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THE BIOLOGY AND ECOLOGY OF VELESUNIO ANGASI (BIVALVIA: HYRIIDAE) IN THE MAGELA CREEK, NORTHERN TERRITORY

Part 1 (Text)

prepared by

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The Supervising Scientist for the Alligator Rivers Region manages the Alligator Rivers Region Research Institute, which conducts, co-ordinates and integrates research relating the effects on the environment of uranium mining in the Alligator Rivers Region.

Supervising Scientist for the Alligator Rivers Region

THE BIOLOGY AND ECOLOGY OF VELESUNIO ANGASI (BIVALVIA: HYRIIDAE) IN THE MAGELA CREEK, NORTHERN TERRITORY.

PART I
(TEXT)

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SUMMARY

The biology and ecology of the freshwater mussel, Velesunio angasi, were investigated from March 1980 to May 1981, in waterbodies of the Magela Creek - a seasonally flowing stream of tropical northern Australia. Features of the biology and ecology of the mussel studied included shell shape and environment, distribution, abundance, population dynamics, reproduction, food ingestion, physiological condition, production, and seasonal changes in any of these.

Three shell forms of V. angasi in lateral outline and obesity were recognisable in the Magela Creek: a winged, billabong or true angasi form, and two ecophenotypic variants - (1) a non-winged and dorsally arched form, and (2) a high, moderately winged and swollen Creek form. Both ecophenotypes appeared to be functionally adapted to maintenance and survival against swift flowing waters, and for aestivation over the Dry season in the braided, sandy creek channel above Mudginberri billabong, respectively. The dorsally arched shells were present only in Mudginberri billabong; progressive dorsal arching culminating in a distinct arcuate form was found at sites of increasing Wet season stream velocity. This trend was accompanied by a decline in relative shell height.

Relative height and obesity were correlated broadly among the billabongs with environmental factors of decreasing eutrophy and increasing depth respectively. Neither correlation, however, could be interpreted in terms of functional morphology and both relative height and obesity were found to be more closely associated with ontogeny; relative height declined with increasing growth rate and obesity increased with increasing age of mussels. There was some evidence to indicate that shells were more obese on silty, unconsolidated sediments which is otherwise suggestive of adaptive morphology.

Young shells (< 1 year old), as yet relatively unaffected by environment, were always typically angasi in form throughout the Magela Creek, i.e. posteriorly winged and truncated.

Differences in distribution and abundance of *V. angasi* for both microhabitat and between-billabong, were clearly evident and quantified in terms of morphometry, hydrology and physicochemical limnology of the billabongs.

Distributional patterns within billabongs were readily quantified in terms of optimal depths or subregions for mussels, delineated mainly by: (1) local seasonal dissolved oxygen concentrations, sufficient levels of which are required for successful recruitment and subsequent development of populations; and (2) suitability of substrates - stable, and firm but yielding sediments are required for maintenance of individuals.

Among all billabongs of the Magela Creek, a correlation was found between mean dissolved oxygen concentration averaged over the seasons, and mean densities of the mussel populations. Apart from dissolved oxygen, no other physicochemical parameter studied was related to mussel distribution and abundance. Between billabongs nevertheless, distributional patterns clearly fell into two categories, those for billabongs lying on the mainstream channel of flow (channel and floodplain), and backflow billabongs. For both billabong types, mean abundances of the mussel populations were related to mean dissolved oxygen concentrations and billabong morphometry. Certain dimensional relations of the latter are argued to be useful indicators of the Wet season flow regime, important for mussel recruitment in billabongs of the through-flow type, or of the amount of water remaining in the backflow billabongs at the end of the Dry, equally critical to the survival of mussels.

Features of the population dynamics of mussels investigated included age and growth, population structure, mortality and mussel movements.

Dark growth rings on the shells of mussels from all waterbodies were shown to be annular in nature, and resulted from late Dry season stresses. These could, therefore, be used to age mussels and to determine other population parameters. von Bertalanffy growth equations were used to describe growth in length of _V. angasi_. No dimorphism in size (and shell shape) was noted between the sexes. Growth rates of mussels between different waterbodies varied widely, being clearly correlated with mean food availability as measured by surface chlorophyll concentrations. Differences in growth rates of mussels within billabongs were accounted for by local differences in food and/or oxygen availability.

Population structures of mussels were compared both within and between waterbodies. Within-billabong patterns in size and age structure were

quantified in terms of depth and different subregions. Both size and age of mussels generally increased with increasing depth in the billabongs, and declined only in the deepest waters of the floodplain billabongs. These patterns are the result of littoral recruitment, instability of the shallows, and oxygen depletion in the deepwaters of the floodplain billabongs.

Recruitment of juvenile, newly metamorphosed mussels onto the sediments of the Magela Creek waterbodies was distinctly seasonal, occurring during the Wet-early Dry seasons. A feature of the age structures of mussel populations between waterbodies, was the irregular nature of those from the floodplain billabongs. Significant proportions of the variation in year class strenth, however, were accounted for by variation in annual stream discharge. This relationship added credence to evidence from distributional studies as to the importance of dissolved oxygen, as manifested through Wet season flow, to juvenile recruitment in these populations.

Age specific mortality rates were estimated for the mussel populations from three billabongs - Georgetown, Mudginberri, and Nankeen which represent backflow, channel, and floodplain types respectively. Longevities of mussels recorded between the different waterbodies were variable with determinations ranging from 11 to 35 years. Maximum ages of mussels among the billabongs were significantly correlated with mean dissolved oxygen concentration. Thus, from known longevities and age specific mortality rates of mussels, the stress imposed by low dissolved oxygen concentrations was believed to be a major cause of mortality of mussels in the Magela Creek waterbodies.

Females appeared to be more susceptible than males to mortality by this cause.

Regular seasonal movements of mussels were observed onto the shallow, flooded banks of Georgetown, a backflow billabong, each Wet season. Annual movements in Buffalo, a deeper channel billabong, however, were negligible, with only some slight evidence of displacement downstream by Wet season flooding.

The reproductive biology of _V_. _angasi_ investigated in the Magela Creek included structure of the breeding population, gonadal development, larval production, and glochidial release and parasitism.

The sexes of _V_. _angasi_ examined in the Magela Creek were separate; hermaphroditism was very occasional and was confined to less than 2% of each of the populations investigated. Gonads of the smallest individuals (< 1 year old) from most populations, appeared to function initially as males. Other than this early protandry no evidence of sex reversal in the adult population was found. The sex ratios of mussels in all environments were biased in favour of males. This was attributed to differential mortality of the sexes; males outlive females in many of the waterbodies. Gonadal maturation was found to be size dependent and was reached by mussels during their first year, at a range in length between 25.0-29.9 and 30.0-34.9 mm. First gravidity of females was found similarly to be size dependent and occurred at a length of approximately 40 mm. This size was attained on average within an age span of from 0.6 to 1.5 years depending on the waterbody. A long and gradual decline in reproductivity with increasing age occurred for female mussels at least in most of the Magela Creek populations.

The timing of spermiogenic and oogenic activity of V. angasi was the same, and both sexes, therefore, were assumed to spawn simultaneously and at a similar intensity. Spawning and larval production were immediate responses to the intensity of gametogenesis. Larval development of mussels in the Magela Creek, from spawning to glochidial maturation, was rapid and during the warmer Wet season months at least could be completed in well under 12 days.

The ubiquity of mature primary oocytes and sperm, the presence of gravid females throughout much of the year in many populations, and the knowledge that larval development is very rapid and that mature glochidia are released in direct proportion to the intensity that they are produced, provided clear evidence that spawning and breeding of V. angasi in the Magela Creek were repetitive and occurred year round. Spawning and breeding were asynchronous among individuals at any given time and locality. Superimposed upon a repetitive reproductive cycle, the relative activity of which was only marginally slowed to any degree by low water temperatures, major interruptions to gonadal activity and larval production were found. These were associated with seasonal lulls in dissolved oxygen concentrations, and with seasonally high turbidities in the billabongs.

The glochidia of V. angasi were found to be unspecific parasites of their fish hosts; from both field and laboratory observations, a total of 19 fish hosts in the Magela Creek were recorded. Bottom feeding and dwelling fishes, and fishes notably inactive in the water column, served disproportionately as hosts to the glochidia. Infections of the toothed glochidia were higher on the gills than the fins of the fish hosts.

The duration of the parasitic period of glochidia of V. angasi was temperature dependent. Metamorphosed juveniles were recorded from a host fish, Glossogobius giurus, on an average of 5 days after infection, at 30° C(shortest period was 48 hours); and on an average of 10 days, at 22° C (shortest period was 96 hours). By monitoring the seasonal incidence of parasitism of glochidia upon the host fish species, G. giurus, it was shown that V. angasi released glochidia throughout the year in direct proportion to their seasonal production. The seasonal pattern of recruitment of mussels in the Magela Creek did not correlate with the seasonal intensity of larval production; breeding was aseasonal and year round, while recruitment was seasonal (see above).

V. angasi in the Magela Creek was observed to be a phytophagous and detritivorous filter feeder, the food comprising unicellular algae and plant detritus. The algal fraction of the ingested material was generally low in the stomachs of mussels. However, algae were assumed to be underrepresented amongst the stomach contents as evidenced by the dominance of digestion-resistant forms. Digestion was assumed to be very rapid in the warm waters of the Magela Creek. Ingestion rates as measured by intestinal fullness were correlated with phytoplanktonic biomass of the environment when the influence of periods of sustained oxygen depletion was excluded from analysis.

(Mussels ceased to feed in waters of very low dissolved oxygen concentration, and reduced their feeding in waters with high concentrations of suspended solids.) This correlation provided some evidence that algae were the chief food source of the mussel. Evidence, however, that unicellular algae were the main utilisable food item and energy source of V. angasi (as opposed to the organic detrital fraction) was found in the correlation between shell and somatic growth and mean abundance of phytoplankton in suspension among the Magela Creek populations; growth was not correlated with the measure of organic detritus. Seasonal shifts in the abundance of major taxa of phytoplankton were noted in the stomachs of mussels. These changes have not previously been detected in the phytoplankton of the Magela Creek waters. Relative to green algae, diatoms were underrepresented in the stomach contents of mussels. However, no other indication of selective feeding was found. Given that a large inorganic fraction was included in the diet moreover, V. angasi appeared to be unselective in its feeding.

Generally, very few significant differences were found in the length/weight relationships averaged over the seasons, between the sexes of mussels from the Magela Creek waterbodies. A diphasic annual cycle was evident in populations where condition was followed at monthly intervals. A major peak in the mid-Dry season and a minor peak in the early-Wet were observed, while lulls in condition were noted at the end of the Dry and again at the end of the Wet. The fluctuations in condition were most clearly related to the seasonal availabiity of food; in 5 out of 8 billabongs, monthly chlorophyll concentrations and condition were significantly correlated. Further, condition and chlorophyll concentration averaged over the seasons were significantly correlated among the billabongs. Thus, the two peaks in condition were generally associated with (1) increasing Dry season eutrophy and (2) major early-Wet, nutrient inputs from a dry catchment. Declines in condition coincided with (1) periods of either increasing turbidity with resultant suppression of algal production, aestivation or with spawning intensity during the latter period of the Dry and (2) progressive oligotrophy of the Wet season waters.

There was evidence that independent of food concentration, condition was depressed during periods of very low concentrations of dissolved oxygen and especially at times of high turbidity in the billabongs. High water temperatures during the late Dry were responsible for peaks in reproductive activity of mussels in the non-turbid Magela Creek billabongs; in oligo-mesotrophic waters, condition declined in response to reproductive activity, while in eutrophic waters, no decline was evident.

Annual production in V. angasi was measured in four of the Magela Creek populations. Production values were high in relation to other published data on freshwater mussels, ranging between 0.39-1.75 g/m^2/year shell free, dry weight. Moreover, gametic and larval production in the mussel, a repetitive breeder, were not included in the estimates. (Larval production would contribute a very significant fraction of total annual production of mussels in many billabongs of the Magela Creek.) Production/Biomass or turnover ratios of V. angasi were exceedingly low, however, varying between 0.07-0.13. These trivial values could be explained by the long-lived nature of the populations, in which adult mortality was low. While the contribution of mussels as food for other trophic levels was probably minimal, the high densities and estimated turnover rates in the soft, acidic waters of some billabongs, suggested that the mussels probably contributed significantly to the nutrient and calcium cycles.

From study of the biology and ecology of mussel populations in the Magela Creek, important roles of V. angasi as an ecological indicator organism of present day and paleoenvironments are advocated. Description and quantification of shell form, densities, growth rates, recruitment, mortality, age structures, and relative condition in relation to environmental factors, may provide valuable baseline data upon which to monitor the effects of environmental disturbance such as potential pollutants, both organic and inorganic. Distributional information about V. angasi could provide useful indications of the local dissolved oxygen environment in waterbodies and, more broadly, of the flow regime in waterways perhaps throughout much of tropical northern Australia. Analysis of the size distribution and growth (shell and visceral) of mussel populations, could additionally indicate the trophic status of the environment seasonally, or integrated over time. Shell form and size might similarly indicate a variety of paleoenvironments with the knowledge of environmental determinants, and interpretations of functional morphologies of shell form.

1 INTRODUCTION

The freshwater mussel, Velesunio angasi, is an appropriate study animal in the environmental programme around the uranium mining ventures in the Alligator Rivers Region. It has potential use as a biological concentrator of possible pollutants in any biological monitoring programme and its inclusion in the Aboriginal diet gives impetus to investigation of the likelihood of contamination of the mussel flesh.

The rationale for the use of mussels as biological monitors of pollution and, more specifically, the strategy of investigation of V. angasi as a potential biological monitor have been outlined previously (Allison and Simpson, 1983). That report also lists the elements measured in mussel flesh during the course of the study, and the reason for their selection.

It is sufficient to reiterate here that a fundamental requirement of the evaluation of V. angasi as a potential biological monitor of pollution and as a possible source of dietary contamination, was to understand the variation in natural levels of elements in the flesh of the mussels. Such variation can be induced by changes in environmental conditions and in the physiology of the mussels themselves. A further basic necessity was to determine the availability (distribution and abundance) of V. angasi in the waterways adjacent to the proposed mining operations.

The biological and ecological studies on V. angasi in Magela Creek have included habitat description, variation in shell shape, distribution, abundance, population dynamics, reproduction, food ingestion, physiological condition, annual production, ecological tolerances, and seasonal changes in any of these. These studies were conducted in parallel with measurements of selected elements in the flesh of mussels from Magela Creek, as well as from a number of other locations (Allison and Simpson, 1983).

Apart from the specific objective to aiding in the interpretation of V.

angasi as a biological monitor of potential pollution, these biological and ecological studies provide information on a prominent member of the aquatic fauna of the Region. As such, the studies form part of the wider objective of understanding the aquatic ecosystem of the Region.

2 THE STUDY AREA

2.1 Geography and climate

The Alligator Rivers Region is situated east of Darwin and abuts the prominent Arnhem Land plateau complex which occupies much of the northeastern portion of the Northern Territory. The Region mainly comprises the catchments of the East Alligator River and the eastern catchments of the South Alligator River, the tributaries of which were the concern of the present studies (Fig.2.1).

The Alligator River systems drain generally in a northwesterly direction to the Arafura Sea from headwaters which arise in the rugged sandstone plateau. After leaving the plateau, the major streams - largely confined to sandy and often braided channels - flow through extensive and extremely flat lowlands, to enter the broad, seasonally - inundated floodplains. The major tributaries including the Magela, Cooper and Nourlangie Creeks, spread widely on entering their floodplains with their drainage lines becoming fragmented. The larger Alligator Rivers however, maintain continuous stream channels. The floodplains finally merge with the tidal flats of the estuaries.

The climate of the Region is monsoonal, like much of far northern Australia, the dominant feature being the two distinct seasons - the 'Wet' and the 'Dry'. The seasons may be variable in length but generally the Wet season extends from November to March and the Dry from May to September, with April and October being transitional (Fox <u>et</u> <u>al</u>., 1977). January, February and March are usually the wettest months (averaging around 300 mm each month), whereas June to September are normally completely dry.

As well as being highly seasonal in incidence, rainfall is also highly reliable (Christian and Aldrick, 1977) and there is little variation in amount throughout the Region, apart from some differences due to local topography. Long-term rainfall records for Oenpelli for example (kept since 1910 and used as representative for the Region), show an annual mean of 1343 mm (coefficient of variation, 21 per cent). Rainfall at Jabiru in the lowlands of the Magela Creek catchment, over an eleven year period to the 1981-82 Wet season, averages annually at 1593 mm (Fig. 2.2). Details of the dynamics of the wet-producing systems are provided in Christian and Aldrick (1977) and Walker et al. (1983a). In short, these systems arise from the change to the humid northwesterly winds at the onset of the Wet, from the dry (continental) southeasterly winds of the Dry season.

Other features of the Region's climate are the high temperatures sustained throughout the year and the small seasonal range of mean monthly temperatures. The seasonal amplitude of mean monthly temperatures is only 5.6°C at Oenpelli (Christian and Aldrick, 1977) and further inland at Jabiru, 7°C (Walker et al., 1983a). A mean daily maximum of 37°C is reached in the period just prior to the Wet, while night temperatures may drop to a minimum of around 17°C in the Dry season between May and August (Oenpelli data).

Mean annual evaporation throughout the Region is estimated to be in the range of 2400-2700 mm, thus exceeding annual precipitation by 800-1200 mm. Mean evaporation is maximal late in the Dry season (about 260 mm in October) and minimal at the height of the Wet (about 100 mm in February) (Christian and Aldrick, 1977).

Day length varies little due to the latitude of the Region, with a maximum of 12.7 hours in January and 11.2 hours in June. Owing to the cloud cover in the Wet season, the least sunshine, 4.5 to 7.5 hours per day, occurs in this period while during the Dry it ranges from 9.7 to 10.2 hours.

2.2 The streams and waterbodies

Wet season flow of the streams in the Region is considerable and is highly variable both throughout the season and from year to year. In the Magela Creek for example, total flow past Jabiru averages about 250 million cubic metres per year, but may be three times this amount in a particularly wet year and only a quarter of the volume in a dry year (Fry, 1979). The annual pattern in the streams, is one of a series of flood peaks following the more heavy periods of rain, superimposed upon a base flow (Hart and McGregor, 1980). Flow commences in an average year about mid December soon after the first substantial rains, declines in the early Dry season and ceases generally about the end of June. The flow pattern for the Magela Creek is shown in Figure 2.3. This figure displays monthly discharge data for the gauging station below Jabiru (GS 821009), over an eleven year period to the 1981-82 Wet season.

While the large rivers, including the Alligator Rivers, maintain a flow in lower sections and estuaries in the Dry season, all other streams including such major tributaries as the Magela, Nourlangie and Cooper Creeks, cease to flow for much of their length. In these streams, flow persists only in upstream sections fed by springs and seepage. During the Dry season, the lowland creek channels and the floodplains dry out, and the creeks contract to a string of small waterbodies. Some water remains until the next Wet season in rock pools on the plateau and in the small waterholes and swamps of the lowlands and floodplains. The small waterbodies left during the Dry season, are known locally in the Northern Territory, as billabongs. Pedantically, the word is somewhat of a misnomer (Walker et al., 1983a), but because of its widespread usage, a billabong will be used here in reference to any waterbody of the lowlands and floodplains.

Three separate billabong classifications - "backflow", "channel" and "floodplain" - have been proposed for waterbodies in the Region; these classifications use geography, morphometry and hydrology (Davy and Conway, 1974; Walker and Tyler, 1979; Hart and McGregor, 1980). Backflow billabongs are situated near the mouths of tributaries to main stream channels of the lowlands and are formed as a result of the damming of the tributary at its mouth by the levee bank of the main stream; channel billabongs are located within actual main stream channels; and floodplain billabongs are depressions or remnants of abandoned channels on the floodplains.

2.3 Limnological features of the Magela Creek waterbodies

It is well known that environment can exert strong influences on freshwater mussels. There is a large literature in particular, describing the often strong relations between mussel morphology and distribution, and environmental factors (see Appendices 1 and 2 respectively). As background therefore to interpretation and to a proper understanding of the biology and ecology of _V. angasi_, pertinent limnological features of stream systems in the Region need also to be well known. The present study of _V. angasi_ was confined to waterbodies of the Magela Creek - a system for which a great deal of other limnological information is available. The following descriptions summarise the relevant morphometry, hydrology and physicochemical limnology of the Magela Creek and its billabongs.

A feature of the billabongs of the Region, is the extraordinary and dramatic changes in hydrology and water quality between the Wet and Dry seasons. This confers on the waterbodies an individual dynamism and a between-billabong heterogeneity that precludes a generalised description of hydrology and physicochemical limnology for the Region. That is, a "typical" billabong cannot be described as might be the case for other waterbodies such as perennial streams and lakes.

2.3.1 Morphometry and hydrology

Figure 2.4 shows the location of the Magela Creek billabongs and Table 2.1 summarises their important morphometric and hydrological features. (The summary is a modified version of that prepared by Walker _et al_., 1983a.) Billabong area and mean depth are standardised to late Dry season conditions (1 November, 1981), the latter calculated from planimetry of prepared bathymetric maps. All bathymetric maps except those of JaJa and Jabiluka billabongs (source acknowledged in Figs. 2.11 and 2.13 respectively) were prepared from data collected during the study. Depth readings were taken at intervals of between 5 and 10 m apart, across transects spaced at 25 m (Georgetown, Gulungul, Corndorl, Mudginberri and Buffalo), 50 m (Nankeen), 75 m (Leichhardt) or 200 m (Island) intervals along the billabong. Aerial photographs, and buoys and stakes aligned at set intervals throughout the billabong, aided with or without a need for compass bearings, were used to set the transects and to determine accurately the relative position of the billabong edge for final mapping. The bathymetric maps of the various billabongs are shown in Figures 2.5 to 2.14. Depths are mostly standardised to late Dry season levels.

At each site over which a depth reading was taken in the preparation of the bathymetric maps, sediment samples were collected by diving, and visually and subjectively assessed for textural character and organic content. These records, supplemented by the observations and some limited determinations of Thomas and Hart (1981) and Thomas et al. (1981) were used as the basis of descriptions of sediment texture. Particle size distributions and percent organic content in the billabong sediments, drawn from the data of the latter reports, are shown in Table 2.2. From these data, mean particle sizes of billabong sediments were estimated, and are also show in that table. For the estimate of overall, mean particle size of billabong sediments, the particle size fraction greater than 63 µm was assumed (from visual observations) to represent very fine to medium sand, which has a mean particle size of 150 µm (Folk, 1968). The different and very distinct types of sediments in billabongs (where these sediments were markedly heterogeneous) are shown on the bathymetric maps. Bathymetric maps that are accompanied with sediment descriptions, are those of Georgetown, Corndorl, Mudginberri, Buffalo, and Leichhardt billabongs.

Gauging stations are located on two creek channel sites, but on only four of the billabongs, to measure discharge and flow rates. Of the billabong stations moreover, only two have been rated for conversion of stage height data to discharge. One of these (GS821023 at Jabiluka) is rated over the 2 km cross-section of floodplain at this point so that discharge cannot be calculated specifically for the billabong. A shortcoming of the computed flow rates (derived from discharge and stage data) is that they represent a mean through the stream cross-sectional area and consequently underestimate velocities through the central channel regions.

Some data are available, however, to show the pattern of decreasing water velocity downstream of the Magela Creek. Table 2.3 displays this pattern, in measured water velocities during rhodamine dye experiments (1979-1980 Wet season) at sites and traverses along the creek (N.T. Dept. Transport and Works, Water Division, 1980).

Walker et al. (1983a) and Thomas and Hart (1981) claim respectively that billabong depth, and the type and distribution of the billabong sediments are good indicators of the current velocity and hydrological characteristics of the billabongs during the Wet. Bathymetry and study of billabong sediments are considered therefore as indirect but valid descriptors, in comparison to direct flow measurements, of the flow regime in billabongs during the Wet.

2.3.1.1 Lowland creek channel

Below Bowerbird and extending downstream to Mudginberri billabong, the Magela Creek flows through a well defined and braided channel. While flow persists throughout the year through Bowerbird and for some distance downstream (several kilometres), through-flow to Mudginberri billabong is accomplished shortly after the first substantial rains of the Wet season (generally between late November and mid December).

During the Wet, the base flow can be interrupted by a number of flood peaks.

These spates can provide substantial discharge and with the confined nature of the channel, stream velocities can be considerable. In the Magela Creek below Jabiru for example, mean, cross-sectional flow rates have been recorded at up to 0.67 m/s (gauging station GS821009, 4 February 1980). As a consequence to the intensity of discharge over the period, the creekbed in this zone is well scoured, and has a mainly shifting, sandy substrate.

Stream flow through the creek channel ceases generally in the early Dry season (end of May) and the creek thereafter is reduced to a number of sandy pools which, depending on the duration of the Dry, may or may not persist until the following Wet. Regardless of their permanence, the creek pools are of no consequence to the present studies.

Vegetation along the banks of the creek channel is extensive and consists mainly of rainforest and some lowland flora. While some occasional Melaleuca and Barringtonia may colonise the actual creekbed, clumps of Pandanus are more common. The many branching roots of the latter are very much a stabilising influence on sections of sandy creekbed. During the Wet, macrophytes are common around the submerged banks of the channel in areas free from shifting, sandy substrates. These act, along with the root systems of the surrounding vegetation, to stabilise the muddy or loamy banks.

2.3.1.2 Backflow billabongs

The backflow billabongs are small, shallow and have shelving banks with mostly organic clay and silt sediments. During the Wet season, extensive wooded (Melaleuca) banks are submerged, and macrophytes grow prolifically in the open shallow waters. Bankside vegetation, however, is sparse during the Dry and macrophytes senesce, with the contracting of the waters. The waters are normally very shallow and turbid by the end of the Dry and over a particularly long Dry, some billabongs may in fact dry out completely.

Hydrologically, backflow billabongs are similar in that they are initially filled by 'backflow' at the commencement of the Wet, when water from the Magela Creek flows over the levee bank separating the billabong from the main creek channel, back up into the billabong. Subsequently, the direction of flow over the levee depends upon the relative flows in the Magela Creek and the billabong feeder stream. Backflow tends to deposit fine sediments and organic material in the billabongs. Flow down the tributary, however, tends to flush them.

Sediments in the backflow billabongs consist of fine grained silt and clay, rich in organic matter (about > 10%) (Thomas and Hart, 1981). Thomas and Hart (1981) attribute these characteristics to the poor flushing and high macrophyte biomass sustained in these billabongs during the Wet season. Observations on the shallowness of the waters (Table 2.1) and on the uniformity and unconsolidated nature of the sediments throughout the billabongs support these views.

An exception to the pattern, however, are the observations for Georgetown billabong. This billabong consists of two basins separated by a sill (Fig. 2.5). The sediments in each basin are mostly silt and clay, and those on the sill have a higher sand content (Fig. 2.5). As observed in the present study and also by Thomas and Hart (1981), as the Wet season progresses and water level in the billabong rises, the main flow pattern into Georgetown is from the Magela Creek at the southern end of the billabong (Fig. 2 of Thomas and Hart, 1981). This is particularly apparent when discharge in the Magela Creek is high, and during one major flood peak for example (March, 1981) very rapid water velocities were observed through the billabong.

Thus, Georgetown billabong can be well flushed during the Wet season, as observed visually, and as evidenced by the comparatively deeper water (Table 2.1) and marked differences in the proportions of sand and clay throughout the billabong. The lower content of organic material present, in comparison to other backflow billabongs - about 11% in sediments of the two basin regions, but as low as 0.1% on the sill (Thomas et al., 1981), further reflects effective flushing and the resultant lower macrophyte biomass sustained in this billabong.

2.3.1.3 Channel billabongs

The channel billabongs positioned in the main Magela Creek channel, are comparatively deep with steep and well-vegetated banks of mainly Pandanus with some Barringtonia and Melaleuca. Macrophytes are uncommon but occur in some shallower waters around the billabong edges, away from strong currents. The sediments are very sandy (as evidenced by the larger sediment particles shown in Table 2.4) and together with the steep banks and overall depth ensure that the waters remain clear throughout the year. The channel billabongs apparently receive seepage input from the surrounding sandy aquifers for some time after the Magela Creek has ceased flowing (Hart and McGregor, 1978).

The sandy sediments which dominate these billabongs indicate that they are well flushed each year, and for the most part accumulation of fine sediments is prevented.

The Magela Creek at Bowerbird billabong is narrow (about 30-40 m wide) and well confined. Because of this and the comparatively steep gradient of the creek here in the escarpment region, stream velocities are exceedingly rapid, having been recorded at up to 1.72 m/s (gauging station GS821008, 4 February, 1980). The billabong, the deepest in the Magela Creek system, is thus well scoured each Wet season, and the sandy bottom here is shifting and unstable.

Mudginberri billabong is in a small transition zone between the lowlands and floodplain. It consequently marks a region of major change in flow characteristics as there is a dramatic reduction in slope of the creek bed at this point (N.T. Dept. Transport and Works, Water Division, 1980). Water velocities at the southern upstream end of this billabong can be considerable, particularly along the western side of the billabong where rapidly flowing water from the creek channel first meets the open water of the billabong. Rhodamine dye experiments have shown dead water and back-flow areas on the eastern side as water from the Creek enters the billabong at the southern end (Smith et al., 1979). The experiments also revealed complex, local turbulence phenomena with depth of this end attributable to the sudden change in depth of the creek as it enters the billabong.

Measurements of stream velocity (under constant discharge) were undertaken during the 1982 Wet season of the present study across a number of transects along the billabong. Figure 2.15 displays the results and clearly confirms that higher flow rates pass through the south-western end of the billabong than in any other part of the billabong until water becomes confined again and leaves through the narrower northern end. Further, under the prevailing flow regime at least, flow rates remained relatively faster along the western side until at least a third of the distance down the billabong. A measure of the stream velocity in the south-western end can be gauged from observation of the sediments in this region (Fig. 2.8). These consist of a fairly soft clay, found only in this reach of the billabong and indicating the prevention of sand deposition, and consequent scouring of the creek bed here. In contrast, sediment observations of a fairly large section of the eastern side of Mudginberri show deposition, the sediments here consisting of relatively high proportions of organic material and finer sediments (Fig. 2.8). Table 2.4 shows the particle size distribution and organic content of the sediments sampled across the transects or at the sites indicated in Fig. 2.16 at the southern end of Mudginberri billabong. These data show the increasing proportions of sand and decreasing organic content (from up to 16%) in the sediments away from the eastern side and immediate western edge of the billabong. From these data, the three major sediment types observed in the billabong (Figs. 2.8 and 2.16) were classified according to particle size distribution and organic content. The correspondence of textural character and organic content with the three sediment types is shown in Table 2.5. The highest Wet season flow rates through the billabong occur over those portions of the billabong with sandy sediments. To some degree, during flood events this sand bed is probably shifting and unstable.

There are two flow paths out of Mudginberri billabong. Both paths inflow to Island billabong, the right channel via Buffalo billabong. As a result of this branching, water velocity through Buffalo billabong is apparently reduced, though by what factor, is not known. From examination of the sediments, much of the billabong is sandy and hence well flushed, although like Mudginberri, a large depositional area exists, but on the western side (Fig. 2.9). These deposits appeared to be similar to those of Mudginberri except for a region along the immediate western edge of the billabong (Fig. 2.9) where more silty and organic, and less consolidated sediments were present. While no analyses were carried out on the sediments to determine the relative fractions, of the major sediments in the billabong, the three coarsest and least organic in nature are assumed to be the same as those in Mudginberri (Table 2.5).

Island billabong is located at the junction of the floodplain and the lowland stream channel of the Magela Creek. During the Wet, the Creek changes from a confined, relatively fast flowing stream into a less defined stream dispersed over a broad floodplain, 1 to 2 kilometres wide, a short distance upstream from Island billabong. Walker _et_ _al_. (1983a) consider Island billabong a 'hybrid', showing characteristics of a channel billabong but showing some affinities with the floodplain billabongs.

Although much of the surrounding weed-choked floodplain is inundated during the Wet, dye experiments have shown that at least under the prevailing flow conditions of the experiments most of the water passed through the open water areas of the billabong, and well ahead of that filtering through the adjacent floodplain (Smith _et_ _al_., 1979).

While no extreme, flood peak velocities are available, a relative measure of flow rate through the billabong can be obtained from Table 2.3. Water velocity through the billabong during the dye experiments (site 5) showed a considerable reduction over that measured only some 2.5 km upstream, the point at which the Creek channel enters the floodplain. Island billabong is the second deepest of the Magela Creek waterbodies (Table 2.1) and this depth together with observations of generally uniform sandy sediments, indicate that the billabong must nevertheless be reasonably well flushed during the Wet. From observations made during the study, sand over a grey, clay bed material dominated the sediments, in accordance with the observations of Thomas and Hart (1981), with increasing amounts of silt towards the banks.

Thomas and Hart (1981) however, over a period of two years regular monitoring of sediments in Island billabong, have noted their changeable character. A 10 to 20 cm deep layer of fine, unconsolidated sediment floc appeared after one Wet season (1979) to be apparently flushed out during a large flood in the following year, re-exposing the underlying sand layer. These authors considered that large flood events probably have a great influence on the distribution of sediments in the Magela Creek system.

2.3.1.4 Floodplain billabongs

The billabongs on the floodplains are relatively deep, less so than channel billabongs, however (Table 2.1), and generally have steep western banks with shelving eastern banks. Bankside vegetation is predominately Pandanus and Barringtonia, but this is variable and does not fringe the banks to the same extent as along the channel billabongs. During the Wet, macrophytes are common around the shallower edges. The deeper open water and some bankside vegetation are the only features which give the billabongs identity at this time, as water from the surrounding floodplain covers them.

Sediments of the billabongs, like the backflow billabongs, are generally composed of coarse silt and clay, but have considerably less (6 to 7%) organic content (Thomas and Hart, 1981). Because of the fine sediments, shelving banks, and being generally the most exposed of all the billabongs, the flooplain billabongs may become very turbid during the Dry.

Despite the width of the floodplain and a fall of only 15 cm in water level between the northern end of Island billabong and 35 km downstream to the East Alligator River (N.T. Dept. Transport and Works, Water Division, 1980), the floodplain billabongs effectively channel much of the water passing down the floodplain. According to the calculations of Thomas et al. (1981), more material is actually flushed from Jabiluka billabong for example, at the beginning of the Wet than could be deposited in it during the Wet season. The aerial photograph in Figure 2.17 shows the billabongs downstream of JaJa during the Dry season, in relation to the broad surrounding floodplain. From this figure, distinct channels can be seen linking the floodplain billabongs (especially between Jabiluka and Nankeen). No studies, however, have yet indicated the extent to which the linking channels are operative during the Wet, or whether in fact they are relict.

Thus, while the floodplain billabongs cannot be considered depositional, dye experiments (Smith et al., 1979) have shown that during the Wet season, Ja Ja billabong at least, is outside the main flow path of water passing through the plains. Observations made during the present study of the sediments around the billabong periphery also indicate a resemblance to those of backflow billabongs. The sediments are the least consolidated of the floodplain billabongs studied, and appeared to have a relatively high organic content. (No data are available, however, on the composition of the sediments.) These observations, in addition to its comparatively shallow nature (Table 2.1), indicate that Ja Ja billabong may be depositional in nature.

Other billabongs, however, effectively channel water passing over the plains. During dye experiments specific to Jabiluka billabong (Smith et al., 1979) flow through the billabong (approximately 100 m in width) was estimated at 43 cumecs. As gauging at Jabiluka is rated over the 2 km wide section of floodplain here (Fig. 2.17), it is estimated from total discharge that 45% of flow across the plains passed through the billabong.

The same experiments showed that the main flow path through Jabiluka billabong is through the relatively narrow southern end. Water is channeled into the open section and does not spread onto the adjacent weed-choked floodplain areas as it moves through the billabong (Fig. 2.18). In addition to the 'funnelling' effect of water through the southern end, intrusion of water into the billabong is apparently subsurface, water entering the billabong during the experiment at a depth of 2.5 m (Fig. 2.19). However, the water moves towards the surface as it moves northward through the billabong (Fig. 2.19).

Thomas <u>et</u> <u>al</u>. (1981) provided additional evidence for the southern end being a "... more energetic environment" from sediment textural analysis, finding less fine silt and clay (69%) in the sediments in this zone than from a sample from the northern end (86%). The sediments of both Jabiluka and Nankeen are similar and are generally distributed uniformly throughout the billabongs. They are described by Thomas and Hart (1981) as being composed of coarse silt and clayey sediments low in organic matter (7%). An exception to the pattern, however, is the very sandy nature of the sediments along a narrow band (5-10 m in width) of the north-eastern edge of Jabiluka billabong. Presumably this reflects the very close proximity of the billabong here to the adjacent sandy lowland soils and reflects localised Wet season runoff from these soils.

Visual observations of Wet season flow through Nankeen billabong indicate that this billabong too, effectively channels floodplain waters. High flow rates, considerably faster than water movement through Jabiluka, were observed, particularly through the narrower northern end of the billabong. No discharge or flow rate data, however, are available for this billabong.

Unlike the other floodplain billabongs, from visual observations of flow and bottom type, there is evidence that Leichhardt billabong may be significantly scoured during the Wet season. This billabong is the narrowest on the floodplain (Fig. 2.12 and 2.17) and considerable water velocities were observed through the billabong during the present studies and have been observed by others (Thomas and Hart, 1981). Accumulation of fine sediments along the central channel section of the billabong is apparently prevented, unlike their uniform coverage throughout the other floodplain billabongs. This central channel region is composed of an extremely consolidated and very fine-textured clay (Fig. 2.12). Another notable feature of the substrate in Leichhardt is the extensive accumulations of deep and extremely unconsolidated detritus along the western edge of much of the billabong (Fig. 2.12). The sediments of the remaining shallower reaches differ from those of Jabiluka and Nankeen, in being composed of grey clay of a very sticky texture and lower in organic content (5.6%) (Thomas and Hart, 1981). Because of the extensive areas of consolidated clays and accumulations of silt-free detritus, and its sheltered nature (bankside vegetation is extensive), the waters of Leichhardt billabong remain relatively clear throughout the year.

Hidden billabong is located to the immediate north of Island billabong and yet contains quite different sediments from the latter. The sediments are similar in texture and in size distribution to those of Leichhardt (Thomas and Hart, 1981); further, a compacted and fine-textured, grey clay layer also appears to dominate central portions of the billabong. As to whether the billabong is scoured to the extent of Leichhardt during the Wet however, is not known.

2.3.2 Physicochemical limnology

Since 1978 a large data base of physicochemical limnology has been collected pertaining to waterbodies of the Magela Creek. Work in the region has been carried out chiefly by four separate study groups: Water Studies Centre, Chisholm Institute of Technology; Environment Department, Pancontinental

Mining Ltd; N.T. Department of Transport and Works, Water Division; and the Botany Department, University of Tasmania. Their data and reports provide the basis of the following descriptions.

2.3.2.1 Temperature

Figures 2.20 and 2.21 display spot monthly minimum temperature of bottom waters of the Magela Creek billabongs since May, 1978 up to and including the duration of the present studies. According to Walker *et al.* (1983a), these values lie approximately midway between the monthly mean maximum and monthly mean minimum air temperatures. While the seasonal fluctuations in water temperature are bimodal, minimum temperatures occur during the mid-Dry and maximum temperatures during the late-Dry.

Table 2.6 shows the surface maximum temperature and bottom minimum and maximum temperatures recorded over a four year period since 1978 for the Magela Creek billabongs. The following generalisations can be drawn from these data: Generally, water temperatures are high and the seasonal range (of the shallower billabongs in particular) is considerable, from a winter low of 20.6°C recorded in bottom waters of Georgetown to a high of 40°C in surface waters of Gulungul during the late Dry.

In standing (still) waters there is generally a thermal stratification with observable differences between the warm surface waters and cooler bottom waters. In the more turbid billabong waters (during the Dry) this temperature differential can be considerable. In the deeper, turbid billabongs (e.g. Nankeen) the reduced penetration of radiation results in comparatively cooler maximum bottom temperatures whereas in very shallow turbid waters (e.g. Gulungul) appreciable heating of the bottom waters is evident. A notable feature of the deeper, turbid water billabongs is for their bottom water temperatures to reach maxima during the Wet and early Dry when waters are clearest and hence radiation penetration is deepest.

2.3.2.2 Dissolved oxygen

Dissolved oxygen concentrations in still waters are dependent upon atmospheric exchange at the water surface and from the reactions of photosynthetic organisms living in the waters. In still waters, changes in both water temperature and photosynthetic rate in particular, can result in considerable diurnal changes in the distribution of dissolved oxygen. Thus, during the day there is an increase in dissolved oxygen concentrations in waters containing dense populations of photosynthetic organisms, while during the night there is a depletion when these organisms respire. Further, if still waters become thermally stratified, bottom waters can become depleted of dissolved oxygen as a result of bacterial decomposition of organic material.

Figures 2.20 and 2.21 show the available dissolved oxygen values (1978-1982) for bottom waters of billabongs of the Magela Creek. The readings were taken in the early morning, the time of the daily minimum of dissolved oxygen. The dawn readings show that most billabongs are considerably undersaturated. Even surface values are often below 50% saturation (3.5-4 mg/l) and according to Walker et al. (1983a), this is in contrast to the status of many temperate lakes whose surface waters always remain close to saturation.

From Figures 2.20 and 2.21 definite seasonal patterns in early morning values of dissolved oxygen are apparent, and these figures along with Walker et al.'s (1983a) accounts are used now to describe these trends.

The dominant feature of the seasonal patterns is the minima early in the Dry (April-June) that apparently pervades the entire water column. The chief cause of this oxygen deficit is the rapid bacterial decomposition of macrophytes, prolific during the Wet in the shallow waters surrounding the waterbodies, and on the floodplain. As water levels decline at the Wet/Dry interchange the large macrophyte biomass senesces and decays, causing a severe oxygen depletion that extends into the open waters of the billabongs.

After the annual senescence of macrophytes, wind-induced circulation patterns and the dynamics of phytoplankton populations in the billabongs determine the oxygen levels for the remainder of the Dry.

The diurnal range of oxygen values in the billabongs can be extreme, and can exceed the seasonal range. The magnitude of these diurnal changes is due mainly to the population densities of the macrophytes and phytoplankton. Phytoplankton levels are considerably higher in the Dry than in the Wet (section 2.3.2.5), and in deeper billabongs without extensive macrophyte beds, phytoplankton populations largely influence diurnal oxygen fluctuations. On 1/8/1979 for example between 0815 and 1520, an extreme range of 21-113% oxygen saturation was recorded by Walker et al. (1983a) in Leichhardt billabong, a waterbody where photosynthesis is chiefly algal. The diurnal fluctuations in the shallow backflow and floodplain billabongs, however, may be more influenced by their large macrophyte biomass, particularly in the early-mid Dry.

Of the Magela Creek billabongs, Jabiluka, Island and Gulungul frequently experienced a mid-Dry maximum of diurnal variation that coincided generally with the peak in chlorophyll levels at this time. The pattern in Leichhardt was typically irregular, involving a number of maxima and minima apparently related to the same erratic fluctuations of its phytoplankton populations (section 2.3.2.5). In other billabongs - Nankeen, Bowerbird and Georgetown, the magnitude of the diurnal flux was small and fairly constant throughout the Dry. Except for Nankeen, this was attributed to the lack of macrophytes and low chlorophyll levels sustained during the Dry in these billabongs. In Coonjimba billabong finally, the magnitude of diurnal variation was large, consistent with the large macrophyte population that persisted throughout the year in this billabong.

In lentic (still water) bodies of tropical regions, difficulties arise in recognising when stratification exists because of the very small temperature changes involved. Walker et al. (1983a) consequently, recognise a "de facto stratification" for billabongs of the Alligator Rivers Region: - at best, only partial mixing has occurred when both thermal and oxygen gradients are present at dawn (indicating that nocturnal mixing was incomplete), and this condition persists over a period of days or weeks, accompanied by a progressive decline in oxygen in the bottom waters.

In the Magela Creek billabongs, a continuum is recognised from transient periods of prolonged stratification, to stratification that is either broken down each night or in fact never develops.

Leichhardt, the most protected billabong on the floodplain, apparently experiences de facto stratification for much of the Dry with frequent periods of anoxia interspersed with periods of mixing. It was the only Magela billabong to experience periods of stratification other than briefly at the Wet/Dry transition. Considerable horizontal variation in oxygen concentrations at any one time was also a feature of the profiles in Leichhardt, and deepwater regions at sites only 10 m apart could differ by more than 10% saturation. Moreover, on more than one occasion, an unexplained rise in oxygen status of deepwaters was observed during the Dry.

In most of the floodplain billabongs, brief periods of deepwater anoxia could also be experienced as the first floodwaters of the Wet reached the billabongs. The cause was attributed to the large amounts of organic material washed into the billabongs, creating a brief peak in oxygen demand before the billabongs were thoroughly flushed.

Jabiluka billabong is prone to periods of days of de facto stratification interspersed with considerable mixing. Periods of stratification, however, were generally limited to the beginning of the Dry when deepwater oxygen values could regularly fall to or close to zero. Walker et al. (1983a) demonstrated one such short period of persistent stratification at the beginning of the Dry (6 days during May 1981) when oxygen concentrations of the waters below 3 m were consistently below 30% saturation (about 3 mg/l).

Nankeen billabong, the most exposed of the floodplain billabongs was frequently well mixed in the early morning during the Dry. While on many occasions bottom waters could be depleted of oxygen, rarely did these values fall to zero. Ja Ja billabong similarly lacked any lasting stratification. This billabong is the shallowest of the floodplain billabongs studied, explaining why instances of stratification were only generally brief.

Although Island billabong was generally iso-oxic, occasional periods of stratification occurred during the early Dry, leading to significant oxygen depletion in the deepwaters.

Both channel billabongs, Mudginberri and Buffalo, as a rule experienced uniform distribution of oxygen throughout the waters. Oxygen was present at relatively high concentration throughout the year, and deepwater depletions were rare.

Periods of stratifications in the backflow billabongs were infrequent and brief, these billabongs being the shallowest of the Magela Creek. Oxygen was generally homogeneously distributed throughout the billabongs and the values were relatively high. The exception to this pattern was in the early Dry for most billabongs, but only in Corndorl, however, was deepwater depletion of oxygen severe at this time or at other times such as during periods of static flow during the early Wet.

2.3.2.3 Chemical characteristics

According to Walker and Tyler (1983a) chemical differences between surface and deeper waters of billabongs in the Region are slight, and single surface samples describe sufficiently the characteristics of the waters at the time of collection. (The absence of any long-term stratification of the Magela Creek billabongs is used to support this claim).

Table 2.7 shows the seasonal means and standard deviations of an array of chemical characteristics of surface waters of the Magela Creek. Coverage is over a four year period (1979-1982) and the data were collated mainly from the N.T. Dept. of Transport and Works, Water Division, supplemented by data of Walker and Tyler (1983a) and those collected during the present studies. Figures 2.22 - 2.23, and 2.24 - 2.25 respectively display monthly values of conductivity (K) - the measure of the total concentration of dissolved inorganic salts in the water, and pH for waters of the Magela Creek billabongs from 1979 up to and including the duration of the present studies. The following description is a brief summary of billabong chemistry according to these figures and as related by Walker and Tyler (1983a).

During the Wet, the sheer intensity of discharge and effective flushing impart a uniform and common water chemistry to all the billabongs. Generally the waters are dilute (K below 20 μScm^{-1}), near neutral (pH's between 6.4 and 7.0) and are dominated by sodium bicarbonate. (The cationic dominance orders are Na > Mg > Ca > K and anionic dominance, $HCO_3 > Cl > SO_4$). During the Dry as the waters in the billabongs evaporate, chemical changes occur but to varying magnitudes, as solutes become concentrated, sediments are resuspended and groundwater enters the billabongs.

By the midpoint of the Dry (July), the uniformity of the Wet season ionic character had gone. Conductivities (17 to 145 μScm^{-1}) and pH's (5.8 to 7.1) now ranged more widely, and the billabongs could be separated into two groupings based on cationic proportions. One grouping, the channel billabongs, had more or less equimolar proportions of Na and Mg while the other, the backflow and floodplain billabongs, had an ionic order Na >> Mg. A further subdivision was evident in anionic character in that the floodplain billabongs became chloride dominated.

By the late Dry (October/November), conductivities (18 to 2600 μScm^{-1}) and pH (a span of 3.8 units) ranged even more widely. Based on cationic proportions, the same groupings were present as during the mid Dry, but according to anionic proportions most billabongs had become chloride dominated while sulphate assumed dominance over bicarbonate in several billabongs.

Thus, while a common water chemistry dominated by sodium bicarbonate characterised the Wet, a diversity in ionic character of the billabongs arose during the Dry, but which could nevertheless be categorised according to particular characters. Some billabongs changed very little while most became sodium chloride dominated, of which some increased significantly in sulphate.

The sodium/magnesium bicarbonate billabongs are made up of the channel billabongs (with the exception of Buffalo). These billabongs are the least changed over the Dry: they maintain the ionic composition of the Wet throughout the year; remain dilute (K ranged from 15 to 30 μScm^{-1}); and pH fluctuations are slight with only a minor downward trend in pH evident. Their chemical stability is attributed to the reduced evaporation and concentration that most other waterbodies experience. This is a result of their low surface to volume ratios (being comparatively deep and narrow) and relative protection by the fringing vegetation.

The sodium chloride billabongs consist of all the backflow billabongs except Corndorl, one floodplain billabong (Leichhardt), and one channel billabong (Buffalo). In these billabongs, there is a change in ionic character over the Dry towards sodium chloride dominance. Where evaporative loss during the Dry is particularly high as in the shallow billabongs of this group, the waters concentrate considerably and conductivities range from 30 to 520 μScm^{-1}. pH values generally decline over the Dry to values as low as 4.0.

The sulphate billabongs include one backflow billabong (Corndorl) all of the floodplain billabongs (except Leichhardt) and Island billabong which in its physicochemistry is intermediate between channel and floodplain categories. In this group, there is the same change to sodium chloride dominance during the Dry (except in Island) but this is accompanied by significant concentration of sulphate. In all of the billabongs conductivity rises sharply during the Dry (except Island) and pH can become very low, particularly in the floodplain billabongs. The low pH values and the concentration of sulphate is apparently from groundwater aquifers, introducing both sulphates and sulphuric acid from the weathering of pyritic minerals (i.e. iron sulphide - a feature of the Region's geology) in the surrounding catchment. While this groundwater influx is considered to be gradual, sudden early Wet season flushes into the floodplain billabongs of runoff from the sulphate-rich and acidic crust that forms on the surface of floodplain soils during the Dry, may occur that are believed to be the cause of occasional, but often major fish kills that develop at the time (Pancontinental Mining Limited, 1981); the sulphate-rich and very acidic waters that result in the billabongs during such influxes, are believed to mobilise aluminium, a known toxicant to fishes, from the sediments.

2.3.2.4 Turbidity

Of the three factors most likely to affect light conditions in billabong waters of the Alligator Rivers Region, namely organic colour (gilvin), turbidity and chlorophyll, turbidity - the presence of suspended, finely divided sediments, has been shown to be the dominant influence (Walker et al., 1983b).

In the Magela Creek, waterbodies can vary from non-turbid to very turbid during the Dry season, and from simple visual observations the billabongs can be so divided. An earlier table (Table 2.6) classifies the billabongs accordingly. The seasonal means of turbidity for the billabongs are similarly shown in Table 2.7 while the seasonal distribution is displayed as monthly values in Figures 2.26 and 2.27. From these data and the report of Walker et al. (1983b) the following generalisations can be drawn.

In most of the billabongs, maximum clarity occurs soon after the creek ceases to flow at the Wet/Dry transition (April-May) when suspended material is allowed to settle. Over the ensuing Dry, the channel billabongs do not experience much further change in triptonic turbidity (i.e. suspended, non-living particles), because of their narrow and sheltered nature, low surface area to volume ratios (as discussed in secion 2.3.2.3), and coarse sandy sediments. For these billabongs, no other discernible trend in water clarity through the Dry is obvious though phytoplankton populations may contribute to the low turbidity (Walker et al., 1983b). Leichhardt billabong behaves similarly for reasons previously discussed (section 2.3.1.4).

By the mid-Dry in most other billabongs, however, namely all the backflow and most floodplain billabongs, more or less rapid deterioration in water clarity has occurred due to the rising turbidity. These rises are attributable to falling water levels permitting wind-disturbance of fine sediments, and probably from some additional disturbance by wallowing buffaloes. The influence of macrophytes in preventing turbulent mixing is important in the shallow backflow billabongs. Thus Georgetown with relatively fewer macrophytes becomes 'dirty' very early in the Dry (Fig. 2.26) in contrast to Gulungul and Corndorl, where the turbulent mixing occurs more or less later and as an abrupt event coinciding with the death of the dense stands of macrophytes in these billabongs.

At the Dry/Wet transition, previously clear and non-turbid billabongs become muddied whereas turbid billabongs are cleansed. During the Wet, water clarity in most billabongs fluctuates, depending on the rate of flow through the billabong. Between floodpeaks when the Magela Creek is not backflowing, Gulungul and Corndorl billabongs for example, can become extremely clear (e.g. Corndorl, February, 1982), whereas Mudginberri billabong in the main stream channel can experience relatively higher turbidities, particularly when the billabong is initially flushed and during proceeding flood events during the Wet (e.g. late December, 1981).

2.3.2.5 Nutrient status and phytoplanktonic productivity

If algal productivity in aquatic ecosystems is limited, the prime causes are most likely to be light and the availability of the two nutrients, phosphorus and nitrogen. Light availability has been discussed in the previous section. The reports pertaining to nutrient status (Walker and Tyler, 1983a), phytoplankton populations (Kessel and Tyler, 1983), and primary productivity (Walker and Tyler, 1983b) are the basis now for the following descriptions on nutrient status and productivity of phytoplankton in the Magela Creek billabongs.

During the Wet, nutrient levels are at their lowest. By world standards, however, total phosphorus levels are high and the billabongs can be regarded as mesoeutrophic to hypereutrophic. Nitrogen: phosphorus (N:P) ratios are low at this time, and the billabongs are ultra-oligotrophic in terms of inorganic nitrogen.

During the Dry, the nutrient status of the channel billabongs remains the same as during the Wet. This is attributed to the lower evaporative concentration that occurs in these billabongs, in addition to the coarse and largely inorganic nature of the sediments.

In the other billabongs, however, nutrient levels rise markedly and continuously as evaporative concentration and internal loading from resuspended sediments proceeeds over the Dry. The process is further accelerated by the congregation in, and use of, these waters by buffalo and large numbers of waterfowl. The rapid increase in nutrients occurs earlier in the floodplain billabongs than in the backflow billabongs, and in addition, inorganic nitrogen constitutes a much higher proportion of the total nitrogen than in the backflow billabongs.

With the exception of the floodplain billabongs, N:P ratios in other billabongs are low and nitrogen is suspected of limiting production, not phosphorus as is usually the case in aquatic ecosystems. Phosphorus levels in all the billabongs indicate hypereutrophy, while inorganic nitrogen levels suggest a range from mesoeutrophic to hypereutrophic on a world scale.

The seasonal distribution of both surface and bottom phytoplanktonic chlorophyll (a direct measure of algal biomass) is displayed as monthly values for the Magela Creek billabongs in Figures 2.28 and 2.29. In general, phytoplankton stocks and productivity increase in all billabongs as nutrient levels rise after the Wet. By the mid-Dry, however, in all backflow and most floodplain billabongs, the increase in chlorophyll concentrations and in productivity is arrested in response to increasing turbidity, even though nutrient concentrations continue to rise. Thus, underwater light conditions deteriorate, preventing phytoplankton productivites from reaching the levels they should on the basis of available nutrients. Only in those waters such as in Leichhardt billabong, where substantial rises in nutrient concentrations occur over the Dry, but where rise in turbidity is mild, do productivities increase for much of the Dry. In this case, phytoplankton is able to capitalise on the optimal nutrient conditions.

In terms of the trophic status and features of the phytoplanktonic populations of individual billabongs, Bowerbird was always unproductive as were generally all of the billabongs during the Wet, particularly when strong flow through the billabong was apparent.

Mudginberri billabong experienced a general rise in trophic status over the Dry, but as nutrient levels never reached the levels attained in the other billabongs, phytoplankton populations were generally checked, despite a suitable light climate. Buffalo billabong apparently behaves in a similar manner. Kessell and Tyler (1983) noted that during the Dry in Mudginberri, there was a general trend towards increasing phytoplankton along the north-south axis of the billabong. In addition, a regular daily pattern of migration of phytoplankton to intermediate depths by the afternoon was found, followed by their dispersion at night through convective mixing. The same phenomenon was found in Leichhardt billabong, and one assumes it is a pattern common to all of the billabongs. At the commencement of the Wet, heavy rains can wash detrital and other material of terrestrial origin into the billabong, producing short-lived but strong increases in chlorophyll (Fig. 2.28), a pattern previously observed in the same billabong by Hart and McGregor (1978).

Island and Leichhardt billabongs are the most productive of the Magela Creek billabongs and both observed the highest populations of phytoplankton biomass. Island billabong experienced maxima in trophic status in the early Dry, while for the remainder of the Dry algal populations fluctuated irregularly.

For reasons already discussed, in Leichhardt billabong there is a trend through the Dry towards higher chlorophylls. The levels attained in fact are the highest of any billabong. The monthly fluctuations in algal biomass, however, are unpredictable and even locally, extremely rapid temporal and spatial variation in the phytoplankton populations (apparently random) are notable and characteristic phenomena of this billabong (Kessell and Tyler, 1983). Like Mudginberri there can be considerable but far less predictable, horizontal heterogeneity of phytoplankton at any one time. (This same horizontal heterogeneity has been assumed for the other billabongs of the Region, and according to Walker and Tyler (1983b) precludes any determinations of whole billabong phytoplankton biomass or whole billabong productivity rates and production budgets from determination at one site).

In Ja Ja, Jabiluka and Nankeen billabongs, chlorophyll levels increased to maxima by the mid Dry, then declined (more or less) as turbidity increased, limiting the algal populations. The backflow billabongs behaved similarly although surface algal scums could produce late Dry season maxima as occurred too during the early Wet season when backflow conditions inputted detrital and other organic matter to the billabongs (e.g. Corndorl, December, 1981).

Finally, according to Walker and Tyler (1983b), the billabongs of the Region at their most fertile are placed in the lower-mid to middle of the range of measured productivities in tropical lakes, and high in comparison with many temperate lakes. Based on chlorophyll concentrations, the billabongs are oligotrophic to eutrophic.

2.3.3 Ecology of the freshwater fishes

The unionacean larva, the glochidium, develops in the marsupial demibranchs of the adult female. In order for further development and growth as a juvenile mussel to take place, a temporary period of obligate attachment to one or more species of fish (with only rare exceptions) is necessary, during which metamorphosis takes place. Dispersal occurs during this parasitic phase. Because of this reliance (and apart from anthropogenic interference), the most important biotic relationship of freshwater mussels is that of their glochidia upon fishes. The population structure and dispersal of Velesunio angasi therefore, are presumably dependent to some degree upon the habits and occurrences of its host fishes. Thus, a brief, background resume of some pertinent aspects of the ecology of freshwater fishes of the Magela Creek, particularly community structure in the various waterbodies and movements, is warranted.

While the Australian freshwater fish fauna is depauperate by world standards, the fish communities of northern Australia, in common with tropical regions generally, are the most diverse in the continent (Lake, 1971). Of the some 170 essentially freshwater fish species native to Australia (Lake, 1971), 45 species - over one quarter of the country's total - occur in the small Alligator Rivers Region of tropical northern Australia (Midgley, 1973; Pollard, 1974). Intensive and ongoing collection of biological and ecological data of the freshwater fishes of the Region, largely concentrating on the catchment of the Magela Creek, has been carried out by research staff of the New South Wales State Fisheries since December 1979. A comprehensive report provided information on various aspects of the biology of the fishes including ecological requirements, movements, community structures and fluctuations in numbers with time (Bishop et al., 1981). Both the latter report and a subsequent article (Bishop, 1983) provide the basis of the following summary.

Baseline information on the biology and ecology of 32 fish species were presented in Bishop et al. (1981); 21 of these species were found abundantly in waterbodies downstream of mining activities of the Ranger Uranium Project Area (Table 2.8). Dynamic seasonal and longitudinal changes were noted in the structure of fish communities in the Magela Creek. These changes are summarised in Table 2.8. Lowest homogeneity was shown between communities in the late Dry season and highest homogeneity in the mid Wet to early Dry seasons. During the Dry, refuge populations of fish species occur in either escarpment, or channel and floodplain zones. These populations may enter the lowlands from either zone following initial creek flow in the Wet season. Thus, the increased homogeneity of the fish community structure shown during the mid Wet to early Dry appeared to correspond to an increased homogeneity of the aquatic environment - Wet season flows relinked Dry seasons refuge areas thereby allowing a greater range of species to become more abundant and widespread. As environmental conditions deteriorated during the Dry season, well-adapted species that did not migrate back to refuge areas after the Wet, were thought to suffer high mortality thereby explaining the decreasing species diversity (or heterogeneity) found in the lowland communities. This was particularly marked in the backflow billabongs, and the unstable late Dry season environment of these billabongs realised both lowest species diversity and lowest abundances of fishes in comparison to the deeper channel and floodplain billabong environments.

Specifically in relation to fish migrations in the Magela Creek, distinct downstream movements to the lowlands by characteristic escarpment species (those fewer species confined to the sandy creek channel shown in Table 2.8) were observed in the early Wet, followed by a return upstream at the end of the Wet season. Similar movements but in an opposite direction, and more obvious considering the larger numbers of species involved, were shown by species characteristic of the channel and floodplain zone. Communities in the lowlands hence, represent a species flux between communities in the upper and lower reaches of the catchment. Thus most of the species in the Region appeared to undertake potadromous migrations (i.e. movements within rivers and their floodplains or from lakes into rivers). At least several, moreover, are known to undertake catadromous migrations to brackish or saltwaters.

Although large concentrations of migrating fish were observed in the channel billabongs during the mid Wet, the abundances were primarily due to the billabongs lying in the mainstream channel of flow of the creek (i.e. migration route); thus aggregations occurred in quieter waters immediately downstream of the torrential input of the sandy creek channel. For most species, migration during the Wet was into the lowlands, particularly into the backflow and floodplain billabongs. Reasons for this response were explained by temporal and spatial patchiness of resources, since: 1) feeding activity was most intense in the Wet in backflow and floodplain billabongs; 2) while breeding activity peaked in the early Wet but declined through the Wet into the early Dry season, it was most intense in backflow billabongs followed closely by escarpment waterbodies, the sandy creek channel and floodplain billabongs; and 3) recruitment was greatest in the mid Wet season, and although more visible in the more downstream billabongs because of the physical displacement of juveniles, was noticeably high in backflow billabongs. Thus, the lowlands were argued to be valuable feeding, breeding and recruitment areas, exploited seasonally by freshwater fishes of the Region.

3 MATERIALS AND METHODS

3.1 The study sites

Study of the biology and the ecology of Velesunio angasi was confined to the Magela Creek waterbodies. Sampling commenced in March 1980 and ceased in May 1982.

Populations from three billabongs were chosen initially for intensive study. As a wide range of habitat types were sought, the selection considered geography, morphometry and hydrology of the waterbodies, in addition to known sites where mussels occurred in reasonable numbers. Thus, in accordance with previous billabong classifications and because of their large mussel populations, Georgetown, Mudginberri and Nankeen billabongs were chosen, being representative of backflow, channel and floodplain billabongs respectively. The wide geographical range of these billabongs (Fig. 2.4) was an additional feature that lent support to their selection.

In July 1980, an additional site was added to the sampling routine. A population of mussels was found along the lowland sandy channel of the Magela Creek between Bowerbird and Mudginberri billabongs. As the creek dries out out at the cessation of flow in the early Dry, the mussels in this reach are obliged to aestivate over the ensuing Dry until the creek flows again at the beginning of the next Wet season.

Mussels were collected monthly from the four waterbodies and except for mussels from the lowland creek channel (hereafter referred to as "creek" mussels), sampling in the billabongs over a two year period was done in a systematic and repeatable fashion. All age classes of mussels were collected quantitatively from defined areas (section 3.2.1) over a variety of habitat types.

Obvious habitat types within the billabongs were substrate and depth. (In addition to any direct effect on mussels, substrate was also indicative of the Wet season flow regime in the mussels' immediate environment - see section 2.3.1). Distance along the billabong was also considered as a check for other subtle (but at that stage unknown) limnological gradients that could act upon the mussels.

With the above considerations in mind, two transects were established across Georgetown billabong (Fig. 3.1). The upstream or southeasterly transect was located largely on the shallow, sandy sill referred to previously (section 2.3.1.2) and the second transect was located across the comparatively deeper silt and clay basin downstream (to the northwest). Mussels were collected from 1m² areas at 5m intervals across the upstream transect, and at 10m intervals across the downstream transect. Both transects thus encompassed a wide range of depths and substrate types.

Five sites were established in Mudginberri billabong (Fig. 3.1) each with a regard to depth, substrate and distance along the billabong. Two downstream (northerly) sites were located in relatively shallow waters over predominately sandy sediments. Two sites were positioned upstream of these (in the southeast) in deeper waters, and over the chiefly detrital sediments of this backflow part of the billabong (section 2.3.1.3). The fifth site was established along the southwestern bank over a stony and clay bed that is well flushed during the Wet season (section 2.3.1.3). No sites were located over the sandy sediments totally free from silt and detrital deposits that occur in the central channel region of the billabong (Fig. 2.8), as mussels here were generally uncommon. Mussels were collected from 2 x 1m² plots at each site, except for the fifth site where 0.25m² was sampled.

The floodplain billabongs of the Region in particular, are renowned for their populations of saltwater crocodile, <u>Crocodylus porosus</u> that become increasingly conspicuous over the Dry season. Nankeen billabong on the Magela

Creek floodplain has an especially large population in comparison to other freshwater billabongs of the Region, and because of this, routine sampling here was restricted. One site only, located at the narrow, downstream (northern) end was established in this billabong (Fig. 3.1). Samples were taken along a transect beginning on the eastern shore across the shelving silt and clay bank, and finishing in the deepest waters approximately halfway across the billabong. A total area of 8m² was sampled across the transect, 1m² at each 3m interval. Sampling thus accounted for the variations in depth, while sediments throughout the billabong were found to be nevertheless reasonably homogeneous (section 2.3.1.4).

Routine samples of creek mussels were generally taken from the section of creek channel betwen Corndorl and Mudginberri billabongs. Because of their habitat (along loamy banks and amongst roots of trees and shrubs, particularly Pandanus) and its extremely variable nature, collections per unit area were not relevant to these populations.

Permanent transects and sites were established in the three billabongs. These were marked by metal stakes in Georgetown and Nankeen, and concrete blocks marked by floating buoys in Mudginberri billabong. Each month the transects and sites were moved 2m downstream (Georgetown) or upstream (Mudginberri and Nankeen) to ensure the same ground was not sampled twice.

By the end of 1980, a wide variation in biological patterns (e.g. growth, reproductive condition etc.) was evident between mussel populations of the four waterbodies, and no common trends were apparent. Consequently, from January 1981 a further four billabongs, Corndorl, Island, Leichhardt and Jabiluka, were added to the routine sampling in the hope that patterns might emerge with the addition of further variety in habitat types and environmental data. Mussels were sampled monthly from each billabong up until May 1981.

In Corndorl, collections were made at one site in the northeastern corner of the billabong (Fig. 3.1). In Island, Jabiluka and Leichhardt billabongs, mussels were sampled quantitatively across transects. These were regularly spaced along the billabong (Fig. 3.2), with one transect being sampled per month, beginning at the first nothern-most transect in January, 1981. Mussels were sampled from 1m² plots at regular intervals across each transect. A total area of at least 10m² (depending upon the billabong width) was sampled and depth and substrate type were recorded at each 1m² plot.

The mussel populations of a further two billabongs, Ja Ja and Buffalo, were sampled during 1981 and 1982 but not on a routine monthly basis. Ja Ja was sampled bimonthly from April 1981 and Buffalo billabong every third month from April 1981. Collections from Ja Ja billabong were taken in the same manner as those from Nankeen but at different sites per collection (Fig. 3.2), while samples from 1m² plots were taken from each of 10 sites (Fig. 3.1) in Buffalo billabong.

3.2 Field procedures

In studies of freshwater mussels to date, collecting has been achieved using a wide variety of sampling techniques - for example dredging, raking, dragging, brailing, tonging, wading and (comparatively recent), sustained diving with SCUBA. Quantitative collection of mussels is not essential to all studies. However, when estimates of abundance or density are needed, (for example when distribution, population dynamics and production are under investigation) an adequate quantitative capability is an important requirement of the sampling device.

It is well known for the marine environment, that most collecting devices including dredges, grabs and corers are at best semi-quantitative in so far as giving an accurate picture of the density and distribution of benthic fauna (McIntyre, 1971). In freshwaters similarly, apart from diving, most samplers are notoriously inefficient when quantitative collecting is required

(Flannagan, 1970). Efficiency is more often dependent upon substrate type. Dredges and grabs for example are known to be ineffective over irregular beds especially hard-packed substrates and rock or debris-strewn bottoms (Stansbery, 1961; Stanczykowska, 1977), so that comparisons of distribution between different habitats of a freshwater body are then often difficult to make. Even over sediments conducive to sampling by these devices, many mussels may be missed. Haukioja and Hakala (1974) found for example that per unit area an Ekman grab collected only one third of the number of mussels collected by hand.

A number of studies nevertheless, have used these supposedly "quantitative" collecting devices when good quantitative data were required (Hendelberg, 1960; Tudorancea and Florescu, 1968; Magnin and Stanczykowska, 1971; Mackie and Qadri, 1973). In other cases several techniques have been used such as hand-collecting and diving in combination with dredges, without any attempt to measure the efficiency of one technique over another (Okland, 1963; Negus, 1966; Lewandowski and Stanczykowska, 1975; Kenmuir, 1980). Even when the inefficiency is recognised in or between sampling techniques (e.g. Lewandowski and Stanczykowska, 1975; Stanczykowska, 1977) no estimates of the mean efficiency of the sampling equipment appear to have been calculated.

It is widely recognised that collection of mussels directly by hand, particularly when aided by SCUBA diving, is by far the quickest and most efficient sampling method. Even when SCUBA is involved, however, "intensive" or "exhaustive" searching by hand alone (Cvancara, 1972; Ghent et al., 1978) is no guarantee of completely efficient sampling. Mussels, especially small specimens, may still be missed (Haukioja and Hakala 1974, 1978a; Coon et al., 1977; Strayer et al., 1981). In studies in which hand collecting alone is employed, only the studies by Haukioja and Hakala (1974, 1978a) have checked the efficiency, by sieving the substrate after handpicking to derive an estimate of the error involved. No mention, however, has yet been made of the size range of mussels that are too small to be collected by hand.

Although collection of small (young) mussels in some quantitative studies is not an important requirement - especially for production estimates where the biomass missed may be practically negligible, the collection of young mussels in studies of distribution and population dynamics is crucial to a proper understanding of recruitment.

Only studies by Negus (1966), Brice and Lewis (1979), Kenmuir (1980) and Horn and Porter (1981) have combined hand collection of mussels by diving with subsequent sampling and sorting of the sediments using scoops for the remaining small mussels. Horn and Porter (1981) used in addition, a diver-operated suction-type dredge at quarterly intervals during the year to collect mussels. The study of Brice and Lewis (1979) was a 'point' sample in time, however, and nor did the studies by Negus (1966) and Kenmuir (1980) collect by this method on a routine seasonal basis. (In the above studies, this type of collecting is assumed totally effective, with no mussels being missed). The study by Horn and Porter (1981) is apparently the only attempt at systematic searching for all age-classes of mussels on a seasonal basis, using diving to collect mussels and sediments. Even when other methods that are apparently non-selective for size have been employed (e.g. dredges) that provide at least a relative measure of the population age structure, seasonal sampling has only been attempted by Negus (1966).

Thus, while it has generally been assumed in the past that young mussels are cryptic and have quite different habitat requirements to those of adults (Isely, 1911; Coker _et_ _al_., 1921; D'Eliscu, 1973; Walker, 1981b), nevertheless few studies have searched systematically for young mussels on a regular temporal basis. When breeding is highly seasonal, such as the case for much of the mussel fauna of temperate regions, young may only appear for a short period of the year, especially if juvenile mortality is high or growth is particularly rapid.

During the present study, diving was used to collect mussels. Virtually unlimited time was available for sampling through the acquisition of a petrol-driven, Hookah compressor; the characteristic and favourably high water temperature for diving; and the comparatively shallow waters (<10m) which never imposed limits upon submerged working times. This is contrary to other studies using diving as the sampling method, where SCUBA invariably provides the air support. In these cases, tanks must be periodically refilled to the detriment of diving time. Limitations of distributional studies due to depth and low water temperature have been commonly cited in temperate regions.

3.2.1 Methods of sampling

Early surveys and collecting of freshwater mussels from the billabongs experimented with a dredge and a toothed, hand-held rake. While the latter was least time-consuming and more effective than the former, the rake was nevertheless inefficient over sandy and debris-strewn substrates and extremely labour intensive particularly under the prevailing hot and generally humid climate. No satisfactory quantitative sampling could be achieved by these methods.

Ultimately five types of sampling were employed to collect freshwater mussels during the present study. The first four methods are variants of diving - free diving with or without a snorkel in depths less than about 1m but aided by a petrol-driven Hookah compressor in deeper waters. The collecting methods are described as follows:

<u>Type 1</u>: Mussels were collected from a confined area, though not from the confines of a prescribed bounded area. The collecting area was roughly a semi-circle with radius the distance of the outstretched hands, with the diver in a kneeling position. Care was taken to sample all size classes of mussels, and to remove all the mussels from an area before moving a short distance and repeating the procedure. To effect this, once all the mussels were thought to

have been removed from a locality (these having been placed in a collecting bag), the sediment was broken up in a systematic mulching fashion to a depth of about 7 cm, and the area rechecked by sight or by touch at least twice for remaining mussels.

In practice, all mussels above 27mm are assumed to have been collected by this method (section 3.2.2.). However, while no size-selection above this length was apparent, nor was any attempt made to relate numbers of mussels to area for density estimates.

Type 2: Using this method, mussels were collected by hand from the confines of a metal-framed quadrat, of dimensions 0.5 x 0.5m (0.25m²) by 7cm in depth with an outer 2cm horizontal lip around the surface. The quadrat was pushed into the substrate as far as the lip (7cm) and all mussels within the frame removed. As in Type 1 sampling, the substrate was then thoroughly broken up to a depth of from 7 to 15cm (depending upon the firmness) and the area re-checked at least twice in a systematic fashion until no further mussels were recovered.

Type 3: Mussels were removed by hand from the confines of the quadrat, in the same manner as before (Type 2). Any debris such as coarse vegetation and sticks was carefully removed; macrophytes were pulled out by the roots, adhering sediment shaken off and the plant discarded; and the substrate was then collected into a scoop (a household plastic dustpan approximately 30cm in width). The contents of the scoop were then placed carefully into a large circular basket made of a rigid plastic mesh. Mesh size was 2.5 x 1.5mm. The basket was held over the quadrat, to ensure that spillages were re-directed into the confined area. Substrate collection was done in a systematic fashion working from one corner and side and finishing in the corner diagonally opposite. All sediment to a depth of 7 cm (the depth of the quadrat) was removed by this method. Care was taken to ensure that, as far as possible, no sediment remained adhering to the side, or collected in the corners of the quadrat.

At the water surface, the sediment and associated debris were thoroughly stirred and washed in the screen basket until all fine material had apparently passed through the mesh. The contents of the basket were then placed in plastic bags for later sorting and examination in the laboratory.

Type 4: This sampling was achieved using a diver-operated, air-lift pump. Mussels were again removed by hand, the sediment lightly broken up, and coarse debris and vegetation removed. Air was then fed via a diving hose into a wide bore (7cm internal diameter) flexible but compressed and reinforced rubber hose, approximately 10cm from the mouth. A nozzle consisting of a 30 cm length of clear perspex or PVC tubing (50 mm internal diameter) was fitted to the mouth of the rubber hose. Water displacement with the resultant Venturi effect, acted to suck up water, sediment, associated debris and mussels through the hose via the inhalent nozzle to the surface where the material was directed by an assistant into the same screen basket as described earlier (Type 3). Sediment was collected in a systematic fashion, working from one side of the quadrat to the other, and to a depth of at least 7cm. The collected material was washed and treated in the same manner as before (Type 3).

Two hoses were used in the study, one of length 6m for deep (Wet season) waters and another of 4m used in the Dry. In shallow water (<3m), the hoses were replaced by PVC tubing (50mm internal diameter) of length appropriate to the depth of water. The pump principle is such that its drawing power decreases with decreasing depth. The pump used in the present study was ineffective in water less than 1m in depth. In water below this depth, the larger and heavier sand particles (and larger mussels) could not be lifted to the surface.

When diving, only for a few months of the year was visibility at the bottom of most of the billabongs sufficient to see more than a metre or so from the diver, and by the time the sediments had been disturbed (the routine practice), visibility was generally negligible in any case. Consequently, touch played a dominant role in the collection of mussels and performance of underwater actions. This did not impair the efficiency of collecting. Even in the clearest billabongs (e.g. Mudginberri) where the mussels were readily visible for much of the year, touch rather than sight was still responsible for most of the collecting actions.

Type 5: This type of sampling describes collection of creek mussels. During the period of creek flow (about December to early June) mussels were collected from likely areas (described in section 3.1 by Type 1 sampling. Over the ensuing Dry the mussels burrow up to 20cm into the surrounding substrate to aestivate. This occurred usually as an abrupt event with the cessation of creek flow, and sampling then involved use of digging implements such as picks and mattocks in compacted soils, aided by the hands in the softer and friable sandy soils. Over the Dry season when digging was involved, care was taken as in Type 1 sampling, to thoroughly search a locality. This meant digging beyond the normal depth at which mussels burrowed, and searching through the exposed soils several times before moving onto the adjacent undisturbed region.

Collection of sediments for later sorting and collection of the small mussels missed by hand (Types 3 and 4 sampling) was limited to Georgetown, Mudginberri, Nankeen and Buffalo billabongs. This was particularly relevant to the first three billabongs, where mussel populations were under most intensive investigation. From July 1981 to the end of the Dry in Nankeen, but throughout the year in Georgetown billabong, sites became increasingly shallow for Type 4 sampling. Thus, as depth declined to below 1m, so too did Type 3 sampling (scooping) replace Type 4 (air-lifting) as the collecting method. By the end of the Dry, 3 of the 8 sites in Nankeen were so affected; in

Georgetown only 4 out of 9 sites in the downstream transect, and none in the upstream transect, could be sampled using the air-lift.

In Nankeen billabong, there was some initial reluctance to spend long periods of time in the water with the knowledge of the attendant crocodile population and potential hazard. The time-consuming task of collecting sediments therefore, did not commence until January, 1981. From June, 1980 to the cessation of sampling, diving in this billabong was done within the confines of a large net as a safety measure. The net was laid in a semicircle about the diver, with both ends anchored to one shore. The net was multifilament and of the floating and sinking type with dimensions: mesh size 20cm (stretched knot to knot); length 75m; and depth approximately 7m. The net was also used for protection in all of the floodplain billabongs during routine sampling.

While mussels were collected from defined areas ($1m^2$) across transects in Island, Ja Ja, Leichhardt and Jabiluka billabongs, invariably the numbers so collected were insufficient for other biological studies. In these cases, Type 1 sampling was employed in the immediate vicinity of the transect but in the shallower water towards the banks, where mussels were most common.

Table 3.1 summarises the various collecting methods used in the Magela Creek waterbodies over the study period.

3.2.2 Sampling efficiency

As different methods were employed to collect mussels between waterbodies and even within the same billabong on any one occasion, it was necessary to check and find the efficiency of the various methods. This was deemed essential for accurate descriptions of distribution and population dynamics. Having found the mean efficiency of the sampling types, these could then be calibrated against one another and the necessary corrections made so that the pertinent features of the mussel's ecology were comparable over the Magela Creek system.

Efficiency was measured against air-lifting, which in the present study was assumed totally effective in so far as collecting all the mussels within a defined area. The basis of this claim were the observations made under optimal conditions of visibility (Mudginberri billabong during the Dry season) when the ability of the air-lift to draw up all substrate and debris within its path was unequivocal. A particular feature of the pump in this regard was its ability to effectively scour and draw up material from the corners and sides of the quadrat.

Apart from observations, an independent check of the efficiency of the air-lift pump was done in the following way: In April 1981, sediment and mussels were air-lifted routinely from the 8.25m² of sites along Mudginberri billabong. No prior hand-collecting was attempted and all material to a depth of 7cm was collected. A further 7cm of the sediment was then air-lifed and collected separately (thus drawing up material over a total depth of 14cm). In the laboratory, the mussels were sorted and separated from the associated sediments and debris. In the upper 7cm of collected substrate 304 mussels were recovered including 43 below 23mm in length, while no mussels were recovered from the underlying 7cm of sediment. Hence, no mussels remained in the confines of the quadrat after collecting the top 7cm of sediment, and air-lifting was assumed a totally effective collecting method.

The above experiment also confirmed observations (by sight and touch) that the mussels did not burrow beyond the depth at which normal siphoning was not possible. This is a phenomenon common to mussels of temperate regions where winter burrowing and apparent "hibernation" are responses to low water temperatures (Stansbery, 1961; Walker, 1981b). Water temperatures were characteristically high throughout the year and never declined to such low levels as to induce the same response in mussels of the Magela Creek billabongs.

Having confirmed the total effectiveness of air-lifting as a collecting method, the effectiveness of hand collecting was then calculated on three occasions (September and October 1981, and May 1982) in Mudginberri billabong. Mussels were collected using Type 2 sampling (hand collecting from quadrats), then air-lifting was used to collect the substrate and remaining mussels. A total area of 24m² was sampled, representing a total of 589 mussels collected. The results are a direct check of the efficiency of Types 1 and 2 sampling which were the sampling procedures in other waterbodies (Table 3.1).

The results of the efficiency check are shown in Table 3.2 . No mussels above 27mm in length were missed by hand collecting and over 60% of mussels between 20-27mm length could still be detected. Mussels below 19mm, however, were too small to be collected by hand.

The efficiency of Type 3 sampling (scooping sediments) was tested in Mudginberri (April and May 1982) and Buffalo (April 1982) billabongs. Mussels and sediments were collected using Type 3 sampling, prior to air-lifting a further 7cm of substrate. A total area of 26m² was sampled comprising a total of 50 mussels collected below 26mm. (Mussels above this size were collected by hand). In the laboratory the mussels were sorted and separated from the sediments according to scooped and air-lifted collection.

From the above experiment 36 mussels were found in the scooped sediments and 14 in those air-lifted. Thus scooping was found to have a mean efficiency of 72% in so far as collecting small mussels less than the size that could be collected by hand. A t-test was applied to the mean lengths of mussels collected by the two sampling methods. This revealed no significant difference ($P > 0.05$) between the two means ($t = 0.319$ on 22 DF). Therefore while scooping failed to collect all the small mussels from a defined area, the size distribution of small mussels so collected was nevertheless unaffected. For samples from Georgetown, Mudginberri and Nankeen billabongs then, a correction factor (of 1.39) was used to correct for numbers of small mussels missed when Type 3 sampling was used.

Although the experiments used to derive scooping efficiency were performed in the deep water of Mudginberri billabong, there was no reason to suspect that the efficiency would be any different in shallower water (<1m). As the methodology was similar over all depths of water, the correction factor is assumed applicable to the shallow sites of Georgetown and Nankeen billabongs where Type 3 sampling was performed. Similarly, the array of sediment types sampled in Mudginberri and Buffalo billabongs was sufficiently broad enough to represent the range found in Georgetown and Nankeen. Any discrepancy that could possibly arise would be from the selective efficiency of scooping between the heavier and more compacted sandy sediments and the lighter silt and detrital or silt and clay sediments. As two main types of sediments were collected from Mudginberri and Buffalo billabongs, a softer silt and detrital sediment and a predominately sandy sediment, a chi-squared test was applied to the proportions of scooped mussels collected from the two sediment types. The test revealed no evidence for an efficiency bias of scooped mussels according to substrate ($\chi^2 = 0.386$, $P > 0.05$).

Presumably the effectiveness of the air-lift lay in its ability to draw up all the sediment from the sides and corners of the quadrat, places where the scoop could not always sample adequately. Further, in some instances it was not always possible to remove underlying debris such as sticks or buried logs, and these invariably interfered with scooping. This bottom type was typical of the two northern sites in Mudginberri billabong. Similarly sticky clay sediments were difficult to sample using the scoop, and at the fifth site in Mudginberri where this sediment was mixed with rocks and stones, air-lifting was virtually the only means of effectively collecting the sediment and small mussels.

3.2.3 Collection of limnological samples

Monthly sampling of mussels was immediately preceded in most instances (i.e. from January, 1981) by collection of limnological samples. (Prior to January

1981, collection and analysis of these samples was carried out by personnel from the Botany Department, University of Tasmania). Water samples were collected in the early morning generally between 0700 and 0830 and coincided therefore with minimum temperatures and importantly, minimum oxygen concentrations. As this was in accordance with the sampling rationale of Walker et al. (1983a) both data sets are comparable.

Collections were made from the bottom and surface waters, over a region where mussels occurred or where mussels were to be sampled. A fixed position in Georgetown, Corndorl, Mudginberri, Buffalo and Nankeen billabongs was sampled monthly but in Island, Ja Ja, Leichhardt and Jabiluka billabongs, water in the vicinity of the monthly transect was sampled.

Surface water samples were taken at 0.1m depth while bottom water samples were collected by diving - that is, by swimming over the bottom sediments while holding and filling the bottles at a 45° angle immediately above the sediments. Constant swimming ensured that the waters from which the samples were taken had not previously been disturbed.

The limnological parameters to be measured from the collected water samples were bottom temperature and dissolved oxygen concentration, surface pH, conductivity and turbidity, and both surface and bottom phytoplanktonic chlorophyll. Of these, temperature and pH were measured directly in the field. The field procedure after collection was as follows:

One of the bottom water samples was fixed for later measurement of dissolved oxygen concentration. The water temperature of the other bottom sample was read by an accurate mercury thermometer, then between 250 and 500 mls of this water was filtered onto Whatman GF-C filters and stored on ice for later chlorophyll analysis. Similarly water from the surface sample was filtered and stored in the same manner for chlorophyll analysis. pH of the surface water sample was measured to the nearest 0.1 pH unit using a submersible glass electrode coupled to a portable Metrohm, Model E604 pH meter. The meter was calibrated against standard pH buffer solutions prior to collection of the water samples. The remaining surface water sample was taken back to the laboratory for measurement of conductivity and turbidity.

3.3 Routine laboratory procedures

All mussels used in routine reproduction and condition studies were processed on the day of collection. This involved excising the flesh and fixing the tissues for later histological examination, or otherwise cutting the mussels open (i.e. cutting the anterior and posterior adductor and protractor muscles) and storing them overnight in refrigerated water. Early experience proved that if mussels were kept any longer (e.g. overnight) before processing, mature females were liable to abort larvae from the inner gills. Hence, the routine laboratory procedure was as follows:

Mussels for reproduction and condition studies were randomly subsampled from the samples taken from the various habitats under study (section 3.1). Generally, mussels less than one year in age, however, were excluded from the subsamples and were dealt with separately. A number for later recognition was etched onto the shells of the selected mussels. The mark was made through the periostracum, with a small electric-powered hand drill (Dremel), fitted with a dental burr.

A number of external measurements of shell dimensions were made to describe the size and shape of mussels. Total length, maximum height and width were measured routinely, this system of measurements being the same as that used by McMichael and Hiscock (1958) except that maximum height was measured on the outside and not on the inside of the shell (Fig. 3.3). Each measurement was made to the nearest 0.5mm and was performed on a measuring board of plastic protected graph paper over a flat wooden base, bounded by two upright horizontal and vertical metal strips. Mussels were placed flush anteriorly and ventrally, or laterally to the bordering strips while another free, upright metal strip was placed flush to the mussel posteriorly, dorsally or laterally to read off the appropriate measurement. The measuring board was used only on mussels greater than 25mm in length. Smaller mussels were measured using Vernier calipers.

Three weights were performed routinely on mussels: total weight (expressed to the nearest 10mg); and flesh and dry weight (both to the nearest 1mg). All weights were taken on a top-pan balance precise to 1mg. Total weight refers to the weight of the whole, intact and live mussel. Flesh was shucked with a scalpel, care being taken to remove all the attached adducter and protracter muscles. Flesh weights were made after draining off the body fluids, and blotting the flesh of surface fluid with absorbent tissue paper. The blotting was performed in a consistent and repeatable fashion on all mussels. The further treatment of the flesh (i.e. fixation and oven-drying) and shells is dealt with in later relevant sections.

Collected substrate material from Georgetown, Mudginberri, Nankeen and Buffalo billabongs was sorted for small mussels on a large, shallow plastic tray. A pair of forceps was used to systematically move and sort the material from one end of the tray to the other, and having inspected all the material, the procedure was repeated in the same manner (i.e. the material was re-sorted).

Measurement of dissolved oxygen, conductivity, turbidity and chlorophyll were performed in the laboratory. Dissolved oxygen concentrations were measured by the Alsterberg azide modification of the Winkler technique (APHA, 1971). Conductivity was measured to the nearest 5 Scm^{-1} with a Metrohm, Model E518 conductivity meter. Turbidity was measured with a Hach 2100 turbidimeter, which gives a measure of the proportion of light scattered by the water at right angles to the incident beam. Filtered chlorophyll samples from field collection were frozen until processed. The determination of chlorophyll involved extraction with 90% acetone, followed by measurement of the absorbance at 750nm, 664nm, 650nm and 647nm (Jeffrey and Humphrey, 1975).

3.4 Data analysis

Where statistical procedures are described, analyses of variance were conducted using the NEVA programme (Burr, 1980); regression analyses using either the BAR3 programme (Chapters 4-6) (Burr, 1975) or the MINITAB statistical package (Chapters 7 and 8) (Ryan et al., 1978); and complex exponential (Chapter 5) and logistic (Chapter 6) models were fitted using the BMDP statistical package for nonlinear regression (Dixon and Brown (Eds), 1979). The analysis of length-for-age data is described in section 6.4.1. Levels of significance of the statistical analyses in the tables, are indicated by the usual conventions of * for $P < 0.05$, ** for $P < 0.01$, *** for $P < 0.001$ or by ns for not significant (i.e. $P > 0.05$).

4 SHELL SHAPE AND ENVIRONMENT

4.1 Introduction

A well recognised characteristic of unionacean bivalves is their high degree of phenotypic plasticity in shell shape. Explanations for why such high morphological variability amongst these forms can be maintained and can be adaptive, have been hypothesised as follows: Expanding largely on the review of Tevesz and McCall (1979), Tevesz and Carter (1980a) reiterated that inherent features of the environments that unionaceans inhabit are the low levels of competition and predation (by comparison with marine environments). Such low biotic selective pressures and the resultant lack of specialisation of freshwater mussels for particular resources such as food, substrate and space, were thought by Tevesz and McCall to have permitted the maintenance of variability; Eagar (1978) and Kat (1983c) added that high variability in shell shape might be adaptive in that it compensates for habitat unpredictability that results from the type of dispersal characteristic of unionids (i.e. via fish hosts). Such dispersal would preclude specialised habitat selection by juveniles.

Amongst the Australian hyriids, variability in shell shape within a single species is reportedly immense, a factor, according to McMichael and Hiscock (1958), accentuated by the vicissitudes of the Australian environment over large areas. For the hyriids (McMichael and Hiscock, 1958; Walker, 1981b), as in other unionacean families, variability is a frustration to taxonomy and to other work in which high species integrity and ease of specific recognition is an essential prerequisite. For Velesunio angasi, the latter consideration has obvious implications for use of the mussel in pollution and biomonitoring work in the Magela Creek. No problems in this regard were expected for the freshwater mussels of the Alligator Rivers Region; according to McMichael and Hiscock, V. angasi is the sole species occurring in the area.

Within the catchment of the Magela Creek, a number of different and clearly distinguishable growth forms may be adopted by V. angasi. Of specific concern, early surveys produced isolated examples of shells from the billabongs that at cursory glance resembled those of a congener, V. wilsonii, a species which V. angasi more closely resembles than any other in the genus (McMichael and Hiscock, 1958). According to the taxonomic descriptions of McMichael and Hiscock, the shell of V. wilsonii is characteristically long with almost parallel dorsal and ventral margins, and an acuminate posterior end (Fig. 4.1); shells of V. angasi differ consistently from V. wilsonii in being notably higher, bearing a fairly pronounced wing and prominent and truncate posterior ridge (Fig. 4.1). For the taxonomy of the Australian fauna, specific recognition, which to date has relied almost solely upon conchological characters, McMichael and Hiscock stressed that specific, subspecific and ecotypic differences could only be discerned by studying large populations of mussels from as wide a range as possible. They believed nevertheless (reaffirmed later by McMichael (1967)), that despite variable shell form, the hyriid species of the Australian environment were discrete taxonomic units that could be recognised easily by the student familiar with the group.

Considerable progress has been made in comparatively recent times in the taxonomy of North American unionaceans, with the use of electrophoresis and the resultant genetic identity that may now be ascribed to species and subspecies (e.g Davis et al., 1981; Kat, 1983b,c). This work marks a new era in the taxonomy of unionaceans that according to Kat (1983a,d) (and probably general opinion) has relied over-excessively on environmentally variable shell characters in the past for species determinations. Nevertheless, despite the anachronism that conchological investigation on its own is assuming, it remains an integral part of an approach in combination with soft-part morphology and electrophoretic techniques, that Kat (1983a,b) thought would be required to resolve taxonomic confusion in unionids. For congeners of some North American unionids not diverged long enough to accumulate genetic differentiation, dissimilarity of shell shape may be the only feature that allows for discrimination among species (Davis et al., 1981; Kat, 1983b).

For species of a genus (such as Velesunio), whose taxonomic separation is based upon apparently distinct, conchological features, analysis of environmental relationships of variability of shell form in populations within a catchment, may provide for resolution and ultimately specific identification of the constitutent forms. Populations so affected by environmentally induced changes (non-heritable) imposed directly on the phenotype, are referred to as ecophenotypes (e.g. McMichael and Hiscock, 1958). Such environmental factors that may affect shell shape among unionaceans include temperature, water depth and flow rate, substrate type, trophic degree and size of the habitat, and water turbulence. These parameters and the resulting induced changes to shell forms that have been documented in the literature, are reviewed in Appendix 1.

The studies by Dell (1953), McMichael and Hiscock (1958) and Walker (1981b) represent the few ecological investigations to have identified ecophenotypic variation within the hyriids. The nature and extent of this variation in some cases has reconciled or ammended existing taxonomic descriptions. No study in the Australasian region, however, has investigated thoroughly ontogenetic variability within a single species, which is critical to the present study in terms of characterising the species integrity of V. angasi.

The limnological heterogeneity that prevailed within and between waterbodies of the Magela Creek, provided convenient environments in which to study the nature and extent of ecophenotypic variation in shell shape of the resident freshwater mussel fauna. Thus, the present investigation sought to describe this variation and its environmental determinants, in addition to describing ontogenetic variation in shell form of specific populations. As known soft-part (McMichael and Hiscock, 1958) and larval (Walker, pers. comm.) differences amongst members of the genus Velesunio are slight, conchological characters will no doubt continue to be important diagnostic features used for species recognition throughout the range of the constituent species. It was hoped from the present study, that apart from affirming the presence of a single species only (V. angasi) in the Magela Creek, some additional insights into, and evaluation of, the present taxonomic distinction between V. angasi and the congener V. wilsonii, would result. These species are separated at present, chiefly by shell character.

Inherent in the evaluation mentioned above, is the extent to which shell description adequately distinguishes between ecophenotypes, and ultimately between species. Relative shell dimensions expressed by ratios, which partly demonstrate shape, were of considerable importance to the taxonomic work of McMichael and Hiscock (1958). Walker (1981b), however, made repeated reference to the inadequacies of relative dimensions (specifically relative height) towards detecting the presence or absence of wing development in particular, in hyriid mussels. Walker found that relative height showed trends in company with the degree of wing development in Alathyria jacksoni, but considerable variations in the relative height ratios (i.e. height/length) tended to conceal rather than to reveal any underlying patterns. While recognition of wing development is more dependent upon angular dimensions, both McMichael and Hiscock, and Walker, argued that their measurement was inappropriate for, and difficult to make upon, living mussels as fully opened valves are required. Relative shell dimensions between length, and height and width, expressed through allometric power functions over the size range of mussels considered in the present investigation, were used to describe variation in shape of mussels in the Magela Creek.

4.2 Methods

The relationships between length and height (i.e. relative height), and length and width (obesity) were chosen for analyses of environmental relationships of shell form variability in V. angasi. These dimensional relations have been most frequently mentioned as changing in predictable fashions from the headwaters of a stream in a downstream direction (section A1.1). If detected therefore, ecophenotypic variation in V. angasi should be evident in these relationships. Relative height most importantly, has been extensively used in taxonomic descriptions of members of the genus Velesunio (McMichael and Hiscock, 1958).

Length, height and width measurements of mussels collected from all of the Magela Creek waterbodies, were made according to the method described in section 3.3. Morphometric data derived from all mussels quantitatively sampled from the routine collections (made between 1980 and 1982, section 3.1), were used in the analyses. Unless otherwise indicated, only adult mussels were used for the analyses (>30 mm in length, section 7.7), as these mussels had been subjected to environmental influence for sufficiently long enough period of time to give a characteristic 'reaction form' for the local environment. The omission of juveniles was further justified in the observation that growth between the size dimensions approached isometry in juvenile mussels; indeed as shown below (section 4.3), some of the relationships between the size dimensions differed significantly between juveniles and adults of a given environment.

Plots of length against height and length against width of adult mussels, clearly indicated differential growth between the various size parameters. The appropriate size variables Y and X therefore were fitted to the allometric power function,

$$Y = AX^b$$

The constants A and b, were calculated using least squares regressions of the log transformed variables. The exponent b, the slope of the linear log-log transformed allometric equation, indicates the relative rate of increase or decrease of the dimension Y in relation to X. The value b therefore, provided a useful quantitative means of describing and comparing growth form variation in relative height and obesity, between different environments (i.e. between-waterbody comparison), and between habitats of the same environment (within-billabong comparison). Errors inherent in the measurement of size are assumed of the same order among each of the various size dimensions. Any biases introduced from measurement error should be consistent therefore, and should not alter or affect the comparisons of growth form variation between different environments. (For comparisons of relative height and obesity between populations, length (Y) is regressed against height and width (X) respectively.)

The approach used in the present study is a departure from previous analyses of ecophenotypic variation in unionaceans, that have relied entirely upon ratios calculated between the size dimensions for shell form comparisons. Ontogenetic variability inherent in these ratios may be minimised by including only data from mussels of a limited size range in the calculations - at the expense, however, of omission of data. As ontogenetic variability is accounted for in the allometric equation, study of ecophenotypic variation in shell form of V. angasi using the slope of the equation, enabled most of the available data to be utilised. The order of increase in the slopes matched the order of increase in allometric intensity at mussel sizes only > 40 mm. (From the data of Tables 4.1 and 4.9, a negative correlation was found between the slope and intercept of the allometric equations describing the relationships between shell length and height, and length and width, among the populations.) For all populations nevertheless, size ranges > 40 mm comprised all or most of the material analysed (see Figs 6.23 and 6.24). Where tests of equality of slopes and intercepts between regression equations were required, analysis of covariance testing was performed.

Environmental parameters assessed as potential correlates of morphological variation in V. angasi were chosen on the basis of previous descriptions in the literature, as having relevance to shell form variation in unionaceans. From the review in section A1.1, these factors include water depth and flow rate, substrate type, trophic degree, and degree of water turbulence. The effect of turbulence upon shell form has been discussed in the literature mainly in relation to large lakes where stunting may result. This stunting reportedly affects overall size independently of relative changes in height and width (e.g. Green, 1972; Ghent et al., 1978). As variation in size of V. angasi is considered in chapter 6, minor consideration is given here to the relationship of water turbulence and shell shape. For between-waterbody comparison otherwise, standardised water depths were obtained from Table 2.1 while broad measures of relative stream velocities between waterbodies were inferred from substrate type (see sections 2.3.1 and 5.2). Sediment characteristics, in terms of percent organic matter and mean sediment particle size, averaged broadly over each billabong are shown in Table 2.2. Trophic degree (as chlorophyll a), and a variety of physicochemical parameters considered, including dissolved oxygen and various measures of hardness, are given in Table 2.7 as averages over the seasons. For within-billabong study, records of depth and substrate at each sampling location were made according to previous descriptions (section 2.3.1). All depth measurements that were made at each site, were standardised to late Dry season levels (1 Nov. 1981). Stream velocities at each of the sampling sites in Mudginberri billabong were taken from the data of Figure 2.15. These measurements were determined for a specific stage of discharge (section 2.3.1.3) but nevertheless are assumed to represent a relative measure of flow rate that is constant between sites, for various intensities of Wet season discharge. The method of determination of mean chlorophyll concentrations averaged over the seasons for each of the sampling sites of Mudginberri and Buffalo billabongs (Tables 4.4 and 4.5), is given in section 6.4.3.1.

4.3 Variation in relative height

The nature of the allometric equations describing relative height and obesity of V. angasi for each of the populations in the Magela Creek waterbodies, was such that height increased relatively slower in relation to length, while width increased relatively faster. While ontogeny could explain this compensation of one shell dimension accompanied by a change in another within populations, among the populations no correlation was found between the same relative shell dimensions. Thus for example, mussels from a population with relatively high shells were not necessarily less obese when compared with other populations. Averaged over all size classes of mussels, environmental influences affected relative height independently of obesity. To demonstrate this, regression analysis was performed between the slopes derived from the allometric equations for relative height and obesity, for the morphometric data of all mussels sampled in each waterbody (Tables 4.1 and 4.9). This analysis showed that the slopes of the respective equations were unrelated ($P > 0.1$).

4.3.1 Between sexes and waterbodies

The allometric regression equations describing the relationship between length and height of mussels, calculated for the sexes separately and combined from each waterbody, are shown in Table 4.1. Neither sex showed any tendency to be higher or lower in relative shell height than the other, and only in 4 out of the 12 Magela Creek populations were significant differences found between the regression coefficients of the equations derived for each sex. Only in one population (Nankeen) did the slopes differ significantly between the sexes. All further calculations and discussions therefore, are based on the equations derived from the data of the sexes combined. For 10 out of the 12 populations, the value of the slope b was greater than unity, indicating that length increases relatively faster than height.

Shell form description

In lateral outline, three shell forms were recognised in the Magela Creek. These are:

1) Billabong form - Except for one form found at a specific site in Mudginberri billabong (described below) the billabong form comprised, appropriately, shells from all billabongs. These shells were the true angasi form in that they were expanded posteriorly, where the elevated dorsal margin was abruptly truncated to produce a pronounced wing (Fig. 4.1). The larger shells in most populations, however, were truncated less abruptly and wing development was less obvious. A decline in relative height accompanied this trend. However, with increasing size of individuals from Nankeen billabong (particularly males), shells showed a tendency to become ovoid in lateral outline, with accompanying increase in relative height. As discussed below, no explanation for this increase in height of males could be advanced.

2) Creek form - These mussels were an ecophenotypic variant of the billabong or angasi form and inhabited the braided, sandy Creek channel above Mudginberri billabong - an environment exposed to rapid water flow during the Wet, with cessation of flow and evaporation of waters over the ensuing Dry. Creek mussels rarely occurred in shifting, sandy substrates; mussels would never survive in the hot, exposed sands during the Dry. Mussels invariably occurred in the rooted mat of aquatic or bankside vegetation, or amongst the roots of Pandanus that stabilised the shifting sands of the creek bed. While the Creek form was distinctly obese (section 4.4), in lateral outline

it resembled the billabong form in that, posterior to the beak, the dorsal margin was always elevated to produce a wing. However, unlike the billabong form, the dorsal margin was truncated less acutely and the postero-dorsal margin was slightly rounded. (In addition, the periostracum was dull and marked by fine growth lines, in contrast to the shiny periostracum of the billabong form.) This form is apparently widespread throughout the geographical range of _V. angasi_ and was described and figured by McMichael and Hiscock (1958, Plate 3) as swollen shells of the holotype _Aparchyria hemesa_, an ecophenotypic variant of _V. angasi_ from the Batavia River, Queensland (location 14, Fig. 4.6).

Although exposed to strong and turbulent currents, the microhabitats of Creek mussels were nevertheless stable, and there was no indication from the shape of these mussels to indicate that the shell morphology is an adaptation to anchorage and probing power of the foot for stability. The overriding environmental influence of shell form appears to be water recession, with the obligation by these forms to aestivate over the Dry season. According to the slope of the allometric equation (Table 4.1) height increased in the shells of Creek mussels faster than length. In company with increasing obesity, the increase in height with age results in an increase in shell volume. This would appear to be an adaptation whereby energy reserves, but particularly water content, are increased over the long and hot Dry season.

3) _Non-winged form_ - Only at one location in Mudginberri billabong was this ecophenotype in its extreme form observed. Shells were of

the arcuate form with curved dorsal margins and reflected ventral margins. The location in the billabong was at site 5 (Fig. 3.1) that lay in direct contact with incoming turbulent and rapidly flowing Creek waters during the Wet season (Fig. 2.15). Mussels at this site were located on either sandy or stony-clay sediments. The characteristic shell outline was strongly reminiscent of the same form of *Margaritifera margaritifera* figured by Eagar (1977, 1978) and was undoubtedly, similarly associated with anchorage and resistance to displacement by strong water currents. The anterior ends of these shells were often strongly eroded. Relative height of the shells of this form was distinctly low, particularly in comparison with shells from other sites in the billabong.

Apart from the general description given above, the index of relative height b, the slope of the allometric regression equation, was found to adequately quantify the various growth forms and character gradients of *V. angasi* in the Magela Creek. This is demonstrated below.

Among the three growth forms just described, young shells were distinctly winged, and of the typical billabong or *angasi* form. However, at a size of only 20 mm, the postero-dorsal margin of the Creek form began to appear slightly rounded. Five young mussels (young of the year) from the Creek were transplanted to Leichhardt billabong in May 1981 to observe the ensuing morphological development of the shell. Mussels were placed in plastic containers filled flush to the rim with sediment. (The containers were the same as used to measure growth rates of mussels in the billabongs, and are described in section 6.2. As no cage effects were observed with growth rates (section 6.3.3.4), shell shape is also assumed unaffected.) The lengths of these shells were 21, 22.5, 23.5, 33.5 and 35 mm. The rounded appearance of the postero-dorsal margin was discernible in all 5 mussels, but was especially evident in the two larger individuals. The mussels were recovered one year later, and had increased in size by an average of 23 mm. The 3 largest shells had assumed the Creek form (that included considerable inflation) while the two smallest had taken on the billabong form (that included relative compression laterally). The rounded postero-dorsal margin was absent in the 'new' billabong mussels and the margin was now abruptly truncated. Thus the distinct ecophenotype from the Creek is committed to its characteristic form only beyond a critical size. In addition to the observation that all young shells are winged, the transplant experiment just described indicates that the various shell forms are ecophenotypic variants only of a wider population of V. angasi in the Magela Creek, that has a common genetic identity.

Environmental correlates of relative height

Using the slope, b, of the allometric equation describing relative height of mussels from each of the waterbody populations (Table 4.1), environmental determinants of the variation in relative height between populations were sought. (A high value of b indicates that relative height of shells in the population is low, while a low value indicates the reverse.) Analysis of covariance testing showed that differences in the slopes and elevations of the allometric regression equations between the 12 Magela Creek populations were highly significant ($P < 0.001$); there was a general trend toward decreasing height of mussels in a downstream direction.

The effect of increasing stream velocity upon shell morphology in the billabongs was to select for or induce growth of a non-winged form. The description of this form is given above. A decrease in height accompanies the progressive dorsal arching and ventral reflection of shells exposed to strong water currents (section 4.3.2). The two environments that experienced the most turbulent and strongest currents during the Wet season were the Magela Creek channel and Mudginberri billabong. The shells of mussels in the populations from these waterbodies, however, were amongst the highest in the Magela Creek (Table 4.1). Thus shell height was unrelated to water velocity and turbulence across all the waterbodies. Similarly sediment characteristics were unimportant; coarse and fine, organic and inorganic sediments contained high or low shells in equal proportions. Water depth and various physicochemical parameters (from Table 2.7) were similarly unrelated to shell height.

The single correlate of relative height that showed a progressive trend along the Magela Creek was apparently the trophic factor, chlorophyll, a measure of algal abundance in the waterbodies. With increasing eutrophy, relative height declined. The relationship between relative height and chlorophyll is plotted in Figure 4.2. A highly significant logarithmic regression equation was fitted to the data. The equation is:

$$Y = 0.887 + 0.0753 \ln X \qquad (P < 0.001,\ r^2 = 0.769)$$

where Y = slope (b) of the allometric equation for relative height, and X = mean chlorophyll a averaged over the seasons (μg/l).
This is a similar relationship as found between population growth rate and chlorophyll described in section 6.4.3.2, where growth rates of mussels were shown to be positively correlated to algal abundance as measured by chlorophyll.

Thus, increasing growth rate is accompanied by decreasing shell height. Just as within populations where height increased relatively slower in relation to length, it is tempting to suggest that the relationship just described and plotted in Figure 4.2, is merely an extension of this ontogenetic principle - i.e. shell height decreases with increasing size. However, there is evidence to suggest that it is growth rate *per se* and not merely size of mussels investigated that determines relative shell height. Allometric equations of relative height for juvenile (young of year) mussels (< 35 mm in length) for populations from Georgetown, Mudginberri, Buffalo and Nankeen billabongs are described in Table 4.2. Mussels in Nankeen billabong are the fastest growing of the populations shown in this Table (section 6.4.2), and it is apparent that juveniles from this billabong also have the lowest shells. Thus, the degree of change in relative height is generally constant between populations, at any given size.

The slope of the allometric equation for relative height of juveniles from Nankeen billabong (Table 4.2), indicated that length increased relatively faster than height and accorded with the relationship plotted in Figure 4.2. Older mussels, however, showed a reverse trend of more rapid increase in height in relation to length. The slopes of the allometric equations of relative height, between juveniles and adults differed only in this population (Table 4.2), and the difference moreover, was highly significant ($P < 0.001$). Relative height therefore, plotted well below the value that could be expected for the given trophic level of the billabong. No explanation for these high shells, ovoid in lateral outline, can be given. They were peculiar mainly to male mussels; the slopes between the allometric equations of relative height of the sexes differed significantly ($P < 0.01$). A synergism between high late Dry season turbidities (and resultant low algal levels) and consistently low seasonal concentrations of dissolved oxygen could be responsible for the ovoid outline of male shells.

4.3.2 Within billabongs

Quantitative data for within-billabong study of variation in relative height were collected from Georgetown, Mudginberri, Buffalo, Leichhardt and Nankeen billabongs. The allometric regression equations describing the relationship between shell length and height for the various sites and depths of the respective billabongs sampled, are shown in Tables 4.3-4.7. The data within each billabong, are generally a composite of those used in the single regression equation averaged over each billabong (Table 4.1), and at all sites and depths morphometric data from a minimum of 50 mussels were used. Regression equations were calculated separately for the sexes of mussels from Nankeen billabong, where the slopes between the respective equations combining all the data (Table 4.1) differed significantly.

In Georgetown billabong, relative height of shells was greater on the sandy, shallow transect located upstream (transect B) as opposed to shells found on the silty, clay and deeper transect downstream (transect A) (Table 4.3). On the same transects, occur younger and older mussels respectively (section 6.5.3.1). The shells of younger mussels are relatively higher in Georgetown billabong (as in most other billabongs) than adult shells. (Compare the slopes of the respective allometric equations of relative height for juveniles and adults shown in Tables 4.2 and 4.1.) Thus, the higher shells observed on transect B are presumably the result of this difference in age structure.

Given the relationship between relative height and trophic status as described above (section 4.3.1), and the observation of a low, dorsally-arched shell form at one sampling site, trophic status and Wet season stream velocity appeared to be obvious potential correlates of relative height in shells between sites in Mudginberri billabong. Relative height (as the slope b, of the allometric equation) is given in Table 4.4, in relation to stream velocity and chlorophyll concentration between sampling sites of Mudginberri. Given that the low relative height of shells (i.e. high value of b) at site 5 is unequivocally a response to rapid Wet season stream velocities (as discussed above), chlorophyll would otherwise appear to be unrelated to relative height. Stream velocity as shown below, however, was negatively correlated with relative height.

Eagar (1948, 1977, 1978) noted that unionaceans shared two contrasting patterns of growth between which there were often few intermediates; the first pattern, a dorsal arched form, was adapted for fast currents, and the second, a straight-hinged form was adapted for quieter waters (see section A1.1). He nevertheless proceeded to illustrate various stages and trends of dorsal arching with decline in relative height, of shells of *Margaritifera margaritifera*, associated with increase in water velocity of the habitat (Eagar, 1977, 1978). Eagar observed that bivalves with progressively more dorsally arched and ventrally reflected shells, tended to survive in stations of increasing water turbulence. Thus, the "progressive" "trends" but "contrasted patterns" with "few intermediates" are seemingly conflicting and contradictory ideas.

The same trend of shell form as described for *M. margaritifera* by Eagar (1948, 1977, 1978) was apparent in the mussels of Mudginberri, a billabong through which the waters of the entire catchment upstream of the floodplain are channelled during the Wet season. An extreme non-winged form with dorsal arching and reflected ventral margin, as described above, was characteristic of the larger mussel shells at a site exposed directly to incoming strong turbulent currents. Winging was also less pronounced in the shells of larger mussels occurring in some unstable sandy sediments exposed to relatively strong currents during the Wet. A decrease in relative height accompanied the progressive trend in loss of definition of the posterior wing. A similar trend by *M. margaritifera* was shown by Eagar (1977, Fig. 1; 1978, Fig. 8). A very significant ($P < 0.01$) negative linear correlation was observed between relative shell height and stream velocity in Mudginberri billabong, indicating that more dorsally arched forms tend to survive in sites of increasing water turbulence. The relationship between relative height and stream velocity is shown in Figure 4.3, along with the fitted linear regression equation.

The Wet season waters emitting from Mudginberri billabong branch, so that water entering the neighbouring Buffalo billabong immediately downstream is considerably reduced in velocity. As a consequence, correlates of relative height of mussels in Buffalo billabong were more difficult to discern (Table 4.5). Both trophic status and Wet season flow rates (as discerned by substrate type) at the sites may influence relative height. Stream velocity (assumed greater over the sandy sediments) may be responsible for the lower shells found on sandy sediments to the north of the billabong (sites 1-4), whereas increasing eutrophy to the south (i.e. increase in site number) may be the cause of lower shells. In relation to height variation in other billabongs (as discerned by the magnitude of spread of the slope, b), differences between relative height of shells between the sites of Buffalo billabong are small.

An increase in relative shell height was found with increasing depth in the floodplain billabongs, Leichhardt and Nankeen (Tables 4.6 and 4.7 respectively). Although the slopes of the allometric equations describing relative height differed significantly between the sexes in Nankeen billabong (Table 4.1), relative height of both sexes increased with depth in a similar fashion (Table 4.7). The relationship between relative shell height and depth for mussels from

Nankeen was plotted therefore, for the data of the sexes combined. Plots of relative shell height and depth, with the associated fitted linear regression equations to describe the relationships, are shown in Figures 4.4 and 4.5 for Leichhardt and Nankeen billabongs respectively.

Growth rates for all size classes (Leichhardt) and in the younger ages (<13 years, Nankeen) decreased with increasing depth, presumably with decreasing eutrophy and increasing oxygen depletion at depth (section 6.4.3.1). Given the relationship found between billabongs, in which relative height declines with increasing eutrophy and growth rates (Fig. 4.2), it might also be assumed therefore, that increasing shell height with depth is also a result of declining eutrophy, and accompanying decrease in growth rate, with depth.

In Nankeen billabong, at approximately half-way through the lifespan of mussels (at about 13 years), growth rates are reversed so that older mussels (>13 years) grow fastest in the deepest waters (section 6.4.3.1). Nevertheless, relative height of shells increases with depth, independently of this growth rate reversal. As shown above (section 4.3.1), mussels are committed to a given growth form beyond a critical size. Presumably therefore, older mussels in Nankeen continue to grow and conform to the lateral outline prescribed them in younger years, and relative height therefore is relatively uninfluenced by trophic and growth rate phenomena.

4.3.3 Geographical variation in juvenile *Velesunio*

In the Magela Creek, morphological variability recorded in the relative height of shells of juvenile *V. angasi* was slight. Although analysis of covariance testing showed that differences between the slopes and elevations of the allometric regression equations of relative height, for juveniles from 4 populations investigated (Table 4.2), were highly significant ($P < 0.001$), compared to adult populations these differences were minor. Within populations, variation between length and height as denoted by r^2 values of the allometric equations, was low for juveniles ($r^2 > 0.97$, Table 4.2) as compared to adults of the same populations ($r^2 > 0.86$, Table 4.1). Moreover, the range in the values of the slopes of the equations for the 4 juvenile populations, was less than 60% of the range recorded in the adult populations from the same waterbodies.

Relative shell height of *V. angasi* from the Magela Creek as shown above, progressively declined with increasing age, and with the environmental influences of increasing eutrophy and (more locally) increasing stream velocity over relatively unstable sediments. These changes to relative height brought about by ontogeny and environment were demonstrated by allometry and by variation in the slopes of the allometric equations between populations respectively. The progressive decline in relative height was generally accompanied by progressive loss of definition of the posterior wing.

According to McMichael and Hiscock (1958) the shells of *V. angasi* and *V. wilsonii* are clearly distinguishable. The shells of *V. angasi* are winged and truncated posteriorly, while the shells of V. wilsonii are never more than slightly winged, being acuminate posteriorly so that the dorsal margin is straight and almost parallel to the ventral margin. Accompanying these features, the maximum height index (MHI = height/length) is reportedly lower in V. wilsonii (46-53%) than in V. angasi (50-60%).

All shells of young V. angasi in the Magela Creek (<35 mm) without exception were strongly winged. This feature was borne out in calculations of relative height of juveniles. Despite significant differences between the slopes of the allometric equations of relative height for the 4 populations investigated (Table 4.2), actual differences in relative height between the populations were minor; the minimum MHI values for example, predicted for the populations from the regression equations, ranged between 59-61 percent.

Thus, the evidence from the present study indicated that the clearly distinguishable outline of the shells of V. angasi, is best exemplified in those of the young mussels relatively uninfluenced by the environment. Low variability in lateral outline of shells of V. angasi in the Magela Creek further, suggested that the young stages provide the most suitable material for which interpopulation comparisons of shell form, without the effect of environment (such as for taxonomic study), may be made. These same virtues were assumed to characterise the young shells of V. wilsonii, after examination of some limited material from a site outside of Mary Kathleen, Queensland (location 9, Fig. 4.6). These shells were characteristically non-winged, and contrasted sharply in form to the winged young shells of V. angasi from the Magela Creek (Fig. 4.1). Both species were clearly distinguished by relative height alone; the MHI values for young of V. angasi ranging from 59-61% (at the least) in the Magela Creek, and of V. wilsonii from Queensland ranging from 44-45% (Table 4.8). These limited observations stimulated enquiry as to whether such differences in relative height between juvenile V. angasi and V. wilsonii were consistent over the broad geographical ranges of both species. Put another way, the question was posed: is relative shell height without the influence of environment, sufficiently bimodal throughout the ranges of both congeners, to clearly separate the species? If this was the case, then morphometry of young shells could provide useful taxonomic differentiation of the two species in regions where doubt was expressed in the species composition.

All records of shell length and height of small V. angasi and V. wilsonii (< 40 mm length) throughout the entire ranges of both species, were kindly forwarded by curatorial staff of the Australian Museum (Sydney). Unfortunately the shells were not personally inspected and thus the relative ages of the constituents, and the environments from where they were collected were unknown. Museum collections for example, may be assumed to be biased toward those from shallow waters. Such environments may include variable habitats such as small, ephemeral creeks that are inhabited by stunted mussels. Some of the V. angasi material forwarded (for example, location 14, Table 4.8) was known to comprise the Creek form, which in the Magela Creek is a relatively high and slow growing shell.

Nevertheless, the very nature of the collections, i.e. probably from similar environments, likely inferred a relative constancy in shell form between the various locations, so that comparisons should still be valid. The morphometric data with respect to species and location are given in Table 4.8, while the locations with respect to geography, species and mean annual rainfall, are shown in Figure 4.6. With the reservations concerning the unknown ages of the constituents and their environments, nevertheless, some points may be made from the data of Table 4.8 and Figure 4.6.

No plots of MHI frequencies were drawn to discern bimodality. However, reasonable separation of the species by relative height alone is apparent from the data of Table 4.8. In regions where the species are sympatric or where the species ranges border, possible misidentifications may have occurred (indicated for locations 1 of V. angasi and 4 of V. wilsonii respectively, Table 4.8). V. angasi for example, has been reported to occur in the catchment of the Victoria River (N.T.) (location 13), suggesting that the individual V. wilsonii reported at location 4 in the same catchment was misidentified. Apart from this exception, the MHI values of V. wilsonii are consistently low.

Relative height of V. angasi is more variable, but apparently much of the variation is accountable for. Despite the fact that the extent of ecophenotypic variation is unknown in the data, it nevertheless appears possible that a geographical cline in relative height of V. angasi exists; individual shells are apparently higher in northern and wetter parts of the range of the species. At more southern and drier parts of the range, however (e.g. locations 11, 12 and 13, N.T.), shells are lower. More thorough investigation, controlling for the environments, will be required to affirm the presence of such a cline.

High species integrity of V. angasi otherwise, is assumed in far northern locations of the Northern Territory, including the Magela Creek (location 16, Fig. 4.6), where MHIs are consistently high. Low variability in relative shell height within and between populations of young mussels, and the high nature of the young shells (MHIs ranging in the very least between 59 and 61%) which are consistently winged and truncate in appearance, leads to the unequivocal conclusion that V. angasi is the sole species occurring in the Magela Creek. If a cline throughout the species range in relative height is actually confirmed, however, species determination may be difficult in more southern latitudes, particularly in areas of sympatry of V. angasi and V. wilsonii or in areas where the ranges border.

4.4 Variation in obesity

Allometric regression equations describing the relationship between length and width of mussels, calculated for the sexes separately and combined from each waterbody, are shown in Table 4.9. In 9 of the 12 Magela Creek populations, females were found to be more obese than males (-indicated by the larger slopes of the regression equations derived for males, as opposed to females). However, only in Georgetown billabong did the slopes of the regression equations differ significantly between the sexes (Table 4.9). In only 3 other populations, moreover, did the intercepts of the equations differ significantly between the sexes. As variation in obesity between populations is described by way of the slope, b, of the regression equations, all further discussions and calculations therefore are based on the equations of the sexes combined. In all populations, the value of b was less than unity, indicating that width increases relatively faster than length.

In terms of obesity, two shell forms were recognised in the Magela Creek, the billabong form and the Creek form. These are the same forms as those described for lateral outline, except that the billabong form here includes both winged and non-winged shells. The Creek form was clearly distinguishable, in being remarkably more obese compared to shells from the billabongs. The causes of this inflation are considered further below.

As found above (section 4.3), averaged over all size classes of mussels and over all waterbodies, variation in obesity occurred independently of changes in relative height. The single most important environmental correlate of obesity was clearly apparent when all data, both within and between populations were amassed. For within-billabong study, quantitative data were collected from Georgetown, Mudginberri, Buffalo, and the floodplain billabongs, JaJa, Leichhardt and Nankeen. The allometric regression equations of obesity for the various sites and depths of the respective billabongs sampled, are shown in Tables 4.10-4.13. Morphometric data from a minimum of 50 shells at each site and depth was used to calculate the regression equations. Both within and between billabongs, obesity was found to increase with increasing water depth. So direct was the relationship across the billabongs in fact, that a single analysis of the data both between and within billabongs was possible. Obesity (as measured by the slope, b, of the allometric regression equations) is plotted with respect to depth, for the data of each billabong in Figure 4.7. (Decreasing values of the slope, b, indicate increasing obesity.) A highly significant ($P < 0.001$) linear regression equation was found to described the relationship between obesity and depth. The equation is:

$$Y = 0.986 - 0.097X \qquad (P < 0.001,\ r^2 = 0.801)$$

where Y = slope (b) of the allometric equation describing the relationship between shell length and width,

and X = water depth (m).

Thus 80% of the variation in obesity of mussel shells recorded in the Magela Creek billabongs, was accounted for by water depth.

A positive correlation was found between age of mussels and depth within most billabongs (section 6.5.3.1). Using mean age and mean billabong depth data (Tables 6.37 and 2.1 respectively), a significant linear regression ($P < 0.05$) was also found between age and depth across all billabongs. (Thus for example, older mussels are found in deeper billabongs.) Given the depth/obesity relationship above and the depth/age correlation, obesity therefore was also linearly correlated with age when the data were regressed across the billabong averages. The linear regression equation found to describe the relationship between obesity and age is:

$$Y = 0.974 - 0.0138X \qquad (P < 0.01, r^2\ 0.654)$$

where Y = slope (b) of the allometric equation describing the relationship between shell length and width,

and X = mean age of mussels (years).

This correlation in fact, is a better one than that calculated using values of obesity and depth averaged over each billabong. Using billabong averages, only 50% of the variation in obesity was accounted for by variation in depth, as opposed to 65% accounted for by variation in age. Thus rather than a direct effect of depth upon obesity (that could only be explained through associated changes in hydrostatic pressure or temperature for example), the most likely explanation for increasing obesity with depth is an ontogenetic one; with increasing age, mussels become more obese. Because older mussels are found in deeper waters of the Magela Creek, the relationship between obesity and water depth may be associative only.

Of other limnological and hydrological factors considered as correlates of obesity in the billabongs, substrate type appeared to be the only influence apart from water depth. Softer and less consolidated substrates tended to support more inflated shell forms. Thus as a general rule, data points lying below the regression line of Figure 4.7 represent more obese forms found on soft organic sediments; noteworthy are the soft and relatively unconsolidated sediments of Gulungul, Corndorl, the shallowest waters of JaJa, and site 2 (Table 4.12) of Buffalo billabong. Conversely, firm sediments supported generally more compressed forms that plotted above the regression line of Figure 4.7; these sediments, for example, characterised Georgetown and Island billabong. Increasing obesity of V. angasi in soft, unconsolidated sediments of the Magela Creek billabongs could be a morphological adaptation enhancing buoyancy and preventing shells from sinking and asphyxiating.

The shells of mussels from the Magela Creek channel, were by far the most inflated of those of any population found in the Magela Creek (Table 4.9). As Creek mussels live in the most shallow sites and are amongst the youngest (Table 6.37) of any population, the degree of inflatedness of their shells therefore, is in direct contradiction to both the depth-obesity and age-obesity relationships just described for billabong mussels. According to Eagar (1978), increase in relative height and obesity provide the most functionally efficient means of increasing bivalve shell volume at the expense of its surface area. Shells of Creek mussels are both the highest and widest in relation to length, than shells of any other population. As discussed previously (section 4.3.1), the resulting increased volume would seem to be an adaptation whereby energy reserves, and especially water content are maximised for the period of aestivation during the hot Dry season.

For comparison with the Creek form from the Magela Creek catchment, mussels were collected from running waters of the East Finnis River, some 280 km west of Jabiru (location 4, Fig. 4.6). Because of possible clinal effects (section 4.3.3), comparison of shell forms over broad geographical areas should be approached with some reservation and caution. Nevertheless, even in relation to neighbouring billabong mussels in the East Finnis River catchment (similar in general appearance to billabong forms from the Magela Creek), the shell form from running waters of the river were notably strongly winged and laterally compressed. The slopes of the respective allometric equations of relative height and obesity for these river shells are given in Tables 4.1 and 4.9. Thus from these Tables, the shells from the East Finnis River are also relatively high and compressed by comparison with populations from the Magela Creek. Compared to the Creek form from the Magela Creek in particular, the river mussels are much less inflated. The two environments differ in that the Magela Creek below Jabiru is ephemeral, whereas the East Finnis River at the site of mussel collection flows all year round. Like the Creek mussels, the microhabitat of the river mussels was relatively stable, with mussels being lodged generally amongst rooted macrophytic and bankside vegetation. As there is no obligation for the river forms to aestivate, the relatively compressed shells are probably an adaptation enabling mussels to orientate themselves better to withstand strong (Wet season) currents. Because of the stable microhabitat presumably, dorsal arching was not observed in the river shells. Thus in two very similar (flowing waters) and yet contrasting environments of ephemeral and permanent streams respectively, occur two contrasting shell forms; one obese and adapted to aestivation, the other compressed and adapted to stability in strong water currents.

4.5 Discussion

Ontogenetic and sexual variability in shell shape

Allometric relationships were found between shell length and height, and shell length and width of V. angasi in the Magela Creek; relative height declined but obesity increased with size. Among unionaceans, allometry is apparently commonly observed between standard shell dimensions (Eagar, 1978) and relative height and obesity may either increase or decrease with age (Eagar, 1948). Agrell (1949) and Crowley (1957) also reported for example, that juvenile unionids were less obese than adults, but the reverse allometry for the same relationships was reported by Ortmann (1920) and Ball (1922). Stream-forms, including the Australian hyriid Alathyria jacksoni (McMichael and Hiscock, 1958; Walker, 1981b) generally decrease in relative shell height with age with progressive dorsal arching of the shell (section A1.2). Changes in relative height of V. angasi were not accompanied by compensatory changes in obesity as have been reported for other unionaceans (Eagar, 1948; Agrell, 1949; Hendelberg, 1960).

Invariably, studies of ecophenotypic variation in unionaceans have relied upon ratios calculated between the size dimensions for comparisons of shell form. Isometric growth is assumed in comparisons of ratios. Thus as also noted by van der Schalie and van der Schalie (1950) and Cvancara (1963), if shells of variable age are compared, even considering only those shells of the adult population, variability caused by allometry is introduced. In the present study allometric equations describing the relative growth dimensions of the adult population were used to study ecophenotypic variation. Ontogenetic variability was thereby accounted for. The extent of departure from unity of the slope of the allometric equations in some extreme populations, indicated that considerable error in comparisons would have occurred had isometric growth between the size dimensions been assumed.

No obvious sexual dimorphism in shell shape was observed in *V. angasi* from the Magela Creek. While females tended to be more obese than males, the differences found between the sexes were generally not statistically significant. Similar, inconspicuous tendencies only have been reported for other unionaceans (Johnson, 1946; Heard, 1975; Dudgeon and Morton, 1983) including hyriids (McMichael and Hiscock, 1958; Walker, 1981b), for the shells of females to be more inflated than males. In these groups, it is generally assumed that ecophenotypic variation in shell form is sufficient to mask any tendency for dimorphism between the sexes. Marked sexual dimorphism in shell features, however, characterise lampsiline unionids (section A1.2). Amongst other features, females are more obese than males particularly over the marsupial regions, an adaptation according to Coker *et al.* (1921) and Anderson and Ingham (1978) allowing for large numbers of eggs to be held in the outer gill marsupia.

Shell shape and environment

Three shell forms of *V. angasi* in lateral outline and obesity were recognised in the Magela Creek: a winged, billabong or true *angasi* form, and two ecophenotypic variants of the true form, a non-winged and dorsally arched form, and a high, moderately winged and swollen Creek form. Indications from descriptions and figures of McMichael and Hiscock (1958) are that the swollen Creek form is an ecophenotype, distinctive in morphology, that is widespread throughout the geographical range of the species. This study, however, is the first to identify such shells as a discrete form of V. angasi and to interpret the functional morphology of such a form. Experiments on transplanting young Creek mussels to a billabong confirmed that the distinctive Creek shell was a phenotypic morph only of the true angasi form, when young shells developed according to the typical form of the resident billabong mussels.

The only immediately apparent environmental trend that accompanied the progessive decrease in relative height of mussels in a downstream direction of the Magela Creek was increasing eutrophy. Increasing eutrophy was also correlated with increasing growth rate of mussels (section 6.4.3.2). Thus with faster growth and increase in size, relative height declined, in company with a progressive loss of definition of the posteriorly expanded wing.

As summarised by Eagar (1948) (see section A1.1), unionacean form is often reported to become more arcuate in terms of lateral outline in swift-flowing waters as opposed to increasingly straight-hinged and winged in slower flowing or still waters. Generally a decrease in relative height accompanies the trend to more arcuate form and increasing stream velocity (e.g. Altnoder, 1926; Dell, 1953; Cvancara et al., 1978; Walker, 1981b). Wet season stream velocities through the Magela Creek waterbodies do not correlate with the relative position of the waterbodies along the Creek, mainly because backflow billabongs occurring upstream do not receive significant flow compared to channel and some floodplain billabongs lower downstream. Thus the trend downstream of decreasing relative height of V. angasi is not correlated with decreasing stream velocity. Moreover the mussels of two populations only, those of the Magela Creek channel and Mudginberri billabong, were affected by rapid stream velocities. Compared with the other populations the shells of these mussels were amongst the highest. The decline in relative height of V. angasi found in the downstream direction of the Magela Creek therefore, is in direct contrast to other reported ecoclines in relative height in riverine mussels (see above references) where an increase in relative shell height can be expected in the downstream direction.

Apart from V. angasi, trophic factors alone were also suggested by Agrell (1949) as affecting various shell dimensions of Swedish unionids including relative height, while Cvancara et al. (1978) implicated nutrient availability as one of a number possible factors affecting relative height of North American unionids with respect to location along a stream. Both studies, however, observed a positive correlation between eutrophy and relative height. The correlation observed for V. angasi was a negative one. Among marine intertidal gastropods, Vermeij (1980) summarised a number of reports for species in which relationships between growth rate and intensity of allometry have been noted. Other than V. angasi, there has been no direct report of this phenomenon in unionaceans although one might ask whether the results of Agrell and Cvancara and co-workers are not suggestive of this. Regardless, no obvious functional advantage can be implicated from the eutrophy/relative height relationship. For V. angasi it is more easily interpreted in ontogenetic rather than environmental terms; with increasing growth rate, relative shell height declines.

Within habitats, such as sites and depths of the same lake, attempts at demonstrating relationships between shell morphology and environment have generally met with little success (Fisher and Tevesz, 1976; Ghent et al., 1978; Horn and Porter, 1981). In relation to lateral outline, Cvancara (1972), however, found a significant decrease in height of two unionid species with increasing depth in lake environments. No causal explanation was offered. Harman (1970) also observed that Anodonta grandis was higher in the littoral than the profundal waters of various lakes studied, and implicated a temperature decline with depth as a possible cause. In contrast to these observations, relative height of mussels in floodplain billabongs of the Magela Creek, increased with increasing depth. The likely cause of this trend to increasing shell height with depth, was argued to be the same factor that determined variation in relative height between waterbodies, namely decreasing eutrophy. Evidence for this association was substantiated in the observation that growth rates of mussels (and thus partly food availability) declined similarly with increasing depth in the same billabongs.

The increase in relative height of male mussels in particular, with age in Nankeen, was exceptional amongst the billabong populations where the pattern was for a general decline in height. This tendency for increased height, however, was not accompanied by more pronounced wing development but with development of a more ovate outline. No causal explanation for this unusual ontogeny can be offered. Thus, these shells became more ovate with increasing depth. Harman (1970) also noted that <u>Lampsilis</u> <u>r</u>. <u>radiata</u> become more ovate in lateral outline with increasing depth in the Finger Lakes of central New York State (U.S.A).

In Mudginberri billabong through which relatively rapid flowing waters pass each Wet season, a negative correlation was observed between relative shell height and stream velocity amongst various sites exposed to more or less strong currents. Associated with the decrease in height of mussels was the development of more dorsally arched and ventrally reflected, and non-winged shells. The correlation between stream velocity and shell height indicated that more dorsally arched forms tend to survive in sites of increasing water turbulence. Eagar (1977, 1978) first provided a functional explanation for this relationship, widely observed amongst stream-dwelling unionaceans (see section A1.1). Dorsally arched and ventrally reflected shells provide a larger pedal gape, which in turn allows a stronger anchorage for the foot in unstable substrates. Shells with curved ventral margins on the other hand were argued by Eagar to have functional advantage over the dorsally arched shells, in providing active movement over the surface of the substrate in quieter environments. In relation to the respective dorsally arched and straight-hinged growth patterns, Eagar (1948, 1977, 1978) referred to these as "contrasting" growth forms between which there were often few intermediates. He nevertheless noted that bivalves with "progressively" more dorsally arched and ventrally reflected shells tended to survive in stations of increasing water turbulence. The same continuum of form was observed for shells of mussels in Mudginberri billabong and progressive dorsal arching (culminating in ventral reflection at one site) was accompanied by decrease in relative height and progressive loss of definition of the posterior wing.

In addition to V. angasi, arcuate shell forms in environments of fast water currents have been noted for various other hyriid unionaceans (Dell, 1953; Walker, 1981b). Walker observed two distinct shell forms of the riverine mussel Alathyria jacksoni, a winged (straight-hinged) and non-winged (dorsally-arched) form, characteristic of mussels from moderate and fast water currents respectively. Few intermediate forms were observed between these two growth patterns. Although a decrease in relative height accompanied development of the arcuate form, Walker emphasised that the relative height dimension (height/length) was not particularly sensitive to revealing the distinct, dual growth patterns. A continuum of form of V. angasi at sites in Mudginberri billabong, however, was observed with progressive dorsal arching and loss of definition of the posterior wing, in response to increasing current velocity. Relative height as measured by the slope of allometric regression equations relating length and height, revealed this continuum. The same observations are relevant to between-waterbody comparisons in the Magela Creek where increasingly less obvious wing development in association with increasing eutrophy of the environment, was detected by associated changes in relative height. No comparable arcuate form of the congener V. ambiguus in the Murray River in southeastern Australia was reported by Walker (1981b). Walker believed that the mussel was absent from fast-flowing waters because it was unable to maintain a strong anchorage.

As a very general rule, shells of unionaceans tend to become obese in quieter waters such as prevail downstream in streams and in lakes, as opposed to being laterally compressed in more turbulent environments such as in the headwaters of streams and in exposed lake sites (see section A1.1). The functional advantage of increased obesity in quiet waters has generally been given as enhanced buoyancy that prevents shells from sinking into soft, muddy sediments that invariably prevail in these waters (Eagar, 1978; Ghent et al., 1978; Anderson and Ingham, 1978; Tevesz and McCall, 1979; Walker, 1981b, Stern, 1983). Eagar (1978) added that greater obesity would increase the volume of living tissue thereby providing improved metabolic and functional activity to forms from quieter waters. Functional interpretation as to why less inflated and more compressed shells occur in unstable and shifting substrates has been variously offered as adaptations enabling mussels to orientate themselves better to withstand strong currents, and to plough deeper and more supportive furrow paths (Wilson and Clark, 1914; Grier and Mueller, 1926; Clarke, 1973; Anderson and Ingham, 1978; Ghent et al., 1978; Stern, 1983). Clarke (1973) nevertheless, found L. r. siliquoidea to be more obese on shifting and unstable lake sediments than elsewhere. He suggested that these obese forms might be better able to remain in place without being dislodged by turbulent wave action and currents during storms. Other than hydrological factors, increasing eutrophy has also been implicated as a cause of greater obesity of some unionids (Agrell, 1949; Cvancara *et al*., 1978).

Three environmental correlates of obesity in *V*. *angasi* were identified in the present study, namely water depth, substrate type and exposure of mussels due to water subsidence. Only the latter two factors apparently, have functional interpretation. Eighty percent of the variation in obesity found in billabong mussels, was accounted for by variation in water depth. Mussel shells across all billabongs, were found to increase in obesity with increasing depth. The most reasonable explanation for this relationship, however, was forwarded in ontogenetic rather than environmental terms; across the billabongs, mussels become more obese with increasing age, while age of mussels generally, increases with increasing water depth both within and between billabongs. No depth related factors have been implicated in the literature as affecting obesity of unionacean shells, other than the report by Harman (1970) that *Elliptio complanata* decreased in obesity from shallow to deeper waters in lakes in central New York state (U.S.A.). This is the opposite trend to that observed for *V*. *angasi* in billabongs of the Magela Creek.

Softer and less consolidated substrates tended to support more inflated shell forms of *V*. *angasi* among and within the Magela Creek billabongs. Relatively more compressed forms, however, tended to occur on firmer sediments. Increasing obesity of mussels on softer and muddier sediments is presumably an adaptation enhancing buoyancy and preventing shells from sinking and asphyxiating. This observation is in accordance with similar interpretation given above, to the functional advantage of swollen shells of unionaceans in general on soft, muddy substrates. The shell form of the congener, V. ambiguus, is also characteristically swollen on unconsolidated, muddy substrates of lagoons according to Walker (1981b). Sediment type has been related to obesity in only one other study of within-habitat shell form variation in unionaceans. Horn and Porter (1981) found that obesity of a lake population of Lampsilis sp. was correlated with percent organic matter of the sediment. No mention was made, however, as to whether the more organic sediments were softer and less consolidated in nature.

The high and swollen shells of the Creek form inhabiting the braided, sandy channel above Mudginberri billabong, represented a distinct, ecophenotypic variant of V. angasi in the Magela Creek. The microhabitats of these forms were stable enough that the shell morphology did not appear adaptive to anchorage and stability; shells of V. angasi in a permanent stream from another geographical location seemed better adapted to this function in being generally laterally compressed. Dorsal arching and ventral reflection of the shells were also absent in the Creek form, that would suggest increasing stability in flowing water environments. Almost certainly the increased volume resulting from increases in relative height and obesity of the Creek form, are adaptive to aestivation, where the amount of energy reserves and water content are maximised for the dormant period over the hot Dry season. By nature of the tropical, monsoonal climate, small streams in the geographical range of V. angasi are ephemeral. The apparent, widespread occurrence of the

Creek form throughout the range of V. angasi therefore (deduced from the figures and descriptions of McMichael and Hiscock, 1958) suggests that the ecophenotype is adapted broadly to life in streams of annually variable discharge. This study is the first to recognise in an ecophenotype, adaptive morphology to aestivation in unionaceans.

Considerable interest has been held in regard to analysing the environmental relationships of the variability in shell form of present day unionaceans, to provide paleoecological and paleolimnological reconstructions. A general review of this work, including the thorough appraisal and review of the topic of Tevesz and Carter (1980a), is presented in sections A1.1 and A1.2. Indications from the present study are, that relative height only of V. angasi may prove useful for inferring environmental changes in paleoenvironments, or for that matter for inferring present day hydrological or limnological patterns in environments as yet unstudied by man. A distinctive low, non-winged and arcuate shell form is characteristic of environments of unstable, shifting sediments where waters are swiftly flowing for some part of the year at least. Conversely, the relative height of shells with curved ventral margins (as opposed to ventrally reflected margins of the arcuate form) are generally indicative of the degree of eutrophy of the environment from which these mussels were found. This correlation would hold presumably in most environments, despite the fact that no obvious functional advantage can be implicated from the eutrophy (or growth rate)/ relative height relationship. The association is apparently more closely related to ontogeny rather than to any environmentally induced change to shell form.

In spite of a strong correlation found between obesity and depth, it is unlikely that shells of V. angasi will prove to be useful indicators of depth in any broad context. A correlation was found between obesity and age of mussels in the Magela Creek, and because of this ontogeny, depth segregation of different age classes resulted in morphologically distinct groupings correlated but not causally related to any environmental factor. The extent to which the age/depth relationship of mussels between waterbodies of the Magela Creek is fortuitous is not known. Only if age was found to be consistently correlated to depth among populations and causal relations identified, could shells be used to indicate water depth.

Indeed, it would be of interest to learn the extent to which ecoclines reported in the literature, are nothing more than gradients of ontogeny. For example, if obesity was found to correlate with age in unionaceans other than V. angasi, and age was found to increase downstream in a given catchment, functional interpretations given to Ortmann's (1920) 'Law of Stream Distribution' (which states that in a given species, shells tend to become more obese in a downstream direction), may be entirely spurious. Previous studies have largely neglected to account for the effect of ontogeny. The extent of ontogenetic variability found in the length/width relationship of V. angasi, sounds a cautionary warning to future studies of unionacean shell form, to carefully consider its effect before offering interpretations of functional morphologies. Similar advice was offered by Tevesz and Carter (1980b) in relation to the distinction between ontogenetic, and environmentally induced variability in unionacean shell form (see section A1.2).

While the obesity of billabong forms may not be so usefully employed as environmental indicators, the Creek form may provide some value in this regard. The outline and swollen nature of this form is unmistakable and therefore may be usefully employed as an indicator of seasonally ephemeral, stream environments.

Species integrity of V. angasi in the Magela Creek: shell morphometrics and taxonomy

Low variability found in the lateral outline of shells of juvenile V. angasi both within and between populations of the Magela Creek, indicates that these young stages provide the most suitable material for which interpopulation comparisons of shell form, without the effect of environment, can be made. Because V. angasi and the congener V. wilsonii are distinctive in relative height, comparison of relative heights of the young shells of both species, should indicate whether a bimodality of form is present. This in turn would suggest whether or not the species occur alone or in sympatry with one another.

More material in addition to that compiled in the present study will be needed before conclusions regarding the taxonomic value of the young shells can be made. Early indications are, that while the young shells of V. wilsonii are consistently low, relative height of V. angasi is more variable. Some of this variation may be caused by a geographical cline in relative height; shells are apparently higher in northern (wetter) parts of the species' range as opposed to more southern (drier) parts of its range. Latitudinal (McMichael and Hiscock, 1958; Cvancara, 1963; Clarke, 1973) and longitudinal (Clarke and Berg, 1959) clines have previously been detected in unionacean form (section A1.1). Thus determinations of these two Velesunio may be difficult in more southern latitudes, particularly in areas where the ranges of both border or overlap. More morphometric data pertaining to juveniles from regions of sympatry of the two species should enhance future criteria for separation of the two species.

Importantly, high species integrity of V. angasi is assumed in the 'Top End' of the Northern Territory. V. angasi is the sole species occurring in the Magela Creek, on the evidence that amongst juveniles (1) inter- and intrapopulation variation in relative shell height is low; (2) the shells are characteristically high; and (3) the shells are consistently winged and truncate in nature.

Although differences in soft part morphology among congeners of Australian hyriids are too minor for species determinations, McMichael and Hiscock (1958) reported that the siphons of V. wilsonii were lightly pigmented as opposed to the siphons and postero-ventral border of the mantle of V. angasi which were brick-red with black blotches. The pigmentation reported for V. angasi was present in all mussels from the Magela Creek dissected for tissue examination. This feature may prove to be a useful taxonomic discriminant and doubtful determinations using shell features may yet be resolved upon inspection of the siphons and mantle.

5 DISTRIBUTION AND ABUNDANCE

5.1 Introduction

Distributional studies of freshwater mussels range widely in subject and consequently there is a large world literature ranging from surveys recording presence or absence and anecdotal notes on habitat preferences, to sophisticated multivariate descriptions of a species' niche requirements. Interest, both academic and commercial, broadly comprises three areas: to determine factors involved in broad geographical dispersal or to describe local or microhabitat requirements; to assess factors involved in the decline of valuable commercial species (especially of North America) through mismanagement of waterways; and using distributional information and/or shell character or chemical composition data, to assess freshwater mussels for their value in prehistory studies or as indicators of paleohydrology or of present day water quality.

The literature pertaining to distributional studies is comprehensively reviewed in Appendix 2, in relation to these three broad areas of interest, namely: factors affecting distribution of freshwater mussels, including broad geographical dispersal, biotic and abiotic (depth, hydrology and physicochemical limnology) relations - section A2.1; anthropogenic activities - section A2.2; and freshwater mussels as ecological indicators - section A2.3. In the light of the known or implicated factors affecting freshwater mussel distribution elsewhere, a comprehensive investigation of the distribution and abundance of <u>Velesunio angasi</u> was undertaken in the Magela Creek billabongs.

Apart from determining distributional relationships, density data were sought in order to provide accurate measures of biomasses and production within billabongs. In addition, density data would contribute to baseline information upon which to detect potential environmental disruptions in the Magela Creek billabongs. In order to gain such information, distributional patterns (for both microhabitat and between-billabong) needed to be demonstrated and quantified in terms of environmental factors - that is, morphometry, hydrology and physicochemical limnology of the billabongs. Such study of within and/or between-site distributional patterns of freshwater mussels within a drainage system, has to a limited extent been demonstrated and occasionally quantified in relation to environmental factors elsewhere (Cvancara, 1967, 1970; Cvancara et al., 1966; Salmon and Green, 1983) but rarely in Australia (Walker, 1981b) and never for the tropics. Investigation into the distributional relations of an Australian and tropical freshwater mussel therefore was of special appeal.

5.2 Sampling design and field procedure

Density estimates of Velesunio angasi in the Magela Creek billabongs were derived from sampling undertaken during 1980 and 1981.

In relation to the environmental variables that may influence mussel distribution, obvious features to consider were substrate and depth. Most sampling was performed during the mid to late Dry, and thus precluded any measurement of stream velocity, another habitat parameter. However, substrate type is generally regarded as indicative of stream hydrology, and this correlation has been applied to billabongs of the Magela Creek (section 2.3.1). For Mudginberri billabong, data pertaining to velocity and flow patterns through the billabong are available; nevertheless the correlation between substrate type and stream velocity was still used here (Figs. 2.8 and 2.15, section 2.3.1.3).

Measurement of percentage vegetative cover was also precluded from the studies, as by the mid to late Dry much of the rooted vegetation had senesced and disappeared. The presence of macrophytic vegetation in the billabongs during the Wet and early Dry may have affected the observed patterns of mussel distribution. Vegetation, however, predominately occurred in quiet, shallow reaches of the billabongs - fairly abundant in backflow billabongs, common around the edges of the floodplain billabongs and scarce in channel billabongs (including Island). Generally, the same shallow reaches were those preferred by mussels, so that the often-described adverse effects of vegetation upon mussel density (see section A2.1.2) were not obvious. Such effects may nevertheless be felt, particlarly in floodplain billabongs where plants may conceivably restrict Wet season water flow thereby interfering with oxygen availability. Here and elsewhere, however, water plants never occurred in such densities that could be considered restrictive either to water movement or to mussel distribution.

A stratified, random sampling procedure was adopted for Corndorl, Mudginberri and Buffalo billabongs - waterbodies with a variety of substrate patterns. Sampling of musssels in these billabongs was undertaken during the mid-late Dry of 1980. Quantitative samples were allocated randomly to representative substrate and depth regions of the billabongs, derived from prepared maps of bathymetry and substrate type (section 2.3.1). This resulted in all regions of the billabong being sampled, thereby allowing for the detection of additional distributional differences along the billabong that may be related to other trends in physicochemical or other unknown factors.

The potential crocodile hazard precluded similar stratified, random sampling in floodplain billabongs. In Nankeen, the mussels along the banks of five evenly spaced sections of the billabong (Fig. 5.1) were sampled intensively during the late Dry of 1981. The billabong was similarly bathymetrically mapped prior to sampling (sediments of this billabong are reasonably homogeneous - section 2.3.1.4) and as before, quantitative samples were allocated randomly to each representative depth region. Densities in the other floodplain billabongs (Island, JaJa, Leichhardt and Jabiluka) were derived from the routine collections made during 1981 and 1982.

During the 1981 Dry, 8 transects evenly spaced along Bowerbird billabong were sampled for mussels, comprising a total sample area of 45 m^2. Ten transects evenly spaced along Gulungul billabong were similarly sampled during November 1981. Because of the small size of Georgetown billabong at the end of the Dry, and because all microhabitats of the billabong were represented in the two routine transects, density estimates were derived from monthly sampling during the late Dry (Oct-Dec) of 1980 and 1981. No quantitative sampling was undertaken in Coonjimba billabong. (Mussels in Coonjimba were extremely scarce.) However, hand searching by systematically wading through this shallow billabong for over an hour in the late Dry of 1980, gave an approximate idea of the relative abundance of mussels.

Apart from Coonjimba and Georgetown billabongs, sampling of mussels for density estimates was done by hand from the confines of a quadrat. Usually, mussels below 19 mm were missed, collecting by this method. However, most collecting was done at times when growth of newly recruited mussels from the Wet season had surpassed this length (section 6.6.1). For the same reason, in Georgetown by the late Dry, few extra juveniles were incorporated into the density estimates by virtue of the more efficient sampling used then. Finally, recruitment in those billabongs sampled during 1980 (Georgetown, Corndorl, Mudginberri and Buffalo), showed similar patterns to those of 1981 (section 6.6.1) and therefore the abundance estimates in the two years between all of the billabongs of the Magela Creek can be compared.

Records of depth and substrate for all billabongs were made according to previous procedures (section 2.3.1). All depth measurements that were made at each site, were standardised to late Dry season levels.

5.3 The distribution and abundance of mussels along the Magela Creek

Mean densities per substrate and depth interval within the Magela Creek billabongs are shown in Tables 5.1-5.9. (Substrate subdivision does not appear in billabongs where the bottom type is reasonably homogeneous.) No mussels occurred along any of the transects across

Bowerbird billabong.

The spatial dispersion of the populations was determined using the method described by Elliott (1977). The null hypothesis of a random distribution of mussels over a homogeneous environment was tested by comparing the field population with a theoretical Poisson distribution. The departure from randomness gives an index of the degree of population aggregation. Values of variance (S^2)/mean($\bar{x}$) greater than 1 indicate some degree of clumping, whereas in a Poisson series, the variance is equal to the mean. The significance of the departure from unity is assessed by the chi-squared test:

$$\chi^2 = \frac{(n-1)S^2}{\bar{x}} \qquad \text{where } n = \text{number of samples.}$$

Significant ($P < 0.05$) departure from unity ($S^2 > \bar{x}$), and hence contagious distribution is indicated in Tables 5.1-5.9.

From inspection of the tables, generally within a particular habitat there was significant clumping at high densities, but random dispersion at low densities. This is to be expected (Elliott, 1977). Further, no realistic inferences can be made where sample sizes were low, a factor contributing to nonsignificance of some observations. Finally, there was a suggestion that in deeper waters in some billabongs (Corndorl, Mudginberri and to some extent Buffalo), dispersion was random despite comparatively high densities and large sample sizes.

Total numbers of mussels per habitat area of a billabong were extrapolated using the mussel density data and the extent of habitat areas derived from planimetry of the prepared bathymetric and substrate description maps. The estimated mussel totals for each habitat were then summed to provide a grand total for each billabong. From this figure, and using the total billabong area figures, mean density estimates of mussels averaged over the billabongs were derived and are shown in Table 5.10. Mean densities ranged widely between billabongs and no broad trends are apparent when geographic location of billabongs is considered.

5.4 Environmental determinants of distribution and abundance

5.4.1 Within billabongs

In relation to depth and substrate data, two-way analysis of variance was performed on the habitat density means wherever applicable to determine whether there were significant differences in population density among depths or in density among different substrates.

5.4.1.1 Depth

Apart from Georgetown, in all of the Magela Creek billabongs studied, an optimal, intermediate depth was found at which mussel densities reached a maximum. Henceforth this depth is referred to as the "preferred depth".

<u>Backflow billabongs</u>

In Georgetown billabong, no significant difference in density among different depths was found. Mussel distribution in this billabong is strongly modified by the seasonal flooding and subsequent evaporation of the waters. Considerable recruitment occurs in the shallow waters of this billabong during the Wet and early Dry, in addition to significant migration here from deeper waters (sections 6.6.1 and 6.8.1 respectively). By the late Dry when densities were recorded, mussels have retreated and are concentrated in the remaining waters, with no discernible pattern of depth distribution.

Mussels were absent from the shallowest reaches of Gulungul billabong (<0.3 m) during the late Dry of 1981. Presumably the mussel distribution was affected by the previous Dry of 1980 at the end of which the billabong almost dried up. Peripherally inundated regions in late 1981 were presumably exposed over the same period in 1980. Mussel densities were maximal at 0.5 m. Although a quadratic relationship appeared an appropriate model of the depth distributional data for depths greater than 0.1 m, the fit was insignificant ($P>0.05$) reflecting the few depth intervals sampled (Fig. 5.2).

Analysis of variance revealed no significant differences in mussel density among depths in Corndorl billabong when data were analysed with the two major substrate types of the billabong. However, partitioning of the sum of squares (SS) due to depths into linear, quadratic and residual components revealed a significant ($P<0.05$) quadratic effect. (The residual component was also significant ($P<0.05$) indicating possibly, that a more sophisticated model may have been appropriate had more depths been sampled.) As significant substrate effects were apparent in this billabong (section 5.4.1.2.1), regression equations describing the relationship between densities and depth for both substrate types, and their levels of significance are shown in Table 5.11. The relationships are plotted in Fig. 5.2. Preferred depths are similar (1.0 m) for both substrate types.

Channel billabongs

No significant (P>0.05) and highly significant (P<0.001) differences were revealed in density among depths in Mudginberri and Buffalo billabongs respectively. As for Corndorl billabong, however, partitioning of the depths SS revealed highly significant quadratic effects in both waterbodies (P<0.001). As significant substrate effects were also revealed (section 5.4.1.2.1), regression equations were calculated separately for the different substrates (Table 5.11) and are plotted in Fig. 5.3. Preferred depths varied with substrate type, tending to be greater with decreasing organic content and softness of the sediments. This was revealed also from Fig. 5.4 which shows the combined sediment relationships for each billabong. The preferred depth in Mudginberri billabong with firmer, less organic sediments was greater than in Buffalo.

Floodplain billabongs

Data from Nankeen billabong for which large numbers of between-site observations were available (Table 5.9), were analysed for between-site and depth differences. Highly significant differences were revealed in mussel density among depths in this billabong (P<0.001). As homogeneous sediments are a feature of the floodplain billabongs, the density data of each floodplain billabong were combined and analysed in a single AOV. This test revealed significant depth relationships ($P<0.05$) when averaged over the billabongs and very significant differences in densities among billabongs ($P<0.01$). Plots of densities and depths for each billabong suggested complex nonlinear relationships (Fig. 5.5). An appropriate exponential model of the form:

$$Y = Ae^{-\alpha x} - Be^{-\beta x} \quad \text{where } Y = \text{density}, X = \text{depth}$$

was chosen to describe the depth distributional relationship (see section 3.4). The regression equations are described in Table 5.12 and plotted for each floodplain billabong in Fig. 5.5. Although not always apparent (e.g. Island billabong with its low densities), a notable feature of the relationships between density and depth in floodplain billabongs was their skewed nature and shallow preferred depths in comparison to those of backflow or channel billabongs.

Depth relationships in all billabongs

Table 5.13 shows the preferred depth as derived from the predictive regression equations for each of the Magela Creek billabongs. Where two or more substrates were present in a billabong, the combined regression equation was used.

Of the factors previously suggested in the literature as restricting mussels from depth (section A2.1.2, Depth), in the relatively shallow and warm waters of the Magela Creek billabongs, finer and unconsolidated sediments and low dissolved oxygen levels with increasing depth are probably most relevant. Notable in the distributional patterns was the skewed depth distribution of mussels towards shallower waters in the floodplain billabongs. The deep waters of these billabongs were particularly susceptible to Dry season stratification and deoxygenation (section 2.3.2.2), strongly suggesting that this factor was the direct cause of the observed, relatively shallow preferred depths. Mean dissolved oxygen levels of Nankeen averaged over 3 years of data and typical of the pattern in other floodplain billabongs (Walker et al., 1983a) are plotted with density and against depth in Fig. 5.5. A correlation between decreasing density and mean dissolved oxygen was evident.

Both channel billabongs, however, do not stratify nor become deoxygenated to the extent of the floodplain billabongs. The preferred depths, presumably by way of the response of the mussels to the lack of deoxygenation, were notably greater, optimising in all likelihood the advantages of deepwater distribution. Also, as previously noted, the preferred depths tended to be greater with decreasing organic content and increasing consolidation of the sediments. This may also be related (at least partly) to microhabitat oxygen availability. Higher organic content of particular sediments presumably increases the oxygen demand of the surrounding waters, a factor accentuated with increasing depth and therefore likely to restrict mussels to shallower waters.

Some stratification and deoxygenation were evident in the backflow billabongs studied (section 2.3.2.2), factors that may have limited numbers of mussels in deep water regions. In addition, the sediments of these waterbodies are fine and unconsolidated (section 2.3.1.2); from observations, the softness increased with depth (though not confirmed quantitatively). Mussels may sink and asphyxiate in such sediments.

It might also be argued that the actual depth of billabongs is important in determining the preferred depth of mussels. Figure 5.6 shows a scatter plot of preferred depth against mean depth of billabongs. Above a threshold depth (approximately 0.5 m), mussel density is apparently maximised at a depth proportional to the depth of the billabong. Nevertheless, the preferred depths of mussels in the two channel billabongs (Nos. 12 and 14 in Fig. 5.6) were disproportionately greater than the mean billabong depths. In the deeper billabongs where oxygen relations are likely to be most important, some correlation was also evident between preferred depth and mean dissolved oxygen (averaged over the seasons) (Fig. 5.6). Perhaps the relatively shallower preferred depth in Nankeen (No. 29) is a luxury afforded by the very turbid waters in this billabong at the end of the Dry (section 2.3.2.4) that may shelter mussels against high water temperatures at this time. Possibly the strongest evidence of the importance of low dissolved oxygen concentrations in causing the relative absence of mussels at depth is provided in the shape of the depth distribution curves. While the effect of high water temperatures and/or desiccation and predation should restrict mussels from shallow waters equally across the billabong types sampled, the skewed nature of the floodplain billabong relations strongly suggests that the stresses imposed by low concentrations of dissolved oxygen at depth here necessitates a bias to shallow water distribution. The skewed effect in floodplain billabongs is shown in the calculations of preferred depths relative to mean billabong depth when viewed over all billabongs (Table 5.13). Significantly, in all (and in only these) the floodplain billabongs (Nos. 16 to 29), the preferred depths are shallower than the mean billabong depths.

5.4.1.2 Hydrological regime of the Wet

5.4.1.2.1 Substrate and stream velocity

Backflow billabongs

Analysis of variance revealed no significant differences in the density of mussels found among the different substrates within Georgetown billabong. Although densities were comparatively low on substrate 'D' (Table 5.1), this bottom type occurs at the edge of the billabong (Fig. 2.5), and by the late Dry, much of the population has moved away from these littoral regions (section 6.8.1). The bottom types in Georgetown billabongs are possibly the most diverse of any billabong on the Magela Creek ranging from very fine silt and clay to coarse, sandy sediments. Of relevance to mussels, however, is that all of the substrates are firm yet yielding.

In the Wet seasons of both 1980 and 1981, flood events (February 1980 and March 1981) displaced large numbers of mussels from Georgetown depositing them on a shallow, flooded meadow immediately downstream of the billabong. No censuses were undertaken, but hundreds and possibly thousands (1980) of mussels were believed to have been carried away. Some mussels burrowed into sandy patches amongst the grassed area and presumably aestivated over the ensuing Dry but the vast majority trapped on impenetrable substrates and unable to burrow, succumbed either to intolerably high water or air temperatures as the shallow waters retreated. Such flood events are not uncommon in the region during the Wet season and thus must account for fairly regular and relatively significant mussel mortality in Georgetown. The Magela Creek's high water route through Georgetown has been previously described (section 2.3.1.2) and undoubtedly all substrates in the central portions are unstable during flood events. The sandy sediments, however, must be particularly unstable and shifting at such times. The Dry season density estimates therefore give no measure of the instability of the central and especially sandy sediments, as migration has occurred from the shallows into this region by this time.

While the bottom type of Gulungul billabong was relatively homogeneous (apart from observed differences in consistency, section 5.4.1.1), there were significant differences ($P<0.05$) in the density of mussels occurring between the two major substrates of Corndorl billabong. Higher densities occur on the more inorganic and coarser sediments of the northern bank (Fig. 5.2). These sediments, being less silty and firmer than those of the other bottom type, may be more conducive to both post-larval settlement and maintenance of adult populations. As the silt and clay sediments of Gulungul are similar to those of Corndorl, the mussel population in Gulungul may also be reduced for the same reasons.

Channel billabongs

As previously mentioned, no mussels were found on the shifting, sandy sediments of Bowerbird billabong. No significant differences were found in mussel density among the major three substrate types in Mudginberri billabong. However, partitioning of the substrates SS revealed significantly fewer ($P<0.05$) mussels occurring on sand than on the other finer and more organic sediments. In Buffalo billabong, highly significant differences ($P<0.001$) were revealed in density among the four major bottom types. No significant differences, however, were found in densities between sand and the other finer and more organic sediments after partitioning of the SS.

Differences in density on the three finer, more organic sediments were tested for between both channel billabongs. No significant differences were found between billabongs, but a significant difference ($P<0.05$) was revealed in density among the different bottom types. No sediment analyses were performed on the softest and most organic substrate type in Buffalo billabong. The three sediments were ranked on a scale of 1-3 in order of increasing organic content and decreasing particle size (also see section 2.3.1.3). The substrates SS was then partitioned into linear and residual components. This revealed a highly significant linear effect ($P<0.001$) with densities declining with increasing organic content and decreasing particle size of the sediments (Fig. 5.7).

The significantly lower densities of mussels on clean swept sandy sediments in Mudginberri were undoubtedly due to the shifting nature of the sediments, particularly during flood events in the Magela Creek (see section 2.3.1.3). Because of the branching of the creek as it leaves Mudginberri billabong, reduced stream velocities pass through Buffalo billabong. The densities of mussels in the corresponding sandy sediments of Buffalo, were notably higher (Table 5.5) as a result and, importantly, did not differ from densities occurring on the other sediments of the billabong.

Significantly fewer mussels occurred as the sediments of both billabongs increased in organic content and became siltier and increasingly unconsolidated. Two factors may be responsible for this. In the worst situations, mussels may be unable to maintain their station in the unconsolidated sediments of Buffalo billabong (substrate E, Table 5.5). Otherwise, the silty sediments may interfere with breathing or juvenile settlement. Alternatively or additionally, as mentioned earlier the organic sediments may also create microhabitat oxygen demands detrimental to maintenance of either juvenile or adult mussel populations. Finally, it was notable that the highest densities for the major bottom types occurred in sediments immediately out of range of the main Wet season stream flow; that is, in sediments that were neither too fine and silty nor too organic (substrate B, Table 5.4) and that occurred in Mudginberri, the best aerated billabong on the Magela Creek.

Floodplain billabongs

As in all of the floodplain billabongs, mussels were scarce at depth in Island billabong. Such parts of the billabong were subject to oxygen depletions in the early Dry (section 2.3.2.2). In addition, however, much of the area was sandy and to some extent may be shifting and unstable during flood events. Further, the same area has been reported to be covered by an unconsolidated sediment floc on a past occasion (section 2.3.1.3). The detrimental effects of silt deposition upon mussels has already been mentioned. All three factors - oxygen depletions, shifting substrates and periodic silt deposition, have the potential to restrict mussels from the central, deep regions of Island billabong.

JaJa, Jabiluka and Nankeen billabongs each have reasonably homogeneous sediments although a sandy strip occurs along the eastern bank of Jabiluka billabong (section 2.3.1.4). Table 5.8 lists the densities occurring on the sandy sediments and those of the firm silt and dry sediments in Jabiluka. No significant differences ($P>0.05$) were revealed in the density of mussels occurring between either sediment type.

Three sediment types occur in Leichhardt billabong: soft but firm silt and clay; extremely compacted clay; and extremely unconsolidated, silty vegetation and detritus. Significant differences ($P<0.05$) were found in the density of mussels occurring among the three substrates, and further partitioning of the substrates SS revealed significantly more mussels ($P<0.01$) occurring on silt and clay than on the other sediments.

All billabongs

Analyses of densities occurring on different sediment types of the Magela Creek billabongs revealed the unsuitability of some for maintenance of mussel populations. In the extreme, sediments comprising the sandy bottom of Bowerbird and the loose vegetation and compacted clay of Leichhardt billabong were completely unsuitable for mussels, being either shifting, too soft or too hard. To a lesser degree, the sandy sediments of Mudginberri (and occasionally Georgetown) and the gradient towards finer and more organic sediments in both channel billabongs also provided less suitable habitats. Such comments are applicable also to the even less consolidated organic, silt and clay sediments of Corndorl billabong and presumably Gulungul. Firm and yielding substrates, regardless of their texture and grain size had the highest densities. Such bottom types include sand, silt and clay, soft clay and sand with little silt or organic material.

5.4.1.2.2 Flow patterns in some floodplain billabongs.

Jabiluka billabong

Fig. 5.8 shows graphically the distribution and abundance of mussels in relation to depth along Jabiluka billabong. Clearly the southern end of the billabong had the highest density of mussels and, notably along the most southerly transect, densities reached a peak in the deepest regions. Mussels were generally absent from deep regions - particularly in floodplain billabongs, and as these deeper waters had lower oxygen tensions, dissolved oxygen status of the water appeared to be clearly implicated in regulating densities of the mussels.

Entry of water into Jabiluka billabong during the Wet season has been previously described (section 2.3.1.4, Figs. 2.18 and 2.19). Water is effectively funnelled through the relatively narrow southern end, entering the billabong at depth and moving towards the surface as it moves northward through the billabong. Presumably, the Wet season bottom waters at the southern end of the billabong are reasonably well oxygenated as the water is moving (being funnelled) and has just left the relatively shallow floodplain. As the waters progress through the billabong, velocities presumably decline in wider reaches and importantly move to the surface, so that the bottom further northward must be relatively deprived of oxygen.

Some pertinent points from other parts of these studies (sections 6.6 and 7.10.1) can be made at this stage: 1) larval production in female mussels of the Magela Creek billabongs is correlated with availability of dissolved oxygen; 2) as a consequence, periods of low discharge through floodplain billabongs during the Wet lead to some oxygen depletion and resultant inhibition of larval production or even abortion of larvae from the female gills; 3) recruitment of metamorphosed juveniles in channel and floodplain billabongs is distinctly seasonal, occurring in the Wet season; 4) juvenile mussels are especially sensitive to low levels of dissolved oxygen (when compared with adult tolerances - see Appendix 6); and 5) recruitment of mussels from floodplain billabongs, as measured by strength of year classes, is significantly correlated with total Wet season discharges. Oxygen availability both during the Wet and early Dry is apparently critical to successful recruitment of young. Larval development and juvenile survival depend upon an adequate oxygen supply during these periods when larvae are both produced and young recruited. The correlaton between recruitment and Wet season discharge therefore is hardly surprising and is to be expected especially for floodplain billabongs where the effects of low dissolved oxygen would be most strongly felt. It is hypothesized therefore that the deepwater entry of presumably well oxygenated water into the southern end of Jabiluka during the Wet enhances both larval production and subsequent juvenile survival. This region therefore records comparatively high densities of mussels.

Nankeen billabong

From the findings of the distribution and abundance of mussels in Jabiluka billabong, a general hypothesis that Wet season flow is an important determinant of distribution and abundance of mussels in billabongs on the Magela Creek is proposed and argued as follows.

To provide adequate oxygenation, current velocities need to be of sufficient strength as waters in stronger currents presumably carry more oxygen. Assuming a constant discharge along a given section of stream, stream morphometry can determine current strength as a smaller cross-sectional area at a given point will result in stronger currents than a larger area.

From visual observations of the Wet season flow through Nankeen billabong, the course of peak flow (as might be expected) was through the deepest section of the billabong (Figs. 2.14 and 5.1), along the left-hand or western bank. As mussels were virtually absent from the deepest portions of the billabong (Table 5.9), the billabong can be considered as comprising two distinct environments - a west and an east, separated by an uninhabitable deep portion. Thus, the 5 transects sampled along the billabong can now be considered as 10 sampling stations as at each transect, both east and west banks were sampled (Fig. 5.1).

On the premise that current strength may determine local distribution and abundance, the cross-sectional area, as a measure of current velocity, was estimated at each station. Cross-sectional area was calculated from the product of billabong width, from the bank to the deepest point of the transect, and the mean depth of the cross-section. A mean density for each cross-section was also calculated. All morphometric data were taken from the prepared bathymetric map (Fig. 2.14). Cross-sectional area and mean density for each sampling station are plotted in Figure 5.9. (Cross-sectional area has been converted to a reciprocal to provide a positive association.)

Analysis of variance revealed very significant ($P<0.01$) differences in mussel density among the different stations in Nankeen billabong even prior to establishing a relationship between current strength and distribution and abundance. From Table 5.9 it is clear that mussel density along the west bank (even numbered stations) was considerably higher than that along the east bank. (A t-test applied to the two overall density means, averaged over either side of the billabong, revealed a highly significant difference (P<0.001)). As Wet season flow passes alongside the west bank closely, it would follow that this bank would receive comparatively well oxygenated water via the stronger currents, so enhancing recruitment and survival of mussels. For the eastern bank, however, mussels were most numerous in shallower waters out of range of the peak current. It is conceivable that during periods of low discharge during the Wet, flow might be barely discernible in these reaches.

Unlike for Jabiluka, there is no knowledge as to the exact pathway of water flow into Nankeen billabong during the Wet. Because of this, interpretation of Fig. 5.9 could be unclear. However, a meandering and apparently relict channel exists between Nankeen and Jabiluka billabongs (Fig. 2.17). Nothing is known of its Wet season competence but because it represents the lowest ground on the floodplain in this region (being still filled with water towards the late Dry) it is tempting to suggest some flow at least must pass along it during the Wet. If this is the case, then at least some (perhaps most) water from the floodplain would enter the billabong via this right hand channel some distance downstream from the southern extremity.

Assuming this pattern of flow occurs, a reasonable interpretation can be made of Fig. 5.9. Firstly, the assumption of constant discharge along the billabong is invalidated, because in the extreme case of all Wet season flow entering the billabong via the described channel, then stations 9 and 10 (Fig. 5.1) are placed outside the main stream of flow. If similar subsurface entry of (presumably) well oxygenated water from the floodplain is the case for Nankeen, as it is for

Jabiluka billabong, then according to the hypothesised flow pathway (Fig. 5.1) the bottom regions to benefit from this water are those around station 8. Accordingly, for their given cross-sectional areas, stations 9 and 10 have fewer mussels than might be expected, while station 8 has far greater densities. If these three stations are considered anomalous for reasons of some peculiar water entry phenomenon, and are neglected from further calculations, a significant linear correlation ($P<0.05$) is found between the reciprocal of cross-sectional area and mean density for the other stations (Fig. 5.9). That is, where stream flow is strongest (as measured by small cross-sectional areas) densities of mussels are highest.

As many assumptions have been made in the above interpretation of distributional patterns in Nankeen billabong, confirmatory evidence must await the collection of more hydrological data relating to the exact pathways of waterflow into the billabong. The significant differences in densities between east and west banks of the billabong at this stage, however, provide some evidence that the more turbulent and presumably better oxygenated environment of the west bank during the Wet in some way enhances recruitment of mussels. In relation to the anomalous patterns of distribution and abundance for stations 8, 9 and 10, some further comments are possibly valid. Well into the Dry season (July) flow continues to pass through the floodplain billabongs (N.T. Dept. Transport and Works, Water Division, 1980). Even if during the Wet, water entry into Nankeen via the meandering floodplain channel is not a significant source, by the early Dry it may well be the major channel source of the little water left flowing through the Magela Creek. In all likelihood, the retreating waters reach such low levels that the only point of entry of water into Nankeen billabong can be via this route. If this is so, the subtle and perhaps unmeasurable early Dry season entry of water may enhance survival of newly recruited mussels at station 8 where the effects of the incoming trickle of waters would be most immediately and significantly felt. Further, presumably no flow would pass over the bottom regions of stations 9 and 10 at this stage.

Hydrological patterns in other billabongs may also explain local patterns in distribution and abundance. The highest densities of mussels in Mudginberri billabong are recorded on the stony and clay sediments (substrate D, Table 5.4) along the southwestern bank (Fig. 2.8). This site is well flushed during the Wet season (Fig. 2.15, section 2.3.1.3) enhancing the oxygen status until flow into the billabong ceases (about June). Larval production and recruitment must presumably benefit from the improved aerobic conditions here. Additionally, however, the stability and non-silty nature of these sediments must also benefit recruitment and consequent maintenance of adult populations. Another soft clay region in Buffalo, also has the highest densities of mussels for the billabong (Substrate F, Table 5.5, Fig. 2.9). No details of localised flow patterns are available for Buffalo billabong, other than that the bed of dense mussels was observed to lie close to (on the left-hand side) the main channel of flow. Flow from Corndorl Creek or from the Magela Creek has been observed to pass close to the gravelly sediments along the northern bank of Corndorl billabong (Fig. 2.7). This may account in part for the large population of mussels in these sediments, although significant flow in either direction through the billabong is probably infrequent, considering the small catchment of Corndorl Creek and the relatively large discharges needed in the Magela Creek to create significant backflow events.

Finally, consideration needs to be given to the habits of host fishes in explaining the observed distributional patterns of V. angasi described above. It may be less the mussel's intolerance to low flow regimes and consequent low dissolved oxygen levels that determines distribution and abundance than it is the host fishes intolerance to these conditions. By seeking strong flowing and well oxygenated waters, the Wet season distribution of fish may inadvertently affect that of the mussel. Presumably, however, there are other areas to which a fish can move to avoid poor oxygen conditions. Avoidance may be affected by vertical and lateral movements into shallower waters for example. More information is needed on the Wet season distribution of fishes in billabongs. Finally, mussel shells have been found in the meandering channel between Jabiluka and Nankeen billabongs. Fish therefore occur in the channel during the Wet season. The presence of shells may reflect the relative permanence of water left at the end of the Dry for mussel survival or more likely, that the channel is used in relation to fish migration. The latter instance adds credence to the suggestion that the channel may be competent.

5.4.2 Correlates of distribution and abundance between billabongs.

Multiple regression analysis

Having examined several environmental influences on the distribution and abundance of mussels within billabongs, the identification of parameters responsible for broader distributional patterns between billabongs was sought. Under normal circumstances, between-site variation in physicochemical limnology of a perennial stream the size of the Magela Creek, might be expected to be minor or even negligible. However, strongly seasonal influences and geographic effects impart a marked heterogeneity to the water chemistry of the Magela Creek billabongs (section 2.3). Because of the large variation in between-billabong distribution and abundance of mussels and in water quality, and the substantial quantitative data base of both mussel densities and billabong limnology, the opportunity to assess the influence of environmental parameters on the distribution of freshwater mussels was presented.

A large array of physicochemical parameters was chosen for the analyses, representing monthly measurements over approximately three years of data collection. The chemical parameters are listed in Table 2.7 and were chosen, on the basis of previous descriptions in the literature, as having relevance to regulation of mussel species or to the physiological tolerances of mussels. Literature pertaining to these known or implicated effects has been reviewed in section A2.1.3; briefer reviews in relation to similar types of analyses have been provided by Green (1971) and Sepkoski and Rex (1974). The chemical parameters comprised the following groups: relevant to shell formation and maintenance (pH, Ca, total hardness, carbonate hardness, bicarbonate concentration, total alkalinity); salinity (conductivity, K, Cl); trophic conditions (dissolved and total organic carbon, nitrate, ammonia, % organic matter of sediments, chlorophyll); other major ions (Mg, noncarbonate hardness); turbidity and suspended solids; and dissolved oxygen. Other relevant environmental parameters chosen were sediment characteristics (percent organic matter, mean sediment particle size) (Table 2.2) and mean depth (Table 2.1).

Stepwise multiple regression was used to assess the relationships between mussel abundance and the limnological variables. Sediment particle sizes were converted to phi units (Folk, 1968) as recommended by Green (1971) and the arcsine transformation was used to express percentage organic content of sediment. Scatter plots of each other environmental variable against the dependent variable, (mean billabong density) (Table 5.10) were made to determine the suitability of transformations. Log transformations were made and a quadratic term included where appropriate. The significance of a quadratic term would indicate a unimodal relationship between abundance and the relevant environmental gradient.

Unfortunately, because N.T. Water Division did not sample from Leichhardt billabong, some chemical data are missing (Table 2.7). Therefore, two multiple regression analyses were performed, one omitting all data from Leichhardt, and the other utilising data common to all billabongs. Few data are available also for Buffalo billabong.

Because of the close proximity of Buffalo billabong to Mudginberri and the similar characteristics of both billabongs, however, a similarity in physicochemical limnology was assumed. From comparison of chemical data collected over a year between both billabongs (Walker and Tyler, 1983b; Water Division data, N.T. Department of Transport and Works), this assumption appears reasonably well justified especially when the large total variation between all billabongs is considered. Thus, the values for 16 parameters were assumed common to both billabongs.

In terms of the relative importance of the independent variables in influencing and predicting densities of mussels between billabongs, only dissolved oxygen was significantly correlated with density in both analyses. With data from Leichhardt billabong omitted, dissolved oxygen accounted for 63% of the variation in density ($P<0.01$), and when included, accounted for 53% of the variation ($P<0.05$). The relationship between mean dissolved oxygen and mean billabong density of mussels is plotted in Figure 5.10. The linear regression equation is described:

$$Y = -13.518 + 5.702X \qquad (P<0.01,\ r^2 = 0.540)$$

where Y = mean billabong density (numbers/m^2) and X = mean dissolved oxygen (mg/l).

Billabongs lying on the mainstream channel

The importance of dissolved oxygen (DO) in determining mussel distribution and abundance within and between billabongs, led to consideration of perhaps even better prediction of mussel abundance between billabongs.

It appeared conceivable firstly, that DO as manifested through Wet season flow patterns might influence mussel densities among billabongs. Flow patterns were at least already implied in the local distributions of mussels in two floodplain billabongs, Jabiluka and Nankeen. Wet season DO as a major factor in affecting successful recruitment among billabongs, could therefore be regarded as a possible determinant of mussel distribution and abundance. This is particularly pertinent to billabongs lying on the mainstream channel of the Magela Creek, where recruitment occurs in the Wet season and as such is presumably influenced by prevailing DO concentrations at this time. Accordingly, these billabongs are treated separately from those billabongs lying off the main channel of flow (backflow billabongs and JaJa billabong).

Rather than using spot monthly readings of DO, (which are presumably influenced to a considerable degree by fluctuating and highly variable daily discharges, section 5.4.1.2.2), mean cross-sectional area may be a more appropriate measure of current strength and associated DO concentration because it integrates the discharge characteristics of particular billabongs. (The rationale behind this statement has been argued previously.) Implicit in the use of such a morphometric index, is the assumption that discharge is constant over all billabongs. Although discharge is obviously proportional to catchment area and increases in a downstream direction, some compensation is made for by branching of the Magela Creek waters below Mudginberri billabong and some degree of dispersal of waters over the broad floodplain. Thus, while all Magela Creek water would not be channelled through the floodplain billabongs, no measure of between-billabong variation in discharge is available. Regardless, a relationship exists between billabong morphometry and mean Wet season (January-April) DO (calculated from the data of Figs. 2.20 and 2.21) suggesting that slower flow rates through the larger billabongs are indicative of lower mean DO concentrations during the Wet (Fig. 5.11). While the Magela Creek waters branch downstream of Mudginberri, all water upstream flows through the billabong, contributing to the anomolously high mean Wet season DO level. Thus when Mudginberri is omitted from the regression analysis, the relationship between depth and Wet season DO in the remaining five billabongs is not significant, but there is a significant correlation ($P<0.05$) between both mean width and mean cross-sectional area, and Wet season DO (Fig. 5.11). No further significance to the prediction of Wet season DO was obtained after addition of cross-sectional areas to the width/DO regression, but cross-sectional area accounted for 89%, in comparison to mean width which acounted for 78%, of the variation in Wet season DO. Cross-sectional area was retained therefore in further analyses, on the grounds that it has more underlying significance and stronger hydrological basis for influencing and predicting Wet season DO.

Both mean cross-sectional area and mean Wet season DO were regressed against mean density of mussels of each billabong (Figs. 5.12 and 5.13 respectively). Both linear regressions were significant ($P<0.05$), Wet season DO accounting for 67%, and cross-sectional area 68%, of the variation in mean density (Figs. 5.13 and 5.12). Again, however, cross-sectional area was retained for further analysis, on the basis that it provides an integrated and quickly determined measure of mean Wet season DO. The linear regression equation describing the relationship between cross-sectional area and density is:

$$Y = 26.094 - 0.107X \qquad (P<0.05,\ r^2 = 0.676)$$

where Y = mean billabong density and X = mean cross-sectional area.

The model (Fig. 5.12) thus far considers prediction of density in terms of billabong morphometry reflecting flow and oxygen, available for Wet season recruitment. However, from the multiple regression analysis, mean density over all billabongs is correlated with mean DO averaged over the year (Fig. 5.10).

It can be argued that adequate DO not only enhances larval production and recruitment, but also survival of newly recruited mussels that were found to be particularly susceptible to low concentrations of DO (section 5.4.1.2.2). Therefore the addition of mean DO averaged over both Wet and Dry seasons may improve the model. The morphometry of Leichhardt billabong for example might suggest a higher density than actually occurs there (Fig. 5.12). However, the low mean DO concentration in this billabong (Table 2.7) suggests that poor survival of recruits affects the distributional patterns.

Thus, a two-compartmental model of density prediction was evaluated: one component, billabong morphometry, considers Wet season flow characteristics and their influence on recruitment; and the other, mean DO averaged over the seasons, considers the survival of recruits throughout the year. As biological models may be expected to be multiplicative rather than additive, a simple model was constructed thus:

$$\text{Mean density} \propto \frac{\text{mean dissolved oxygen concentration}}{\text{mean cross-sectional area}}$$

for a particular billabong. A high value in the numerator, suggests a high density and vice versa. A low value in the denominator also implies a high density (and vice versa). Thus for example, a 'small' billabong with adequate DO should expect high mussel densities as opposed to a 'large' billabong with low DO values.

The predictive model of density for billabongs lying on the mainstream channel of the Magela Creek is shown in Figure 5.14. For predictive purposes a linear model provided a sufficient fit of the data, and the fitted regression equation is:

$$Y = -7.325 + 663.98X \qquad (P < 0.001,\ r^2 = 0.978)$$

where Y = mean density (numbers/m^2)

$$\text{and } X = \frac{\text{mean DO concentration}}{\text{mean cross-sectional area}} \quad (\text{mg/l/m}^2)$$

The derived model has significant predictive value, despite other factors not being fully considered. The model for example, assumes that the Wet season discharge through each billabong is the same. To what extent this assumption is invalidated however, is not known; regardless, however, Wet season DO and billabong morphometry were correlated. Inimical substrates affect the density figures in Mudginberri and Leichhardt billabongs respectively (section 5.4.1.2.1), so that as far as the model is concerned, the densities in these two billabongs were somewhat underestimated. Further, the relationship is extremely simplistic. While no environmental parameter other than dissolved oxygen was significantly correlated to density, some other unmeasured parameter (not yet implicated in the literature) may be important. Fish relations for example are not considered; however, fish hosts are present throughout the year in all of the billabongs studied (sections 2.3.3 and 7.14). Nevertheless, the model makes good biological sense: dissolved oxygen is strongly implicated in mussel abundance throughout the Magela Creek billabongs (hardly surprising considering the characteristic low seasonal values in the billabongs); flow characteristics in billabongs lying on the mainstream channel of Magela Creek influence oxygen availability during the Wet, presumably therefore, affecting recruitment; and mean DO levels averaged over all seasons must presumably have a marked influence on survival of newly recruited mussels.

Finally, it is a significant observation that (although not shown on Fig. 5.14) only billabongs receiving constant flow from the Magela Creek fit the relationship, reflecting presumably, the importance of stream flow and oxygen availability to the Wet season recruitment that occurs in these billabongs. Backflow billabongs and JaJa, a floodplain billabong, do not receive regular flow from the Magela Creek and other factors presumably influence their patterns of mussel distribution and abundance.

Backflow billabongs

The significant correlation between mean DO and mean billabong density (Fig. 5.10) was derived from all the Magela Creek billabongs and therefore DO status presumably is as important in backflow billabongs as it is in other billabongs. Discharge, however, is not a critical factor in determining recruitment and the observed high densities of some of these billabongs at least suggest they are adequately oxygenated when recruitment occurs (late Wet - early Dry season, section 6.6.1). The shallow waters of these billabongs must presumably enhance the DO levels when recruitment occurs especially as recruitment occurs in their littoral zones (section 6.6.1).

Depth is critical to the mussel populations of these billabongs in other ways, however. Shallow waters at the end of the Dry may leave mussels exposed to lethally high water temperatures, desiccation or predation. Deeper backflow billabongs then, might be expected to harbour a greater abundance of mussels. Presumably, however, a threshold depth is met which acts in an opposite direction, inhibiting recruitment as still, deep water during the Wet may become deoxygenated. (JaJa billabong is one example of this type, discussed below.)

On the premise that both mean DO concentration and water depth affect the recruitment and survival of mussels in backflow billabongs, and in the absence of any other significant environmental factor (see earlier 'Multiple regression analysis'), a model based on mean DO and water depth was proposed to explain density patterns among backflow billabongs. The model was constructed thus:

Mean density = mean DO x water depth, for a particular billabong. The model is based on the observation that deep, and adequately oxygenated backflow billabongs realise a greater abundance of mussels. A logarithmic model provided the best fit of the data (Fig. 5.15) and the fitted regression equation is of the form:

$$Y = 10.034 \ln X + 1.987 \qquad (P<0.05,\ r^2 = 0.932)$$

where Y = density (numbers/m^2) and X = mean DO x depth (m.mg/l). Again, the derived model has significant predictive value and the theoretical basis for its validity is reasonable. However, the analysis is based on only a few billabongs. Further, some substrate effects were also observed to influence the distributional patterns in these billabongs (section 5.4.1.2.1). Shifting sands in Georgetown billabong, and soft, unconsolidated sediments in at least Gulungul and Corndorl billabongs supported a reduced abundance of mussels. No consideration, however, was given to the sediment characteristics of these billabongs towards predicting mussel densities. The derived equation, nevertheless, presents a reasonably adequate model. More backflow billabongs within the Region need to be studied to test its present validity.

Finally, it is a notable feature, that JaJa billabong was a misfit to both predictive models. It does not lie on the mainstream channel of flow of the Magela Creek, nor does it have the morphometric, hydrological and limnological characteristics of backflow billabongs of the Magela Creek catchment. Its location on the floodplain but off the mainstream channel, and relative depth in comparison to other backflow billabongs, means that it possibly does not receive adequate flow and oxygenation during the Wet to realise the higher densities expected from its morphometric appearance.

5.5 Discussion

Distributional patterns within billabongs

As might be expected in distributional studies of benthic organisms (Elliott, 1977), at higher densities, the local distributions of *Velesunio angasi* populations within specific habitats of the Magela Creek billabongs, are clumped. Demonstration of this distributional pattern in other freshwater mussel species, however, is uncommon (Kenmuir, 1980; Salmon and Green, 1983). Apart from being caused by differences in microenvironment, the clumped distribution of mussels may effectively enhance fertilization and reproduction as suggested by Tudorancea and Florescu (1968), in the lotic but also lentic phase of a billabong's seasonal cycle.

The depth distributional relationships of *V. angasi* follow the patterns reported elsewhere of an abundance maximised at an intermediate depth. However, the pattern elsewhere is invariably of a skewed relationship between depth and density, with a preferred depth occurring in relatively shallow waters in comparison to the overall depth distribution (Okland, 1963; Cvancara, 1972; Haukioja and Hakala, 1974; Lewandowski and Stanczykowska, 1975; Ghent *et al.*, 1978; Kenmuir, 1980; Strayer *et al.*, 1981). This pattern was repeated only in the floodplain billabongs of the Magela Creek. Presumably a number of factors, as reported, may inhibit colonisation of deeper waters in both lentic and lotic environments; in the generally shallow, warm water and low oxygen status billabongs of the Magela Creek, however, low dissolved oxygen, and in some instances siltier and less consolidated sediments at depth, were considered most likely to restrict mussels.

A number of lines of evidence were found to support the idea that low dissolved oxygen concentrations restrict mussels at depth: the mean oxygen concentrations of the billabongs by world standards are low (Table 2.7); in all billabongs some deepwater oxygen depletion, to a greater or lesser degree is felt at some stage of the year; in floodplain billabongs where the effects of deoxygenation are most obviously felt, the depth distributional relationships are skewed with mussels preferring shallow depths especially when compared to the preferred depth of mussels in channel billabongs; a correlation between the decline in mean dissolved oxygen levels and mussel densities in one floodplain billabong, Nankeen, is shown (Fig. 5.5); it is argued that the cause of preferred depths tending to be greater with decreasing organic content and increasing consolidation of the sediments in channel billabongs is more likely to be related to microhabitat oxygen demand at depth in the more organic sediments; and finally, in the deepwater billabongs, a correlation is observed between preferred depth and mean dissolved oxygen averaged over the seasons (Fig. 5.6). In studies elsewhere, seasonal oxygen depletions in the deepwaters of Plover Cove in tropical Hong Kong were implied as the cause of the shallow water distribution of Anodonta woodiana (Dudgeon and Morton, 1983); mussels are absent from waters deeper than 11 m in tropical Lake Kariba because oxygen levels at greater depths could reach levels low enough to cause mortality (Kenmuir, 1980); and deepwater anoxia was similarly believed to be the cause of the shallow water distribution of mussels in Fort Loudon Reservoir, Tennessee

River (USA) (Isom, 1971).

Siltier, less consolidated sediments in the deepwaters of Gulungul and Corndorl billabongs may limit mussel distribution at depth. The smothering effect of silt was suggested by both Fisher and Tevesz (1976) and Ghent _et al_. (1978) as a possible factor restricting mussels from the deepest waters of certain lakes. However, some deepwater oxygen depletions have also been observed in these billabongs (section 2.3.2.2) and this factor may at least partly account for the observed distributional patterns.

As could be expected, populations of _V. angasi_ were absent from, or scarce on, shifting sands, compacted, or extremely unconsolidated sediments. Even the gradient towards decreasing consolidation of organic and silty sediments showed a decline in mussel densities. This was observed in Mudginberri and Buffalo billabongs but whether the nature of the sediments _per se_ or the presumed microhabitat oxygen demand of more organic sediments (or both) are inhibitive, is not known. The significantly lower densities of mussels on the unconsolidated silt and clay substrate than on the silt and gravel substrate in Corndorl billabong suggest that the nature of such sediments in both Gulungul and Corndorl billabongs is a restrictive factor to maintenance of mussel populations.

In the channel billabongs, the evidence suggests that the restrictive factor(s) of organic and silty sediments acts upon the young mussel, most likely the newly metamorphosed juvenile. Bronmark and Malmqvist (1982) believed that fine sediment particles might interfere with feeding and respiration in Unio pictorum; and reduced growth rates of Elliptio complanata on muddy substrates have been observed (Kat, 1982). A significant increase in size, however, of V. angasi was observed with increasing organic content of the sediments. Although age also increased over the same gradient, growth rates were also higher (section 6.4.3.1). This suggests that the finer organic sediments at least do not interfere with normal growth and development of adult populations of mussels in the channel billabongs. Juveniles, however, may be particularly susceptible to silty environments, or to microhabitat oxygen deficiencies that organic sediments may render (Negus, 1966; Howard, 1922; Ellis, 1931).

Evidence as to the same age specific mortality induced by the sediments in the backflow billabongs is inconclusive; a significant decrease in mussel size was observed in Corndorl billabong but generally an increase in size was noted in Gulungul (section 6.5.2.1). No depth related growth rate data are available for either billabong, but older and larger mussels might be expected in the permanent deeper waters of Gulungul, as the billabong occasionally dries up. Apart from migrations away from the depths, higher mortality of mussels (and therefore reduced densities) in the depths of either billabong could arise from the smothering effects of the silty sediments upon adults (Fisher and Tevesz, 1976; Ghent et al., 1978). Substrate interference to maintenance, feeding and respiration of adults may also reduce the growth rates of mussels in at least Condorl, as found by Kat (1982). Thus, silty organic sediments described above have in common some degree of unconsolidation that is presumably inimical to juvenile settlement but in its extreme form is probably prohibitive to normal growth and maintenance of adult populations. However, there is no evidence that sediment particle size *per se* is in any way restrictive to distribution and abundance of *V. angasi*. This was revealed from the multiple regression analysis of mussel densities between billabongs in which no sediment particle size effect was found. At the extremes of particle sizes, within some of the finest sediments (silt and clay) in Nankeen and the coarsest (sand) in Mudginberri (Table 2.2), comparable and high densities were recorded (Table 5.10). Both sediment types are firm and yielding and within these constraints no substrate preference of *V. angasi* could be shown. These observations support the contention of others that within the provisions of firm and yielding sediments, bottom type, whether muddy or gravelly, is unimportant in regulating distribution of mussels (section A2.1.3, *Hydrology*).

Apart from creating shifting sands or soft, silty and organic sediments in the backflow regions that are either conducive or inimical to mussels, water flow exerts other strong influences on distributional patterns of mussels in the Magela Creek. The localised distribution of mussels in at least two floodplain billabongs were attributed to Wet season flow patterns which, through oxygen availability, enhance larval production and recruitment of mussels. Thus, wherever strongest flow occurred - at the southern end of Jabiluka billabong and along the west bank of Nankeen, highest densities of mussels were recorded. This pattern was also observed in Mudginberri and Buffalo billabongs where highest densities of mussels occurred in stable clay sediments exposed immediately to the side of the full force of current through the billabong. Elsewhere where mussels have been reported as most commonly occurring near or on the full force of current, the optimal conditions of the locations for extracting food, soluble mineral materials and oxygen from the water are implied or suggested (Evermann and Clark, 1917; Cvancara _et_ _al_., 1966; Simmons and Reed, 1973; Brönmark and Malmqvist, 1982). In the Magela Creek, however, current strength is believed to provide optimal aerobic conditions for mussels during the Wet, enhancing recruitment in these regions. The higher densities found here are assumed to be a direct reflection of higher Wet season oxygen concentrations and better subsequent survival of metamorphosed young.

In summary, patterns of distribution and abundance of mussels observed within billabongs of the Magela Creek, are doubtless modified by hydrological and limnological events occurring during the lotic and lentic phases of the creek's seasonal cycle. Localised water flow may render some substrates shifting and unstable, or otherwise provide optimal aerobic conditions for mussel recruitment. In the absence of significant flow, other loose and unstable, silty sediments may develop that support more or less fewer mussels. Dry season events that presumably modify distribution of mussels, include: declining water levels and subsequent increases in water temperatures and predation in shallow waters; and while the location of fish hosts (from visual and fish collecting observations), is often over shallow waters, the lower densities of mussels from deeper waters is additionally, doubtless a function of the lower concentrations of dissolved oxygen occurring here. Each of the Dry season events modifies the preferred depths of mussels occurring in the billabongs.

Distribution and abundance of mussels between billabongs

In the very soft and acidic waters of the Magela Creek, any marked differences between billabongs in measures of chemical parameters important to shell formation and maintenance might be considered critical to the distribution and abundance of mussels. The absence, however, of any significant correlation between such measures and densities of mussels within billabongs, presumably reflects the small variation in mean concentrations when values are compared among billabongs, and of course, reflects the marked tolerance of *Velesunio angasi* to acid softwaters. This latter point is made even more remarkable when it is learnt that a negative (but insignificant) correlation was found between calcium concentration and mussel abundance. Mussel densities in Mudginberri for example, are amongst the highest of any billabong but mean calcium concentrations in this billabong (0.47 mg/l) are amongst the lowest (Table 2.7). Elsewhere, although considered important to mussel development, the interpretation of water hardness values is complicated by lack of data to show levels at which hardness determines presence or absence of any species (Fuller, 1974), and occasionally its assumed importance in restricting mussels from some regions has later been challenged (Harman, 1969; Harman and Berg, 1970). At least several species of freshwater mussel of the northern hemisphere are reported to be equally tolerant of softwaters: for example, *Anodonta* spp. (Green, 1980); *Elliptio complanata* (Strayer, 1981); and *Margaritifera margaritifera* (Hendelberg, 1960; Stober, 1972).

While no significant correlation was found between pH and mussel abundance between billabongs, a noted feature of the shells of some mussels from Jabiluka billabong was their paper-thin consistency. The waters of Jabiluka are amongst the most acidic of any billabong (mean pH = 5.5). While there has been little evidence specifically relating the absence of mussels to the natural acidity of prevailing waters (Harman, 1969), valve erosion at low pH has been observed by a number of workers (Coker et al., 1921; Jewell, 1922; van der Schalie, 1938; Tudorancea, 1972). As to whether low pH causes premature mortality of mussels in Jabiluka through this corrosive effect, however, is not known.

The absence of correlations between any measure of salinity and mussel abundance comes as no surprise. The waters of the Magela Creek are generally quite dilute, as gauged by the low mean conductivity levels between billabongs (Table 2.7). Specific measures of salinities (potassium, chloride) are low and well within upper levels thought responsible for the absence of mussels from regions in North America (Cvancara, 1967, 1970; Imlay, 1973) and Australia (Dean, 1968).

No trophic factor was implicated in the observed distributional patterns between billabongs. In fact, most trophic measures (chlorophyll, total organic carbon, percentage organic matter of sediments, nitrate and ammonia) were negatively (but nonsignificantly) correlated with mussel density, an observation contrary to the findings of others where increasing eutrophy is thought responsible for increased species diversity and abundance (Clarke and Berg, 1959; Okland, 1963; Sepkoski and Rex, 1974; Kenmuir, 1980; Strayer et al., 1981; Brönmark and Malmqvist, 1982). Thus, food availability is not limiting to mussel abundance. Rather increasing eutrophy realises fewer mussels, possibly partly explained by its effect on oxygen concentrations. Highly productive billabongs may experience overnight oxygen depletions, an observation for example, accounting in part for the low seasonal mean concentration in Leichhardt billabong (Table 2.7, section 2.3.2.2). In relation to its effect on DO concentration, it might be argued thus, that some billabongs are excessively enriched with nutrients (e.g. Leichhardt). This enrichment, however, is not reflected through any direct toxic effect of nitrogenous wastes. Ammonia levels for example, are well within the limits reported to be toxic or responsible for absence of mussels in other drainages in North America (Fuller, 1974; Horne and McIntosh, 1979).

Likewise, no significant adverse effects were observed from high turbidities and suspended solids. In fact, two billabongs, Georgetown and Nankeen become highly turbid during the Dry season and yet observe amongst the highest densities of mussels in the Magela Creek. While high turbidities adversely effect larval production (section 7.10.1), recruitment in all billabongs occurs at times when waters are reasonably clean (Wet- early Dry season). In other drainages, mussels are similarly unaffected by turbidity; high densities of mussels have been recorded in consistently and highly turbid waters both in North America (Cvancara, 1967, 1970) and Australia (Walker, 1981b). There was similarly no evidence of adverse siltation effects upon mussels in the Magela Creek. Siltation has been observed in Island billabong (section 2.3.1.3), and because of its close proximity to mining activities, might be expected in Coonjimba billabong. However, in neither billabong were dead shells observed in the substrates that might indicate some past catastrophic event. The deepwaters of Island billabong normally experience Dry season oxygen depletions, a factor already strongly implicated as the main inhibitor of mussel distribution at depth in the billabongs. Apart from smothering effects, however, siltation may also indirectly affect benthic forms by its shallowing effect, resulting in increases in bottom water temperatures or early evaporation of waters (Chutter, 1969); or silt may retain organic matter and create oxygen demands immediately above the sediments (Ellis, 1936). Both factors may effectively reduce recruitment and survival of juvenile mussels at least. The waters of Coonjimba billabong are both shallow, and low in dissolved oxygen concentrations.

The concentrations of most heavy metals in the Magela Creek are naturally low (Fox _et_ _al_., 1977) and even the increments in some metal concentrations over the Dry (copper, lead and zinc) in some billabongs are apparently not responsible for major fish kills. Freshwater mussels might be assumed to be more tolerant than fish to most pollutants and in fact _V. angasi_ has been shown to be markedly more tolerant than fish of the Region to some selected toxic metals (Skidmore and Firth, 1983). However, aluminium toxicity mobilised through highly acidic and sulphate-rich waters is believed to cause fish kills observed in some floodplain billabongs during early Wet season flushes (section 2.3.2.3). Some mussel deaths have been observed on a few occasions in these billabongs in association with fish kills and Morley _et_ _al_. (1983) suggested that aluminium may be the similar toxicant. Considering the broad tolerances of mussels to associated acidity and anoxia that might occur with the kills (unpublished observations) the same aluminium toxicity at this stage appears a plausible explanation for the deaths. Small numbers (<100) of dead mussels were observed on any one occasion and the events therefore, are assumed to have had an insignificant effect on mussel abundance in the affected billabongs, especially when related to total density figures.

In relation to other known adverse effects of low DO upon V. angasi - inhibited larval production and therefore recruitment (section 7.10.1), and relative juvenile sensitivity (Appendix 6) - it comes as no surprise therefore that mean DO concentration was significantly correlated with mussel abundance in the Magela Creek, the only physicochemical parameter in fact, to do so. The importance of low levels of DO in determining distributional patterns of mussels has received little attention in ecological studies, other than noting the broader tolerances to low DO of quiet water species (Horne and McIntosh, 1979; Walker, 1981b; Fuller, 1974; Kenmuir, 1980); the high sensitivity of young mussels to low DO (Ellis, 1931); the absence of mussels at depth in lentic environments (Coker et al, 1921; Bates, 1962; Isom, 1971; Fuller, 1974; Kenmuir, 1980; Dudgeon and Morton, 1983); or absence elsewhere wherever DO dropped occasionally to as low as 3 mg/l (Grantham, 1969; Isom, 1971) or 2 mg/l (Kenmuir, 1980).

Adult populations of V. angasi are exceedingly tolerant of low DO, surviving under experimental conditions for months in anoxic waters (Appendix 6). This tolerance appears even more remarkable in view of the large and apparently thriving populations inhabiting billabongs of generally low oxygen status, where for long periods DO concentrations of waters may be consistently below 3 mg/l (section 2.3.2.2). These observations undoubtedly place V. angasi amongst the most tolerant species to low DO concentrations yet studied. Other tolerant species reported include Amblema plicata and some Anodonta spp., quiet water mussel species of North America (Fuller, 1974).

While juvenile V. angasi are particularly sensitive to low DO concentrations, the lower observed densities of mussels on some silty and organic sediments in channel billabongs at least, were attributed to a sensitivity by juveniles to the silty and unconsolidated nature of these sediments and/or to microhabitat oxygen demands that such sediments may create. This degree of sensitivity in agreement with the observations of others (section A2.1.3) indicates that the habitat requirements of juveniles are quite specialised. Isely (1911), Coker et al., (1921) and Kenmuir (1980) believed in fact, that any consideration of ecological factors inimical to mussel life should be directed towards the juvenile habitat, as adults could live in environments where young would perish. Thus, further analysis of distributional data was based on the observations that successful recruitment and survival of young are dependent upon adequate oxygen concentrations.

Because mussels occur in billabongs where no appreciable flow is present, stream flow per se is not regarded as essential to recruitment. Flooded peripheral zones in shallow backflow billabongs where recruitment occurs are presumably well oxygenated. In deeper billabongs, however, without the same shelving and shallow banks, recruitment is more dependent upon the supply of oxygen maintained through water flow during the Wet season. At the depths that mussels are recruited, any significant respite in flow may quickly lead to some degree of oxygen depletion which in turn may adversely affect recruitment.

In billabongs lying on the main channel of flow of the Magela Creek, successful recruitment was argued to be related to adequate oxygen as manifested by stream discharges, while survival related to concentrations prevailing over the entire year. Distribution and abundance of mussels in these particular billabong types therefore, are effectively a function of Wet season flow patterns and mean seasonal oxygen concentrations. The resulting derived model was of exceptionally good predictive value. How fortuitous was the resulting goodness of fit of density data, however, remains for further study, yet in combination with known low dissolved oxygen effects, and within-billabong distributional patterns, a good case is presented to recommend _V. angasi_ as a valuable indicator of stream flow patterns in the Magela Creek and perhaps in other monsoonal discharge systems of the Northern Territory or indeed throughout tropical northern Australia. Within the Magela Creek for example, its distribution and abundance in particular billabongs partly indicate a billabong's competence and channelling efficiency during the Wet. Within-billabong distributional patterns indicate local flow effects and the patterns observed within Nankeen billabong for example, strongly implicate at least partial competence of the 'relict' channel lying between Jabiluka and Nankeen billabongs. Such knowledge of hydrology and flow patterns of the Magela Creek is essential to future management, by way of a proper understanding of the likely pathways of potential pollutants. Indeed the distribution and abundance of mussels over all of the Magela Creek billabongs are correlated with mean dissolved oxygen concentrations. Knowledge therefore of the abundance of mussels in a billabong indicates the general aerobic status of its waters. In pollutional terms, such knowledge is valuable in that poor oxygen relations, but especially pesistent anoxia in a billabong, may have implications as to the likelihood of mobilisation of metals in a soluble and available toxic form under low redox conditions (Walker _et al_., 1983a).

The sensitivity of juvenile _V. angasi_ to low dissolved oxygen concentrations will undoubtedly make the species a particularly valuable indicator of the types of pollution in which oxygen concentrations are severely affected. Excessive organic enrichment is one such type, and in this respect the species might have value as an indicator of nonpolluted waters much as Horne and McIntosh (1979) advocated, as the presence of _V. angasi_ indicates at least adequate oxygen concentration at a generally regarded critical time of the year for biota - the Wet-Dry interchange (Walker _et al_., 1983a). Little is known of the sensitivity of _V. angasi_ to other pollutants (Skidmore and Firth, 1983) but if juveniles are as sensitive to their effects as they are to low dissolved oxygen, populations of _V. angasi_ may be sensitive pollutional indicators and may be used to mark the downstream area of full biological recovery in a polluted stream (Simmons and Reed, 1973).

In relation to the environmental determinants of distribution - dissolved oxygen and stream morphology, it is to the best of knowledge, the first time attempts at quantifying distributional patterns of freshwater mussels between sites of a drainage system have been made, although previous surveys have eluded to obviously or at least potentially important determining factors (Cvancara, 1967, 1970; Walker, 1981b). Walker (1981b) also considered water flow, as a reflection of the supply of oxygen, the single most important factor governing the relative distributions of Velesunio ambiguus and Alathyria jacksoni in the Murray River in Australia. Both species have distinct preferences for slow-flowing and still waters, and river environments respectively and with the analysis of other such complementary animal-groups, Walker (1981b) suggested study may provide useful insights into the ecology of the Murray-Darling system with its characteristic river and floodplain environments. V. angasi like V. ambiguus is a species at least as tolerant of still waters, a factor borne out in consideration of its wider geographical range, in monsoonal seasonally flowing systems of tropical drainages. Analysis of its distributional patterns elsewhere could provide valuable insights into the aerobic status of waterbodies, which in deepwater billabongs may reflect regional and local Wet season flow patterns.

6 POPULATION DYNAMICS

6.1 Introduction

In view of the large stocks of mussels in billabongs of the Magela Creek (Chapter 5) and the very large fraction of the total benthic biomass that these comprise (unpublished determinations), study of the population dynamics of Velesunio angasi was deemed important from the point of view of providing basic information needed to assess the influence of its populations in the energy budgets (via production estimates) of billabongs on the Magela Creek. Growth data, while essential for determining other population parameters (e.g. age structure, mortality) were also needed for proper understanding and determination of structure of the breeding populations. Finally, various population parameters (growth rates, recruitment relationships, mortality rates and age structure) could conceivably provide valuable baseline data upon which to monitor the effects of environmental changes such as potential pollutants. These are further indicator roles in which V. angasi might be employed.

Aspects of the population dynamics of V. angasi undertaken, included age and growth, size and age structure, recruitment, mortality, and movements. Literature reviews appropriate to these studies appear in Appendix 3. While considerable attention has been devoted to the dynamics of freshwater mussel populations in North America and Europe (see Appendix 3), very few comprehensive studies have been carried out on populations of either Australian or tropical freshwater mussel species. Walker (1981b) studied aspects of the ecology of freshwater mussels in the Murray River in temperate Australia, and Kenmuir (1980) and Dudgeon and Morton (1983) studied tropical species in Zimbabwe and Hong Kong respectively. On both counts therefore, the present study from tropical northern Australia greatly adds to an area lacking in knowledge.

6.2 Materials and methods

Quantitative field sampling and later subsampling of mussels in the laboratory for use in determining population parameters have been described earlier (sections 3.3 and 5.2). The method of age determination is described below (section 6.3.2).

The growth of individually marked mussels was monitored at regular intervals in Georgetown, Corndorl, Mudginberri, Island, Leichhardt and Nankeen billabongs. Marks and numbers for later recognition were engraved on the dorsal portion of the left shell, as described in section 3.3. Plastic containers filled with the surrounding billabong sediments were used to hold the mussels. Between 5 and 6 containers were used in each billabong and the density of mussels placed in each container was approximately the same as that prevailing on the surrounding substrates. The containers were filled flush to the rim with sediments and embedded well into the bottom substrates of the billabong. Thus, water circulation around the mussels placed on the surface of the container's sediments was unimpeded and the level at which siphoning occurred was almost the same as those mussels siphoning on the nearby sediments. Fine fishing mesh (2 cm stretched knot-to-knot) covered the mussels to prevent them moving out of the containers. Containers were placed in waters at depths closely approximating those "preferred" by mussels for the particular billabong (section 5.4.1.1) and were always close to a station that was, or had been used in routine collecting (section 3.1).

In this way, the growth of at least 60 marked mussels in each billabong was monitored at approximately 3 to 4 month intervals over the course of at least an 18 month period. The regular measurements of growth in length, were performed in the field and individual mussels were never out of the containers nor water for more than 15 minutes. Dead mussels were replaced during these occasions.

No inhibition of growth by the handling involved in marking was ever apparent. This was indicated by the fact that newly marked mussels added to the containers from time to time to replace dead mussels, grew at comparable rates at the subsequent inspection and measurement, to mussels of similar size which had been resident in the containers for some time.

In addition to growth rate measurements of mussels made at regular intervals, other measured and marked mussels were scattered free into the surrounding sediments about the containers, remaining undisturbed for later recovery toward the end of the study (April-May, 1982).

A major mark-recapture programme was undertaken in Buffalo billabong to observe the migratory patterns of mussels in deep billabongs over the course of a year. Approximately 8,000 mussels were collected, marked and individually allocated to, and released over, predetermined gridded portions of the billabong during May 1980. The billabong was gridded by way of 22.5 x 22.5 m quadrats (Fig. 6.39) marked by buoys. Bankside markers ensured that the pattern was exactly repeatable twelve months later when the buoys were reset, and mussels recollected.

The sex of individual mussels was determined according to methods described in section 7.3.

6.3 Age determination

Background

Study of some of the population parameters of Velesunio angasi such as growth, age structure and mortality, largely depended upon finding a suitable and accurate method of age determination. Three standard methods have been used to determine the growth rate and age of bivalve molluscs (Haskin, 1954): (1) study of length frequency distributions; (2) release and recovery experiments; and (3) use and interpretation of annual growth rings.

For freshwater mussels (as in marine bivalves), analysis of annual cessation rings on the shells is regarded as rapid and efficient, and is by far the most common aging method in population studies. Haukioja and Hakala (1978a) have extensively reviewed the techniques and methodology as they apply to freshwater mussels. In most bivalve populations, the differences in successive modes in size frequency distributions are of limited use in aging, as generally there are only one or two peaks - adults, or young of the year and adults. Release and recovery studies are also infrequently employed, as an extended period of time is required to produce reliable results and growth between individuals of the same habitat may be highly variable. Nevertheless, in populations of freshwater mussels from the tropics where growth interruption lines have been difficult to interpret, length frequency analysis has been used to age seasonal breeding species (Dudgeon and Morton, 1983), and release and recovery experiments used to determine age and growth rates of continuous breeders (Kenmuir, 1980).

The use of shell rings produced by a cessation of growth, for age determination, is dependent upon confirming their annual or periodic nature. Chamberlain (1931) and Stansbery (1961) and recently McCuaig and Green (1983), reviewed the developmental studies that first described the microstructure of the conspicuous interruption bands which led to ascertaining their annual nature in the shells of freshwater mussels from temperate climates. In short, Coker et al. (1921) showed that doubling-up of outer shell layers was formed by repeated startings and stoppings of growth in late autumn and early spring, giving the appearance of a dark, broad and compound band on the shell. Other disturbance rings were the result of only single duplications of shell while winter rings showed several repetitions. In both earlier and subsequent studies, moreover, a seasonal growth pattern of mussels was shown by Lefevre and Curtis (1910), Isely (1914) and Sebestyen (1942), with growth ceasing over the winter period; and a one-to-one correspondence between successive winters and added shell annuli during mark-recovery experiments shown by Lefevre and Curtis (1910), Coker et al. (1921), Isely (1931), and Sebestyen (1942).

In temperate regions, false annuli are believed to result from: water shrinkage and drought; rapid temperature fluctuations in summer; summer reproduction; seiches; transport or stranding by floods; pollution; or even tagging and handling (Isely, 1914; Coker et al., 1921; Crowley, 1957; Stansbery, 1961; Negus, 1966; Walker, 1981b; McCuaig and Green, 1983). While true winter annuli are noted to be more heavily marked (Coker et al., 1921, Negus, 1966), other criteria have been drawn up for distinguishing these from other disturbance rings (Chamberlain, 1931; Stansbery, 1961; Tevesz and Carter, 1980b). Nevertheless, some workers have been reticent to use shell annuli as the basis of age determination, while others have expressed caution and suggested that considerable experience might be needed to distinguish true rings (Crowley, 1957; Okland, 1963). The shells of some species are inherently difficult to age as growth lines are ill-defined or closely packed: e.g. Margaritifera margaritifera (Roscoe and Redelings, 1964), Elliptio complanata (Matteson, 1948; Ghent et al., 1978; Strayer et al., 1981) and certain small creek species (van der Schalie and van der Schalie, 1963). Otherwise, the nature of the environment may render some shells more difficult to age than elsewhere. Shells of mussels from lentic environments for example, have notably regular spaced and distinct annuli, and are free of false rings as found in river-dwelling mussels; this has been attributed to the less marked fluctuations in seasonal temperature changes in large bodies of water such as lakes (Brown et al., 1938; Stansbery, 1961; Tevesz and Carter, 1980a). Finally, Comfort (1957) noted that growth rings provided reliable age estimates, where estimates are confined to species and to localities, and where a fixed and consistent pattern of rings can be confirmed.

6.3.1 Seasonal growth pattern

Having established that distinct rings are present on the shells of mussels, a prior assessment as to their annularity or shorter-term pattern of consistency might be gained from monitoring the sequence of shell growth throughout the course of a year or more (Jones, 1983). While growth of mussels in temperate climates slows down or ceases during winter, droughts and the silt carried by monsoonal floods were suggested by Tevesz and Carter (1980a) as possible factors that might cause growth interruption in mussels from warmer or tropical regions. Late Dry season food depletions were believed by Kenmuir (1980) to slow the growth rates of mussels in Lake Kariba at this time, while growth of _Anodonta_ _woodiana_, in Plover Cove Reservoir was also retarded in the late summer Dry (Dudgeon and Morton, 1983). Dudgeon and Morton did not suggest causal factors in the growth decline of mussels, but the period is associated with thermal and oxygen stratification of the reservoir while temperatures are at their summer high (c. 23° C).

Growth rates of _Velesunio_ _angasi_ were monitored regularly in a number of billabongs on the Magela Creek (section 6.2). Figure 6.1 shows the pattern of seasonal growth of mussels in representative billabongs, expressed as percentage of the growth completed over an 18 month period. (Figures 6.5 and 6.6 show the marginal increments of shell growth from the last annulus to the shell edge, monitored monthly in representative billabongs. These may be used to complement the patterns shown in Figure 6.1).

The pattern of growth of mussels inhabiting the braided creek channel above Mudginberri billabong (section 3.1), was not studied. A clear seasonal growth cycle, however, is preordained for these populations. As they are obliged to aestivate over the Dry (Jun.-Nov.), growth can only occur during the Wet and early Dry.

The seasonal growth patterns of mussels in Georgetown and Nankeen billabongs are representative of those in the majority of billabongs on the Magela Creek and are typical of all other backflow billabongs and other floodplain billabongs that become turbid late in the Dry (Coonjimba, Gulungul, Corndorl, Hidden, Ja Ja and Jabiluka). Growth begins with the initial replacement of turbid waters by early Wet season flushing (Dec.-Jan.), is most rapid in the early Dry and continues but steadily declines as waters become turbid again between the mid to late Dry (Fig. 6.1). Apparently growth is related to availability of food which for V. angasi comprises unicellular algae and detritus (section 8.3). A partial measure of available food is chlorophyll content of the waters as shown in Figures 2.28 and 2.29. Algal populations are suppressed by increasingly turbid waters (section 2.3.2.5), a factor presumably responsible for growth cessation of mussels during the late Dry.

Growth rates of mussels in Mudginberri and Island billabongs were highest from the late Wet until the late Dry. During the Wet, growth rates of mussels were low. These billabongs are well, to reasonably well, flushed in the Wet (section 2.3.1.3) and at these times algal populations are stifled. Figures 6.5 and 6.6 further exemplify the pattern in Mudginberri billabong of minimal shell growth during the Wet season. Growth in these billabongs, however, was also suppressed late in the Dry (Fig. 6.1) despite this being a time of high algal productivity in both waterbodies (Figs. 2.28 and 2.29). Algal blooms themselves may be the cause of deterioration in water quality over the late Dry. In addition to causing stressful overnight oxygen depletions, sudden crashes in algal populations that have been observed in at least Island billabong at these times, reduce the available food temporarily, and cause even more general and severe bottom water anoxia (Walker et al., 1983a). A close correspondence is observed between shell growth and relative condition (i.e. body weights) of mussels in the late Dry. In the channel billabongs condition declines in the late Dry (section 8.7.1) when larval production is at its peak (section 7.10.1). Presumably the energy channelled into reproductive effort at this time is at the expense of both shell and somatic growth. Further, other stresses are observed during the late Dry in channel billabongs. Their generally non-turbid nature may impart a stressfully warm environment upon bottom dwelling mussels with the onset of summer (Table 2.6). (Low water temperatures of course, are not factors of importance to growth of mussels in the Region. Lowest water temperatures recorded in the Magela Creek (Table 2.6) are still some 10°C warmer than levels generally reported to induce dormant behaviour in temperate species.)

Mussels in Leichhardt billabong showed the slowest growth rates from the late Wet to mid Dry. This period coincides with a time of often severe oxygen depletions to which this billabong is particularly susceptible (section 2.3.2.2). These periods of hypoxia may suppress metabolic processes including feeding in mussels. This phenomenon may also explain a similar but less marked pattern of growth retardation of mussels in Island during the early Dry, a billabong also notably deficient in oxygen at this time (section 2.3.2.2). The Dry season of 1981 was a particularly severe one in terms of oxygen depletions in Leichhardt (Fig. 2.21), and presumably the growth rates of mussels in this billabong at this time are not always suppressed to the extent shown in Figure 6.1 each and every year. As in the channel billabongs, growth of adult mussels at least, in Leichhardt billabong was also retarded during the late Dry (Fig. 6.1), despite high observed chlorophyll values at these times (Fig. 2.29). The dynamics of algal populations, high reproductive efforts and/or high temperature in the relatively clean waters may explain the reduced growth rates. A further result of stress is the reported kills of a proportion of mussels in Leichhardt billabong with the initial Wet season flushes (section 5.5).

6.3.2 Method of age determination

In the present study, growth interruption rings on the shells were used to age mussels, while length frequency distributions and release and recovery experiments were used in part as checks against, and to validate the aging method. Shells of <u>Velesunio angasi</u> show quite distinct growth interruption rings that in most cases are spaced regularly and consistently in mussels from the same location. An annual pattern to the rings was most likely given the seasonal nature of the environment and especially after having ascertained clear seasonal growth patterns for mussels in most billabongs. Aging by shell annuli was particularly appealing in view of the rapidity and accuracy with which determinations could be made, especially in consideration of the large numbers of mussels needed to be aged from the quantitative samples.

Strong transmitted light as used by several workers (Chamberlain, 1931; Stansbery, 1961; Coon _et al_., 1977; Walker, 1981b) greatly assisted the aging method. Placed immediately behind the shell (generally the left valve), the dark growth bands stood out in bold relief against the lighter background of the surrounding, thinner shell material.

The prominent bands on the shells of _V. angasi_ were always obvious and distinct along the postero-lateral axis, and in populations from some shallow backflow billabongs (Gulungul and Corndorl), did not always extend circumferentially to the anterior portion of the valve. Apart from some older shells from Mudginberri and Buffalo billabongs, the appearance of the dark growth bands was highlighted by new and lighter Wet season growth. From confirmatory shell measurements (section 6.3.3.2), these bands were shown to be annular and were laid down during the late Dry season in accordance with the observed seasonal growth patterns.

The usual difficulties as found by most workers (Okland, 1963; Magnin and Stanczykowska, 1971; Coon _et al_., 1977; Haukioja and Hakala, 1978a) were experienced in discerning the closely packed annuli of older individuals. These problems were particularly pertinent to the old (> 20 years) and stunted mussels that are commonly found in still, backwater regions of Mudginberri and Buffalo billabongs. A needle-tipped pointer was an aid in these cases, in the often painstaking task of moving outwards along the postero-lateral axis, and separating and counting the crowded annuli. For difficult (old) shells, three age determinations were made. These determinations never varied by more than three and rarely by two years amongst all of the shells aged. A further difficulty in age determinations of older shells was found in individuals from stony sediments (e.g. station 5 in Mudginberri, section 3.1), where the region about the umbo was badly eroded. However, in accordance with the method of Stansbery (1961) who reported similar problems, by knowing the general periodicity of the annuli in the particular environment, and by noting the spacing represented by the remaining annuli on the mussels in question, the number of missing annuli could be estimated. Such eroded shells were uncommon, but in long-lived species such as <u>Margaritifera margaritifera</u> erosion is such a problem in older specimens, that valves are aged by counts of the annual layers in the ligament (Hendelberg, 1960; Björk, 1962; Stober, 1972; Smith, 1976; Bauer, 1983).

A feature of the shell appearance of juvenile (young-of-year) mussels from non-turbid billabongs (channel billabongs and Leichhardt) was the general absence of a distinct, dark annulus formed at the end of their first Dry season. While growth is continuous throughout the first year in mussels from these environments, nevertheless, a colour change in the shell was generally discernible between the seasons. Invariably, thicker and darker Dry season shell growth followed by abrupt, thinner (presumably faster) and lighter shell growth accompanied the appearance of the shell between Dry and Wet seasons.

Less prominent, false bands were characteristic of the shells of mussels from floodplain billabongs, particularly Nankeen and Jabiluka. The nature and distinguishing feature of false annuli in the shells of various freshwater mussel species have been reviewed by Chamberlain (1931), Stansbery (1961) and Tevesz and Carter (1980b). Major properties of vagueness, incompleteness, and irregularity are ascribed to false annuli. However, true annuli in shells of individuals from particular environments were also notably incomplete (see above) while the false annuli observed on individuals from floodplain billabongs were often of a regular nature lying between the more prominent true annuli. Nevertheless, while false annuli were generally incomplete, their distinguishable characteristic was their vagueness and thinness. The often regular appearance of the false annuli and their occurrence generally in shells from floodplain environments were strongly indicative that the regular and annual oxygen depletions that occur in these billabongs during the early Dry (section 2.3.2.2) were the cause of the minor interruption to shell growth. A thin and false ring was also a feature of the shells of juvenile (young-of-year) mussels from Mudginberri and Buffalo billabongs. The ring was also traceable to the early Dry season (from back-calculated growth measurements), again suggestive of the sensitivity of juveniles to the even less marked depletions in oxygen (Fig. 2.20) that accompany the cessation of flow through these billabongs in the early Dry season.

In practice, the annual rings of mussel shells from most billabong environments were not difficult to interpret. Difficulties arose in two environments only, Mudginberri and Buffalo, in which the exact ages of some old mussels were not determinable. However, in view of the small numbers of difficult shells and the careful approach taken to aging these, it is unlikely that these errors alter in any way the appearance of the age structure of the populations of the two billabongs. As expected from the marked seasonality of their environment, the shells of mussels inhabiting the creek channel above Mudginberri were by far the easiest to age. Mussel shells from turbid billabongs also possessed pronounced and easily interpretable annual growth rings. Individuals from Island and Leichhardt billabongs are fast-growing (section 6.4.2) and relatively short-lived (section 6.6.3), factors that ease the interpretation of growth bands considerably as noted by Haukioja and Hakala (1978a) in populations of *Anodonta piscinalis*. It was notable finally, that the growth bands of shells from Leichhardt were similarly laid down during the late Dry season, so that the stresses that arise then are apparently of more marked effect than early-mid Dry season oxygen depletions that were presumed to have slowed growth of mussels here during the 1981 Dry season.

All shells of mussels subsampled and used for subsequent reproductive and condition studies (section 3.3) were aged.

6.3.3 Validation of the aging technique

Graham (1929) listed five separate procedures for testing the validity of age determinations. While these methods have been applied extensively to studies of fish populations, they are nevertheless applicable to any fisheries problem. Growth studies with freshwater mussels are particularly well suited to such analysis. The methods (modified for molluscs) are: the occurrence of discrete length-frequency distributions which correspond with the age determinations; the study of annual, cyclical changes in shell morphology; observations of the progress of dominant year-classes; the recovery of marked individuals after a known interval; and the observation of individuals confined in tanks or ponds. Jones (1983) added that for marine bivalves, while counts of internal bands from sectioned shells were far more accurate than conventional studies on external shell growth patterns, annual shell periodicities either way could be substantiated by monitoring the seasonal growth patterns throughout the course of a year or more, or by using stable or radioactive isotopes to determine growth rates.

Rather than the above methods, Chamberlain (1931), Crowley (1957) and Walker (1981b) argued that the consistency and regularity of the disturbance lines and the uniformity of the growth curves for freshwater mussel populations justified the assumption of their annularity. Walker (1981b) conceded, however, that further substantiation was required. Other authors have effectively argued that in temperate zones, (1) the regularity and clarity of the rings on shells from lake environments; (2) their conspicuous and inherent nature in shells of particular species (e.g. Anodonta), or (3) previous substantiation of their annularity in either similar environments or in the same species elsewhere, were valid grounds for assuming annularity in the growth bands of the shells in question.

In populations of V. angasi in the Magela Creek, regularly and consistently spaced rings on the shells of individuals from the same environment, and a uniformity of the derived growth curves between populations (section 6.4.2) were observed. Moreover, a seasonal growth pattern of mussels was found that corresponded to shell patterns of alternating seasonal growth and growth cessation. Nevertheless for unequivocal justification of the aging method, it was possible to satisfy three of Graham's (1928) five above criteria for validation completely, and one partially.

6.3.3.1 Length-frequency distributions

Aided by knowledge of the time of impoundment and subsequent colonisation by mussels, Dudgeon and Morton (1983) found year classes of Anodonta woodiana in Plover Cove represented by fairly discrete peaks in the monthly length frequency distributions. Subsequent analysis of the peaks enabled them to age mussels and estimate growth properties of the mussel population. Walker (1981b) also found length frequency distributions of Alathyria jacksoni in the Murray River, useful aids to interpreting the age structure of its populations at various sites along the river. In the Crapina-Jijila marshes, however, Tudorancea (1969) considered length frequency analysis an inefficient aid in growth studies of mussels as distinct modes were only present for the first two years of life, after which considerable overlap of age classes occurred.

Although seasonal recruitment of V. angasi occurs in billabongs of the Magela Creek, similar observations to those of Tudorancea (1969) were made showing that length frequency distributions were of limited value as progression in the modes of the first two year classes only, could be followed. For the two age classes nevertheless, age as determined by modal peaks corresponded in every case to age as determined by shell annuli, thus partially substantiating the aging method. Figures 6.2-6.4 show the monthly length frequency distribution of mussels collected from Georgetown, Mudginberri and Nankeen billabongs respectively, populations for which quantitative and non-selective sampling was accomplished (section 3.2.1). Two age classes can generally be distinguished as discrete modes, particularly for populations from Georgetown billabong where growth during the first year is not particularly rapid by comparison to populations from Mudginberri and Nankeen. For young-of-year mussels, growth rates from all populations are clearly discernible, as the modes progress through the season to the position previously occupied by the next older age group.

6.3.3.2 Shell morphology

By measuring the distance from the shell margin to the last-formed annulus at regular intervals throughout the season it should be possible to demonstrate the time of annulus formation (and importantly that only one such ring is formed each year), when an abrupt change occurs at a critical time from relatively wide marginal bands to extremely narrow widths. This method has been used to substantiate age determinations of some marine bivalves (Okera, 1976; Taylor and Venn, 1978) while Negus (1966) used a variation of the technique for validating her age determinations of freshwater mussels in the Thames. By recording the months when winter rings first became visible, Negus was able to demonstrate their time of formation and annular nature.

Monthly measurements of marginal shell increments were made on shells from Georgetown, Mudginberri and Nankeen billabongs for the two year period of the study. Mean values are plotted according to appropriate age divisions, against time of year in Figures 6.5 and 6.6. Marginal increments were standardised for age by multiplying mean values by the mean age of mussels used in the particular age division. In old mussels (> 10 years), a faint transparent edge was found along the shell margins of most individuals during the early Wet, and was interpreted as new shell growth beyond a newly formed annulus. Figures 6.5 and 6.6 clearly show that the marginal bands in shells from all billabongs and age classes reach a maximum in the late Dry (December) but decrease suddenly during January following formation of the new ring. The pattern of ring formation was identical in both years of sampling and between all billabongs, and occurred during the Dry-Wet interchange, thus demonstrating its similar timing and establishing its annual nature in backflow, channel and floodplain environments.

6.3.3.3 Dominant year classes

Haukioja and Hakala (1978a) showed that growth rings in one Finnish population of _Anodonta piscinalis_ were formed annually, as a dominant year class in the population moved its position in the age distribution one step to the right each year.

Dominant year classes were present in many of the mussel populations from billabongs of the Magela Creek. They were especially conspicuous in all of the floodplain billabongs. Figures 6.7 and 6.8 show the age distributions of mussels between years sampled, from populations in a number of billabongs. Clearly, each strong year class appears as a successively older age class in progressive sampling years lending very strong evidence to the assumption that the shell rings are in fact annular.

6.3.3.4 Growth of marked individuals

A number of workers have successfully verified the annular nature of shell annuli of temperate freshwater mussels, from mark and recovery experiments. Mussels are released in the field and upon recovery, the number of rings that have appeared over the elapsed period has been shown to correspond to the number of winters that have passed (Lefevre and Curtis, 1910; Coker _et al_., 1921; Altnöder, 1926; Isely, 1931; Sebestyen, 1942; Negus, 1966; Ghent _et al_., 1978; Haukioja and Hakala, 1978a).

Marked mussels in Georgetown, Mudginberri and Nankeen billabongs that were released around the confined individuals in plastic containers (section 6.2) were recovered after a period encompassing two Wet seasons. Details of the times of release and recovery, lengths at release, recovery and at successive annuli upon recovery, and estimated ages at recovery are shown in Table 6.1. On all shells, a faint but discernible false check due to handling was observed at the length corresponding to the time of release. As expected, for older mussels, no more shell growth was observed between the short period from the time of release until the end of the first Dry season. Nevertheless, on all shells, the added area of growth was divided by two distinct rings representing the periods of growth cessation during the late Dry seasons of 1980 and 1981. While no mussels older than 20 years were recovered, it is conceivable that some difficulties may have been faced in discerning added annuli on their shells, as growth of these individuals, particularly in Mudginberri billabong, is exceedingly slow (section 6.4.2).

Kenmuir (1980) aged mussels in Lake Kariba according to mark recovery data. With age determined by shell annuli for one species, the resulting closeness of the two sets of calculated results suggested to him that the growth cessation lines were in fact true annuli. A comparison of the growth data derived from both mark recovery and shell annuli measurements were also used as an independent check on the accuracy of the latter aging method for <u>Velesunio angasi</u>.

Data from marked mussels placed in containers were used in the analyses. Growth data for only a few individuals spanned the entire study period. Much data, however, was available that covered both shorter time spans (< 18 months) and different seasons. Gulland (1969) described a method of fitting a growth curve to mark recovery data obtained at unequal time intervals, whereby the instantaneous rate of growth, approximated by ($\frac{l_2 - l_1}{t_2 - t_1}$) is plotted against the mean length ($\frac{l_1 + l_2}{2}$), where l_1 and l_2 are the lengths at times t_1 and t_2 respectively. Analysis of the resulting fitted regression line provides estimates of the constants L_∞ and K of the von Bertalanffy growth equation, used to describe the length for age relationship in populations of V. angasi, and considered in more detail in section 6.4. Thus, the intercept on the X-axis provides an estimate of L_∞, and the slope an estimate of -K. Instantaneous growth rate is plotted against mean length in Figure 6.9 for mussels in Georgetown, Mudginberri and Nankeen billabongs. If growth across the entire size range of mussels were to conform to the von Bertalanffy growth model, the resulting plots would be linear. Clearly this is not the case, and the youngest age class does not conform. This is examined in greater detail in section 6.4. The relevant point here is that growth data for young-of-year mussels were rejected whenever the von Bertalanffy model was fitted. Using regression lines fitted to growth data of adults, resulting estimates of L_∞ and K for a number of billabong populations were derived and compared with estimates calculated from shell annuli data from section 6.4.2 (Table 6.2).

The results indicate the limitations when deriving growth rate data from mark recovery experiments that run over a relatively short period of time. Most of the growth data was obtained during 1981, a year in which chlorophyll values (and hence, presumably food availability) were low in comparison with data from previous years (Walker and

Tyler, 1983b), especially in the floodplain billabongs (Fig. 2.29). Thus it is observed from Table 6.2, that L_∞ values are lower and K values higher (the two parameters being interrelated, Ricker, 1975) in mark recovery data derived from most of the floodplain billabongs. Nevertheless, estimates of the constants compare reasonably well between the two methods used to estimate growth rate data. Importantly, differences in estimates of the constants (or growth rates) between different billabong populations are constant between both methods. The generally close similarity between the growth parameters derived from both methods is further evidence that shell annuli in Velesunio angasi from billabongs of the Magela Creek, can be used for accurate age determinations.

6.4 Growth

6.4.1 Growth description

Asymptotic growth equations have been widely used to describe growth in animals, as they fit the empirical data adequately enough, and because their constants have been interpreted as having at least some biological meaning. Using the growth of freshwater mussels as an illustration, Haukioja and Hakala (1979) made a thorough appraisal of asymptotic growth equations. They concluded that none of the parameters of the equations had any significant biological validity, when comparisons of parameters derived from different populations were made. The best known and most commonly used growth equation in fisheries assessments, is the von Bertalanffy equation (von Bertalanffy, 1957). It has come under criticism over the reality of asymptotic growth (Knight, 1968) and with specific reference to marine bivalves, has been shown to provide an inadequate description of the growth of the early stages (Theisen, 1973; Yamaguchi, 1975). Nevertheless, when applied to appropriate data, the von Bertalanffy equation is generally considered a good approximation of observed growth curves. In relation to growth of marine bivalves for example, Brousseau (1979) found the equation a valuable model when comparisons of growth patterns in single-species populations were made, providing large numbers of animals were used and the entire size range of animals was considered, especially the older age classes.

Although widely applied to growth of marine bivalves, it is only in recent times that the von Bertalanffy equation has been used to describe growth of freshwater mussel populations (Kenmuir, 1980; Walker, 1981b; Dudgeon and Morton, 1983; McCuaig and Green, 1983). Coon _et al._ (1977) used general power functions to describe growth of freshwater mussels in pools of the Mississippi River. For some North American populations of _Anodonta grandis_ growth does not tend to a maximum length and therefore growth according to the von Bertalanffy equation is invalid (Green, 1980). For these populations, Green (1980) developed a growth model that did not assume an asymptotic size.

As applied to linear growth, the von Bertalanffy growth equation is:

$$l_t = L_\infty [1 - e^{-K(t-t_0)}]$$

where l_t = length at any given time t,

L_∞ = the theoretical average maximum length,

K = the growth constant indicating the rate at which length approaches L_∞ ,

t_0 = the calculated time at which length is equal to zero.

Conventionally, the suitability of the von Bertalanffy growth model for growth rate data has been tested using Walford plots of lengths at consecutive ages. With asymptotic growth and a constant decrease of growth rate with age, the mean age values should give a linear relationship on a Walford-graph where the slope of the line is equal to e^{-K}, and the intersection of the line and the 45° diagonal from the origin, is at the asymptotic value of length, L_∞ (Walford, 1946). Variations of the Walford plot may be used to test the suitability of other growth models for growth rate data. Kaufmann (1981) presented techniques involving such variations of the Walford plot, for determining which of several growth curves - exponential, power, Gompertz, logistic, as well as the von Bertalanffy - could best fit growth data. Other than the von Bertalanffy model, the appropriateness of a particular growth curve is indicated by the linearity of the relationship between specific growth rate and size, after the axes have been suitably transformed.

Using Kaufmann's (1981) methods with growth rate data of V. angasi, untransformed plots of specific growth rate and size consistently gave the best linear fit of data from among all the Magela Creek populations. This indicated that the von Bertalanffy model was the most suitable of the models tested. Walford plots are shown in Figure 6.10 for mean length for age data from representative mussel populations in Georgetown, Mudginberri and Nankeen billabongs. From Figure 6.10, and exemplifying the results of the Kaufmann technique just described, it is clear that for most billabongs and age classes, linear relationships of lengths at consecutive ages are found, indicating that the von Bertalanffy model sufficed for the growth data.

As observed from the plots (Fig. 6.10), however, and from others drawn for populations in other waterbodies (not shown), growth of young-of-year mussels does not conform to the growth equation. Because of this unconformity, the Walford plots of growth data of V. angasi resembled to some extent those of the arctic population of A. grandis studied by Green (1980); Green found that a quadratic model more adequately described the relationships in the Walford plots. With the assumption of nonlinearity, he derived a model for the population that did not assume an asymptotic size. For all populations of V. angasi, however, inclusion of a quadratic term in the Walford plot relationships added no extra significance over the linear model. This indicated asymptotic growth of the populations (and therefore growth according to the von Bertalanffy model).

Thus, the cause of nonlinearity in the Walford plots was the inclusion of growth data of young-of-year mussels only. As recommended by Ricker (1975), therefore, this age class was rejected whenever the von Bertalanffy curve was fitted to the growth data. The value for K (the slope of the Walford line) of the Georgetown mussel population changes with age with two growth stanzas either side of a length of about 55 mm. This is a common enough phenomenon in fish populations (Ricker, 1975), and also in some marine bivalve populations where Johannsen (1973) for example, represented growth of Venerupis pullastra with two von Bertalanffy equations about a critical size. Different growth stanzas were sufficiently uncommon (see Corndorl, Fig. 6.11 and section 6.4.3.2) in populations from other billabongs to warrant that only one equation be used to describe growth of each billabong population. Although this probably led to some loss of precision in the values of the growth constants, a single equation was nevertheless a more useful aid for comparisons between the growth of populations in all waterbodies.

Computations of the von Bertalanffy growth parameters were performed using the interative method developed by Allen (1966). Whilst this method is regarded as amongst the most precise (Ricker, 1975), additional advantages are: the allowance for data collected at any age interval; the parameters of the equation may be calculated using individual observations (thus making use of all the available data); and estimates of the limits of error (confidence limits) of the parameters are provided. Individual lengths and ages of mussels at the time of collection were used in the computations. To set specific ages, it was necessary to have suitable arbitrary reference points of the times of larval metamorphosis and annulus formation. Annulus formation is seen with early Wet season flushing of the creek (section 6.3.3.2), and 1 January served as a suitable and convenient reference date for this. The times of juvenile settlement were extrapolated from mean lengths for age data of juveniles collected about the time of recruitment as depicted in Figures 6.2-6.4 and elsewhere (not shown). These dates are: Georgetown - 7 March; Mudginberri, Buffalo, Island - 10 January; Nankeen - 11 March. For other waterbodies these data are not available, but for the general knowledge that recruitment occurred during the Wet. A mid-Wet season date of 1 February therefore was arbitrarily set for the time of recruitment in these places.

6.4.2 Growth within and between waterbodies

Within billabongs

Growth data were available between sampling stations in Georgetown, Mudginberri and Buffalo billabongs, and between different depths in the floodplain billabongs, Leichhardt and Nankeen. Sampling stations within the billabongs are the ones used for routine monthly collections, as described in section 3.1. Tables 6.3-6.7 show the parameters of the von Bertalanffy growth equation and their 95 per cent confidence intervals (calculated by Allen's (1966) method) for mussels within different localities of the billabongs. The equations were calculated at each site, for each sex separately, and overlap in the confidence intervals for a particular parameter, indicated that no significant differences were observed between the sexes. In practice, sexual differences were rarely found and the parameters calculated for the sexes combined only are shown. In Georgetown billabong, however, marked sexual differences in growth patterns were observed within sites, and Table 6.3 shows the parameters calculated separately and combined for the sexes. Clearly from Tables 6.3-6.7, growth rates may differ considerably between mussels at different sites of the same billabong (and occasionally between the sexes at the same site), and apparent trends and their significance are discussed in section 6.4.3.1.

Between waterbodies

The variation in growth between waterbodies was more marked than within billabongs. For between-waterbody comparisons therefore, growth data were combined for each waterbody. Tables 6.8-6.19 show the means, standard deviations, 95% confidence intervals and ranges of lengths for each age class of mussel in the different waterbodies, calculated separately and combined for the sexes. From these data the enormous variation in size range within a particular age class is most apparent, and shows that mussel size from small samples may bear little resemblance to age. Further, this factor is offset only to a minor degree when within-billabong variation is considered. (Data not shown.) von Bertalanffy growth parameters were calculated separately and combined for the sexes from these data (Table 6.20). Again, from the confidence limits of both data sets, growth differences between the sexes are trivial, and all further comparisons were based upon the growth parameters calculated for the sexes combined (Table 6.20). von Bertalanffy growth curves calculated for the combined sexes, are shown with means and confidence limits of size at each age interval, for the different waterbodies in Figures 6.11 and 6.12. Marked differences are noted in the growth rates of mussels between different waterbodies. Apparent trends and causes of the disparities are discussed in section 6.4.3.2.

6.4.3 Environmental determinants of growth

Of the three parameters of the von Bertalanffy equation, L_∞ , K and t_0 , L_∞ and K are interpreted as having intrinsic physiological significance, by which growth within populations may be studied or compared between populations. Haukioja and Hakala (1979) concluded that asymptotic growth parameters in general, were unsuitable for comparing growth between populations of Anodonta piscinalis. However, they found the von Bertalanffy equation least unsuitable for producing parameters for comparisons between populations and did not rule out the possibility that the parameters in general may be correlated with some environmental factors or other parameters of growth. Haukioja and Hakala recommended length at a critical annulus for comparing growth rates between populations but stated that this criterion would not be valid if the groups compared had clearly different final lengths. McCuaig and Green (1983), however, used analysis of covariance of linear Walford regression equations to test hypotheses about perturbations that might bring about differences. With such analysis, they found the parameters apparently quite sensitive to hypothetical perturbations, with subsequent changes to population growth.

The constants, L_∞ and K, derived from growth equations of mussel populations in the Magela Creek, were fairly easily interpreted, together clearly dictating the form of growth within and between the populations in most waterbodies. With the aid of hypothetical growth curves, they were of considerable use for investigating some important factors that might determine growth patterns of mussels. These factors are discussed below.

Reiterating, as an aid to the following discussion, the constant L_∞ is the theoretical asymptotic size of a organism while K describes the rate at which this value is approached. Both Ralph and Maxwell (1977) and Brousseau (1979) considered the constant K of interest, because it could be used to make comparisons of the rate of growth of different (bivalve) species or of the same species from different environments. Use of the parameter in isolation in this manner, however, must be viewed with caution for as Ricker (1975) states, K is a growth coefficient, not a growth rate. A relatively large K value for example, merely suggests that the asymptotic size is approached relatively early in life, while a lower K value may yet describe a population whose growth rate at all ages is higher. Thus growth rates in between-population comparisons can only be studied with knowledge of both K and L_∞ . Ricker (1975) states that for any given initial size of an organism, a larger K means a smaller L_∞ and thus slower growth from that time onward. Ricker's mathematical basis and argument for this statement (p.221) is apparently incorrect (V. Bofinger and W. Taylor, pers. comm.) on the basis of assuming the variable l_t to be a fixed and constant value. Nevertheless, the statement is probably true for most populations, including at least marine bivalves (Theisen, 1973).

With respect to the interpretation of and interrelationships between the growth constants of the von Bertalanffy equations derived for mussel populations within and between waterbodies of the Magela Creek, three types of comparative growth relations were found. The hypothetical types are shown in Figure 6.13. In type A relations, both populations reach the same maximum size (L_∞), but at a slower rate for those on the bottom curve, characterised by a lower K. In type B relations, a smaller K means a larger L_∞ (and vice versa). Over the whole lifespan nevertheless, lower K populations are faster growing than populations with successively higher K values. A smaller K may also mean a larger L_∞ , but for type C relations, higher K populations may reflect faster growth rates relatively earlier in life before being surpassed in growth rate by lower K growth for the remainder of the lifespan.

Beverton and Holt (1957) noted that K could be regarded as independent of the level of feeding but might be expected to vary with certain environmental factors such as temperature. (These comments were directed to temperate fish species.) These authors provided evidence that the parameter W_∞ (asymptotic weight, $W_\infty \propto L_\infty{}^3$) was affected by variations in food consumption. Even if changes in K occurred for various levels of food consumption, Beverton and Holt suggested that K may be expressed in terms of W_∞ and from the theoretical point of view then only W_∞ need be used in attempting to predict the growth rate in given circumstances. In the Magela Creek populations, type B relations were typical of between- and most within-billabong comparisons of growth (see below). Thus L_∞ , in a loose sense, in type B comparisons is more indicative of growth rate throughout all life-stages (by nature of the shape of the curves) than the false impression that K values on their own would suggest. In any case, L_∞ and K were mostly negatively correlated in type B relations (section 6.4.3.2). As only food availability was of interest as a quantitative determinant of growth rates, and as L_∞ may (1) on theoretical grounds be dependent upon the feeding level, (2) be indicative of overall growth rate and (3) nevertheless be correlated with K in type B comparisons, the parameter L_∞ only was considered for study. A further reason for the choice of L_∞ as a measure of growth rates, is that it was a more conservative parameter, not influenced to the same degree as K, to weighting of the age classes and varying age structures.

Regression analyses were performed where each parameter, L_∞ and K, was regressed against itself where the parameter was derived from computations using individual observations, as opposed to unweighted mean observations for each age class. The analyses showed highly significant correlations in both cases ($P<0.001$), but K calculated with unweighted means accounted for only 77% of the variation in K calculated from individual observations, as opposed to a high 95% of the variation in L_∞ derived from individual observations that was accounted for by L_∞ derived from unweighted means. Thus, differences in sample sizes and age structures between billabong populations that were used to compute the growth equations, affect K more than L_∞ . The constant K in relation to growth is apparently more complex in its interpretation than L_∞ . Further discussion on its significance is made in the following sections.

6.4.3.1 Within billabongs

The mussels on the shallower and sandier transect of Georgetown billabong represented the only population in the Magela Creek where sexual differences in growth rates were observed (Transect B, Table 6.3). Over the entire size range, females grew at a significantly faster rate than males (i.e. a type B relation, Fig. 6.13). Mussels in this region of the billabong regularly move onto the adjacent flooded peripheral shores during the Wet (section 6.8.1). Growth on the flooded shores during this time occurs at a faster rate than of mussels in deeper waters (unpublished observations and data). Some differential movement of females onto the peripheral shores was observed at these times (section 6.5.1), but whether these differences are enough to explain why females might overall grow more quickly than males, however, is not certain. With growth data combined, growth between mussels on the two routine transects of Georgetown billabongs is one of type A as illustrated in Figure 6.13. Both populations reach the same asymptotic size, but the population on the shallow, sandy transect does so at a faster rate than the population on the deeper, muddy transect. The preponderance of younger mussels on the shallower transect (mean age of 4.20 years as opposed to 6.54 years on the deeper transect) may have considerable influence on the values of the parameters of the growth equation here. Young mussels predominate in the billabong generally (Fig. 6.29) and the values of K and L_∞ derived from individual observations of the mussel population in the billabong as a whole, are 0.290 and 62.8 mm respectively, as opposed to corresponding values of 0.164 and 67.4 mm when the parameters were calculated from unweighted data of mean lengths for each size class. In the former, calculations were biased towards the younger age classes, but the unweighted data favoured the older age classes. Thus the type A relation between the two transects can be best explained at this stage by the difference in age structures of the two populations.

Tables 6.4 and 6.5 show the von Bertalanffy growth parameters calculated for data between the routine sampling stations in Mudginberri and Buffalo billabongs respectively. Growth within each billabong varies considerably. The growth relations when plotted were of Type B (Fig. 6.13), and only a few populations in Buffalo billabong contradicted this pattern. Thus asymptotic size indicated growth rates of populations within the billabongs, and was used as the dependent variable denoting growth quality of mussels in subsequent correlations of environmental determinants of growth.

As L_∞ may theoretically be expected to vary with food availability, chlorophyll levels as a measure of this, were compiled for different regions of the two channel billabongs. For Buffalo billabong, crude estimates of chlorophyll content of the waters were available only. The waters of the 10 sites sampled in the billabong were analysed on two occasions during 1981 for chlorophyll. The levels and mean values are shown in Table 6.22. Within-billabong variation of chlorophyll in Mudginberri, was reported in Kessell and Tyler (1983). Chlorophyll concentrations were calculated fluorometrically on four occasions during 1980 and 1981, over different regions of the billabong. The data in Kessell and Tyler (1983) for each sampling occasion, are divided into 5 equal ranges of chlorophyll concentration, classed from lower to higher concentration as 1-5, and mapped over the respective billabong regions. The concentrations on these occasions (in arbitrary units) and mean values, over the routine sampling stations for mussels are shown in Table 6.21. From the limited data, there is a trend in both billabongs for chlorophyll concentrations (and presumably primary productivity), to be higher at the southern end of the billabongs, and over the more organic sediments (stations 6 and 7 in Buffalo, and 3 and 4 in Mudginberri Fig. 3.1). Chlorophyll concentrations were regressed against asymptotic size of mussels between the different sites of both billabongs. For Mudginberri billabong, a very significant ($P<0.01$) logarithmic correlation was found (Fig. 6.14), whilst for Buffalo, a significant ($P<0.05$) linear correlation was found between asymptotic size and chlorophyll concentration (Fig. 6.15). Both results provide good evidence that food availability as measured by algal concentrations, is a chief determinant of mussel growth rates within billabongs. Whilst mussel growth rates are generally highest over the organic sediments, of further interest is the observation that on some of these sediments (station 3 in Mudginberri, and station 2 in Buffalo) mussels grow faster than the surface chlorophyll values would suggest. This may be an artifact of the small sample numbers that comprise the mean chlorophyll values, but may suggest that in addition to the nutrients made available for algal production, breakdown and resuspension of the organic material in the sediments conceivably provides an additional, and unmeasured detrital food supply for mussels here.

Plots of the growth curves for mussels from different depths of Leichhardt and Nankeen billabongs (Tables 6.6 and 6.7 respectively), showed Type B relations for Leichhardt and Type C relations for Nankeen billabong (Fig. 6.13). Thus growth rates in Leichhardt billabong decrease with depth. A similar pattern is observed in Nankeen for about the first 13 years of life, before overlap of the curves (Fig. 6.13) reverses the growth rate order, and growth rates actually increase with depth. Declines in food supply and temperature with depth have elsewhere been used to explain decreases in mussel growth rates with depth (see Appendix 3).

Some limited chlorophyll data are available between the surface and bottom waters of both billabongs as a check of differences in food availability with depth that may correlate with growth rates. Over a 10 month period (Fig. 2.29), surface chlorophyll concentrations in Leichhardt billabong averaged 15.5 as opposed to 13.3 μg/l in the bottom waters. Over 9 months of readings in Nankeen billabong, surface chlorophylls averaged 7.0 as opposed to 9.1 μg/l for bottom water concentrations. Thus, decreasing food availability might explain the growth rate decline of mussels with depth, in Leichhardt billabong, and vice versa for the greater maximum lengths attained at depth in Nankeen. In Leichhardt billabong, decreasing oxygen tensions with depth (notably severe in this billabong, section 2.3.2.2) very likely reduce the time available for feeding, further adding to the growth rate reduction of mussels with depth here. While decreasing oxygen concentrations with depth in Nankeen might similarly explain the slower growth rates of mussels at depth at least for the relatively younger age classes, some other overriding factor reverses this pattern later in life. Apart from perhaps increasing food availability with depth that might support better growth in the later years, shallow water stunting later in life might also explain the pattern. Nankeen billabong is possibly the most exposed billabong on the Magela Creek, and becomes extremely turbid during the latter period of the Dry season (section 2.3.2.4). Wave-induced resuspension of the silty sediments no doubt, is quite severe in the shallow waters of the billabong at this time. The wave action and/or the high amounts of suspended solids that may interfere with feeding, may reduce growth rates of mussels in the shallow waters (section 6.1). If this is the case, then the factor(s) are apparently selectively inhibitive to the growth of the later year stages.

6.4.3.2 Between waterbodies

Growth curves calculated for populations of mussels from each waterbody (Figs 6.11 and 6.12) when compared with one another are of Type B relations (Fig. 6.13). Thus as K increases, L_∞ becomes smaller (and vice versa), and L_∞ is indicative of growth rate over all age classes. A significant ($P<0.05$) negative, linear correlation was found between the estimates of L_∞ and K calculated with data from each waterbody (Fig. 6.16). (Not enough growth data were available for Gulungul and Hidden billabongs for the estimates of their growth parameters to be considered reliable. The data from these billabongs are hence omitted from Fig. 6.16 and from further calculations and discussions.)

From Figures 6.11, 6.12 and 6.16 some general statements may be made. A low K constant is indicative of a population whose growth is continuous throughout the whole lifespan, whereas a high K indicates maximum size is attained relatively earlier in life. The former populations occur in billabongs where food availability is high (shown later) for much of the year and which is capitalised upon by even the older age groups (Island, JaJa, Leichhardt and Jabiluka). In other waterbodies, the food supply may be low (Georgetown, Magela Creek channel, Buffalo), or relatively more abundant (Nankeen), but nevertheless is available for only a short period of the year. Growth in these waterbodies is apparently accomplished earlier in life and the older age groups do not grow much on a low food supply, nor capitalise upon a more abundant but short-lived supply.

From Figure 6.16, Corndorl and Mudginberri populations (points 9 and 12 respectively) have apparently anomalous K values, being lower than might be expected in relation to the values of the parameter in other waterbodies. The Mudginberri population shows a steady increase in size over the whole life span (Fig. 6.11). The food supply in this billabong on average is low, but is probably more evenly spread out over the year (Fig. 2.28). This factor, in addition to the general equitableness of the billabong waters by comparison to the other waterbodies (e.g. low turbidity, high oxygen content), may be more conducive to growth throughout the lifespan of individuals in the population. In Corndorl, growth of the mussel population is in two stanzas either side of an age of 12 years (Fig. 6.11). The older year classes appear to be growing at a different and faster rate than the younger ages. This might be attributed to either some major and abrupt shift downwards in food abundance over the years, or selection may favour faster growing individuals at some stage in life. The latter suggestion is conceivable in unstable and shallow, backflow environments where, if the waterbody occasionally dried up, only the larger individuals of the early year classes may survive by virtue of their higher tolerances to desiccation (unpublished data). Thus, the growth pattern of the Corndorl population is an anomaly and the presence of two growth phases results in a relatively low K constant when the growth equation is derived from the pooled population data.

As asymptotic size, L_∞, may be regarded as dependent upon the level of feeding, a relationship was sought between L_∞ estimated for each waterbody population and algal production as measured by mean seasonal chlorophyll concentrations (Table 2.7). Figure 6.17 shows the relationship. Neither a Gompertz nor logistic curve adequately fitted the data, and a line of best fit was drawn by eye. The comparatively low L_∞ estimated for the mussel population in Leichhardt billabong (No. 24), is no doubt due to a preponderance of young mussels in the billabong and a corresponding lack of size classes of greater age (Figs 6.12 and 6.30). Each has the effect of lowering the asymptotic size in a weighted calculation. Nevertheless and clearly, growth rates can be predicted quite accurately and simply with knowledge of mean chlorophyll concentrations. With the regression equation of the constant K in terms of L_∞ (Fig. 6.16), the growth dynamics of individual mussel populations can be even better understood.

6.5 Population structure

6.5.1 Distribution of the sexes in billabongs

Sex was determined for large numbers of mussels between the routine sampling stations (Georgetown, Mudginberri and Buffalo) and/or different depth regions of billabongs (Georgetown and the floodplain billabongs). Chi-squared tests were performed to determine whether or not the sexes were distributed evenly across the different habitat types sampled within each billabong. Data from floodplain billabongs were tested alone, and lumped together in a single test across all billabongs. No trends in sex ratios within billabongs were evident, and the chi-squared tests revealed no significant deviations in any case of the proportions of the sexes between sites or different depths of billabongs that would suggest that the sexes were unevenly distributed.

An additional test was performed in Georgetown, for data of sex distribution of mussels across the shallow, sandy transect that incorporated shallow inundated banks during the Wet season. Adult mussels make seasonal movements up onto, and back away from the inundated shore (section 6.8.1). 36 out of 69 adult mussels (52%) collected from the inundated shore were female as opposed to 429 out of 895 adults (48%) along the entire transect. However, a chi-squared test, revealed that there was no differential movement of females onto the flooded shore ($\chi^2 = 0.55$, $P>0.25$).

6.5.2 Size distribution

6.5.2.1 Within-billabong patterns

Length was measured of all mussels that were sampled for density estimates in the different habitats of the billabongs. The sampling rationale and methods are described in section 5.2. While density estimates for Georgetown billabong were derived from late Dry season sampling, size data, however, were obtained from the routine monthly collections made over the entire duration of the study. Mean lengths per substrate and depth interval within the Magela Creek billabongs are shown in Tables 6.23 - 6.28. Two-way analysis of variance was performed on the habitat means wherever applicable to determine whether there were significant differences in mean lengths among depths or in mean lengths among different substrates.

Depth

No significant differences were found in size among depths in Georgetown, nor in size between locations ($P > 0.05$) when data were analysed according to depths and the two routine transects sampled in the billabong. However, partitioning of the sum of squares (SS) due to depths into linear, quadratic and residual components revealed a very significant ($P < 0.01$) linear effect. With the data of both transects pooled, however, further regression analysis showed a very significant ($P < 0.01$) quadratic relationship. The regression equation is described in Table 6.29, and the relationship plotted in Fig. 6.18. Thus mussel size increases with depth in Georgetown, reflecting the observations that recruitment occurs in the shallow reaches of the billabong, and young mussels move into deeper waters with age (sections 6.6.1 and 6.8.1). A slight decrease in size was recorded in the deepest reaches of the billabong (Fig. 6.18). This can be attributed to slower growth rates of mussels here rather than the presence of younger age classes, because mean age increases with depth in the billabong (Fig. 6.25). This might be due to oxygen deficiencies at depth, or more likely to the high amounts of suspended solids that occur during the Dry season and which are generally inhibitive to algal production at these depths (and hence food availability) (Fig. 2.28). Suspended solids might also interfere with the normal feeding processes if the load is greater with increasing depth in the billabong.

In Gulungul billabong, mussel size tends to increase with depth (Table 6.24), though not enough depth intervals were sampled for a significant regression to be fitted to the data. It would appear almost certain that the older age classes would dominate at depth, as the billabong occasionally dries out, and mussels in deeper waters would be more likely to survive these periods. Analysis of variance showed no significant differences in size among depths in Corndorl when data were analysed according to the two major substrate types of the billabong. Partitioning of the depths SS, however, revealed a significant ($P < 0.05$) linear effect. As no substrate effects were found, the data were pooled. The resulting linear regression equation is described in Table 6.29, and the relationship plotted in Figure 6.19. Unlike Geogetown and Gulungul, mussel size in Corndorl billabong <u>decreases</u> with increasing depth. Again, either decreasing mean ages or growth rates with depth can account for this observation. Unfortunately no age data are available in relation to different depths of this billabong. Nevertheless, both decreasing oxygen tensions and consolidation of the sediments with increasing depth were observed in Corndorl. Both factors have the potential to reduce growth rates of mussels and even induce early mortality, thus shortening the lifespan of mussels at depth. Low oxygen concentrations may effectively shorten the period available for feeding, thereby affecting the growth rates of mussels, or effectively alter the age structure to favour younger mussels by killing off older mussels. The siltier environment associated with the very soft sediments of the deepest waters may also interfere with feeding, and with age, more energy may be required to maintain a hold in the soft sediments to the detriment of energy allotted to growth. When the sediments are extremely soft, mussels may reach a threshold size which the sediments are unable to support and mussels may consequently smother and die prematurely. This factor, however, cannot explain why mussel size decreases with depth over the relatively more consolidated sediments along the northern bank of the billabong (Table 6.25). The sediments, are notably siltier with increasing depth. From the limited information, food availability may not be a factor in reducing growth rates with depth, as chlorophyll concentrations tend to be greater at depth in Corndorl (Fig. 2.28). Shoreward migration with age to avoid the deepwater stresses mentioned above could explain the observed size distribution.

No significant differences were found in mussel size among the different substrate types in either Mudginberri or Buffalo billabong. Data among substrates were pooled for each billabong, and a single analysis of variance was again used to test for differences in mussel sizes (1) between billabongs, and (2) among different depths. No differences were found in sizes between billabongs, but significant differences occurred in size among depths ($P < 0.05$). While partitioning of the depths SS revealed a very significant linear effect ($P < 0.01$) with the data of both billabongs pooled, further regression analysis showed an even more significant ($P < 0.001$) logarithmic relationship between mussel size and depth. The regression equation is shown in Table 6.29 and plotted in Figure 6.20. The increase in mean size of mussels with depth in the channel billabongs is caused by, at least, an increase in mean age over the same gradient (Fig. 6.26). To some extent, primary productivity is also high over the deepest portions of these billabongs (Tables 6.21 and 6.22), and so the larger sizes of mussels are partly related to the higher growth rates here.

Mean length among the 10 sampling stations in Nankeen billabong did not differ significantly. Nor were significant differences found in size among different depths when averaged over the sites. An analysis of variance was performed with size in relation to billabongs and depth, over the five floodplain billabongs. No significant differences were found in mussel size among billabongs, nor in size among depths. However, partitioning of the depths SS showed a significant quadratic effect ($P < 0.05$). The relationship is described in Table 6.29 and plotted in Figure 6.21. An intermediate depth is found at which size reaches a maximum in the floodplain billabongs. Again, the relationship is mirrored by the same pattern in the age distribution of mussels in these billabongs, where a maximum age occurs at the same intermediate depth (Fig. 6.27).

In general, size variation of mussels in relation to depth in the Magela Creek billabongs, can be explained by the same variations in mean age. No age related data were available for Gulungul and Corndorl billabongs, but if size in these billabongs is a reflection of the age distribution (as in the other billabongs) then mean age increases with depth in Gulungul but decreases with depth in Corndorl. If this is the case, then substrate- and/or oxygen-related factors might best explain why older mussels avoid or succumb in the deeper reaches of Corndorl billabong.

Substrate

As seasonal movements of at least a portion of the Georgetown population are likely to bring mussels into contact with a variety of the sediment types of this billabong (section 6.8.1), no analysis of size distribution in relation to substrate was undertaken here. Nor did the relatively homogeneous sediments of Gulungul and the floodplain billabongs provide opportunities for such study. As mentioned earlier, no significant differences were found in mussel sizes between the two substrate types in Corndorl billabong.

No significant differences were found in mean size of mussels among different substrates in either Mudginberri or Buffalo billabongs. Using mean sizes per substrate type over all depths sampled, differences in sizes were tested for among comparable substrates in both billabongs. No significant differences were found in mussel sizes between the two billabongs, but significant differences were found in sizes among the different substrates ($P < 0.05$). As for the analysis performed in section 5.4.1.2.1, the four sediments were ranked in order of increasing organic content and decreasing particle size. The substrates SS was then partitioned into linear and residual components. This revealed a very significant linear effect ($P < 0.01$) with mean sizes increasing over the gradient from sand, to the relatively siltier and increasingly unconsolidated and organic sediments (Fig. 6.22). While the more organic sediments generally harbour relatively older mussels in the channel billabongs (section

6.5.3.1), the increase in mean size over the gradient of increasingly organic sediments can also be attributed to the same trend in faster growth rates of mussels as previously found (section 6.4.3.1).

6.5.2.2 Between waterbodies

For size distribution analysis between all waterbodies, quantitative data from all routine monthly collections were used. This meant that only in the billabongs - Georgetown, Mudginberri, Buffalo and Nankeen - did non-selective sampling ensure that all the size classes were represented (section 3.2.1). Nevertheless, for size classes above about 20 mm (section 3.2.2), the data between waterbodies are assumed comparative. Table 6.30 shows the mean lengths, their standard deviations, maximum and minimum lengths and sample sizes of mussels recorded from all waterbodies. Figures 6.23 and 6.24 show the length frequency distributions of mussels from the various waterbodies. From these figures an ubiquitous adult mode is apparent. This large and often single mode reflects similiar, unimodal age distributions (Figs 6.29 and 6.30), where overlap in size of the adult age classes is considerable, and where young mussels may be sparse or approach adult size very rapidly. The trough between the juvenile and adult mode of the Mudginberri, Buffalo and Nankeen mussel populations, represents high seasonal recruitment followed by significant juvenile mortality before the young approach adult size. Only in Georgetown billabong do the size distributions represent regular year-to-year recruitment where numbers of mussels gradually decrease with increasing age (Fig. 6.29). The bimodality of Gulungul size distributions is a direct reflection of a trough of missing age classes in the age structure of mussels in the population (section 6.7.3).

The mean sizes of mussels in the different waterbodies (Table 6.30) is clearly related to differences in growth rates, even though the mean length is overestimated to some (slight) degree in populations where very small mussels were not collected or were uncommon. Like asymptotic size (L_∞) therefore, mean length correlates with mean chlorophyll concentration of the waters, the latter reflecting a measure of food availability. No statistical treatment of these data, however, was undertaken.

6.5.3 Age structure

The age data derived from mussels collected at routine monthly intervals in the waterbodies, were used for the following age structure analysis.

6.5.3.1 Within billabongs

Sufficient quantitative data were available for Georgetown, Mudginberri, Buffalo, Leichhardt and Nankeen billabongs, for within-billabong study. Because of the seasonal movements of mussels over the sediments in Georgetown, the limited number of sampling stations within Mudginberri and Buffalo, and the relatively homogeneous bottom types of Leichhardt and Nankeen billabongs, analyses were restricted to relationships between age and depth only. Mean ages per depth interval within the billabongs are shown in Tables 6.31 - 6.34. Again, two-way analysis of variance was used as the test basis for studying these relationships.

No significant differences were found in mean age among depths in Georgetown, but a significant difference in mean age of mussels ($P < 0.05$) was found between the two routine transects sampled in the billabong. Mussels on the sandy, shallow transect were significantly younger than those further downstream on the muddy and relatively deeper transect. While partitioning of the depths SS would most likely have yielded a significant linear effect, plots of mean ages and depths for each transect suggested logistic relationships would be more appropriate models. The fitted functions are described in Table 6.35 and are plotted for each transect in Figure 6.25. As for the same pattern in size distributions within the billabong, the increase in age with depth along each transect can be interpreted by peripheral recruitment, with young mussels moving into deeper waters with age. Presumably, this response is a gradual one and is a reaction to falling water levels and increasing water temperatures that accompany the progress of each Dry season. By the end of particularly dry years especially, mussels would be left in the little remaining waters, of the deepest portions of backflow billabongs. The observation is probably modified to some degree by the increased mortality that might be expected in the shallows from desiccation, high water temperatures and mammalian predation.

For the same depth intervals in Georgetown billabong, mussels are younger on the shallow, sandy transect than further downstream on the deeper, muddy transect. Recruitment on the shallower transect is disproportionately high. 885 out of 2436 mussels collected on this transect were less than a year old compared to only 493 out of 2658 further downstream. The large numbers of juveniles on the shallower transect therefore have a significant influence on the mean age structure here. The shallower transect is also presumably, a less stable environment than further downstream. In particularly dry years, high mortality may result from high water temperatures, desiccation and predation. This region of the billabong is also susceptible to scouring during Wet season floods, and the population on the sandy sediments may be periodically removed during such events (section 5.4.1.2.1). It is tempting to suggest that the significant recruitment observed over this transect is some form of density dependent compensation for the relatively fewer adults that occur here. Conditions here, however, may be particularly well suited to the needs of juveniles as opposed to elsewhere (section 6.6.1).

Significant ($P < 0.05$) and highly significant ($P < 0.001$) linear regression relationships were found between mean age and depth in Mudginberri and Buffalo billabongs respectively. The regression equations are described in Table 6.36 and plotted in Figure 6.26. Mean age increases with increasing depth in both billabongs. Unlike Georgetown, there was little evidence to show that recruitment was higher in the shallower waters or that mussels moved to deeper waters with age (section 6.6.1). To some degree, the deeper reaches of the billabongs are out of the mainstream flow, where silt and detritus are able to settle. Thus older mussels occur on these sediments in Mudginberri (sites 3 and 4 in Table 6.32) and to some extent in Buffalo billabong (sites 2, 6 and 7 in Table 6.33). Some sandy sites in both billabongs are presumably relatively unstable and shifting, and younger mussels may be expected there because of this. Sites 1 and 2 in Mudginberri (Table 6.32) and sites 8, 9 and 10 in Buffalo (Table 6.33) are examples of these. Site 8 in Buffalo occurs in a narrow neck of the billabong (Fig. 3.1), where stream velocities were observed to be particularly high during the Wet. The shifting sands here bear few mussels but those that are present are relatively young. The mussels in fact, were so young for the observed depth that the site was omitted from calculation of the linear regression equation (Fig. 6.26). Nevertheless, other sandy sites in Buffalo billabong harbour relatively older mussels (sites 1 and 4) and are therefore presumably quite stable. The clean waters of both billabongs can expect relatively high bottom water temperatures particularly over the late Dry (Table 2.6). The warmer environment in the shallower reaches may be stressful and thereby stimulate mussels to move to deeper waters. The higher temperatures may also increase metabolic rates enough to induce an earlier mortality of mussels in the shallows much as suggested for other bivalves (Appendix 3). High growth rates were found for mussels in some shallow reaches of Buffalo billabong (Fig. 6.15).

Highly significant differences were found in mean age among billabongs, and in mean age among depths ($P < 0.001$) when data were analysed according to the five floodplain billabongs. Partitioning of the depths SS showed highly significant ($P < 0.001$) quadratic effects. Significant quadratic relationships between age and depth were found for Leichhardt ($P < 0.01$) and Nankeen ($P < 0.001$) billabong. The regression equations are described in Table 6.36 and plotted in Figure 6.27. An intermediate depth is found in the floodplain billabongs at which age reaches a maximum but about which mean age of mussels decreases. In the floodplain billabongs, recruitment occurs in the littoral zones (section 6.6.1), and either progressive movement to deeper waters with age, increased mortality in the shallows, or both, may explain the progressive increase in age of mussels with depth. Movements are presumably associated with avoidance of the resuspended silty sediments that are likely to be accentuated in the shallows, avoidance of high water temperatures, desiccation and predation. Mussels might also suffer significant mortality from these factors and even the higher growth rates of mussels in at least the early life stages in the shallows, by some physiological mechanism, might shorten the life span. Mussels reach a maximum age at an intermediate depth beyond which they become progressively younger. Older mussels could conceivably migrate shoreward with increasing age to avoid the hazards associated with the greater depths. Significant mortality of older mussels at greater depths is also likely. Dissolved oxygen depletions that may be severe at depth in the floodplain billabongs are almost certainly the major stresses that induce both movement of older mussels away from, and premature mortality of the older age classes in, the deepest reaches of the billabongs.

In all of the billabongs studied, mean age increases with increasing depth. Both increased mortality in the shallows, and avoidance with increasing age of these regions with all their hazards can account for this observation. Only in floodplain billabongs, were mean ages observed to decrease at the greater depths, again adding strong support to the view (section 5.4.1.1) that deep water oxygen depletions are particularly stressful to mussels in these environments.

6.5.3.2 Between waterbodies

As for comparison of size distributions between billabongs, nonselective sampling in Georgetown, Mudginberri, Buffalo and Nankeen billabongs biases the age structures of their mussel populations. This bias as argued in section 6.5.2.2 is minor considering the rapid growth of juveniles and is assumed to have no major and significant effect on mean age of the populations. These comments are made even more relevant when it is considered that for 1981 and 1982 when sampling was most concentrated, recruitment in fact was relatively poor in those billabongs where young mussels may have been missed (section 6.6.2). An exception to this rule, however, are the populations in the Magela Creek channel in which there is apparently regular year-to-year recruitment. Thus, recruitment and collection biases were not large enough to adversely affect comparisons between waterbodies.

Mean ages, their standard deviations, maximum and minimum ages and sample sizes of aged mussels from the Magela Creek waterbodies are shown in Table 6.37. Figures 6.28 and 6.29 show the age frequency distributions of mussels from the various waterbodies in relation to the year of recruitment of the particular age classes. A feature of these figures (also from Table 6.37), is the considerable variation in life-spans between populations of mussels. Whilst longevity and mortality are discussed elsewhere (section 6.7), a general observation is that populations are long-lived, indicating low adult mortality.

The age distributions (accounting for age, classed according to year of recruitment) of populations from some waterbodies show a gradual decrease in numbers from the youngest age class to the oldest, indicating regular year-to-year recruitment. This is a feature of the Georgetown billabong population, and is also shown for the Magela Creek channel, although the very young age classes were inadequately sampled. Although dominant year classes are present in the Mudginberri and Buffalo mussel populations, the gradual decline in numbers over the lifespan suggests that recruitment is fairly regular. Irregular age distributions characterised the populations in other billabongs signifying irregular, and in most cases, considerable, year to year variation in recruitment, or occasionally significant adult mortality.

Bell-shaped age distributions are thought to typify stable populations and where the bell is skewed to the left, the populations can be regarded as increasing and virile. When mean age is compared to maximum age in the mussel populations of the Magela Creek (Table 6.37), it is always much less than half the value of the latter. Thus these populations may be thought of as young and increasing. For most mussel populations studied elsewhere, the typical bell-shaped nature of their age distributions is explained by an absence of the youngest age classes. However, irregularity rather than a bell-shaped nature characterised the age distributions of populations in the present study, and young were present in all numbers from abundant to scarce. If young were uncommon, it was because they were inadequately sampled or recruitment (for reasons governed by the prevailing environmental conditions, section 6.6.2) was poor over the relevant periods of the study. There was no evidence that young were scarce because they occupied a habitat remote from that of the adults (section 6.6.1). Thus despite some 'typical' appearances ascribed to the age frequency distributions of freshwater mussels and the very general interpretations given to their shapes, an ecological basis for the variation and irregularity in some age distributions of mussel populations in the Magela Creek can be ascribed in a quantitative manner to environmental factors that affect both recruitment and mortality. Using the population age distributions as portrayed in Figures 6.28 and 6.29, the following two sections pertaining to recruitment and mortality explain how these age structures are modified by the factors that determine recruitment and death rates.

6.6 Recruitment of metamorphosed juveniles

6.6.1 Seasonal and spatial occurrence

Seasonal occurrence

Non-selective sampling of mussels in the Magela Creek was carried out in four billabongs (section 3.2.1). Monthly length-frequency distributions for the populations in three of the billabongs, Georgetown, Mudginberri and Nankeen, are shown in Figures 6.2-6.4. Generally, only Wet season conditions provide the clean, well oxygenated waters needed for growth and development of the newly metamorphosed juvenile. These requirements are reflected in the seasonal nature of recruitment of mussels in the billabongs (Figs 6.2-6.4).

Juvenile mussels in Georgetown billabong are recruited in the shallows during the Wet to mid-Dry - that is, from February to as late as August (Fig. 6.2). The relatively protracted period of settlement of young mussels here, reflects the provision of clean, aerated waters in the littoral zones over this period. Later in the Dry, the extremely turbid waters are inhibitive to larval production and presumably to larval development. It is likely too, that significant mortality of juveniles that settle late in the recruitment period occurs from the high amounts of suspended solids. These might be expected to interfere with normal gill functioning of the sensitive young mussel. Thus, distinct juvenile modes progress through the late Dry showing the clear seasonality of recruitment (Fig. 6.2).

Significant recruitment in Mudginberri occurs when Wet season flow is discernible through the billabong between January and May (Fig. 6.3). Dissolved oxygen concentrations are highest in the billabong at these times (Fig. 2.20). In the relatively deep waters otherwise, even the slightly depressed levels of oxygen during the Dry are apparently sufficiently stressful to prevent larval settlement and development. This might be readily understood for the silty and organic sediments of the deepest parts of the billabong where microhabitat oxygen availability is likely to be relatively low and where silt may clog the gills of the young. Some minimal recruitment occurred, however, throughout the Dry season in Mudginberri (Fig. 6.3). This was observed mostly at site 2 (Figure 3.1) where waters are shallower and the sediments less organic and silty than elsewhere. Juveniles could also be found on sandy littoral areas at the southern end of the billabong in the late Dry. These sites are presumably better aerated than elsewhere. However, the juvenile length-frequency modes that occur in the mid to late Dry do not progress, and so mortality of the small Dry season recruits appears to be high. Fish predation may be more intense in the clean waters of the Dry, or periodic lulls in oxygen availability that accompany the cycles of algal blooms in the billabong later in the Dry (section 2.3.2.2) may be destructive.

Recruitment in the floodplain billabongs is probably the most seasonal and synchronised for the waterbodies as dissolved oxygen is of sufficiently high concentration and turbidity generally minimal only during the Wet season. Newly recruited mussels were observed in Nankeen billabong between February and May (Fig. 6.4). Severe oxygen depletions that accompany the Wet-Dry interchange (section 2.3.2.2) prevent larval settlement in the mid Dry in Nankeen and presumably the other floodplain billabongs. Although oxygen concentrations may be relatively high in the mid to late Dry, the high turbidity observed in Nankeen at these times, inhibits larval production and subsequent recruitment. Dissolved oxygen concentrations in the clean, late Dry season waters of Island and Leichhardt billabongs are probably not sufficiently high enough for significant recruitment then. Both deepwater oxygen depletion and turbidity are likely to prevent Dry season recruitment in the heavily vegetated backflow billabongs, Gulungul and Corndorl as well. It is conceivable however, that in well oxygenated littoral zones as in Georgetown, some recruitment might occur well into the Dry in either billabong. In at least Gulungul billabong, however, flooded littoral regions have an unsuitable bottom sediment of hard-packed clay. In any case, waters may recede too rapidly over the broad shallow basin for juveniles to retreat in time to deeper waters.

As a general rule then, mussels are recruited seasonally into the Magela Creek waterbodies in a relatively short period for respective populations, within the broader time span of the beginning of the Wet to the mid Dry.

Spatial occurrence

Tables 6.38-6.40 show the numbers of juvenile, young-of-year mussels quantitatively sampled in Mudginberri, Buffalo and Nankeen billabongs respectively, in relation to both adults sampled and habitat. Chi-squared tests were used to discern differences in the proportions of juveniles in relation to adults in the different habitats. Such differences might indicate different habitat requirements of the young.

A graphic representation of recruitment patterns was chosen for Georgetown billabong (Fig. 6.30). Shown in this figure is the population structure of mussels during 1981, along the shallow, relatively sandy transect upstream in the billabong. Newly recruited mussels (< 20 mm in size) appear from May to about August in the shallow reaches of the transect, moving progressively to deeper regions as the waters recede. The recruitment pattern was not as pronounced on the northern shore of the transect (Fig. 6.30), nor on the deeper, muddy transect downstream. This is explained partly because the inundated shallows of these regions were steep and not very extensive, and/or the bottom types comprised mostly unsuitable, hard-packed mud. The occurrence of juveniles in the shallows is almost certainly related to the habits of the host fishes that were notably active amongst the weeded littoral zones at the time of juvenile mussel recruitment. It is conceivable that some additional deepwater oxygen depletions may also have restricted settlement elsewhere over this period.

Chi-squared tests revealed highly significant differences ($\chi^2 = 108.8$, $P < 0.001$) among the different sites sampled in Mudginberri, and no significant differences ($\chi^2 = 12.41$, $P > 0.05$) in Buffalo billabong, in the proportions of young relative to adults. Strong currents flow through Mudginberri billabong, and the distribution of juveniles might therefore be expected to be influenced considerably by flow patterns. More juvenile mussels were found at site 3 than might be expected, while fewer were found at sites 1 and 5 (Table 6.38). Particularly high flooding occurred in February 1980 and March 1981 that may have been responsible for sweeping juveniles away from sites 1 and 5 where currents would be expected to be stronger in relation to other sites (Fig. 2.15). Site 3 is a backwater area into which juveniles are probably swept during high discharge events, and might be expected to record relatively larger numbers of juveniles. The silty and organic sediments here may nevertheless be the cause of significantly higher mortality of juveniles over the ensuing Dry if the site receives flood refugees on a regular annual basis. By contrast, currents through Buffalo billabong during the Wet are considerably reduced, and the young are notably evenly dispersed over the billabong (Table 6.39). The sandy sites, 1 and 8, can be expected to receive stronger currents very extensive, and/or the bottom types comprised mostly unsuitable, hard-packed mud. The occurrence of juveniles in the shallows is almost certainly related to the habits of the host fishes that were notably active amongst the weeded littoral zones at the time of juvenile mussel recruitment. It is conceivable that some additional deepwater oxygen depletions may also have restricted settlement elsewhere over this period.

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When data were grouped according to five depth zones in Nankeen (0.0-0.49; 0.5-0.99; 1.0-1.49; 1.5-1.99; 2.0-2.49 m), highly significant differences were found in the proportions of young to adults, among the different depths ($\chi^2 = 35.7$, $P < 0.001$). When the proportions of young relative to adults were plotted against increasing depth, the proportion declined with depth (Fig. 6.31). A significant ($P < 0.05$) negative exponential regression equation was found to describe the relationship, shown in Figure 6.31. (The percentages of the dependent variable were transformed using a complementary log-log function as described in section 6.6.2). Thus from this Figure, and from earlier data (section 6.5.3.1), the occurrence of juveniles differs significantly from the adults, and recruitment is highest in the shallows. The marginal waters of the floodplain billabongs are reasonably well vegetated during the Wet, a feature that apparently attracts fish to the shallows. The occurrence of juvenile mussels in the shallows therefore is presumably related to the same distribution of their hosts. Further, deepwater oxygen depletions which juveniles are particularly susceptible to, undoubtedly restrict the young to the shallows either through causing higher mortality of young at depth or by stimulating movement away from the depths.

Thus in billabongs with shallow shelving banks, juveniles occur in different habitats than those of the adults. Occurrence in the shallower waters is presumably related to the habits of the host fishes, and the higher oxygen concentrations that occur there. Otherwise, differences between juvenile and adult occurrence appear to be related to dispersal by stream currents, and conceivably by the influence of that factor upon local fish habits and locations. None of the observed differences in habitat of juveniles and adults could be attributed to the need by juveniles of quite specific sediment types. Young were common in soft, crumbly mud and detritus in Georgetown, fine silt and clay in Nankeen (homogeneous at all depths) and from sand, grading to organic and silty soft sediments in backwater regions, of Mudginberri and Buffalo billabongs. These sediments range widely in texture and consistency, and possibly the least suitable are those silty sediments in the backwater regions of the channel billabongs. On these sediments of site 3 of Mudginberri billabong, however, are recorded the highest proportion of juveniles to adults of any other site, and within any other billabong (Tables 6.38 - 6.40).

6.6.2. Factors affecting recruitment

The occurrence of recruitment during the Wet, and earlier evidence (section 5.4.1.2), strongly implicate Wet season flow as an important determinant of juvenile recruitment in, at least, billabongs lying on the mainstream channel of the Magela Creek. As a supplier of dissolved oxygen, Wet season discharge is especially critical to populations within the heavily vegetated, floodplain billabongs where minimal or intermittent flow under the prevailing, warm conditions of the Wet, quickly produces deoxygenating conditions. Low dissolved oxygen concentrations (as mentioned earlier, section 5.4.1.2.2) are inhibitive to larval production in female mussels, and detrimental to newly-recruited juveniles. From Figure 6.29, a number of dominant year classes are apparent in the age structures of mussel populations in the floodplain billabongs. The peak in year class strength occurs in mussels recruited during either the 1973/1974 or 1974/1975 Wet seasons. Discharge data available for the gauging station below Jabiru (GS 821009, Fig. 2.3), show a number of wet years at about these times.

As observed in the floodplain billabongs, the Wet/Dry interchange is a period of regular, and often severe oxygen depletion. This period therefore might be expected to be critical for juvenile survival. If the Wet season were to end early, a relatively large period of warm weather remains until the cooler period (commencing in about May) under which deoxygenating conditions may be more pronounced. If Wet season flow were to continue relatively late into the season, only a short period of warm weather would remain before the cooler nights of the Dry effectively mix the water column, breaking down stratification and reducing periods of anoxia. Further, a protracted and late finish to the Wet not only means a longer breeding season and enhanced recruitment, but also provides a longer growing season for the juvenile. From experimental observations (Appendix 6), tolerance to anoxia increases with increasing mussel size, and so the larger the juveniles are in size at the end of the Wet, presumably the better are their chances of survival when deoxygenating conditions begin. Thus, the most dominant year class in the floodplain billabongs originates from the 1974/1975 Wet season (Fig. 6.29). This Wet was not the highest in terms of total discharge, but significantly, the April discharge was the highest (Fig. 2.3) and so the late finish to the Wet may presumably have enhanced recruitment for the reasons mentioned above. It is also significant that this dominant year class occurred in Island, Leichhardt and Jabiluka billabongs, where anoxia at the Wet/Dry interchange is most pronounced (Fig. 2.21). A limitation to this correlative approach, however, is that Dry season oxygen concentrations are presumably also responsible for post-recruitment survival. Information as to when the Wet season finishes gives by no means complete prediction of the oxygen relations in billabongs that are likely to prevail throughout the ensuing Dry.

Regression analysis was used to test for correlations between discharge and recruitment in the floodplain billabongs. Although a gauging station is located on the floodplain at Jabiluka billabong (GS 821017), records held are not extensive, and because of the complexity of flow patterns on the floodplain, reliable rating and gauging by the station is not as yet guaranteed (N.T. Dept. Transport and Works, Water Division, 1979). More extensive and reliable records, however, are held for the gauging station upstream near Jabiru (GS 821009). For the limited and reliable data that is available, a good correlation of discharge exists between the two gauging stations (N.T. Dept. Transport and Works, Water Division, 1980). (It is notable, however, that flow begins earlier and ceases earlier at Jabiru than on the floodplain at Jabiluka.) Monthly discharge data for the 9 year period from the 1971/1972 to the 1979/1980 Wet season from the gauging station below Jabiru were used in the analyses. Because of the similarity in age structure between mussel populations in all of the floodplain billabongs (Fig. 6.29), the year class data were combined. Strength of year class for each billabong, was calculated as a proportion of the total numbers of mussels of all the age classes recruited over the 9 year period that discharge records had been kept. An averaged proportion was then calculated for each year class, for the floodplain billabongs. It is conceded, however, that the regression analysis used would result to some degree in crude and inaccurate correlations, as the error introduced because of natural mortality effects was not considered. Although mortality in one floodplain billabong (Nankeen), over the 9 year period of life considered here, amounted to less than 10 percent (Fig. 6.36), this value is probably higher in billabongs where anoxic periods (likely to be a significant cause of mortality, section 6.7.3) are more severe, such as in Leichhardt billabong.

Systematically, various discharge combinations were regressed against year class strength (the latter arcsine transformed). Total discharge for the Wet season for instance, may not be so meaningful if most of the flow occurred in one relatively short period that did not leave time for either larval production, the parasitic phase or sufficient growth before the effects of deoxygenation at the end of the Wet were felt. A critical two or three month period of the Wet for example, may be all that is required to effectively determine recruitment. Thus, discharge was tested one month at a time (e.g. December discharge against strength of year class, January discharge against strength of year class, etc.), then discharge combined for two month periods, and so on, discharge adding cumulatively until total discharge was regressed against year class strength. The final test used was a multiple regression analysis, regressing all months, December to May for the 9 year period of discharge data against recruitment.

As shown in Table 6.41, many significant correlations ($P < 0.05$) were found between discharge and year class strength. (A few of the plots indicated that an exponential model may have provided a slightly better fit to the data. However, with the exception of the equation described below, these were not calculated.) It is notable that the latter months of the Wet are heavily represented in the regressions, especially where combined periods of discharge were shortest. This adds strong supportive evidence to the claim that late Wet season flow is most critical to juvenile recruitment and subsequent survival. While a few discharge periods bore stronger correlations to year class strength over others ($P < 0.01$), no one correlation was outstanding. For descriptive purposes, an adequate model nevertheless was considered to be that regression equation combining all of the significant discharge that might be felt through the floodplain billabongs, namely the period January to May. (From discharge data at Jabiluka, significant stream flow begins in January and extends well into May, whereas upstream at GS 821009, flow is not nearly as discernible during May.) The linear regression equation for this period is described in Table 6.41. An exponential model, however, shown in Figure 6.32 provided a better fit to the data ($P < 0.01$). The model was derived by transforming the percentages of the dependent variable with a complementary log-log function, log(-log(1-Y/100)). The regression equation is:

$$Y = 100(1-EXP(-0.043EXP(0.00234X))) \quad (P < 0.01,\ r^2 = 0.653)$$

where Y = year class strength (percent)

and X = total discharge for the period January to May ($m^3 \times 10^{-6}$).

Hence, total discharge between January and May accounted for 65 percent of the variation in year class strength of mussels in the floodplain billabongs over the 9 year period of discharge records.

The best fit of the linear multiple regression equation, however, accounted for all (100%) of the variance in year class strength. The multiple regression equation is:

$$Y = 0.178 - 0.0017X1 + 0.0012X2 + 0.0004X3 + 0.0011X4 - 0.0017X5 + 0.002X6 \quad (r^2 = 1.000)$$

where Y = Year class strength (arcsin ✓ (Y in percent/100), radians)

X1 = December,

X2 = January,

X3 = March,

X4 = April,

X5 = May.

X6 = June discharge (m^3 x 10^{-6}).

Table 6.42 shows the significance levels of the regression variables. December, January, March and April discharge are important variables. April discharge is by far the most important variable (Students t = 82.05) followed by March and January (Table 6.42). Thus, it is predicted that late Wet season discharge (March and April) enhances recruitment. Discharge, however, at the extremities of the Wet (December and May) has a negative effect on recruitment. (The negative sign is uninterpretable.) Nevertheless, the sign and significance levels of the January, March and April variables are more easily interpreted. High January discharge (the first significant flushing that the floodplain billabongs receive) presumably results in early juvenile metamorphosis and settlement. While February discharge is almost always greater than in January (Fig. 2.3) high discharge in March and April further enhances recruitment and lengthens the growing season of those mussels recruited as early as January. Thus by the end of the Wet, early recruits may be of considerable size, and the late finish of the season might nevertheless shorten the period that the young are exposed to low dissolved oxygen environments.

The shorter period of time over which mussels were sampled, and the bias against the small juveniles in the collections precluded analysis of the 1980/1981 and 1981/1982 Wet season recruits. The multiple regression equation, however, predicted relatively good recruitment in the 1980/1981 Wet (about half the strength of the most dominant (1974/1975) year class) but only about half this value again for the strength of the 1981/1982 Wet season year class. Early indications from Nankeen billabong at least, where non-selective sampling was performed, are that these values may in fact be quite accurate. Hence the multiple regression equation as it stands appears to be an adequate model, having significant predictive value. Further discharge data and information on mussel age structure in the floodplain billabongs will presumably increase the predictive value of the model. The generalised model, moreover, could be recalculated using data from individual billabongs, so that recruitment might then be predicted for specific floodplain billabongs.

From Figure 6.28, it is apparent that recruitment in Corndorl billabong follows the same year to year pattern as in the floodplain billabongs. Presumably this reflects the fact that this heavily vegetated billabong behaves in a similar fashion to the floodplain billabongs at the end of the Wet, with periods of deoxygenation (section 2.3.2.2). Therefore, protracted or extended Wet seasons also enhance recruitment here and similar correlations can be assumed. In the channel billabongs, Mudginberri and Buffalo, recruitment is much more regular, with much slighter evidence that high discharge and extended Wet seasons benefit recruitment. Presumably this reflects the observation that neither billabong becomes significantly deoxygenated at the Wet/Dry interchange, and survival of recruits therefore, is less dependent upon the amount of water discharged through the billabong during the Wet. Even in the Magela Creek channel where recruitment is very regular, the beneficial effects of the extended 1974/1975 are felt in the slightly elevated age class peak in the population (Fig. 6.28). Dominant age classes in Gulungul billabong finally, may be more influenced by remaining waters left in the billabong at the end of the Dry, than by Wet season discharge patterns themselves. Significant mortality of mussels might be expected if the billabong were to dry out. Further discussion about the age structure of this population therefore, is dealt with in section 6.7.3.

6.7 Mortality

6.7.1 Survival between the sexes

Plots of sex ratios with age were made to discern whether at any stage in the lifespan of mussels within particular waterbodies, differential mortality occurred. From the plots, it was clearly apparent that sex ratios of Velesunio angasi within several billabongs, changed with increasing age. The relationships are shown for these populations in Figure 6.33. In billabongs where changing sex ratios were observed, invariably the proportion of females appeared to decline, at least in the latter years of life (Fig. 6.33). Regression analysis was performed using sex ratio and weighted age data of the oldest age classes, systematically including younger age classes until the correlation became insignificant ($P > 0.05$). From the next age class onward therefore, it could be said that the proportion of females significantly declined with age. Such relationships were found in mussel populations in Mudginberri, Island, JaJa and Leichhardt billabongs. The same regression approach was used for the data from Jabiluka billabong, but in reverse order, in which the proportion of females significantly increased with age (Fig. 6.33). The linear regression equations and the range of ages over which significant correlations between sex ratio and age were found ($P < 0.05$), are shown in Table 6.43.

While the age variations observed in the sex structure of mussel populations might indicate differential mortality of the sexes, other interpretations are available. Tudorancea (1969) indicated that the variations in sex ratios of freshwater mussels arose from sex transformation with age. He found more male Unio tumidus both at younger and older ages, while females outnumbered males in the middle years. While no significant quadratic effects could be found using individual observations of sex ratio and age, nevertheless the same trend as found by Tudorancea is apparent in the sex ratios observed throughout the lifespans of mussel populations in some Magela Creek billabongs (Fig. 6.33).

The notion of major sex transformations occurring within the lifespan of V. angasi is considered in section 7.5, but it is of interest to this discussion that the proportions of females in some billabongs decline at older ages. It might be expected that associated with the approach of old age in organisms, are a physiological weakening and increasing intolerance to environmental stresses. It is worth noting that the populations in which the numbers of females decline with old age in the Magela Creek, are mostly from the floodplain billabongs where a common major stress is their poor oxygen relations. Whether the decline in the numbers of females at older ages is due to either a sex transformation, higher mortality with increasing age, or both, it is tempting to suggest that of either sex, the females might be expected to be more stressed at age. Higher demands are presumably placed upon the physiology of female mussels because the gills serve an additional function of harbouring and nurturing the larvae. In low oxygen environments therefore, older female mussels may be hard pressed to find sufficient oxygen and yet perform the additional gill functions of feeding and larval brooding. In fact, at low environmental oxygen levels, larval production by female mussels in the Magela Creek billabongs is inhibited (section 7.10.1). Thus as a sexual strategy, reproductive effort might be optimised at older ages in environments with poor oxygen relations, by production of male gametes. Alternatively or additionally, because females may be more vulnerable to stresses at old age, their lifespan might be expected to be considerably shortened. The latter interpretation is strongly suspected (sections 7.5 and 7.6).

6.7.2. Estimation of survival rates

Because quantitative samples were taken systematically over a two year period of collecting, opportunities were available to estimate age specific mortality in mussel populations from Georgetown, Mudginberri and Nankeen billabongs. Age specific mortalities are of considerable interest in population studies because as mortality usually varies greatly with age, is then possible to elucidate the forces underlying the crude, overall population mortality (Odum, 1971). For freshwater mussel populations, age specific mortality rates have been estimated for populations of <u>Margaritifera margaritifera</u> (Bauer, 1983) and <u>Anodonta anatina</u> (Negus, 1966). Bauer's (1983) estimates were based upon ratios of living mussels in every age class and numbers of empty shells, while Negus (1966) compared the proportions of mussels within specific age classes, between successive years for her estimates. Otherwise, both Haukioja and Hakala (1978b) and Green (1980) estimated the mortality of the oldest part of certain Anodonta populations, by analysis of catch curves.

In the present study, both catch curve analysis and ratios of mussel numbers in specific age classes, between successive years were used to estimate age specific mortality. All mussels collected from the routine monthly samples in Georgetown, Mudginberri and Nankeen billabongs were used in the analyses. A proportion of the samples of adult mussels from Georgetown and Mudginberri billabongs were unaged (section 3.3). The mussels belonging to this proportion were assigned an age according to the overall proportions of adult age classes estimated earlier (section 6.5.3.2). Age frequency distributions were then constructed for the three populations, pooling numbers of mussels within specific age classes collected over the two year period, without regard for the year of recruitment. Thus, young of year mussels ('0' years, Fig. 6.34) comprised 1980, 1981 and 1982 recruits and so on; no year class therefore was biased by the shorter or longer period of collecting. The age distributions are shown in Fig. 6.34.

From Figure 6.34, it is clear that recruitment in Georgetown billabong is fairly constant and the age frequency distributions show a gradual decrease in numbers with increasing age. Mortality rate in this population therefore could be estimated from catch curve analysis (Ricker, 1958). By this method, the natural log of mussel numbers is regressed against age. Mortality rate (M) which is constant over all age classes, is found from the slope (b) of the resulting negative linear regression, by means of the equation:

$$(m = 1.0 - e^{b} y)$$

Recruitment in Mudginberri and Nankeen billabongs was less regular, and the method of Negus (1966) was used to estimate age specific mortalities. Survival was estimated by comparing the numbers of one age class collected in the second year to those of the same cohort collected in the previous year. For example, survival at the end of the first year of life was found from the ratio:

$$\frac{\text{Number of 1-year-olds in 1981/1982}}{\text{Number of 0-year-olds in 1980/1981}}$$

, each year represented by the period June to May inclusive. The resulting ratios were plotted with increasing age and a line fitted by eye to predict annual survival rate for each age class (Fig. 6.35). Both small sample numbers and inaccurate age determinations precluded the estimation of survival rates for the final 11 years of life of mussels in Mudginberri billabong by this method. Catch curve analysis therefore was used for this oldest portion of the population, in which mortality is estimated from the slope of the semi-log regression between mussel numbers and age as described above. Although this method assumes that recruitment is regular and mortality constant in the population concerned, year to year fluctuations in recruitment in Mudginberri billabong are fairly slight (Fig. 6.28) while mortality nevertheless appears to approach a constancy at greater ages, from the trend apparent in the survival values of the ages immediately preceeding (Fig. 6.35). Instantaneous mortality rates were calculated according to the relationship:

$$S = (1.0 - M) = e^{-z}$$

where S = annual survival rate,

M = annual mortality rate,

Z = instantaneous mortality rate.

The values for age specific annual survival rates and instantaneous mortality rates of mussel populations in Mudginberri and Nankeen billabongs are shown in Table 6.44 Using these smoothed data and the mortality rate estimated for the Georgetown population (see below), survivorship curves were drawn for the three populations, where survival is plotted against age, under the conditions of regular year-to-year recruitment (Fig. 6.36).

The negative exponential equation relating mussel numbers and age for the Georgetown population was calculated to be:

$$Y = 1735e^{-0.286x} \qquad (r^2 = 0.825,\ P < 0.001)$$

where Y = numbers of mussels

and X = age in years.

From this relationship, the annual mortality rate (M) was found to be 24.9 percent, and the instantaneous mortality rate therefore, 0.29. If recruitment were regular, the age structure of the mussel populations in Georgetown, Mudginberri and Nankeen billabongs would appear as shown in Figure 6.36. (An implicit assumption in drawing up the survivorship curves shown in Fig. 6.36, is that survival found between successive year classes of mussels collected over the present two year study period, has been the persistent pattern in time.) The concave curve of the Georgetown mussel population indicates a constant specific rate of mortality over the entire life span. The populations in Mudginberri and Nankeen billabongs, however, display "stair-step" types of survivorship curves (Odum, 1971), where survival undergoes sharp changes between different age groups. Both populations harbour intermediate age classes in which mortality is insignificant. This high survival phase is most pronounced in Mudginberri billabong where it extends for some 10 years. In both Mudginberri and Nankeen billabong populations, however, mortality is highest in the earlier and older age classes (Fig. 6.36). Further discussion of these curves in relation to mortality causes is made in the following section.

6.7.3 Mortality causes and longevity

Some causes of mortality of freshwater mussels in waterbodies of the Magela Creek have previously been mentioned or suggested, in a general manner in Chapter 5. Further information regarding these and other factors is presented here. Predation, drought, flooding and anoxia are believed to be the main causes of mortality of <u>Velesunio</u> <u>angasi</u> in the Magela Creek.

Little information and circumstantial evidence was gained over the period of the study as to the chief predators of freshwater mussels in the Region. Aboriginal man both in the past and present is a very significant predator of mussels from shallow waters over the Dry season. In the Magela Creek, evidence of his collecting activities (via observations or shell middens) was found in the braided Magela Creek channel in the early Dry, and later in the season, in Georgetown, Corndorl, Mudginberri and Buffalo billabongs. The pattern of incision marks on shell fragments in other middens, was identical to the description by Fisher (1973) for predation by water rats (Hydromys) in southern Australia. Significant Dry season predation by water rats was observed in shallow billabongs, and was especially evident at the Wet-Dry interchange in the Magela Creek channel above Mudginberri. Shell fragments have been found in the stomachs of turtles in the Region, and mussels form a major component of the diet of certain populations of one species in particular, Emydura australis, and to a lesser extent in Carettochelys insculpta (J. Legler, pers. comm.). Otherwise, mussels are almost certainly preyed upon heavily in the juvenile stages by fish, and shell fragments at least, have been observed in the stomachs of certain catfishes: Hexanematichthys leptaspis; H. australis; and Neosilurus sp. (Bishop et al., 1981). Juvenile mussels have been found among the stomach contents of Glossy Ibis (Plegadis falcinellus, P. Dostine, pers. comm.). Similarly, White Ibis (Threskiornis molucca), observed feeding in the shallows of Georgetown billabong, were strongly suspected of taking juvenile mussels that were present here in large numbers during the mid Dry season (Fig. 6.30). This bird species has also been noted to prey upon mussels in southeastern Australia (Vestjens, 1973).

Prolonged Dry seasons presumably, are a major factor in explaining the general absence of mussels from shallow backflow billabongs. The direct causes of mortality may be increased predation and high water temperatures in the shallow waters remaining at the end of the Dry or from direct exposure and desiccation if the waters dry up completely. From accompanying experimental studies, V. angasi tolerated temperatures above 45° C before 50 percent of the population succumbed, and adults survived out of water (but indoors and away from direct exposure to sunlight) for several months. Juveniles, however, are less tolerant of dehydration. Accompanying outdoor experiments also showed that mussels reacted to falling water levels by burrowing, thereby avoiding the effects of high water temperatures in the surrounding shallow waters. However, in sediments where mussels cannot burrow, high water temperatures and exposure to sunlight were fatal. Burrowing in sandy sediments is also of little survival value as the poor insulative properties of sand provide little protection from high ambient temperatures. Mussels that burrow in muddy sediments increase their chances of survival, but cracks that appear in drying mud nevertheless expose a proportion of mussels to either the lethal effects of dehydration or direct sunlight.

Young of year mussels might be expected to be particularly vulnerable in a shallow backflow billabong such as Gulungul after a prolonged Dry season. Three age classes dominate the age distributions of the mussel population in Gulungul billabong: those derived from the Wet seasons of 1972/1973, 1973/1974 and 1980/1981 (Fig. 6.28). Gauge height data for the billabong are unavailable for these periods, but discharge data are available for the period 1971 to 1979 in the small, feeder stream (Gulungul Creek) upstream of the billabong (GS 821012, N.T. Dept. Transport and Works, Water Division, 1980). Presumably these data give some indication as to how early the billabong begins to fill with Wet season waters and how late in the Wet water is discharged into the billabong. Early filling of the billabong in particular (say, November), is assumed to mean that the billabong did not dry out in that particular year. The months of late and early Dry season discharge into the billabong (May, June, November and December) were regressed against year class strength of mussels (Fig. 6.28). (The percentages of the dependent variable were arcsine transformed.) November discharge only was significantly correlated with year class strength according to the linear regression equation:

$$Y = 0.218 + 0.525X \ (r^2 = 0.659, P < 0.05)$$

where Y = year class strength over the relevant period (arcsin √ (Y in percent/100), radians)

X = total discharge at gauging station 821012 during November (m^3 x10^{-6}).

This result indicates that juvenile survival is enhanced in those years in which Gulungul billabong does not Dry out significantly. The 1980/1981 year class was not included in the regressions because of the lack of discharge data. The billabong, however, did not dry up and depth by the end of 1981 still averaged 0.3 m (Table 2.1), a year in which juveniles were also quite common (Fig. 6.28). Better prediction of year class strength in Gulungul billabong might be achieved when billabong gauge height data replace stream discharges, as water levels in the billabong may not necessarily strongly correlate with discharge upstream of the billabong.

Flooding has been mentioned as a significant factor affecting mussel distribution and abundance in some billabongs of the Magela Creek (section 5.4.1.2.1). Flood events preclude habitation on sandy sediments in particular waterbodies, and in Georgetown billabong at least, were responsible for large scale displacement of mussels (section 5.4.1.2.1). The mussels that were swept downstream of the billabong, succumbed either to intolerably high water temperatures or air temperatures as the shallow waters about them retreated.

Juvenile mussels are particularly sensitive to low dissolved oxygen concentrations (Appendix 6), an observation already strongly implicated in recruitment success or failure in particular billabongs of the Magela Creek (section 6.6.2). There is little evidence, however, that the periods of low dissolved oxygen concentration observed in the floodplain billabongs are severe and stressful enough to cause mass mortality of adult mussels at these times. No mussel kills were observed that could be attributed to the direct effects of anoxia during the seasonal declines in dissolved oxygen in the billabongs. From experimental observations, adult mussels in fact may survive for prolonged periods (months) without oxygen (Appendix 6). It is conceivable nevertheless, that the cumulative effect of seasonal dissolved oxygen depletion over periods of years, may prove stressful enough to weaken the physiological tolerance of adult mussels and thus perhaps shorten the lifespan of mussels in the environments prone to these conditions. Whether the mussel kills that accompany fish kills at the Dry-Wet interchange (section 5.5), are significant factors in explaining mortality in the floodplain billabongs, is uncertain. The low numbers of dead mussels observed on one of these occasions in Leichhardt billabong at least, indicate that the effects are not severe, but the stressful factor, like anoxia, may conceivably weaken the tolerances of mussels.

In the light of knowledge of observed or likely causes of mortality of mussels, the age structure of mussel populations (Fig. 6.28 and 6.29), longevities (Table 6.37) and age specific mortalities (Fig. 6.36), the factors underlying the overall population mortality in waterbodies may now be better understood:

In the shallow backflow billabong of Georgetown, mortality is constant over all age classes (Fig. 6.36). Late Dry season stresses presumably account for much of the loss in mussel numbers from year to year. These stresses include: high turbidities and associated low food availability; high water temperatures and dehydration if water subsidence is particularly rapid; and increased mammalian predation. Flood events during the Wet presumably account for regular loss of mussels when these are physically displaced from the billabong (section 5.4.1.2.1). All age classes nevertheless are equally vulnerable to mortality by whatever cause.

No evidence was found of avian and mammalian predation in Nankeen, nor any other floodplain billabong, but turbidity and low food availability may be possible causes of mortality during the late Dry. Unlike Georgetown, mortality is low in Nankeen for mussels of younger ages between 3 and 5 years (Fig. 6.36). Whatever the causes of mortality in the billabong, these age classes therefore are the most tolerant and vigorous. The very youngest and older age classes of the population suffer highest mortality. The youngest age classes may be expected to be preyed upon more heavily than other age classes. As shown later, low dissolved oxygen concentrations are probably major causes of mortality of mussels in the Magela Creek billabongs. The effects of course are most pronounced in the floodplain billabongs where the youngest and perhaps oldest age classes of mussels may be least tolerant to their effects.

The environment in Mudginberri billabong, however, is apparently a most favourable one for mussels. Water quality is particularly equitable year round, with waters remaining clean, well oxygenated and adequately supplied with food. The deeper waters of the billabong moreover ensure that mammalian predation at least is relatively low. Thus, mussels in this billabong (and in Buffalo billabong for which these comments may also apply) are the longest-lived, and for a period of some ten years in the intermediate ages no discernible mortality is apparent (Fig. 6.36). Predation is almost certainly intense in the youngest years, and perhaps to some degree in the oldest age classes as well. Senescence, presumably, accounts for much of the increase in mortality at greater ages.

Longevity varies widely between mussel populations of different waterbodies (Table 6.37). Drought and dehydration may be factors that determine the maximum ages of mussels in Gulungul billabong and the ephemeral Magela Creek channel. Otherwise, dissolved oxygen appears to be at least one important factor that determines longevity of mussels in billabongs which presumably never dry out completely. A significant correlation was found between mean, dissolved oxygen concentration of billabongs and the maximum ages of mussels ($P < 0.05$). The linear regression equation is described and plotted in Figure 6.37. Because they affect maximum ages attained, dissolved oxygen concentrations in billabongs presumably have considerable influence upon the mortality of at least the oldest proportion of the mussel populations. In billabongs where the concentrations are particularly low (e.g. Leichhardt), the effects of anoxia might be expected to act upon all the age classes. These results again (see

Chapter 5) testify to the significance of dissolved oxygen conditions in billabongs, to the general well being and development of mussel populations.

6.8 Movements

6.8.1 Lateral movements in a shallow backflow billabong.

Figure 6.30 shows the seasonal distribution of mussels in relation to location along the shallow, sandy transect sampled routinely in Georgetown billabong (Fig. 3.1). Movements were marked along this transect - particularly the southern end, as the sediments here are fairly soft and the slope of the banks fairly gentle. As seen from the figure, adult mussels (> 20 mm in size) move up onto the peripheral seasonally-inundated and weeded shallows during the Wet season. During the Wet and early Dry, juvenile mussels are recruited in these shallows (section 6.6.1) and both young and adults move back into deeper waters as the waters recede over the ensuing Dry.

The migration of adults onto the banks during the Wet season may be associated with feeding, reproduction or avoidance of the shifting sandy sediments of the central portions of the billabong. Faster growth rates were observed for adult mussels in the peripheral, shallow waters during the Wet (unpublished observations) indicating that food availability was higher in these reaches. Greater somatic growth and larval production might also be expected under these conditions. Further, as fish frequent the weeded shallows, the movements of mussels into these regions during the Wet therefore coincides with their distributional patterns, thus facilitating parasitism of the fish by the glochidial larvae. Between the February and March samples (1981) floods displaced large numbers of mussels from the billabong (section 5.4.1.2.1). The central sandy reaches of the transect shown in Figure 6.30, are notably depauperate of mussels during March. Although some mussels may have been washed away from these central regions during the floods, nevertheless others apparently moved up or were washed onto the flooded banks over this time as both proportions and numbers of mussels were higher on the banks than at previous sampling occasions. Movements therefore, may be made in response to water movement. Receding water levels initiate a response to move to deeper water in avoidance of high water temperatures and exposure.

6.8.2 Movements in a deep channel billabong

Of the some 8,000 mussels marked and released in Buffalo billabong, 591 of these were recovered twelve months later. 58 of the recovered mussels had moved beyond the 506 m^2 quadrats over which they were originally released. The movements in relation to numbers and direction in the billabong are shown in Figure 6.38. 17 of the movements occurred at the very southern end of the billabong, and were made in response to falling water levels during the late Dry season. The mussels were placed in shallow waters during May 1980 and moved to deeper waters as the sandy sediments became exposed during the Dry. Thus when these individual movements are discounted, 7.1 percent of the remaining recovered mussels had moved beyond the quadrats originally allocated them, for reasons other than receding water levels and imminent exposure.

The size of the quadrats over which mussels were released was designed to detect fairly large scale movements of mussels. The distances travelled into adjacent quadrats for example, could not be considered substantial as mussels initially replaced near the edge of a quadrat need only have moved a few metres at the most, to a new one. Thus, only two recoveries had moved sufficiently over the period for their movements to be termed significant. These movements occurred at the northern end of the billabong, over sandy sediments, and the shortest distances that the two mussels could possibly have moved were 50 and 70 metres respectively (Fig. 6.38). It is almost certain, however, that both movements occurred as a result of displacement downstream by Wet season floods. The sandy sediments of the billabong were probably to some degree shifting during a large flood event in March 1981.

Chi squared tests were used to discern whether the movements throughout the billabong were random or not. Those movements involving responses to falling water levels were not included in the tests. An initial hypothesis to be tested was that the frequency of movements was the same in all four directions, north, south, east and west. Movements in a direction between two vectors were divided and aportioned equally to both directional vectors. Thus a northwest movement was considered half a north movement and half a westward movement. Very strong evidence was found against the hypothesis of random movement by mussels ($\chi^2 = 27.44$, $P < 0.001$). Tests were then conducted to discern whether northward movements were significantly more frequent than movements in other directions; whether southward movements were less frequent than movements either east or west; and whether movements were equally frequent both east and westward. Northward movements were far more frequent than movements in any other direction ($\chi^2 = 24.59$, $P < 0.001$), and southward movements less frequent than movements either east or westward ($\chi^2 = 4.59$, $P < 0.05$). No differences were found in the frequencies of movements either east or westward ($\chi^2 = 0.40$, $P > 0.05$). Thus mussels moved predominantly northward or in a downstream direction, and moved least of all southward or upstream. No substrate related tests were conducted, but over half the movements (27 out of 41) were over sandy sediments.

Undoubtedly, the northward movement of mussels in the billabong was the result of a displacement downstream by a large flood event during March 1981, that rendered the sandy sediments of the billabong especially, slightly unstable and shifting. In spite of the significant movement downstream, only a small proportion of recovered mussels (7.1%) had moved beyond the initial plots to which they were allocated, and only two recoveries (0.3%) had moved a distance beyond 25 metres. Other than floods and receding waters over the shallows, presumably no other factor initiates a response in mussels to move far in a lifetime in the deep channel billabongs. In the deeper floodplain billabongs, however, deepwater anoxia might provide such a stimulus (section 6.5.3.1).

6.9 Discussion

The conspicuous dark rings that characterise the shells of <u>Velesunio</u>

angasi in all freshwater environments of the Magela Creek were shown to be annular in nature. By following the guidelines as set out in section 6.3.2 for distinguishing the annual growth rings these can be used to age mussels from the Magela Creek and presumably from other freshwater environments of the Region. The present study provides the first unequivocal evidence that rings on the shells of mussels from tropical environments may be used in age determinations. Indeed, the study provides the first substantiation that an Australian freshwater mussel species can be aged by this means.

Decreases in seasonal growth in mussels from waterbodies of the Magela Creek were attributed to food and oxygen depletions, and aestivation. Food depletions and aestivation were assumed to be the most obvious cause of growth cessation of mussels during the late Dry that resulted in the annual growth interruption bands of mussels in all environments. However, less conspicuous factors such as the channelling of energy into reproduction, increasing water temperatures, the fluctuating dynamics of algal populations and their effect upon oxygen conditions, and metal toxicity were also believed to be late Dry season causes of annular cessation rings. Late Dry season stresses were also found by Kenmuir (1980) and Dudgeon and Morton (1983) to retard mussel growth in the tropics. Thus, Tevesz and Carter's (1980a) suggestion that the silt load carried by Wet season floods might be the cause of growth cessation and annularity in the shell rings of tropical species of freshwater mussel may be incorrect and has yet to be demonstrated. Drought (McMichael, 1952) and low winter temperatures (Walker 1981b) are believed to be the main causes of growth cessation of mussels in other parts of Australia.

Despite some peculiarities in the growth of mussels at various life stages in Georgetown and Corndorl billabongs, and the unsuitability of growth data of young-of-year mussels, the von Bertalanffy growth equation proved to be an adequate model of growth description of mussel populations in the Magela Creek. This was confirmed by the conformity of growth data to linear Walford plots and by the close fit of the computed curves to the data. The von Bertalanffy growth equation has been used elsewhere to describe the growth of freshwater mussels (Kenmuir, 1980; Walker, 1981b; Dudgeon and Morton, 1983; McCuaig and Green, 1983), although it cannot be assumed that the model will always provide an adequate description of their growth (Green, 1980). Very few significant differences were found between growth rates of the two sexes and size for age data were therefore pooled for growth comparisons of mussels within and between waterbodies. If any trends were apparent they were towards a tendency for female mussels to grow slightly faster than males. However, in billabongs where females were underrepresented in the older age classes (section 6.7.1) the differences in growth rates were least obvious. Elsewhere female mussels may grow more quickly than males (Chamberlain, 1931; Haukioja and Hakala, 1978a) but similarly the differences are trivial.

Growth rates in relation to food availability were studied between mussel populations within and between waterbodies. Asymptotic size, L_∞ , of the von Bertalanffy growth equation, was used to compare growth between different populations. This parameter reflected growth rate differences throughout the lifespans of mussels in the populations compared, and has a stronger theoretical basis (over the parameter K of the equation) for use in the types of comparison in which growth rates are related to food abundance (Beverton and Holt, 1957). Growth rates were found to vary quite considerably within billabongs. Within Mudginberri and Buffalo billabongs, significant correlations were found between growth rate and food availability. Growth rates of mussels decline with depth in Leichhardt billabong and similarly for the earlier age classes of mussels in Nankeen. Food and oxygen depletions with increasing depth may account for these reduced growth rates. Growth rates of older age classes of mussels in Nankeen billabong, however, are reduced in the shallower waters. This was believed to be associated with an interference to feeding of these later year stages, by wave-induced resuspension of the silty sediments during the Dry season. Growth rates varied widely between mussel populations of different waterbodies, being clearly correlated with mean food availability. The effect upon growth of mussels in waterbodies in which food abundance is low or the growing season short, is for maximum size to be attained relatively early in life and for little growth to occur in the older year classes. In more productive billabongs, or billabongs in which food is available over a relatively longer period of the year growth is discernible throughout most of the lifespan.

Very few studies have compared quantitatively, growth rate differences of freshwater mussels between different populations and in relation to possible environmental determinants. Haukioja and Hakala (1978a, 1979) recommended using the mean length of the third annulus in the shells of mussels, which have just passed their third winter, for growth comparisons between populations. Ghent _et al_. (1978) used mean height of mussels at the fifth annulus for growth comparisons of lake populations of Anodonta grandis at different depths. Haukioja and Hakala (1979), however, admitted that the choice of a specific annulus for comparison was subjective and that the criterion would not be valid if the groups compared had clearly different final lengths.

Elsewhere, as for Velesunio angasi, growth rate differences of freshwater mussels within sites of streams (Brönmark and Malmqvist, 1982), over a depth gradient in lakes (Appendix 3), and between different sites of the same lake (Harman, 1970; Cvancara, 1972; Kenmuir, 1980) have been attributed at least partly to differences in food supply. This same factor has also been suggested as the cause of growth rate differences of mussels between different streams (Björk, 1962) and different lakes (Okland, 1963). Growth rates of mussels in the Magela Creek generally, were observed to increase downstream in accordance with increasing primary productivity in that direction. The phenomenon has been observed in streams of temperate regions too (Altnöder, 1926; Cvancara et al., 1978; Walker, 1981b). Cvancara and co-workers observed that a downstream increase in nutrients (and hence greater food availability) might also explain the observed growth rate differences of mussels. Walker thought, however, that increasing temperatures in the downstream direction were probably the cause of the observed growth disparities. The shallow water stunting of the older age classes at least, in the exposed environment of Nankeen billabong has also been a commonly observed phenomenon in exposed lake habitats elsewhere (Appendix 3). Brown et al. (1938) attributed the stunting effect to extra energy expended by mussels in maintaining their station in the unstable environments, and/or to food supply reductions that might prevail in exposed habitats.

Within sites, growth rates have been reported to decline with increasing mussel density (Kat, 1982) and with increasingly softer sediments of finer particle sizes (Brönmark and Malmqvist, 1982; Kat, 1982). Mussel densities of V. angasi were amongst the highest in the Magela Creek on the stony, clay sediments in Mudginberri and Buffalo billabongs (Table 5.4 and 5.5). At these sites, however, (site 5 in Mudginberri, Fig. 6.14 and adjacent to site 10 in Buffalo, Fig. 6.15) were recorded the highest growth rates of mussels in either billabong and high mussel densities therefore had no bearing upon reduced growth rates of the mussels. Kenmuir (1980) also found highest growth rates of mussels in Lake Kariba, amongst sites where densities were greatest. Higher growth rates of V. angasi were found upon the finer, silty and organic sediments of the two channel billabongs than food availability as measured by algal concentrations might suggest (section 6.4.3.1). The substrates possibly provide an additional detrital food supply for mussels here. While these sediments are fine and slightly unconsolidated, they obviously neither interfere with feeding nor cause mussels to expend constant energy towards retaining their position to any degree that would result in reduced growth rates. Thus, no competition for food resources was evident amongst mussels of the Magela Creek environments, nor was evidence found that growth rates were reduced over soft, silty sediments.

Apart from higher water temperatures, faster growth rates of freshwater mussels between different but neighbouring streams (Björk, 1962; Clarke, 1973) and lakes (Green, 1980) have otherwise been attributed to increasing water hardness. No measure of water hardness between different waterbodies of the Magela Creek (Table 2.7), however, was correlated with growth rate of mussel populations in different waterbodies, as measured by asymptotic size, L_∞ , of the von Bertalanffy growth equation ($P > 0.05$).

The broad aspects of the population structure of V. angasi studied in relation to habitat and environmental patterns in the Magela Creek were distribution of the sexes, and size and age distribution. No significant deviations were found in the proportions of the sexes between sites or different depths of billabongs in the Magela Creek that would suggest that the sexes were unevenly distributed. Cvancara (1972) similarly noted no apparent trend in sex ratio with depth in a lake population of freshwater mussels in North America.

In billabongs in which habitat related age structures were studied, size distributions closely mirrored the patterns evident in age distribution. Thus, both size and age of mussels were generally observed to increase with increasing depth in billabongs. In Georgetown billabong and the floodplain billabongs, this distributional pattern can be partly attributed to the recruitment of juveniles that was observed in the shallows. Presumably higher mortality in the shallows, and migration of older individuals to deeper waters to avoid high, Dry season water temperatures, exposure and increased predation, are further factors that modify the distributional patterns. In other studies, juveniles are generally noted to be more frequent in shallower waters than adults (section A2.1.3). Both Okland (1963) and Kenmuir (1980) similarly attributed the increase in size and age with depth, to the shallow water recruitment of juveniles, and to the unstable environment of the shallows that results in higher mortality of mussels or that induces a migration of older mussels to deeper waters.

In Mudginberri and Buffalo billabongs, recruitment of juveniles is not necessarily confined to the shallows, but is apparently more influenced by Wet season flow patterns through the billabongs. The occurrence therefore of older mussels in the deeper waters of these billabongs is more difficult to explain, especially as extensive bottom areas of barely discernible slope lie between depth contours (Figs 2.8 and 2.9). The shallower waters of both billabongs, however, comprise mostly sandy sediments which are to some degree unstable during peak discharge events in the Magela Creek. Higher water temperatures can also be expected about the sediments of the shallower waters of these clean water billabongs, that either stimulate movement away from the shallows or perhaps increase the metabolic rates to such a degree as to reduce longevity of mussels here. Okland (1963) at least, thought the lack of younger mussels in the shallows of Lake Borrevann might partly be explained by selective mortality of faster growing individuals there. In both channel billabongs, moreover, mammalian predation is presumably higher in the shallows during the late Dry than elsewhere.

While older individuals are less common in the shallows, in the floodplain billabongs they are also less common at the greatest depths. Okland (1963) observed a similar phenomenon in Lake Borrevann in which the oldest mussels predominated at intermediate depths. As suggested by Okland, deepwater oxygen depletions may stimulate movement of older mussels away from, and induce higher mortality of the older age classes in the deepest reaches. In Corndorl billabong, mean size of mussels was also observed to decline with depth. The deep waters of this billabong are seasonally deprived of oxygen, and harbour softer unconsolidated sediments than elsewhere. Older mussels may avoid or succumb in the deeper reaches of the billabong under these conditions. Both Fisher and Tevesz (1976) and Ghent et al. (1978) for example, explained the absence of mussels from the depths of certain lakes, by possible asphyxiation in the soft, unconsolidated sediments there. Kat (1982) at least, observed reduced growth rates of mussels on soft, muddy sediments. Both growth rates and mean age of mussels in the channel billabongs are relatively higher on the more silty and organic sediments. Obviously these are not so soft that mussels require a constant energy expenditure to maintain a footing or even asphyxiate, as is conceivable in the deeper waters of Corndorl billabong.

The age distributions of mussel populations between the different waterbodies were characterised by long-lived individuals, and various types of recruitment patterns were evident. Populations from Georgetown, the Magela Creek channel, and Mudginberri and Buffalo billabongs displayed reasonably regular decreases in numbers from juveniles to the oldest age groups, indicating regular year to year recruitment. This type of age distribution is noted in many freshwater mussel populations except for the absence of the very youngest age classes (van der Schalie and van der Schalie, 1963; Tudorancea and Florescu, 1968; Tudorancea and Gruia, 1968; Tudorancea, 1969, 1972; Magnin and Stanczykowska, 1971; Kenmuir, 1980). Thus, in the Magela Creek, are represented some of the only known populations of mussels in which year to year variation in recruitment is minimal or exceedingly low. Invariably, the youngest age class is reported to be absent in studies of freshwater mussels. If the youngest age class was absent from any population in the Magela Creek, however, it was not because their habitat was so remote from that of adults, nor because of a specialised substrate requirement. The absence of young was attributed to inadequate sampling and poor conditions for survival of newly recruited mussels. The age distributions of populations from other billabongs, notably floodplain billabongs, were uneven and characterised by dominant year classes. This type of age distribution indicates irregular recruitment and is also common in freshwater mussel populations elsewhere (Negus, 1966; Haukioja and Hakala, 1978b; Walker, 1981b; and Strayer et al., 1981). No terminal populations of mussels were found in the Magela Creek, and because the age distributions are skewed to the left, the populations in all waterbodies can be regarded as increasing and virile (Zaika, 1973).

An ecological basis for the variation in year to year recruitment in freshwater mussel populations has never previously been quantified in terms of important environmental factors. Discharge patterns, particularly during the late Wet season, accounted for significant proportions of the variation in year class strength of mussel populations in the floodplain billabongs of the Magela Creek. Higher Wet season discharge, particularly late in the Wet season, was argued to result in both enhanced larval production in adult female mussels and subsequent recruitment, and better survival of newly-recruited mussels during the early Dry season. While drought was found to be a major factor adversely affecting recruitment of Alathyria jacksoni in the Murray River (Walker, 1981b), recruitment of Velesunio angasi in the floodplain billabongs, best resembles recruitment patterns of mussels in the Crapina-Jijila marshes. Tudorancea (1969, 1972) found that recruitment of Unio tumidus into the marshes was enhanced by high seasonal flooding of the Danube River. Strong year classes were traced back to years of high flooding in the Crapina populations.

Little evidence was found as to whether mussel populations in the Magela Creek could be regulated in a density dependent fashion. Both Kenmuir (1980) and Brönmark and Malmqvist (1982) thought that settlement of young mussels could be suppressed by adults when adult densities were high, and enhanced when adult densities were low. Recruitment onto the shallow and unstable, sandy transect in Georgetown was observed to be exceptionally high over the study period. Adult mussels are relatively scarcer in this region of the billabong than elsewhere and thus the age distribution might influence the recruitment patterns. However, the habitat requirements of the young may be exceptionally well met in the shallows of this transect, and recruitment might always be greater here.

The same causes of mortality of V. angasi in the Magela Creek have been reported or implicated for mussel populations elsewhere. These factors are predation (sections A2.1.2 and Appendix 3), drought and rapid subsidence of waters (Björk, 1962; Okland, 1963; Tudorancea, 1969, 1972; Walker, 1981b), flooding (section A2.1.3) and anoxia

(Björk, 1962; Okland, 1963; Walker, 1981b; and section A2.1.3). In broad comparisons between waterbodies, no evidence was found of growth selective or density dependent mortality. Comfort (1957) stated that slower growing molluscs tend to be longer-lived. Thus, Björk (1962), Okland (1963) and Haukioja and Hakala (1978a) considered that growth selective mortality operated on some freshwater mussel populations. Using asymptotic size (L_∞) from the von Bertalanffy growth equation as a measure of growth rate, and maximum age of mussels recorded from each waterbody, no significant correlation was found between growth rate and longevity ($P > 0.05$) that might indicate growth selective mortality. Tudorancea and Gruia (1968) believed that high densities of *Unio crassus* in a site in the Nera River shortened their lifespan. Again, however, no correlation was found between mean density of mussels and longevity in waterbodies ($P > 0.05$) that would suggest density dependent mortality. In fact the highest densities of mussels were recorded in the two channel billabongs, Mudginberri and Buffalo, where the longest-lived mussels in the Magela Creek were also found.

The proportions of female mussels in some billabongs of the Magela Creek were found to decline in the older year classes. This was also found by Tudorancea (1969) for the older ages of *Unio tumidus*, and might indicate differential mortality of females or sex transformations with age. Nevertheless, the occurrence of the phenomenon mainly in the floodplain billabongs suggests that the females, by virtue of the additional gill functions of larval brooding, are stressed by the low oxygen conditions of these environments.

The only significant events in the past that were believed to explain mortality and low numbers in the age classes of the age distribution, were the effects of drought upon young of year mussels in Gulungul billabong. A correlation was found between year class strength of mussels, and presumed late Dry season drying up of the billabong. Juvenile V. angasi are less tolerant of dehydration than adults. Both Tudorancea (1969) and Walker (1981b) interpreted missing age classes in the age distributions of mussel populations to the devastating effects of past periods of high winds and wave action, and severe drought respectively. More recently, Bauer (1983) found correlations between mortality rates and organic pollution in populations of Margaritifera margaritifera in North Bavarian streams.

Indirect assessments of the factors underlying overall population mortality of mussels in the Magela Creek, however, were gained from estimation of age specific mortality rates for populations in three billabongs, in combination with knowledge of longevity of mussels in different populations. Mortality in the Georgetown mussel population was found to be more constant throughout the life span, apparently an exceedingly rare observation in animal populations (Odum, 1971). In both Mudginberri and Nankeen billabongs however, mortality at intermediate ages is minimal and even negligible, while mortality in the youngest and oldest age classes is highest. Negus (1966) also found mortality of Anodonta anatina in the Thames River to be negligible in the intermediate ages, while Green (1980) suggested that mortality in the youngest ages might be expected to be higher than in the intermediate ages.

Late Dry season stresses and increased mortality would be likely to be severe enough in the shallow and unstable environment of Georgetown billabong to expect more or less constant mortality of mussels. Flood events, stranding and dehydration by receding waters, high water temperatures, high turbidities and mammalian predation might be expected to account for regular and constant loss of mussels from the billabong annually. At the other extreme, mussels in Mudginberri billabong suffer negligible mortality for a period of some ten years or so at intermediate ages, and the billabong is apparently a most favourable one for mussels. Water quality in the billabong remains unspoiled throughout most of the year and in addition to the relative depth of water left in the billabong at the end of the Dry season, contributes to a relatively stress-free environment. Most of the year classes in Nankeen billabong, however, are observed to decline from year to year. While water quality deteriorates in the late Dry season, the added stress of oxygen depletion during the Wet-Dry interchange is conceivably the factor that might contribute most to mortality of mussels in the billabong. Across all billabongs, a significant correlation was found between maximum age and mean dissolved oxygen concentrations, suggestive that mortality in the oldest age classes at least, is more influenced by dissolved oxygen than any other factor.

Longevity of V. angasi in the Magela Creek varied considerably between waterbodies, with determinations ranging from 11 to 35 years. While anoxia, and the ephemeral nature of other waterbdies may contribute to a shortened lifespan, other equitable environments such as those prevailing in Mudginberri and Buffalo billabongs are apparently most conducive to mussel development, and long lifespans may be expected. Comparable light-shelled species in Europe, North America, Asia and Africa generally live from 10 to 15 years (Appendix 3). In Australia, the congener Velesunio ambiguus along the Murray River was estimated to live to 11 years while the heavier shelled mussel, Alathyria jacksoni was estimated to live to 29 years (Walker, 1981b). In suitable environments therefore, V. angasi lives to a greater age than comparable forms elsewhere. The genera Velesunio and Alathyria both belong to the subfamily Velesunioninae. Further studies on species in the subfamily may reveal that members are generally longer-lived, and may resemble more the longevities found for thicker shelled species in North America (Appendix 3). The wide range in longevities found in V. angasi for various waterbodies in one small catchment, nevertheless, exemplifies the importance of environmental quality upon mussel well-being. (The longevities themselves in fact, further accentuate how diverse and heterogeneous the various freshwater environments of the Magela Creek are in relation to water quality.) Thus, it is conceivable that a species with circumboreal distribution such as Margaritifera margaritifera should vary even more greatly with respect to the maximum ages attained. Criticism of the reports of the extreme ages attained by this species therefore (Thompson et al., 1980; Dudgeon and Morton, 1983), may not be entirely valid because they did not fully consider the environmental and phylogenetic influences on longevity.

Mussel movements over a lifetime in selected environments of the Magela Creek were likely to be very limited in the absence of sufficient stimuli. In an equitable, stress-free environment where

Wet season stream velocities are not particularly strong, such as in Buffalo billabong, this is probably to be expected (Evermann and Clark, 1917). Thus in Buffalo, only 7.1% of mussels were observed to have moved beyond the 506 m² quadrats to which they were allocated one year previously. Most of the movements appeared to be associated with slight displacement downstream from Wet season flood events. Significant movements, apparently regular and seasonal, were observed over a shallow, sandy transect in Georgetown billabong. The stimulus for mussels here to move onto the shallow, seasonally inundated banks during the Wet season may arise for a number of reasons: avoidance of the unstable, and shifting sandy sediment in the centre of the transect; better feeding conditions at the edges of the billabong; and to increase the chances of parasitizing the host fishes with the glochidial larvae. Elsewhere, movement of mussels over unstable sediments and in response to rising water levels in lotic environments has also been observed (Coker et al., 1921; Björk, 1962; Kat, 1982; Salmon and Green, 1983). Similarly, both seasonal movements related to feeding (Tudorancea, 1972) and reproduction (Ellis, 1931; Yokley, 1972; Brönmark and Malmqvist, 1982), have been noted in various other freshwater mussel populations. In both Georgetown and Buffalo billabongs, mussels were observed to retreat to deeper waters in response to receding water levels over the Dry season. Again, this has been a commonly observed phenomenon in other mussel populations (Coker et al., 1921; Björk, 1962; Tudorancea, 1972; Fuller, 1974; Kenmuir, 1980; Salmon and Green, 1983), and is a response attributed to avoidance of dehydration, high water temperatures and increased predation. The seasonal migrations of mussels in Georgetown billabong most resembled the movements of mussels in the Crapina-Jijila marshes;

migrations in the marshes occur onto seasonally inundated floodplains for feeding and reproduction; and mussels retreat into deeper waters as the waters recede during the summer (Tudorancea, 1972). Thus, rising and falling water levels in shallow water environments, significant water movement, and conceivably anoxia in the floodplain billabongs are possible stimuli that initiate responses in *V. angasi* to movement in environments of the Magela Creek.

Finally, in addition to the indicator role that distributional information about *V. angasi* can offer (i.e., of the flow regime in waterways and the dissolved oxygen environment in waterbodies, section 5.5), further roles can be advocated with knowledge of the population dynamics of the mussel in the Magela Creek. For example, there have been no previous attempts in studies of freshwater mussel populations to demonstrate quantitatively, temporal variations in recruitment patterns related to environment; to calculate age specific mortalities for the entire age distribution in a relatively undisturbed environment; nor to show significant correlations between growth rate and size distribution, and algal productivity. *V. angasi* therefore, may be used as an indicator of environmental impact, and of past and present environments much as suggested by Tevesz and Carter (1980a). In association with distributional data, it is conceivable that recruitment patterns and mortality estimates that differ significantly from baseline data collected in the present study, could indicate environmental change in the Magela Creek brought about by anthropogenic activities such as pollution.

While distributional information about *V. angasi* indicates the long-term oxygen status of freshwaters (section 5.5), growth rate data are clearly correlated with algal production and therefore may indicate the trophic status of a waterbody. Because of the correlation between growth rate and water temperatures (e.g Negus, 1966), both freshwater and marine mussels in temperate environments have already been suggested as useful palaeothermometers, indicators of thermal pollution or in interpreting past and present climates at sites uninhabited by man (Tevesz and Carter, 1980a; McCuaig and Green, 1983; Jones, 1983). Similarly, it is conceivable that throughout the Region and indeed perhaps throughout its wider geographical range in tropical northern Australia, analysis of the size distribution and growth rates of populations of V. angasi will assist in the knowledge of limnology of both past and present environments. Oxygen relations and trophic status of freshwaters are fundamentally important limnological parameters, and a good understanding of both relationships may be gained from data on distribution and abundance, and size and growth rate data of mussels respectively. Thus V. angasi may prove a useful 'palaeotrophic' indicator or may be useful in interpreting the trophic status of tropical freshwaters previously unstudied. Additionally, in terms of pollution, growth rate data that exceed the rates calculated from baseline data might indicate forms of mild organic pollution in waterways. Such uses of freshwater mussels have not previously been suggested.

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THE BIOLOGY AND ECOLOGY OF VELESUNIO ANGASI (BIVALVIA: HYRIIDAE) IN THE MAGELA CREEK, NORTHERN TERRITORY

Part 2 (Text) (Contd)

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Supervising Scientist for the Alligator Rivers Region

THE BIOLOGY AND ECOLOGY OF <u>VELESUNIO ANGASI</u> (BIVALVIA: HYRIIDAE) IN THE MAGELLA CREEK, NORTHERN TERRITORY

PART II
(TEXT CONTD)

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Report to the Office of the Supervising Scientist
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7 REPRODUCTION

7.1 Introduction

Reproduction in freshwater mussels has been extensively investigated and is reasonably well understood for the unionaceans of northern temperate climes. The North American fauna in particular, has received considerable attention and in general two phases can be recognised in the progress of studies in this region: (a) commercial interest in freshwater mussels in the early 1900's led to a spate of broad, general studies concerned primarily with discovering means of rearing mussels or restocking heavily exploited and depleted populations (Lefevre and Curtis, 1910, 1912; Surber, 1912; Coker et al., 1921; Howard, 1922); (b) more intensive and specific investigation has been carried out only in comparatively recent times, part of the impetus for this work being the threat made to species whose ranges have been significantly reduced by anthropogenic changes to their environments. Indeed attention in regard to the latter has not only been directed at North American unionids (e.g. Trdan, 1981; Trdan and Hoeh, 1982; Zale and Neves, 1982, a,b,c) but at species equally endangered in parts of Europe, e.g. Margaritifera margaritifera (Bauer, 1979; Young and Williams, 1984 a, b).

By comparison, reproduction in freshwater mussels from the tropics and southern latitudes has received scant attention. Although the broad anatomical and life stage differences that distinguish the southern mutelaceans and hyriid unionaceans from northern forms have been described (e.g. Fryer, 1961; Parodiz and Bonetto, 1963), breeding patterns and life cycles for the vast majority of mussels are unknown.

Among tropical freshwater mussels, documentation of the sexuality and breeding seasons (Bloomer, 1931; Lomte and Nagabhushanam, 1969; Ghosh and Ghose, 1972; Nagabhushanam and Lohgaonker, 1978) and parasitic stages (Seshaiya, 1941, 1969) of the Indian unionids Lamellidens and Parreysia, is the most extensive. More comprehensive, ecological studies however, are few and comparatively recent. Noteworthy are Kenmuir's (1980, 1981 a, b) investigations of the reproductive biology of two mutelids, Aspatharia wahlbergi and Mutela dubia, and the unionid, Caelatura mossambicensis, in Lake Kariba and Lake Mcllwaine, Zimbabwe. Fryer's (1961) thorough study was the first description of the parasitism and development of a mutelid haustorium (Mutela bourguignati of Uganda) upon a host fish. Otherwise, the only other study of significance is a reasonably complete account of reproduction in Anodonta woodiana in Plover Cove, Hong Kong carried out by Dudgeon and Morton (1983).

Very few studies have investigated the reproductive biology of the hyriids of the Australasian region, though the situation has improved in temperate Australia somewhat in recent times. Glochidia have been described and fish hosts found for Hyridella menziesi (Percival, 1931), Velesunio ambiguus (Hiscock, 1951; McMichael and Hiscock, 1958; Walker, 1981b), H. drapeta (Atkins, 1979), and Alathyria jacksoni (Walker, 1981b). Published reports include glochidial descriptions of an additional five species - A. p. pertexta, A. profuga, H. australis (McMichael and Hiscock, 1958), H. australis, H. depressa and Cucumerunio novaehollandiae (Jones and Simpson, in prep.); while there are unpublished records of at least a further three - V. angasi, V. moretonicus and Westralunio carteri (Walker, pers. comm.). Thus the glochidia of eleven of the seventeen Australian hyriids have been described. From observations made of the appearance of glochidia (Percival, 1931; McMichael and Hiscock, 1958; Atkins, 1979) and of brooding females (Walker, 1981b; Jones and Simpson, in prep.), the probable breeding seasons of a number of species from temperate Australasia (section A4.3) have been inferred. Collection of material for the studies by Walker (1981b) and Jones and Simpson (in prep.) was regular and seasonal and thus the breeding seasons of the species involved are more or less confirmed. Among the species studied by Jones and Simpson, gonadal and larval development of C. novaehollandiae were also described.

The above review accentuates the paucity of knowledge regarding the reproduction of both tropical and Australian freshwater mussels. No Australian or South American hyriid, has been thoroughly investigated in all aspects of its reproductive biology. The study of reproducton in Velesunio angasi therefore provides an important contribution to the knowledge relating particularly to the hyriids, and also to freshwater mussels of the tropics. Important aspects of the reproduction of V. angasi studied included gonadal development, structure of the breeding population, larval production, glochidial release and parasitism. Worldwide information of this completeness for populations from specific locations is available for only a number of unionacean species, namely: Elliptio complanata (USA) (Matteson, 1948); Pleurobema cordatum (USA) (Yokley, 1972); Anodonta cygnea (Italy) (Giusti et al., 1975); four (sympatric) lampsilines (USA)

(Zale and Neves, 1982 a, b); and A. woodiana (Dudgeon and Morton, 1983), while collectively, the reproductive biology of Margaritifera margaritifera throughout its holarctic range is well known (Murphy, 1942; Bjork, 1962; Roscoe and Redelings, 1964; Smith, 1976, 1979; Bauer, 1979; Young and Williams, 1984 a, b).

Literature reviews appropriate to the following sections on gonadal development and structure of the breeding population, larval production, and glochidial release and parasitism, appear in Appendix 4, sections A4.1 to A4.3 respectively.

A. GONADAL DEVELOPMENT

7.2 Materials and methods

The material for histological study was taken from sexually mature mussels, randomly selected from the collections made monthly in Georgetown, the Magela Creek channel, Mudginberri and Nankeen billabongs (section 3.3). Collectively, a diversity of billabong types was represented, each varying considerably in limnological character. Nevertheless, rationalising the large amount of material to be processed, the annual gametogenic cycle of Velesunio angasi was followed more closely in Mudginberri billabong than in the other waterbodies. In this environment, regular seasonal patterns were apparent in larval production but seasonal changes in water quality were least discernible in comparison to the other waterbodies. The pattern of larval production in the reasonably equitable environment of Mudginberri, apparently represented a baseline breeding cycle. In other waterbodies, interruptions to this pattern caused by regular and seasonal fluctuations in oxygen concentration (Nankeen), turbidity (Georgetown and Nankeen) and exposure and inundation (Magela Creek channel) might occur. Description of this background breeding cycle assumed priority in the studies undertaken here.

Individuals collected between June 1980 and May 1981 were used for study. Monthly samples from Mudginberri billabong were processed over this period, while quarterly samples taken in June, September, December 1980, and March 1981 from Georgetown and Nankeen, were used. Aestivating mussels collected during November and December 1980, and submerged mussels taken in January 1981 from the Magela Creek channel, were processed. Each monthly sample comprised five individuals of each sex. Specimens were fixed in Bouin's solution and preserved in 70% ethanol. Sections were taken transversely through the central visceral mass at 6 μm and stained with Mayer's haematoxylin and alcoholic eosin.

No broad stages of gonadal maturation could be assigned to individuals as superficially the sections of testes and ovaries bore a resemblance between all individuals, sites and collection dates. The gonads were mature and sperm and primary oocytes present year round. The more subtle changes in gonadal condition, however, were quantified in the following manner:

For the testes of each individual, the proportion of the different spermatogenic stages was determined in 5 seminiferous tubules. The tubules chosen were spaced evenly across the section dorsally to ventrally (i.e. at predetermined intervals), and were selected using an eyepiece graticule. Camera lucida drawings of each tubule in relation to the different stages were made upon graph paper, and the relative areas of each spermatogenic stage determined by counts of the squares filled with the respective cell type. Sperm in the lumen of the tubules were present in more or less varying densities. To account for this variation, the areal presence of sperm was ranked according to an arbitrary scale, 1-5, of density. The relative areas of sperm was then adjusted accordingly. The values of the relative areas of each spermatogenic stage for the 5 tubules were averaged and a percentage composition by cell type was determined for the testes of each individual. 50 cells of each spermatogenic stage were measured under an oil immersion lens, using an eyepiece graticule.

Measurements and counts of the free primary oocytes were used to assess the female gonadal cycle. Oocyte counts were made on each of 25 follicles. Five fields of view were selected and located in the same manner as described for the testes. Within the field of view, the numbers of oocytes within each of 5 adjacent follicles were counted. A mean number of oocytes per follicle averaged over the 25 counts, was calculated for each individual. Simultaneously, at each field of view selected in the ovaries, the diameters across both axes of all oocytes through which the nucleus had been sectioned, were measured using an eyepiece graticule. For each individual, data were accumulated on at least 20 oocytes. After averaging the values of the two measurements made of each oocyte, a mean oocyte diameter was calculated for each individual.

7.3 Sex determination

7.3.1 Sexual dimorphism in shell size and shape

In the Magela Creek waterbodies, there is a tendency for female Velesunio angasi to grow slightly faster than males; in billabongs where females were underrepresented in the older age classes, however, differences in growth rates were least apparent (section 6.4.2). In only 2 of the 12 populations sampled, were significant growth disparities (as determined by the confidence intervals about the parameter, L_∞, of the von Bertalanffy growth equation) observed between the sexes (Table 5.20).

With respect to shape, there were no tendencies observed between relative height (i.e. in relation to total length) and sex (section 4.3.1). Of the populations sampled both males and female tended to have higher or lower shells equally. In only one billabong, moreover, did the slope of the length-height regression differ significantly between the sexes. In 9 of the 12 waterbodies, females tended to be more inflated (wider) than males (section 4.4), yet in only one billabong did the slope of the length-width regression differ significantly between the sexes.

The conclusion reached is that while obesity is the only morphometric index that consistently portrays a sexual dimorphism, nevertheless differences between the sexes in either growth rate, relative height or obesity are trivial and none of the indices has a broader application to sex determination. External shell characters in most instances therefore, could not be used to confidently predict sex of

V. angasi in the Magela Creek.

7.3.2 Internal anatomy

For routine work, sex was determined by both morphology of the inner gills and nature of the gonads ('visceral sex', Heard, 1975).

The inner gills of female *V. angasi* are modified as marsupia and are easily distinguishable from either the male or non-marsupial condition. While McMichael and Hiscock (1958) have described the anatomy and structure of the marsupial and non-marsupial demibranchs of *V. angasi*, for practical recognition their appearance in mussel populations from the Magela Creek is as follows. The inner, marsupial gills of females are notably thickened and the striation of the modified water tubes appears uniformly regular and even over the entire gill. Generally the gills are pigmented a light tan and this coloration is similarly uniform throughout the gill. The non-marsupial condition comprises both pairs of gills in males and the outer pair in females. These gills are conspicuously thinner, and the structure of the water tubes gives the appearance of a very irregular striation and reticulation throughout. Coloration is similarly variable both across the gill and between individuals where in the latter instance, the range in colour may vary from light tan to a deep, crimson red. Although the gill may be uniform in coloration, in most cases an irregular, yellow-orange pigmentation is prominent at its base, losing intensity over the remainder of the gill. Only in female mussels from the Magela Creek channel, was the marsupial appearance restricted to a portion of the inner gills. In these mussels, the marsupium occupied between one and two thirds of the gills, the remainder having the non-marsupial appearance.

Determination of the visceral sex in V. angasi was easily accomplished as the gonads were in a mature condition year round. By piercing the visceral mass with a probe, the ripe, yolky oocytes of females exuded and were clearly visible as minute, white specks amongst the body fluids. The body fluids similarly exuding from males, however, mainly comprised a white, milky fluid containing spermatogenic products (of which sperm predominated, section 7.4.2). For mussels from Georgetown, Mudginberri, the Magela Creek channel and Nankeen billabong, the body fluids containing the gonadal products were in all instances smeared upon microscopic slides and examined under high power magnification to confirm the nature of the gonadal tissues. The gravid condition of many of the females throughout the year in most populations, greatly assisted in determining sex.

For individuals from all populations, sex was determined both by the presence or absence of marsupial, inner gills and by puncturing the visceral mass to observe the exuded gonadal products. With few exceptions (section 7.5), there was always a consistent correlation between the visceral sex and sex as determined by inner gill morphology.

7.4 Gonad histology

Velesunio angasi is dioecious and only very occasional individuals are hermaphroditic (section 7.5). The gonads of both sexes ramify the visceral mass and within the follicles and tubules the various gametogenic stages develop.

7.4.1 Stages of gametogenesis

Stages of sperm maturation

The follicles or seminiferous tubules of the testes, each contain discrete cell aggregations or 'nests' of the various spermatogenic stages arranged in successive layers so that cells in the more advanced stages occur more or less regularly in succession towards the centre of the tubule (Fig. 7.1 B). In the spermatogenesis of V. angasi, six distinct stages were observed.

1. Spermatogonia - These cells have a mean nuclear diameter of 4.1 μm and are slightly angular in appearance. No cytoplasm is observed and the nucleus is compact and basophilic. Spermatogonia always occurred in nests adjacent to the tubule walls (Figs 7.1 C and D).
2. Sperm morulae - These are large multinucleate structures, each drupel of which resembles in appearance the spermatogonium. Collectively they have a mean diameter of 11.0 μm . Sperm morulae are often associated with spermatogonia and occur more or less singly scattered along the periphery of the tubule walls (Fig. 7.1 C).
3. Primary spermatocytes - Division of the spermatogonia produces primary spermatocytes which have a mean nuclear diameter of 5.3 μm. The nuclei of these rounded cells are slightly granular in appearance as dense chromatin material is abundant. Primary spermatocytes occur in nests more or less centripetal to the spermatogonia (Fig. 7.1 D).
4. Secondary spermatocytes - These cells, produced by divisions of

the primary spermatocytes were rarely observed. This is in accordance with the observation of Tranter (1958); apparently division is very rapid at this stage. The nuclei are characteristically granular in appearance and measure 3.5 μm in mean diameter. Secondary spermatocytes when present, occur in nests adjacent to the primary spermatocytes (Fig. 7.1 D).

5. Spermatids - The secondary spermatocytes divide to produce spermatids. The nuclei of these spherical cells have a mean nuclear diameter of 2.7 μm, and resemble the spermatogonia in staining quality. Invariably, the spermatids occurred in large nests outside the central body of spermatozoa (Fig. 7.1 D).

6. Spermatozoa - The transformation of the spermatids into spermatozoa occurs in the centre of the tubule lumen. The nuclei of these small cells stain intensely and homogeneously and are bullet-shaped in appearance, having mean dimensions of 3.8 x 1.4 μm (Figs 7.1 C and D).

Oocyte maturation

The classification of oocyte maturation stages was based on the general scheme used by Tranter (1958) for describing the histological changes in the ovaries of the Australian pearl oyster, *Pinctada albina*.

Oogonia and early previtellogenic oocytes (oocytes 1 and 2 of Tranter, 1958) stain heavily as little observable cytoplasm is present in these cells. They are found imbedded in the follicle walls and were infrequently observed in the sectioned material.

At the onset of vitellogenesis, the oocyte becomes attached to the follicle wall amongst the nutritive granules, by a flat broad base of attachment (Fig. 7.2 C). The cytoplasm of the semi-oval cell stains less heavily than the nucleus (oocyte 3).

The oocyte increases in size and the cytoplasm stains more heavily as yolk accumulates (Fig. 7.2 C). The base of attachment constricts and the stalked oocyte becomes almost spherical in appearance (oocyte 4).

By this stage, the oocyte has grown towards the centre of the lumen; final detachment from the follicle wall occurs and the ripe oocyte lies free in the lumen (Fig. 7.2 C). After detachment, the cell is termed the free or primary oocyte.

Amongst the sectioned material, no atretic oocytes were ever observed.

7.4.2 Seasonal histological changes in the gonads

7.4.2.1 The testes

Examination of the proportions of spermatogenic stages calculated for each individual from the one time and location, revealed little variation in the relative proportions between the 5 individual testes. Because of this similar appearance, the proportions were averaged over the 5 individuals to provide a combined composition by cell type for each month and location. The relative proportions of spermatogenic stages observed for each month and waterbody are shown in Figure 7.3.

Having calculated the relative proportions of spermatogenic stages, it is apparent that spermatogenesis occurred throughout the year as indicated by the presence of most of the early stages in the testes at any one time. The relative equitability of the environment in Mudginberri in particular, is reflected in the similar constancy at which spermatogenesis takes place in males throughout the year in this billabong (Fig. 7.3). However, elsewhere periods of inactivity were noted. Inactive phases were recognised by relative absence of the stages of typical spermatogenesis (spermatocytes and spermatids). In accordance with the findings of others (Ropes and Stickney, 1965; Heard, 1975; Jones and Simpson, in prep.), most of the spermatogenic activity is atypical during these phases, activity being directed towards production of sperm morulae. The characteristic appearance of the testes at these times is shown in Figures 7.1A and C. Sperm morulae, spermatogonia and spermatozoa (residual?) are chiefly observed. Atypical and typical spermatogenesis are nevertheless not mutually exclusive events, and sperm morulae are often found amongst the typical spermatogenic units (e.g. Magela Creek channel, January; Mudginberri, June, July, September; Nankeen, September - Fig. 7.3). Inactive phases where found in the testes of males in Georgetown during the early-mid Dry (June and September), in the testes of aestivating Creek mussels (November and December) and early Dry season testes in Nankeen (June).

Other than the periods stated above, the testes were otherwise active, and spermatozoa were dominant. Activity in Mudginberri mussels was discernible throughout the year. The appearance of the testes during active phases is shown in Figures 7.1 B and D. Spermatozoa and the stages characteristic of typical spermatogenesis dominate the tubules.

Active gonads with the presence of sperm (and ripe oocytes) throughout much (if not all) of the year, is concomitant with the notion that spawning in V. angasi is repetitive. This could be expected in equitable, warm-water and tropical environments, and in relation to the testes, implies that sperm is continuously produced and released throughout the year. The actual presence and quantity of sperm in the seminiferous tubules therefore, give no indication of the intensity of spermiogenesis and resultant spawning, as the sperm is constantly in a state of flux. Rather, under these circumstances, the presence and abundance of the stages of typical spermatogenesis - spermatocytes and spermatids (but especially the latter) may be expected to reflect spermiogenic activity and subsequent release of sperm, i.e. spawning intensity.

Spermiogenic activity of V. angasi in the present study was found to respond to the same factors that influence oocyte and larval production in the female cycle. To demonstrate this, the following regression analyses were performed. In the reproductive cycle of the female, larval production (% of females brooding embryos and larvae in the marsupia at any one time and location) was extensively studied and environmental correlates that might influence it, determined. (Larval production nevertheless, directly and immediately reflects the simultaneous production of oocytes occurring in the ovaries, section 7.4.2.2.) Larval production for the same period and locality was regressed against each of the spermatogenic stages occurring in the testes. Both variables were arcsine transformed, and the results of the linear regressions for each spermatogenic stage and location are shown in Table 7.1. As a whole year's data were analysed from Mudginberri billabong, more confidence is stored in the conclusions drawn from these results. From the results in general, the following conclusions and remarks can be made:

1. The abundance of spermatids correlated positively with larval production. In Mudginberri billabong this correlation was high and a very significant regression relationship was found ($P < 0.01$). This same relationship was the strongest found in Nankeen billabong. These results indicate that spermiogenesis and spawning in males occur with the same intensity as larval production (and thus oocyte production and spawning) in females.

2. In the three billabongs, all stages of typical spermatogenesis correlated positively with larval production.

3. The relative compactness of sperm in the tubules (the 'empty' category of Table 7.1) correlated negatively with larval production, indicating that spermiogenesis and larval production proceed with the same intensity. In Mudginberri, this relationship was significant ($P < 0.05$), even though sperm abundance declined over the same gradient. The latter suggests that spawning of males in Mudginberri billabong is exceedingly intense and that sperm release is a continuous event, peaking with larval production.

4. The presence of sperm morulae (and thus atypical spermatogenesis) in the tubules correlated negatively with larval production (and also spermiogenic activity).

5. Spermatogonia appeared to play a passive role in cycles of spermatogenesis as they were constantly present in the tubules (Fig.

7.3). Their omnipresence indicates that they act as a reservoir of germ cells for all spermatogenic redevelopment.

Of the factors that promote larval production (and therefore oocyte production) in the billabongs, increasing water temperature (Mudginberri and Georgetown) and oxygen concentration (Nankeen), and decreasing turbidity (Georgetown) are strongly implicated (section 7.10.1). According to the relationships found in point 1. above therefore, spermiogenic activity responds to these same factors. Thus, it appears likely that the intensity of spawning in both sexes of V. angasi is simultaneous.

Of final interest is the observation that spermatogenesis proceeded apparently uninterrupted in mussels from the Magela Creek channel, aestivating during November and December. Normal physiological processes such as gametogenesis in V. angasi therefore, are not suspended during dormancy. Increasing ambient temperatures were presumably responsible for the increase in spermatogenic activity observed in Creek mussels over the period encompassing aestivation and subsequent inundation (January).

7.4.2.2 The ovaries

Superficially it was assumed that owing to the presence of primary oocytes in the ovaries year round, in association with the gravid condition of the marsupia for much of the year, oogenesis and spawning in female V. angasi occurred throughout the year. However, the exact nature, intensity and timing of the events could not be shown without investigating the seasonal activity and development of oocyte maturation in the ovaries. The oogenic cycle in the ovaries was followed by monitoring seasonal changes in the size and numbers of primary oocytes. In the ovaries of both temperate (e.g. Zale and Neves, 1982a; Jones and Simpson, in prep.) and tropical (Dudgeon and Morton, 1983) unionaceans, either the absence of primary oocytes or a sharp decline in oocyte diameter immediately after a period of reproductive maturity has been assumed to indicate that spawning had occurred.

For each location and sampling period, a mean oocyte number per follicle and mean oocyte diameter were calculated from the individual observations averaged for the 5 sectioned ovaries. The values and 95% confidence intervals about the means, are shown in Table 7.2. From microscopic inspection of the ovaries, changes and patterns in oocyte sizes between individuals, localities and sampling periods were not visually discernible. However, periods of inactivity just as in the male gametogenic cycle, or a partially spawned appearance in the ovary, were readily observed by visual assessment of oocyte numbers in the follicles. In a relatively inactive or partially spawned ovary, primary oocytes were noticeably fewer (Fig. 7.2 A) than in the active ovary (Fig. 7.2 B).

Mean oocyte number

Both oogenic activity in terms of mean numbers of primary oocytes per ovarian follicle, and the percentage of gravid females observed over all individuals examined from the same monthly collections, are plotted with respect to billabong and against time in Figure 7.4. Clearly, the ovaries and marsupia are in close communication with each other and there is an immediacy of response to the intensity and activity of oogenesis by spawning and subsequent production of larvae. The breeding pattern is apparently a repetitive one for unlike distinct, seasonal breeding cycles observed elsewhere, spawning in V. angasi does not result in an immediate fall in oocyte numbers in the follicles. Rather oocyte and subsequent larval production occur simultaneously, and the only indication of a spawning stress was observed in Mudginberri billabong (for which the seasonal cycle is complete) when between July and November, the intensity of larval production was apparently so high that a lag in oogenic activity was observed (Fig. 7.4).

For the 12 monthly observations in Mudginberri billabong, analysis of variance (AOV) testing was performed to discern whether the mean oocyte numbers of the 5 observations differed when they were partitioned according to the different stages of gravidity observed in the respective marsupia. Although considered in detail in a later section (section 7.9), the marsupial condition for the purposes of this analysis, was classified: 'empty'; with 'developing larvae'; and 'mature larvae'. The analysis revealed no significant difference ($P > 0.05$) in oocyte numbers among the different marsupial states. The mean oocyte numbers determined were: 4.50 (empty); 4.15 (developing larvae); and 5.30 (mature larvae).

When the partitioned data were replotted with respect to season, however, particular patterns emerged (Fig. 7.5). In the active phases of the oogenic and larval cycles (from the peaks in activity observed in Fig. 7.4), least oocytes were observed in the gonads of females simultaneously brooding developing larvae (Fig. 7.5). This is to be expected as presumably, individuals either (1) with empty marsupia that have recently discharged their larvae and whose marsupia are ready to receive a new batch of eggs or (2) with fully developed glochidia, have had a longer period since the previous spawning for the gonads to have recovered. During relatively inactive phases of the oogenic and larval cycles (Fig. 7.4), however, least oocytes were observed in the ovaries of females with empty marsupia (Fig. 7.5). Various environmental factors at these times inhibit or retard gonadal and larval development (section 7.10.1), and apparently females with empty marsupia represent a condition in which oogenesis is slowed to such an extent that not enough eggs are availble for spawning and subsequent brooding.

<u>Mean oocyte diameter</u>

Oogenic activity in terms of mean oocyte diameters, and the percentage of gravid females observed from the same monthly collections, are plotted with respect to billabong and against time in Figure 7.6. Seasonal patterns in oocyte diameters are less obvious than the patterns involving oocyte numbers. Only the diameters of free, primary oocytes were measured and presumably a relatively advanced, developmental threshold is required before the oocytes break away from the follicle wall. Tranter (1958) in fact, thought it doubtful whether there would be any further growth of primary oocytes after they had broken free into the lumina of the ovarian follicles in

Pinctada albina. However, assuming eggs discharged into the marsupia are of a constant size, then the differences in sizes of free, primary oocytes observed in the lumina of the ovarian follicles of V. angasi between sampling periods and locations (Table 7.2), are themselves evidence that either vitellogenic growth, or expansion of the eggs must occur here. (It was noted for V. angasi nevertheless, that larger eggs were produced in higher trophic environments - Georgetown, Mudginberri, Nankeen billabongs - in that order, Fig. 7.6.)

An interpretation of the data of Figure 7.6 is as follows. During periods of gonadal activity (as previously discerned by mean oocyte numbers in the follicles) larger eggs are closely associated with increased spawning and intensity of larval production (Mudginberri between July and November; Nankeen in September). Only after a period of peak ovarian activity and larval development does the effect of repetitive spawning finally outpace oocyte development, reflecting in smaller egg sizes (Georgetown in March, Mudginberri in December and April). During inactive phases in the ovary, the fewer oocytes present (Fig. 7.4) are nevertheless fully matured and developed. Their larger size (Fig. 7.6) suggests that they have accrued and developed for some period of time in readiness for the next spawning (Georgetown between September and December; Mudginberri between January and March; Nankeen in June and March). The small egg sizes observed in Mudginberri during July, the coolest month, are best explained by a retardation of oogenesis caused by low water temperatures.

Exceptions to the above patterns (e.g. Nankeen in December) may also be explained after partitioning individual observations according to different stages of gravidity. AOV testing in Mudginberri billabong revealed a significant ($P < 0.05$) difference in oocyte size among the different marsupial states (as classified earlier). Multiple range testing (least significant different test: Zar, 1974, p. 151) showed that while the oocyte means of individuals with empty marsupia (47.9 µm) and ones bearing mature larvae (48.9 µm) were compatible, the oocyte means in individuals bearing developing larvae (43.2 µm) were significantly lower than either ($P < 0.05$).

When the partitioned data were replotted with respect to season (Fig. 7.7), the same general patterns emerged as were discovered when mean oocyte number was partitioned according to the different stages of gravidity. Active ovarian development resulted in larger eggs in females both brooding mature larvae and with empty marsupia. (The same interpretation of this phenomenon can be given to oocyte diameter, as was previously given in relation to oocyte number.) During inactive phases, however, some females with empty marsupia bore larger eggs in the ovaries than those with developing larvae in the marsupia (Georgetown in September, Mudginberri in June, Nankeen in December). As mentioned above, this might reflect additional development available for the eggs owing to their retention in the ovaries for relatively prolonged periods.

Overall

Oogenic activity in terms of production of primary oocytes is best represented by mean numbers of oocytes per ovarian follicle. That the pattern of larval production may be directly superimposed upon that of oogenic activity reflects the close communication of the ovaries and marsupia: the intensity of oogenesis is immediately reflected in the intensity of larval production. A series of repetitive breeding cycles is concomitant with this description. (Very strong evidence for the latter is given in section 7.15.2.) Knowledge of primary oocyte size adds supplementary information concerning recognition of peaks in spawning intensity (marked by declines in oocyte diameter) and periods of ovarian recovery (indicated by increases in oocyte diameter when oocyte numbers are low).

Evidence from the previous section (section 7.4.2.1) suggests that the timing of both spermiogenic at least, and oogenic activity (and therefore spawning of both sexes) is the same, and both cycles are presumably therefore, influenced by the same environmental factors (described in section 7.10.1).

Finally, just as spermatogenesis proceeded uninterrupted in aestivating mussels from the Magela Creek channel between November and December (1981), so too oogenic activity proceeded uninterrupted (Table 7.2). Both mean primary oocyte numbers and diameters increased over the period, presumably in response to increasing ambient temperatures. Inundation during January resulted in decreases in oocyte numbers and sizes presumably as a result of spawning.

B. STRUCTURE OF THE BREEDING POPULATION

7.5 Hermaphroditism and sexual integrity

Among the mussels from Georgetown, Mudginberri and Nankeen billabongs, and the Magela Creek channel sexed by inspection of gonadal smears, individuals were occasionally found in which both ripe eggs and sperm were present. Heard (1975) classified occasional hermaphrodites amongst normally dioecious unionids as male or female hermaphrodite, according to the predominant gonad prevailing. Smears, however, are known to be a less reliable technique both for determining the presence of hermaphroditism and for assessing the comparative abundance of ovarian and testicular tissue (Heard, 1975). Having determined by smears that the gonads were of an hermaphroditic nature, the assignment into male or female hermaphroditic categories was made according to inner gill morphology: male hermaphrodites possessed non-marsupial inner gills while the inner gills of female hermaphrodites were marsupial in appearance.

The incidence of hermaphroditism according to different age classes of mussels from the populations investigated, is shown in Table 7.3, while seasonal incidence of hermaphroditism amongst male and female hermaphrodites is displayed in Table 7.4. Among the individuals histologically sectioned, occurred 6 hermaphrodites; 3 of these had not previously been discovered from gonadal smears. Thus the incidence of hermaphroditism among the populations studied, as shown in Table 7.3 needs to be corrected for cases where the condition is undetected by smears. Assuming that the incidences are only half represented, nevertheless hermaphroditism in _V_. _angasi_ is uncommon and is confined to less than 2% of each of the populations investigated (Table 7.3).

The nature of the gonads of sectioned hermaphrodites is given in Table 7.5. Testicular tissue predominated (5 out of 6 cases), and the discrete ovarian follicles or testicular tubules were mostly confined to distinct regions of the gonad (5 out of 6 cases) (Fig. 7.2 D). In contrast, the majority of known North American hermaphroditic unionids either bear gonads with monoecious acini (in which both eggs and sperm are produced) or gonads with intermingled zones of male and female acini (Heard, 1975). Only one hermaphrodite sectioned in the present study displayed the latter condition (Table 7.5).

Summarising known information on North American unionids, Kat (1983d) states that hermaphrodites reproducing chiefly as males are either very uncommon or when present in appreciable numbers contain less than 5% female tissue. In _V_. _angasi_ the predominant visceral sex of hermaphrodites corresponded with the morphology of the inner gills in 5 out of 6 cases (Table 7.5). If the same relationship is applicable to all the hermaphrodites examined, then hermaphrodites of _V_. _angasi_ in the Magela Creek reproduce both as males and females more or less equally. Twelve male and 14 female hermaphrodites were detected by gonadal smears (Table 7.4). Moreover, the ovarian follicles in male hermaphrodites occupied more than 5% of the gonadal tissue (Table 7.5). Thus the nature of hermaphroditism in the hyriid _V_. _angasi_ differs from that found in unionids. According to Kat (1983d), unionids reproducing chiefly as females are common and are highly variable with respect to the amount of male tissue found in the gonad. While male and female hermaphrodites were equally common, nevertheless the gonads of female hermaphrodites of V. angasi are apparently equally variable. Two individuals with female inner gills contained testicular tissue varying from less than 40% to more than 90% (Table 7.5). This observation accords with Kat's (1983d) hypothesis that disruption of hormonal levels determining sex by developmental error should result in considerable variability in male:female gonadal ratios among females as the sex of females is hypothesised to be determined by high hormone levels.

Hermaphroditism has been previously implicated as providing evidence of sex reversal in unionids (e.g. Bloomer, 1934, 1935, 1939). The possibility of consecutive, rhythmical consecutive, and alternative sexuality (Coe, 1943) was investigated in V. angasi.

Consecutive sexuality is sex reversal in which there is a single change in the functional sexuality of the individual, usually from male to female (Coe, 1943). Protandry is one such example. Chi-square analyses were performed on the data of Table 7.3 to discern whether occasional hermaphrodites were distributed evenly amongst the age classes of the various populations studied. No evidence against the hypothesis of equal distribution ($P > 0.05$) was found, although the chi-square value of the Mudginberri data was high ($\chi^2 = 39.4$ on 31 DF). The incidence of hermaphroditism amongst the large numbers of young of year mussels examined in this billabong is disproportionately high (Table 7.3).

Inspection of Table 7.6 reveals that the sex ratios of young of year mussels are often strongly biased in favour of males, particularly in populations where smaller individuals are well represented (Georgetown and Mudginberri billabongs). Sexual maturity in V. angasi is size dependent (section 7.7) and from Table 7.7 it is apparent that the gonads of small individuals function initially as males. (This observation is best exemplified in populations in which larger sample sizes are available.) The apparent protandry is not the result of an earlier maturation of males; once mussels exceed 30 mm in length, few immature and indeterminate gonads are found (Table 7.7) and yet the proportion of females still remains relatively low.

Presumably amongst juveniles, protandry is accompanied by hermaphroditism in which the dominant gonad does not necessarily correlate with inner gill morphology. No histology was undertaken to investigate this, however. Further, an intermediacy should be noted in the inner gills between the marsupial and non-marsupial condition of at least some individuals. This was not observed. Presumably the change in morphology occurs very rapidly. In any case the distinction between marsupial and non-marsupial gills in mussels so small is not always so clear.

In section 6.7.1, significant declines were noted in the proportions of females, with increasing age in some mussel populations of the Magela Creek. Long term mark-recapture studies may be needed to determine whether consecutive sexuality is the cause of these declines. However, there is very little evidence to suggest that this form of sex reversal did occur in the populations in question as: 1) incidence of hermaphroditism, that may suggest a sex change, is overall very low; 2) in Mudginberri billabong where a rapid decline in the proporton of females was observed over the oldest age classes (Fig. 6.34), no noticeable increase in the incidence of hermaphroditism was noted (Table 7.3); and 3) significantly, visceral sex and the dominant gonad of hermaphrodites, are consistently correlated with morphology of the inner gills of mature mussels regardless of their age. For these populations, differential mortality between the sexes may be the best explanation available for the observed change in sex ratio with age (section 6.7.1).

Rhythmical consecutive sexuality is observed where the initial phase is male, followed by a series of alternating female and male phases throughout life (Coe, 1943). For the reasons given in points 1) and 3) above, it is very doubtful that this type of sexuality characterises populations of _V_. _angasi_ in the Magela Creek.

Alternative sexuality is a sex reversal in which adults function seasonally as separate sexes. No patterns were observed in the seasonal incidence of hermaphrodites amongst the different populations (Table 7.4) that were suggestive of a sex change confined to a definite period of the year at least. Figure 7.8 shows the seasonal fluctuations observed over the study period in the sex ratios of mussels between the different populations of the Magela Creek. The decline in the proportion of females observed during the Wet-Dry interchange (April and May, 1981) in Jabiluka billabong suggested a strategy whereby females changed sex in response to the anoxic environment that prevailed at the time. During January of the following Wet season (1982), known female mussels from the respective billabongs (sexed by observing individuals aborting larvae in the laboratory) were marked and subsequently released in Jabiluka and Mudginberri. Upon recollection at the end of May (1982), all individuals were found to be female, showing that no sex change had occurred over the period.

Nevertheless while no more than random sampling error is assumed to account for the seasonal fluctuations observed in the sex ratios in most populations, definite patterns were discernible in both Georgetown billabong and the Magela Creek channel (Fig. 7.8). Both patterns are almost in phase with one another, and two cycles are apparent each year. The proportion of females is lowest at the end of the Dry and again at the end of the Wet. Peaks in proportions of females are observed in between these periods.

Although the sexes tend to occupy different habitats in different seasons in Georgetown billabong (section 6.8.1), the nature of sampling in this billabong using transects, was such that no sampling biases were likely (section 3.1). In Georgetown as in all the billabongs, visceral sex consistently correlated with morphology of the inner gills of mature mussels, regardless of season. Moreover, hermaphrodites were least common in this billabong (Table 7.3), both factors arguing against alternative sexuality. No satisfactory explanation is available to explain the seasonal patterns in sex ratios observed in Georgetown billabong. (The only apparent environmental factor that resembles the diphasic pattern is water temperature but the relationship between temperature and sex ratio in

V. angasi is unknown.)

During 1981, a peak in female proportions was observed in Creek mussels at the onset of aestivation (July), and declined over the entire period of dormancy (up to Demember). It is tempting to suggest that the rigours of dormancy promote a strategy whereby it is energetically more expedient somehow, for these mussels to aestivate as males. The highest proportion of hermaphrodites was observed in this mussel population (Table 7.3), and of further note is that the inner gills of females are not entirely marsupial in appearance (section 7.3). A sex reversal is therefore not inconceivable for mussels from the Magela Creek channel, particularly in consideration of the rigours of their environment.

In conclusion, it is highly unlikely apart from protandry, that sex reversal occurs seasonally or throughout the adult life of billabong populations of V. angasi (and in all likelihood that of the Magela Creek channel). Hermaphroditism is only occasional, and by all appearances sexual integrity in V. angasi is high. Further long-term investigations are required to determine the causes of the observed fluctuations in the sex proportions of mussels in Georgetown billabong and the Magela Creek channel. Sampling biases may yet explain the patterns.

Among various North American unionids studied by Kat (1983d), occasional hermaphroditism among populations of predominately dioecious species was found to be associated with the presence of digenean trematodes within the gonads. Cercarial infections were also noted in the gonads of V. angasi. In severe cases gametes were entirely absent and mussels were rendered functionally sterile by the sporocysts (Fig. 7.1 E). No doubt all heavily infected individuals were detected by gonadal smears. Histology, however, showed that 2 out of 5 infections found were so light that they were not previously detected by smears.

The seasonal occurrence of cercarial parasitism as determined by gonadal smears is shown for the different waterbodies in Table 7.8. Corrected infection rates from histological observations are also given in this table. The infection rates overall are low, but during the Dry season in Georgetown billabong up to 10% of the population was infected. Infections in mussels from the Magela Creek channel and Mudginberri and Nankeen billabongs invariably occurred only during the Wet season. In Georgetown, however, peak infections were observed during the mid Dry and were associated with a period of low physiological condition (body weights) of mussels (section 8.7.1). Because of the generally low incidence of infections observed, the reproductive potential of populations of V. angasi was presumably not affected to any significant degree. Female mussels, however, are apparently more susceptible to infection than males (Table 7.8).

There was no correspondence between incidence of cercarial infection and occasional hermaphroditism in the Magela Creek waterbodies. In fact the Georgetown billabong population had the highest incidence of cercarial infection but the lowest incidence of hermaphroditism, whilst the reverse situation applied to the population from the Magela Creek channel. Presumably very high incidences of parasitism (up to

80% in Kat's (1983d) populations) are required in order for trematodes to cause hermaphroditism via disruption to hormonal levels. Errors in developmental processes are likely to be responsible for observed hermaphroditism amongst populations of V. angasi in the Magela Creek. That the incidence of hermaphroditism is highest in the Magela Creek channel, where normal metabolic processes such as filtering and reproduction are periodically brought to an abrupt halt at the onset of dormancy each Dry season, is supportive to this hypothesis.

7.6 Sex ratio

The sex ratio of mussel populations in the Magela Creek varied with age. In most waterbodies (and probably in all populations) the primary gonad is apparently male (section 7.5) and within several billabongs a decline in the proportion of females with age was observed (Fig. 6.34). In one or two populations moreover, seasonal fluctuations in sex ratios were discerned (section 7.5, Fig. 7.8).

Averaged over seasons and age classes, however, the proportion of females in the waterbodies invariably falls below a 1:1, male:female sex ratio (Table 7.6). Tests of departure from a 1:1 sex ratio were performed on the proportions, using the normal approximation to the binomial test (Zar, 1974, p. 289). Significant departure from equal proportions of the two sexes ($H: p = 0.5$) resulted for populations from Jabiluka ($P < 0.05$) and Buffalo and Leichhardt ($P < 0.01$) billabongs.

The low proportions of females observed may partly be explained in terms of longevity, and dissolved oxygen concentration in the billabongs. The longest-lived populatios are found in Mudginberri and Buffalo billabongs and in Mudginberri at least, males live significantly longer than females (section 6.7.1). It is notable, however, that both environments in which females are most underrepresented - Jabiluka and Leichhardt billabongs (Table 7.6), have the lowest mean concentrations of dissolved oxygen, averaged over the seasons, of the populations sampled (Table 2.7). This finding adds further strength to the claim that low dissolved oxygen concentrations are most stressful to females, and the decline observed in the proportions of females with increasing age are very likely the result of this stress (section 6.7.1). Low values of dissolved oxygen that are at least periodic in most of the billabongs, may partly explain why the proportions of females are invariably always lower than those of males.

7.7 Age and size at sexual maturity

Gonadal maturation in V. angasi was determined by examination of smears for the presence of spermatozoa or primary oocytes. From Table 7.7 it is apparent that gonadal maturity is size dependent, and the mature gonad is first distinguishable from the undifferentiated gonad somewhere between the size ranges 25.0-29.9 and 30.0-34.9 mm. These size classes generally lie well within the growth attained by mussels in their first year in all study populations (Tables 6.9-6.19).

Gonadal maturity was followed in more detail in juvenile mussels from Mudginberri billabong. Gonadal smears were made of 79 young of year mussels at various times during 1981. All mussels greater than 30 mm in length possessed mature gonads. Details of the gonadal appearance of all mussels below this size are shown in Table 7.9. Below 30 mm, the sex of most individuals cannot be reliably determined. Age at gonadal maturation can be determined from the data of Table 7.10. 50% of mussels reach maturity at approximately 0.5 years of age, while all mussels are mature by an age of 0.8 years. Mature gonads may be found in individuals as young as 0.2 years.

The mean sizes of female young of year mussels in which brooding larvae were found, were used to determine the age and size at which mussels first spawned and brooded young. The results for a number of populations are shown in Table 7.11. (Details of the developmental stages of the larvae are given in section 7.9). The broader range in size at first gravidity, as compared to the size range at gonadal maturation, is more apparent than real, partly because of low sample size, and because larval production is very sensitive to various limnological factors such as temperature, dissolved oxygen and turbidity (section 7.10.1). The greater size recorded of females brooding young in Leichhardt billabong for example, resulted from anoxic conditions during the early Dry seasons that prevented brooding at an early age (section 7.10.1). The minimum mean sizes at which females were first observed brooding young (Table 7.11) are therefore assumed to be the sizes at which females in most populations may potentially spawn and become gravid. Thus first gravidity like gonadal maturity is size dependent and occurs at a size of approximately 40 mm.

Again age and size at which females first brooded young was studied in greater detail in Mudginberri billabong. The marsupial condition of all females collected during September, October and November 1981 is shown in Table 7.12. No brooding young were found in mussels below a size of 36.0 mm, and most females greater than 38 mm in length were gravid. The mean age at first spawning and brooding in Mudginberri billabong, extrapolating to the population as a whole, is reached at approximately 0.8 years (Table 7.10).

Assuming a size at first spawning and brooding of 40 mm, and extrapolating from the growth data of Tables 6.9-6.19, the mean age at first spawning and brooding lies within an age span of from 0.6 to 1.5 years (Table 7.11) depending upon the growth rates of mussels within the various waterbodies. In all populations, however, sufficient growth is reached by a more or less significant proportion of individuals, that some spawning and brooding by young of year mussels occur.

7.8 Senescence

The percent of gravid females with respect to age is plotted in Figures 7.9 and 7.10, for each of the Magela Creek waterbodies. In 7 out of the 10 populations, gravidity was observed to decline significantly with age. The populations in which significant declines were noted and the respective regression equations describing the relationships are shown in Table 7.13. Both linear and quadratic weighted regression equations were fitted to the data (the dependent variable being arcsine transformed), but in only two populations

(Leichhardt and Jabiluka billabongs) was the quadratic model appropriate (Table 7.13).

There was a decline in gravidity with age in most of the populations of V. angasi in the Magela Creek. This decline appears to operate over much of the life-spans of mussels in the various populations (Figs 7.9 and 7.10). Larval production correlates directly with the mean number of primary oocytes in the ovarian follicles of V. angasi (Fig. 7.4). Thus with increasing age, oogenesis and oocyte production decline in activity. In the largest of the females histologically sectioned (85 mm from Nankeen billabong), the ovarian follicles were entirely devoid of primary oocytes - an unusual occurrence in all of the mussels sexed and sectioned. No attention was paid to the likelihood of the same decline in reproductive activity in male V. angasi. Superficially, no discernible changes were noted in the testes from the many gonadal smears made, and from the sections examined. In both sexes, however, condition (relative body weight) was noted to decline with age (section 8.7.2). Declining reproductive activity is compatible with this observation.

The data of Mudginberri, Buffalo, Leichhardt and Jabiluka billabongs clearly indicate a peak in reproductive potential reached in the fourth, fifth, third and sixth years of life respectively (Figs 7.9 and 7.10) after which a long and gradual senile or post-reproductive phase occurs. In other waterbodies, the full reproductive potential is reached in the very first year or so of life (Figs 7.9 and 7.10).

In all probability the long and gradual senile phase of declining reproductive activity V. angasi is limited to or most prominent at least in females. Again the protracted nature of the decline in reproductive potential, may be suggestive of a physiological weakening of females by Dry season stresses (e.g. turbidity and anoxia) to which they are particularly sensitive to by virtue of the brooding, feeding and respiratory function of the gills. Repetitive spawning (section 7.11) might further exacerbate the decline. A post-reproductive and senile phase in females of V. angasi provides further supportive evidence that females are shorter-lived than males amongst several populations at least in the Magela Creek (section 6.7.1).

C. LARVAL PRODUCTION

7.9 Stages and rate of larval development

Stages of larval development

The development of brooding young of V. angasi was observed and divided into three stages. Such a classification was originally thought useful for determining the times of spawning, incubation period, the period of glochidial release and the number of broods of larvae produced per year. All developmental stages were studied under low power microscopy, using living material. Photomicrographs of the stages are shown in Figure 7.11. The large amounts of yolk material present in the early embryological stages precluded any attempts at studying the cleavage processes. By all accounts nevertheless, the appearance of the developmental stages of larvae of V. angasi apparently does not differ greatly from the records of Lillie (1895) and Wood (1974a) for unionids.

Although a continuum of development is present in embryogenesis (Fig. 7.11), and therefore the classifications are rather arbitrary, certain morphological features were very characteristic of each stage. Including the non-gravid condition, the larval classifications are as follows:

'Empty' - No developing embryos or larvae were present in the marsupia.

'Early larvae' - The developmental continuum of early larvae is shown in Figure 7.11 A-C. Early larvae included developmental stages from zygote through all cleavage divisions to at least gastrulation. The embryonic appearance ranged from an early spheroid (Fig. 7.11 A) to a more advanced elliptical (Fig. 7.11 B-C) mass of cells enclosed within a vitelline membrane. Apparently the larger dorsal end is the rudimentary, ectodermal shell gland. No other morphological features, however, characterise the embryos. (The stages represented in Fig. 7.11 A-C are relatively advanced embryos.)

'Developing larvae' - Other than minor (largely unrecognisable) cellular developments, the most discernible feature of the developing larvae following gastrulation, is the appearance and development of the larval adductor muscle. Developing larvae are shown in Figure 7.11 D-F, and the adductor muscle is apparent as a cross band of striated tissue within the centres of the larvae. In the latter stages of this developmental phase, slight invagination of the larval mantle is apparent (seen in the right-most larvae in Fig. 7.11 F).

'Glochidia' - The chief distinguishing feature of the transformation phase of young larvae into glochidia is the continuing invagination of the larval mantle to affect the bifid condition of the mature larva. Accompanying this movement is the formation of the larval shell. As yolk is absorbed, the shell becomes progressively thinner until the typical translucent appearance of the mature glochidium is reached. The various glochidial stages are shown in Figure 7.11 G-I. Early glochidia (Fig. 7.11 G) are enclosed in the vitelline membrane. The shell margins are not necessarily partitioned fully and remain untoothed. Mature glochidia are invariably free of the vitelline membrane, and possess well developed teeth (Fig. 7.11 H) and a sticky, larval thread (Fig. 7.11 I).

Accompanying each of the developmental stages is a corresponding change in colour of the larvae when observed in the intact marsupia, brought about by yolk absorption and shell formation. Early larvae appeared white to pale yellow; developing larvae, yellow to light brown; and glochidia, a light to a darker shade of tan. Development in fact could be followed on colour changes alone. However, the embryos and larvae of all gravid females dissected were sorted into stages microscopically. No unfertilised eggs were encountered, and without exception developmental stages were highly synchronised, indicating that the young mature and are released from the mother at the one time. Finally, in eutrophic waters (e.g. Island, JaJa, Jabiluka and Leichhardt billabongs) the larval masses were noted to fill the entire inner gill of females. In other populations, the portion of the gill used to incubate young was generally restricted to the inner two thirds.

Rate of larval development

Because 1) larval development was not synchronised between individuals collected at the same time and location, 2) females brooded young continuously for most of the year, and 3) the developmental time was very short in relation to the monthly interval between samples, the staging of larval development performed routinely on gravid females did little towards assisting the determination of the rate at which young develop in the marsupia. Faced with the same problems, Kenmuir (1981b) monitored the developmental rate of larvae in tropical Lake Kariba by periodically prising open the valves of marked female mussels from the lake, probing the marsupial gills with sharp-pointed forceps and staging the larvae so sampled. The results achieved by these methods, however, must be viewed with some suspicion. Disturbance of brooding females commonly results in abortion (noted by Kenmuir (1980) himself, amongst many other authors - see section A4.2), and the resulting patterns observed may merely reflect the attempts of the disturbed mussels at re-etablishing the marsupial brood with a subsequent alteration in the release date.

Interruptions to larval development in mussels from the Magela Creek populations occurred often, and resulted from adverse environmental conditions (section 7.10.1). During these periods, it was common for all females to have aborted brooding young or to be inhibited from further production of larvae. Use was made of this phenomenon in ascertaining the rate of larval development in V. angasi in the Magela Creek. Having sampled mussels in a synchronised condition of empty marsupia, the subsequent sampling date at which mature larvae reappeared in the marsupia indicated the rate of larval development.

From Figures 7.12-7.14 it is seen that recovery, after such periods of non-gravidity, to the stage of mature larvae present in the marsupia can occur by the time of the proceeding monthly collection. Glochidia appeared after 40 days in Island (Jun./Jul., 1981), 41 days in Corndorl (Jan./Feb., 1982), 42 days in Leichhardt billabong (Jun./Jul., 1981) and 44 days in the Magela Creek channel (Dec./Jan., 1981). All of these periods encompass both winter and summer months, and therefore even for the slowest rates in winter, larvae had developed within a 40-42 day period. Sampling at shorter intervals was carried out in Corndorl billabong (Nov./Dec., 1981) and in the Magela Creek channel (Nov./Dec., 1981), for which recovery after a period of cessation in larval production was noticed (Figs 7.12 and 7.13). Glochidia appeared after 15 days in Corndorl and after 12 days in the Magela Creek channel. Of interest is the observation that the latter population had been aestivating 12 days prior to collection in December, 1981; subsequent inundation resulted in immediate spawning and very rapid development of active, mature glochidia, free of the vitelline membrane. Larvae were probably mature even for some days prior to collection.

Development rates are presumably affected by temperature, and larvae may require a longer period to develop during the winter than the minimum rate of 12 days recorded during the summer. However, the winter rate does not exceed 40 days and is probably much closer to the maximum of 12 days noted during summer.

7.10 Seasonal pattern of larval development

7.10.1 Between waterbodies

Seasonal breeding activity of V. angasi in relation to larval production was determined by compiling the monthly occurrences of the gravid stages recorded over the entire period of investigation, for each of the study populations. Larval production in each of the populations, represented by histograms of the monthly marsupial appearance of females, is shown in Figures 7.12-7.14. From these figures, it is apparent that at any one time and location, all developmental stages of larvae may be present in different individuals comprising the population. The asynchronised nature of larval development within the populations and the observation that larval production can occur over the entire year were superficially suggestive of repetitive breeding in V. angasi (substantiated in section 7.11).

Seasonal patterns of larval production were discernible within most of the waterbodies, but rarely was the same pattern common between any two locations. Major interruptions to larval production in particular were a feature of several populations, especially those from the floodplain billabongs (Figs 7.12-7.14). Thus the seasonal appearance of larval production varied quite considerably amongst the waterbodies.

While no one obvious environmental variable was the cause of the marked variations observed both within and between the billabongs, several factors - of climatic and limnological nature, seasonal in occurrence, and in combination - were strongly implicated to affect the patterns of larval production. A largely aseasonal breeding cycle was evident for V. angasi populations in the Magela Creek. Within this general perspective, however, a background breeding pattern dependent upon temperature was apparent while superimposed upon this, the cycle was shown to be interrupted by adverse environmental conditions, especially the effects of dissolved oxygen and turbidity. The effect of temperature upon larval production was clearly evident in Mudginberri billabong as shown in Figure 7.15, while the significance of turbidity in Georgetown (Fig. 7.15), and dissolved oxygen in Nankeen (Fig. 7.15) and the other floodplain billabongs (Fig. 7.16) could also clearly be demonstrated. (It is worth noting that larval production in V. angasi merely mirrors the intensity of oogenesis (section 7.4.2.2). Therefore the measure of the response of larval production to various environmental factors is in turn a measure of the response of gonadal activity.)

Having delineated several environmental variables of importance to larval production, attempts to model the breeding cycle over all billabongs and within billabongs, were made using a multiple regression approach. Independent variables chosen were temperature, dissolved oxygen, turbidity, chlorophyll and time. The inclusion of chlorophyll and time of year, was made on the assumption that the former is a measure of food availability, of conceivable importance to larval production, while the latter was included as a measure of other (unmeasured) seasonal effects. Such effects may include aspects of the physiology of the mussel itself, e.g. relative condition and previous spawning history.

While the choice of temperature, dissolved oxygen, turbidity, chlorophyll and time was fixed, stepwise multiple regressions were performed on the untransformed data, various transformations of the data and on various multiplicative combinations of the data from each billabong, to determine whether or not transformations were required and whether consistent synergistic or antagonistic effects among the variables were present. The results indicated that a log transformation of dissolved oxygen only was required for the regression analyses (also indicated from inspection of the residuals of appropriate regressions). No other significant factors resulted that were suggestive of consistent synergism or antagonism amongst the variables. Multiple regression analyses were performed on the five independent variables against monthly larval production (percent of gravid females, arcsine transformed) of each billabong. An equation was also derived using the data of the billabongs combined.

The resulting multiple regression equations are shown in Table 7.14. An AOV of the regression coefficients over the billabongs showed very strong evidence against the assumption that all 8 regression equations estimated the same population regression ($P < 0.001$). Even when the billabongs were grouped according to the hydrological classifications of backflow, channel and floodplain, the equations within the groups still differed in each case ($P < 0.001$). Nevertheless, within the broad billabong types, some environmental influences were strong and common in effect. Three environmental factors at least have a very significant bearing upon the patterns of larval production observed amongst the different billabongs:

1) Temperature - The major determinant of larval production in Mudginberri billabong is apparently water temperature (Table 7.14), and increasing water temperature is conducive to production of young (as might be expected). The relationship between monthly larval production and temperature for Mudginberri billabong is shown in Figure 7.15, and a highly significant linear regression equation ($P < 0.001$) was found to describe it (Table 7.15). The environment in Mudginberri billabong is the most equitable and temperate of all the Magela Creek waterbodies, and dissolved oxygen is generally adequate and turbidity very low year round. The breeding pattern in this billabong therefore, apparently represents a background cycle, primarly dependent on water temperature. Except for Nankeen, the sign of the partial regression coefficient for temperature amongst the billabongs was consistently positive and in two other billabongs (Georgetown and Island) the variable was significant ($P < 0.05$) in the regression equation (Table 7.14).

2) Turbidity - At high concentrations, suspended solids (as measured by turbidity) had a mostly negative effect upon larval production. In Georgetown, the 'dirtiest' of the Magela Creek billabongs, the relationship is clear (Fig. 7.15), and a highly significant linear regression equation ($P < 0.001$) was found to describe the relationship between monthly larval production and turbidity (Table 7.15). The significant, but positive sign of the partial regression coefficient

for turbidity in Nankeen billabong is ambiguous. No correlation was found between larval production and turbidity when the variables were regressed on their own, and the significance of the parameter in the multiple regression equation is suggestive of intercorrelation between the other independent variables. Similarly, in the non-turbid and marginally turbid billabongs, the positive sign of the coefficient in the regression equations (Table 7.14) may merely reflect increasing algal production that turbidity partially measures during the Dry season. Thus, at high loads only, suspended solids apparently inhibit larval production, very likely through an effect of interference to normal gill functioning of brooding females.

3) Dissolved oxygen - In all but one billabong, the partial correlation coefficients of dissolved oxygen in the multiple regression equations are positive. It is particularly noteworthy that the coefficients in three of the five floodplain billabongs are significant (Table 7.14), and it is clear that dissolved oxygen has a marked influence upon larval production in these billabongs (Fig. 7.16). In four of the five floodplain billabongs, significant linear regression equations were derived to describe the relationships between dissolved oxygen and larval production (Table 7.15).

From Figure 7.16, larval production is suppressed at each Wet-Dry season interchange (April-June), apparently in response to the same seasonal lulls observed in dissolved oxygen concentration. Later in the Dry, however, the same correspondence is not so clear. At these times algal populations have increased and the resultant respiratory lull measured in early morning dissolved oxygen concentration may be followed by a supersaturated reading in the afternoon as a result of photosynthesis (section 2.3.2.2). At the Wet-Dry interchange, however, algal populations are low and the effects of the relative anoxia resulting from macrophytic decomposition are sustained, in all likelihood, throughout much of the day. Thus, the response of larval production to dissolved oxygen concentration may be an integrated measure of the sustained effect of low dissolved oxygen. Spot monthly readings of dissolved oxygen are probably of little value in this regard. Nankeen is limnologically the least productive of the floodplain billabongs and presumably dissolved oxygen concentrations are less dependent upon algal blooms. The close correspondence of larval production to dissolved oxygen in this billabong therefore (Fig. 7.15), may indicate that the early morning readings of dissolved oxygen are an effective measure of the daily concentration. In spite of an apparent relationship between dissolved oxygen and chlorophyll, however, no multiplicative combination of the two variables resulted in any consistent and significant patterns from the stepwise regressions.

At low sustained concentrations, dissolved oxygen must either inhibit further larval production (via reduced oogenic activity, section 7.4.2.2) or induce abortion in brooding females. In the former, relative anoxia is assumed to directly interfere with oogenesis at least, while in the latter the brooding larvae may impose a serious respiratory burden upon the mother or conceivably, themselves asphyxiate if their development occurs more or less independently of the parent.

4) Overall - Because larval production responds differently to the

same environmental conditions between billabongs no overall model can accurately predict larval production given a limited set of variables as used in these analyses. In any case, on statistical grounds, an equation derived from the data of all the billabongs for predictive purposes is invalidated. Thus within billabongs larval production may respond in a predictable fashion to the immediate environment; yet responses averaged over all billabongs differ sufficiently to suggest that control of breeding is also influenced by more complicated physiological mechanisms. Other unmeasured, environmental influences and synergistic and antagonistic effects may also be influential to breeding.

Nevertheless, the combined equation as derived in Table 7.14 whilst not providing significant predictive value (having a low coefficient of determination of 39%), indicates by way of the sign and significance levels of the coefficients a measure of the relative importance of the environmental parameters studied, to larval production. According to the multiple regression equation, the strongest influence of the environmental factors studied is dissolved oxygen. Above a threshold value, the influence of dissolved oxygen is not particularly marked, but at low sustained concentrations breeding of mussels is suppressed. Increasing water temperatures also significantly enhance breeding, while suspended solids at high concentrations inhibit it. Algal abundance (as measured by chlorophyll) as a source of food available to mussels is apparently unimportant in determining larval production.

In the Magela Creek channel, the availability of water appears to be the only requirement for breeding as mussels were observed in a gravid condition for the entire duration of the Wet season (Fig. 7.12). Breeding commences almost immediately after the Creek begins to flow in about December, continues through the Wet season and ceases at the cessation of flow prior to aestivation in about May. Continuous breeding over the Wet season is no doubt enhanced by the high oxygen concentration of the flowing waters and generally low loads of suspended solids.

7.10.2 Within billabongs

The percentages of gravid females observed within each depth interval over the study period, were estimated and plotted according to depth and/or sampling location in Georgetown, Mudginberri and Buffalo (Fig. 7.17) and Leichhardt and Nankeen (Fig. 7.18) billabongs.

Given that larval production generally declines with mussel age (section 7.8), and that age is related to depth in the billabongs according to the relationships described in section 6.5.3.1 and shown in Figures 6.25-6.27, the relationships drawn here are merely the inverted images of Figures 6.25-6.27. Thus larval production decreases with depth in Georgetown, Mudginberri and Buffalo billabongs (Fig. 7.17) in response to increasing age over the same gradient. (The significance of the encircled point in Buffalo billabong shown in Figure 7.17, is considered in section 6.5.3.1). In Leichhardt and Nankeen billabongs, larval production is least at intermediate depths (Fig. 7.18), corresponding to the sites where the oldest mussels are found. The relationship found in Nankeen billabong, however, is not exactly an inversion of the quadratic relationship between age and depth as shown in Figure 6.27. Larval production at the shallowest and greatest depths (Fig. 7.18) was less than might be expected, as the youngest age classes are heavily represented here. The effects of anoxia may be assumed to be most pronounced at depth, possibly explaining the suppressed breeding at the deepest station. At the shallowest depth, wave-induced resuspension of the silty sediments during the Dry season (see section 6.4.3.1) may interfere with larval brooding, again perhaps explaining the slightly reduced breeding activity here.

7.11 Duration of incubation and frequency of brood production

The correlation between the percent of brooding females and the incidence and intensity of parasitism of the host fishes by the glochidia over the seasons (section 7.15.2), clearly indicates that larvae are released from the mother as soon as they have matured. From the data of section 7.9 therefore, larvae are brooded and released within at most 12 days during summer and within at most 40 days (probably much shorter) during winter. Unfortunately, it is not known over what time span the larvae are released to ascertain more precisely the duration of an entire reproductive cycle, from one brood to the next. Possibly the period of release of glochidia is no longer than a week. A very conservative estimate would place the period at two weeks. In all likelihood therefore, an entire reproductive cycle is completed within a period of two weeks and one month.

When reproductive activity is most intense in the waterbodies, few females were found in a non-gravid condition, for often prolonged periods (e.g. Sept.-Dec., 1980 in Mudginberri billabong, Fig. 7.12). This indicates that a rest period between broods is extremely short during these phases of activity, and females are therefore breeding repetitively. Based upon an estimate of one month for the duration of an entire reproductive cycle, and considering that in most billabongs, there are active phases in which one cycle is immediately followed by another, it is likely that as many as 9 broods are produced each year. If cycles are of fortnightly duration, it is conceivable that as many as 15 broods may be produced each year. The duration of a reproductive cycle, however, needs to be properly ascertained.

D. GLOCHIDIAL RELEASE AND PARASITISM

7.12 Materials and methods

Natural infections

Fish collections from several billabongs of the Magela Creek, were made at various times of the year to investigate glochidial infections of *V. angasi*. Wherever possible (several instances) advantage was taken of the catches of other investigators involved in fish autecological studies in the Region. Only catches made in billabongs and sites known to harbour mussel beds, however, were utilised. Fish were collected by seining the shallows on or adjacent to mussel beds, while gill netting was performed in some deeper sites mainly for capture of the larger fish species. The sampling dates and sites of collection are shown in Table 7.16. All fish from a catch were fixed in 10% formalin and subsequently transferred to 70% ethanol for later inspection of glochidial infections. When individuals of a fish species were particularly numerous, subsamples only were taken and preserved.

Having ascertained early in the study that Glossogobius giurus, the flathead goby, was a host for the glochidia of V. angasi, regular monthly collections were made of the fish from Mudginberri billabong during 1981 and 1982, to monitor the seasonal incidence of parasitism. G. giurus is benthic in habit and fish were collected by diving over sites where mussels occurred, using small dip nets for their individual capture. An effort was made each month to capture at least 20 fish. However, during the late Dry season of 1981 (Sept.-Dec.), water clarity deteriorated to such an extent that fish were difficult to locate. Sample numbers were therefore low during these months (Table 7.17).

In the laboratory, fish were inspected under a dissecting microscope for the presence of encysted glochidia. These were conspicuous as small, semi-opaque tubercles on the host's tissues. Rationalising the time required to inspect the fishes for presence of glochidia, inspections were made of the fins only unless otherwise indicated (section 7.1).

Laboratory induced infections

The duration of the parasitic period of the glochidia of V. angasi upon a host fish, G. giurus, was determined in the following manner:

Fish were collected from Mudginberri billabong two weeks prior to experimentation to allow naturally occurring infections to be voided. Individuals were kept in billabong water (from Mudginberri) throughout the study and, during the experiments, water was changed daily. Prior to experimentation fish were fed, but were starved during the experiments.

Each trial comprised artificial exposure of the fish to glochidia, at a specific water temperature. Two trials were performed, at 22°C during the Dry season of 1981, and at 30°C during the Wet season of 1982. Six fish were used in each trial, and each fish was held in a 1 litre glass beaker individually aerated. All beakers were held in a waterbath where water temperature was thermostatically controlled to within 1°C. A barrier of nylon gauze mesh was placed a few centimetres above the bottom of the beaker through which newly metamorphosed larvae could pass, to prevent them being fed upon by fish.

Mature glochidia from 5 or 6 mussels collected from Mudginberri billabong, were used to infect fish. Glochidia were excised from the marsupial gills of mussels, placed in a water-filled petri dish, agitated and mixed, and then pipetted into the beakers holding the fish. Only glochidia free of the vitelline membrane and with active, snapping movements were used in the infections. Fish were exposed to the glochidia for several minutes, after which they were transferred to fresh beakers and water to begin the parasitic phase.

After initial infection, fish were removed from the beakers every 24 hours and the bottom debris individually siphoned and carefully collected into water-filled petri dishes for microscopic inspection. (Fish were again transferred to fresh beakers and water.) Newly metamorphosed larvae were readily discernible from sloughed glochidial shells by their opaque shells (indicative of the new internal structures), and by occasional and conspicuous movements of the feet. At each individual inspection, the number of metamorphosed juveniles was recorded. The bottom debris of each beaker was inspected for at least 3 days after the last juveniles were found.

A number of other fish species were exposed to artifical infections to determine whether or not they were host for the glochidia of V. angasi. In these cases, the procedures were followed according to the previous descriptions of infections of G. giurus, except that the trials were run at 22°C only, and for Leiopotherapon unicolor and Lates calcarifer, 3 and 1 individuals respectively were tested. The single individual of L. calcarifer was placed in a 40 l perspex aquarium for the duration of the trial. The presence of metamorphosed juveniles in the bottom debris was the criterion that a fish species was host to the glochidia of V. angasi.

7.13 Site of attachment of the glochidia upon the host fish

The body surfaces of individuals of 4 species of fish only, naturally infected with glochidia of V. angasi, were thoroughly examined to determine the sites of attachment. These species were Ambassis (spp. complex), Glossogobius giurus, Oxyeleotris lineolatus and Tandanus ater. Internal surfaces examined were mouth, opercula and gills, while external surfaces comprised the fins and body surface other than the fins. The mean numbers of encysted glochidia found on each of the fish tissues in relation to fish species, number of fish examined, and sampling location, are shown in Table 7.18.

For each species examined, encysted glochidia were proportionately more common on the internal body surfaces than on the external surfaces. For individuals of each fish species, the number of glochidia recorded were combined for both the internal and external body surfaces. From these data, a mean number of glochidia per individual was estimated for both internal and external body surfaces, for the 4 naturally infected fish species. A chi-square test was performed over the data of the 4 species to determine whether or not there were disparities between the species in the relative proportions of glochidia found on the internal and external body surfaces. No evidence was found against the hypothesis that the relative proportions of glochidia on either body surfaces were the same between gall 4 fish species ($\chi^2 = 2.92$, 3 D.F.). In all of the data a tendency was found for the benthic feeding G. giurus and T. ater to harbour proportionately more gill infections, as might be expected. (Ambassis spp. are more commonly observed in mid-waters, while O. lineolatus frequents the benthos, but is less dependent upon it for food - Bishop et al., 1981).

To discern whether total body infections were correlated with those observed only on the external body surfaces, the mean number of infections with respect to internal (Y) and external (X) body surfaces were subjected to regression analysis over the four species. The resulting linear regression equation ($Y = 0.72 + 2.36X$) proved non-significant (2 degrees of freedom only, $P < 0.20$), but correlation between the infections observed on each of the body regions was relatively high ($r^2 = 69\%$). Similar regression analysis was performed between internal and external (fins only) infections over the individual data for G. giurus. As this species was used as a monitor of glochidial release over the seasons (section 7.15.2), and as only fin infections were scrutinised, it was important to demonstrate that fin and internal body infections were correlated. Using the data that comprised the observations in Table 7.18, a very significant linear regression equation was found to describe the relationship between internal infections (Y) and infections on the fins (X) of G. giurus. The regression equation is:

$$Y = 7.573 + 2.17X \qquad (P < 0.01,\ r^2 = 0.344).$$

Further observations are required over a wider range of fish species with a broad range of habits, to confirm whether or not attachment of glochidia to the fish body is proportionately higher on the internal surfaces (chiefly the gills) than the external surfaces (mainly fins). Although the chi-square test used here showed that there were no disparities, between the species examined, in the relative proportions of glochidia found on the different body surfaces, 3 of the 4 fish species are chiefly bottom-dwelling. Gill infections therefore could have been expected to be higher than fin infections in the 3 bottom-dwelling species. Nevertheless, considering that many of the fish species from the Magela Creek feed from or on the bottom (apparent in the data of Bishop et al., 1981), gill infections generally, may prove to be higher than fin infections. This is contrary to the general observation, that hooked or toothed glochidia tend to parasitise the external surfaces of their host fish (see section A4.3).

7.14 The host fish species and host specificity

Observations on natural infections of glochidia of V. angasi, upon the fins of fish species from various Magela Creek billabongs, are summarised in Table 7.19. The sampling periods that comprise the total number of fish examined for each billabong are given in Table 7.16. The percent of gravid female mussels recorded at each sampling period (Table 7.16), and a mean percent of gravid females observed overall are given in Tables 7.16 and 7.19 respectively.

The order at which species appear in Table 7.19 is based more or less upon highest to lowest incidence (% of fish infected) and intensity (mean number of glochidia per infected fish) of infection when the data from all billabongs were averaged. While the order may change slightly as gill infections are scrutinised more, early indications are that differences between fish species in the site of attachment of glochidia are slight (section 7.13, above). Therefore the results of Table 7.19 while not providing total data on incidence and intensity of infection, nevertheless provide an adequate measure of the relative degree of infection between the different fish species. It should be noted, however, that particularly in view of the observation that gill infections outnumber fin infections (section 7.13), some low infections were possibly missed. The list of Table 7.19 therefore, may possibly be an underestimate of the total number of known hosts occurring from the observations on natural infections.

Trdan and Hoeh (1982) emphasised that the designation of a fish species serving as a suitable host required a combination of observations on naturally encysted glochidia and artificial laboratory infections. The artificial infections performed on the six fish species tested in the present study (Table 7.20), resulted in successful metamorphosis of glochidia. A diversity of families, sizes and life habits were represented in these species, suggesting that host fish specificity of V. angasi is low if existing at all. The natural infections observed on the fish species shown in Table 7.19 therefore, are likely to indicate that glochidia have the potential to parasitise and successfully metamorphose from the respective species.

The 19 known fish hosts of the glochidia of V. angasi are shown in Table 7.20. The ranking is based upon an order thought to represent most to least important host to V. angasi. By 'importance' is meant the number of glochidia that would eventually metamorphose from a fish species under field conditions, and is fairly subjectively scaled according to information on overall abundance of a fish species throughout the Magela Creek (Table 2.8), and its incidence and intensity of infection of glochidia (Table 7.19).

From Table 7.19 both incidence and intensity of infection, are low in fish species of the Magela Creek, even considering that gill infections are not represented. Thus the highest intensity of infection is observed on G. giurus which bears upon the fins a mean number of 4.1 glochidia per infected fish or 16.5 glochidia upon all the body surfaces (using the regression equation from section 7.13). Seventy-three percent of G. giurus were found infected, and the next highest incidence of infection was for Amniataba percoides where only 40% of the individuals were found infected. These results are somewhat surprising given that densities of mussels from all the sampling sites were high, and that high proportions of gravid female mussels were present in the populations at any one time (Table 7.16).

As mentioned above, no evidence was found of host fish specificity of V. angasi and in relation to natural infections specifically, no one fish family stood out as having a consistently higher incidence or intensity of infection than another. Infections are apparently more influenced by fish behaviour than any other factor. The feeding guilds of fish species identified as hosts to V. angasi are shown in Table 7.20. Generally speaking, bottom dwelling and feeding fishes observed highest incidence and intensity of infection.

All species listed in Table 7.20 are known to feed in both benthic and mid-water habitats (Bishop et al., 1981), although Toxotes chatareus and Melanotaenia splendida tend to inhabit and feed in mid- and surface waters. G. giurus feeds exclusively on the benthos explaining no doubt the high infections observed on this species (Table 7.19). Ambassis spp., Glossamia aprion and Oxyeleotris lineolatus from direct observations, were notably inactive in the water column. The latter two species probably capture prey in an ambush fashion, observing long periods of inactivity between predatory movements. This relative inactivity may provide more opportunities for infection. Scleropages jardini, Lates calcarifer, Megalops cyprinoides, Strongylura kreffti and Leiopotherapon unicolor are no doudt more active in their predatory habits and in all likelihood, may not often frequent the benthos. This may account for the generally low infections observed on these species. The fins of the eeltailed catfishes Tandanus ater and Porochilus rendahli are probably not particularly suitable for glochidial infections, as the membranes between the fin rays may be too coarse and slimy for attachment. Similarly the fins of larger individuals of S. jardini, L. calcarifer and O. lineolatus may prove too coarse for glochidial attachment. In the eeltailed catfishes at least, however, the gills have been shown to bear relatively large infections (section 7.13). Not enough samples were collected of many species, however (Table 7.10), to speculate upon the relative degree of infection.

7.15 Glossogobius giurus as a monitor of glochidial release

7.15.1 Duration of the parasitic period

The mean numbers of newly metamorphosed juveniles of V. angasi per infected G. giurus are plotted at daily intervals subsequent to initial infection, and with respect to temperature in Figure 7.19. At lower temperatures (22° C) the duration of the parasitic period was protracted, and the period of larval metamophosis spanned 3-15 days after initial infection. Recovery of juveniles was greatest on the 11th day. At higher temperatures (30° C), however, the duration of parasitism was very short (Fig. 7.19) and the period of metamorphosis spanned a relatively short period of 9 days, i.e. 2-10 days after infection. Greatest recovery of juveniles was on the 6th day.

Thus, there was a relationship between the duration of the period of metamorphosis of glochidia of V. angasi, and water temperature. Metamorphosed juveniles were recovered earlier from the host fish at 30° C than 22° C. Liberation from the host tissues was more protacted at 22° C, but at either temperature, metamorphosed juveniles left the fish during the middle of the period of parasitism. It was noted during the trials that those glochidia encysted after 2 days generally continued development through to metamorphosis. Very few sloughed off glochidia were found in the bottom debris after 2 days. At 22° C at least, the duration of the parasitic period was observed to be similar in all 6 species artificially infected (Table 7.20). Thus, the duration of attachment by glochidia of V. angasi does not appear to be influenced by host species to any extent.

7.15.2 Seasonal incidence of parasitism

The mean number (per fish) of encysted glochidia of V. angasi (and standard deviation) parasitising G. giurus from Mudginberri billabong during 1981 and 1982 are shown in Table 7.17. The monthly means are plotted with monthly percentages of gravid female mussels from the billabong observed over the same period, in Figure 7.20. All of the fish collected by diving, exceeded 60 mm. Only infections upon the fins of these fish were observed and counted. However, infections on the fins were significantly correlated with infections recorded on other body regions of G. giurus during March 1981 (section 7.13). There is no reason to suspect that the same correlation would not hold at other times of the year, as the same habits of G. giurus and habitat, were observed year round. Therefore the infections observed on the fins, although only relative, nevertheless directly reflect the actual monthly intensities of infection.

From Figure 7.20, monthly intensity of infection of G. giurus clearly correlates with the monthly percentage of gravid female mussels. Thus, glochidia are released from the marsupia after a very short developmental time. Release of glochidia from brooding mussels, as monitored by the intensity of infection of G. giurus, is in direct proportion to their seasonal production. Given that water temperatures in Mudginberri billabong always exceed 25° C and average 28.2° C over the seasons (from the data of Fig. 2.20), recovery of metamorphosed juveniles from the host fishes would span a period no longer than two weeks; most recovery averaged over the seasons would be accomplished only 8 days after infection (extrapolating from the data of section 7.15.1 above). Thus the seasonal intensity of recruitment (with only a slight lag phase) is in direct proportion to glochidial production. (This same relationship is assumed to apply to the other Magela Creek waterbodies as well.) From Figure 7.20 therefore, recruitment would appear to be greatest during the latter period of the Dry season (Aug.-Dec.) in Mudginberri. From the data of section 6.6.1, however, recruitment of V. angasi in billabongs of the Magela Creek is clearly seasonal and occurs during the Wet and early Dry seasons in association with periods of highest dissolved oxygen content. Thus, there is a marked seasonal disparity between the intensity of larval production and subsequent metamorphosis of larvae (Figs. 7.12-7.14) and actual recruitment of juveniles observed in the sediments of the Magela Creek waterbodies. This apparent anomaly in aseasonal breeding but seasonal recruitment of V. angasi is discussed below.

E. DISCUSSION

Gonadal development

But for very occasional hermaphrodites (see below), the sexes of V. angasi are separate, in accordance with the general condition prevailing in freshwater mussels. As in the majority of species, sex can be determined by both gonadal appearance and by morphology of the marsupial gills. Sex in V. angasi is readily determined by gonadal smears, as ripe eggs and sperm in sexually mature mussels are present year round. Nevertheless, for all practical purposes sex is most easily and reliably determined by gill morphology alone, as consistent correlation is found between sex as determined by identification of gametes and sex as determined by inner gill morphology.

In unionaceans from temperate regions, gametogenesis generally continues throughout the year, but is most intense during the warmer months when more or less synchronised spawning occurs (Matteson, 1948; van der Schalie and van der Schalie, 1963; Stein, 1969; Yokley, 1972; Giusti et al., 1975; Heard, 1975; Smith, 1979; Zale and Neves, 1982a; Jones and Simpson, in prep.). Even in tropical climates oogenesis is reportedly slowed in the cooler seasons; spermatogenesis nevertheless, may continue unabated throughout the year, and spawning may be protracted over the warmer months (Lomte and Nagabhushanam, 1969; Ghosh and Ghose, 1972; Nagabhushanam and Lohgaonker, 1978; Dudgeon and

Morton, 1983). Thus in unionaceans from all climates, seasonal gonadal activity is influenced to a lesser or greater degree by water temperature. The presence of spermatozoa and primary oocytes in the respective gonads of the sexes of V. angasi throughout the year, suggested that gametogenesis was a continuous event. Nevertheless, while gonadal activity was found to be synchronised between males and females, relatively inactive phases, as identified by presence of stages of atypical spermatogenesis in the testes and by fewer numbers of primary oocytes in the ovaries, could be recognised. As in all other unionaceans studied, gonadal activity in V. angasi could also be shown to be responsive to water temperature. However, superimposed upon an apparent repetitive reproductive cycle (the relative activity of which is only marginally slowed to any degree by low seasonal water temperatures), major interruptions to gonadal activity were observed that were associated with seasonal lulls in dissolved oxygen concentrations and with seasonally high turbidities in the billabongs. These factors are further considered below.

That the period of spermatogenic activity invariably overlaps the same period of oogenic activity in unionaceans, has been interpreted as meaning that sperm are released over a timespan that overlaps ovulation in females, thus ensuring successful fertilisation (e.g. Matteson, 1948; Dudgeon and Morton, 1983). The timing of spermiogenic and oogenic activity of V. angasi is the same, and both sexes therefore are assumed to spawn both simultaneously and at a similar intensity. As sperm are present in the testes at all times of the year, however, it is probable that some sperm are released even during inactive phases of spermatogenesis. Absence of spawning in females moreover, is most conspicuous when for brief periods the marsupia in some populations may be entirely devoid of brooding larvae.

Further consideration of the breeding patterns observed in populations of _V. angasi_ from the Magela Creek is given below.

Structure of the breeding population

Hermaphroditism in _V. angasi_ is very occasional and in the Magela Creek was confined to less than 2% of each of the populations investigated. In North American unionaceans similarly, when hermaphroditism is encountered amongst predominately dioecious species, incidence is reportedly low (Kat, 1983d). The incidence of hermaphroditism in _V. angasi_ is the first reported for any hyriid. The nature of hermaphroditism in _V. angasi_ differs from other unionaceans, but whether these differences are representative for the hyriids as a whole of course, is not known. Unlike North American unionaceans with monoecious acini or gonads with intermingled zones of male and female acini (Heard, 1975), the discrete follicles or tubules of hermaphroditic _V. angasi_ were mostly confined to discrete regions of the gonad. Further, hermaphroditic unionids of North America reproduce chiefly as females and if male hermaphrodites are present, generally less than 5% of the gonadal tissue is female (Kat, 1983d). In _V. angasi_, however, hermaphrodites reproduced both as males and females more or less equally. Moreover, the ovarian follicles in male hermaphrodites occupied more than 5% (between 10 and 40%) of the gonadal tissue.

Kat (1983d) found an association between presence of cercarial trematodes within the gonads and occasional hermaphroditism among populations of predominately dioecious species of unionids. No such association was observed in populations of V. angasi, however, where incidence of parasitism was generally low (up to 10% infected at any one time), and seasonal in nature. Because of the low incidences of infection, the reproductive potential of mussel populations in the Magela Creek is assumed not to have been affected to any significant degree by cercarial parasitism. High incidences of cercarial infections observed in some unionids, however, have been shown to have severely affected the reproductive potential of respective populations (e.g. Zale and Neves, 1982a; Kat, 1983d).

Both evidence for (Bloomer, 1934, 1935, 1939; Tudorancea, 1969, 1972) and against (Heard, 1975; Dudgeon and Morton, 1983; Young and Williams, 1984a) sex reversal in unionaceans have been presented. From limited mark-recapture studies on known female mussels and from the close correlation observed between sex as determined by the gonad and sex as determined by inner gill morphology in animals from all seasons and of all ages, sex reversal is assumed to be absent from adult populations of V. angasi in the Magela Creek. Heard (1975) reached a similar conclusion in relation to the sexuality of various North American anodontines. Declines in the proportions of females with age observed in a number of populations in the Magela Creek can best be explained by differential and age selective mortality between the sexes. Tudorancea (1969, 1972) observed this phenomenon in some European unionids. Seasonal patterns were observed in the sex ratios of mussels from both Georgetown billabong and the Magela Creek channel. While sampling biases may affect the patterns observed in Georgetown, both long and short term mark-recapture studies would be needed to resolve the question of sex reversal in V. angasi for the respective populations.

Hermaphroditism in adult populations of V. angasi is apparently the result of none other than developmental error in sexual determination. Such cause has also been implicated for hermaphroditism in other normally dioecious bivalves including unionaceans (e.g. Coe, 1943; van der Schalie, 1970; Kat, 1983d). However, the relatively high incidence of hermaphroditism observed in young of year mussels in Mudginberri billabong, did provide evidence suggestive of consecutive sexuality in the form of protandry. In fact the gonads of the smallest individuals of V. angasi from most populations function initially as males. Protandry observed at about the time of sexual maturity may prove to be the general rule for unionaceans (Bloomer, 1939; Tudorancea, 1969, 1972; Kat, 1983d).

In relation to the question of sexuality in V. angasi in the Magela Creek, it is concluded that apart from early protandry, sex reversal appears to be absent. Hermaphroditism occurs at a low incidence in all populations investigated and otherwise the dioecious condition is a stable one and sexual integrity is high.

The sexes of V. angasi in the Magela Creek populations are biased in favour of males. Apart from age specific differences in sex ratios males live longer than females in many of the waterbodies, which presumably accounts for the observed disparities in proportions of the sexes. Repetitive spawning and periods of anoxia in particular waterbodies may be causes of selective mortality of females. Elsewhere, the literature shows that there may be more or less predominance of either sex in freshwater mussel populations (section A4.1). However, no statistical evidence has been presented to show that sex ratios vary from 1:1 in any population studied, nor has speculation been offered as to possible reasons for observed disparities from a sex ratio of unity.

Gonadal maturity in V. angasi is size dependent, and is initiated between the size ranges 25.0-29.9 and 30.0-34.9 mm. This length is reached by most mussels during their first year. First gravidity is similarly size dependent, occurring at a size of approximately 40 mm. This mean length is reached within an age span of from 0.6 to 1.5 years depending upon the waterbody. Such early maturity may be the general rule amongst species of freshwater mussels from the tropics. Kenmuir (1980) observed gravid females of 2 out of 3 species studied in Lake Kariba between the ages of 1 and 2, while Dudgeon and Morton (1983) observed that Anodonta woodiana was mature by the end of the first year in Hong Kong. Other fast growing temperate species, also mature at a relatively early age (Table A4.1), but generally never in the first year. Warm, equitable water temperatures, presumably enhance rapid gonadal maturation.

After a peak is reached in reproductive potential relatively early in life, for female mussels at least, in most populations from the Magela Creek a long and gradual decline in reproductivity with increasing age occurs. The same phenomenon has previously been noted only for two

European unionids (Haranghy *et al*., 1964), while a post-reproductive phase (a decline with age) is reportedly absent in many other species of freshwater mussel (Scruggs, 1960; Stansbery, 1967; Heard, 1975; Kenmuir, 1980). The decline in reproductive effort of female *V. angasi* in the Magela Creek with age is suggestive of a physiological weakening of mussels by certain environmental stresses to which they, because of the brooding habit, may be particularly vulnerable - e.g. turbidity and anoxia. Repetitive breeding is also, presumably, taxing to the reproductive physiology of female mussels. Both sexes nevertheless, showed a decline in relative body weight in the oldest age classes of most of the Magela Creek populations, corroborative evidence (section 8.7.2) of general senescence in *V. angasi*.

Larval production

Larval development in *V. angasi*, from initial spawning to glochidial maturation, is exceedingly rapid and may be completed during the Wet season months at least, in well under 12 days. This time span is the shortest recorded of any species of freshwater mussel, although some North American *Quadrula* spp. may complete development in 2 weeks (Lefevre and Curtis, 1912). A longer period for larval development has been found in other tropical freshwater mussels: 4 weeks in *Anodonta woodiana* (Dudgeon and Morton, 1983) and 3-5 weeks for species from Lake Kariba (Kenmuir, 1981b).

The ubiquity of mature primary oocytes and sperm, the presence of gravid females throughout much of the year in many populations, and the knowledge that larval development is exceedingly rapid and that mature glochidia are released in direct proportion to the intensity that they are produced, provided clear evidence that spawning and breeding of V. angasi in the Magela Creek are repetitive. Elsewhere, such intensity of larval production is apparently matched only in the mutelids Mutela bourguignati (Fryer, 1961) and M. dubia, and the unionid, Caelatura mossambicensis (Kenmuir, 1981a) from tropical Africa. Other tropical species are distinctly seasonal in their breeding - e.g. Anodonta woodiana (Dudgeon and Morton, 1983), although protracted and/or repetitive breeding during the warmer months have been observed for Indian unionids (Seshaiya, 1969; Lomte and Nagabhushanam, 1969; Ghosh and Ghose, 1972; Nagabhushanam and Loghaonker, 1978) and for the mutelid, Aspatharia wahlbergi in Lake Kariba (Kenmuir, 1981a).

Amongst temperate tachytictic breeders from northern climes, multiple broods and repetitive spawning during the warmer months have been observed (e.g. Yokley, 1972; Wood, 1974a) and even some bradytictic forms have been shown to reproduce repetitively over the summer (Heard, 1975). Data from the temperate Australian hyriids also indicates that many of the species studied to date may have the potential to produce a number of broods during the warmer months (Hiscock, 1951; McMichael and Hiscock, 1958; Atkins, 1979; Walker, 1981b; Jones and Simpson, in prep.). Different climatic regions across latitudes appear to be largely influential in determining the reproductive patterns of the respective freshwater mussel groups. Providing warm temperatures are sustained for a long enough period of time, multiple broods may be the norm, suggesting that the breeding of freshwater mussels may be largely opportunistic.

Both wide temporal and spatial variations were found in the breeding patterns of _V. angasi_ between the different populations of the Magela Creek. The superficial appearance observed was one of a number of different populations each breeding in a pattern peculiar to the respective waterbody. Intraspecific variation in the timing and frequency of breeding over a broad geographical range (Giusti _et al_., 1975; Kenmuir, 1981a,b; Dudgeon and Morton, 1983), or on a more regional scale between neighbouring lakes (Kenmuir, 1981b) or sites of the same river (Walker, 1981b; Young and Williams, 1984a; Jones and Simpson, in prep.) have been attributed to climatic and temperature variations between the various localities. Otherwise both interpopulation (Bjork, 1962; Heard, 1975; Haukioja and Hakala, 1978b; Young and Williams, 1984a) and even intrapopulation variations (Porter and Horn, 1980) in the timing and frequency of reproduction of intraspecifics have been left unexplained.

Interpopulation variation in breeding patterns of unionids recorded at the specific level was attributed by Dudgeon and Morton (1983) to adaptations to conditions peculiar to local environments, whilst Heard (1975) concluded that breeding cycles were apparently not influenced entirely by conspicuous environmental factors such as water temperature and presence or absence of current. Reproductive timing amongst unionaceans has been linked to the habits and activities of the host fishes (section A4.3) although no evidence has been provided to indicate that the activities of the host fishes may influence the timing and frequency of breeding cycles between specific populations of freshwater mussels.

Seasonality in other environmental factors has largely been ignored in terms of its influence upon reproduction in freshwater mussels. Numerous authors, nevertheless, have drawn attention to the sensitivities of gravid female mussels to stressful environmental conditions such as high water temperatures and oxygen deficiences under laboratory conditions (section A4.2). Under field conditions, however, only Matteson (1955) has observed abortion in gravid mussels, in response to unseasonally warm, shallow waters. While breeding of V. angasi in the Magela Creek in equitable and stress-free environments conforms to a cycle apparently temperature dependent, the breeding patterns in other billabongs are clearly interrupted by seasonal deficiences in dissolved oxygen concentrations and seasonally high turbidities.

In V. angasi from the Magela Creek, spawning and larval production are immediate responses to the intensity of gametogensis. Although a background reproductive cycle dependent upon temperature, and which may be interrupted by the aforementioned seasonal stresses, is suggested for mussel populations of the Magela Creek, no overall model could be derived to show this. Prediction of breeding patterns within billabongs may be good, but responses between billabongs to the same environmental parameters differ sufficiently to suggest that control of breeding is also influenced by more complicated physiological mechanisms. Physiological condition of the mussels themselves (e.g. body weights, previous spawning history) in addition to other unmeasured, environmental influences are also presumably, influential to reproductive patterns.

Nevertheless, this study is the first to attempt an elucidation of the factors that may influence breeding patterns, in a species of freshwater mussel that breeds largely aseasonally. The results clearly implicated two other environmental variables apart from water temperature that are influential to breeding in freshwater mussels - namely dissolved oxygen and turbidity. It would be of interest to investigate the extent to which environmental parameters other than water temperature and implicated host fish habits and activities, influence reproductive cycles in other species of freshwater mussel.

Glochidial release and parasitism

From both field and laboratory observations, a total of 19 fish hosts are known for the glochidia of V. angasi in the Magela Creek. In accordance with the observations for unionaceans in general (Kat, 1984) including the Australian hyriids (Atkins, 1979; Walker, 1981b) therefore, it appears that V. angasi also has little host specificity. Considering the comparative richness of the fish community of the Region (section 2.3.3), it is unlikely that a record of at least 19 fish hosts observed for V. angasi will ever be surpassed by another Australian hyriid confined to a specific catchment. Further hosts of V. angasi are likely to be discovered moreover, as gill infections are more closely scrutinised. Only two North American anodontines are known to parasitise a larger number of fish hosts (over 30) than V. angasi (Trdan and Hoeh, 1982), though these reports pertain to known hosts over the entire ranges of the species concerned. As more tropical species are examined, however, even these records are likely to be surpassed.

Both incidence and intensity of infection by glochidia of V. angasi are low overall in fish species of the Magela Creek. This finding accords with other natural infections recorded in unionaceans elsewhere (section A4.3). The result might be expected for V. angasi as Trdan (1981) observed a negative correlation between the number of species serving as hosts for the glochidia of particular unionids and the infection rate (percent infected and intensity).

While both host specificity and infection rates are low in V. angasi, nevertheless, some species were observed to serve disproportionately as hosts. Bottom feeding and dwelling fishes in the Magela Creek and fishes notably inactive in the water column (e.g. Glossogobius giurus, Ambassis spp., Glossamia aprion, Amniataba percoides) had higher infections than species inhabiting the mid- and surface waters (Toxotes chatareus, Melanotaenia splendida) or species with active predatory habits (e.g. Leiopotherapon unicolor, Lates calcarifer). Elsewhere, hosts occurring in sympatry with mussels may have heavy infections of glochidia (Surber, 1912; Lefevre and Curtis, 1912; Percival, 1931; Fuller, 1974; Giusti et al., 1975; Kenmuir, 1980; Zale and Neves, 1982 a,b; Kat, 1984).

For four species of fish whose body surfaces were thoroughly examined for glochidial infections, infections were observed to be higher on the gills than the fins. This is contrary to the general observation, that hooked or toothed glochidia tend to parasitise the external surfaces of their hosts (section A4.3). More species of fish from all habitat types need to be examined, however, before conclusions concerning the distribution of glochidia of V. angasi on the fish hosts can be drawn. Nevertheless, there are many recorded exceptions to the general rules concerning the site of attachment of glochidia upon the host tissues (section A4.3). The glochidia of Anodonta cygnea for example are of the hooked variety, but Giusti et al. (1975) found large burdens of infections upon the gills of bottom feeding, host fishes than upon predatory fishes. Upon further examination, this may also prove to be case for infections of the glochidia of V. angasi. Dartnall and Walkey (1979) concluded that such factors as fish size and feeding behaviour of fishes might interact to determine the distribution of the glochidia on fish hosts. Among the few other Australian hyriids (larvae of the toothed variety) whose host fishes are known, the glochidia of Hyridella drapeta apparently attach exclusively to the gills of host fishes (Atkins, 1979). Other velesunionines, however, chiefly parasitise the fins and general body surface of their hosts (Hiscock, 1951; Walker, 1981b).

As for other unionaceans studied, temperature appeared to be the most important factor determining the duration of the parasitic period of glochidia of V. angasi. Metamorphosed juveniles were recovered from host fish on average after 5 days at a water temperature of 30° C, and after 10 days at 22° C. Recovery of metamorphosed juveniles occurred as shortly as within 48 hours after infection at 30° C, and within 96 hours at 22° C. Thus larval metamorphosis in V. angasi is exceedingly rapid, and is matched only by some Indian unionids which may complete the parasitic period in 3 days (Seshaiya, 1969 - Table A4.2). The glochidia of some temperate unionids also have a rapid metamorphosis -

Anodonta grandis and *A. imbecilis* were observed to complete the parasitic phase on average 6 and 8 days respectively after infection at summer temperatures (Trdan and Hoeh, 1982). Seshaiya (1969) thought that the rapid metamorphosis observed for the larvae of *Lamellidens* spp. might be an adaptation to the environmental conditions of the tropics. No reference was made, however, as to what these conditions might be. Larval metamorphosis in *V. angasi* though, is probably no shorter than that which might be expected for any unionacean under the same warm environmental conditions prevailing in the Magela Creek.

By monitoring the seasonal incidence of parasitism of glochidia upon a host fish species, *Glossogobius giurus*, it was shown that *V. angasi* releases glochidia throughout the year in direct proportion to their seasonal production. Thus metamorphosed glochidia drop from the fishes onto the sediments throughout the year - again, in direct proportion to their seasonal production. However, recruitment of *V. angasi* in the Magela Creek is seasonal and occurs during the Wet and early Dry seasons in association with periods of highest dissolved oxygen content (section 6.6.1). It would seem therefore, that much of the energy expended in producing larvae during the Dry season is wasted as little recruitment occurs during these times. A better strategy would seem to be for mussels to accrue reserves and to breed only during the Wet season when conditions are ideal for recruitment.

However, the fact that some Dry season recruitment is observed at all, may be the clue to understanding the aseasonal and continuous breeding pattern of *V. angasi*. Populations of *V. angasi* have a very high reproductive potential, chiefly as a result of early maturation, repetitive spawning, and high longevity. In the deeper billabongs, overall densities are mainly affected by Wet season flow regimes (section 5.4.2). For all the considerable reproductive effort expended by individuals nevertheless, minor (and presumably constant) recruitment has been observed in all of the billabongs during the Dry. In billabongs where low densities of mussels are observed such as in Jabiluka, it is conceivable that a significant proportion of the population are the result of Dry season recruitment, as anoxia at the Wet-Dry interchange may kill many of the Wet season recruits.

Thus environments may be envisaged where breeding during lentic phases results in significant recruitment, and thereby is a successful strategy ensuring the continuation of the population. Over the entire geographical range of V. angasi, a monsoonal climate occurs. However, annual precipitation and stream discharges over this range may be considerably lower than those observed in the Alligator Rivers Region. Low dissolved oxygen concentrations in part may limit Dry season recruitment in the Magela Creek populations. Nevertheless it is likely that in drier regions of its range, there are lentic environments where dissolved oxygen concentrations are sufficiently high to allow major recruitment of V. angasi throughout the year.

In the broader context of the recent climatic history of the Australian environment, the year round breeding strategy of V. angasi may be better appreciated. From the scenario presented by Galloway and Kemp (1981), warmer and considerably wetter phases characterised Australian climates during the Early Tertiary. In the perennial streams of the time, year round breeding for freshwater mussels was presumably the norm. From the Middle Miocene onwards, there has been a general trend to dryness over the continent. Fluctuating climates characterised the Lower and Middle Pleistocene and the trend to dryness culminated in relative aridity between 30,000-17,000 years B.P. With this increasing aridity, streams presumably became intermittent. Also, wet seasons in monsoonal belts at the height of this dry period, were (presumably) of less intensity than those experienced today. Thus, the reproduction of the freshwater mussels was probably modified under the fluctuating and relatively arid environments to one of opportunistic breeding superimposed on a year-round potential.

Past climates have been drier and more variable than those observed today, and recruitment of _V. angasi_ during periods of low and fluctuating discharges, and under lentic conditions has presumably, ensured the continuation of the species. The opportunistic breeding pattern of _V. angasi_ thus, may have been retained as a guarantee against fluctuating climates and environments.

8 FOOD INGESTION, CONDITION AND ANNUAL PRODUCTION

8.1 Introduction

Despite the often reported dominance of freshwater mussels from the second trophic level benthic fauna in lakes and streams, and hence their implicated importance in the processing of energy and nutrients, comparatively few studies have been undertaken to investigate the contribution made by mussels to the nutritional dynamics of freshwater ecosystems. Feeding relationships, the incorporation of ingested material into the body, and the relative contribution of the assimilated tissues to the overall economy of freshwaters in fact, are the least well understood aspects of the ecology of freshwater mussels.

From the standpoint of such basic information as to what freshwater mussels feed upon, only a limited number of attempts have been made to determine specifically the nature of the particulate organic matter strained from the water by these filter-feeding forms, and the dynamics of this filtration process. Apart from a number of general statements that appear in the literature based mostly upon cursory observations of the food items observed in the guts of freshwater mussels, the only comprehensive investigations were undertaken 60 to 70 years ago - for North American unionids by Allen (1914, 1921), Coker *et al*. (1921) and Churchill and Lewis (1924). Annual variations in the composition and abundance of the ingested particulate matter have never been investigated in freshwater mussels.

Similarly, seasonal fluctuations in body weight i.e. condition, as a part measure of the availability of food resources, are poorly understood. Although annual variation in the weight of the soft parts of freshwater mussels have been noted to be high (Haukioja and Hakala, 1978b), minor fluctuations are more generally assumed (e.g. Cameron et al., 1979). Huebner (1980) emphasised, however, that seasonal changes in body weights must be accounted for in the estimates of biomass of mussel populations for population and community energetics studies. Huebner's study in fact is the only one to date to have investigated seasonal body weight fluctuations in populations of freshwater mussels. Condition indices, however, have been derived by Tudorancea and Gruia (1969) and Haukioja and Hakala (1978b) for between-population study of body weight variations.

Studies of the contribution of production and biomass of various species of freshwater mussel to the functioning of ecosystems have been completed by Negus (1966), Tudorancea and Florescu (1968) and Tudorancea (1972), Magnin and Stanczykowska (1971), Lewandowski and Stanczykowska (1975), Coon et al. (1977), Kenmuir (1980), and Strayer et al. (1981).

In at least several billabongs of the Magela Creek, the standing crop of Velesunio angasi is considerable. Studies of the benthic macroinvertebrates apart from V. angasi conducted currently with those of the present, indicated that V. angasi was the major constituent of the benthos, dominating in terms of biomass by over 95% (P. Outridge, unpublished data). As basic information required for estimating the role and importance of the large standing crop of V. angasi in the economy of the freshwaters of the Magela Creek, studies of food ingestion, condition and annual production were undertaken in the waterbodies. No comparable studies have been undertaken on any hyriid unionacean, and the only study for other tropical freshwater mussels is that of Kenmuir (1980) who estimated annual production of the mussels of Lake Kariba, Zimbabwe.

A. FOOD INGESTION

The present investigation sought to determine: what Velesunio angasi ingested; the seasonal changes in the composition and abundance of the ingested particles; and whether or not selectivity of the ingested materials could be ascertained.

8.2 Materials and methods

Material for dietary study was collected from Georgetown, Mudginberri and Nankeen billabongs. Rationalising the time required for investigation, 5 monthly collections from each billabong, taken over the period 1981 and 1982 were used for study. The choice of the time intervals at which mussels were collected was made in order to maximise observed peaks and lulls in body condition (Figs 8.2 and 8.3). Thus, mussels were sampled at mid-Dry and early-Wet season peaks, at late-Wet and late-Dry season lulls and at early-Dry season increases in condition (Figs 8.2 and 8.3). The collection dates for each billabong are given in Table 8.1. An additional collection was made from Mudginberri billabong during June 1980, for selectivity studies (section 8.4).

Mussels to be used in dietary studies were taken from the routine sampling sites of the billabongs during the monthly collections (section 3.1). After collection, mussels were immediately placed in 50% ethanol that was kept on ice both in the field and for some period of time back in the laboratory. Such treatment after collection ensured that digestion or the passage of food materials through the digestive system was prevented. The collection times at which mussels were preserved was constant for each sample, and were always within one or two hours prior to midday.

Fifteen adult mussels randomly selected from each collection provided the material for study. In bivalve molluscs including unionaceans (Allen, 1914), digestion is virtually completed in the stomach. According to Morton (1970), food in the stomach of Anodonta is subjected to extracellular digestion by fragmentation spherules from the digestive diverticula and enzymatic breakdown by the crystalline style, and intracellular digestion as the food is passed into the digestive diverticula itself. For studies of relative digestibilities of the ingested particles therefore, the respective contents of both stomach and intestine were processed. The shucked visceral mass of each individual was dried at room temperature for an hour, prior to longitudinal dissection through the centre of the firmed mass. The relative amount or fullness of ingested material present in both the bulbous stomach and the first loop of the intestine was scored from 0 (empty) to 5 (full). The contents of both stomach and intestine were removed and stored in 70% ethanol.

To determine the relative organic and inorganic fractions present in the ingested material, the stomach and/or intestinal contents of 5 mussels from each sample were combined and dried to a constant weight at 40° C. The ash content was then determined by burning off the organic matter in a muffle furnace at approximately 500° C for 20 hours. It must be stressed that the organic fraction determined by this method is an underestimate, as alcoholic preservation is known to chemically alter organic material. By what factor the fraction is underestimated is not known. The relative weight loss nevertheless, is assumed constant between all samples.

To determine and identify the relative algal fractions of the ingested material, a portion of gut content from each of 10 individuals from each monthly sample, was mounted on a glass slide according to the method of Prescott (1980), for microscopic inspection. Identification of the phytoplankton was based upon the regional key of Ling and Tyler (in press) and the key of Prescott (1980). Working in a systematic fashion across the slide, the first 50 algal units were identified under high power microscopy to genus, but mostly to species. This numerical limit was chosen because often no further plankton could be found on the slide. The algal fraction of the ingested material was determined from areal proportions. Using a 1 mm^2 gridded eyepiece graticule, the number of grid squares (out of 100) at each of 10 fields located at random on each individual slide, superimposed upon algal units and unidentified material (both organic and inorganic) were counted. The number of grid squares containing algal units and unidentified material were summed respectively over the 10 fields. A mean proportion of phytoplankton was then averaged over the 10 individuals from each sample.

8.3 Seasonal changes in the composition and abundance of the gut contents

Composition of ingested material

The relative fractions of the ingested material for each sample are given in Table 8.1 and relative to various environmental parameters in Table 8.2. In general, the proportions of the ingested fractions - phytoplankton, organic detritus, and inorganic material are considered approximate only. The dominance and absence of various algal taxa in the ingested material can be explained by either differential digestibility and/or possible selectivity of some groups (see section 8.4). Thus overall, the algal fraction is almost certainly underestimated and a proportion of the organic detrital fraction probably comprises some broken down and digested algal cells. Further, the total organic fraction is likely to be underestimated because of error involved in the ashing procedure (see above). Between samples nevertheless, biases are assumed to be constant, and comparisons may still be made.

From the data of relative fractions of the ingested material (Tables 8.1 and 8.3-8.5) and from the relationships between the stomach contents of mussels and various environmental parameters (Table 8.2), some general statements may be made:

1) No zooplankters were observed in the guts of V. angasi.

2) As observed by Coker et al. (1921) for unionids (for which the only comparable data are available), the algal fractions in the stomachs of V. angasi are generally low. In V. angasi the values range from 1 to 27% of the ingested materials. While Coker et al. (1921) observed that the phytoplankton normally found in natural waters rarely amounted to more than 20% of the suspended organic material, partial and complete digestion of some algal forms in the stomachs of V. angasi are almost certainly responsible in part for the low representation of algae (see below).

3) As graphically portrayed in Figure 8.1, a correlation is observed between the amount of phytoplankton in water samples and the proportion found in the stomachs of mussels collected simultaneously. The phytoplankton observed in Georgetown during August 1981, considering the high turbidity of the waters (Table 8.1), was presumably restricted to the surface waters (see section 2.3.2.5) and may not have been accessible to mussels. Under such circumstances, a low proportion of algae found at this time in the stomachs of mussels from this billabong could be expected.

4) The only other pattern apparent for the remaining ingested organic and inorganic fractions observed in the stomach contents over the seasons was that the inorganic fraction overall was higher in Georgetown than the other billabongs. This billabong also had the highest turbidities (Table 8.2).

Gut fullness

The fullness indices of ingested material present in the stomach and first loop of the intestine averaged over the individuals of each monthly sample, are shown in Table 8.2. As relative fullness is a measure of feeding intensity, the indices calculated in Table 8.2 are assumed to be synonymous with 'ingestion rates' (Winter, 1978). To discern the effect of the environmental variables shown in Table 8.2 upon ingestion rates of mussels, multiple regression analysis was performed over the data of all billabongs, with either stomach or intestinal fullness as the dependent variable, and chlorophyll, turbidity and dissolved oxygen as the independent variables.

Using stomach fullness as the dependent variable, the only significant relationship was observed in an untranformed regression equation where the partial regression coefficient of dissolved oxygen was (positively) significant ($P < 0.05$). Presumably this reflects an immediate suppression to feeding caused by overnight and early morning oxygen depletions such as were commonly recorded in Nankeen (April, June, August) and occasionally in Georgetown (April) (Table 8.2).

Intestinal fullness is likely to be a better integrated measure of the daily ingestion rate, because the contents are less likely to be voided (vomited) in response to preservation as might be the stomach contents, and further, are less likely to be influenced by the immediate limnological environment prevailing prior to collection. In a multiple regression analysis using log transformations of the independent variables, relationships (but not particularly strong ones, $P < 0.1$) were found between ingestion rate, and dissolved oxygen and chlorophyll. Increased concentrations of either dissolved oxygen or chlorophyll are suggestive of increased ingestion rates. In the same regression equation, turbidity had a negative (but negligible) effect upon food ingestion.

In the floodplain billabongs specifically, however, the sustained effect of anoxia during the early Dry season must have a profound effect upon food ingestion. From Table 8.2 it is evident that in Nankeen billabong, despite high algal concentrations during June 1981, feeding is suppressed probably because of low (sustained) dissolved oxygen concentration. Multiple regression analysis was performed over the data of all billabongs, using intestinal fullness as the dependent variable, and omitting the data from Nankeen during June. In a linear model, all three partial regression coefficients proved significant and Student t values were a follows: chlorophyll, 4.11 (11DF, $P < 0.01$); turbidity, -2.25 ($P < 0.05$); dissolved oxygen, 2.58 ($P < 0.05$). Needless to say, the linear regression equation between intestinal fullness and chlorophyll with the omitted Nankeen data, also proved significant ($P < 0.05$). This indicates that ingestion rates increase with increasing algal concentration; the effect, however, is overridden during periods of low sustained oxygen concentration, when feeding is suppressed. (The inclusion of temperature data to the above analyses indicated that temperature had a negligible effect upon ingestion.)

Food value of the organic fractions

There are indications from the above data, that both the algal fraction of the diet and overall ingestion rates increase in response to increasing phytoplankton in the waters. No seasonal measures of suspended organic detritus are available, but similar cycles in suspended detritus to those of phytoplankton might be expected. More data would be required to discern whether it is the algal populations alone, by some influence upon a preferential feeding behaviour of mussels, that are responsible for the amounts of food ingested. Nevertheless, to affect ingestion rates, food concentration is presumably at submaximal levels (Jorgensen, 1975; Winter, 1978).

Regardless of the influences of ingestion rates, there are good indications that phytoplankton is the chief utilisable food source of V. angasi. The strongest evidence of this relies upon the general observation that growth of bivalves normally varies with food levels present in the environment (Jorgensen, 1975). Growth of V. angasi in the Magela Creek, is directly related to algal concentrations (section 6.4.3.2). The other utilisable food source is suspended organic detritus, which appears to comprise the main bulk of the ingested material of mussels (see above). An averaged measure of suspended organic detritus over the seasons and between the billabongs, is provided in Table 2.7, as total organic carbon. Growth rate of mussel populations as measured by L_∞ of the von Bertalanffy growth equation (Table 6.20), was not correlated with this parameter.

Further indications of assimilation efficiencies between algae and detritus are provided in Table 8.1. A decrease in carbon content of the ingested fractions is observed with the passage of food through the gut. From analysis of the data in Table 8.1, the loss of organic material between the stomach and intestine varied from 0 to 16% in the four samples that were processed. During August 1981 in Mudginberri, data pertaining to the algal and organic detrital fractions of both stomach and intestinal contents were available. Approximately 14% of the organic material was lost between the stomach and intestine; of this proportion, a 46% loss of algae was recorded, but only an 8.3% loss of organic detritus. Whilst this might indicate preferential digestibility of algae, nevertheless, presumably a proportion of the wastes from algal digestion in the intestine may now comprise the unidentified organic detrital fraction, thereby underestimating to some degree loss of the organic detritus. Data on relative fractions of algae and detritus between sites of the gut are inconclusive, and proper feeding experiments using a variety of different diets would be required to estimate properly the assimilation efficiencies of algal and detrital food sources. As far as these studies are concerned, growth rate data suggest that the chief utilisable food source of *V. angasi* is unicellular algae. This accords with the general case that living phytoplankton has a higher food value than either bacteria or detritus in the diets of suspension feeders (section A5.1). In terms of ingestion nevertheless (as opposed to digestion), *V. angasi* may be regarded as a phytophagous and detritivorous filter-feeder.

8.4 Composition and selectivity of ingested phytoplankton

Species composition

The combined percentage composition of phytoplankton genera observed in the stomachs of the 10 individuals of each monthly sample was calculated, and is shown in Tables 8.3-8.5 for Georgetown, Mudginberri and Nankeen billabongs respectively. Highest to lowest species diversity of phytoplankton in the guts of mussels from the 3 billabongs was found to be in the following order: Georgetown, Mudginberri, and Nankeen billabongs.

Two studies relating to phytoplankton populations in the Magela Creek billabongs have been completed: that by Pancontinental Mining Limited (1981), and by Kessell and Tyler (1983). Unfortunately neither source provides comprehensive information upon seasonal changes in the composition and abundance of phytoplankton populations within any of the billabongs. Kessell and Tyler (1983) recorded that motile flagellates especially, but also passively floating desmids (Zygnematales), Chlorococcales, and diatoms dominate the phytoplankton of the Magela Creek. Their studies were mainly confined to the Dry season, and no seasonal data were presented. Pancontinental Mining Limited (1981) provided some limited information on seasonal changes in phytoplankton in the floodplain billabongs of the Magela Creek. They recorded representative species occurring in blooms in the billabongs, and noted in general that 46 species or 36% of the total flora recorded in the billabongs belonged to the Zygnematales. (This is apparently consistent with most Australian freshwater systems where desmids are the dominant taxa.) Pancontinental Mining Limited (1981) noted no apparent differences in taxonomic composition of phytoplankton populations inhabiting billabongs during either Wet or Dry seasons.

Seasonal patterns, however, were apparent in the species composition of phytoplankton ingested by mussels of the Magela Creek. The number of species ingested by mussels was highest in all billabongs during the Wet season (Table 8.3-8.5). Motile flagellates (Dinophyceae and Euglenophyceae) dominated the ingested photoplankton during the Dry. Desmids (Zygnematales) and Chlorococcales were underrepresented in the material from the turbid billabongs during the Dry (i.e. months prior to December 1981, Tables 8.3 and 8.5), but generally dominated in the material from all billabongs collected during the Wet. Assuming that ingestion in *V. angasi* is unselective (see below), these major shifts in species diversity between the seasons were a feature of the dynamics of the phytoplankton populations of the billabongs over the study period. Such patterns, however, have apparently been previously undetected in the plankton of the billabong waters.

Selectivity of ingested phytoplankton

Unfortunately, no water samples were taken with the mussel collections from the billabongs to allow for direct comparison of phytoplankton composition in the guts of mussels and in the surrounding waters. Kessell and Tyler (1983), however, sampled the waters of Mudginberri billabong intensively, over an 11 day period from 24 June to 4 July 1980, recording species present on each consecutive day. Their results in terms of the number of days over which genera were present in the waters (out of 11 days), in relation to the generic composition of the phytoplankton observed in the stomachs of mussels collected on 15 June 1980 are shown in Table 8.6. From the 11 day record of Kessell and Tyler reasonable stability of the phytoplankton populations was apparent with no major shifts or trends in species composition over the period. It is unlikely therefore, that the species composition observed in the waters should have differed to any marked degree from that present 9 days earlier at the time that mussels were sampled.

The water samples of Kessell and Tyler (1983) were taken by towing a net in the open waters of the billabong. Thus, while these samples were not taken from immediately above the benthos, nevertheless a uniformity between different depths of the billabong in algal species composition is assumed. This assumption is justified in that the shallow waters of the Magela Creek billabongs including Mudginberri (section 2.3.2.2) are generally well mixed. Further, algae are not restricted to the surface of the clean waters of Mudginberri and Kessell and Tyler noted regular daily patterns of migration of algae in the billabong, including dispersion at night.

From comparison between the algal composition present in the plankton and in the stomachs of mussels (Table 8.6), it is immediately apparent that the ingested phytoplankton is a poor representation of that present in the water. The phytoplankton of the Magela Creek is diverse and from a water sample from any of the billabongs, 80-100 species can generally be expected (Kessell and Tyler, 1983). The number of species (27) found in the stomachs of mussels from Mudginberri billabong during June 1980, amounted to only one third of that which could be expected from the surrounding waters (Table 8.6). With the same counting procedure (i.e. a total of 500 phytoplankton units) from monthly samples from the billabongs, the total number of species of algae recorded in the stomach varied but rarely exceeded 80 (Tables 8.3-8.5).

The low numbers of algal species observed in the stomachs of mussels, compared to the high numbers found in the plankton could be the result of either 1) differential digestibility or 2) selection against certain algae by mussels.

Evidence of differential digestibility is as follows. The composition of phytoplankton in the stomachs of mussels is characterised by very dominant genera (Tables 8.3-8.5); notable are *Trachelomonas*, *Peridinium* and *Cosmarium* spp. Almost all of the *Trachelomonas* comprised *T. oblonga*, which apparently is consistently represented in algal blooms throughout the Magela Creek (Pancontinental Mining Limited, 1981; Kessell and Tyler, 1983). None of the individual species of the preceding listed genera, however, dominate in the plankton to anywhere near the extent that they are represented in the stomachs of mussels. Analysis of intestinal contents also shows that the dominant taxa are consistenty represented, unchanged in form, in the digested material (see August 1981 in Mudginberri billabong, Table 8.4). Their dominance in the stomach contents of mussels therefore, indicates that these forms are resistant to digestion. The cell wall of *Peridinium* is an armoured thecate; the cell wall of *Cosmarium* is surrounded by a gelatinous sheath; and the *Trachelomonas* cell is enclosed in a rigid, mineralised and nonliving lorica. As also noted by a number of authors therefore (e.g. Allen, 1921; Ten Winkel and Davids, 1982), these spherical algae may pass through the alimentary canal of freshwater bivalves undigested, because of resistant cell walls.

Although species identifications with the material at hand were reliable, with preservation and digestion, the subtlety of form of some algae may have been lost, resulting in some inadvertant misidentification, or lumping of species of similar appearance. This error, however, is assumed minimal and with proper perusal, it is more likely that phytoplankton with naked cell walls will be found to be underrepresented amongst the ingested algae; this would indicate that these forms are rapidly digested in the stomach of V. angasi. In the warm waters of the Magela Creek, this is almost certainly the case and overall, algae should tend to be underrepresented in the stomach contents. Comparison of the phytoplankton composition between that of the stomach content and that suspended in the environment therefore, is unlikely to yield satisfactory results in selection studies, and to properly determine whether V. angasi selects its food, controlled feeding experiments would be required.

Evidence for selection against certain algae is as follows. The number of diatom species in the plankton of the Magela Creek waters is reportedly low, by comparison with the high species numbers of green algal forms. The normally digestion-resistant diatoms are apparently underrepresented in the stomach contents (Table 8.6). Even considering that many broken frustules (presumably of the larger ornate forms such as Asterionella) were observed (but not recorded because they were unidentifiable), tests of the smaller diatoms (e.g. Eunotia) were rarely seen, even though they were commonly recorded in the plankton (Kessell and Tyler, 1983). Gale and Lowe (1971) concluded that Sphaerium transversum fed unselectively, despite the fact that diatoms were underrepresented amongst the ingested phytoplankton. Further, it is quite probable that very large phytoplankton forms (e.g. Netrium, Asterionella) are omitted from the diet of V. angasi, and that a size range (but a large one) of algae is preferred.

Because the number of diatom species (and the taxa of very large algae) represented in the plankton are small in relation to the green algae, selection by V. angasi against diatoms and large algae may account for only minor underrepresentation of algae found in the guts of mussels. The weight of evidence therefore, favours the view that V. angasi generally feeds unselectively, and that algae are underrepresented in the stomachs of mussels because some species are digested much more rapidly than others. Apart from a size selection - if indeed present at all and an unexplained absence of diatoms, further evidence of unselective feeding is presented in that V. angasi includes a large inorganic fraction (silt) (Table 8.2) in the diet. On this criterion alone, i.e. the failure to discriminate between organic and inorganic ingested materials, other authors have decided that respective bivalve species are unselective in their feeding (e.g. Churchill and Lewis, 1924; Nasr, 1984). Further strength to unselective feeding in V. angasi is advanced, given that a wide array of algal taxa at some time or another are represented in the stomach contents (Tables 8.3-8.5).

That the proportions of inorganic particles are not even higher in the guts of mussels from turbid environments (e.g. Georgetown and Nankeen during the Dry season, Table 8.2) is probably explained by the efficiency of retention of particles by the gills. Bivalves can generally retain particles no smaller than 1 μm in diameter

(Jorgensen, 1975). The suspended particles that comprise the turbidities observed in the Magela Creek billabongs, however, are generally less than 0.45 μm in size (Walker et al., 1983b).

B CONDITION

8.5 Wet/dry weight conversions

The flesh of 50 individuals from each of the routine monthly samples from the billabongs (30 individuals from each of the routine samples from the Magela Creek channel) was weighed (section 3.3), and oven dried at 65°C to a constant weight. All dry weights were made to the nearest 1 mg.

Plots of flesh (or wet) weights against dry weights clearly indicated nonlinear relationships within the sexes and waterbodies and showed that water content of mussels decreased with increasing size. Log-log transformed regression equations therefore were calculated to describe the relationship between wet and dry weight. The linear transformed equations are shown for each waterbody, and for sexes separate and combined in Table 8.7. Within any one waterbody, there are generally no significant differences found between the slopes and intercepts of the regressions for each sex (Table 8.7). However, using an analysis of covariance test, very strong evidence ($P < 0.001$) was found against the hypotheses of equal slopes and means of the combined-sexes regressions of each waterbody. A single regression equation using the data from all billabongs therefore, cannot be used to describe the wet/dry weight relationship of mussels from the Magela Creek.

8.6 Length/weight relationships between sexes and waterbodies

Of six external shell dimensions (length, height, inflation, profile, girth and circumference) used to predict biomass of a number of unionid species, it was concluded by Golightly and Kosinski (1981) that functions with the variable shell length as the independent variable, provided accurate and adequate models. Thus even early results using the theoretically ideal dimension, inner shell volume, were quickly abandoned in the present study when it was learnt that as accurate (if not better) prediction of biomass could be obtained using shell length alone. In addition to its virtue of accurate prediction, length has been argued to be the best dimension for field use because of its ease of measurement, and because it is the largest dimension, thus minimising measurement error. Further, its extensive use in the literature facilitates comparison of biomass estimates between various environments (Golightly and Kosinski, 1981).

Using dry weight as the dimension of biomass in the present investigation, log-log transformed regression equations were calculated to describe the relationship between shell length and dry weight. The linear transformed equations are shown for each waterbody, sexes separate and combined in Table 8.8. Only in 3 out of 10 waterbodies were significant differences found between the slopes and/or intercepts of the regressions for each sex (Table 8.8).

To follow changes in the length/weight relationship or condition of the sexes of V. angasi between seasons and locations of the Magela

Creek, the relationship between length and dry weight for all data of the Magela Creek, sexes, locations and seasons combined, were used as a baseline to which the weight of individual mussels of a specific size and from any season and location could be compared. The linear, tranformed regression equation for all mussels combined, is described in Table 8.8.

8.7 Relative condition

The condition of individual mussels, relative to the entire Magela Creek community sampled over the study period, was calculated according to the method of Le Cren (1951) for fish studies, using the formula:

$$K = \frac{W_0}{\hat{W}} \qquad (1)$$

where K = relative condition,

W_0 = observed weight,

$\hat{W}$ = expected weight.

$\hat{W}$ was calculated by substituting the length of individual mussels into the regression equation determined for the combined Magela Creek data (Table 8.8).

8.7.1 Between sexes and waterbodies

Relative condition is shown for male and female mussels (means 95% confidence limits) from Georgetown, Mudginberri and Nankeen billabongs, and the Magela Creek channel at monthly intervals in

Figure 8.2; from Corndorl, Island, JaJa, Leichhardt and Jabiluka billabongs at bimonthly intervals, and from Buffalo billabong at intervals of three months, in Figure 8.3.

In waterbodies where condition was determined at monthly intervals, a diphasic annual cycle of condition is apparent (Fig. 8.2). A major peak in condition during the mid-Dry season (July-September) and a minor peak during the early Wet season (January-February) are observed. Condition is lowest at the end of the Dry (December) and again at the end of the Wet (March-April). Generally speaking, the peaks in condition coincide with periods when food availability (phytoplankton and organic detritus) is greatest, while the lulls correspond to periods of lowest food concentration (see below). In billabongs where condition was determined bimonthly, only a Dry season peak in condition was immediately discernible. Nevertheless, food availability again, appeared to be chiefly responsible for the patterns observed.

Generally, the condition of females was lower than males at any one time and location (Figs 8.2 and 8.3). Rarely however, were the disparities between the sexes significant. The lower condition of females is probably best explained by the repetitive spawning observed in V. angasi, which can be assumed to be more taxing upon the physiology and energy reserves of females than males. Nevertheless, periods were observed when the condition of females exceeded that of males. These periods were associated with either less intensive spawning of females (e.g. late Dry season in Nankeen, Fig. 8.2) or with lag phases in which the condition cycle of females was occasionally observed to fall behind that of males (e.g. January-March 1981 in Mudginberri and the Magela Creek channel; August-December in JaJa). The latter is possibly the result of the lag that would be observed in the weight of females (as opposed to males) retaining brooding larvae.

While the condition cycles appeared to be broadly associated with seasonal abundances and deficiencies in food availability, other climatic and limnological factors from the literature (sections A5.1 and A5.2) have been implicated as affecting either condition or feeding activity of bivalves. Chief amongst these factors are temperature, turbidity, and dissolved oxygen. As was the case for larval production therefore (section 7.10.1), attempts were made to model the condition cycle over all billabongs, or at least within the billabongs, using a mutliple regression approach. Just as was found for larval production the analyses can indicate at least, the contribution of the various climatic and limnological factors towards determining the cycles of condition.

Dry weights and thus condition, were measured and only determined bimonthly in most billabongs. To utilise all of the available data for analysis therefore, the individual wet weights of mussels examined every other month in these billabongs, were converted to dry weights by using the appropriate regression equation (Table 8.7). Relative condition was then calculated for the data in question using the formula (1) described above. Within the alternate months when condition was determined by actual dry weights, condition was also calculated using the conversion of wet to dry weight, for comparison of the estimates. Condition (males and females combined) as derived by the two methods is plotted monthly for the appropriate billabongs in Figure 8.4. The closeness of fit generally observed between the estimates at any one time and location was sufficient justification for including the condition data from all months in the analyses.

The same independent variables as were chosen for larval production were included in the analyses performed on condition, namely chlorphyll, turbidity, dissolved oxygen, temperature and time. (The basis for the inclusion of time in the analyses was the same as presented in section 7.10.1.) Appropriate transformations were decided according to the criteria given earlier (section 7.10.1). Log transformations of chlorophyll, turbidity and dissolved oxygen were used. No multiplicative combinations of the variables were suggested for the analyses. For the dependent variable, condition, the data of both sexes combined were analysed, as differences in body weights between the sexes of V. angasi were generally not significant (Figs 8.2 and 8.3).

Multiple regression analyses were performed on the five independent variables against monthly condition of mussels from each billabong, and on the data of the billabongs combined. The resulting regression equations are shown in Table 8.9. Results of AOVs of the regression coefficients over the billabongs and over groups of hydrologically similar billabongs showed very strong evidence, in both cases, against the assumption that all the regression equations estimated the same population regression ($P < 0.001$). The absence of consistent and significant correlations between condition and environmental factors within billabongs and groups of billabongs indicated that the effects of the various factors were either minimal, masked by other environmental factors, or mediated and controlled more by internal physiological mechanisms rather than realised by an immediate response of body weight to any of the factors.

As noted for larval production (section 7.10.1), the equation derived from the data of the billabongs combined, is a useful descriptive model, giving a general indication of the importance of the various environmental parameters studied, to condition averaged over the Magela Creek. Because condition was calculated relative to the entire Magela Creek data, however, the values of condition at the peaks and lulls do not necessarily correspond between the billabongs. To some extent therefore, the correlations using the combined equation may be expected to be low for independent variables such as temperature and dissolved oxygen whose range in values is similar between billabongs. The results of the regression equations may be summarised as follows:

1) Turbidity - With respect to the regression equations derived from the data of individual billabongs, the sign of the partial regression coefficient of turbidity in the turbid billabongs, Georgetown and Nankeen is positive (significant at $P < 0.01$ in Georgetown, Table 8.9). From the evidence given below, these relationships are assumed associative only, and the seasonal trends of both condition and turbidity are merely coincident. In several billabongs, turbidity and chlorphyll are intercorrelated (Table 8.10) and as shown below, turbidity may obscure the relationship between condition and chlorophyll within these billabongs.

Averaged over all billabongs, the sign of the partial regression coefficient of turbidity is negative (Table 8.9), indicating that increasing turbidity is inhibitive to weight gain. In highly turbid billabongs, food availability (phytoplankton at least) might be expected to be low owing to reduced light penetration through the water column. However, as discussed below, this effect in the Magela Creek billabongs, might only be felt during the late Dry season. In highly turbid waters, additional energy might be expended by mussels in sorting and rejecting the suspended solid load from the surrounding waters. Across all billabongs, nevertheless, the influence of turbidity upon condition is apparently not a strong one.

2) Temperature - The significant, negative partial regression coefficient of temperature ($P < 0.05$) in the regression equation from Nankeen billabong suggested merely coincidental, seasonal trends of both condition and temperature. However, given the correlation between spawning intensity of mussels and temperature in Mudginberri billabong (section 7.10.1), the significant, negative coefficient of temperature ($P < 0.01$) for Mudginberri suggests that condition declines directly in response to increasing reproductive activity. Over all billabongs, the effect of temperature upon condition is nevertheless negligible.

3) Dissolved oxygen - The availability of sufficient oxygen is doubtless conducive to weight increase, and a consistently positive sign of the partial regression coefficient was observed among the billabongs. During June 1981 in Leichhardt billabong, a decrease in

weight of mussels was observed (Fig. 8.3) in association with deoxygenation of the billabong at the time. The suppressed condition of mussels observed between April and June 1981 in Island might similarly be explained in terms of the relative anoxia found in the billabong over this time. Presumably filtering and feeding activities cease during periods of anoxia. Nevertheless, over all billabongs, the influence of dissolved oxygen upon condition is apparently minimal.

4) Chlorophyll - Averaged across all billabongs, trophic conditions are apparently the only significant influence of the magnitude of weight variations of mussels. Thus food availability as measured by chlorophyll, was the only significant partial regression coefficient ($P < 0.001$) in the regression equation using the combined Magela Creek data. Within billabongs, the relationship between chlorophyll and relative condition is partly obscured by intercorrelation between turbidity and chlorophyll (Table 8.10). However, in 5 out of the 8 billabongs, significant regressions were found between seasonal chlorophyll concentrations and condition (Table 8.10).

Weight increment and decline of _V_. _angasi_ in the Magela Creek, are depicted as smoothed and averaged responses to food availability. The monthly measure of food availability (algae) for mussels, however, is not necessarily highly correlated with monthly measurements of chlorophyll. Algal concentrations in the Magela Creek are highly variable both temporally and spatially (Kessell and Tyler, 1983). While the chlorophyll value averaged over the seasons might be a good indicator of the trophic status of the particular environment generally, the spot monthly readings measured in each billabong might not necessarily be the best measure of algal abundance from a month to month basis. This may explain the poor correlations observed between seasonal condition and chlorophyll within billabongs (Table 8.10). (Indeed the weight variation observed in V. angasi might be a good integrated measure of seasonal trends in the trophic status of the waterbody in question.)

Thus, with increasing algal production over the Dry season, a weight increase of mussel flesh is generally observed (Figs 8.2 - 8.3). As stated above, this increase is depicted as an integrated response to food availability. That the period generally coincides with a decline in water temperature, would indicate that respiratory and maintenance costs also decline, thereby availing more energy for growth. Condition peaks during the mid-Dry season in most billabongs.

An ensuing decline in weight is found until the end of the Dry (December) in turbid billabongs (Georgetown, Corndorl, JaJa, Jabiluka, Nankeen) and one non-turbid billabong (Mudginberri) (Figs 8.2 - 8.3). Suppressed algal production due to increasing turbidity is depicted as the cause of weight loss of mussels in turbid billabongs, while a temperature increase and associated spawning intensity are probably the cause of the decline in condition of mussels from Mudginberri. Apparently algal abundance is high enough in the non-turbid billabongs, Island and Leichhardt, that no discernible weight loss occurs with spawning intensity over the Dry season. Weight variations of mussels in these billabongs may be more directly related to oxygen and food availablity.

During the early Wet season, a minor peak is again observed in condition, most evidently in waterbodies where condition was determined monthly (Fig. 8.2). With major early Wet season flushes into the billabongs, dramatic influxes of nutrients into the billabongs occur with associated major peaks in algal production (section 2.3.2.5). These nutrient fluxes apparently decline in intensity, with each major ensuing spate of the Wet season. Thus significant, but nevertheless sporadic and short-lived increases in algal production, in addition to detrital material, probably characterise the waters of the early Wet season. The measurements of chlorophyll taken during the early Wet (December - January) in the present study do not necessarily depict this. (Note, however, the high chlorophyll value recorded for Corndorl billabong during early flushes in December 1981, Fig. 2.28.) The weight gain of mussels observed during the early Wet season, is undoubtedly associated with significant but short-lived increases in algal concentrations. As nutrients are flushed through the catchment with the progression of the Wet, the flowing waters become increasingly oligotrophic and mussel condition reaches a seasonal low at the end of significant Wet season discharge.

Seasonal increases and declines in condition of mussels correspond broadly to the same patterns of fluctuations in algal production observed in the Magela Creek billabongs. Using the data of the respective variables averaged over the seasons for the billabongs, a significant linear regression equation ($P < 0.05$) was found to describe the relationship between mean condition and mean chlorophyll concentration. The relationship is plotted in Figure 8.5 and the regression equation is:

$$Y = 0.595 + 0.046X \qquad (P < 0.05,\ r^2 = 0.575)$$

where Y = mean relative condition
and X = mean chlorophyll concentration (μg/l).

Thus, relative condition of mussels averaged over the seasons is clearly dependent upon the trophic status of the waters. This relationship is taken as further independent evidence that phytoplankton is probably the main utilisable food and energy source for V. angasi.

From Figure 8.5, it is interesting to note that condition of mussels from the non-turbid billabongs (Mudginberri, coded 12; Buffalo, 14; Island, 16; Leichhardt, 24) plotted above the regression line, while the values of the other, non-turbid billabongs plotted below the line. This suggests that energy is expended (at the expense of somatic growth) by mussels in clearing the filtering apparatus of inorganic particles and/or that ingestion in V. angasi may cease or be reduced under conditions of high turbidity. The observation is in agreement with the negative influence of turbidity upon weight increase suggested in the negative sign of the partial regression coefficient from the combined multiple regression equation (Table 8.9).

The mean condition value averaged over the seasons, of mussels from the Magela Creek channel, was not included in the above regression equation describing the relationship between seasonal condition and algal abundances. Of the populations from the Magela Creek waterbodies, the shells of these mussels are exceptionally inflated (section 4.4), and flesh weights therefore, are disproportionately high in relation to mussel length. These mussels consequently, have the highest conditions relative to the other Magela Creek populations (Figs 8.2 and 8.3).

In terms of annual patterns, a diphasic cycle of condition as shown for other populations, is shown for mussels from the Magela Creek channel (Fig. 8.2). An early Wet season peak in condition corresponds presumably to nutrient (and detrital) flushes in the Creek. A seasonal low in body weights occurs at the end of the period of major discharge (March). However, as the Creek is reduced to a trickle and eventually to a series of lentic pools (from March to August), algal populations apparently build up in sufficient concentration for condition of mussels to improve. Condition peaks just at the period when mussels are obliged to aestivate with water subsidence. Energy reserves are depleted over the dormant phase of the mid-late Dry, until feeding recommences at the onset of the Wet season.

8.7.2 Between age classes

Mean condition with respect to age is plotted in Figures 8.6 and 8.7 for each of the Magela Creek waterbodies. Both linear and quadratic weighted regression equations were fitted to the data. Significant regression relationships as described in Table 8.11, were found in 9 out of the 10 populations. In the Mudginberri, Island, JaJa and

Jabiluka populations, the quadratic model was appropriate whereas the linear model was used in the Georgetown, Corndorl, Buffalo, Island, Leichhardt and Nankeen populations. In particular billabongs, mussel condition increased over the earliest ages, peaked at an intermediate age, and declined over the oldest age classes (Mudginberri, Buffalo, Island, JaJa, Nankeen - Figs 8.6 and 8.7). In Buffalo billabong, the decline in condition was noted only amongst the oldest age classes (> 25 years). In other billabongs, a decline in condition was observed over the entire life-span of mussels (Georgetown, Corndorl, Leichhardt).

The increase in condition observed amongst the younger age clases of mussels in several billabongs (and the Magela Creek channel) can be attributed in part at least, to the allometric relationship between length and width of mussels in the Magela Creek (section 4.4). Larger mussels are more inflated than smaller mussels and therefore tissue weight is proportionately greater in the larger individuals of a population.

Senility (Comely, 1978) or the increased energy requirements for basal metabolism that would result in less food being made available for growth (Hickman and Illingworth, 1980), have been suggested as causes of a decline in condition observed amongst the older age classes of respective marine bivalve species. The decline in condition invariably observed amongst the older age classes of mussels of the Magela Creek populations (Figs 8.6 and 8.7), corroborates the evidence of section 7.8, that reproductive functioning of V. angasi, declines with age. That this decline is at least one factor contributing to the relative weight decrease of mussels, is shown by the fact that in female mussels at least, gravidity and oogenic activity decline in intensity with age (section 7.8). Relative weight loss can be assumed to accompany these changes therefore, as significantly fewer oocytes and subsequent larvae are produced.

8.7.3 Within billabongs

The mean condition of mussels sampled in Georgetown (Fig. 8.8), and Leichhardt and Nankeen billabongs (Fig. 8.9) was plotted according to depth. As was found for within-billabong study of larval production (section 7.10.2), the relationships shown in Figures 8.8 and 8.9 could generally be explained in terms of the known condition-age relationships as discussed above (section 8.7.2) and the age-depth relationships as described in section 6.5.3.1. Some exceptions to the expected patterns, however, were noted. At shallow depths, the condition of mussels in Georgetown and Nankeen billabongs was the reverse of the patterns that could be expected if they were to accord with known condition-age and age-depth relationships. Thus, the youngest mussels occur at the shallowest depths (< 0.5m Nankeen, < 1.5m - Wet season levels - Georgetown) in these billabongs yet their condition was amongst the lowest observed and not the highest as might be expected from section 8.7.2 above (Figs 8.8 - 8.9). To some extent, the anomalous patterns observed in Georgetown may be explained in terms of the seasons that mussels were collected. Waters less than 1m in depth represented the peripherally inundated shallows of the Wet season. The condition of mussels collected at this time was generally low (Fig. 8.2). As discussed in an earlier section (section 6.4.3.1) nevertheless, at the shallowest depths in either Georgetown or Nankeen billabong, wave-induced resuspension of the silty sediments during the Dry season might interfere with the normal filtering processes. Extra energy may be expended by mussels feeding in highly turbid waters (see above, section 8.7.1). For greater depths (> 0.5m Nankeen, > 1.5m Georgetown) and all depth intervals of Leichhardt billabong otherwise, condition accords with the patterns as could be expected from known condition-age and age-depth relationships.

No depth relationships could be shown for the condition of mussels within Mudginberri and Buffalo billabongs. Although age and depth relationships have previously been shown for mussels from these billabongs (section 6.5.3.1), condition does not vary greatly over the life-spans of mussels from either billabong (Fig. 8.6). Nevertheless, in both billabongs relationships were found between mean condition of mussels at the particular sampling sites and mean chlorophyll concentration (calculated for these sites as described earlier in section 5.4.3.1). The relationships between mean condition of mussels and chlorophyll concentration are plotted in Figure 8.10 for Mudginberri and Buffalo billabongs. Condition of mussels clearly improves with increasing chlorophyll concentration.

Thus, between relatively widely spaced sampling sites of a billabong such as in Mudginberri and Buffalo, trophic conditions may be expected to affect relative condition. Otherwise, age and local turbidity effects may influence the patterns of relative condition observed over a depth range at a sampling station, such as were observed in Georgetown, Leichhardt and Nankeen billabongs.

C ANNUAL PRODUCTION

8.8 Biomass

The lengths of individuals that were used to determine the density estimates of mussels in each billabong (section 5.3, Tables 5.1-5.9), were converted to dry weights, using the appropriate length/weight regression equation (Table 8.8). The mean shell free, dry weight of mussels per unit area was then calculated according to habitat types within the billabongs (Tables 8.12-8.19).

From the data of Tables 8.12-8.19 no overall mean biomass (per unit area) was calculated for each billabong. Cursory but reliable approximations, however, range as follows: <5 g dry weight/m², Jabiluka < Gulungul < Island; 5-10 g/m², Georgetown; 10-15 g/m², JaJa < Leichhardt < Corndorl; 15-20 g/m², Buffalo < Mudginberri < Nankeen. The biomass ranking thus, is similar to the billabong density ranking (Table 5.10), except that the high density of mussels in Georgetown (second highest of the billabongs) realises a small biomass (fourth lowest) because of the slow growth rates exhibited by mussels in this billabong (section 6.4.2).

8.9 Annual production in selected billabongs

Annual production of V. angasi was estimated in several billabongs of the Magela Creek - Georgetown, Mudginberri, Leichhardt and Nankeen. The choice of billabongs was made according to the variety of hydrological and trophic types represented in the Magela Creek.

Biomass and production estimates were computed from the population data using method 1 of Crisp (1971). This is the method used by other workers (Table A5.1) to estimate biomass and production in respective freshwater mussel populations. Biomass was obtained from the product of density (n) and mean weight (b), and production from the product of density and change in mean weight (b) (where b at age n = $b_n - b_{n-1}$) of each age class. Density of mussels of each age class was obtained from the product of the grand, mean density of mussels (per m^2, Table 5.10) and the proportion of the total age structure that individuals of the respective age class comprised (Figs 6.29 and 6.30). Biomass of individuals of each age class was calculated by converting age to length according to the appropriate von Bertalanffy growth equation (Table 6.20), and converting length again to dry weight using the appropriate length/weight regression equation (Table 8.8). Step by step computations (following Lewandowski and Stanczykowska, 1975) used to calculate annual production and biomass of the various age classes of *V. angasi* in the respective billabongs, are presented in Tables 8.20 - 8.23.

As expected (Waters, 1977), the turnover ratio (P/B) of *V. angasi* in the Magela Creek, decreases with increasing age of mussels (Tables 8.20 - 8.23), as a result of decreasing growth rates with age. P/B ratios calculated for all age classes, are relatively constant between populations, ranging from 0.07 to 0.13. The population from Leichhardt observes the highest ratio (0.13). This population is one of the youngest in the Magela Creek (Figs 6.29 - 6.30), and as growth is continuous over the entire life span (Fig. 6.12) even the oldest mussels are nevertheless contributing to production (Table 8.22). Proportionately more older mussels comprise the mussel populations from Georgetown, Mudginberri and Nankeen billabongs, however (Figs 6.29 - 6.30). As growth is insignificant in the oldest age classes (Figs 6.11 - 6.12), these mussels contribute little if any to the total annual production (Tables 8.20, 8.21 and 8.23 respectively). P/B ratios therefore are relatively low (0.071 - 0.088) and variations can be attributed to the relative contributions of the oldest age classes to the biomass of the respective populations. Thus in accordance with the predictions of Waters (1977), P/B ratios of V. angasi in the Magela Creek are generally a function of longevity and the relative contribution of the oldest mussels to production.

D. DISCUSSION

Food ingestion

The absence of animal remains (notably zooplankters) amongst the ingested stomach contents of mussels from the Magela Creek billabongs, was taken as evidence that V. angasi is a phytophagous and detritivorous filter feeder. Thus, these observations are in accord with those of other workers that the food of freshwater mussels is chiefly of plant origin (Evermann and Clark, 1917; Coker et al., 1921; Hendelberg, 1960; Clarke, 1973). Others, however, have recorded zooplankters amongst the ingested gut contents of mussels (Allen, 1921; Churchill and Lewis, 1924), and both Pennak (1953) and Fuller (1974) concluded that these forms were important as food value for freshwater mussels. Zooplankters are generally absent from the diet of other freshwater bivalve forms and marine bivalves (section A5.1).

Based on reports that much of the phytoplankton ingested by freshwater mussels passed through the digestive tract intact and unchanged by the digestive processes, Fuller (1974) concluded that algae were overestimated as food value. Thus, the observation of only partial digestion of algae is a widespread one amongst dietary studies of bivalves (section A5.1), and it is well known that some diatoms and flagellates bear tests or cellulose cell walls resistant to digestive enzymes. Coker et al. (1921) recorded moreover, that generally less than 5% of the ingested stomach contents of mussels examined, comprised diatoms and unicellular green algae. They concluded that detritus formed the main fraction of the food of freshwater mussels.

Similarly, in the stomachs of V. angasi examined, the algal fractions were generally low ranging from 1 to 27% of the ingested materials. Moreover, the dominant genera of algae present in the stomachs, notably Trachelomonas, Peridinium and Cosmarium, are all forms with resistant cell walls - which in other studies have been shown to pass through the digestive tract undigested (e.g. Allen, 1921; Coker et al., 1921; Ten Winkel and Davids, 1982). These forms in V. angasi were also noted beyond the stomach, present in an undigested condition. The very presence of dominant, digestion-resistant algae in the stomachs, however, is taken as evidence that algae overall were underrepresented amongst the ingested material; that is, more sensitive forms presumably ingested along with the more resistant algae (assuming that ingestion is unselective), must undergo rapid breakdown and digestion. This is almost certainly the case considering the comparatively high water temperatures sustained over the year in the Magela Creek (> 20° C), that would accelerate the digestive processes. Allen (1921) and Coker _et_ _al_. (1921), also recorded dominant and resistant algae amongst the ingested contents of the gut. Unfortunately, no data were presented in either study to allow assessment of the extent to which both individual algal forms and the bulk proportion of phytoplankton present in the gut contents of the unionids were underrepresented as well.

Intestinal fullness of ingested material was argued to be the best integrated measure of feeding activity and ingestion rates of _V_. _angasi_. A positive correlation was found between the ingestion rate and phytoplanktonic biomass of the environment when the influence of periods of sustained oxygen depletion was excluded from analysis. (During periods of relative anoxia, there was no evidence of feeding regardless of the levels of algae in the plankton.) A strong correspondence was also noted between the proportion of algae in the stomach and the biomass of phytoplankton present in the surrounding waters. More studies would be needed to discern whether feeding intensity is dependent only upon the living algal component of the organic material in suspension. In this instance the appetite of mussels would be solely dependent upon algae even if ingestion was unselective. This would indicate that algae was the main utilisable food item. Both algal and detrital abundance in the suspension of the waters of the Magela Creek, however, may be simultaneous, especially if much of the detritus is of phytoplanktonic origin. A correlation between ingestion rate in bivalves and food concentration in the environment, is generally interpreted as meaning that food is at submaximal levels (Jorgensen, 1975; Winter, 1978).

Nevertheless, while the cycles of living and dead algae could be assumed to be the same in water suspensions, the abundances of phytoplankton and total organic carbon averaged over the seasons in the Magela Creek billabongs do not correlate (see Table 2.7). This would suggest that the chief component of the organic detritus in suspension in the billabongs, is not of phytoplanktonic origin. Almost certainly the material is of a macrophytic or allochthonous nature considering that the levels of total organic carbon are highest in billabongs lying off the mainstream channel of flow of the Magela Creek (backflow billabongs and JaJa) where macrophytes are prolific and where deposition during the Wet season is relatively high.

Jorgensen (1975) and Winter (1978) state that growth in bivalves is dependent upon the amount of food ingested. In V. angasi periods of maximal uptake of food averaged over the billabongs was correlated with the abundance of phytoplankton in suspension. Importantly, both shell (section 6.4.3.2) and somatic growth (section 8.7.1) of mussels between the billabongs are correlated with algal abundance averaged over the seasons. No correlations were found between growth and mean, total organic carbon (as a measure of suspended organic detritus). These relationships strongly suggest that phytoplankton is the chief utilisable food and energy source of V. angasi. (No correlations between algal abundance i.e. trophic status, and growth rates of freshwater mussels have been clearly demonstrated within a drainage system in the literature. Green (1972, 1980) found evidence that calcium is a limiting factor to shell growth of some North American unionid populations. However, between European lakes, higher trophic environments realise bigger and heavier Dreissena polymorpha, according to Stanczykowska (1978).)

That algae may be underrepresented in the stomach contents of freshwater mussels, and nevertheless pass through the digestive system in large proportions undigested, would not appear to be justification, on the results of the present study, for assuming that algae are overestimated as food value (Coker et al., 1921; Fuller, 1974). That algae were underrepresented in the guts of V. angasi, was almost certainly an artifact caused by the differential digestibilities of the various algal types. In relation to digestibility moreover, Allen (1914, 1921) showed that digestion was dependent upon the demand for nutrition; starved mussels were capable of digesting normally resistant diatoms. As further evidence, Moore (1975) and Jorgensen (1975) state that living phytoplankton is superior to both bacteria and detritus in terms of utilisable energy in the diets of deposit and filter-feeders respectively. According to Wallace et al. (1977), even diatoms potentially have a high food value in the nutrition of filter-feeders.

Species composition of the phytoplankton ingested by V. angasi was highest during the Wet season. Motile flagellates (Dinophyceae and Euglenophyceae) dominated the ingested phytoplankton during the Dry, while over the same period desmids (Zygnematales) and Chlorococcales were generally absent in material collected from turbid waters. The latter forms, however, dominated in all of the material collected during the Wet. These seasonal shifts in the abundance of major taxa of phytoplankton have not previously been detected in the plankton of the Magela Creek waters (Pancontinental Mining Limited, 1981; Kessell and Tyler, 1983).

Various interpretations have been advanced as to whether freshwater mussels exercise selectivity over ingested materials. Allen (1914, 1921) concluded that selection is exercised - mussels avoiding particles of no food value such as silt, and rigidly excluding injurious substances. Coker *et al*. (1921) and Churchill and Lewis (1924), however, reported that mussels fed unselectively, noting the presence of inorganic debris amongst the ingested food. Coker *et al*. (1921) added that the ingested stomach contents were similar to those found in the environment in type and proportion. Both studies indicated that rejection of unwanted substances was accomplished by mussels ceasing to feed whenever these were present. The results of feeding experiments conducted by Brönmark and Malmqvist (1982) suggested that unionids have a sorting and selection capability.

Because digestion is apparently rapid in the stomach of *V. angasi*, the algal forms present were underrepresented. The ingested phytoplankton is a poor representation of that present in the water and selection therefore could not be determined by direct comparison between the content of the stomach and the phytoplankton suspended in the environment. Controlled feeding experiments would be required to resolve the question of whether or not *V. angasi* shows preference among the types of food available for ingestion. Certainly, relative to green algae, diatoms are underrepresented in the stomach contents. Finding no other indication of selection in *Sphaerium transversum*, Gale and Lowe (1971) also found comparatively fewer diatoms in the guts than in water samples. Broadly speaking nevertheless, given that a significant inorganic fraction is included in the diet (not all of which could possibly have comprised the inorganic constitutent of phytoplanton and organic detritus), *V. angasi* is unselective in its feeding. On the same grounds both freshwater (Churchill and Lewis, 1924) and marine (Nasr, 1984) bivalves have been termed unselective feeders. It is unlikely that selection amongst algal forms (other than diatoms) occurs, moreover, given that at one time or another most of the taxa are represented in the stomach contents.

Among other lamellibranchs, corbiculaceans apparently exhibit very little selection over potential food items; the freshwater bivalve *Dreissena polymorpha* may be selective; and opinion is as equally divided, as it is amongst studies of freshwater mussels, as to whether marine bivalves are selective in their feeding (section A5.1).

Other than there being an increase of ingestion rate of mussels with increasing food concentration, there were clear indications from regression analyses that ingestion was also affected by dissolved oxygen and turbidity. Mussels apparently reduced their feeding and ingestion rates in response to both low environmental levels of dissolved oxygen and to high concentrations of suspended solids. The suppressive effect of low, sustained dissolved oxygen concentrations upon ingestion appears to be of overriding influence to any other environmental factor. While the reaction of freshwater mussels to anoxia can be assumed to be a cessation of water filtration (noted in laboratory experiments with *V. angasi*), energy might also be conserved in turbid waters by reducing or ceasing filtering activities (as discussed below). Suppression of feeding has been observed during periods of low dissolved oxygen in both freshwater (Gale and Lowe, 1971) and marine bivalves (Riisgard and Randlov, 1981). Peddicord (1977) thought that the marine bivalve Rangia cuneata probably reduced or ceased filtering activities during periods of high turbidity to conserve energy required to sort and reject silt particles. No evidence was found to indicate that V. angasi reduced feeding activity with decreasing water temperature as other temperate bivalves including freshwater forms respond (Matteson, 1955; Gale and Lowe, 1971; Winter, 1978).

Condition

Few significant differences were found in the length/dry weight relationships of male and female mussels from the Magela Creek populations, using regression equations calculated on data averaged over the seasons. In plotted condition cycles, however, the condition of females plotted generally below that of males at any one time and place. Rarely though were these differences in condition between the sexes significant. Repetitive spawning is presumably more taxing upon female reproductive physiology of V. angasi than males, which may explain the disparities. Occasionally the condition of females exceeded that of males. These periods were mostly associated with reduced reproductive activity of females.

Very few comparative data are available on the length/weight relationship or condition of the sexes of freshwater mussels between seasons and locations. For North American unionids nevertheless, Cameron et al. (1979) found generally no differences in the length/weight relationship between sexes while Huebner (1980) recorded only slight seasonal changes between the sexes. Huebner found that female Anodonta grandis and Lampsilis radiata exhibited higher body weights than males during the period of glochidial brooding. By contrast, in V. angasi brooding females were mostly of lower condition than males. Female mussels in the Magela Creek, however, may be assumed to constantly channel a greater contribution of energy into reproductive effort at times of peak larval production. Few data are available on similar aspects of sexual differences in condition of marine bivalves. Apparently sexual differences at any one time are insignificant (e.g. Comely, 1978).

In waterbodies in which condition of V. angasi was followed monthly over a two year period, a diphasic annual cycle was apparent. A major peak in the mid-Dry season and a minor peak in the eary-Wet were observed, while lulls in condition were noted at the end of the Dry and again at the end of the Wet. Food availability appeared to be the major factor determining seasonal increases and declines in condition.

From the multiple regression analyses performed on condition and environmental data from individual billabongs and from the billabongs combined, only several significant, partial regression coefficients resulted. Of these, only a few were interpretable. A negative coefficient of temperature for the Mudginberri data suggested that condition declined indirectly in response to increasing temperature, but directly in response to associated increasing reproductive activity. Food availabiity (phytoplankton) as measured by chlorophyll was the only significant coefficient in the regression equation using the combined Magela Creek data. In 5 out of the 8 billabongs moreover, significant regressions were found between monthly chlorophyll concentrations and condition.

Thus, the two peaks in condition were generally associated with (1) increasing Dry season eutrophy and (2) major early-Wet, nutrient inputs from a drought-stricken catchment, that resulted in short-lived but significant increases in trophic conditions in the waterbodies. Declines in condition coincided with (1) periods of either increasing turbidity with resultant suppression of algal production, aestivation (Magela Creek channel) or with spawning intensity (Mudginberri), during the latter period of the Dry and (2) progressive oligotrophy of the Wet season waters.

In the few comparative studies of weight fluctuations of freshwater mussels, however, Cameron et al. (1979) and Golightly and Kosinsky (1981) found only minor seasonal variations in the length/weight regressions of unionids. Haukioja and Hakala (1978b) recorded considerable annual variation in condition of Anodonta piscinalis, but did not describe the seasonal changes, nor the factors that might influence them. Huebner (1980) in contrast, reported on seasonal body weight fluctuations of A. grandis and Lampsilis radiata. Both species peaked in condition in spring. Seasonal weight changes were attributed to whether or not females were brooding larvae, differences in food availability and quality of the environment and to possible disparities between tissue and shell growth. Seasonal weight increases of Dreissena polymorpha in European lakes occur at the time of gonadal development. In marine bivalves for which cycles are well known, condition generally peaks with gonadal maturation, and falls following spawning; a correspondence is also observed between gonadal maturation and periods when food resources are abundant (section A5.2).

In contrast to both freshwater and marine bivalves from temperate regions where seasonal reproductive activity largely influences weight changes, condition in V. angasi is mainly influenced by food availability. Weight variations are largely independent of reproductive activity. The only apparent exception to this general rule, was the weight decline noted in mussels from Mudginberri billabong during the late Dry season. As food concentrations in this billabong are relatively meagre (by comparison with other non-turbid billabongs such as Island and Leichhardt), the intensive breeding activity observed in the late Dry was sufficient to outpace any weight increase; a net decline in weight resulted. In non-turbid billabongs that exhibited comparative eutrophy over the latter period of the Dry season, however (Island and Leichhardt), no decline in condition was noted in association with increased breeding intensity.

The effects of dissolved oxygen and temperature, upon condition of mussels amongst the billabongs were very likely underestimated from the results of the multiple regression equation averaged over the billabongs. This was because condition was estimated relative to the entire Magela Creek community and thus the magnitude of peaks and lulls in condition did not necessarily coincide between billabongs.

Nevertheless, their effects as discerned from the respective coefficients in the regression equations derived for each billabong, were either negligible or inconsistent in sign. Overall, the effect of temperature was negative but nevertheless, negligible except for the specific case of Mudginberri billabong mentioned above. Dissolved oxygen was conducive to weight increase but the effect was only noticeable in some floodplain billabongs at the Wet-Dry interchange, when condition was noticeably depressed in mussels sampled from anoxic waters.

The influence of temperature upon condition of bivalves reported in the literature is ambiguous. Increasing temperature may influence or may be associated with an increase in food availability, in which case condition may improve (Stanczykowska, 1977; various marine bivalves reported in section A5.2). Otherwise respiratory costs may increase with increasing temperature, thereby reducing energy available for somatic growth (Huebner, 1980; Dudgeon and Morton, 1983). Hickman and Illingworth (1980) observed that mean condition and latitude were negatively correlated in marine bivalves, and that broadly, temperature and condition were negatively correlated. With respect to dissolved oxygen, as mentioned above, both marine and freshwater bivalves have been reported to reduce feeding activites under conditions of oxygen depletion. Presumably body weights are affected during these periods of inactivity. V. angasi also reduces its feeding activity in oxygen-stressed environments.

Using data averaged over the seasons for each billabong, a significant linear relationship was found between mean condition and mean chlorophyll concentration when the data from all billabongs were regressed. A feature of the plotted relationship was the observation that the condition of mussels from non-turbid environments was comparatively higher than that of mussels from turbid billabongs. This substantiated the evidence from the combined multiple regression equation of all the Magela Creek data, in which the partial regression coefficient of turbidity was negative. Of further note, was the observation that the condition of mussels inhabiting the shallow reaches of the turbid billabongs (Georgetown and Nankeen) was visibly depressed, presumably because of wave-induced resuspension of the silty sediments that may be expected to be most pronounced here. All the evidence indicates that either filtering activity is reduced in turbid waters or that extra energy is expended by mussels in feeding under the conditions. Peddicord (1977) also observed depressed condition in marine clams feeding in turbid waters. The same conclusions as drawn by Peddicord are relevant to V. angasi, namely, extra energy might be expended in cleaning the filtering apparatus of mussels feeding in dirty waters, and filtering may nevertheless be reduced under these conditions. (A reduction in feeding activity of mussels feeding in turbid waters was noted - see above.)

Very few accounts of variations in condition of freshwater bivalves between sites have been described in relation to possible factors of influence. At high densities, condition in some species is reportedly reduced, presumably as a result at least, of competition for available food resources (Tudorancea and Gruia, 1968; Stanczykowska, 1964, 1977). Stanczkowksa (1977) reported that weight variations of Dreissena polymorpha between European lakes were in proportion to trophic conditions.

Between billabongs of the Magela Creek, flesh weights of V. angasi are also dependent upon trophic conditions. As condition is largely independent of environmental factors other than chlorophyll, relative weight of V. angasi may prove, regionally, to be a valuable indicator of the trophic status of billabongs. This value may be even better appreciated when applied to weight variations recorded temporally within specific waterbodies. Weight variation over time in V. angasi is depicted as a smoothed and averaged response to food availability. Condition is presumably then, an integrated measure of trophic status for which productive and unproductive periods in waterbodies may be identified. This measure of trophic degree may not be so reliable in clean, oligo-mesotrophic waterbodies such as in Mudginberri (section 2.3.2.5) where spawning intensity in the warm waters of the late Dry, may affect body weight independently of food availability.

The indicator role suggested here for V. angasi may be corroborative of a similar role advocated earlier (section 6.9) for which growth rates (as measured by L_∞ of the von Bertalanffy growth equation) were argued to be useful, integrated measures of trophic status of waterbodies averaged over the seasons. Condition data may be usefully employed to identify (in most cases) the trophic status of waterbodies within that timespan.

Annual production

Waters (1977) stated that production rates of organisms in tropical regions could be expected to be several times the levels of the same groups from temperate regions. In relation to known production rates of freshwater mussels from temperate and tropical regions (Table A5.1), annual production of V. angasi (values ranging between 0.39 and 1.75 g shell free, dry weight) in billabongs of the Magela Creek is high, but not of the order indicated by Waters. Moreover, production of gametes in V. angasi, a repetitive breeder, is not included in the production estimates. Larval production especially, would amount to a very significant fraction of total annual production in some environments of the Magela Creek, given that reproductive cycles may be completed within a month (section 7.11). The production estimates calculated in this study therefore, may be grossly underestimated.

P/B or turnover ratios of V. angasi (0.07 - 0.13), are amongst the lowest recorded of any freshwater mussel (Table A5.1). By comparison with other mussels studied, however, V. angasi is one of the longest -lived freshwater mussels known (Chapter 6). Thus, while the P/B ratio is reasonably constant for a group of organisms and is generally independent of environmental influences, it is clearly a function of voltinism (life spans) (Waters, 1977). The ratio therefore may be expected to be low in long-lived populations, because of the accumulation of production with age.

The low P/B ratios observed generally in freshwater mussel communities and low production rates in comparison to the total macrobenthic production, have been variously interpreted (section A5.2), as indicating that freshwater mussels contribute very little in terms of biomass and energy to predators of the trophic level above.

Short-lived corbiculaceans, and marine bivalves by comparison may be important food sources to animals in higher trophic levels. Negus (1966) noted, however, that juvenile freshwater mussels may be significantly preyed upon. Negus added that in populations where recruitment was regular, mussel flesh of individuals that died each year, would contribute an amount of food approximately equal to annual production to scavenging fish and invertebrates, and decomposers. (Mussel flesh for animals that are consumed, has a very high caloric content - Tudorancea and Florescu, 1968).

It must be reiterated that production (and therefore the P/B ratios) of V. angasi in the Magela Creek may be severely underestimated because of the omission of the contribution by gametic and larval production. Thus, apart from providing food for predators in the juvenile stages, or for scavengers and decomposers when death occurs by natural causes, the same trophic levels may utilise the considerable production of wasted reproductive products.

Although probably utilised to only a minor degree as food for other trophic levels, mussels may contribute to the functioning of ecosystems in other important ways. At high densities, the filtration ability of mussels has been estimated (or argued) to be significantly important to the nutrient cycles of aquatic environments and to their general circulation of materials (section A5.3). Using filtration rates estimated for European unionids (Lewandowski and Stanczykowska, 1975), the entire mussel population in Mudginberri billabong (680,000 - Table 5.10) is estimated to filter almost 5 Ml of water daily. At a Dry season volume of 177 Ml of water in the billabong, this represents an exceedingly rapid turnover equivalent to the entire volume by filtering mussels, every 36 days. During the filtration process, large amounts of seston are filtered out to return to the sediments in the form of faeces and pseudofaeces. This process results in acceleration of the breakdown of nitrogenous wastes, thereby providing nutrients at rapid disposal for plankton, and bacteria-enriched seston as food for other benthic fauna. Thus at high densities the large biomass of V. angasi must play a significant role in the nutrient cycles and towards organic enrichment of the bottom sediments of billabongs. Lewandowski and Stanczykowska (1975) suggested that movement of mussels present at high densities may also be important in mixing the bottom sediments.

Mussels may also play an important role in the calcium cycles of particular aquatic environments, notably in soft, acid waters (Green, 1980). Preliminary calculations suggest that V. angasi when present at high densities, may play a significant role in the calcium cycles of some Magela Creek billabongs. In the soft, acid waters of Mudginberri billabong for example, 3.9 Mg of calcium is present in the shells of living mussels. This is approximately 19 times the amount of calcium dissolved in the water. Assuming a dissolution rate of one year for empty shells in the warm acid waters, and an annual mortality rate of mussels of 10% (from the data of Table 6.44), an amount of calcium almost twice that present in the water is freed annually, to be either flushed from the billabong during the Wet, accumulate in the sediments, used for shell growth of mussels or importantly, taken up in other biological pathways.

Thus in summary, although direct predation upon V. angasi is probably minimal in the adult life, dead material and significant (but undetermined) annual production of reproductive products and newly recruited young would be provided to organisms of other trophic levels for consumption. Considering the enormous biomass of mussels in some billabongs, their filtration ability may be assumed to contribute most significantly to the ecological functioning of the environments. The mussel must almost certainly play an important role in the nutrient cycles and general circulation of materials in the Magela Creek billabongs. The extent of the importance of V. angasi in the calcium cycles of the billabongs remains to be determined. Early estimates, however, suggest that empty mussel shells may provide a significant potential source of calcium to various biological pathways.

9 GENERAL DISCUSSION

The study of Velesunio angasi in the Magela Creek, has contributed a significant fund of knowledge to the biology and ecology of freshwater mussels in general, particularly to the southern hyriid unionaceans and tropical mussels for which little information is presently available. While specific findings have been brought to attention in the relevant sections, some general aspects of the study of V. angasi with respect to adaptations and life strategies, merit some final discussion in comparative relation to the freshwater mussels from Australasia, tropical regions and worldwide. Finally, some specific aspects of the biology and ecology of V. angasi are re-presented as deemed worthy of consideration in future studies of the mussel or indeed for studies of freshwater mussels generally.

McMichael and Iredale (1959) recognised in the Australian hyriids, a complete gamut of physiological and ecological adaptation, from species incapable of withstanding desiccation to any degree, to those fully adapted to drought conditions. As typical forms, McMichael and Iredale mentioned (a) the genera Hyridella and Cucumerunio, occurring in the relatively well watered, perennial east coast streams of Australia - as intolerant of desiccation, and (b) the velesunionines, V. ambiguus and V. wilsonii, which can survive for months or even years without water. The most primitive members of the Australian hyriids are the velesunionines, comprising the genera Velesunio, Alathyria and Westralunio (McMichael and Hiscock, 1958). Representative species of this subfamily occur in all principal drainage divisions of Australia. Three species of the genus Velesunio

- *V. ambiguus*, *V. wilsonii* and *V. angasi*, are the most widely distributed of the Australian fauna, and collectively their ranges almost completely superimpose the ranges of all other species.

While only the velesunionine hyriids occur in inland Australia, members of only the genus *Velesunio* appear to be specificially adapted to the vicissitudes and aridity that are features of this vast expanse of the continent. The inland species, *Alathyria jacksoni* for example, is intolerant of still-water environments (Walker, 1981b). At the extreme, *V. wilsonii* which is found in drier parts of Australia than any other hyriid, reportedly aestivates during droughts in the bottom sediments of semi-permanent waterholes; it has been recorded as surviving for 3 years in a box in the laboratory without water (McMichael and Iredale, 1959). *V. ambiguus* has preferences for still or slow flowing waters throughout its range, and is in fact intolerant of fast flowing riverine environments; in company with these habitat preferences, the mussel is markedly resistant to desiccation and has demonstrated ability to survive at least short-term anoxia (Walker, 1981b).

V. angasi does not occur in inland Australia, but nevertheless shares physiological and ecological attributes in common with *V. wilsonii* and *V. ambiguus* described above. Indeed, one may forward the view that *V. angasi*, by nature of its environment, will eventually prove to be amongst the most tolerant of the Australian hyriids to environmental rigours. Occurring in tropical monsoonal drainages, extreme variations are inherent in the quality of the freshwater environments inhabited by the mussel from season to season, as the result of the annual cycle of alternating flooding and drought. As a consequence, V. angasi is adapted to a broad range of conditions from riverine, to still-water and ephemeral environments. Exemplifying these environmental extremes, constrasting ecophenotypic forms of the mussel are found, functionally adapted for life in swift-flowing waters and seasonally dry river beds. Comparable ecophenoptypes apparently are not found in V. ambiguus and V. wilsonii. (The relatively larger size attained by V. wilsonii, however, is presumably a factor contributing to burrowing powers and increased volume - behavioural and morphological attributes that would be necessary to enhance survival during periods of aestivation.) V. angasi is well adapted to life in still, Dry season waters that may be seasonally depleted of oxygen, and that may become hot and shallow. Physiological adaptations to these environmental conditions include: (1) a remarkable tolerance to anoxia (V. angasi is amongst the most tolerant species of freshwater mussel to anoxia yet reported) - adult musels may survive for months in anoxic waters; (2) tolerance to desiccation - while the Creek form aestivates over each Dry season, billabong mussels were similarly shown to survive for months out of water; and (3) a tolerance to high water temperatures - 50% of experimental mussels succumbed at water temperatures exceeding 45° C.

Thus, over vast areas of Australia occur at least a few freshwater mussel species, belonging to the genus Velesunio, that are adapted to still-water, ephemeral and drought-prone environments. V. angasi at least, however, is equally adapted to life in streams seasonally flooded by torrential Wet season rains.

Other than information related broadly to tolerances and adaptations, specific comparative information on other life-history attributes of the Australian hyriids is lacking. V. angasi in the Magela Creek, is apparently a longer-lived mussel than the two temperate velesunionines of the Murray River, V. ambiguus and Alathyria jacksoni, studied to date. While temperate hyriids are seasonal in their breeding, the effect of the northern tropical clime upon reproduction in V. angasi is reflected in much higher reproductive potentials. This potential is realised by sexual maturity reached at a very early age, repetitive breeding throughout the year, rapid larval development and ensuing development of the parasitic larvae, and long-lived populations with low adult mortality. Like other hyriids studied to date, the glochidia of V. angasi appear to be non-specific parasites of their fish hosts.

Despite warmer and less marked annual fluctuations in water temperatures in tropical than in temperate regions, the monsoonal climate of the tropics and subtropics, nevertheless confers a seasonality to many physiological processes of freshwater mussels from these regions. Because of regular, alternating wet and dry seasons, species are presumably well adapted at least to still water environments. The mutelids of tropical and subtropical Africa, according to Kenmuir (1980) are well adapted to life in disconnected pools of the dry seasons. Kenmuir reported forms resistant to desiccation and capable of aestivating, and others with demonstrated ability to withstand extremely low oxygen concentrations found in deeper pond type habitats during the dry season. This situation is strongly paralleled in similar adaptations of V. angasi to the rigours of the tropical climate of northern Australia.

Although seasonal growth patterns have been noted in tropical mussels, the study of _V. angasi_ in the Magela Creek is the first to provide unequivocal evidence that growth rings on the shells of tropical freshwater mussels are annular in nature and may be used to age mussels. _V. angasi_ is longer-lived than other tropical species yet studied. Seasonal temperature fluctuations appear to be sufficiently large to preclude year round breeding in tropical unionids studied north of the equator. _V. angasi_ in northern Australia and freshwater mussels from tropical Africa are the only reported species in which year round, repetitive breeding occurs. In most tropical species studied to date, various developmental processes are speeded up in the prevailing warm waters; mussels mature at an early age, and larval development and metamophosis during the parasitic phase are rapid.

Several investigators have observed that a close zoogeographical relationship exists between the mussel faunas of Africa, Australasia and South America; collectively they form a group clearly separable from species from the northern hemisphere (Walker, 1981a). Other than taxonomic and zoogeographic similarities, however, from the limited studies so far undertaken, it is doubtful that the Australian hyriids differ from the northern unionaceans much in the way of general living requirements. A degree of ecological similarity has been assumed for freshwater mussels as a group in such things for example as feeding ecology and microhabitat tolerances (Tevesz and McCall, 1979; Strayer, 1981; Davis _et al_., 1981). Nevertheless, fundamental differences in climate and the type of environment inhabited by mussels (lotic or lentic) may impose adaptations and life strategies upon the various species shown by often profound differences in aspects of their biology and ecology. Some of these broad differences among the Australian hyriids and tropical freshwater mussels have been discussed above.

A tentative suggestion offered here, is that the Australian hyriids may be ecologically dissimilar in broad reproductive strategies and ecological tolerances, to other unionaceans from the northern hemisphere. The more temperate, drier and vicissitudinous nature of the Australian environment may yet be shown to be features that have lead to: (1) protracted and opportunistic breeding (within constraints of temperature regimes), where species have a capacity or potential to produce a number of broods per year; (2) an absence of host specificity of the glochidial larvae; and (3) broad environmental tolerances, when the fauna is viewed collectively. In view of the relatively harsh and rigorous environments of the African continent, these attributes may well extend to the mutelids; V. angasi is most similar in biology and ecology to tropical mussels of Africa than to other tropical unionids. Further research will reveal the truth or fallacy in these hypotheses. It should be stressed for example, that potential for multiple broods may be more prevalent in northern unionaceans than was previously thought (e.g. Heard, 1975); the glochidia of some unionid species are unspecific parasites (e.g. Kat, 1984); and that individual unionids in North America at least, are equally as tolerant of desiccation (van der Schalie, 1940) and anoxia (Fuller, 1974) as some hyriids and mutelids.

According to Kat (1984), present understanding of many basic life-history attributes of unionaceans in general, is poor. Thus, specific findings on V. angasi in the Magela Creek have contributed to a better understanding of unionacean biology and ecology. The studies have provided some information on areas of conflict or contention in the literature, and further, have exposed some salient features that may be worthy of attention in future studies of freshwater mussels generally. In the sequence that they appear in the text, these features of interest are:

1) Shell form and environment - Obesity and relative height were correlated broadly among the waterbodies with environment (depth and eutrophy respectively). Neither correlation, however, could be explained in terms of a functional morphology and both obesity and relative height were found to be more closely associated with ontogeny; obesity increased with increasing age and relative height declined with increasing growth rate of mussels. Thus future studies of shell form in unionaceans must carefully consider the effect of ontogenetic variability before interpretations of functional morphologies are offered. Ecoclines in shell form both within and among habitats may be nothing more than gradients of ontogeny.

2) Microhabitat preferences - A diversity of findings have been forwarded in the literature in relation specifically to whether or not bottom type is important or not in determining mussel distribution and abundance (section A2.1.2, Hydrology). While bottom type is more closely correlated with relative water

movement, particle size of the sediment per se was found to have no effect upon distribution and abundance (and for that matter, growth rate) of *V. angasi* in the Magela Creek. Providing sediments are firm yet yielding, bottom type whether muddy or gravelly is unimportant in regulating mussel distribution. More attention needs to be paid to the degree of associated water movement in studies of microhabitat preference, itself perhaps a reflection of the tolerances of various species to local oxygen conditions and maintenance in strong currents. Further, the degree of consolidation of the sediment needs to be reported in future studies; fewer mussels were found in the Magela Creek on muddy sediments that were unsupportive, loose and silty in nature.

3) Dissolved oxygen - A strength of the present study was an elucidation of environmental factors (in quantitative terms) that influence and govern aspects of the biology and ecology of *V. angasi*. The analyses revealed that dissolved oxygen was by far the most influential environmental factor to the development and well being of mussel populations in the Magela Creek. Dissolved oxygen concentration was a highly significant correlate of larval production, subsequent recruitment and abundance of mussels within and among billabongs, life-spans of mussels (especially females), and feeding activity of mussels in the billabongs. Future studies, particularly of still-water species, must direct more attention to the influence of dissolved oxygen in all aspects of biology and ecology.

4) Juvenile mussels - Invariably, the youngest age class is reported

to be absent in most population studies of freshwater mussels. Juveniles were relatively common amongst the populations in the Magela Creek. If the youngest age class was absent from any population, it was not because their habitat was remote from that of adults, nor because of a specialised substrate requirement. Rather, the absence of young was attributed to inadquate sampling or poor conditions for survival of newly recruited mussels. Other studies of freshwater mussels have attributed the scarcity of juvenile mussels in part to their cryptic appearance and specialised habitat requirement. Future studies would do better to use sampling methods designed to retain the juvenile mussels, and adopt a methodology whereby all possible habitats are quantatively sampled.

5) Longevity - Criticism has been levelled at the diversity of reports of the extreme ages attained by _Margaritifera margaritifera_ throughout its holarctic range (see Apendix 3). A wide range of longevities was found in _V_. _angasi_ in populations of the Magela Creek (11-35 years). Life spans were found to be positively correlated to mean dissolved oxygen concentration. Thus a species as widely distributed as _M_. _margaritifera_ should vary even more greatly with respect to the maximum ages attained across its range. Therefore criticism of the reports of the longevities attained by this species may be unjustified because environmental (and phylogenetic) influences have not been considered.

6) Breeding activity - Reproductive investigation of _V_. _angasi_ in the

Magela Creek demonstrated that two other environmental variables apart from water temperature were influential to breeding activity - namely dissolved oxygen and turbidity. The effect of environment other than temperature, has essentially been ignored in terms of its influence upon reproduction in freshwater mussels. There is obviously much potential for further study of this matter in other species of freshwater mussels. For example, V. ambiguus and Alathyria jacksoni in the Murray River in southeastern Australia, were observed by Walker (1981b) to peak in larval production in spring and late summer/early autumn. Do both species have the potential to breed over the entire summer, and is the potential curtailed in mid summer by some seasonal, adverse physicochemical factor such as suppressed dissolved oxygen concentration or high turbidity?

7) Glochidial attachment - With the limited data at hand, glochidial infections of V. angasi appear to be higher on the gills than the fins of the host fishes. This is contrary to the general observation, that hooked or toothed glochidia tend to parasitise the external surfaces of their hosts (section A4.3). As more species are studied, host fish activities (as in the present study) will probably assume more important in explaining discrepancies in the site of glochidial attachment. The glochidia of the Australian hyriids are of the toothed variety. The glochidia of one other hyriid (H. drapeta - Atkins, 1979) attaches exclusively to the gills of the host fishes.

8) Food of mussels - Unlike some reports for North American unionids

that zooplankters feature in the diets (section A5.1), V. angasi in the Magela Creek is strictly phytophagous and detritivorous. Fuller (1974) concluded that algae were overestimated as food value for freshwater mussels, on the basis that much phytoplankton ingested by mussels passed through the digestive tract undigested. While the algal fractions were found to be low in the stomachs of V. angasi, the presence of mostly digestion-resistant forms in the stomachs strongly indicated that algae overall, were underestimated amongst the ingested material; much of the algae was assumed to undergo rapid breakdown and digestion. The evidence strongly indicated that phytoplankton is the chief utilisable food and energy source of V. angasi. Strong correlations were found between shell and somatic growth of mussels, and algal abundance averaged over the seasons among the populations. No correlations were found between growth and the measure of suspended organic detritus. With further investigation, Fuller's conclusion above, may be found to be invalid for freshwater mussels generally.

Ingestion rates in V. angasi were correlated with phytoplankton concentrations in the surrounding waters. To what extent, however, food intake is solely dependent upon algal concentration in the waters, independent of the levels of organic detritus would require further study. In such an event, the appetite of mussels would be solely algal-dependent even if ingestion was unselective, and would provide more evidence that algae is the main utilisable food item. To the best of knowledge, this type of feeding behaviour has not been demonstrated in bivalves.

9) Selectivity of ingested particulates - There is debate as to whether freshwater mussels exercise selectivity over ingested materials (see section A5.1). Because of differential and rapid digestion of algae in the guts of _V. angasi_, controlled feeding experiments are needed to resolve the issue of whether or not the mussel shows preference among the types of food available for ingestion. However, because a significant inorganic fraction is included in the diet, _V. angasi_ can be regarded as unselective in its feeding; this finding is in accord with most comparable studies of feeding in freshwater bivalves.

In relation specifically to the biology and ecology of _V. angasi_ in the Magela Creek, or indeed throughout the geographical range of the mussel, the present study has exposed some features of interest that are worthy of further attention. In brief point form, these features are:

- Shell morphology of juvenile mussels in northern Australia may hold promise for species determinations in regions of doubtful species composition. Is the shell morphology of juvenile _V. angasi_ and _V. wilsonii_ (unaffected by environment) sufficiently distinguishable that the two species may be recognised by relative height alone?
- Does a latitudinal cline exist (as suggested) in the relative height of _V. angasi_ across the geographical range of the species?
- Regular seasonal fluctuations were observed in the sex ratios of mussels from Georgetown billabong and the Magela Creek channel. Was this the result of a sampling bias, or are the mussels from these populations alternatively sexual?

- The seasonal recruitment pattern of V. angasi in the Magela Creek, did not correlate with the seasonal intensity of larval production. Thus breeding was aseasonal and year round, while recruitment was seasonal, occurring in the Wet-early Dry season. With known sensitivities of juveniles to low dissolved oxygen concentrations, dissolved oxygen immediately above the bottom is presumed to be insufficient during the Dry for juvenile survival. Lack of recruitment during the Dry season is presumably the indirect result of the high macrophytic productivity of far northern Australia; decomposing plant material creates a high biochemical oxygen demand in the bottom waters of the billabongs for much of the year. What then, is the pattern of recruitment of V. angasi in other regions of its geographical range?
- While evidence suggested that V. angasi selected against diatoms in its feeding, to what extent, if any, does the mussel show preference in the size and type of green algae ingested? Further, is food intake solely dependent upon the algal concentration in the water, independent of the levels of detritus?
- High densities of mussels and estimated turnover rates of the water, suggest that V. angasi may play a significant role in the nutrient and calcium cycles of some Magela Creek billabongs. What is the extent of the contribution by mussels to these cycles? Also there is an indication that overall production is grossly underestimated because high gametic and larval production were not considered in the estimates. What contribution to overall production is gametic and larval production of V. angasi in the Magela Creek waterbodies?

Finally, attention is drawn to the contribution of the present study of the biology and ecology of _V_. _angasi_, to the current intensive investigations being undertaken in the Alligator Rivers Region. Research activity in the region is aimed primarily, at acquiring a general knowledge and understanding of the aquatic ecosystems, and at assessing various biological means of monitoring potential pollutants in the waterways.

In most billabongs of the Magela Creek, _V_. _angasi_ is by far the most dominant member (in terms of biomass) of the second trophic level benthic fauna. At high densities, annual production, with the addition of larval and gametic production, is likely to be quite high. More importantly, however, it is probable that mussels contribute significantly to the nutrient and calcium cycles of many of the billabongs. The extent of this contribution has been suggested above, as worthy of further study.

The study of _V_. _angasi_ has provided essential biological and ecological information that may be used to evaluate the potential of the mussel as a biological monitor of pollution in the Alligator Rivers Region. Importantly moreover, the studies themselves have demonstrated repeatedly the potential value that the mussel may have as an indicator organism. This potential may be realised in pollutional, but also in paleoenvironmental and present day environmental contexts as well, by studies of distribution and abundance, shell form and size, and population structure and dynamics of mussels.

The sensitivity of juvenile _V_. _angasi_ to low dissolved oxygen, may make the mussel a particularly valuable indicator of the types of pollution in which oxygen concentrations are severely affected. Excessive organic enrichment is one such type, and because densities of mussels were correlated with mean dissolved oxygen concentrations, knowledge of long-term changes in abundance of mussels may usefully indicate the aerobic status (and thus polluted nature) of waterbodies. A correlation was also found between both growth rate and relative condition, and algal productivity, and thus long-term studies of growth of mussels might also be employed to identify forms of mild organic pollution. Because of the sensitivity of juveniles to low concentrations of dissolved oxygen - and presumably other toxicants, mussels in the Region may have value as indicators of nonpolluted waters, and might be used to mark the downstream areas of full biological recovery in polluted streams. With baseline data pertaining to environmental correlates of recruitment, mortality and growth rates, V. angasi has considerable potential as an indicator of environmental impact in the Alligator Rivers Region.

Densities of mussels reflect local and regional Wet season flow patterns in the mainstream channel of the Magela Creek, as a result of the reliance upon adequate dissolved oxygen sustained throughout the Wet for successful recruitment. For the complex flow patterns on the floodplains of drainage systems in the Alligator Rivers Region therefore, (and presumably in other locations under monsoonal influence), study of the distributional patterns of V. angasi may assist in unravelling the pathways of water movement. In present day environments as yet unstudied by man, distributional data, and growth rate and condition data may usefully and rapidly indicate to the investigator some measure of the overall aerobic and trophic status of the environment in question. Further, condition data in most environments of the Magela Creek at least, was an integrated measure of seasonal trophic status. Thus, estimations of condition may usefully identify productive and unproductive periods in a particular environment.

Shell size and form of V. angasi on a regional scale at least, may be useful indicators of paleoenvironments. While shell size and relative height may indicate 'paleotrophic' conditions, an arcuate shell form and distinctive, swollen Creek form may respectively indicate (a) environments of relatively unstable, shifting sediments where waters are swiftly flowing for some part of the year at least; and (b) seasonally ephemeral, stream environments.

Overall, the present study of V. angasi in the Magela Creek, has shown how a valuable store of limnological and hydrological information, may be gleaned from ecological studies of freshwater mussels.

APPENDICES

1 - 6

APPENDIX 1

VARIATION IN SHELL SHAPE

A1.1 Shell shape and environment

Tevesz and Carter (1980a) have recently reviewed the environmental relationships of shell form variability in unionaceans. Walker (1981b) similarly reviewed the subject, and completed analyses of shell form variability appropriate to some Australian hyriids. The review of Eagar (1948) has provided a convenient reference material to the habitat relationships of shell shape in unionaceans. Eagar summarised much early anecdotal literature and collated a number of generalisations that have largely been substantiated by subsequent studies; the observations effectively exemplify the long known fact that the considerable variation inter- and intraspecifically in unionacean shell form, is of a systematic nature. While variation in shell size (including the effect of stunting) is considered in Chapter 6, observations on obesity (width/length), and lateral outline (see later) may be summarised from the work of Eagar as follows:

Variation in obesity

1. In a given species, lake forms are recognisably more obese than river forms.
2. Within a single drainage system, river forms tend to increase in obesity downstream (following Ortmann's (1920) 'Law of Stream Distribution').
3. Obesity tends to be positively correlated with stream size and negatively correlated with water velocity.

Variation in lateral outline

1. Arcuate forms with curved dorsal margins and straight or more typically reflected ventral margins, are generally found in small streams or rivers of swift-flowing water.
2. Shells with curved ventral margins, a long hinge-line, and posterior ends expanded or strongly developed, are more typical of lakes or rivers of relatively slowly flowing waters.
3. Relative height (height/length) is often negatively correlated with water velocity, although positive correlations have been recorded.
4. There is usually some correlation between obesity and relative height of shells.

The functional morphological explanation of Eager's (1948) conclusions regarding the shape-environment correlations, particularly those in relation to lateral outline, had remained largely speculative until recent studies and reviews by Eagar (1977, 1978). In relation to lateral outline, Eagar's (1977) experiments with Margaritifera margaritifera showed that the functional advantage of the arched dorsal and reflected ventral form lay in the provision of a larger pedal gape, and associated increase in shell weight. The increase in pedal gape and extra shell weight, allowed a stronger anchorage and increased probing power for the foot in the unstable substrates of stream habitats subjected to strong and turbulent water currents. The lighter shells with curved ventral margins and long (and stronger) hinge-lines, however, were argued to have functional advantage over the heavier, dorsally arched shells, in providing active movement over the surface of the substrate in quieter environments. Thus the two contrasting patterns of growth appear to be consistently related to two contrasting functional activities, each typical of forms from habitats differing in water velocity (Eagar, 1977, 1978).

Eagar (1978) extended his explanations on functional morphologies to provide ecological meaning to Ortmann's (1920) 'Law of Stream Distribution' which states that shell form tends to increase in obesity downstream. Eagar argued that greater obesity provided a functionally efficient means of increasing volume of living tissue, thereby providing improved metabolic and functional activity to these forms from quieter waters. In addition, increased obesity in relatively still waters should enhance buoyancy and prevent shells from sinking into soft sediments that may prevail in quieter waters. Eagar stated that these generalisations would also apply to lake forms, which are recognisably more obese than river forms.

In relation to Eagar's (1948, 1977, 1978) generalisations upon the functional morphology of obesity and lateral outline summarised above, specific contributions made to the understanding of shell form in unionaceans are as follows:

As previously described, Eagar (1977, 1978) provided the first functional explanation of the correlation between stream velocity and lateral outline of unionaceans. Early workers provided no explanation for the observation of increasing height of mussels in the downstream direction of streams (e.g. Grier and Mueller, 1926), although Altnöder (1926) recognised that a correlation existed between dorsal arching in _M. margaritifera_ and increasing stream velocity. Other studies on this species (Clarke and Berg, 1950; Hendelberg, 1960; Bjork, 1962; Roscoe and Redelings, 1964), and various unionids (e.g. Evermann and Clark, 1917) had left the problem largely unresolved, being preoccupied with distinguishing between the variation induced by the environment as opposed to ontogeny. Cvancara _et al_. (1978) thought generally that the lower shells of _Anodonta grandis_ and _Lampsilis radiata_ found in the upper reaches of the Sheyenne River (USA) were better adapted to the current.

Amongst hyriid unionaceans, Dell (1953) recorded that relative height in _Hyridella_ from New Zealand, increased from flowing to still water environments. In the light of Eagar's (1977, 1978) interpretation given to the lateral outline of unionaceans from stream environments, Walker (1981b) recognised two distinct growth patterns of _Alathyria jacksoni_ in the Murray River (Australia) - a 'winged' or straight-hinged form and a 'non-winged' or dorsally-arched form. Each growth pattern was characteristic of mussels from moderate and fast water currents respectively. Walker found that a decrease in relative height generally accompanied development of the dorsally arched shell, but emphasised, however, that this relative dimension showed considerable variation, tending to conceal rather than to reveal the dual nature of the growth patterns.

Ortmann (1920) first proposed the general 'law' that river forms of mussel species within a single stream tend to increase in obesity downstream. The observation has been substantiated by others (e.g. Ball, 1922; Grier and Mueller, 1926; van der Schalie, 1938; Cvancara et al., 1978), but nevertheless not all species accord to the general rule. Ortmann found evidence for example, that the trends were similar only for species of primitive taxonomic grouping. Similarly the relationship may not always hold for the same species in different streams. Cvancara et al. (1978) found that obesity of Anodonta grandis increased downstream in the Sheyenne River but not in the Turtle River, North Dakota (Cvancara, 1970). Although Clarke (1973) reported that A. grandis is a highly variable unionid, other studies have indicated that the mussel is conservative in relation to phenotypic plasticity; it has generally been found to vary little in shape between most habitats (Cvancara and Harrison, 1965; Cvancara, 1972; Green, 1972; Ghent et al., 1978).

Various workers have suggested that the occurrence of less inflated and compressed shells in small streams or headwaters, was an adaptation enabling mussels to orientate themselves better to withstand strong currents (Wilson and Clark, 1914; Grier and Mueller, 1926; Clarke, 1973; Anderson and Ingham, 1978). This explanation of functional morphology is generally complementary to Eagar's (1978) interpretation described above, that explained increasing obesity of mussels from quieter portions of rivers, or from lakes. Matteson (1955), however, recorded various small-stream species as having highly obese dorsal portions and highly truncate posterior ends - just the reverse morphological appearance that might be expected under the prevailing conditions. (See Eagar's (1948) generalisations above.) Matteson proceeded to describe how such a truncate form at least, might enable mussels to burrow deeply into the sediments, thereby assisting in maintenance of a hold in strong currents.

Horn and Porter (1981) summarised the findings of a number of early North American studies comparing flowing water and lake forms of the same species. These studies in addition to that of Anderson and Ingham (1978) reported a greater degree of inflation of forms from lake environments. Clarke (1973) nevertheless, reported that Fusconaia flava was more obese in large streams than in any other environment.

A number of studies have corroborated, partly, the functional explanation given by Eagar (1978) for the higher obesities noted in lake forms of a given species. Ghent et al. (1978) argued that the wide ventral angle and lightweight shell of A. grandis were morphological adaptations permitting the animal to present a broad bearing surface to a soft-silt, deep-water substrate on which a mussel of narrower ventral angle might smother. (The thin-shell, and ovoid and slightly winged shape of a form of Velesunio ambiguus recorded from shallow, soft-muddy lagoon environments in southeastern Australia by McMichael and Hiscock (1958) and Walker (1981b), may serve a similar function.) The narrow ventral angle and heavier shell of Elliptio complanata from lake environments conversely, were thought by Ghent and co-workers as being ideally suited to life in hard-sand, wave-swept reaches. Such a shell would allow the mussel to plough deeper and more supportive furrow paths. Stern (1983) corroborated the findings of Ghent _et_ _al_. (1978), but in relation to a stream habitat, where obese and compressed species were characteristic of mud and sand substrates respectively. Anderson and Ingham (1978) and Tevesz and McCall (1979) also suggested that the moderately inflated and thin shelled form of _Lampsilis_ _radiata_ _siliquoidea_, would enhance its buoyancy in soft sediments. Tevesz and McCall added, moreoever, that the form might permit the retention of enough water between the valves to flush away any shallow silt covering from the siphon areas.

In further relation to stability in the substrates of lake environments, Clarke (1966, 1973) reported that the anterior-beak length/length ratio was highest in specimens of _A_. _grandis_ from the sandy sediments of large lake habitats. This suggested to Clarke that the large foot volumes inherent in these forms were physically selected for, enabling mussels to maintain their positions in exposed habitats and on shifting substrates. This functional morphology has a similar analogy therefore to that interpreted by Eagar (1977, 1978) for the increased stability in fast-current stream environments offered by the large pedal gape of dorsally arched shell forms.

Shell form in different species nevertheless, does not always appear to respond in the same morphological direction under similar environmental conditions. Clarke (1973) for example, found _L_. _r_. _siliquoidea_ to be more obese in large lakes than elsewhere. He suggested that these more obese forms with lower surface to volume ratios might be better able to remain in place without being dislodged by turbulent and shifting currents that occur in lakes during storms. The relative obesity recorded for this species contrasts sharply with the relatively compressed form of _E_. _complanata_ recorded by Ghent _et_ _al_. (1978) in similar habitats. As mentioned above, a similar contradictory shell form was reported by Matteson (1955) in small-stream species, than had generally been reported for forms in small streams and headwaters.

Sediment type, and water turbulence and flow have not been the only implicated factors determining shell morphology. For Swedish unionids, Agrell (1949) observed that such features as anterior development, relative height and obesity were positively correlated with eutrophication. Amongst factors such as taxonomic differences, stream velocity and sediment type, Cvancara _et_ _al_. (1978) indicated that nutrient availability could account for differences recorded in relative height and obesity of unionids in the Sheyenne River (USA). Between Canadian lakes, Green (1972) found that factors such as shell height, width and inside volume were apparently conservative variables in relation to measured environmental variables, including sediment type.

The above review has been concerned so far with comparison of growth forms between quite different environments, such as prevail between quiet and still water, and turbulent and flowing water environments. Between similar habitats (e.g. lakes) or within the same habitat, the following findings in relation to a given species have been reported. Between lakes, the results of Green (1972) (above) suggest little variation in unionacean form. Within lakes, Fisher and Tevesz (1976) and Horn and Porter (1981) reported generally no significant relationship between shell morphology and various environmental variables such as depth and sediment type. Of three species studied by Horn and Porter, however, obesity of one species, Lampsilis sp., was positively correlated with percent organic matter of the sediments. No causal relation was inferred. Both Cvancara (1972) and Ghent et al. (1978) found that shell morphology of A. grandis did not change with depth in respective lake environments, although Cvancara found a significant decrease in height of L. r. luteola and Anodontoides ferussacianus with depth. Again no causal explanation was offered. In central New York state, Harman (1970) noted that E. complanata decreased in obesity from shallow to deeper waters in the Finger Lakes; that A. grandis was relatively higher in the warmer littoral waters than the colder sublittoral and profundal waters of three lakes; and that L. r. radiata had ovate shells in the depths of the Finger Lakes as opposed to a more typical lateral outline in littoral waters.

The above discussions have described the nature and extent of the broad intra-specific variation characteristic of shell shape in unionaceans, from or between a variety of habitats and environments. Surprisingly, present understanding of the forces that manifest this considerable phenotypic plasticity in natural populations, is poor. Although both selection by the environment and direct phenotypic response by unionaceans are implicated, the relative contribution of these forces to shell form is not clear. Tevesz and Carter (1980a) described studies that evidenced phenotypic modifications of shell morphology in unionaceans following the damming of a stream; shell form in the populations from the newly created lakes quickly assumed some of the proportions characteristic of lake-dwelling forms. However, these observations are apparently ambiguous in interpretation because some of the observed influences were apparently related to human interference. Eagar (1978) described transplant experiments of a marine bivalve that had been transferred to new environments. Phenotypic changes of shell shape took place immediately, and in the same direction as those found in shells on the neighbouring sediments. However, in relation to the shell form of stream-dwelling unionaceans at least, Eagar felt that both selection and phenotypic moulding were operative, but that selection by the environment probably played the major role.

Character variation in shell form along ecological gradients, such as occur for example along the length of a stream are termed ecoclines. Ecoclines are clearly distinguishable from character gradients or clines reported over relatively large geographical areas in that the latter are largely independent of local environmental effects. They are most clearly evident when these effects are controlled for by the sampling of similar habitats (Cvancara, 1963; Walker, 1981b). Cvancara (1963) found evidence of a geographical cline in shell character of species of Lampsilis in North America. He observed that relative height and obesity increased toward lower latitudes suggesting that the three subspecific forms may represent only one species. Clarke and Berg (1959) reported a similar geographical cline in subspecies of Lampsilis radiata across central New York state. The claim, however, was refuted by Harman (1970). In Canada, Clarke (1973) observed generally, that northern populations of unionids were often more compressed than southern large-stream counterparts. McMichael and Hiscock (1958) found a cline in the anterior to beak/total length ratio of the hyriid, Velesunio ambiguus. The ratio tends to decrease in higher latitudes.

Finally, attention must be drawn to the interest that unionacean shell form has held in regards to paleoecological and paleolimnological reconstruction. Analyses of the environmental relationships of the broad variability in shell form of present day species, provide potentially, a useful means of inferring corresponding environmental changes in ancient aquatic ecosystems. The studies of Eager (e.g. 1948, 1977, 1978) are particularly noteworthy in demonstrating how shell form-habitat information may be used to reconstruct the habitat of fossil species.

Nevertheless, with inadequate ecological information on present day shell form - habitat relationships, such paleoenvironmental reconstructions may be incorrect. In a thorough appraisal of the topic, Tevesz and Carter (1980a) concluded that a common shortcoming of most form-habitat studies was that explanations of functional morphology for observed correlations, were largely speculative. This situation has possibly been remedied to some extent by the experimental work of Eagar (1977, 1978) (which Tevesz and Carter apparently did not have access to), in regards to interpretation of the lateral outline-stream velocity correlation. However, sufficient diversity of findings in the obesity-habitat relationship have been recorded to suggest that generalisations about the functional morphology of obesity in unionaceans need to be cautiously applied. Obese shells for example, may be adaptive for life on soft muddy sediments, but such forms are not always present in relatively still-water environments upon these sediments (Clarke, 1973; Cvancara _et al_., 1978). Thus, reconstruction of the paleoenvironment from fossil forms of this phenotype in various geological strata may be incorrect. As the phenotypic response by different species to the same environmental conditions may differ (e.g. Ortmann, 1920; Cvancara _et al_., 1978), reconstruction of paleoenvironments require in the very least, specific information concerning functional morphologies of present day forms of individual species. Even after explaining the adaptive morphology of the various forms, Green (1972) and Anderson and Ingham (1978) warned of the danger in applying present-day results determined for one geographical region, to data from another. Data applied beyond a regional scale may be suspect where geographical clines in shell form exist.

A1.2 Sexual and ontogenetic variability

Only for lampsiline unionids is sexual dimorphism in shell features marked. Reportedly, females of various species are more obese, higher and thicker-shelled, and are distinguishable from males both visually and statistically (Coker _et al_., 1921; Ball, 1922; Anderson and Ingham, 1978; Kat, 1983d). The obese condition of the female shell is generally most pronounced over the marsupial regions and Coker and co-workers, and Anderson and Ingham thought this condition was an adaptation allowing for large numbers of eggs to be held in the outer gill marsupia. Anderson and Ingham added that the thicker shell of female _Lampsilis_ might provide protection as the inflated form of the shell generally would be less resistant to wave action or stream currents.

For other unionaceans (Johnson, 1946; Heard, 1975; Dudgeon and Morton,

1983) including hyriids (McMichael and Hiscock, 1958; Walker, 1981b), females may also be more inflated than males. The dimorphism, however, is far less conspicuous than in lampsiline unionids, and if present at all, may only be detected by statistical testing. Ecophenotypic variation in shell morphology is generally assumed sufficient to mask any tendency for sexual dimorphism in these groups.

Unionacean shell form may be markedly influenced by ontogeny, and bivariate analysis between standard variables generally reveals allometric relationships (Eagar, 1978). Relative height and obesity for example, may either increase or decrease with growth (Eagar, 1948). In relation to obesity, Ortmann (1920) and Ball (1922) recorded that young unionids were more obese than older specimens. Agrell (1949) and Crowley (1957) nevertheless, reported that juveniles of the respective unionids studied, were less obese than full-grown specimens. In stream-forms at least, however, generally a decrease in relative height with age can be expected, with progressive development of dorsal arching of the shell (Evermann and Clark, 1917; McMichael and Hiscock, 1958; Clarke and Berg, 1959; Hendelberg, 1960; Bjork, 1962; Roscoe and Redelings, 1964; Walker, 1981b). Eager (1948) remarked that changes in one shell dimension appeared almost invariably to be accompanied by changes, possibly compensatory, in other shell dimensions. Agrell (1949) and Hendelberg (1960) for example, reported that relative height and obesity were positively correlated.

Because environmental influences which mould shell form are expressed only in older individuals, such specimens give the characteristic 'reaction form' (Eager, 1948), and most workers have included only the older shells in their calculations. Indeed several authors have stressed that material should only comprise individuals which have been subjected to environmental influence for a sufficiently long period of time (e.g. Agrell, 1949). van der Schalie and van der Schalie (1950) and Cvancara (1963) added that a source of variability in many shell form-environment studies could be due to using shells of variable age.

In relation to sexual and ontogenetic variability, Tevesz and Carter (1980a) sounded a cautionary note to studies where unionacean shell form was used as an indicator of environmental change. Because of such variablity, habitat segregation of different age classes or sexual morphs for example, could result in morphologically distinctive groupings that might be correlated with, but not necessarily causally related to environmental factors. They added that correlation between relative shell dimensions added to the difficulty in distinguishing between fortuitous, rather than causally related, correlations between shell form and environment.

APPENDIX 2

DISTRIBUTION AND ABUNDANCE

A2.1 Factors affecting the distribution of freshwater mussels

A2.1.1 Broad geographical dispersal

Transport by fish in relation to sea level changes, stream confluences, and coastal flooding as well as transport by animals other than fishes have been considered to be important factors in relation to broad geographical dispersal (van der Schalie, 1945; Clarke, 1973; Sepkoski and Rex, 1974; Walker, 1981b). There has been debate as to whether stream confluence is the best explanation for the natural distributional patterns observed (van der Schalie, 1945, 1963) or whether it is only one of several ways by which mussels have dispersed from one drainage system to another (McMichael and Hiscock, 1958; Walker, 1981a). With respect to dispersal by animals, attachment to the feet of, or undigested fish material carried in waterfowl have been suggested as significant dispersal mechanisms of freshwater mussels - particularly of some species within the Australasian region (McMichael, 1958; McMichael and Hiscock, 1958; Walker, 1981a).

Other than the aforementioned means of broader geographical dispersal, other ecological and physiological factors are involved in between- and within-drainage distribution, and that of the microhabitat preferences of a species. Factors involved can be grouped into biotic, hydrological and physicochemical categories. The relationship of the physicochemical environment in determining the range of a single species is poorly understood (Fuller, 1974; Haukioja and Hakala, 1974). Inconsistent or contradictory reports of relative importance of the various factors in determining the distribution and abundance of freshwater mussels have led some (Fuller, 1974; Tevesz and McCall, 1979) to consider that many species have quite broad tolerances for different water types and habitats. Anodonta for example, is an ubiquitous North American genus that is seemingly indifferent of water type (Fuller, 1974; Green, 1980). Nevertheless, other species have a limited geographical distribution and/or apparent habitat restrictions. Margaritifera margaritifera has a holarctic distribution but within its range is restricted to unpolluted and perennial, softwater streams (generally acidic in nature) in localities free of silt deposition (Boycott, 1936; Hendelberg, 1960; Björk, 1962; Roscoe and Redelings, 1964; Stober, 1972; Bauer, 1983). Even for this species, however, there is some doubt as to whether the distribution is limited by water hardness per se, and exceptions to the softwater occurrence have been noted (Boycott, 1936; Björk, 1962). In Middle Europe, the species is considered a glacial relict and physiographic isolation from a former, broader circumpolar distribution has been used partly to explain its apparent stenotopy (Jungbluth, 1978).

A2.1.2 Biotic relations

The most important biotic relationship and chief dispersal phase of freshwater mussels are with the brief parasitic period of the larval glochidium upon fish. As noted by Walker (1981a), few references have been made to the role of fish in mussel dispersal, mainly because little is known of the host preferences of particular mussel species. Kat (1984), however, presented a thorough review of parasitism in unionacean bivalves. He concluded that the parasitic relation between the mussel and its host fish, would tend to reduce the unpredictability of the freshwater habitat as it applied to the juvenile mussel. Because of their specialised habitat requirements (by comparison with other freshwater bivalves), Kat thought it would be of advantage for unionaceans to form an association with a fish that shared the same habitat requirements, so that dispersal over long distance occurred with much more habitat fidelity.

Apart from their broad ecological tolerances, it is a noted feature of widely distributed and abundant species (e.g. Anodonta in North America (Fuller, 1974; Trdan and Hoeh, 1982), Velesunio ambiguus in southeastern Australia (Walker, 1981a,b)) that they parasitise a large number of host fishes. In relation to broad geographical dispersal, however, rarely are the ranges of distribution of mussel species and their host fishes the same. Generally the mussel's range is smaller than that of the host suggesting that other factors act to exclude mussels from their potential range (van der Schalie and van der Schalie, 1963; Strayer, 1983). Walker (1981a) made similar comments with respect to the geographical range of waterfowl, considered to be possibly important passive agents of dispersal of Australian freshwater mussels.

Within a drainage system, fish hosts are regarded as especially significant in determining presence or absence of mussels (van der Schalie, 1938). Examples of abrupt cessations in the distributions of both mussels and their fish hosts above barriers such as waterfalls are cited in evidence of this (Fuller, 1974). Isolated but general accounts imply that fish hosts are even more significant in determining local distribution of mussels. The recruitment of young in particular sites of a stream (e.g. eddies, along edges of reed beds) for example is claimed to be directly affected by the habits and activities of fish hosts (Coker et al., 1921; Negus, 1966; Cvancara, 1967, 1970). Cvancara (1970) believed that fish hosts were of more importance than bottom type in determining distribution of mussels in the Red River Valley (USA) as many species of mussels occurred on a variety of substrate types. Differences in the species composition of mussels between localities of a Swedish stream were thought by Norelius (1967) to be related only to host fish distribution at the time of metamorphosis. For lake populations, Kenmuir (1980) thought the local abundances of two species of mussel in tropical Lake Kariba (Zimbabwe) were more directly influenced by the habits of their fish hosts than by any other factor. Finally, Strayer et al. (1981) could find no physical or chemical factor to account for the low density of mussels in an oligotrophic lake in New Hampshire (USA) and hinted at fish host limitation, as fish in oligotrophic waters were likely to be scarce.

The relationship between freshwater mussels and their fish hosts in determining mussel distribution is obviously important but poorly understood. As commented aptly by Strayer et al. (1981): "It would be desirable to have more information on the role of fish-mussel relations in mussel population dynamics."

Other significant biotic effects upon mussel distribution include mammalian predation. Published accounts describe how muskrats in North America can feed heavily upon mussels and in fact severely restrict the shallow water distribution of some species (reviewed in Fuller, 1974; Strayer, 1983). In both North America (Fuller, 1974) and Australia (Walker, 1981b) consumption by aboriginal man is considered to have had a significant effect on mussel populations in the past.

Other bivalves may affect the local distribution of freshwater mussels. Three lampsiline species occur in Lake Waccamaw, eastern North and South Carolina (USA); the percentage of samples having a lampsiline was increased if other lampsiline species were present suggesting a gregariousness among the three species (Porter and Horn, 1983). While no causal mechanism was suggested by Porter and Horn, clumping of conspecifics was previously thought by Tudorancea and Florescu (1968) to represent an adaptation ensuring successful fertilization. Clumping of conspecifics may result from environmental heterogeneity but also can occur in homogeneous environments, which has often been reported but rarely quantitatively assessed, as done by Kenmuir (1980) and Salmon and Green (1983).

Filter-feeders are generally assumed not to partition the environment for food and space (Kraemer, 1979). Competitive advantage according to Fuller (1974) was no more than a superior reproductive ability of some mussel species. Tevesz and McCall (1979) in reviewing literature concluded that niche widths of unionids were much broader than marine filter-feeders and attributed this to a relative absence of predation and competition in the freshwater environment. Strayer (1981) in explaining the broad microhabitat tolerances of unionids in some Michigan (USA) streams, attributed them in part to the absence of competition in these environments where densities were low and space and food superabundant.

Nevertheless, it is the belief of others, that competitive exclusion between bivalves is real, and that competition is reduced and species diversity greatly increased through both spatial and temporal partitioning of the environment. In evidence, Harman (1972) and Sickel (1980) cite substrate preferences of species in lakes and streams; Green (1971) used multiple discriminant analysis of bivalve lake molluscs in central Canada to show that separation was primarily on a trophic basis; Stern and Felder (1978) and Trdan and Hoeh (1982) cite spatial and temporal differences in encystment of larvae of sympatric unionids on host fishes in evidence of resource partitioning to reduce competition for available hosts. The pattern of distributional segregation of two unionid species in a Swedish lake outlet, led Bronmark and Malmqvist (1982) to conclude that interspecific interactions were suppresssing establishment of young conspecifics and the other species in a very productive habitat. Finally, in undisturbed river habitats in North America, Kraemer (1979) argued that Corbicula, an introduced bivalve, competed with indigenous freshwater mussels for substrate.

The final significant biotic factor of consideration is the influence of vegetation on mussel distribution. Invariably, rooted vegetation is reported to have a negative influence on mussels (Coker et al, 1921; Boycott, 1936; Pennak, 1953; Tudorancea and Florescu, 1968;

Cvancara, 1972; Fuller, 1974). A number of factors are considered to contribute to the restricted distribution of mussels by vegetation: plants and their decayed material contribute to finer, less consolidated sediments in which to burrow; plants may compete with mussels for bottom space; restrict movement of mussels; interfere with glochidial and juvenile settlement; and effect water movement so modifying the oxygen regime and delivery of food (Coker et al., 1921; Tudorancea and Florescu, 1968; Cvancara, 1972, Bronmark and Malmqvist, 1982). Only Salmon and Green (1983) have reported a positive association of rooted vegetation and mussel distribution and abundance. In the lotic environment under study, they implied that vegetation stabilised the microhabitats of mussels by decreasing water turbulence. In a newly created tropical lake (Lake Kariba, Zimbabwe) the benthic habitat (including a lamellibranch population - Corbicula) was markedly enriched after invasion of three plant species (McLachlan, 1969). Significantly, the large freshwater mussel populaton of the lake (Kenmuir, 1980) was not part of the association. In other lentic studies, only those by Lewandowski and Stanczykowska (1975) and Fisher and Tevesz (1976) have reported no association, positive or negative, between mussel density and aquatic vegetation.

A2.1.3 Abiotic relations

Depth

Quantitative descriptions of mussel distribution and abundance in relation to water depth are comparatively recent (Cvancara, 1972) and follow initiation of SCUBA investigation and the ease and accuracy with which it has contributed to study.

In lakes, the relationship is a predictable one and a preferred depth range is sought by most species, from occurrence in minimum depths of 5-8 cm of water (Lampsilis radiata siliquoidea in the Canadian Interior Basin (Clarke, 1973)), to a maximum of between 18-31 m (Anodonta grandis in Lake Michigan USA (Reigle, 1967)), and 30 m (Elliptio complanata in central New York lakes, USA (Harman, 1970)). Within the preferred depth range, an optimal depth - generally shallow, is reached by most species at which densities are at a maximum and beyond which densities steadily peter out (Okland, 1963; Cvancara, 1972; Haukioja and Hakala, 1974; Lewandowski and Stanzykowska, 1975; Fisher and Tevesz, 1976; Ghent et al., 1978; Kenmuir, 1980; Green, 1980; Strayer et al., 1981). As a general rule found by these same authors, the optimal or preferred depth does not exceed 3 m for species so far studied, although A. grandis in Lake Bernard, Ontario (Canada) reaches maximum densities between 2.5-12 m (Ghent et al., 1978) and species in tropical Lake Kariba (Zimbabwe) occur between 3-12 m (Kenmuir, 1980).

Causal factors in the pattern of depth distribution in lakes have generally only been hypothesized. Exposure, temperature extremes, wave action, silt-recirculation and predation are believed to restrict mussels from marginal zones (Coker et al., 1921; Matteson, 1948; Fuller, 1974; Marshall, 1975; Fisher and Tevesz, 1976; Kenmuir, 1980; Green, 1980). Finer, silty and unconsolidated sediments; low dissolved oxygen; decreasing water temperature (thus slowing metabolism, reproduction and growth; less water turbulence to bring and keep in suspension living or dead food material; reduced light penetration and its effect on living food; increasing water pressure; the absence of fish hosts at depth; and changing water chemistry, with increasing depth - all have been suggested as important factors restricting mussels to relatively shallow waters (Cvancara, 1972; Fuller, 1974; Haukioja and Hakala, 1974; Fisher and Tevesz, 1976; Ghent _et al_., 1978; Kenmuir, 1980; Strayer _et al_., 1981).

Surprisingly, little attention has been paid to the role of low dissolved oxygen in explaining the absence of mussels at depth, although the lakes in question are generally claimed to be adequately oxygenated. Coker _et al_. (1921) and Fuller (1974) stress its importance in general statements. Okland (1963) observed periods of inferior oxygen conditions in the deeper parts of Lake Borrevann, Norway but did not draw any conclusions between this and the corresponding absence of mussels. Plover Cove in tropical Hong Kong experiences seasonal deoxygenation of the hypolimnion in the dry season. As _Anodonta woodiana_ is distributed in the shallow waters near the margins of this reservoir, Dudgeon and Morton (1983) considered it unlikely that the species would experience the same wide fluctuations in oxygen concentrations. Mussels occur over a wide range of depths (3-12 m) in the waters of Lake Kariba, Zimbabwe, (Kenmuir, 1980); the waters of this lake are adequately oxygenated at most depths but the oxygen levels at greater depths (> 11 m) are thought too low for both mussels and their fish hosts to survive. In man-made impoundments the effects of low dissolved oxygen have received some attention. Bates (1962) attributed the gradually diminishing fauna in the Kentucky Reservoir, Tennessee River (USA) partly to decreasing oxygen tensions. In a similar vein, Isom (1971) attributed the net loss of 60 species of mussels in the Fort Loudon Reservoir (Tennessee R.) to periodic oxygen sag.

Study of the depth distributions of mussels in lotic environments is not as relevant as in lentic environments because, as emphasised by Stern (1983), depth is no more than a reflection of current velocity and substrate type. Thus both Haukioja and Hakala (1974) and Stern (1983) report in lotic distributional studies that bottom type is more significant than depth in determining distribution. Negus (1966), however, found a lake-pattern of distribution of mussels in the Thames River, England. No causal factors were suggested but presumably water turbulence in the central (and deeper) portions was one factor. Both unsuitable bottom type and strong water currents restrict mussels to shallow waters in the Neva River, Rumania (Tudorancea and Gruia, 1968). Similarly, the shallow water occurrence of mussels in the Middle Thames River, Ontario was attributed to advantages of associated low currents (Salmon and Green, 1983). In contrast, mussels in a Swedish lake outlet occurred in largest numbers in the central, deepest portions where Bronmark and Malmqvist (1982) believed reduced chances of desiccation, more food and less vegetation to restrict movement made this environment more favourable. (Water turbulence and velocities in the central portions of the outlet presumably never exceeded levels at which mussels are physically displaced.)

In a manner akin to tropical, monsoonal drainages, the Crapina-Jijila marshes of Rumania receive annual floodwaters from the Danube River. The annual flooding modifies the distribution and abundance of freshwater mussels in the marshes; during the flooding mussels are widely dispersed, but undertake extensive migrations as the waters subside. Thus, densities are greatest at the end of the subsidence period when waters have contracted. If flooding subsidence is too rapid, mussels may be stranded, severely affecting populations (especially new recruits) in some years (Tudorancea and Florescu, 1968; Tudorancea, 1972).

Finally, in relation to water subsidence and shallow water effects, Marshall (1975) noted that apart from stranding large numbers of mussels in shallow regions, added implications of extreme water level fluctuations typical of impoundments in Zimbabwe are the marked effects on water chemistry. Although the tolerance limits of some species of mussels to high water temperatures have been determined specific evidence of the restriction of freshwater mussels from shallow waters by high water temperatures is lacking. The general statements made earlier are the only references to the effects of high water temperatures upon mussel distribution.

Hydrology

There is a considerable literature on the influence of hydrological factors (water body type, substrate and/or flow regime) on freshwater mussel distribution and abundance. Much of the material is descriptive, and from recent quantitative studies, especially in relation to habitat preferences, some conclusions may be misleading or contradictory.

It is a commonly observed phenomenon that the freshwater mussel fauna of larger streams and lakes with regular water renewal, are more abundant and diverse than of smaller tributaries, ponds or still lakes (Evermann and Clark, 1917; van der Schalie, 1938; Pennak, 1953; Cvancara, 1967; Green, 1972; Sepkoski and Rex, 1974; Kenmuir, 1980). The wider range of available habitats in larger waterbodies and in particular, where there is a continuous and strong current in large streams, are generally thought to enhance faunal development. Boycott (1936) adds that larger bodies of water may also contain more species by virtue of the fact that the chances of importation have been greater.

The effects of current in relation to bringing about faunal enrichment have been ascribed to the constant supply and change in oxygen, food and minerals and to the enhancement of fertilization (Evermann and Clark, 1917; Coker *et al*., 1921; Boycott, 1936; Pennak, 1953). In the absence of significant flow (that is, in lakes and impoundments, intermittent streams or streams of low discharge), the mussel fauna is often observed to be impoverished, a factor variously attributed to resultant low dissolved oxygen, high water temperatures, desiccation, increased concentration of salts, predation and fewer fish hosts or the restriction of their dispersal at low discharge (Coker *et al*., 1921; Cvancara and Harrison, 1965; Norelius, 1967; Cvancara, 1967, 1970; Imlay, 1973; Horne and McIntosh, 1975; Kenmuir, 1980; Strayer, 1983). The effect of discharge is considered particularly important in the Crapina-Jijila marshes of Rumania, where mussel recruitment is mainly influenced by flooding of the Danube River. Years of significant and long lasting floods enhance development of mussel populations through phytoplankton blooms (Tudorancea, 1969, 1972).

References to the habitat preferences of different species are numerous but often general in nature, describing broadly (and occasionally specifically) how each species is more commonly found in a particular type of waterbody, or in particular conditions or regions of the waterbody (Coker et al., 1921; Boycott, 1936; van der Schalie, 1938; van der Schalie and van der Schalie, 1950; Cvancara and Harrison, 1965; Clarke, 1973). Quantitative measures of the habitat preferences and specific requirements of species in relation to broad dispersal are uncommon. Studies by Green (1971, 1972) and Strayer (1983), represent the only attempts of defining niche or habitat requirements over a wide geographical range.

Within a particular drainage system, studies on the habitat and microhabitat preferences of species are common, and often diverse in findings - particularly in regard to substrate preferences. Some bottom types are inimical to the establishment and maintenance of mussel communities. Mussels are rarely found on shifting sand or silt, bare rock or unconsolidated muds and silts - substrates in which the foot cannot penetrate and function effectively as a holdfast structure or into which mussels would rapidly sink and asphyxiate (Ellis, 1931; Boycott, 1936; Clarke and Berg, 1959; Marshall, 1975; Fisher and Tevesz, 1976; Strayer et al., 1981; Suloway, 1981). With respect to soft and unconsolidated muds, Kat (1982) found that even though a species might occur in these (e.g. Elliptio complanata), the constant energy expenditure needed to maintain a station effectively lowered the fitness of individuals, as shown by reduced growth rates resulted. Kat regarded these substrates therefore, as low quality microhabitats. Yet it is this degree of tolerance to soft substrates that partly explains the broad distribution of some species of freshwater mussel. Anodonta grandis for example, can live in softer, siltier bottoms than most other species (Evermann and Clark, 1917; Ghent et al., 1978), an adaptation contributing to its widespread occurrence in lakes.

The shape and size of particular species may determine their habitat requirements. The lightweight and ovate shell of A. grandis for example, enables the species to 'float' upon fine silty muds (Ghent et al., 1978). The swollen shell of Velesunio ambiguus may perform a similar function in similar habitats in Australian waterways (Walker, 1981b). Various other reports draw attention to the occurrence of larger and heavy-shelled species in headwaters, large rivers or wave swept shores of lakes in correspondingly coarser substrates, and of smaller and/or thin-shelled species in quieter and siltier, muddy environments (Jewell, 1922; Coker et al., 1921; Clarke and Berg, 1959; Ghent et al., 1978; Horne and McIntosh, 1979). It has been generally suggested that larger and heavier shells assist in maintaining the station of mussels in turbulent environments. Horne and McIntosh (1979) correlated the flow patterns and corresponding type of stream bottom with the distribution of various sized species in the Blanco River, central Texas (USA). Coon et al. (1977) considered that the number of heavy-shelled species in pools of the Mississippi River had increased in recent times as these were probably better able to anchor in the relatively unstable sand substrates that have developed over the same period.

Between the extremes of inimical substrates, from clean sand/soft silt to coarse gravel/stiff clay, Coker et al. (1921) believed there was a great variety of bottom types that could be used by various species of mussels. Yet they considered that bottom type was of first importance in governing distribution in rivers at least. In more recent studies, bottom type has been considered important in determining mussel distribution and abundance (Harman, 1972; Haukioja and Hakala, 1974; Fisher and Tevesz, 1976; Horne and McIntosh, 1979; Sickel, 1980; Bronmark and Malmqvist, 1982; Stern, 1983; Salmon and Green, 1983) or unimportant (Cvancara and Harrison, 1965; Dean, 1968; Cvancara, 1970, 1972; Green, 1971, 1972, 1980; Tevesz and McCall, 1979; Walker, 1981b; Strayer, 1981; Kat, 1982; Porter and Horn, 1983).

Some apparent discrepancies in conclusions of the above studies can be accounted for and qualified as follows. Absence from inimical substrates and maintenance of location in others - according to the shape and size of species, can account for much of the published work relating to apparent selection of bottom type by different species. Nevertheless, although substrate type is generally recognised as a reflection of the flow regime or local turbulence, emphasis often tends to be placed, in lotic studies at least, on "preference" or "selection" for sediment type per se rather than any regard for the physiological tolerances of species to some condition which is related to relative water movement - such as oxygen availability. A much cited work is that of Harman (1972) who concluded that the type of substrate influenced species distributions of molluscs. While his study dealt mostly with gastropods, in relation to freshwater mussels he considered that their needs were soft but firm substrates in which to anchor. Harman (1972) listed quite specific sediment requirements of several species which in earlier studies in the same region (Clarke and Berg, 1959; Harman, 1970) were reported to be broader. Further, both a progressive increase in mussel species and substrate type were noted in three lakes studied. Harman (1972) admitted, however, an increase in the trophic status over the three lakes that may have contributed to the observed distributional patterns; also, in the largest lake, the dispersive capabilities were much greater.

Other than species size being correlated with occurrences in particular substrates, the study by Bronmark and Malmqvist (1982) concluded that particle size of the sediments was important in determining distributional patterns of Unio pictorum. The presence of the species was positively correlated to particles of size 0.25-0.5 mm; smaller particles were thought to interfere with feeding and respiration while larger particles were believed to interfere with locomotion.

Tevesz and McCall (1979) presented the most convincing conclusions in relation to the bottom type requirements of freshwater mussels. Within the accepted provisions of soft, yet firm substrates, their reviews of past surveys and studies led to the conclusion that the requirements of most species are in fact quite broad. Selection within the variety of bottom types that can be used by the various species, are most readily explained in terms of (a) mussel shape and size and resultant stability of location, and (b) physiological tolerances of various species to varying flow regimes, themselves expressions of oxygen status at least.

In studies of the microdistribution of freshwater mussels in lotic environments, flow patterns have been found to be important determining factors. The absence of mussels from too vigorous and turbulent currents has been mentioned previously. Where currents are less vigorous, studies have shown relationships between mussel distribution and current strength. Mussels in the Middle Thames River, Ontario were most often found in stable, low current regions where Salmon and Green (1983) considered minimal turbulence, a steady food supply, minimal siltation and enhanced reproduction as optimal conditions for the presence of mussels. Similarly in the Murray River (Australia), Walker (1981b) found mussels grouped in gentler currents along the innermost margins of meanders or in regions of sharp bends where the flow changed abruptly. Otherwise and in presumably stable substrates, the characteristic habitat of various mussel species from other lotic studies, has been found to be along banks, in the centre, or in other sites exposed directly to the current (Evermann and Clark, 1917; Björk, 1962; Cvancara et al., 1966; Simmons and Reed, 1973; Bronmark and Malmqvist, 1982; and earlier references to Margaritifera margaritifera). Such locations are generally believed to provide optimal conditions for extracting food, soluble mineral materials and oxygen from the water; Evermann and Clark (1917), Roscoe and Redelings (1964) and Cvancara et al. (1966) reported further evidence of this in the observations that most mussels in their study sites were oriented with siphons directed upstream or directly into the current.

Good evidence of the flow requirements of some essentially riverine mussel species is provided in the observations of the local occurrences in man-made impoundments. Marshall (1975) and Kenmuir (1980) found highest numbers and largest sizes of mussels in Lake McIlwaine and Lake Kariba, Zimbabwe respectively, in the river section of the lakes, attributing the observed distributions partly to increased numbers of fish hosts and to an absence of or nevertheless tolerance by mussels to siltation in the river section. Walker (1981b) considered water flow the single most important determinant of the distribution of the two species of mussel in the Murray River. Velesunio ambiguus occurs in slow-flowing and still waters while Alathyria jacksoni is characteristic of areas of moderate to strong currents. In an irrigation reservoir on the river (Lake Mulwala), A. jacksoni predominates along the old river channel where water continues to flow most strongly while in the surrounding quiet water, V. ambiguus is dominant.

Walker (1981b) suggested that the presence or absence of the above species from particular flow regimes was more directly related to their oxygen requirements. V. ambiguus could survive in deoxygenated water for short periods, while A. jacksoni was intolerant of short period anoxia. Mention has been made of the study of mussels in the Blanco River, central Texas in which Horne and McIntosh (1979) found species distributed according to a correlation between increasing shell size and stream velocity. The authors observed in addition, that the most tolerant species of low dissolved oxygen were found in habitats away from faster water, while the least tolerant were generally confined to swifter flowing habitats. Both studies suggest that much can be learnt of the habitat requirements of freshwater mussels when their oxygen requirements and tolerances to low dissolved oxygen levels are fully evaluated.

Final consideration of the habitat requirements of freshwater mussels must account for the life habits of juveniles. Almost invariably it is remarked in studies of mussels, that juveniles are rarely found. Apart from the difficulties in collecting small mussels and their rapid growth rates (section 3.2.1), their scarcity is generally attributed to their sensitivites and vulnerability to stresses and predation, or to their quite different habitat requirements (Lefevre and Curtis, 1910; Isely, 1911; Coker _et al._, 1921; D'Eliscu, 1973; Fisher and Tevesz, 1976; Kenmuir, 1980; Green, 1980).

Bottom type, streamflow and turbulence, and water depth are factors considered of prime importance in determining distribution of juvenile mussels. Isely (1911) found juveniles of various riverine species in fairly swift water from a bottom of course gravel. He suggested such environments provided a constant supply of food and oxygen, were frequented by fish and were free from shifting sand and silt accumulations. Negus (1966) found other riverine juveniles along the edges of reed beds and beneath landing stages, in sediments of fine shelly gravel, rich in organic matter. Such habitats were places where fish were known to congregate, and the sediments were silt free. Howard (1922) believed that species generally required clean, silt-free bottoms for survival, yet successfully raised one species (_Lampsilis luteola_) in crates in the Mississippi River, despite an accumulation of 2-3 cm of silt over the juveniles per week. As the crates were located in current-swept reaches of the river, the influence of adequate oxygen supply is almost certainly implicated in juvenile survival, especially as young mussels generally are known to be more susceptible to low dissolved oxygen levels than adults (Ellis, 1931). Water depth in most environments is mentioned as an important requirement (Isely, 1911; Coker _et al._, 1921; van der Schalie, 1938; Matteson, 1955; Green, 1980) and young mussels are often reported to occur in shallow waters close to the water margins. Finally, Isely (1911) and Coker _et al._ (1921) believed that any consideration of ecological factors inimical to mussel life should be directed towards the juvenile habitat as adults could live in environments where young would perish.

Physicochemical limnology

Fuller (1974) has provided the most recent review on the effects of physicochemical parameters on the physiological ecology, and levels for successful maintenance of unionid mussel populations. Most attention has been directed (in the chemical ecology of mussels) on the influences of water hardness and salinity in determining mussel distribution. However, the influence of any chemical factor in determining distribution is poorly understood for there has been scant work on the limits of tolerance of mussels for any chemical parameter.

The availability of dissolved calcium carbonate, important in shell formation, has in the past been considered critical to the maintenance of mussel populations (Coker _et al._, 1921; Boycott, 1936; Pennak, 1953; Clarke and Berg, 1959; Tudorancea, 1972; Isom and Yokley, 1973). Fuller (1974) agreed that hardness (as $CaCO_3$) was essential to mussel development but added that no published levels were available at which hardness determined presence or absence of a particular species. Fuller (1974) cited studies which gave limiting levels of various chemical parameters that reflected availability of dissolved $CaCO_3$, to the unionid fauna of particular regions, but listed other works which recorded their presence at much lower levels. While the broader geographical distribution of some species is believed to be determined by hardness (Boycott, 1936; Clarke, 1973), nevertheless other contrary findings are available in the literature - for example, the significance (Coker et al., 1921) or insignificance (Sepkoski and Rex, 1974) of water hardness in determining mussel distribution in the Atlantic slope waters of eastern United States, or more locally its importance (Clarke and Berg, 1959) or unimportance (Harman, 1969; Harman and Berg, 1970) in central New York state (USA). Evidence to show the reliance of a single species upon calcium and/or carbonate availability is very limited. Green (1972) used multivariate statistics to show that the distribution of Lampsilis radiata in some central Canadian lakes was apparently influenced by carbonate availability. The remaining studies pertain to the occurrence in and tolerance of other species to softwaters: Margaritifera margeritifera is found in softwater lakes and streams (referenced earlier); Green (1980) stated that Anodonta in North America commonly occurs in softwaters; and Strayer (1981) argued that lack of calcium (2-3 mg/l) was not a factor limiting the population of Elliptio complanata in Mirror Lake, New Hampshire (USA).

A suggested means by which soft, poorly buffered waters may affect mussels, is indirectly as the result of freely available carbonic acid, which in harder waters combines with calcium in solution to form bicarbonate (Coker et al., 1921; Harman, 1969; Fuller, 1974). Fuller (1974) smmarised studies relating to the adverse physiological effects of low pH upon mussels. Apart from observed effects of valve erosion at low pH, however, (Coker et al., 1921; Jewell, 1922; van der Schalie, 1938; Tudorancea, 1972) distributional studies are mixed in findings and suggest if anything, an indifference by species to acidity. In a naturally acid stream in Illinois (USA) (pH 5.6-6.8), Jewell (1922) recorded 9 species, apparently abundant and influenced more by bottom characteristics than by water type. The lack of mussels in the acid-degraded zone of a polluted stream receiving acid drainage in Virginia, was thought by Simmons and Reed (1973) to be caused by effects of siltation and altered fish populations rather than any direct effect of acidity. In river systems on the eastern seaboard of the United States, Sepkoski and Rex (1974) found a significant correlation between hydronium concentration and species numbers, believing the result accounted for the low numbers of species in two rivers of high acidity. The rivers ranged in pH from 4.3 to 5.9, but were, however, also high in chlorides (Johnson, 1970), a chemical factor also believed to be restrictive to mussels (Cvancara, 1967, 1970). Matteson (1955) placed mussels in a strongly acidic lake (pH 4.4-6.1) and noted that their reaction over a period was akin to that of aestivation, with the valves tightly closed. The findings of Jewell (1922) mentioned earlier, however, suggest that residents may behave differently. Harman (1969) thought that in central New York streams, reduced abundances of mussels were not caused by the low levels of water hardness, as much as by the rapid (and detrimental) changes in pH values associated with the soft waters. Finally, other species have been noted to be specifically tolerant of or actually partial to, acid waters: Margaritifera throughout Europe and North America (see earlier references and especially Bauer, 1983); Anodonta in North America is often found under acidic conditions (Green, 1980); and the density of Leptodea ochracea in Lake Waccamaw, North and South Carolina (USA) was found by Porter and Horn (1983) to be negatively correlated with increasing pH.

Of the chemical factors limiting mussels in the Red River Valley in North Dakota and Minnesota USA, Cvancara (1967, 1970) believed chloride content to be ecologically most significant. In the Turtle River, no live mussels were recorded at chloride levels of 87 ppm or more, derived from surrounding saline soils (Cvancara and Harrison, 1965). Sepkoski and Rex (1974) found a significantly negative correlation between dissolved solids and species number of mussels in streams of the Atlantic coast (USA), but could not interpret the result other than perhaps representing low species numbers in the saline drainage systems of Florida. Green (1972) found that part of the ecological separation of Lampsilis radiata and Anodonta grandis in central Canadian lakes had to do with the high sensitivity of A. grandis to sodium chloride. For both species, high NaCl concentration had an apparently deleterious effect on shell deposition. In South America, the distribution of Hyriidae is correlated with salinity, and mussels are absent when salinity exceeds 2500 ppm (Bonetto et al., 1962). Dean (1968) showed a similar restriction of Hyridella drapeta in Victorian streams (Australia) to salinities less than 300 ppm.

In the Murray River, prevailing salinities are generally high from returning irrigation water, but are nevertheless not of sufficient concentration to affect the two resident species, Velesunio ambiguus and Alathyria jacksoni. Both species are thought unlikely to be affected by salinities below 3.5 g/l (Walker, 1981b). Other occurrences in relatively saline waters were recorded for Anodonta woodiana in tropical Plover Cover Reservoir (Hong Kong); Dudgeon and Morton (1983) recorded their initial presence in the reservoir in 1972 when chloride levels ranged between 100-200 mg/l (Morton, 1977).

Imlay (1973) found that unionaceans were highly sensitive to the direct effects of potassium and believed high natural levels (>7 ppm) in waterways were responsible for the absence of mussels from certain regions in North America.

The effect of water depth and flow regime as a reflection of oxygen status and their bearing on mussel distribution has been discussed previously. Apart from the studies already mentioned, the role of dissolved oxygen in determining freshwater mussel distribution and abundance has received relatively little attention other than broad general statements. The factor may be unimportant in large perennial rivers. In other waterbodies its effect may only be felt at critical times of the year, necessitating seasonal measurement and precluding spot, isolated measurements typical of most studies.

Apart from the broad correlations made by Horne and McIntosh (1979) and Walker (1981b) between physiological tolerances to low dissolved oxygen of particular species, and their habitat reqirements, Fuller (1974) has summarised enough studies to further demonstrate the broader tolerances of quiet water species over characteristic riverine species. Selected pool species in North America (Amblema plicata and Anodonta spp.) were tolerant of anoxia for at least short periods, other riverine species required 2.5 ppm of dissolved oxygen for survival (Fuller, 1974). Kenmuir (1980) found that Caelatura mossambicensis, a deep pool species in Zimbabwe, could survive dissolved oxygen levels of 2 ppm, but succumbed below this level. Forty seven percent of the mostly fluvial mussels tested by Horne and

McIntosh (1979) were dead after 7 days at dissolved oxygen levels of between 0-0.5 mg/l. Ellis (1931) stated that young mussels were very sensitive to oxygen reduction, and that adults became inactive when oxygen tension was reduced to 20% saturation or less.

Fuller (1974) cited the work of Grantham (1969) who found no mussels in the Mississippi River where dissolved oxygen occasionally dropped as low as 3 mg/l. In the Fort Loudon Reservoir, Tennessee River, dissolved oxygen content of water near the bottom averaged about 3 mg/l with periodic lows of less than 1 mg/l when measured in the summers of 1965-68. The same regions have recorded a catastrophic loss of 60 native endemic mussels since impoundment (Isom, 1971). Kenmuir (1980) recorded no mussels in Lake Kariba at depths greater than 11 metres. Oxygen levels at these depths could fall below 2 ppm, concentrations known to be lethal to the mussels of the lake. The absence of mussels from organically rich pools below a sewage effluent in the Blanco River, Texas (USA) was attributed to periods of slow moving waters which could experience extreme fluctuations in oxygen concentrations (Horne and McIntosh, 1979). In organically enriched streams, Gaufin and Tarzwell (1952) believed that nocturnal deficiency in dissolved oxygen was the critical factor determining the distribution of stream organisms, especially when modified by seasonal flow characteristics (Tarzwell and Gaufin, 1953). Finally, one consequence of anoxia is the production of hydrogen sulphide from decomposition of non-living organic material. While nothing is known of its effect on freshwater mussels, it is at least harmful and toxic to fish (Ellis, 1937).

Reference has previously been made to the evidence for and against the limitation on mussel distribution by food availability, and the trophic separation of bivalves to avoid competition. Other studies have implicated trophic factors as the causes of increased species diversity and abundance in some regions: Clarke and Berg (1959) observed that sandy, shallow and eutrophic lakes in New York state were the most productive with respect to mussel species and densities; Okland (1963) found highest densities of mussels in Lake Borrevann, Norway, in the eutrophic shallows and summarised other work that found that the population density of Anodonta piscinalis in European lakes increased with increasing degree of eutrophy; in coastal streams of eastern United States, Sepkoski and Rex (1974) found a significant correlation between species number and nitrate concentration; and in Lake Kariba, Kenmuir (1980) found highest densities of mussels in waters of highest trophic status.. Whether food limitation is the cause of low densities in oligotrophic waters, however, is questionable. Strayer et al., (1981) argued that food and calcium were not limiting in Mirror Lake, New Hampshire, a soft, oligotrophic lake, but that low mussel densities may have more to do with a corresponding paucity of fish hosts, also likely to be scarce in oligotrophic waters.

Excessive organic enrichment of waterways, however, has adverse effects on mussels. Fuller (1974) summarised the work of Starrett (1971) who found no mussels in the Illinois River (USA) wherever ammonia concentrations exceeded 6.0 ppm. In tolerance tests to ammonia on five species of local mussels from the Blanco River central Texas, Horne and McIntosh (1979) found levels of 5 mg/l ammonia (as NH_4^+-NH_3) lethal to 40 percent of the mussels tested in 7 days. This level of sensitivity was believed in part to explain the absence of mussels from organically polluted sections of the Blanco River. Lewandowski and Stanczykowska (1975) found no mussels in the vicinity of local sewage outflow into Lake Mikolajskie (Poland) at values of 20 mg/l ammonia (as N-NH_4).

The effect of turbidity, especially in its severest form, has received considerable attention in relation to freshwater mussel distribution. Cvancara (1967, 1970) suggested turbidity may possibly be important in restricting mussels from the lower sections of some tributaries in the Red River Valley (USA), but added that turbidity in the Red River itself is consistently high but yet large numbers of species apparently thrive in its waters. High turbidities and siltation characterise waters of the Murray River in Australia, yet Walker (1981b) could find no evidence of any adverse effects upon mussels and even suggested that siltation and erosion might conceivably provide more available habitats in the extensive silt-derived substrates. Further, Tevesz and McCall (1979) believed, after reviewing the literature, that the absence of bivalves from soft bottoms had nothing to do with any inability to feed and respire effectively in turbid waters.

In its most severe form however, i.e. unnaturally high turbidities of unnaturally long duration, detrimental and often catastrophic effects upon mussels are observed. Erosion silt is harmful to mussels in a number of ways: it screens out light thereby reducing the food supply; smothers out sedentary biota during periods of sudden inundations following floods; interferes with feeding, mussels remaining closed 75-90% of the time; and retains organic matter, carrying it to the bottom and thereby increasing the oxygen demand immediately above the stream floor (Ellis, 1931, 1936, 1937). Chutter (1969) adds that in regions of seasonal rainfall in South Africa, shifting silt and sand lead to shallowing and a resultant increase in temperature of the bottom waters, thereby indirectly and adversely affecting stream fauna. Wave-induced, silt-recirculation in the shallows of Lake Kariba was believed by Kenmuir (1980) to stifle young mussels and subsequent development of shoals there.

A2.2 Anthropogenic activities

Much attention has been directed to the steady decline of freshwater mussels in waterways since the 1900's particularly in the Mississippi River drainage, where commercial exploitation of valuable species has been greatest and distribution and abundance of many species significantly affected. In the Mississippi drainage, overharvesting and dam construction in particular, have led to serious declines in species abundance and diversity (Fuller, 1974).

The adverse effects of impoundments upon mussel fauna are well documented and include: siltation caused by the obstruction to flow; changes in the fish fauna both within and upstream of impoundments and the elimination of fish migration from downstream; changes from riverine mussel fauna to species typical of quiet waters; increased hydrostatic pressure; and decreases in oxygen tensions (Lefevre and Curtis, 1910; Ellis, 1931; van der Schalie and van der Schalie, 1950; Scruggs, 1960; Bates, 1962; Isom, 1969; Imlay, 1972; Yokley, 1972; Isom _et al_., 1973; Fuller, 1974; Coon _et al_., 1977; Kenmuir, 1980).

In Australia, the abundance of Alathyria jacksoni an essentially riverine mussel in the lower Murray River, is thought to have declined in relatively recent times as a consequence of the extensive impoundment of the river in this region (Walker 1981b).

Industrial, municipal or domestic pollution are often mentioned in general statements in studies, as affecting the decline of species in waterways (Coker et al., 1921; Ellis, 1931; van der Schalie, 1938; Clarke and Berg, 1959; Cvancara, 1967, 1970; Green, 1980; Suloway, 1981; Bauer, 1983). Bauer (1983) actually found a positive correlation between mortality rates of Margaritifera margaritifera populations in North Bavarian streams and the degree of organic pollution in the streams. Fuller (1974) reviewed the adverse effects of some pollutants, including wood product wastes, organic enrichment, acid mine wastes, and some heavy metals upon freshwater mussels. Other comprehensive studies and reviews on the effects of pollutants include acid drainage in the North Anna River (Simmons and Reed, 1973) and organic enrichment in the Blanco River, central Texas (Horne and McIntosh, 1979). The specific findings of these studies have already been discussed (section 5.1.1.3).

Finally, the introduction of the Asian clam, Corbicula manilensis, into North American waterways during the 1930's (Kraemer, 1979) has led a number of investigators to wonder as to whether it has contributed to the decline of native mussels through competition (Bates, 1962; Isom, 1968; Isom and Yokley, 1968; Coon et al., 1977; Horne and McIntosh, 1979). Anatomical, ecological and physiological factors that have contributed to the broad tolerances to stresses, rapid colonisation and abundance of C. manilensis have been summarised by Kraemer (1979) and Horne and McIntosh (1979). Kraemer (1979) argued, however, that while Corbicula abounds in heavily managed waterways where substrates are altered and often unstable, in relatively unmanaged rivers, the species does not show the same runaway distribution and biomass, and lives in a competitive role with indigenous mussels.

A2.3 Freshwater mussels as ecological indicators

Freshwater mussels are particularly well suited as indicators of palaeoenvironments, the activities of early man, or of present day water quality for a number of reasons: mussel shells preserve well; mussels often have particular habitat needs; shell size and shape are usually very responsive to the surrounding environment; mussels are sedentary; they absorb simple compounds directly from the water or feed from the basic trophic levels; they are long-lived and, being continually exposed to their environment, integrate variable water conditions (Tuthill, 1967; Cvancara, 1967; Green, 1972; Horne and McIntosh, 1979).

In relation to palaeoenvironments, mussels in North America at least have been used in deciphering drainage history. Mussel distribution has been used to interpret post-glacial stream confluences: van der Schalie (1939) for example used as evidence, the strength of commonness of mussels in both the Tennessee and Alabama Rivers to indicate that both rivers were once connected, mussels being carried across the divide by fishes during the period of confluence. Cvancara (1967) suggested mussels may be useful in indicating historical changes in river discharge in the Red River Valley (USA). As some species are peculiar only to larger rivers of the valley, their presence in terrace sediments suggests a greater discharge in a particular river at some previous time. Similar rationale can be made for other species indicative of smaller rivers or tributaries (Cvancara, 1967). Lee and Wilson (1969) used the differences in Sr/Ca ratios of recent shells and ancient midden shells to indicate historical changes in palaeohydrologic conditions. Ecotypic shell forms have been suggested as offering reliable palaeohydrologic and palaeolimnologic data on at least a regional basis: in normally smooth-shelled species, rough growth interruption lines may indicate water temperature rises and/or declining water levels (Tuthill, 1967); as prediction of environment from <u>Lampsilis</u> <u>radiata</u> shell morphology in central Canadian lakes is possible, Green (1971) suggested the analysis of shell shape of fossil shells could be made to predict and describe the environment in which particular strata were laid down.

The distributions of some Australian mussel species were cited by Iredale and Whitley (1938) and later McMichael and Hiscock (1958) in support of a 'fluvifaunula' concept - that the principal drainage divisions in Australia supported more or less distinct assemblages of river animals. Walker (1981a) reviewed the idea and arguments. He concluded that the degree of overlap of species appeared too great to warrant the recognition of separate zoogeographic provinces and hence mussels in Australia did not provide effective support for the fluvifaunula concept. Of interest, however, is the correspondence between the ranges of a few mussel species and the geographic boundaries of the fluvifaunular provinces. The range of <u>Velesunio angasi</u>, one such species, nearly coincides with the Leichhardtian province (Walker, 1981a).

As the niches of some North American bivalves have been found to be trophically defined, their potential use and value as indicators of both past and present trophic stages of lakes has been suggested independently by Green (1971) and Clarke (1979).

Finally, in relation specifically to present day environments, interest has been held in recent years in the assessment and value of freshwater mussels as biological monitors of water quality. The topic has been reviewed by Fuller (1974), Horne and McIntosh (1979), Walker (1981b; 1984) and Simpson (1982). Present knowledge as to their value as indicators of pollution in chemical terms is growing and this forms a large part of the work on <u>Velesunio</u> <u>angasi</u> in the Northern Territory (Allison and Simpson, in press). Freshwater mussels apparently have great value as indicators of the "biological recovery zone" (Simmons and Reed, 1973) or at least as indicators of nonpolluted waters. Simmons and Reed (1973) noted that species diversity indices of benthic invertebrates were insensitive to the detection of pollution below a point source into the North Anna River, Virginia (USA), owing to the dominance of insect species. However, the molluscan fauna, including 3 freshwater mussel species, did not re-establish itself for some distance below the pollution source, and Simmons and Reed (1973) considered these organisms therefore more sensitive pollutional indicators and used them to mark the downstream area of full biological recovery. Horne and McIntosh (1979) reaffirmed an earlier suggestion of Ingram's (1957), that mussels may have value as indicators of nonpolluted waters as their presence indicates at least high dissolved oxygen and other associated physicochemical conditions of clean waters. The absence of formerly present "clean water" species was argued to be a more significant indication of polluted waters than the presence of known pollution resistant forms. Mussels in the Blanco River, Texas, sections of which are organically enriched, are known to be sensitive to low dissolved oxygen levels to varying degrees (Horne and McIntosh, 1979).

APPENDIX 3

POPULATION DYNAMICS

Considerable attention has been devoted to study of the dynamics of freshwater mussel populations. Early work on determining population parameters of freshwater mussels focussed mainly on age and growth, important basic requirements for understanding the ecology of commercially valuable species (Lefevre and Curtis, 1910; Isely, 1914; Coker *et al*., 1921; Ellis, 1931; Chamberlain, 1931). More recently, as the dominance of freshwater mussels in the total benthic biomass of many freshwater ecosystems has become increasingly realised, their likely importance in the links of food chains and influence in energy and nutrient budgets, has attracted attention. As the basis for assessing the functional role of freshwater mussels in ecosystems (chiefly by way of secondary production estimates), thorough knowledge of the structure of mussel populations has been an important prerequisite (Okland, 1963; Negus, 1966; Tudorancea and Florescu, 1968; Tudorancea and Gruia, 1968; Magnin and Stanczykowska, 1971; Tudorancea, 1972; Lewandowski and Stanczykowska, 1975; Coon *et al*., 1977; Green, 1980; Kenmuir, 1980; Strayer *et al*., 1981). Otherwise, study of aspects of the population dynamics of important or formerly valuable commercial species of freshwater mussel, has identified terminal populations and even elucidated factors affecting their decline in regions severely affected by anthropogenic activites and changes (Ellis, 1931; Scruggs, 1960; Hendelberg, 1960; Isom, 1969; Coon *et al*., 1977; Bauer, 1983).

By far the bulk of relevant information on freshwater mussel populations has been devoted to methods of aging (see below, section 6.3), as this information is a basic prerequisite for determining other population parameters such as growth, population structure, recruitment, mortality and annual production. A notable feature of this considerable literature, however, is a dearth of studies that have validated the aging technique (section 6.3.2). Because of this, several authors have doubted and contested the longevities recorded for some populations of mussel. *Margaritifera* in particular, from inferences from its growth rate is reported to live from 60 to 100 years in both Europe and North America (early studies summarised in Comfort, 1957; Hendelberg, 1960; Stober, 1972). Even though Altnöder (1926) had earlier shown growth lines of *M*. *margaritifera* in one German population to be annual from direct observations of growth over the course of one year, Thompson *et al*. (1980) questioned the accuracy of estimates of its longevity in general, because growth rate is known to be highly variable between individuals of this species so that large specimens might merely be fast-growing. On the basis that other unionids rarely lived beyond 10-15 years, Dudgeon and Morton (1983) similarly, contested Stober's (1972) reported longevity of 67 years for a north American population of *M*. *margaritifera*.

In relation to the accusations by Thompson and co-workers just cited, Comfort's (1957) observations support the claims that generally, large shells represent high growth rates rather than extreme age. Thus while growth rates between individuals are generally noted to be highly variable, an inherent feature of unionid populations (Tevesz and Carter, 1980a), nevertheless much of the variation in growth may be accounted for sexually or by way of broad aspects of the environment. Tevesz and Carter (1980a) recently reviewed some of these environmental relationships of shell growth in unionacean bivalves.

Prior to discussing factors that may cause variability in growth within a particular species, differences in growth rates between different mussel groups at least, are reported to be related to shell form. Heavy shelled forms (e.g. subfamilies Ambleminae and Megalonaiadinae) often grow more slowly than thin shelled forms (e.g. Anodontinae and Lampsilinae) (Isely, 1914; Grier, 1921 in Stansbery, 1961; Coon *et al.*, 1977).

Few studies have explored the possibility of growth rate differences between the sexes of individual species of freshwater mussel. Tevesz and Carter (1980a) noted that Lampsiline unionids generally, are often markedly sexually dimorphic in shell features including size. Chamberlain (1931) for example, showed that female *Lampsilis anodontoides* in North America are faster growing in the sexually active phase of life. Judging from the growth data, however, differences are apparently minor. Female *Anodonta piscinalis* in Finland similarly grow faster with the onset of maturity, but according to Haukioja and Hakala (1978a), differences are so minimal that measurements for both sexes can be pooled in growth studies.

In temperate regions generally, growth is invariably reported to decline or cease during winter in response to declining temperatures (section 6.3). While drought may cause growth cessation in warmer climates (McMichael, 1952), Tevesz and Carter (1980a) suggested that high amounts of suspended solids during wet season flooding in tropical regions might conceivably arrest growth. Very little information is available on growth of freshwater mussels in the tropics, but at least Kenmuir (1980) has suggested that seasonal differences in growth rates of mussels in Lake Kariba, Zimbabwe are probably related to food availability. Thus temperature and trophic degree are at least two environmental determinants implicated in shell growth.

Within habitats, growth patterns of freshwater mussels have been shown to vary with several environmental factors, of both biotic and abiotic nature:

Density effects on mussel growth are reportedly few, and mixed in findings. Kat (1982) found some evidence that growth rates of *Elliptio complanata* in stream environments were greater for each size class, at or below observed densities as opposed to densities greater than those usually observed in the stream. Conversely, however, Kenmuir (1980) recorded the largest (and presumably faster growing) mussels in Lake Kariba, in regions of highest density suggesting to him that no competition for resources was evident amongst mussels of the lake.

Reports of substrate effects on growth are ambiguous in interpretation. Brönmark and Malmqvist (1982) found that growth rate of *Unio pictorum* decreased immediately downstream of a Swedish outlet. While fine sediment particles increasing downstream, could explain the observed growth patterns in that these may interfere with feeding and respiration, food quality (as measured by chlorophyll a) was also found to decline downstream. Kat (1982) showed that growth rates of E. complanata were reduced on muddy substrates. He believed such sediments reduced feeding efficiency of mussels, as a constant energy expenditure would be required in order that they retain their position. It was conceded, however, that muddy substrates reflected reduced flow regimes and that weaker currents probably supported less nutritive material (Kat, 1982). In Lake Erie, growth of Amblema plicata inhabiting fine-grained sediments in deep water is reduced. Such environments according to Stansbery (1970) reflect reduced currents, these affecting growth rates.

In lakes, growth rates of mussels are invariably reported to decrease with depth (Okland, 1963; Reigle, 1967; Stansbery, 1970; Haukioja and Hakala, 1978a; Ghent et al., 1978; Strayer et al., 1981; McCuaig and Green, 1983). Ghent et al. (1978) found that stunting of Anodonta grandis was smoothly progressive, and that the predictable effect was consistent with similar and expected gradual declines in food supply and/or water temperatures with depth that might suppress metabolic rates. Similarly, stunting in relation to more exposed lake habitats is an unequivocal observation (Coker et al., 1921; Brown et al., 1938; van der Schalie and van der Schalie, 1950; Stansbery, 1961; Green, 1972; Clarke, 1973; Tevesz and Carter, 1980a). Brown et al. (1938) suggested that either wave action alone may produce the stunting effect, as mussels would require a continuous effort to stay in place; food supply or availability may be reduced over exposed habitats; or that stunting might be due to a series of factors associated with degrees of wave action or exposure.

Between habitats or sites, again growth rates may vary considerably (e.g Margaritifera, Altnöder, 1926). Much of the variation, however, can be explained by limnological factors, in particular, temperature, trophic status and water hardness. In streams, M. margaritifera in Germany (Altnöder, 1926), A. grandis in the Sheyenne River, USA (Cvancara et al., 1978) and Alathyria jacksoni in the Murray River, Australia (Walker, 1981b) generally grow more rapidly in a downstream direction. While trophic status might be expected to increase downstream (Cvancara et al., 1978), Walker (1981b) suggested that increasing temperatures recorded downstream in the Murray River would impart a longer growing season on mussel populations, which may account for differences in growth rates. In the Thames River, higher growth rates of Anodonta anatina at one site were attributed by Negus (1966) to artificial heating of the river there by effluent from a nearby power station, which caused earlier breeding in the local population and provided it with a longer growing season. Coker et al. (1921) believed that the limiting factor of growth in thick shelled species particulary, was not so much the organic food supply as the mineral food supply. Björk (1962) for example, attributed higher growth rates of M. margaritifera between populations in two streams in southern Sweden to both higher trophic degree and increasing water hardness. Similarly, Clarke (1973) observed that streams in the Canadian interior basin that flowed through limestone often supported larger specimens than elsewhere.

Higher growth rates of mussels between different sites of the same lake have been attributed to higher water temperatures (Cvancara, 1972) and/or increasing eutrophy (Harman, 1970; Cvancara, 1972; Kenmuir, 1980). Between different but neighbouring lake populations in North America, Green (1980) found evidence that calcium availability was the cause of growth rate differences of mussels. Okland (1963) on the other hand, attributed higher growth rates between the mussel populations in two Norwegian lakes, to higher summer temperatures in the shallower lake, in addition to higher levels of domestic sewage there.

The type of environment that mussels inhabit may have profound influences on their growth. Lake populations of a given species are generally noted to be smaller than their counterparts in nearby streams (Evermann and Clark, 1917; Coker _et al_., 1921; Brown _et al_., 1938; Harman, 1970; Clarke, 1973; Walker, 1981b), while both individuals in, and species associated with small streams or creeks are smaller than those in large rivers (Clarke, 1973; Tevesz and Carter, 1980a). Coker _et al_. (1921) believed the disparities in growth between rivers and lakes were caused by the deficiency in mineral and organic food in lakes over rivers, where currents kept food matter in suspension. While Brown _et al_. (1938) maintained that the more favourable conditions ascribed to streams could not be supported with limnological facts, presence of currents appear nevertheless to be implicated. Walker (1981b) found for example, better growth of _Velesunio ambiguus_ in the Murray River proper or impoundments on the river in which there was regular water renewal, over populations in still waters. Clarke (1973) noted that mussels in general reached their largest sizes in rivers close to and draining lakes. This may be a trophic phenomenon in that draining waters immediately downstream of lakes (Brönmark and Malmqvist, 1982) and impoundments (Fuller, 1974) are generally noted to be nutrient enriched compared to waters further downstream. Harman (1970) recorded greater growth of individuals of a given species in central New York in nutrient-rich streams as opposed to growth in the cold, deep and nutrient-poor Finger Lakes. Finally, Evermann and Clark (1917) attributed the stunted populations of mussels in Lake Maxinkuckee (USA) not to food (apparently abundant), nor to the absence of current, but to close inbreeding and the absence of "new blood" in the populations.

The effect of temperature on growth rates of freshwater mussels is most effectively observed in latitudinal comparisons. Comfort (1957) states that in mollusc species in general with wide climatic ranges, individuals from colder climates are longer-lived and slower growing than those from warmer climates. Thus the growth rate of _Margaritifera margaritifera_ is noted to be considerably higher in southern Swedish localities (Björk, 1962) than in northern, arctic sites (Hendelberg, 1960). Stober (1972) suggested the even faster growth of _M. margaritifera_ in Montana (USA) over Swedish populations could in part be due to the lower latitudes of his site. Negus (1966) thought that growth of _Anodonta anatina_ in the Thames River was less than that recorded in Norwegian lakes, as summer temperatures were higher in Norway. Populations of _Anodonta_ and _Lampsilis_ in extreme northern, peripheral populations in Canada grow very slowly and Clarke (1973) noted that the maximum sizes reached, were much less than those in more southerly populations. Chamberlain (1931) noted that the growth rate of _Lampsilis anodontoides_ in North America was higher in southern and middle portions of its range than in northern portions and that further south, higher average temperatures coupled with the longer growing season were two likely factors producing greater growth rates.

A final observation in regard to growth rates are their relations to longevity. As noted by Comfort (1957) above, slower growing molluscs tend to be longer-lived. Segerstrale (1961) noted in relation to the marine bivalve, Macoma baltica for example, longer-lived populations in the deepest localities, were accompanied by a slowing of growth rate with increasing depth. In relation to freshwater mussels, M. margaritifera is not as long lived in southern Sweden as in northern Sweden, a factor attributed by Björk (1962) to faster growth and pearl fishing that shorten its lifespan. Okland (1963) suggested the lack of older mussels in the shallows of Lake Borrevann might be due to the shortening of life attained when growth was accelerated by, for example, higher temperatures. Haukioja and Hakala (1978a) found evidence of growth-selective mortality in some freshwater mussel populations. However, while mortality was observed to be higher in individuals that grew faster, in other populations there was evidence that selective mortality operated on slow growers and in other populations still, did not operate at all.

A feature of long-lived animal and plant populations is the irregular nature of their age distributions (Krebs, 1978). Thus invariably, the age structure of freshwater mussel populations in various freshwater ecosystems is reported to be uneven, and characterised by dominant year classes and long-lived individuals - the result of irregular and considerable year to year variation in recruitment, and low adult mortality (Negus, 1966; Haukioja and Hakala, 1978b; Walker, 1981b; and Strayer et al., 1981). An inherent feature of the age structure of freshwater mussel populations, is the absence of the very youngest age group. This imparts to age frequency distributions a bell-shaped nature. Where intermeidate age groups of mussels are most abundant (Brown et al., 1938; Lewandowski and Stanczykowska, 1975; Smith, 1976; Coon et al., 1977), populations are generally regarded as stable (Krebs, 1978). For most age distributions of molluscs, however, the mode is skewed to the left hand part of the curve (Zaika, 1973), and the predominance of younger age groups indicates increasing populations. This type of age distribution is noted in many freshwater mussel populations (van der Schalie and van der Schalie, 1963; Tudorancea and Florescu, 1968; Tudorancea and Gruia, 1968; Tudorancea 1969, 1972; Magnin and Stanczykowska, 1971; Kenmuir, 1980). In other populations, the mode of the dominant age groups may occur in the right hand part of the curve indicating declining populations. This has been reported in exploited (Hendelberg, 1960; Bauer, 1983) and even unexploited (Stober, 1972) populations of Margaritifera margaritifera in Europe and North America, and in populations of mussels following impoundment or embankment (Scruggs, 1960; Tudorancea, 1969, 1972). No freshwater mussel populations have been found in which there are gradual and regular decreases in numbers from juvenile young-of-year to the oldest age group, indicating regular recruitment from year to year.

Age structures of course, are affected by birth and death rates. In relation to recruitment, the notable and reported absence of young mussels in most freshwater environments generally, and suggested or implicated causes have been discussed previously (sections A2.1.3 and 3.2). While some causes of juvenile scarcity have been briefly reviewed by Lewandowski and Stanczykowska (1975) and Kat (1982), for the sake of completeness, causes have been attributed as follows: to small sizes and consequent sampling biases against the young; high growth rates of juveniles; different habits and habitat preferences than adults; whereas adults are generally clumped, juveniles may be dispersed considerably after leaving the host fishes; irregular year to year recruitment; and pollution and other adverse anthropogenic changes to the environment that juveniles may be particularly sensitive to.

With respect to the present study, variation in year to year recruitment and the habitat preferences of juveniles were of particular interest. Literature relating to spatial patterns of recruitment has been previously described (section A2.1.3). While the unevenness of the age distributions of mussel populations indicates considerable differences in annual reproductive success (Lewandowski and Stanczykowska, 1975; Haukioja and Hakala, 1978 a, b), there has been little attempt at demonstrating temporal variations in recruitment patterns related to environment. Both density dependent and independent factors, however, have been suggested as important regulating factors in freshwater mussel populations.

Fish breeding activities coinciding with release of glochidia were thought by Okland (1963) and Negus (1966) to be important factors leading to successful recruitment. Okland's observations are of interest in that a particularly dominant year class was observed in only two of the three stations studied in Lake Borrevann (Norway) - the only stations where breeding behaviour of the host fishes was observed, thus demonstrating how localised successful recruitment can be. Droughts and floods have been held responsible for annual reproductive success or failure. Bimodality of the length frequency distributions of Alathyria jacksoni populations along middle tracts of the Murray River, were attributed by Walker (1981b) to high mortality and absence of recruitment during a severe drought in 1967 and 1968. Similar troughs in size distributions suggested that recruitment was poor in 1975 and 1976 when widespread and prolonged flood in the river apparently adversely affected recruitment. In the Nera River (Rumania) too, young age classes of Unio crassus are uncommon in upstream stations but predominate lower downstream; Tudorancea and Gruia (1968) believed young mussels were swept away from the upper reaches to be carried into the quieter waters further down. In the Crapina-Jijila marshes of Rumania, however, recruitment of mussels is enhanced by flooding from the Danube River, and in the absence of flooding mussels fail to breed; strong year classes and successful recruitment of Unio tumidus in fact could be traced back to years of high floods in Crapina populations (Tudorancea, 1969, 1972).

Odum (1971) writes: "There is evidence that populations have a "normal" or stable age distribution towards which actual age distributions are tending. Once a stable age distribution is achieved, unusual increases in natality or mortality result in temporary changes, with spontaneous return to the stable situation." Amongst the evidence, Odum cites the suppression of reproduction for several years following unusual survival of year classes of some fish populations. Both Kenmuir (1980) and Brönmark and Malmqvist (1982) believed mussel populations could be regulated in a density dependent fashion. Brönmark and Malmqvist (1982) observed high densities of mussels in a Swedish lake outlet. Such habitats were high quality in terms of food, oxygen and substrate availability, and scarcity of young was attributed by these authors to suppression of establishment by adults. Kenmuir (1980) similarly observed few young mussels where adult densities were high, but where adult populations had been devastated by earlier drawdown in Lake Kariba, large conentrations of young and rapid recolonisation were observed. Thus recruitment rates in stable and long-lived mussel populations might be expected to be very low, by virtue of the fact that age distribution influences natality in populations (Odum, 1971).

The long life-span of freshwater mussels generally, suggests low adult mortality (Comfort, 1957; Strayer *et al.*, 1981). Nevertheless, apart from physiological longevity, death may occur prematurely in freshwater mussel populations from a number of causes. Some of the factors have been discussed previously (Appendix 2), but again for the sake of completeness, the various causes of mortality have been attributed as follows: life spans may be growth selective (see above); while various predators of freshwater mussels have been recorded, muskrats and aboriginal man are thought to have severely reduced the shallow water distribution of some species in Europe and North America (section A2.1.2). In Australia, water rats (Dean, 1968; Fisher, 1973; Walker, 1981b) and various species of birds (Vestjens, 1973; Fisher, 1973) have been observed to prey upon freshwater mussels, while aboriginal man in the past at least, must have been an important and significant predator (Walker, 1981b); droughts, drawdown in impoundments or rapid subsidence of waters may devastate mussel populations through effects of desiccation, anoxia or direct exposure to predators (Björk, 1962; Okland, 1963; Tudorancea, 1969, 1972; Marshall, 1975; Kenmuir, 1980; Walker, 1981b); winds and high wave action during storms may throw mussels up onto shores where survivors may become food for various predators (Tudorancea, 1969, 1972; Walker, 1981b); and adverse anthropogenic changes such as pollution, impoundment, siltation and overharvesting may similarly devastate populations (section A2.2). In addition to these causes, density dependent affects have been suggested as inducing early mortality in mussel populations. In the Nera River (Rumania), high densities of mussels downstream were believed by Tudorancea and Gruia (1968) to shorten the life span of *Unio crassus* populations; in evidence the population here comprised mostly young individuals, in relatively poor condition (according to flesh weights) when compared with other stations.

As in recruitment patterns, attempts at interpreting age distributions in relation to significant and devastating mortality effects in the past have been few. In the Crapina-Jijila marshes, a past two year period of high winds and wave action (that throw juvenile mussels onto the shores), was believed to be responsible for the low numbers of two corresponding age classes in the age distributions of mussels (Tudorancea, 1969). Bimodality in the length frequency distributions of *Alathyria jacksoni* in middle tracts of the Murray River was shown by Walker (1981b) to be caused by a severe two year drought in the river during 1967 and 1968. *A. jacksoni* is intolerant of both dehydration and anoxia (Walker, 1981b). Mortality rate of all the age classes in populations of *Margaritifera margaritifera* in streams of North Bavaria, was shown by Bauer (1983) to rise steeply with increasing degrees of organic pollution.

Because of the irregularity in recruitment and long life spans of freshwater mussel populations, few attempts at estimating mortality rates have been made (Negus, 1966; Haukioja and Hakala, 1978 b; Green, 1980; Bauer, 1983). While mortality is generally easier to estimate in the older age classes, it has been suggested (Green, 1980) and found (Negus, 1966) that mortality rates at intermediate ages are lower or negligible in comparison to the oldest part of the population, but at the earliest ages are also probably high (Tudorancea, 1972; Green, 1980). With respect to sexual differences in mortality rates, in populations of freshwater mussels in which growth selective mortality worked against slow growers, Haukioja and Hakala (1978a) found that males suffered higher mortality than females. Elsewhere, changing sex ratios with age have been interpreted as modification or transformation of sex (Tudorancea, 1969).

In relation to physiological longevity, the life spans of light-shelled species throughout the northern hemisphere are remarkably and consistently similar. Species of the subfamilies Unioninae, Anodontinae, Lampsilinae generally live from 10 to 15 years in Europe (Boycott, 1936; Crowley, 1957; Björk, 1962; Okland, 1963; Haranghy *et al*., 1964; Negus, 1966; Norelius, 1967; Tudorancea and Gruia, 1968; Tudorancea, 1969; Lewandowski and Stanczykowska, 1975), North America (Chamberlain, 1931; Pennak, 1953; Magnin and Stanczykowska, 1971; Coon *et al*., 1977) and tropical Asia (Dudgeon and Morton, 1983). Coon *et al*. (1977) noted that heavier shelled mussels of the subfamilies Ambleminae and Megalonaiadinae in North America, however, in addition to their slower growth rates, often live longer than mussels of the previously mentioned subfamilies. Thus, species of *Elliptio* may live from 16 to 20 years (Ghent *et al*., 1978; Strayer *et al*., 1981), *Quadrula* from 20 to 50 years (Lefevre and Curtis, 1910; Comfort, 1957), *Pleurobema* over 30 years (Scruggs, 1960) and *Megalonaias* from 25 to over 50 years (Comfort, 1957; Coon *et al*., 1977).

Light-shelled mutelids in tropical Lake Kariba in Africa have comparable age spans to similar shell forms in the northern hemisphere, of between 10 and 12 years (Kenmuir, 1980). Similarly, in Australia, the lighter shelled *Velesunio ambiguus* is estimated to live to 11 years along the Murray River, and the heavier shelled riverine mussel, *Alathyria jacksoni*, 29 years - again comparable estimates to figures recorded for similar shelled forms in Europe and North America (Walker, 1981b).

Vastly different estimates for the life span of *Margaritifera margaritifera* throughout its circumboreal range but also within countries, however, have been reported. In North America, two populations in central Massachusetts (USA) were reported to live from between 19 and 23 years (Smith, 1976), while in Montana, maximum ages of 67 years were found (Stober, 1972); in southern Sweden *M. margaritifera* was believed to live from 19 to 24 years (Björk, 1962) and up to 116 years in arctic Sweden (Hendelberg, 1960); and in North Bavaria maximum ages amongst five rivers studied ranged from between 60 and 110 years (Bauer, 1983). While exploitation, pollution and growth-selective mortality have been used to explain differences in the longevity of *M. margaritifera* (Björk, 1962; Bauer, 1983), doubts over its extreme longevity (mainly because of the aging technique), have been previously mentioned. There is little doubt that the aging method needs to be validated for each regional population of Margaritifera studied. Even though growth has been shown to vary considerably in this species regionally, it is curious that extreme age *per se* should be questioned, given that bivalves generally are long-lived and that some marine species may live beyond 100 years (Jones, 1983). Shells of *Arctica islandica* for example, have been reported with up to 150 growth increments, apparently annual in nature (Thompson *et al.*, 1980).

Apart from studies of growth in relation to habitat and environmental patterns, other aspects of the population structure of freshwater mussels in relation to habitat have been little studied. With respect to distribution of the sexes, Cvancara (1972) noted no apparent trend in sex ratio with depth evident in *Lampsilis radiata luteola* populations in Long Lake, Minnesota (USA). In relation to size and age distributions, different habitat requirements of young mussels have already been discussed. Within habitats generally, for example, juveniles are often found in shallower waters than adults (section A2.1.3).

Kenmuir (1980) found that mussels increased in size (and presumably age) with increasing depth in Lake Kariba. While more young were recruited in the shallows than elsewhere, drawdown and exposure increased mortality in the shallows or prompted migration of older individuals to deeper waters; mortality due to predation and siltation was argued to be higher in the shallows than elsewhere (Kenmuir, 1980). In Lake Borrevann, Okland (1963) not only found younger *Anodonta piscinalis* individuals in the shallows (0.4 m) but also in deeper waters (6 m) while the oldest mussels were found at intermediate depths (3-5 m). Okland suggested that the lack of old shells in the shallows might be due to: the unstable environment of the shallows that increases mortality (e.g. ice, drought, wave action, or predation); selective mortality of the faster growing individuals in the shallows; local recruitment effects that may favour the shallows; and dispersal to greater depths with age). He thought the occurrence of younger mussels at greater depths might be a result of periodic oxygen depletions that either shorten the life-span of mussels here or induce migrations upwards towards more favourable habitats. Conversely, in Lake Mikolajskie, Lewandandowski and Stanczykowska (1975) found reverse trends to those of Kenmuir (1980) and Okland (1963) in size distributions. Smaller individuals of *A. piscinalis* occurred at intermediate depths, while larger mussels were found in the shallows and deeper regions. *Unio tumidus* individuals on the other hand, became smaller with depth. No explanation for the observed distributional patterns was provided by the authors, and interpretation is made even more difficult as habitat related growth rates were not studied. A final observation in relation to size distributions in lakes is that of Green (1980) who found that the size of *Anodonta grandis* in a small arctic lake was more related to slope of the bottom than to depth, with mean length decreasing with decreasing slope. No causal explanation was offered.

Within microhabitats of streams, a vertical stratification of age classes has been observed with larger and older mussels in a superficial position, and smaller and younger mussels occurring deeper in the sediments (Bjork, 1962; Tudorancea and Gruia, 1968). Little comparison has been made of age distributions within habitats otherwise. Between sites of the Nera River, however, as mentioned earlier, Tudorancea and Gruia (1968) thought age distributions were influenced by currents, with juveniles being swept away from upstream into quieter reaches downstream.

The structure of mussel populations at any given time and place may of course be considerably altered or modified where movements and migrations of individuals are significant. Early thoughts on freshwater mussel movements reached the conclusion that adult mussels rarely if ever moved about, especially in the absence of suitable stimuli and hence that mussels probably lived close the the place that they first settled (Lefevre and Curtis, 1910; Evermann and Clark, 1917; Coker et al., 1921; Ellis, 1931). The only significant movements were believed to be associated with the rapid migrations possible in the parasitic stage upon fish, and that otherwise locomotion played a minor part in the distribution of mussels (Coker et al., 1921; Pennak, 1953). In transplant studies, Isely (1914) found very little evidence of migration in various stream species. While he noted that lighter-shelled species were considerably more active than heavier-shelled mussels (also noted by Lefevre and Curtis, 1910), he also believed that they probably would not migrate far from the point where they dropped from the fish.

Recent thought in relation to total movement over a lifespan is mixed in conclusion. In stream populations, Strayer (1981) found only 2.2% of mussels associated with trails in the substrate that would suggest recent movements. He thought most mussels would not move about much. Salmon and Green (1983) argued, however, that by nature of the instability of the lotic environment, mussels would be expected to move about to some degree in response to various stimuli such as raising or falling water levels. Frequent reports of considerable fluctuations in community composition and population densities suggested to Kat (1982) a considerable degree of mobility of adult mussels. Kat himself observed high rates of migration of Elliptio complanata in stream environments and thought it conceivable that movements of mussels whose fish hosts had small home ranges might be greater than the larval dispersal distance upon the fish. Ghent et al. (1978) observed random horizontal movements of mussels in Lake Bernard (Canada), but that relatively large proportions of time (up to 30%) were spent engaged in such movements.

An undisputed claim of most observers is that juvenile mussels are much more active than older mussels (Evermann and Clark, 1917; Coker et al., 1921; Kat, 1982), a phenomenon believed to be related to the active searching by juveniles for suitable habitats after dropping from the host fishes (Lefevre and Curtis, 1910; Isely, 1911; Howard, 1922).

Freshwater mussels may respond to various stimuli. Movements may be initiated by pressure, temperature or light (Coker et al., 1921). Bright light for example stimulates movement to deeper waters away from the shallows and their associated hazards (Fuller, 1974). Flooding induces a movement to shallow waters, while receding waters stimulates withdrawal of mussels to deeper waters (Coker et al., 1921; Björk, 1962; Tudorancea, 1972; Fuller, 1974; Kenmuir, 1980; Salmon and Green, 1983). Coker et al. (1921) suggested the stimulus to move to shore during floods was an accommodation to light conditions as floodwaters are invariably turbid. At other times, mussels may exhibit a positive geotaxis (Matteson, 1948) and actively seek and find their optimum depth when they are experimentally displaced (Isely, 1914; Matteson, 1948). Imlay (1972) however, observed little response of displaced mussels when the displacement occurred either in the wrong season or was artificial. Siltation is one such unnatural event and rather than mussels not responding quickly enough to its smothering effects (Ellis, 1931), Imlay believed the unnatural coverings (that may occur at an atypical season) probably do not trigger the natural response mechanism of mussels for digging themselves out. (The implications of Imlay's study invoke a cautionary note to studies and experiments whose results rely upon the responses of mussels following artificial displacement).

Some environments are apparently move conducive to activity in mussels than others. Evermann and Clark (1917) observed for example that mussels were generally quiescent in deeper lake waters. Margaritifera margaritifera was found to be more active over sandy sediments in streams (Björk, 1962). Brönmark and Malmqvist (1982) believed that large sediment particles would probably have a restrictive influence on mussel locomotion. Less movement was observed by Elliptio complanata on muddy substrates than sandy ones in streams, as these sediments are not exposed to the currents and mussels must therefore rely on their own efforts to move (Kat, 1982). Other mussels may affect the migratory behaviour of individuals, and in displaced mussels at artificially high densities in comparison to lower densities, Kat (1982) observed most movement of and distances travelled by individuals.

During winter in temperate regions, freshwater mussels generally become inactive and bury deeper into the sediments (Isely, 1914; Evermann and Clark, 1917; Matteson, 1948; Pennak, 1953; Stansbery, 1961; Roscoe and Redelings, 1964; Walker, 1981b). While Evermann and Clark (1917) and Coker et al. (1921) observed migrations to deeper waters prior to winter, van der Schalie (1938) and Pennak (1953) claimed these responses were related to receding water levels during autumn rather than decreasing temperatures. Lewandowski and Stanczykowska (1975), however, observed migration of lake Unio tumidus populations into shallow waters with the approach of summer.

Other seasonal patterns of movements, mainly in depth distribution, have been noted by various authors. Seasonal, but unspecified movements of Anodonta spp. have been noted by Salmon and Green (1983). Regular shoreward migrations by spawning mussels of various species have been observed (Ellis, 1931; Yokley, 1972; Brönmark and Malmqvist, 1982). Such reproductive behaviour is believed to be correlated with the increased chances of parasitising host fishes, also noted to be more active in the shallows at these times (Ellis, 1931; Yokley, 1972). Tudorancea (1972) observed both active autumnal migrations associated with reproduction and spring feeding migrations in populations of Anodonta piscinalis in the Crapina-Jijila marshes.

A final and important consideration in the literature relating to the study of the population dynamics of freshwater mussels, is the recent interest in their value as indicators of environmental impact and of past and present environments.

On the basis that unionids can be accurately aged, Tevesz and Carter (1980a) reviewed the potential ways in which unionids may be usefully employed to monitor environmental change. Baseline information available on population dynamics (e.g. age structures, mortality rates) could be used to compare new information with, and to test for, possible perturbations in the environment brought about by pollution or other anthropogenic activities. If the typical period of the year of mortality for individuals of a population could be ascertained for example, it might be possible to tell whether "kills" were natural or man-induced.

Tevesz and Carter (1980a) cited Negus' (1966) study in which she showed the close correlation between increasing growth rates of Anodonta anatina as reflected by relative widths between annuli, and water temperatures. Such information might make unionaceans useful as relative palaeothermometers (ibid) or as indicators of thermal pollution (McCuaig and Green, 1983). Similar information is available for marine bivalves, and Jones (1983) suggested such records may prove useful in monitoring environmental disturbances (natural or man-made) or in interpreting past and present climates at sites uninhabited by man.

Lampsilis radiata and Anodonta grandis are unionids with wide geographical distributions in North America and about which much ecological information is known including growth rate differences related to natural environmental variability. As such, McCuaig and Green (1983) considered these unionids valuable research organisms, and showed how growth rate parameters derived from aging studies could be used to test hypotheses about changes in the environment such as long-term temperature changes, or presence of pollutants.

APPENDIX 4

REPRODUCTION

A4.1 Gonadal development and structure of the breeding population

In the Unionidae for which much information is available, the sexes are separate; some species are occasionally or simultaneously (i.e. consistently) hermaphroditic (Pennak, 1953). Among the hyriids and mutelids of the southern hemisphere, there is no indication from the available literature to suggest other than the dioecious condition.

Apart from limited dimorphism in shell shape and size amongst freshwater mussel taxa (Appendices 1 and 3 respectively), the sex is most precisely determined by the nature of the gonads which are imbedded in the upper part of the foot, and which ramify much of the visceral mass. In addition, the sex of most individuals can be determined by morphology of the marsupial demibranchs i.e. one or both pairs of gills of the female that are modified as marsupia in which the developing young are incubated and mature (Heard, 1975). In the hyriid Velesunio ambiguus for example, Walker (1981b) distinguished males and females by the anatomy of the innermost marsupial gill. In non-gravid females, the marsupium was recognisable as a slightly thickened portion of the gill whilst in gravid females, was noticeably extended and swollen with developing larvae. The inner gills of males resembled the outer gills of both males and females. Walker (1981b), however, could not distinguish females from males by this method. For dioecious species in which a gravid condition for the female is the norm, the sexes may be easily distinguished for much of the time by gill morphology alone (van der Schalie and van der Schalie, 1963). Kat (1983d) states of other species, nevertheless, that microscopic examination of the demibranchs may be needed to discriminate non-breeding males from females.

Kat (1983d) in a study of hermaphroditism among unionids, was impressed with the stability of the dioecious system of reproduction. Not only is the occurrence of simultaneous hermaphroditism infrequent (the predominant mode of reproduction for only 6 out of 220 North American species), but among the proportion of predominately dioecious species in which hermaphroditic individuals are encountered (30 out of 101 examined) such incidence is low (Kat, 1983d).

For unionaceans that reproduce predominately as hermaphrodites as well as separate sexes, are reported species for which ratios of males, females and hermaphrodites in various populations vary considerably. Thus, regional differences have been recorded of the sexual composition of a simultaneous hermaphrodite, Anodonta imbecilis in North America (van der Schalie, 1970; Heard, 1975); the ratios of males, females and hermaphrodites of Anodonta cygnea in Britain are constant for, but vary between populations (Bloomer, 1930, 1934, 1935, 1939); in Italy A. cygnea is reported to be dioecious (Giusti et al., 1975); and whilst Margaritifera margaritifera is normally dioecious throughout its holarctic range (e.g. Smith, 1979; Bauer, 1979; Young and Williams, 1984a), a North American population was found by Heard (1970) to be hermaphroditic. Heard (1975) found a variety of sexual strategies among several anodontine species studied over North

America, showing that hermaphroditism was not phylogenetically determined. Nor have different reproductive modes been found to be consistently related to habitat type per se (Heard, 1975; Kat, 1983d). Both van der Schalie (1970) and Heard (1975), although recognising that hermaphroditism had selective value under particular environmental conditions, could not demonstrate any environmental factor that indicated a causal relation with sexuality. Dudgeon and Morton (1983) thought it appropriate to consider the sexual strategies of these bivalves as a balance between the tendency for hermaphroditism and sexual separation. They cited the study of Coe (1941) who believed the sex differentiating mechanism of bivalve molluscs to be so delicately balanced between the two sexual tendencies, that relatively slight differences in environmental conditions could be potent in determining which of the two aspects would be realised.

The study of Anodonta imbecilis by Kat (1983d) has been the first to propose hypotheses to account for the selective value of different reproductive modes in freshwater mussels from a variety of habitats and population densities. Kat believed dense populations in reservoirs and sparse populations in streams for example, were subject to fundamentally different sexual selection pressures acting on ratios of allocation to male and female gonadal products. Several hypotheses to account for the considerable variability in the ratio of male:female gametes produced by A. imbecilis were presented, based on population density, nutrient and sperm availability, mode of fertilisation and limitation of brood space.

Among populations of predominately dioecious species, Kat (1983d) found occasional hermaphroditism to be generally associated with the presence of digenean trematodes within the gonads. Kat suggested that these parasites could secondarily or directly alter levels of sex determining hormones in the infected individuals. However, trematode parasitism was not implicated as the cause of occasional hermaphroditism by either van der Schalie (1970) and Heard (1975) for other populations and species investigated. Developmental errors in sexual determination though, have also been implicated as the cause of such hermaphroditism (Coe, 1943; van der Schalie, 1970; Kat, 1983d).

Occasional hermaphroditism and variable sex compositions among freshwater mussel populations have been linked to possible forms of sex reversal. Amongst the evidence of this is cited seasonal and age specific variations in sex ratios, and exceptions to the normal correspondence of visceral sex and marsupial demibranch morphology. Apart from occasional and simultaneous hermaphroditism, Coe (1943) recognised a further three types of sexuality less common to bivalves: (a) consecutive sexuality, in which there is a single change in the functional sexuality of the individual (usually male to female); (b) rhythmical consecutive sexuality, where the initial phase is male, followed by a series of alternating female and male phases throughout life; and (c) alternative sexuality, in which adults function seasonally as separate sexes. In an extensive study of hermaphroditism in British populations of Anodonta cygnea, Bloomer (1934, 1935, 1939) found that the morphology of the outer, marsupial demibranch did not always correlate with visceral sex amongst various populations, suggestive that individuals changed sex at least seasonally (alternative sexuality). Hermaphroditism was not confined to any particular age of animal in some populations (Bloomer, 1935) but in others, the gonads functioned as males at first maturity (consecutive sexuality) (Bloomer, 1939).

Tudorancea (1969, 1972) found age and seasonal variations in the sex structure of Unio tumidus and U. pictorum in the Crapina marsh of Rumania. Males predominated in the youngest and oldest age divisions, while females were most common at intermediate ages. During the breeding season females were the dominant sex while for the rest of the time, males predominated. Both phenomena were suggestive to Tudorancea of consecutive and rhythemical consecutive sexuality respectively.

For populations of Anodonta woodiana in Plover Cove, Hong Kong (Dudgeon and Morton, 1983) and Margaritifera margaritifera in streams of Scotland (Young and Williams, 1984a) individuals were found to be either male or female throughout the size range of the species with no suggestion of changing sex with age. Similarly Heard (1975) concluded that sex reversal was absent from several North American populations of Anodonta, noting that visceral sex (or the dominant gonad of hermaphrodites) consistently correlated with morphology of the marsupial demibranchs, regardless of season and age of mussels. In a North American population of M. margaritifera, however, Smith (1979) noted a slight male over female dominance in the youngest age classes. However, as males matured earlier than females, no protandric tendencies were suspected.

Kat (1983d), nevertheless, found the primary gonads of two normally dioecious unionids and one simultaneous hermaphrodite to be spematogenic. He believed sex determination among dioecious species to be controlled by hormonal levels, with juveniles tending toward maleness due to low levels of sex-determining hormones; true males continued with such low levels while the female condition resulted from high levels. Kat attributed the higher variability in male:female ratios of gonadal tissue amongst female hermaphrodites to the higher hormonal levels hypothesised to determine the female condition. The observed early-maleness in above-mentioned studies therefore (Bloomer, 1939; Tudorancea, 1969, 1972) accord with Kat's (1983d) hypothesis of protandry amongst unionids. In bivalves generally, Coe (1943) observed in normally dioecious species that occasional hermaphroditism commonly occurred in the young at the first reproductive season, and that in cases of alternative sexuality, the male phase was often indicative of immaturity. Protandry of the type proposed by Kat (1983d) for at least the unionids he studied, would place these species in the category of consecutive sexuality.

In considering sex ratios of all individuals from a population averaged over time, the literature shows that there may be predominance of males (van der Schalie and van der Schalie, 1963; Tudorancea, 1969; Yokley, 1972; Walker, 1981b; Zale and Neves, 1982a) or females (Boycott, 1936; Smith, 1979; Kenmuir, 1980; Dudgeon and Morton, 1981; Young and Williams, 1984a). However, no author has provided evidence to show that sex ratios vary significantly from 1:1 in any population of freshwater mussels studied.

Age at sexual maturity for freshwater mussels is invariabily reported as either the earliest age at which the gonads mature or at which gravid females are found. (Presumably the lag between gonadal maturation and spawning for most species, nevertheless, is no more than one breeding season.) Haukioja and Hakala (1978b), however, reported age at maturity as the time at which half the females had glochidia in the gills for the first time. Table A4.1 summarises the available literature concerning age at maturity. From these studies some generalisations can be made. Amongst temperate species investigated, thicker-shelled and slower growing species (e.g. Quadrula spp., Pleurobema) are slower to mature than the thinner-shelled and faster growing species (e.g. anodontines and lampsilines). Tropical species (Seshaiya, 1969; Kenmuir, 1980; Dudgeon and Morton, 1983) by comparison mature at a very early age reflecting presumably, the equitable and higher water temperatures sustained for gonadal maturation and rapid shell growth. Conversely, Margaritifera margaritifera, is the slowest freshwater mussel known to reach maturity reflecting presumably the circumboreal range of this animal and consequent slow development and growth.

Gametogenesis in unionaceans from temperature climates is typically continuous throughout the year, though brief periods of inactivity may occur immediately after spawning, while the process usually proceeds at a slower rate over the winter (Matteson, 1948; van der Schalie and van der Schalie, 1963; Stein, 1969; Yokley, 1972; Giusti et al., 1975; Heard, 1975; Smith, 1979; Zale and Neves, 1982a; Jones and Simpson, in prep.) While gametogenesis is most intense during the summer months, spawning, a more or less short and synchronised event in temperate species, occurs during the warmer months ranging between early spring and early autumn. Water temperature is generally assumed to be the cue responsible for initiating spawning.

In tropical climates, gametogenesis has been studied in Indian (Lomte and Nagabhushanam, 1969; Ghosh and Ghose, 1972; Nagabhushanam and Lohgaonker, 1978) and east Asian (Dudgeon and Morton, 1983) unionids. While spermatogensis is reportedly continuous throughout the year, inactive phases in oogenesis as occur in temperate species have also been reported, and this is related to the cooler winter temperatures. Spawning in Anodonta woodiana occurs in the spring (Dudgeon and Morton, 1983) but for the Indian unionids studied, nevertheless, spawning for individual species is protracted, extending over most of the warmer months.

The period over which sperm are present in the testes, is invariably reported to be much broader than that over which ripe ova are present in the ovaries. This has been interpreted as meaning that sperm are released over a timespan that overlaps ovulation in females, thus ensuring successful fertilisation (e.g. Matteson, 1948; Dudgeon and Morton, 1983).

A product of atypical spermatogenesis (i.e. where typical meiotic stages are absent) in bivalves are multinucleate structures termed sperm morulae. They are reportedly widespread in unionids (van der Schalie and Locke, 1941; Bloomer, 1946; Smith, 1979) and hyriids (Heard, 1975; Jones and Simpson, in prep.) and are seasonal in appearance, being present in male follicles prior to spermiogenesis. Coe and Turner (1938) believed most sperm morulae underwent cytolysis prior to the period of typical spermatogenesis. Heard (1975), however, contested this, and provided some evidence to show that the

Table A4.1 Age at gonadal maturity and/or first gravidity reported for the species of freshwater mussels studied worldwide to date.

SPECIES	Region	Authority	Age at gonadal maturity	Age at first gravidity
Margaritifera margaritifera	Scotland	Young and Williams (1984a)	-	12
M. margaritifera	Sweden	Bjork (1962)	20	-
M. margaritifera	U.S.A.	Smith (1979)	7 (male)	-
North American unionids	"	Pennak (1953)	1-8	-
Anodonta grandis	U.S.A.	van der Schalie and Locke (1941)	2	-
A. imbecilis	"	Stansbery (1967)	2	-
A. imbecilis	"	Coker *et al*. (1921)	2	-
Anodonta spp.	"	Heard (1975)	-	4-6
A. piscinalis	Finland	Haukioja and Hakala (1978b)	-	2-3
A. woodiana	Hong Kong	Dudgeon and Morton (1983)	1	-
Villosa nebulosa	U.S.A.	Zale and Neves (1982a)	3	-
V. vanuxemi	"	"	"	-
Medionidus conradicus	"	"	"	-
Lampsilis fasciola	"	"	"	-
L. luteola	"	Coker *et al*. (1921)	2	-
L. (Proptera) laevissima	"	"	1	-
Actinonaias ellipsiformis	"	van der Schalie and van der Schalie (1963)	3	-
Amblema plicata	"	Stein (1969)	4	-
Pleurobema cordatum	"	Yokley (1972)	<4	-
P. cordatum	"	Scruggs (1960)	6	-
Plagiola donaciformis	"	Coker *et al*. (1921)	2	-
Quadrula spp.	"	"	4-8	-
Lamellidens spp.	India	Seshaiya (1969)	2	-
Unio tumidus	Rumania	Tudorancea (1969)	3-4	3-4
Caelatura mossambicensis	Zimbabwe	Kenmuir (1980)	-	1
Velesunio ambiguus	Australia	Walker (1981b)	-	3-4
Alathyria jacksoni	"	"	-	3-4
Aspatharia wahlbergi	Zimbabwe	Kenmuir (1980)	-	2-3
Mutela dubia	"	"	-	1-2

structures completed metamorphosis to provide spermatozoa.

A final factor in relation to gonadal development, is the effect upon the reproductive potential of freshwater mussels of parasitism by digenean trematodes. Invariably, their presence in the viscera is reported to result in partial or complete castration. Kat (1983d) reported up to 85% infection of Lampilis radiata by trematodes in some of the North American populations he studied. Over 30% of individuals of Villosa vanuxemi examined by Zale and Neves (1982a) were similarly infected, and many of the older mussels were found to be rendered functionally sterile. van der Schalie and van der Schalie (1963) reported lower infection rates in Actinonaias ellipsiformis (<2%) while in the hyriid Velesunio ambiquus, parasitism is apparently uncommon (<1%) (Angel, 1961)

Noting that the oldest mussels were reproductively active, displaying normal gametogenesis and gravidity, Scruggs (1960), Stansbery (1967), Heard (1975) and Kenmuir (1980) concluded that no post-reproductive (cessation of reproduction) or senility phase (decline in reproductive activity) occurred in the respective populations of freshwater mussels studied. In studies of aging in European populations of Anodonta cygnea and Unio pictorum, however, Haranghy et al. (1964) noted that variability in the ovary increased with age, while no changes were noted in the gonads of males. In the ovaries of some females, large numbers of mature oocytes were found; in others, mature oocytes were hardly observed; while in others again the ovaries were disorganised and atrophied. Thus while the processes of spermatogenesis and production of apparently viable oocytes continued even in quite old mussels, Haranghy et al. (1964) concluded that for the most part, a post-reproductional period could be assumed for the two unionids.

A4.2 Larval production

The unfertilised eggs of freshwater mussels, having found their way from the ovaries to the water tubes of the marsupial demibranchs, are fertilised by sperm taken in through the inhalent siphon. While the eggs of most species are fertilised more or less at the one time, spawning in some unionids, e.g. Unio spp. (Lillie, 1895; Tudorancea, 1969), Pleurobema cordatum (Scruggs, 1960; Yokley, 1972), is intermittent and all stages of development may be found in the marsupia of individuals at a given time. Evermann and Clark (1917) noted that gravid females were fewer than expected in lake populations of freshwater mussels compared to those from neighbouring rivers, as more opportunities of fertilisation of ova were available in flowing waters. Other studies, nevertheless, report that unfertilised eggs are rarely found in populations of mussels (Coker et al., 1921; Matteson, 1955; Wood, 1974a; Smith, 1976). The number of developing larvae brooded in the marsupia has been estimated to range generally from between several thousand and 3 million, depending upon the species and size of the animal (Coker et al., 1921; Pennak, 1953; Kenmuir, 1980). Gestant females from Scottish populations of Margaritifera margaritifera, however, can harbour from between 3-4 million larvae (Young and Williams, 1984a), while individually up to 17 million young may be produced.

Amongst unionids and margaritiferids, the marsupia may comprise all four gills, the two outer gills, or only special parts of the outer gills, depending upon the species (exobranchiate condition, Lefevre and Curtis, 1912), while they are contained in the inner gills only (endobranchiate condition) amongst the southern hyriids and mutelaceans.

In relation to larval development, Lillie (1895) gave a detailed account of the anatomy and morphology of developing and mature glochidia of Anodonta and Unio. The study of Matteson (1948) and the more detailed work of Wood (1974a) corroborated Lillie's observations for Elliptio and Anodonta species respectively. Otherwise, numerous workers have studied the seasonal and developmental continuum of embryogenesis in only a cursory manner for the purposes of determining the period of fertilisation, the period and duration of incubation, and number of annual broods of respective mussel populations (e.g. Scruggs, 1960; Yokley, 1972; Heard, 1975; Smith, 1976; Trdan, 1981; Kenmuir, 1981a; Zale and Neves, 1982a).

The duration of larval development, from fertilisation to glochidial maturation is relatively constant amongst species of freshwater mussels, as embryonic development occurs chiefly during the warmer months. Studies have shown in fact, the dependence of embryonic development upon temperature (Matteson, 1948; Yokley, 1972; Wood, 1974a). Development during spring and summer is very rapid (Lefevre and Curtis, 1912), maturation for example being completed in 2 weeks in Quadrula spp. (Lefevre and Curtis, 1912), 4 weeks in Elliptio complanata (Matteson, 1948) and from 16-45 days in Margaritifera margaritifera (Harms, 1909; Smith, 1976). Maturation during late summer and autumn is slower, for example 8 weeks of Anodonta (Wood, 1974a) 7-8 weeks for the four lampsilines studied by Zale and Neves (1982a) and 9 weeks for the hyriid Cucumerunio novaehollandiae (Jones and Simpson, in prep.). Amongst tropical species studied, maturation is completed in 4 weeks in Anodonta woodiana (Dudgeon and Morton, 1983) and 3-5 weeks for species from Lake Kariba (Kenmuir, 1981b). Even in tropical species, maturation during the cooler winter months is reportedly delayed (Kenmuir, 1981b).

In temperate regions of North America (Lefevre and Curtis, 1912; Coker et al., 1921; Pennak, 1953; Clarke and Berg, 1959; Clarke, 1973; Kat, 1984) and Europe (Harms, 1909; Negus, 1966; Tudorancea, 1969, 1972; Wood, 1974b; Haukioja and Hakala, 1978b; Dartnall and Walkey, 1979), general breeding patterns are well known. Two broad reproductive patterns are recognised according to the length of time over which larvae are brooded in the female marsupia. Long-term or bradytictic breeders, spawn during mid-late summer. The glochidia develop during autumn and early winter, but are not released from the marsupia until the following spring and early summer. Short-term or tachytictic breeders, spawn in early spring and release glochida in late summer and early autumn. The anodontine and lampsiline unionids generally belong to the first category of breeders while amblemine unionids, and margaritiferids belong to the second category.

Among the tachytictic breeders, Unio spp. (Negus, 1966; Tudorancea, 1969) and Pleurobema cordatum (Scruggs, 1960; Yokley, 1972) bear all stages of larval development in the marsupia during summer, and as embryogenesis proceeds so rapidly, multiple release of glochidia is possible each year.

Of the tropical species of freshwater mussel, Seshaiya (1969) found glochidia in the marsupia of Lamellidens during July and August, and again during December, indicating annual production of at least two broods of larvae at extremes of season. The African mutelids Mutela bourguignati (Fryer, 1961) and M. dubia, and unionid, Caelatura mossambicensis (Kenmuir, 1981a) breed throughout the year in tropical Africa, spawning and brooding repetitively (Kenmuir, 1981b). Aspatharia wahlbergi, however, in Lake Kariba breeds seasonally, Kenmuir (1981a) finding gravid individuals only during the summer months. Kenmuir (1981b) attributed repetitive spawning to the warmer environment of tropical waters that presumably stimulated spawning and breeding activity in mussels. Winter lulls in the breeding intensity of repetitive spawners were also noted by Kenmuir (1981b). Kenmuir (1981a) suggested that flowing water may be needed to stimulate breeding in A. wahlbergi, a known riverine mussel. Dudgeon and Morton (1983) reported seasonal breeding of Anodonta woodiana in Plover Cove, Hong Kong, with late spring spawning followed by glochidial release until mid summer. Dudgeon and Morton suggested that cooler autumn and winter temperatures might slow glochidial development in Anodonta from temperate regions, thereby contributing to the bradytictic condition (i.e. brooding of glocidia overwinter). The short incubation period in A. woodiana (one month) was believed to result from much higher winter temperatures sustained in Plover Cove.

Seasonal variations of glochidial release amongst the bradytictic Anodonta over a broad geographical range - Britain (Negus, 1966; Dartnall and Walkey, 1979), Italy (Giusti et al., 1975) and North America (Heard, 1975; Wiles, 1975), were attributed in part by Giusti et al. (1975) to result from temperature variations that may stimulate differential release over a wide latitudinal gradient. Giusti et al. (1975) stressed the importance of determining the exact period of appearance of glochidia upon fish in order to draw conclusions concerning the duration of reproductive cycles. Monitoring glochidial release by periodic examination of host fishes and by drift in fact, is assuming increasing importance in evaluating seasonal breeding cycles of unionaceans (Giusti et al. 1975; Wiles, 1975; Dartnall and Walkey, 1979; Porter and Horn, 1980; Trdan, 1981; Zale and Neves, 1982a; Dudgeon and Morton, 1983; Young and Williams, 1984a).

Of the hyriids of temperate Australasia, distinct seasonality in breeding cycles has been reported only for Cucumerunio novaehollandiae (Jones and Simpson, in prep.). This species breeds in autumn in southeastern Australia. Otherwise, breeding may be more protracted. The glochidia of Hyridella drapeta (Atkins, 1979) for example were observed on fish throughout the year. Except for the months when no fish were available for examination (between May and September), glochidia of Velesunio ambiguus were always present on their fish hosts (Hiscock, 1951). However, peak infections on the hosts of H. drapeta were noted during spring (Atkins, 1979), while inspection of the marsupia of V. ambiguus by Walker (1981b) showed two peaks in glochidial production, one in spring and another in late summer and early autumn. Alathyria jacksoni showed similar patterns to V. ambiguus in larval production (Walker, 1981b). McMichael and Hiscock (1958) suggested breeding of Hyridella was seasonal in southeastern Australia, occurring from spring through to summer. Jones and Simpson (in prep.) substantiated this claim for three sympatric Hyridella species, further adding that a series of synchronised, repetitive breeding cycles were likely for H. australis during the warmer months. Percival (1931) found 'ripe' glochidia in the marsupia of H. menziesi from New Zealand, from the end of November to the end of January.

The Australasian hyriids therefore, appear to have broader breeding periods than counterparts in northern temperate regions, and all have the potential to produce more than one larval brood per year. This may possibly reflect the milder and more equitable climates of the southern temperate latitudes. Latitudinal variations have been previously implicated (e.g. Kenmuir, 1981a,b; Dudgeon and Morton, 1983) as having some effect on reproductive patterns of freshwater mussel groups.

Apart from the great variety recorded in the periods of gametogenesis, glochidial incubation and release among the different species of freshwater mussels (Dudgeon and Morton, 1983) considerable temporal and spatial variations in breeding patterns have also been reported at the intraspecific level. Connor (1909) and Porter and Horn (1980) observed that the time of breeding of individuals of the same species from the same location varied from season to season, attributable by Connor (1909) at least, to climatic variation. Over a broad geographical range, Margaritifera margaritifera has been reported to produce one (Smith, 1976; Young and Williams, 1984a) or two (Wood, 1974a; early North American studies cited by Smith, 1976) broods of larvae each breeding season, while Bjork (1962) noted regional differences in glochidial release in Sweden. Haukioja and Hakala (1978b) also noted variation in reproductive timing among Finnish populations of Anodonta piscinalis. North American populations of A. imbecilis may complete one or several cycles throughout the breeding season. Presumably climatic differences account in part for these disparities observed in breeding patterns between the various localities. On a more regional scale however, A. peggyae in Florida may complete two cycles in the year in lakes or only one in streams (Heard, 1975). In Zimbabwe, differences in breeding patterns of freshwater mussels between Lake Kariba and Lake McIllwaine were attributed by Kenmuir (1981b) to temperature variations. Within the same stream, the differences in water temperatures between upstream and downstream sites may result in variations in timing of respective breeding cycles (Walker, 1981b; Young and Williams, 1984a; Jones and Simpson, in prep.). Even within the same lake, Porter and Horn (1980) recorded unexplained variations in the time of breeding of mussels between different zones, in the same season.

Heard (1975), recording two sympatric and congeneric Anodonta that had completed one and two annual breeding cycles respectively, concluded that breeding cycles might not be influenced entirely by conspicuous environmental factors such as water temperature and presence or absence of current. In relation to glochidial release at least, a number of workers have drawn attention to the correspondence of time of release of glochidia and the habits and activities of the host fishes; or among sympatric species different periods of release may have resulted from competitive interactions amongst each other for a limited number of hosts (e.g. Kat, 1984). Fish relations thus, are other factors that may influence the seasonal breeding patterns of freshwater mussels.

A further factor that has received little attention, is the effect of adverse environmental conditions (other than low water temperatures) upon the reproductive cycle of freshwater mussels. The lack of consideration is even more surprising given the known sensitives of gravid females (see below) and that potentially stressful environmental conditions (e.g. high water temperatures, periods of high or low discharge, turbidity) may in certain environments be highly seasonal.

Numerous authors have noted that gravid freshwater mussels are sensitive to sudden changes in water temperature, rough handling, toxic substances, starvation and especially oxygen deficiency and imperfect aeration of the water, responding under these conditions by aborting eggs and larvae (e.g. Lefevre and Curtis, 1912; Coker et al., 1921; Allen, 1921; Matteson, 1948, 1955; Hiscock, 1951; Tudorancea, 1969; Yokley, 1972; Young and Williams, 1984a).

In relation to low dissolved oxygen concentration, resultant abortion is assumed to occur in order that the gills may be more effectively employed for respiration. Lefevre and Curtis (1912) noted a correlation between the number and portion of gills used as marsupia and susceptibility to abortion. Species using all four gills (e.g. Quadrula) were notoriously sensitive to disturbances and imperfect aeration of the holding water; species of Anodonta, however, using only two gills and possessing other structural modifications of the gills to enhance water circulation, rarely aborted under these conditions. Gravid Lampsilis ventricosa were shown by Matteson (1955) to be more sensitive than nongravid individuals to anoxia. He determined a mean threshold for the gravid mussels at which abortion occurred at approximately 1.8 mg/l dissolved oxygen higher than nongravid ones. Allen (1921) cited studies that showed that the volume of water siphoned in the gravid condition was much less than in the nongravid condition. Allen showed that the feeding processes of freshwater mussels were similarly hindered in gravid females. He indicated that the modifications made in the marsupia were adaptations for water circulation about the eggs and larvae, sufficient for the aeration of these but not of the mother. Thus the gravid gills are unable to meet all the demands (brooding, feeding and respiration) made upon them (Allen, 1921).

In relation to field conditions, Matteson (1955) observed abortion in gravid Lampsilis ventricosa in spring, in unseasonally warm, shallow waters.

A4.3 Glochidial release and parasitism

Kat (1984) recently presented a thorough review of parasitism in unionacean bivalves mainly as it applies to the North American and European fauna. A survey of glochidial hosts of the North American unionaceans as well as a review on the subject had earlier been collated by Fuller (1974). Walker (1981b) also presented a synopsis of the subject and completed studies appropriate to hyriid unionaceans. While no better review of the literature is possible at this stage, the following survey provides an adequate background for the studies presented here.

The mature glochidium, free from the vitelline membrane is a bivalved shell which, depending upon the group, may or may not bear teeth or hooks at the tip of each valve. A thin tissue of mantle cells lines the inner surface of the valves and some of these cells possess fine sensory hair-like projections. The two valves are cross-banded by a single adductor muscle and in some groups enclose a long and sticky larval thread.

The glochidia of Australian hyriids are uniformly subtriangular and toothed but variation in size and shape between species is not as slight as originally thought by McMichael and Hiscock (1958), Atkins (1979) and Walker (1981b). Jones and Simpson (in prep.) noted that the glochidia of Cucumerunio novaehollandiae and Hyridella australis are much smaller than those of species previously described, and those of the former species possess a unique shell sculpture. With the addition of H. depressa, all three species also bear either a pair of hooks on each valve (C. novaehollandiae and H. australis) or a single bifurcated hook (H. depressa). The glochidia of other Australian species described, bear single, individual hooks upon each valve. Larval threads have been reported on the glochidia of H. drapeta (Atkins, 1979) and Velesunio ambiguus (Hiscock, 1951; Walker, 1981b). Walker (1981b) reported that the glochidial shell margin of V. ambiguus is marked by fine ridges, thought to assist in attaining a firm hold on host tissue. With respect to the genus Velesunio at least, Walker (pers. comm.) has found no observable differences in morphology and morphometry between species.

Studies of glochidia have shown morphology and morphometry to be of useful taxonomic importance. Glochidial morphology has been used to distinguish broad groups of freshwater mussels (Parodiz and Bonetto, 1963) while morphometry has been used to distinguish congenerics and even conspecifics (Wiles, 1975; Rand and Wiles, 1975). Rand and Wiles (1975) noted, however, that identification of glochidia to species within a genus was still a formidable problem wherever congenerics occurred. Variation in size (Tudorancea, 1972; Walker, 1981b) and structure (Porter and Horn, 1980) observed between glochidia from the same parent moreover, does not make the task of separating morphologically similar larvae of congenerics any easier. McMichael and Hiscock (1958) considered that the larval stages of Australian hyriids would be of limited value taxonomically. However, the larvae of Hyridella in southeastern Australia differ sufficiently (Jones and Simpson, in prep.) to suggest that differentiation of species within the genus may be a relatively simple procedure.

While all unionaceans with known life histories exhibit a period of obligate parasitism on a vertebrate host, Anodonta imbecilis at least, has been reported to complete development to the juvenile stage in the marsupial demibranchs (Howard, 1914) or to be discharged by the mother to parasitise fish in the usual manner (Heard, 1975; Stern and Felder, 1978). Walker (1981b) cites an unconfirmed report that an isolated population of Velesunio ambiguus could also apparently pass through metamorphosis in the parental marsupia.

Water temperature may be the direct stimulus required for release of glochidia from the parent, a number of workers having recorded diurnal, day to day, and seasonal fluctuations in numbers of planktonic or parasited glochidia as a function of temperature variation (Tudorancea, 1972; Atkins, 1979; Dartnall and Walkey, 1979; Zale and Neves, 1982a; Dudgeon and Morton, 1983; Young and Williams, 1984a). Fish habits, have assumed increasing importance in determining the seasonal timing and duration of glochidial release. While Coker et al. (1921) and Young and Williams (1984a) have drawn attention to the correspondence of host fish activity and temperature cycles, release of glochidia has been shown to coincide with host fish migrations (Davenport and Warmuth, 1965), breeding activities of the host fishes (Yokley, 1972; Zale and Neves, 1982a, b; Kat, 1984) and the seasonal presence of the fishes over mussel beds (Zale and Neves, 1982a, b). Seasonal differences in timing and duration of glochidial release amongst sympatric species are thought by some authors to be indicative of selection to avoid competition for fish hosts (Stern and Felder, 1978; Trdan and Hoeh, 1982; Dudgeon and Morton, 1983; Kat, 1984).

While the glochidia of lampsiline unionids are discharged into the water through minute pores in the marsupial gills, other unionaceans discharge glochidia through the exhalent siphon. Various behavioural mechanisms and structural modifications are used by some lampsilines by which females enhance successful attachment of glochidia upon the hosts. Mimicry of the mantle flaps is used by these species to imitate the appearance and pulsating actions of prey items of fish; disturbance of the structures by predatory host fishes results in the release of glochidia by the female (Evermann and Clark, 1917; Harman, 1970; Clarke, 1973; Kraemer, 1979; Zale and Neves, 1982b). Otherwise, glochidial attachment to the host may be enhanced by the suspension of glochidia in a network of mucous threads (Matteson, 1948, 1955; Yokley, 1972; Atkins, 1979). Host fishes may even be attracted to these suspended particles as food items (Yokley, 1972; Dartnall and Walkey, 1979). Other devices are available for assisting glochidial attachment: glochidia may descend through the water in an opened condition, thus slowing downward movement (Matteson, 1955); the larval thread itself may act as a dragline or by its long and sticky nature aid in direct attachment (Wood, 1974b).

The refrigerated glochidia of Anodonta grandis remained viable for approximately 8 months according to Trdan and Hoeh (1982). Under normal field situations, however, glochidia may survive up to 14 days in the plankton (Pennak, 1953; Telda and Fernando, 1969; Fuller, 1974). The viability of the glochidia of Alathyria jacksoni and Velesunio ambiguus spanned from 50% of the glochidia dead after 5 days at 25°C, to 15 days at 12°C (Walker, 1981b).

Although the glochidia of a number of unionacean species have been shown to parasitise and successfully metamorphose from tadpoles (Seshaiya, 1941; Walker, 1981b); these species normally parasitise fish. The only known host of Simpsoniconcha ambiqua in North America is the salamander, Necturus maculosus. This is the only documented exception to the rule that parasitism and subsequent glochidial metamorphosis is normally completed upon a fish host.

One or more species of fish are host to the unionacean glochidium. Strict species specificity in which the parasite is limited to only one host - e.g. Elliptio complanata (Matteson, 1948), Simpsoniconcha ambiqua (Howard, 1951), Anodonta implicata (Davenport and Warmuth, 1965), Pleurobema cordatum (Yokley, 1972), Villosa vanuxemi (Zale and Neves, 1982a), appears to be exceptional. While the maximum number of reported hosts for any unionacean glochidium exceeds 30 (for A.

grandis - Trdan and Hoeh, 1982), using Fuller's (1974) review on the number of parasitic relationships elucidated up to then, Kat (1984) estimated that North American species averaged 4.5 hosts each. From this figure, Kat concluded that host specificity in unionaceans was low, proposing that this was the result of an inability to predict the exact identity of the fish that would come into contact with the discharged glochidia.

Australian hyriids apparently observe little host specificity. Walker (1981b) recorded a variety of native fish endemic to the Murray River drainage that served as hosts for *Velesunio ambiguus* (10 fish species) and for *Alathyria jacksoni* (8 species), while larval metamorphosis could be completed on several exotics. Atkins (1979) similarly reported that the fish, native to the respective study areas are the normal hosts of *Hyridella drapeta* (2 endemics and 1 exotic) and *H. depressa* (2 endemics). The intensity of infection reported for *H. drapeta* ranged from 1-36 glochidia per fish, and for *H. depressa*, 6-37. Percival (1931) noted high infections of up to 6 glochidia on the two recorded host fishes (individuals of which were less than 1 cm in length) of *H. menziesi*.

While host specificity may be low, some fish groups serve disproportionately as hosts to freshwater mussels. Hosts occurring in sympatry with mussels may observe heavy infections. Thus, nesting and territorial centrarchids (Fuller, 1974; Zale and Neves, 1982, a, b; Kat, 1984), molluscivorous fish (Surber, 1912; Fuller, 1974; Kat, 1984) or bottom feeding or dwelling fish in general (Surber, 1912; Lefevre and Curtis, 1912; Percival, 1931; Giusti *et al*., 1975; Kenmuir, 1980) may be heavily infected and host many different species of mussel.

Generally, the intensity of glochidial infection upon host fishes is reportedly low (Surber, 1912; Evermann and Clark, 1917; Coker *et al*., 1921; Darntall and Walkey, 1979; Trdan, 1981; Young and Williams, 1984a). Only 8.9% of the 3671 fish examined by Coker *et al*. (1921) during the warmer months for example, were infected. The mean number of glochidia per infected fish was 125 while the range was 1-416. From his own studies and reviewing previous work, Trdan (1981) noted a negative correlation between the number of species serving as hosts for glochidia of particular unionids, and the infection rate (percent infected and intensity). Where host specificity is high, Trdan proposed that ecological and behavioural factors became important in the initial host-parasite contact, leading to conditions which support a high intensity of infection, a high percentage of the population infected, or a combination of both. Dartnall and Walkey (1979) also drew attention to factors such as viability and dispersal of discharged larvae, behaviour of larvae and hosts, and whether or not glochidia are released en masse, in influencing the intensity of infection upon host fishes. Mussel density (Stern, 1978; Bauer, 1979; Kat, 1984) and the immune reaction of the host that strengthens with repeated infections (Fuller, 1974; Stern, 1978; Kat, 1984) are also factors of influence.

Attachment to the host tissues relies mostly on chance, but both tactile and chemical stimuli trigger glochidial attachment (Lefevre and Curtis, 1912; Wood, 1974b; Young and Williams, 1984b). Glochidia cannot discriminate between proper and unsuitable hosts at initial attachment and the well developed immune response reacts to slough off glochidia after 4-7 days (Kat, 1984) if these are attached to unsuitable hosts.

Glochidia are ectoparasites on the fins, gills and body surface of fishes. Hooked or toothed glochidia generally attach to the exterior or strong and exposed parts of the fish host (such as the fins) whereas hookless glochidia generally parasitise the soft and fine gill filaments. There are many recorded exceptions to this rule, however (Wiles, 1975; Giusti et al., 1975; Meyers and Millemann, 1977; Atkins, 1979; Dartnall and Walkey, 1979; Zale and Neves, 1982c). However, Dartnall and Walkey (1979) concluded that availability of larvae, fish size, type of food selection and feeding behaviour might interact to determine the distribution of the glochidia on fish hosts. Giusti et al. (1975) found for example that the gills of bottom feeding, host fishes harboured more glochidia of Anodonta cygnea (larvae of the hooked variety) than predatory fishes.

Of the toothed, Australasian hyriids, the glochidia of Velesunio ambiguus (Hiscock, 1951; Walker, 1981b) and Alathyria jacksoni (Walker 1981b) chiefly parasitise the fins and general body surface of their hosts, and few instances of gill infestation were recorded in field collections. General body surface parasitism has been observed for Hyridella menziesi (Percival, 1931), although the glochidia of other Hyridella species may attach to both gills and general body surfaces (Atkins, 1979). The glochidia of H. drapeta apparently attach exclusively to the gills of host fishes (Atkins, 1979).

Among sympatric unionaceans, Stern and Felder (1978) observed the glochidia of two different species concurrently parasitising different areas of the same fish host (fins and gills). They thought this mechanism may have evolved to reduce competition for the same host in sympatric species.

Encysted glochidia appear as small, semi-opaque tubercles on the host tissues. Qualitative changes involving organogenesis occur during encystment but only in a few species (Surber, 1912; Wiles, 1975; Young and Williams, 1984b) do the glochidia increase in size while still encysted.

A summary of the periods of parasitic duration upon host fishes, reported for a wide range of freshwater mussel taxa distributed worldwide, are summarized in Table A4.2. From these data, it is apparent that for temperate unionaceans under summer conditions, the parasitic period generally lasts from 10-30 days. Although factors such as nutritive condition of the host (Lefevre and Curtis, 1912) and larval maturity (Coker et al., 1921; Zale and Neves, 1982b) may modify the time of metamorphosis, temperature is considered to be the most important factor determining the duration of the parasitic period. Thus, Lamellidens from tropical India has a very short parasitic stage, lasting in the prevailing warm waters for only several days (Seshaiya, 1969). The glochidia of Margaritifera margaritifera overwinter on fish in Scotland (Young and Williams, 1984b) and in two of the five populations studied by Bauer (1979) in Bavaria. Bauer found that the time at which glochidia completed development (before or after winter) was genetically determined rather than determined by environmental factors. In Massachusetts (USA) however, temperatures

Table A4.2 Duration of the parasitic period upon host fishes (and amphibia) in relation to temperature, reported for the larvae of species of freshwater mussel studied worldwide to date.

Species	Region	Authority	Duration of parasitic period (days)	Temperature (°C)
Margaritifera margaritifera	Scotland	Young and Williams (1984a)	290	?
M. margaritifera	Bavaria	Bauer (1979)	c. 14-270	?
M. margaritifera	U.S.A.	Fustish and Millemann (1978)	84	12
M. margaritifera	"	Smith (1976)	36	?
M. margaritifera	"	Roscoe and Redelings (1964)	28-35	?
Anodonta grandis	"	Trdan and Hoeh (1982)	6	21
A. imbecilis	"	"	8	21
A. californiensis	"	D'Eliscu (1973)	26-27	20
A. cygnea	Europe	Harms (1909)	80	8-10
"	"	"	12	20
Villosa nebulosa	U.S.A.	Zale and Neves (1982b)	38-105	16.5
"	"	"	10-21	24.7
V. vanuxemi	"	"	28-49	16.7
"	"	"	8-17	25.0
Medionidus conradicus	"	"	10-20	16.0
Lampsilis fasciola	"	"	30-47	19.2
L. radiata siliquoidea	"	Coker *et al*. (1921)	12-28	?
L. r. siliquoidea	"	Tedla and Fernando (1969)	98	?
Symphynota costata	"	Lefevre and Curtis (1912)	74	10
S. complanata	"	"	14-16	16
"	"	"	9-13	17.8
Elliptio complanata	"	Matteson (1948)	18	?
Simpsoniconcha ambigua	"	Howard (1951)	210	?
Pleurobema cordatum	"	Yokley (1972)	14-18	21
Unio sp.	Europe	Harms (1909)	26-28	16-17
Lamellidens spp.	India	Seshaiya (1969)	3	29-30
"	"	"	6-8	24-25
Velesunio ambiguus	Australia	Hiscock (1951)	22-23	20-22
V. ambiguus	"	Walker (1981b)	22-24	18
"	"	"	16-18	25
Alathyria jacksoni	"	"	22-24	18
"	"	"	16-18	25
Mutela bourguignati	Uganda	Fryer (1961)	25	24-25
M. dubia	Zimbabwe	Kenmuir (1980)	21	25-28

? Not reported

may be sufficiently high over the warmer months that glochidia of M. margaritifera develop quickly enough to achieve full development and drop off the hosts before or after the summer peak in temperature (Smith, 1976). Similarly the glochidia of Lampsilis radiata siliquoidea from Minnesota (USA) are released from the hosts in late summer, but may overwinter as parasites in cooler regions (Trdan, 1981).

APPENDIX 5

FOOD INGESTION, CONDITION AND ANNUAL PRODUCTION

A5.1 Food ingestion

There is difference of opinion over many aspects of the feeding ecology of freshwater mussels, particularly in regard to the potential food items that are ingested and that may be assimilated and whether or not mussels are selective in the types of particles ingested.

All freshwater mussels are suspension feeders, and interspecific differences in feeding among the various species are apparently minimal (Evermann and Clark, 1917; Coker et al., 1921). Bronmark and Malmqvist (1982), finding no significant difference in the size distribution of particles ingested by two sympatric unionids, argued that suspension feeders should be generalists where variability of the food resource is high and predictability low.

A variety of observations on the food of mussels, however, has accumulated. Some have claimed or observed that the food is of plant origin: Evermann and Clark (1917) recorded mud and algae in the guts of unionids but noted that the food of lake mussels comprised more algae and organic material than the chiefly mud component found in river mussels; Coker et al. (1921) thought detritus formed the main bulk of the food of freshwater mussels, and observed that vegetable food was preferred to animal substances; the food of Margaritifera margaritifera was recorded by Hendelberg (1960) as consisting mainly of vegetable detritus; and finally Clarke (1973) states broadly, that all Unionidae are phytophagous filter-feeders. Others believe any suspended material will serve as food for mussels: Allen (1914) thought the gut contents comprised any finely divided, living or decaying tissue; nutrients including fats in solution according to Coker et al. (1921) may be assimilated; Allen (1921) stressed the importance of nannoplankton including bacteria in the diet of mussels; Churchill and Lewis (1924) recorded that the stomach contents included microscopic animal and plant forms, and debris or detritus resulting from the decay and disintegration of such forms; the food of mussels according to Pennak (1953) consists of zooplankton, phytoplankton and organic detritus; and according to Fuller (1974), the diet consists primarily of detritus and animal plankters - he considered that algae were commonly overestimated as food value.

Fuller's (1974) conclusion above was no doubt influenced by observations such as those of Coker et al. (1921) that much of the algae and diatoms passing through the digestive tract of freshwater mussels remained intact and unchanged by the digestive processes. This has been observed not only in other studies of freshwater mussels (Allen, 1921; Churchill and Lewis, 1924), but for corbiculaceans (Gale and Lowe, 1971), other freshwater forms (e.g. Dreissena polymorpha - Ten Winkel and Davids, 1982), and marine bivalves as well (e.g. Coe and Fox, 1944 ; Jorgensen, 1975; Hildreth, 1980). In accordance with this observation, it is well known that certain forms such as diatoms and some flagellates are immune to digestive enzymes by nature of their resistant tests or cellulose cell walls. However, Allen (1914, 1921) concluded that ingestion was continuous but digestion discontinuous and dependent upon demand for nutrition; he showed that resistant diatom species frequently found undigested, were digested when fed to starved mussels. It is of further significance that in terms of utilisable energy, living phytoplankton in the diet of filter- and deposit-feeders has been found to be superior to both bacteria and detritus (Moore, 1975; Jorgensen, 1975). Wallace et al. (1977) added that the high oil or fat content of diatoms may contribute significantly to the nutrition of filter feeders.

With respect to the food of juvenile freshwater mussels, Matteson (1948) noted that none of the common items of the adult diet were seen to be ingested by the young. He thought it possible that the young might utilise considerable quantities of bacteria and dissolved organic material. Howard (1922), however, stated that the food of juveniles appeared to be similar to that of the adult, namely microscopic plants and animals. For the marine oyster, Pinctada margaritifera at least, Nasr (1984) noted that the variety of food increased as the oyster grew older.

In other freshwater bivalves, very few zooplankters have been observed in the diet, which generally comprises algae and detritus (Gale and Lewis, 1971; Wallace et al, 1977; Stanczykowska, 1977). A similar situation may apply to the diet of marine bivalves (e.g. Fox, 1936; Nasr, 1984).

Controversy still exists as to whether bivalves exercise selectivity over ingested particulates. Based mainly on comparisons of stomach contents to the suspension in surrounding waters and the direct observation of various particles on the exposed pallial surfaces, various interpretations have been advanced. In relation to freshwater mussels, Allen (1914) concluded that selection is exercised at the inhalent siphon, palps, and mouth, mussels avoiding most material with no food value and rigidly excluding injurious substances. While the apparent absence of sand and silt from the stomach contents was indicative of selection to Allen (1914, 1921), the inorganic debris present in the ingested materials examined by Coker et al. (1921) and Churchill and Lewis (1924) suggested to these authors an absence of selection. Coker et al. (1921) noted further, that the stomach contents corresponded to the composition of the surrounding plankton, in type and proportions. Rejection of potential food items was thought by the preceding authors to be accomplished not by ciliary sorting but by ceasing to feed when unwanted substances were present. Churchill and Lewis (1924) felt tht everything small enough (whether of nutritive value or not) and not active enough to escape was ingested by mussels; from the heterogeneous mass, the alimentary canal digested and absorbed what it could with the rest passing on. Nevertheless, on Allen's (1914) results, it has been assumed by some, that freshwater mussels exercise some selection over ingested food materials (Pennak, 1953; Clarke and Berg, 1959). Bronmark and Malmqvist (1982) in feeding experiments upon freshwater mussels, noted that the particle size distribution of a charcoal slurry found in the guts of two unionids was significantly smaller than that in the surrounding waters, indicating a sorting and selection capability.

Amongst other freshwater forms, corbiculaceans apparently exhibit very little selection (Gale and Lowe, 1971; Wallace et al., 1977; Hornbach et al., 1984). Gale and Lowe (1971) noted, however, that fewer diatoms were represented in the guts of Sphaerium transversum than in water samples, while the dominance of a few forms of diatoms in the guts of Pisidium (Neopisidium) conventus suggested possible selection to Heard (1963). Dreissena polymorpha according to Ten Winkel and Davids (1982), may select for the size and type of algae ingested, but the selection apparently fails when the animal is starved. According to various authors, marine bivalves may (e.g. Fox, 1936; Bernard, 1974; Hughes, 1975) or may not (e.g. Winter, 1978; Nasr, 1984) exercise active selectivity over ingested materials.

Various environmental factors may influence feeding in bivalves. Some freshwater bivalves have diurnal rhythms of feeding (Jorgensen, 1975; Winter, 1978; Walz, 1978; McCorkle et al., 1979). Notably, the hyriid Velesunio ambiguus observes the greatest number of shell openings during the night (3-6 a.m.) (Hiscock, 1950). With increasing food concentration, bivalves generally increase their ingestion rate; a threshold value is reached, however, beyond which the rate remains constant (Winter, 1978). In practice, nevertheless, ingestion (and therefore growth) is normally submaximal and tends to vary with food levels (Jorgensen, 1975). Ingestion rates also increase with increasing temperature (Winter, 1978) and in freshwater bivalves feeding may cease in winter (Matteson, 1955; Gale and Lowe, 1971). In both freshwater (Gale and Lowe, 1971) and marine bivalves (Riisgard and Randlov, 1981) feeding may be suppressed during periods of low dissolved oxygen. Hornbach et al. (1984) observed that filtration rates of the sphaeriid Sphaerium striatinum peaked in association with reproductive condition of the animal rather than with levels of food or temperature.

A5.2 Condition

Studies of body weight variations (i.e. condition) in freshwater mussels are few, and generally cursory in nature. Using shell length versus dry weight regression equations, Cameron et al. (1979) found generally no differences between sexes or sizes of mussels, and only minor variations of body weights with season in some unionids studied. Golightly and Kosinsky (1981) observed similarly, that the length/weight relationships for other unionids species were similar between locations and seasons. Using a condition index based upon flesh weights in relation to shell length of Anodonta piscinalis to depict the availability of resources at a certain time and place, Haukioja and Hakala (1978b) recorded, however, that annual variations in condition were considerable. No factors influencing the observed fluctuations were elucidated.

In a more thorough investigation, Huebner (1980) studied seasonal body weight fluctuations of A. grandis and Lampsilis radiata using length/dry weight regression equations. Body weights fluctuated seasonally and both species peaked in condition in spring. Huebner accounted for seasonal weight changes according to whether or not females were brooding larvae, by differences in food availability and quality and by possible disparities between tissue and shell growth. Other than the period when higher body weights were recorded for females brooding glochidia in the marsupia, differences in body weights between the sexes were absent. In other studies, Tudorancea (1969) observed that flesh weights of Unio tumidus were higher in the Crapina than the Jijila marshes of Rumania; using a condition index, Tudorancea and Gruia (1968) observed that condition of U. crassus in the Nera River (Rumania) was highest where densities were minimal and vice versa. In the latter study, Tudorancea and Gruia thought that the poor condition of mussels measured at high mussel densities was due to poor nourishment (presumably from competition amongst individuals for food at least).

In studies of other freshwater bivalves, Stanczykowska (1964) observed very small body weight variations of Dreissena polymorpha within European lakes, but considerable variations between lakes. As in the Nera River for U. crassus, condition of D. polymorpha was highest where densities were lowest, and vice versa. Stanczykowska pointed to the deleterious influence of overcrowding. In later studies, Stanczykowska (1977) recorded seasonal weight increases of D. polymorpha at the time of gonadal development, while between lakes, the main factor affecting variability in body weight was attributed to trophic conditions. Higher trophic conditions either felt directly, or indirectly through higher water temperatures and lowest mussel densities (i.e. a reduction of competition), resulted in higher body weights of mussels. Stanczykowska noted that algal blooms of specific, unpalatable algae could inhibit food intake and result in a decline in body condition in some populations of D. polymorpha. The same phenomenon has been reported in marine bivalves by Pieters et al. (1980).

In contrast to freshwater forms, condition cycles in marine bivalves are well known. Generally condition peaks in summer and falls in winter, in association with gonadal maturation and spawning respectively (e.g. Hughes, 1970; Peddicord, 1977; Comely, 1978; Newell and Bayne, 1980; Hickmann and Illingworth, 1980). Several authors have drawn attention to the correspondence between food availability (as measured by algal concentrations) and condition (Taylor and Venn, 1979; Newell and Bayne, 1980; Pieters et al., 1980; Hickman and Illingworth, 1980). Thus bivalves time the resource-consuming phase of reproduction to coincide with periods when food resources are abundant.

Hickmann and Illingworth (1980) and Shafee (1980) noted, however, that seasonal changes in condition were quite complex, and resulted from a variety of factors including food, temperature and metabolic activities of bivalves. Hickman and Illingworth (1980) observed generally, that mean condition and latitude were negatively correlated in marine bivalves, and that broadly, temperature and condition were inversely related. Dudgeon and Morton (1983) thought that in organisms generally, high prevailing temperatures would cause an increase in respiration (i.e. maintenance costs), thereby reducing energy available for somatic growth.

High suspended solids have also been implicated as the cause of poor condition in marine bivalves. Peddicord (1977) found that condition of Rangia cuneata was lowest on mud substrates. The mud per se was thought to have no effect upon condition, but the high suspended solids prevailing above the substrates were thought to necessitate frequent cleaning of the filtering apparatus. Peddicord thought that considerable energy might be consumed in filtering the solids, compacting them into pseudofaeces and ejecting them. He suggested that clams probably reduced or ceased their filtering activities during periods of high turbidity to conserve the energy required to sort and reject particles.

Noting that condition decreased with increasing size, various authors have concluded that the same bivalve species exhibit a senility phase (e.g. Comely, 1978). Hickman and Illingworth (1980) thought that the lower condition observed in larger individuals of Perna canaliculus, might be caused by the increased energy needed for basal metabolism; this requirement would result in less food available for somatic growth. Amongst freshwater mussels, Haukioja and Hakala (1978b) noted that condition of Anodonta piscinalis over a number of populations correlated negatively with length of the reproductive life span.

A5.3 Annual production

Production, or the rate of tissue elaboration of organisms, is in terms of ecosystem functioning, the means by which energy is made available for transmission from one trophic level to another (Waters, 1977). Production and biomass studies allow an evaluation of the roles of the constituent species of a community. Considerble interest therefore has been expressed in the annual turnover ratio, i.e. the ratio of production to standing stock (P/B), as a means of assessing the contribution made by organisms to the functioning of ecosystems. Generally, for a given group of organisms, the P/B ratio is reasonably constant and according to Waters (1977) for aquatic organisms, is usually independent of environmental factors such as water fertility and temperature. Annual P/B ratios are most clearly a function of voltinism (life spans), and expanding and/or short-lived populations observe a high ratio as opposed to overcrowded, stunted and long-lived populations that may observe a much lower ratio. The ratio therefore, decreases with increasing life span, because growth rates are high in the early years.

Known biomass, annual production and P/B ratios of freshwater mussels (shell free, dry weight) from various ecosystems are summarised in Table A5.1. The P/B ratios as expected (Waters, 1977) are relatively constant for the group, and variations are apparently related to the age distributions of the respective communities. (Ratios may be expected to be inversely related to the individual life span of mussel populations.) From Table A5.1, low P/B ratios (as discussed below) are typical of freshwater mussel populations. Thus, although the standing crop of freshwater mussels may be very high, the annual production is reportedly low especially in comparison to the total macrobenthic production. The low P/B ratios observed, have been variously attributed to the long-lived nature of mussel populations and the consequent accumulation of large amounts of organic matter over a number of years (Negus, 1966; Tudorancea and Florescu, 1968; Magnin and Stanczykowska, 1971; Lewandowski and Stanczykowska, 1975; Strayer et al., 1981). Except for predation in the earliest age classes (Negus, 1966), the low ratios indicate that freshwater mussel communities play a trivial role in the ecosystem, in terms of their contribution of biomass and energy to the predators of the trophic level above.

Short-lived corbiculaceans, by contrast with freshwater mussels, are an important food source to animals in higher trophic levels, and observe much higher P/B ratios, generally in the range 1-4 (e.g. Hamill et al., 1979). Marine bivalves also contribute significant

Table A5.1 Annual production, biomass, and turnover (P/B) ratios reported for freshwater mussel communities from various freshwater ecosystems worldwide.

Ecosystem	Biomass (g/m²)	Production (g/m² /year)	P/B	Source
Thames River (UK)	12.1	2.1	0.17	Negus (1966)
Lac Saint-Louis (Canada)	0.71	(0.07)*	(0.10)	Magnin and Stanczykowska (1971)
Lac des Deux Montagnes (Can.)	8.6	1.7	0.20	"
Crapina pool, Danube River (Rumania)	4.8	1.1	0.23	Tudorancea (1972)
Mikolajskie Lake (Poland)	0.20	0.07	0.35	Lewandowski and Stanczykowska (1975)
Mississippi River (USA)	3.26	0.482	0.15	Coon _et_ _al_. (1977) (_Amblema_ _peruviana_ only)
Lake Kariba (Zimbabwe)	2.55	0.876	0.34	Kenmuir (1980)
Mirror Lake (USA)	0.05	0.006	0.12	Strayer _et_ _al_. (1981)
"	0.74	0.057	0.08	" (shells)

* Value apparently incorrect according to Strayer _et_ _al_. (1981).

biomass and energy to predators of the trophic level above, and ratios may range from 0.15 to 2.6 (Hibbert, 1976). Production in the freshwater bivalve Dreissena polymorpha in Europe, is low, but P/B ratios are higher than those observed for freshwater mussels, ranging from 0.42-0.65 (Stanczykowska, 1977).

While predation upon freshwater mussels (including D. polmorpha) is thus generally unimportant, nevertheless, mussels may contribute in other profound ways to the functioning of ecosystems. Firstly, mussel flesh (consumed by predators, scavengers or decomposers) has a very high caloric content to pass on to other trophic levels (Tudorancea and Florescu, 1968). Negus (1966) reasoned that mussels dying each year in a population with regular recruitment would provide an amount of mussel flesh approximately equal to annual production as food for bottom feeding fish, scavenging invertebrates and decomposers. In addition, a small amount of organic material (approximately 2.8%, Cameron et al., 1979) present in the shells would also return to the ecosystem on decomposition.

At high densities, the filtration ability of mussels has been estimated or argued to be significantly important to the nutrient cycles of ecosystems and to the general circulation of materials in aquatic enviroments. Filtration, and biodeposition of faeces by mussels abundant in organic matter, are thought to provide significant cleansing and purification of waters (Tudorancea and Florescu, 1968; Lewandowski and Stanczykowska, 1975); and significant acceleration of the breakdown of nitrogenous wastes to provide nutrients for plankton and other benthic fauna (Tudorancea and Florescu, 1968; Lewandowski and Stanczykowska, 1975; Walz, 1978; Stanczykowska, 1978; Kenmuir, 1981c). Lewandowski and Stanczykowska (1975) added that movements of mussels present at high densities may be important in stirring and mixing the bottom sediments. Mussels may also play an important role in the calcium cycles of some aquatic environments (Green, 1980).

Finally, Waters (1977) emphasised that production estimates in themselves are important as indicators of the general well-being of an ecosystem. Pre-disturbance estimates of production for example, may provide baseline data upon which to monitor the effects of environmental perturbations, natural or anthropogenic. Anthropogenic effects may include pollutants - thermal, organic or inorganic; sedimentation; or any other general alteration of the habitat.

APPENDIX 6

TOLERANCES OF VELESUNIO ANGASI TO ANOXIA

Mussels from the floodplain billabongs of the Magela Creek are seasonally exposed at the Wet-Dry interchange (April-June) to low concentrations of dissolved oxygen and even anoxia, often for prolonged periods. A number of detailed laboratory and field experiments were conducted over the study period to test the tolerance of *Velesunio angasi* to these low concentrations of dissolved oxygen. A brief summary of one laboratory study only is reported here; the experiments demonstrate the tolerances of various age classes of *V. angasi* to anoxia.

Experiments were conducted during the Wet-Dry interchange of 1982 (April-May). Three age classes of mussels were tested: young-of-year mussels recruited at the very recently finished 1981/1982 Wet season; 1-year old mussels; and >1-year old mussels (i.e. all other age groups). All 1-year old and older mussels were collected from Nankeen, representing a floodplain billabong. Unfortunately, recruitment of mussels during the 1981/1982 Wet season was poor in the floodplain billabongs (see Fig. 6.4) and young-of-year mussels therefore were collected from Mudginberri, a channel billabong.

Mussels were placed in stoppered reagent bottles holding approximately 11 litres (range, 10.72-11.12 l) of clean and aerated billabong water. Five bottles were used for each of the 3 age classes of mussels tested. Each bottle held 20 (1-year old and >1-year old) or 25 (young-of-year) mussels. Mussels from each age class were distributed amongst the 5 bottles such that in each bottle mussels of the entire size range were represented. Experiments were initiated when aerators were removed from the bottles and stoppers were replaced. Continuous aeration, however, was maintained in one bottle from each age group as a control, for the duration of the studies. Dissolved oxygen (DO) concentrations were measured in each bottle at the beginning of each experiment and at daily intervals subsequently, using a Hach Model 16046 portable dissolved oxygen meter. The meter was calibrated prior to the daily measurements.

After stoppering the bottles, aerobic respiration of mussels brought DO concentrations to anoxia (defined as <0.5 mg/l) after 144, 30 and 24 hours for young-of-year, 1-year old and >1-year old groups respectively. After DO concentrations had reached anoxia, levels were maintained at this concentration (as described below) for the duration of the experiment. Water in each bottle was changed every 24 hours from commencement of the experiments for young-of-year mussels, and every 48 hours for the other two age groups. At each change of water, mussels were removed from the bottles and inspected. Dead animals were discarded while live ones were returned to bottles containing clean water of the same DO concentration that prevailed prior to inspection. DO concentrations were regulated in this way by bubbling nitrogen gas through the new water in each bottle. The entire procedure from removal of mussels to replacement in re-stoppered bottles of clean water was always completed in less than 5 minutes. If dead mussels in the 1-year old and >1-year old groups were observed at daily inspection prior to the routine 48 hour water renewal, they were removed immediately to prevent fouling of the water. (Dead mussels were recognised by excessive and continuous gaping after agitation of the bottles.)

The experiments were maintained, as described above, until all mussels from each age group had died. No mussels from any age group died prior to DO concentrations reaching anoxia. Similarly, no mussels in the control bottles died over the duration of the experiments. A summary of the counts made of mussels that had succumbed to the anoxic conditions at progressive days (young-of-year) or fortnights (1-year old and >1-year old) is given in Table A6.1 below.

Table A6.1 Numbers of mussels recorded dead after each day (young-of-year) or fortnight (1-year old and >1-year old) of exposure to anoxic conditions.

AGE GROUP	DAY OR FORTNIGHT											
	1	2	3	4	5	6	7	8	9	10	11	12
Young-of-year	1	9	16	20	22	18	8	1	2	1	-	-
1-year old	0	2	4	6	8	13	14	8	13	5	0	4
> 1 year	0	11	23	27	25	3	3	3	3	-	-	-

Young-of-year mussels were least tolerant to anoxia. Mortality in this group was observed between 1-10 days after waters had become anoxic. Greatest mortality was observed on the 5th day after waters reached anoxia. In contrast, however, adult mussels (>1-year old) were exceedingly tolerant to anoxia and survived up to several months in anoxic waters. 1-year olds were particularly insensitive to anoxia, and mussels in this age group survived for up to 24 weeks under these conditions; greatest mortality was found 14 weeks after waters became anoxic. Older mussels (i.e. >1-year old) survived for up to 18 weeks in anoxic waters, while greatest mortality was observed only after 8 weeks.

The likelihood and extent of a genetic difference in the tolerances to anoxia between mussel populations from different billabongs remains to be tested. Thus, while young-of-year mussels from Mudginberri are exceedingly intolerant to anoxia in comparison with the other age groups of mussels from Nankeen billabong, it is possible that juveniles from Nankeen could be less sensitive than those from Mudginberri. Nevertheless, while such differences in the tolerances of mussels of the same age class between two such billabongs of opposing aerobic status may be found to be significant, it is highly likely that the tolerances of juveniles and adults from the same billabong would still be significantly different.

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THE BIOLOGY AND ECOLOGY OF *VELESUNIO ANGASI* (BIVALVIA: HYRIIDAE) IN THE MAGELA CREEK, NORTHERN TERRITORY

Part 3 (Tables)

prepared by

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The Supervising Scientist for the Alligator Rivers Region manages the Alligator Rivers Region Research Institute, which conducts, co-ordinates and integrates research relating the effects on the environment of uranium mining in the Alligator Rivers Region.

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Table 2.1 Broad morphometric and hydrological features of the Magela Creek billabongs sampled during the study.

Billabong classification	Billabong name	Area (m^2)	Mean Depth (or depth range)	Sediments
Backflow	Georgetown	16230	0.65	Fine silt and clay + localised sand
	Coonjimba	< 20000	(0-1)	Fine silt and clay
	Gulungul	29469	0.30	Fine silt and clay
	Corndorl[1]	28560	0.4	Fine silt and clay + localised sand and gravel
Channel	Mudginberri	53615	2.16	Sand + localised silt and detritus
	Buffalo	12863	2.05	As for Mudginberri
"/Escarpment rockpool	Bowerbird	<100000	(0-10)	Rock and sand
"/Floodplain	Island	150231	2.32	Sand with silt and clay
Floodplain	Hidden	< 20000	Unknown	Coarse silt and sticky or compact clay
	JaJa(nth)	22114	1.26	Coarse silt and clay + detritus
	Leichhardt	83782	1.92	As for Hidden
	Jabiluka	100544	2.17	Coarse silt and clay
	Nankeen	174664	1.87	Coarse silt and clay

1. Includes only that section of the billabong shown in Figure 2.7.

Table 2.2 Particle size distribution, mean particle size and percent organic content of sediment samples taken in October 1979 (according to Thomas and Hart, 1981), and November 1978 (according to Thomas <u>et al</u>., 1981), from the Magela Creek billabongs.

		Percent of Total Sediment				Percent Organic Content In			
Billabong		Sand and Organics (> 63 μm)	Silt and Clay (63-20)	Fine Silt and Clay (20-2)	Clay (< 2)	Sand and Organic Fraction	Silt and Clay Fraction	Total Sediments (mean value)	Mean Sediment Particle Size (μm)
Georgetown	1	6	16	50	28	1.6	10.3	9.0	31.7
	2*	12	2	[85]		nd	nd		
	3	31	9	38	22	nd	7.6		
	3*	11	7	30	51	nd	nd		
Gulungul	1	25	[75]			9.3	14.3	13.5	32.5
	2*	14	17	14	54	nd	nd		
	3*	9	15	19	57	nd	nd		
Corndorl		35	[65]			nd	13.7	12.0	59.2
Mudginberri		84	[16]			nd	3.0	6.9	136.5
	*	99	<1	[1]		nd	nd		
Island	1	75	3	16	6	11.3	5.3	9.0	97.3
	1*	100	[<1]			nd	nd		
	2	4	4	83	9	nd	16.3		
	3*	69	2	[28]		nd	5.2		
Hidden		52	11	29	8	nd	14	nd	85.9
Leichhardt	1	3	16	66	15	nd	4.9	9.7	22.4
	2	8	18	60	15	2.2	10.1		
Jabiluka	1	21	36	28	16	4.4	4.7	4.7	31.8
	2*	7	7	29	57	nd	nd		
	3*	12	18	25	44	nd	nd		
Nankeen		12	34	35	19	2.4	5.3	5.0	29.8
	*	10	13	21	55	nd	nd		

* Nov 1978; 11 other records from Oct. 1979.

Table 2.3 Stream velocities calculated at various sites of the Magela Creek during dye experiments in February 1979. (Source - N.T. Dept. Transport and Works, Water Division, 1980).

Sample Site	Distance from Injection Point	Velocity of Travel Between Sites (m/s)
0-50 m downstream of Georgetown billabong	0.0	0.0
1-GS821009 [Downstream of Jabiru]	3.8	0.45
2-GS821018 [Southern end of Mudginberri billabong]	11.5	0.58
3-Magela Creek as enters floodplain	13.5	0.37
4-Y-shaped billabong	14.1	E 0.08
5-GS821023 [Northern end of Island billabong]	16.0	E 0.13
6-Floodplain north of Island	17.5	0.04
7-Floodplain cross section at JaJa	19.5	E 0.02
8-Floodplain cross section between JaJa and Jabiluka	22.9	E 0.04

E = Estimate
GS = Gauging Station.

Table 2.4 Particle size distribution, percent organic content and percent moisture of sediment samples taken in October 1980, from sites in Mudginberri billabong. (Sites shown in Fig. 2.16.)

Sampling location [in Fig. 2.16]	Percent of Total Sediment: sand and organics (> 63 μm)	silt and clay (63-2)	Clay (<2)	Percent Organic Content	Percent Moisture
A5	83.3	13.5	3.2	20.9	61.6
A15	74.5	19.5	6.0	10.7	53.8
A25	94.6	1.4	4.0	4.9	29.9
A35	95.9	2.9	1.2	1.9	28.4
A45	98.2	1.6	<0.5	0.9	22.0
A60	98.7	1.1	<0.5	0.6	22.5
A90	89.7	7.7	2.6	3.9	41.5
B25	74.2	19.4	6.4	15.5	57.2
C25	92.0	5.2	2.8	3.6	38.2
D25	91.8	5.8	2.4	6.4	48.1

Table 2.5 Particle size fractions and organic content of the three major sediment types that characterise Mudginberri billabong. (Sediments shown in Fig. 2.8.)

Sediment (code)	Percent of total sediment that is sand (> 63 μm)	Percent organic content
Sand (A)	95 - 100	< 0.5 - 2
Sand, with a little (B) silt and detritus	92 - 95	2 - 5
Sand, with silt and and detritus (soft) (C)	74 - 92	5 - 21

Table 2.6 Water clarity, and surface and bottom temperature extremes recorded in the Magela Creek billabongs over a four period (1978 to 1981). (Source - Walker *et al.*, 1983a and present study.)

Billabong	Max. surface temperature (° C) (date)	Max. bottom temperature (date)	Min. bottom temperature (date)	Water Clarity during Dry Season
Mudginberri	35.6 (29/11/78)	32.3 (16/11/78)	23.7 (20/6/78)	Non-turbid
Buffalo	33.2 (25/11/78)	31.3 (25/11/78)	23.1 (23/6/78)	
Island	34.6 (10/11/78)	31.6 (17/12/80)	24.0 (6/7/79)	
Leichhardt	34.5 (12/12/80)	32.5 (18/12/78)	22.5 (19/7/78)	
Gulungul	40.0 (6/12/77)	33.7 (22/12/78)	21.3 (30/7/79)	Turbid
Coonjimba	39.0 (6/11/78)	32.0 (3/1/78)	22.3 (29/7/78)	
Corndorl	36.5 (14/12/77)	31.8 (5/12/78)	22.1 (20/6/78)	increasing turbidity
Jabiluka	37.7 (19/12/80)	32.3 (13/3/79)	23.4 (20/7/78)	
JaJa	34.8 (11/12/78)	31.0 (6/4/81)	22.0 (17/7/78)	
Nankeen	37.0 (12/1/78)	31.0 (4/1/78)	23.6 (12/7/80)	
Goanna	37.3 (11/11/78)	31.9 (11/11/78)	21.4 (19/6/78)	
Georgetown	36.0 (15/12/77)	29.5 (3/1/78)	20.6 (16/6/78)	

Table 2.7 Mean values averaged over the seasons (and standard deviations) of physicochemical parameters measured monthly in the Magela Creek billabongs over a four year period (1978 to 1981). Values are from surface readings, except for dissolved oxygen (bottom readings).

Physicochemical parameter (unless indicated, measurement in mg/l)	Billabong										
	Georgetown	Coonjimba	Gulungul	Corndorl	Mudginberri	Buffalo	Island	Jaja	Leichhardt	Jabiluka	Nankeen
dissolved oxygen	4.72 (1.25)	2.82 (1.38)	3.59 (1.35)	3.20 (1.88)	5.06 (0.95)	4.00 (0.69)	3.10 (1.77)	3.15 (1.65)	2.41 (1.82)	3.02 (1.52)	3.55 (1.78)
pH (no units)	6.04 (0.73)	6.21 (0.39)	5.73 (0.77)	6.30 (1.20)	5.89 (0.69)	5.78 (0.73)	5.45 (0.61)	5.75 (1.01)	6.10 (0.65)	5.50 (0.72)	5.72 (0.71)
conductivity (μScm^{-1})	34.7 (17.1)	53.4 (31.8)	45.3 (40.7)	53.4 (47.0)	21.3 (6.7)	23.3 (5.9)	28.8 (11.7)	88.6 (72.0)	83.1 (59.8)	70.1 (59.2)	107.6 (82.9)
turbidity (NTU)	107.4 (93.7)	14.6 (9.8)	10.2 (11.6)	23.6 (38.8)	4.8 (2.0)	5.0 (2.2)	5.6 (2.6)	39.8 (50.2)	5.8 (4.9)	23.7 (23.3)	39.4 (41.7)
suspended solids	259.0 (511.0)	109.0 (183.0)	128.1 (270.1)	175.7 (621.4)	7.2 (4.1)	-	8.7 (4.2)	49.0 (68.8)	-	28.0 (39.0)	72.1 (121.0)
surface chlorphyll a (μg/l)	7.49 (5.36)	-	-	9.33 (4.52)	7.97 (5.66)	7.75 (5.28)	14.16 (12.77)	14.66 (12.23)	29.63 (39.24)	21.28 (37.91)	10.73 (9.93)
total hardness	6.19 (2.26)	3.30 (2.20)	4.27 (1.94)	6.46 (3.62)	6.33 (4.58)	-	5.75 (2.18)	11.85 (10.12)	-	22.68 (24.91)	29.94 (34.14)
carbonate hardness	4.33 (2.68)	3.30 (2.20)	3.33 (2.13)	4.52 (2.06)	3.80 (1.50)	-	2.50 (1.77)	1.95 (2.11)	-	2.80 (2.77)	3.21 (2.61)
non-carbonate hardness	2.13 (2.92)	-	1.58 (2.80)	1.44 (2.74)	0.57 (0.83)	-	3.50 (3.19)	9.65 (10.74)	-	7.43 (8.34)	10.37 (10.41)
bicarbonate	5.81 (3.92)	11.00 (4.70)	5.95 (4.33)	8.50 (5.25)	4.81 (1.73)	-	3.20 (2.19)	2.54 (2.58)	-	3.29 (3.49)	3.95 (3.51)
Ca	0.67 (0.29)	0.42 (0.32)	0.51 (0.26)	1.12 (0.67)	0.47 (0.10)	-	0.73 (0.27)	1.17 (1.07)	-	1.19 (1.02)	1.87 (1.60)
Mg	1.10 (0.41)	0.55 (0.35)	0.73 (0.33)	0.90 (0.51)	0.74 (0.23)	-	0.96 (0.38)	2.17 (1.80)	-	1.72 (1.14)	2.24 (1.51)
K	0.84 (0.54)	1.96 (1.41)	1.48 (1.72)	1.85 (1.82)	0.42 (0.26)	-	0.58 (0.33)	2.48 (2.28)	-	1.91 (1.52)	2.49 (1.91)
Cl	4.64 (3.69)	8.00 (7.73)	7.31 (8.26)	11.55 (12.60)	3.29 (1.73)	-	4.04 (1.75)	11.21 (8.25)	-	10.29 (9.14)	22.16 (19.73)
dissolved organic carbon	7.07 (6.31)	12.78 (14.60)	8.29 (6.79)	11.18 (17.72)	5.05 (4.48)	-	4.56 (2.17)	9.72 (5.56)	-	5.87 (3.34)	7.43 (4.84)
total organic carbon	8.68 (10.66)	16.32 (19.83)	16.34 (19.44)	11.03 (18.37)	5.37 (5.17)	-	8.19 (7.88)	11.10 (7.34)	-	6.52 (3.21)	7.54 (4.77)
nitrate	0.241 (0.38)	0.440 (0.976)	0.184 (0.378)	0.072 (0.213)	0.032 (0.047)	-	0.132 (0.637)	0.250 (0.380)	-	0.315 (0.434)	1.104 (2.175)
ammonia	0.03	0.280	0.255	0.142	0.009	-	0.008	0.592	-	0.199	0.147

Table 2.8 Seasonal resume of fish community structure (relative abundance) recorded for the Magela Creek waterbodies over the period late 1978 to early 1979. (Source - Bishop et al., 1981)

WATERBODY

FISH SPECIES	GEORGETOWN			COONJIMBA			MAGELA CREEK CHANNEL			GULUNGUL			CORNDORL			MUDGINBERRI			BUFFALO			ISLAND			JAJA			LEICHHARDT			JABILUKA			NANKEEN		
	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED	LD	MW	LW/ED
Melanotaenia nigrans							+	++	++																								+			
Leiopotherapon unicolor						+	+	++	+		++	+			+		+										+								+	
Melanotaenia maculata	++	++	++	+	++	+++	++	+++	++	+	++	++		++	++	+	++	++	+	++	+++	+	++	++	++	++	++	+	++	+++		++	+++	+	+	++
Hephaestus fuliginosus								+																												
Pingalla sp.									+																											
Neosilurus hyrtlii							+																													
Tandanus ater			+			+		+			+			+	+	++		++	++		+	+		+		+		+			+	+		+	+	
Scleropages jardini																						+														
Porochilus rendahli	+		+			+				+		+	++		++						+		+				+	+		+			++			+
Toxotes lorenzi																																				
Amniataba percoides	+	+	+	+			+		++			+		+	+	+		+		+	+	+	+						++						++	
Megalops cyprinoides			+			+		+				+		+				+			+	+	+		+			+	++	+			+		+	+
Ambassis macleayi								+	++	+								+		++	++	+		++			+++									
Syncomistes bulteri																		+																		
Glossamia aprion		+	++			+			+	+		+	++		+		+		+					++	++		+	+		+	+		++	+	+	+
Toxotes chatareus		+	+	+	+	+			+			+		+	+	+				+	+	+	+			+									++	
Mogurnda mogurnda				+			+		+	++		+			+						+				+	+	+		+							
Strongylura kreffti			+	+	+	+	+	+	+		+	+			+		+	+			+		+		+		+		+	+			+		+	
Craterocephalus marjoriae							+++	++	++	+																										
Craterocephalus stercusmuscarum		++	+	+	++	+	+++	++	++		+	+				+	+	++	+	++	+	+	+++	+	+	++	+	+	++	+	+	++	++	+	++	
Nematalosa erebi	+	++	++	+	++	++		+	+	++	++	++		+	++		++	+	+		+	+		+	+	+			+		+	+		+		
Denariusa bandata	+	+	++	++		+			++	++	+	++	++		+		++		+	+	+	++	+	++	++	++	++	+		+	+	+	+	+	+	++
Oxyeleotris lineolatus	+		+	+		+			+			+		+	+		+							+	+		+			+		+			+	
Ambassis agrammus	+++	+++		+++	+		++	++	+++	++	+		++	++	+++	+++	+++		++	+				++	+++	+		+++			+++	++	++	+++	++	++
Pseudomugil tenellus				+	+				+		+			++	+						+			+	+	+	+				+	+		++		
Ambassis sp.				+++			++		++				++									+	++						++	++						
Hexanematichthys leptaspis	+		+		+			+			++	+		+	+	+	+	++	++		+	+		++	+			+	++	+	+	+	+	+	++	++
Glossogobius giurus	+						+									++	+	+	+					+												
Liza diadema																					+				+											
Ophisternon gutturale																								+	+											+
Lates calcarifer		+																	+									+								
Hypseleotris compressus																			+			+			+			+				+		+		

Table 3.1 Sampling methodology of mussels for the Magela Creek waterbodies.

Waterbody	Study period	Sampling type
Georgetown	March - May 1980	Rake; 1
	June - December 1980	3
	January 1981 - May 1982	3; 4
Mudginberri	March - May 1980	Rake
	June - December 1980	3
	January 1981 - May 1982	4
Nankeen	March - May 1980	Rake
	June - December 1980	2; 3
	January 1981 - May 1982	3; 4
Lowland creek channel	July 1980 - May 1982	1; 5
Corndorl	January 1981 - May 1982	1
Island	January 1981 - May 1982	1; 2
Leichhardt	January 1981 - May 1982	1; 2
Jabiluka	January 1981 - May 1982	1; 2
Buffalo	April 1981 - April 1982	4
JaJa	April 1981 - April 1982	1; 2

Key to sampling types:

1. Collected by hand, without a quadrat.
2. Hand collection from the confines of a quadrat.
3. Hand collection and sediment scooping from the confines of a quadrat.
4. Hand collection and air-lifting of the sediments from the confines of a quadrat.
5. Digging and sorting of exposed sediments for aestivating mussels. (No quadrat.)

Table 3.2 Sampling efficiency of Type 2 sampling (hand collection from the confines of a quadrat) in Mudginberri billabong.

Length of mussel (mm)	No. of mussels collected by hand (Type 2 sampling), prior to air-lifting	No. of mussels subsequently air-lifted
2	0	0
3	0	0
4	0	6
5	0	2
6	0	5
7	0	3
8	0	1
9	0	0
10	0	0
11	0	0
12	0	0
13	0	0
14	0	0
15	0	1
16	0	0
17	0	0
18	0	0
19	1	1
20	3	1
21	1	1
22	2	1
23	1	0
24	1	2
25	2	3
26	1	0
27	5	1

Table 4.1 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of adult mussels (> 30 mm length) in the Magela Creek waterbodies (and East Finnis River) for sexes separate and combined. Equation is of the form: $\ln L = a + b\ln H$ where L = shell length (mm), H = maximum shell height (mm). Levels of significant differences between the slopes and intercepts of the equations derived for each sex (as shown by analysis of covariance testing) are indicated.

WATERBODY	Regression and correlation coefficient	Sex		
		male	female	combined
Georgetown	a *	0.355	0.404	0.373
	b	1.058	1.045	1.053
	r^2	0.947	0.926	0.938
	n	962	896	1858
Gulungul	a	0.311	0.514	0.415
	b	1.058	1.000	1.028
	r^2	0.950	0.969	0.958
	n	42	37	79
Corndorl	a	0.331	0.333	0.331
	b	1.067	1.066	1.067
	r^2	0.897	0.902	0.899
	n	496	441	937
Magela Creek channel	a **	0.704	0.767	0.733
	b	0.939	0.922	0.931
	r^2	0.947	0.942	0.945
	n	596	541	1135
Mudginberri	a	0.309	0.303	0.306
	b	1.066	1.068	1.067
	r^2	0.896	0.866	0.883
	n	1018	942	1960
Buffalo	a	0.310	0.462	0.373
	b	1.060	1.017	1.042
	r^2	0.879	0.850	0.862
	n	721	614	1334
Island	a	0.318	0.207	0.271
	b	1.071	1.100	1.083
	r^2	0.929	0.910	0.920
	n	451	418	869
Hidden	a	0.213	0.068	0.193
	b	1.097	1.135	1.102
	r^2	0.922	0.926	0.925
	n	24	24	48
JaJa	a	0.179	0.138	0.161
	b	1.117	1.127	1.121
	r^2	0.903	0.917	0.910
	n	173	180	353
Leichhardt	a **	0.095	0.008	0.054
	b	1.143	1.164	1.153
	r^2	0.890	0.908	0.898
	n	470	383	853
Jabiluka	a	0.205	0.219	0.220
	b	1.108	1.103	1.103
	r^2	0.895	0.895	0.896
	n	458	391	848
Nankeen	a	0.709	0.525	0.612
	b **	0.959	1.011	0.986
	r^2	0.849	0.866	0.857
	n	967	910	1877
Finniss River	a	-	-	0.232
	b	-	-	1.073
	r^2	-	-	0.934
	n	-	-	30

* $P < 0.05$
** $P < 0.01$

Table 4.2. Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of juvenile mussels (< 35 mm lenght). Equation is if the form: $lnL = a + bLnH$ where L = shell (mm), H = max. shell height (mm). Significant differences between the slopes and intercepts of the equations derived separately for juveniles and adults from the same billabongs (as shown by analysis of covariance) are indicated.

Billabong	Regression and correlation coefficient			
	a	b	r^2	n
Georgetown	0.411 ***	1.028	0.978	1522
Mudginberri	0.358 ***	1.029	0.991	648
Buffalo	0.359 ***	1.031	0.992	201
Nankeen	0.298 ***	1.075 ***	0.994	112

*** $P < 0.001$

Table 4.3. Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of adult mussels (sexes combined), in relation to depth and samplinfg transect in Georgetown Billabong. Equation is of the form: $lnL = a + blnH$ where L = shell length (mm), H = max. shell height (mm). Location of the transects is shown in Fig. 3.1.

TRANSECT	Depth (m)	Regression and correlation coefficient		
		a	b	r^2
A	0.0-0.49	0.350	1.059	0.931
	0.5-0.99	0.303	1.073	0.936
	> 1.0	0.349	1.061	0.947
B	0.0-0.49	0.360	1.057	0.948
	0.5-0.99	0.371	1.055	0.937

Table 4.4 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of adult mussels (sexes combined), in relation to Wet season stream velocity and mean chlorophyll a concentration (arbitrary units) at different sites in Mudginberri billabong. Equation is of the form: lnL = a + blnH where L = shell length (mm), H = maximum shell height (mm). Location of the sites is shown in Figure 3.1.

SITE	Regression and correlation coefficient			stream velocity (m/sec)	mean chlorophyll concentration
	a	b	r^2		
1	0.292	1.069	0.992	0.125	1.47
2	0.311	1.063	0.995	0.100	1.67
3	0.289	1.069	0.996	0.106	2.32
4	0.339	1.055	0.991	0.045	2.89
5	0.268	1.084	0.992	0.191	3.14

Table 4.5 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of adult mussels (sexes combined), in relation to sediment type and mean chlorophyll a concentration at different sites in Buffalo billabong. Equation is of the form: $\ln L = a + b\ln H$ where L = shell length (mm), H = maximum shell height (mm). Location of the sites is shown in Figure 3.1.

SITE	Regression and correlation coefficient			Mean chlorophyll concentration (μg/l)	Sediment type
	a	b	r^2		
1	0.329	1.052	0.802	6.60	sand
2	0.374	1.039	0.833	5.95	silt
3	0.297	1.062	0.882	5.62	sand
4	0.328	1.053	0.870	5.62	sand and silt
5	0.279	1.070	0.858	6.68	sand and silt
6	0.293	1.063	0.802	8.83	silt
7	0.281	1.066	0.736	8.83	silt
8	0.365	1.046	0.865	8.67	sand
9	0.285	1.069	0.826	8.25	sand and silt
10	0.373	1.047	0.851	8.74	sand and silt

Table 4.6 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of adult mussels (sexes combined), in relation to depth in Leichhardt billabong. Equation is of the form: $\ln L = a + b \ln H$ where L = shell length (mm), H = maximum shell height (mm).

Depth (m)	Regression and correlation coefficient		
	a	b	r^2
0.25-0.49	-0.027	1.182	0.969
0.50-0.74	-0.543	1.321	0.944
0.75-0.99	-0.119	1.204	0.942
1.00-1.24	0.053	1.155	0.854
1.25-1.49	0.224	1.107	0.904
1.50-1.74	0.240	1.097	0.823
1.75-1.99	-0.019	1.168	0.939
2.00-2.49	0.480	1.028	0.913
> 2.49	0.243	1.092	0.905

Table 4.7 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and height of adult mussels, sexes separate and combined, in relation to depth in Nankeen billabong. Equation is of the form: $\ln L = a + b \ln H$ where L = shell length (mm), H = maximum shell height (mm).

Depth (m)	Regression and correlation coefficient	Sex		
		male	female	combined
0.2	a	0.474	0.281	0.371
	b	1.030	1.080	1.056
	r^2	0.950	0.927	0.934
0.4	a	0.417	0.116	0.293
	b	1.041	1.131	1.079
	r^2	0.888	0.899	0.888
0.6	a	0.671	0.221	0.388
	b	0.971	1.097	1.050
	r^2	0.853	0.924	0.898
0.9	a	0.736	0.573	0.658
	b	0.951	0.997	0.973
	r^2	0.851	0.893	0.871
1.2	a	0.583	0.963	0.704
	b	0.993	0.890	0.961
	r^2	0.923	0.800	0.881
1.6	a	0.991	0.530	0.712
	b	0.880	1.009	0.958
	r^2	0.776	0.880	0.840
1.9	a	1.083	0.757	0.923
	b	0.854	0.941	0.897
	r^2	0.714	0.871	0.789
2.3	a	0.850	0.960	0.891
	b	0.918	0.889	0.907
	r^2	0.900	0.821	0.860

Table 4.8 Shell length, maximum shell height, MHI (Maximum Height Index = height/length), and mean MHI of small individual *Velesunio angasi* and *V. wilsonii* (< 40 mm) from various localities in northern Australia. Records are from the Australian Museum (Sydney). Location of the coded sites of collection is shown in Figure 4.6.

SPECIES	Length (mm)	Height (mm)	MHI (%)	Mean MHI (%)	Location (code)
V. wilsonii	35.5	18.0	51	51	Lennard R., W.A. (1)
	39.5	21.1	53	53	Fitzroy Crossing, W.A. (2)
	28.5	15.1	53	53	SE of Kununurra, N.T. (3)
	23.4	13.9	59*	59	Victoria R. area, N.T. (4)
	29.6	15.1	51	51	Stewart R., Qld (5)
	31.0	15.8	51		
	29.1	15.7	54	51	Cairns, Qld (6)
	33.1	15.9	48		
	38.2	20.8	54	54	Ravenshoe area, Qld (7)
	25.5	12.5	49	47	Cooper Ck, near Nebo, Qld (8)
	47.0	20.6	44	44	Corella R., Qld (9)
	34.7	15.6	45		
	30.6	13.5	44		
	29.4	12.9	44		
V. angasi	37.9	20.9	55	56	Glenelg R., W.A. (1)
	41.3	25.1	61		
	49.7	25.4	51*		
	33.9	19.1	56	56	Upper Liveringa, Fitzroy R., W.A. (2)
	27.0	17.8	66	66	Fly Ck, S. of Darwin, N.T. (3)
	15.0	9.8	65		
	37.0	21.8	59	59	Manton Dam, S. of Darwin, N.T. (3)
	32.4	19.7	61	59	Howard Springs, E. of Darwin, N.T. (3)
	16.9	9.7	57		
	37.8	21.8	58		
	35.9	21.5	60		
	32.1	19.3	60		
	34.4	19.8	58		
	37.2	22.2	60		
	39.6	23.7	60		
	20.9	11.6	56	58	S.E. of Howard Springs, N.T. (3)
	21.7	13.0	60		
	38.5	22.2	58		
	38.9	23.6	61		
	30.6	18.0	59		
	35.8	19.5	54		
	30.8	17.2	56		
	14.5	8.9	61	61	Arnhem H'way near Stewart H'way, N.T. (3)
	28.4	16.8	59	59	Humpty Doo, N.T. (3)

* possible misidentifications

Table 4.8 (Ctd)

SPECIES	Length (mm)	Height (mm)	MHI (%)	Mean MHI (%)	Location (code)
V. angasi	32.2	19.3	60	60	Stuart H'way, 60 km S. of Darwin, N.T. (3)
	39.2	24.1	61	61	Trib. of Sth Finnis R., N.T. (4)
	31.3	18.9	60		
	28.0	19.1	68	64	Wildman R., N.T. (5)
	34.4	22.0	64		
	30.2	19.9	66		
	39.6	24.0	61		
	36.8	23.2	63		
	28.6	16.4	58	58	Daly R. Road area, N.T. (6)
	32.0	18.3	57	61	Nourlangie Ck, N.T. (7)
	35.2	22.5	64		
	35.1	21.6	62		
	35.4	19.2	54	54	Nellie Ck, N.T. (8)
	33.4	17.6	53		
	40.0	23.9	60	60	Pine Creek, Stuart H'way, N.T. (9)
	34.2	21.8	64		
	39.6	21.8	55		
	33.1	20.6	62	62	S. of Katherine, N.T. (10)
	37.7	19.5	52	54	Brandy Bottle Ck, Victoria H'way, N.T. (11)
	28.5	15.8	55		
	29.9	16.7	56		
	28.8	16.3	57		
	15.4	8.0	52		
	36.1	19.6	54	55	Crawford Ck crossing, N.T. (12)
	30.8	16.7	54		
	33.1	18.6	56		
	30.4	16.4	54		
	29.1	16.2	56	56	Humbles Ck, Victoria R. area, N.T. (13)
	34.1	20.6	60	61	Batavia R., Cape York, Qld (14)
	29.1	18.5	64		
	37.4	22.4	60		
	37.9	22.1	58	58	Nesbit, R., Cape York, Qld (15)
	25.8	15.5	60	60	Rocky R., E. Cape York, Qld (15)
	39.0	21.5	55	56	Silver Plains Stn, Cape York, Qld (15)
	36.5	19.2	53		
	37.3	21.3	57		
	32.8	18.1	55		
	31.5	17.8	57		
	34.5	20.6	60		

Table 4.9 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and width of adult mussels (> 30 mm length) in the Magela Creek waterbodies (and East Finnis River) for sexes separate and combined. Equation is of the form: $\ln L = a + b \ln W$ where L = shell length (mm), W = shell width (mm). Levels of significant differences between the slopes and intercepts of the equations derived for each sex (as shown by analysis of covariance testing) are indicated.

WATERBODY	Regression and correlation coefficient	Sex		
		male	female	combined
Georgetown	a	1.125	1.245	1.180
	b *	0.978	0.938	0.960
	r^2	0.918	0.909	0.915
	n	710	650	1359
Gulungul	a	1.223	1.334	1.280
	b	0.924	0.887	0.905
	r^2	0.964	0.978	0.970
	n	42	37	79
Corndorl	a *	1.490	1.481	1.483
	b	0.849	0.850	0.850
	r^2	0.881	0.902	0.891
	n	439	368	807
Magela Creek channel	a **	1.861	1.897	1.879
	b	0.698	0.689	0.694
	r^2	0.893	0.899	0.895
	n	508	476	984
Mudginberri	a	1.528	1.555	1.540
	b	0.843	0.834	0.839
	r^2	0.861	0.837	0.850
	n	714	682	1396
Buffalo	a	1.660	1.705	1.680
	b	0.793	0.779	0.786
	r^2	0.819	0.829	0.824
	n	719	614	1333
Island	a	1.395	1.436	1.413
	b	0.881	0.868	0.875
	r^2	0.921	0.889	0.906
	n	451	418	869
Hidden	a	0.823	1.492	1.033
	b	1.063	0.850	0.995
	r^2	0.957	0.743	0.894
	n	24	24	48
JaJa	a	1.543	1.544	1.519
	b	0.845	0.845	0.852
	r^2	0.902	0.893	0.899
	n	172	180	353
Leichhardt	a	1.453	1.460	1.455
	b	0.869	0.864	0.867
	r^2	0.927	0.918	0.923
	n	470	383	853
Jabiluka	a	1.436	1.399	1.423
	b	0.875	0.886	0.879
	r^2	0.917	0.907	0.914
	n	458	391	849
Nankeen	a	1.412	1.415	1.395
	b	0.888	0.887	0.893
	r^2	0.852	0.877	0.870
	n	670	684	1354
Finnis River	a	-	-	1.313
	b	-	-	0.901
	r^2	-	-	0.848
	n	-	-	30

* $P < 0.05$
** $P < 0.01$

Table 4.10 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and width of adult mussels, sexes separate and combined, in relation to depth and sampling transect in Georgetown billabong. Equation is of the form: $\ln L = a + b\ln W$ where L = shell length (mm), W = shell width (mm). Location of the transects is shown in Figure 3.1.

TRANSECT	Depth (m)	Regression and correlation coefficient	Sex		
			male	female	combined
A	0.0-0.49	a	1.086	1.261	1.001
		b	0.990	0.931	1.019
		r^2	0.894	0.903	0.903
	0.5-0.99	a	1.332	0.914	1.293
		b	0.904	0.885	0.919
		r^2	0.911	0.902	0.908
	> 1.0	a	1.064	1.176	1.177
		b	0.999	0.960	0.958
		r^2	0.891	0.925	0.901
B	0.0-0.49	a	1.004	1.135	1.023
		b	1.022	0.977	1.017
		r^2	0.942	0.919	0.935
	0.5-0.99	a	1.041	1.139	1.138
		b	1.011	0.976	0.976
		r^2	0.934	0.907	0.915

Table 4.11. Regression and correlation coefficients of the allometric equations describing the relationship between shell length and width of adult mussels (sexes combined), in relation to depth at different sites in Mudginberri Billabong. Equation is if the form: lnL = a + blnW where L = shell length (mm), W = shell width (mm). Location of sites is shown in Fig. 3.1.

SITE	Regression and correlation coefficient			depth (m)
	a	b	r^2	
1	1.585	0.822	0.821	1.8
2	1.633	0.809	0.746	1.6
3	1.890	0.725	0.769	2.6
4	1.960	0.703	0.720	2.9
5	1.879	0.734	0.760	2.2

Table 4.12. Regression and correlation coefficients of the allometric equations describing the relationship between shell length and width of adult mussels (sexes combine), in relation to depth at different sites in Buffalo Billabong. Equation is if the form: lnL = a + blnW where L = shell length (mm), W = shell width (mm). Location of sites is shown in Fig. 3.1.

SITE	Regression and correlation coefficient			depth (m)
	a	b	r^2	
1	1.756	0.759	0.782	2.3
2	1.937	0.701	0.788	2.4
3	1.570	0.820	0.884	1.8
4	1.803	0.741	0.814	2.2
5	1.727	0.772	0.792	2.2
6	1.809	0.744	0.729	2.1
7	1.723	0.773	0.756	2.0
8	1.994	0.688	0.750	3.1
9	1.700	0.781	0.811	1.6
10	1.575	0.825	0.853	1.8

Table 4.13 Regression and correlation coefficients of the allometric equations describing the relationship between shell length and width of adult mussels (sexes combined), in relation to depth in floodplain billabongs of the Magela Creek. Equation is of the form: $\ln L = a + b\ln W$ where L = shell length (mm), W = shell width (mm).

BILLABONG	Depth (m)	Regression and correlation coefficient		
		a	b	r^2
JaJa	0.0-0.99	1.455	0.871	0.916
	1.0-1.99	1.539	0.846	0.905
	> 2.0	1.730	0.786	0.821
Leichhardt	0.0-0.99	1.421	0.877	0.953
	1.0-1.99	1.474	0.861	0.951
	> 2.0	1.703	0.784	0.902
Nankeen	0.0-0.99	1.282	0.930	0.897
	1.0-1.99	1.487	0.863	0.844
	> 2.0	1.695	0.794	0.802

Table 5.1 Mean density (numbers/m^2) and standard deviation (SD) of mussels in relation to depth and substrate in Georgetown billabong.

Depth (m)		substrate			
		A	B	C	D
0.0-0.9	mean	16.391*	12.423*	14.047*	5.000*
	SD	10.789	5.333	13.485	5.692
	n	15	12	21	6
1.0-1.9	mean	10.771	13.764*	-	-
	SD	3.805	7.626	-	-
	n	9	21	-	-

* Significant departure from random distribution ($P < 0.05$).

Key to substrates:

A. Soft silt and clay
B. Sand with a little silt, clay and detritus
C. Silt, clay and detritus with some sand
D. Friable organic mud.

Table 5.2 Mean density (numbers/m^2) and standard deviation (SD) of mussels in relation to depth in Gulungul billabong.

	Depth (m)					
	0.1	0.2	0.3	0.4	0.5	0.6
mean	0.0	0.0	0.839*	2.000*	2.308	2.000
SD	0.0	0.0	1.267	1.811	1.377	1.256
n	19	40	31	26	13	10

* Significant departure from random distribution ($P < 0.05$).

Table 5.3 Mean density (numbers/0.25m^2) and standard deviation (SD) of mussels in relation to depth and substrate in Corndorl billabong.

Depth (m)		substrate		
		A	B	C
0.0-0.2	mean	0.130	1.000	1.000
	SD	0.344	1.414	0.816
	n	23	5	4
0.21-0.4	mean	0.814	2.750*	2.000*
	SD	0.982	2.712	2.632
	n	43	8	6
0.41-0.6	mean	2.086*	8.400*	0.500
	SD	2.661	5.550	1.000
	n	35	5	4
0.61-0.8	mean	3.600*	13.710*	2.184
	SD	3.451	10.218	2.001
	n	30	10	6
0.81-1.0	mean	4.667*	19.600*	-
	SD	4.029	12.759	-
	n	24	5	-
1.01-1.2	mean	4.000	5.162*	-
	SD	2.303	3.419	-
	n	24	7	-
1.21-1.4	mean	2.875	-	-
	SD	2.050	-	-
	n	24	-	-
1.41-1.6	mean	0.900	-	-
	SD	0.863	-	-
	n	5	-	-

* Significant departure from random distribution ($P < 0.05$).

Key to substrates:

A. Very soft, organic silt and clay
B. Fine gravel with some silt and clay
C. Sand.

Table 5.4 Mean density (numbers/0.25m²) and standard deviation (SD) of mussels in relation to depth and substrate in Mudginberri billabong.

Depth (m)		substrate			
		A	B	C	D
0.0-0.9	mean	0.309*	0.511	2.200	0.613
	SD	0.963	1.098	2.280	1.253
	n	13	5	5	4
1.0-1.9	mean	0.583	3.947*	4.737*	4.800
	SD	0.996	2.953	3.603	2.864
	n	12	19	19	5
2.0-2.9	mean	1.810*	7.304*	4.440*	8.167*
	SD	1.942	4.204	5.370	6.242
	n	63	23	25	6
3.0-3.9	mean	3.587*	7.563*	4.727	-
	SD	4.075	4.427	2.611	-
	n	46	16	11	-
4.0-4.9	mean	4.333	5.667	3.750	-
	SD	2.425	3.786	1.500	-
	n	12	3	4	-
5.0-5.9	mean	3.250	3.350	1.000	-
	SD	1.500	1.725	0.775	-
	n	4	2	11	-

* Significant departure from random distribution ($P < 0.05$).

Key to substrates:

A. Sand
B. Sand with a little silt and detritus
C. Sand with silt and detritus (soft)
D. Soft to stiff clay with rubble.

Table 5.5 Mean density (numbers/0.25m^2) and standard deviation (SD) of mussels in relation to depth and substrate in Buffalo billabong.

Depth (m)		substrate					
		A	B	C	E	F	G
0.0-0.9	mean	0.125	1.500	0.864	-	-	-
	SD	0.354	1.331	1.010	-	-	-
	n	8	5	3	-	-	-
1.0-1.9	mean	3.400*	5.333*	1.134	2.111	5.265*	2.739
	SD	3.026	5.033	0.984	1.056	5.001	2.648
	n	10	3	8	10	4	4
2.0-2.9	mean	5.015*	5.630*	4.645*	2.783	10.200*	7.833*
	SD	3.785	3.589	4.930	1.917	8.438	5.707
	n	66	54	31	37	5	6
3.0-3.9	mean	5.164*	4.581	3.816*	2.429	8.651*	4.800
	SD	3.550	2.514	2.865	2.070	7.226	2.775
	n	61	31	38	7	5	5
4.0-4.9	mean	2.000*	2.490	-	-	-	-
	SD	3.265	2.533	-	-	-	-
	n	4	5	-	-	-	-

* Significant departure from random distribution ($P < 0.05$).

Key to substrates:

A. Sand
B. Sand with a little silt and detritus
C. Sand with silt and detritus (soft)
E. Sand, silt and detritus (very soft)
F. Soft clay with some sand, silt and detritus
G. Soft silt, clay and fine detritus.

Table 5.6 Mean density (numbers/m^2) and standard deviation (SD) of mussels in relation to depth in the floodplain billabongs.

Depth (m)		Billabong			
		Island	JaJa	Jabiluka	Nankeen
0.0-0.9	mean	0.059	4.916	0.568*	17.576*
	SD	0.239	2.843	1.144	26.696
	n	34	12	37	41
1.0-1.9	mean	1.444*	7.385*	1.960	21.492*
	SD	3.193	4.129	1.567	21.848
	n	36	26	25	37
2.0-2.9	mean	2.000*	3.000	0.627*	3.776*
	SD	2.867	2.191	1.134	4.972
	n	19	11	43	29
3.0-3.9	mean	1.028	0.489*	0.0	0.688*
	SD	1.183	1.246	0.0	2.752
	n	36	7	38	28
4.0-4.9	mean	0.471	-	0.0	-
	SD	0.717	-	0.0	-
	n	17	-	9	-

* Significant departure from random distribution ($P < 0.05$).

Table 5.7 Mean density (numbers/m²) and standard deviation (SD) of mussels in relation to depth and substrate in Leichhardt billabong.

Depth (m)		substrate A	substrate B	substrate C
0.0-0.9	mean	8.28*	0.0	-
	SD	10.334	0.0	-
	n	25	1	-
1.0-1.9	mean	10.250*	0.0	-
	SD	6.304	0.0	-
	n	32	4	-
2.0-2.9	mean	5.294*	0.100	0.111
	SD	13.959	0.316	0.333
	n	17	10	9
3.0-3.9	mean	1.500	0.0	0.0
	SD	1.732	0.0	0.0
	n	4	27	2
4.0-4.9	mean	0.300*	-	0.0
	SD	1.414	-	0.0
	n	4	-	1

* Significant departure from random distribution ($P < 0.05$)

Key to substrates:

A. Soft, coarse silt and clay
B. Silt and unconsolidated plant debris
C. Extremely compacted grey clay.

Table 5.8 Mean density (numbers/m²) and standard deviation (SD) of mussels in relation to depth and stations sampled in Jabiluka billabong.

Depth (m)		substrate Sandy	substrate Muddy (soft, coarse silt and clay)
0.0-0.9	mean	0.667	0.548*
	SD	0.516	1.234
	n	6	31
1.0-1.9	mean	0.800	2.250
	SD	1.304	1.517
	n	5	20
2.0-2.9	mean	0.400	0.714
	SD	0.548	1.226
	n	5	35

* Significant departure from random distribution ($P < 0.05$).

Table 5.9 Mean density (numbers/0.25 m^2) and standard deviation (SD) of mussels in relation to depth and stations sampled in Nankeen billabong.

		Station										
Depth (m)		1	2	3	4	5	6	7	8	9	10	Mean
0.0-0.9	mean	2.901	5.636*	2.636*	9.818*	3.455*	8.182*	1.909*	6.636*	1.000*	1.818*	4.394*
	S D	1.943	4.610	3.264	9.293	3.959	7.731	2.071	8.640	1.342	2.892	6.674
	n	64	11	11	11	11	11	11	11	11	11	163
1.0-1.9	mean	2.850	9.273*	3.818*	8.818*	3.545	6.909*	3.273*	10.818*	2.091*	2.727*	5.373*
	S D	1.777	10.248	3.628	9.898	4.906	5.941	3.438	8.035	2.119	4.627	5.462
	n	48	11	11	11	11	11	11	11	11	11	147
2.0-2.9	mean	1.010	1.455	1.000	1.182	1.364	0.545	0.455	2.182*	0.091	0.364	0.944
	S D	0.976	1.214	1.183	1.079	3.264	0.820	0.688	2.401	0.302	0.505	1.243
	n	18	11	11	11	11	11	11	11	11	11	117
3.0-2.9	mean	0.311	0.455	0.0	0.273	0.091	0.0	0.091	0.636	0.0	0.0	0.172
	S D	0.636	0.820	0.0	0.467	0.302	0.0	0.302	0.924	0.0	0.0	0.345
	n	11	11	11	11	11	11	11	11	11	11	110

* significant departure from random distribution ($P < 0.05$).

Table 5.10 Estimated total number and mean density of mussels in the Magela Creek billabongs.

Billabong	Grand mussel total	Billabong area (m^2)	Mean Density (m^{-2})
Bowerbird	0.0	nd	0.0
Georgetown	208,518	15,610	13.358
Coonjimba	nd	nd	0.1 E
Gulungul	33,542	29,308	1.144
Corndorl	189,774	28,560	6.645
Mudginberri	681,029	53,255	12.788
Buffalo	238,730	13,116	18.202
Island	152,827	150,232	1.017
JaJa (Nth)	34,053	10,946	3.111
Leichhardt	356,585	84,440	4.223
Jabikula	70,283	100,544	0.699
Nankeen	1,784,856	174,663	10.219

nd, not determined
E, estimate

Table 5.11 Regression and correlation coefficients, and significance of quadratic regression equations describing the relationship between depth and density in some billabongs of the Magela Creek. Equation is of the form: $Y = a + bX + cX^2$ where Y = density, X = depth (m). Density units are numbers/0.25m^2 except for Gulungul billabong (numbers/m^2). Keys to the sediment types are shown in Tables 4.3 - 4.5 for Corndorl, Mudginberri and Buffalo billabongs respectively.

Billabong	Substrate type	Regression and correlation coefficients				Significance
		a	b	c	r^2	
Gulungul	-	-3.905	23.452	-22.479	0.970	NS
Corndorl	A	-2.664	12.419	-5.843	0.898	*
	B	-12.436	60.446	-35.357	0.668	NS
	combined	-5.520	28.537	-14.960	0.637	*
Mudginberri	A	-1.011	1.725	-0.156	0.859	NS
	B	-2.365	5.894	-0.889	0.976	**
	C	1.052	2.876	-0.521	0.939	**
	combined	-0.803	3.532	-0.529	0.982	**
Buffalo	A	-2.592	5.674	-1.025	0.982	*
	B	-0.406	4.835	-0.942	0.949	*
	C	-0.614	2.336	-0.275	0.735	NS
	combined	-2.045	5.057	-0.951	0.996	**

Table 5.12 Regression coefficients (± standard deviation) of the exponential equation describing the relationship between depth and density in floodplain billabongs of the Magela Creek. (Equation is of the form: $Y = Ae^{-\alpha X} - Be^{-\beta X}$ where Y = density (numbers/m²) and X = depth (m)).

Billabong	Regression coefficients (±standard deviation)			
	A	B	α	β
Island	323.60 (±0.69)	-324.73 (±0.00)	-0.668 (±0.14)	-0.677 (±0.14)
JaJa	2745.23 (±334.54)	-2749.98 (±336.25)	-1.261 (±21.19)	-1.271 (±20.87)
Leichhardt	3101.18 (±6.58)	-3116.69 (±0.00)	-1.393 (±0.16)	-1.416 (±0.17)
Jabiluka	-4556.48 (±0.00)	4554.82 (±1.21)	-1.149 (±0.25)	-1.147 (±0.25)
Nankeen	2377.87 (±16816.47)	-2403.11 (±16804.56)	-2.332 (±0.00)	-2.411 (±0.58)

Table 5.13 Preferred depth of mussels in relation to mean billabong depth and mean dissolved oxygen concentration in the Magela Creek billabongs.

	Billabong								
	Gulungul	Corndorl	Mudginberri	Buffalo	Island	JaJa	Leichhardt	Jabiluka	Nankeen
Billabong code	7	9	12	14	16	22	24	26	29
Preferred depth (m)	0.5	1.0	3.3	2.7	1.9	0.9	0.9	1.3	0.6
Mean billabong depth (m)	0.3	0.4	2.2	2.1	2.3	1.2	1.9	2.2	1.9
Mean dissolved oxygen (mg/l)	3.6	3.2	5.1	4.0	3.1	3.2	2.4	3.0	3.6

Table 6.1 Mark recovery data used to show the correspondence of successive annuli formed and Dry seasons passed, between initial release and final recovery of mussels, in selected billabongs of the Magela Creek.

Billabong	Time of Release	Length at Release (mm)	Time of Recovery	Length at Recovery	Length at successive annuli upon release		Age at Recovery (years)
Georgetown	18/3/1980	48.0	3/4/1982	61.5	53.0	59.0	4
"	"	45.0	"	52.5	49.0	51.5	4
"	"	55.0	"	58.5	56.0	57.5	8
"	"	60.0	"	63.0	61.0	62.5	10
"	"	62.0	"	64.0	62.5	63.5	8
"	"	65.5	"	67.0	66.0	66.5	15
"	"	70.0	"	71.5	70.0	71.0	17
"	3/10/1980	18.0*	3/4/1982	54.0	19.0	37.0	2
"	"	24.0*	"	49.5	25.0	46.0	2
"	"	26.0*	"	53.0	27.5	48.0	2
"	"	26.0*	"	52.5	27.0	48.5	2
"	"	30.0*	"	55.0	30.5	50.5	2
Mudginberri	4/8/1980	25.5*	27/5/1982	48.0	40.0	45.0	2
"	"	24.0*	"	48.5	41.0	45.0	2
"	"	30.5*	"	50.0	44.0	47.0	2
"	"	35.0*	"	53.5	47.0	52.0	2
"	"	36.0*	"	55.0	49.0	53.5	2
"	26/9/1980	54.0	"	57.0	54.0	56.0	6
"	"	56.0	"	59.0	56.5	58.5	8
"	"	61.0	"	62.0	61.0	61.5	15
"	"	62.0	"	63.5	62.0	63.0	16
"	"	70.0	"	71.0	70.0	70.5	19
"	25/10/1980	70.5	"	72.0	70.5	71.5	17
Nankeen	20/9/1980	26.0*	29/5/1982	47.0	28.0	46.5	2
"	"	30.5*	"	51.5	31.0	51.0	2
"	"	25.0*	"	54.0	26.0	52.5	2
"	"	31.0*	"	52.0	32.0	51.0	2
"	"	30.0*	"	46.0	31.0	45.5	2
"	"	45.0	"	57.0	46.0	56.0	3
"	"	53.0	"	58.0	53.0	57.5	3
"	"	60.5	"	63.0	60.5	62.5	8
"	"	67.0	"	68.5	67.0	68.0	9
"	"	71.0	"	73.0	71.0	72.5	15
"	"	72.0	"	73.5	72.0	73.0	18
"	"	63.0	"	65.0	63.0	64.5	14

* young-of-year

Table 6.2 Comparison of estimates of the growth constant (K) and asymptotic length (L_∞) of the von Bertalanffy growth equation, as derived from mark recovery growth data and from shell annuli data.

Billabong	Growth constant, K		Asymptotic length, L_∞ (mm)	
	Annuli	Mark recovery	Annuli	Mark recovery
Georgetown	0.39	0.40	61.5	70.4
Corndorl	0.14	0.37	70.6	65.3
Mudginberri	0.20	0.27	63.6	65.8
Island	0.20	0.26	88.5	84.9
Leichhardt	0.19	0.31	89.7	82.7
Jabiluka	0.14	0.37	90.7	81.3
Nankeen	0.29	0.22	70.0	72.6

Table 6.3 The parameters of the von Bertalanffy growth equation (and 95% confidence intervals) computed from growth data between transects and sexes in Georgetown billabong. Location of the transects is shown in Figure 3.1.

Parameter	TRANSECT A			TRANSECT B		
	males	females	sexes combined	males	females	sexes combined
L_∞	64.36	65.74	64.96	63.05	66.63	64.44
	(62.83, 65.89)	(63.39, 68.08)	(63.64, 66.27)	(61.94, 64.16)	(64.85, 68.42)	(63.50, 65.39)
K	0.206	0.160	0.183	0.385	0.260	0.329
	(0.169, 0.243)	(0.213, 0.198)	(0.157, 0.209)	(0.333, 0.439)	(0.213, 0.307)	(0.293, 0.365)
t_o	-3.613	-5.104	-4.286	-1.493	-2.803	-1.977
	(-4.479, -2.747)	(-6.452, -3.755)	(-5.041, -3.531)	(-1.860, -1.126)	(-3.457, -2.149)	(-2.311, -1.644)

Table 6.4 The parameters of the von Bertalanffy growth equation (and 95% confidence intervals) computed from growth data between sites in Mudginberri billabong. Location of the sites is shown in Figure 3.1.

Parameter	Site				
	1	2	3	4	5
L_∞	59.33	60.43	64.38	64.73	65.09
	(58.39, 60.25)	(59.40, 61.45)	(63.44, 65.33)	(64.01, 65.45)	(63.68, 66.49)
K	0.309	0.247	0.177	0.216	0.180
	(0.239, 0.380)	(0.186, 0.308)	(0.136, 0.218)	(0.171, 0.252)	(0.129, 0.231)
t_o	-3.073	-4.355	-5.955	-4.166	-6.129
	(-4.19, -1.96)	(-5.94, -2.77)	(-7.87, - 4.04)	(-5.64, -2.69)	(-8.52, -3.74)

Table 6.5 The parameters of the von Bertalanffy growth equation (and 95% confidence intervals) computed from growth data between sites in Buffalo billabong. Location of the sites is shown in Figure 3.1.

SITE	Parameter		
	L_∞	K	t_0
1	59.74 (58.89, 60.58)	0.309 (0.217, 0.402)	-2.719 (-4.020, -1.411)
2	62.68 (61.61, 63.75)	0.165 (0.120, 0.211)	-6.201 (-8.807, -3.596)
3	57.66 (56.16, 59.17)	0.230 (0.150, 0.310)	-3.740 (-5.815, -1.665)
4	58.47 (57.70, 59.24)	0.266 (0.199, 0.332)	-3.417 (-4.886, -1.949)
5	64.70 (63.37, 66.02)	0.198 (0.141, 0.256)	-4.740 (-6.764, -2.717)
6	63.69 (61.88, 65.51)	0.160 (0.098, 0.223)	-6.318 (-9.725, -2.912)
7	64.58 (63.26, 65.89)	0.212 (0.143, 0.280)	-4.103 (-6.241, -1.964)
8	63.31 (61.77, 64.85)	0.248 (0.158, 0.339)	-3.869 (-6.116, -1.621)
9	62.59 (61.36, 63.82)	0.245 (0.188, 0.301)	-3.224 (-4.521, -1.968)
10	64.95 (63.96, 65.92)	0.293 (0.233, 0.353)	-2.364 (-3.251, -1.477)

Table 6.6 The parameters of the von Bertalanffy growth equation (and 95% confidence intervals) computed from growth data between different depths in Leichhardt billabong.

Parameter	Depth interval (m)		
	0.0-0.9	1.0-1.9	> 1.9
L_∞	101.96 (87.55, 116.37)	88.61 (81.32, 95.90)	79.12 (54.60, 103.64)
K	0.145 (0.072, 0.218)	0.181 (0.107, 0.254)	0.172 (-0.163, 0.507)
t_0	-3.930 (-5.72, -2.14)	-3.692 (-5.43, -1.96)	-5.461 (-16.74, 5.82)

Table 6.7 The parameters of the von Bertalanffy growth equation (and 95% confidence intervals) computed from growth data between different depths in Nankeen billabong.

Parameter	Depth interval (m)		
	0.0-0.9	1.0-1.9	> 1.9
L_∞	69.69 (68.81, 70.58)	70.85 (69.69, 72.00)	72.42 (68.27, 76.57)
K	0.357 (0.301, 0.414)	0.249 (0.206, 0.291)	0.202 (0.109, 0.295)
t_0	-1.628 (-2.14, -1.11)	-2.638 (-3.47, -1.80)	-2.938 (-5.53, -0.34)

Table 6.8 Length characteristics of age classes of male, female and total mussels sampled from Georgetown billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.00-0.99	male	11	0.90	36.3	3.38	31.0	42.0	34.0, 38.5
	female	3	0.87	33.7	2.52	31.0	36.0	27.4, 39.9
	total	1352	0.52	19.5	9.90	3.0	69.0	18.9, 20.0
1.00-1.99	male	154	1.47	42.0	5.45	25.5	56.0	41.2, 42.9
	female	136	1.53	43.7	4.84	27.0	57.5	42.9, 44.5
	total	453	1.36	40.6	6.81	18.5	62.0	39.9, 41.2
2.00-2.99	male	106	2.40	48.4	4.45	36.5	56.5	47.5, 49.3
	female	111	2.41	49.2	4.37	39.0	60.0	48.4, 50.1
	total	217	2.41	48.8	4.42	36.5	60.0	48.2, 49.4
3.00-3.99	male	119	3.51	52.8	3.74	43.0	65.0	52.1, 53.5
	female	93	3.50	52.5	3.31	42.0	58.0	51.9, 53.2
	total	213	3.51	52.7	3.57	42.0	65.0	52.2, 53.1
4.00-4.99	male	67	4.40	54.8	3.57	43.0	61.0	54.0, 55.7
	female	82	4.37	54.1	4.13	46.0	64.0	53.2, 55.1
	total	150	4.39	54.4	3.88	43.0	64.0	53.8, 55.1
5.00-5.99	male	56	5.50	56.3	3.38	46.0	64.0	55.4, 57.2
	female	57	5.48	55.4	3.95	45.0	64.0	54.3, 56.4
	total	113	5.49	55.8	3.69	45.0	64.0	55.1, 56.5
6.00-6.99	male	66	6.61	57.6	4.09	47.0	67.0	56.6, 58.6
	female	42	6.49	57.1	4.01	49.0	64.0	55.8, 58.3
	total	108	6.56	57.4	4.05	47.0	67.0	56.6, 58.2
7.00-7.99	male	59	7.53	58.7	4.46	48.0	73.0	57.6, 59.9
	female	56	7.44	58.3	4.33	45.0	68.0	57.1, 59.4
	total	115	7.49	58.5	4.38	45.0	73.0	57.7, 59.3
8.00-8.99	male	45	8.54	59.6	4.12	52.5	68.0	58.4, 60.8
	female	58	8.46	60.2	4.59	49.0	69.5	59.0, 61.4
	total	103	8.50	60.0	4.38	49.0	69.5	59.0, 60.8
9.00-9.99	male	53	9.46	60.0	4.99	50.0	70.0	58.6, 61.3
	female	56	9.52	60.1	5.10	51.5	71.0	58.8, 61.5
	total	109	9.49	60.0	5.02	50.0	71.0	59.1, 61.0
10.0-10.99	male	27	10.46	60.6	4.29	51.5	69.0	58.9, 62.3
	female	24	10.45	62.6	4.72	56.0	71.5	60.6, 64.6
	total	51	10.45	61.5	4.57	51.5	71.5	60.2, 62.8

Table 6.8 (Ctd)

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
11.0-11.99	male	24	11.47	60.7	4.49	49.0	69.0	58.8, 62.6
	female	20	11.52	61.4	7.14	52.5	75.0	58.0, 64.7
	total	44	11.49	61.0	5.78	49.0	75.0	59.3, 62.8
12.0-12.99	male	20	12.37	62.0	3.35	55.0	69.0	60.4, 63.6
	female	20	12.52	63.3	5.12	55.0	75.0	60.9, 65.7
	total	40	12.44	62.6	4.32	55.0	75.0	61.3, 64.0
13.0-13.99	male	11	13.56	64.0	2.61	59.0	67.0	62.2, 65.7
	female	8	13.34	61.9	3.29	56.0	65.5	59.2, 64.7
	total	19	13.47	63.1	3.0	56.0	67.0	61.7, 64.6
14.0-14.99	male	19	14.48	65.0	3.40	59.0	72.0	63.4, 66.7
	female	16	14.42	63.3	4.56	57.0	74.0	60.9, 65.8
	total	35	14.45	64.3	4.00	57.0	74.0	62.9, 65.6
15.0-15.99	male	7	15.45	62.4	5.38	54.0	71.0	57.4, 67.3
	female	12	15.43	63.3	5.66	52.0	72.0	59.7, 66.9
	total	19	15.44	62.9	5.43	52.0	72.0	60.3, 65.6
16.0-16.99	male	6	16.46	65.9	3.90	63.0	73.0	61.8, 70.0
	female	3	16.54	61.7	3.75	59.5	66.0	52.4, 71.0
	total	9	16.49	64.5	4.19	59.5	73.0	61.3, 67.7
17.0-17.99	male	6	17.57	66.5	4.23	62.0	73.0	62.1, 70.9
	female	3	17.48	68.8	3.69	66.0	73.0	59.7, 78.0
	total	9	17.54	67.3	3.99	62.0	73.0	64.2, 70.4
18.0-18.99	male	4	18.12	67.0	2.71	65.0	71.0	62.7, 71.3
	female	3	18.80	68.0	6.08	64.0	75.0	52.9, 83.1
	total	7	18.41	67.4	4.04	64.0	75.0	63.7, 71.2
19.0-19.99	male	-	-	-	-	-	-	- -
	female	2	19.61	69.5	2.12	68.0	71.0	- -
	total	2	19.61	69.5	2.12	68.0	71.0	- -
20.0-20.99	male	1	20.02	67.0	-	67.0	67.0	- -
	female	-	-	-	-	-	-	- -
	total	1	20.02	67.0	-	67.0	67.0	- -
22.0-22.99	male	1	22.24	68.5	-	68.5	68.5	- -
	female	1	22.69	69.0	-	69.0	69.0	- -
	total	2	22.46	68.8	0.35	68.5	69.0	- -

Table 6.9 Length characteristics of age classes of male, female and total mussels sampled from Gulungul billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	18	0.75	41.0	3.90	29.0	45.5	39.1, 43.0
	female	16	0.75	39.4	4.30	33.0	49.5	37.1, 41.7
	total	34	0.75	40.3	4.11	29.0	49.5	38.8, 41.7
1.00-1.99	male	3	1.76	50.7	3.21	47.0	53.0	42.7, 58.7
	female	3	1.76	51.7	1.53	50.0	53.0	47.9, 55.5
	total	6	1.76	51.2	2.32	47.0	53.0	48.7, 53.6
2.00-2.99	male	1	2.76	54.5	-	54.5	54.5	- -
	female	-	-	-	-	-	-	- -
	total	1	2.76	54.5	-	54.5	54.5	- -
4.00-4.99	male	2	4.63	56.0	4.24	53.0	59.0	- -
	female	1	4.76	56.0	-	56.0	56.0	- -
	total	3	4.67	56.0	3.00	53.0	59.0	48.6, 63.5
5.00-5.99	male	2	5.76	59.0	0.71	58.5	59.5	- -
	female	-	-	-	-	-	-	- -
	total	2	5.76	59.0	0.71	58.5	59.5	- -
6.00-6.99	male	2	6.76	63.0	4.24	60.0	66.0	- -
	female	-	-	-	-	-	-	- -
	total	2	6.76	63.0	4.24	60.0	66.0	- -
7.00-7.99	male	4	7.76	62.8	4.99	59.0	70.0	54.8, 70.7
	female	8	7.74	61.6	2.24	57.0	64.0	59.7, 63.4
	total	12	7.75	62.0	3.22	57.0	70.0	59.9, 64.0
8.00-8.99	male	6	8.72	66.9	4.09	62.0	73.5	62.6, 71.2
	female	5	8.71	64.1	1.34	62.0	65.5	62.4, 65.8
	total	11	8.71	65.6	3.36	62.0	73.5	63.4, 67.9
9.00-9.99	male	1	9.63	66.5	-	66.5	66.5	- -
	female	1	9.63	63.5	-	63.5	63.5	- -
	total	2	9.63	65.0	2.12	63.5	66.5	- -
10.0-10.99	male	-	-	-	-	-	-	- -
	female	1	10.63	63.0	-	63.0	63.0	- -
	total	1	10.63	63.0	-	63.0	63.0	- -
11.0-11.99	male	2	11.76	75.5	13.44	66.0	85.0	- -
	female	2	11.70	69.5	4.95	66.0	73.0	- -
	total	4	11.73	72.5	8.96	66.0	85.0	58.3, 86.8
12.0-12.99	male	1	12.63	72.5	-	72.5	72.5	- -
	female	-	-	-	-	-	-	- -
	total	1	12.63	72.5	-	72.5	72.5	- -

Table 6.10 Length characteristics of age classes of male, female and total mussels sampled from Corndorl billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01- 0.99	male	1	0.93	35.5	-	35.5	35.5	- -
	total	1	0.93	35.5	-	35.5	35.5	- -
1.00- 1.99	male	16	1.35	37.7	4.42	32.0	47.0	35.4, 40.1
	female	18	1.33	39.1	4.65	33.0	47.0	36.8, 41.4
	total	34	1.34	38.4	4.52	32.0	47.0	36.9, 40.0
2.00- 2.99	male	8	2.47	46.3	2.37	44.0	50.0	44.3, 48.3
	female	10	2.70	47.2	4.41	41.0	55.0	44.0, 50.3
	total	18	2.60	46.8	3.58	41.0	55.0	45.0, 48.6
3.00 3.99	male	21	3.44	50.4	2.64	47.0	56.5	49.2, 51.6
	female	32	3.48	49.2	3.00	42.5	58.0	48.1, 50.3
	total	53	3.46	49.7	2.92	42.5	58.0	48.9, 50.5
4.00- 4.99	male	57	4.57	51.8	3.34	46.0	61.0	50.9, 52.6
	female	48	4.52	51.6	3.74	45.5	63.0	50.5, 52.7
	total	105	4.54	51.7	3.51	45.5	63.0	51.0, 52.4
5.00- 5.99	male	79	5.53	53.9	4.38	45.0	66.0	52.9, 54.8
	female	54	5.53	53.7	4.59	45.0	63.0	52.4, 54.9
	total	133	5.53	53.8	4.45	45.0	66.0	53.0, 54.6
6.00- 6.99	male	77	6.54	56.3	4.58	47.0	66.0	55.3, 57.4
	female	65	6.55	56.4	4.31	45.0	64.0	55.4, 57.5
	total	142	6.54	56.4	4.44	45.0	66.0	55.6, 57.1
7.00- 7.99	male	64	7.36	58.2	4.23	50.0	67.0	57.2, 59.3
	female	61	7.50	58.0	4.95	43.0	67.0	56.8, 59.3
	total	126	7.43	58.2	4.57	43.0	67.0	57.4, 59.0
8.00- 8.99	male	56	8.38	60.8	4.52	51.0	77.0	59.6, 62.0
	female	45	8.40	58.9	4.93	48.0	67.0	57.5, 60.4
	total	101	8.39	60.0	4.77	48.0	77.0	59.0, 60.9
9.00- 9.99	male	33	9.30	60.1	4.91	50.0	70.0	58.4, 61.8
	female	19	9.25	59.2	5.42	45.5	67.5	56.6, 61.9
	total	52	9.28	59.8	5.10	45.5	70.0	58.4, 61.2
10.0- 10.99	male	23	10.1	60.0	5.55	52.0	71.5	57.6, 62.4
	female	13	10.23	59.2	5.79	51.0	70.0	55.7, 62.7
	total	36	10.20	59.7	5.56	51.0	71.5	57.9, 61.6
11.0- 11.99	male	12	11.12	58.8	4.37	53.0	70.0	56.0, 61.5
	female	14	11.21	60.3	6.11	52.0	70.0	56.7, 63.8
	total	26	11.17	59.6	5.33	52.0	70.0	57.4, 61.7
12.0- 12.99	male	5	12.21	63.7	2.39	59.5	65.0	60.7, 66.7
	female	-	-	-	-	-	-	- -
	total	5	12.21	63.7	2.39	59.5	65.0	60.7, 66.7
13.0- 13.99	male	4	13.35	68.8	2.36	67.0	72.0	65.0, 72.5
	female	6	13.26	65.7	5.47	56.0	73.0	59.9, 71.4
	total	10	13.30	66.9	4.58	56.0	73.0	63.6, 70.2
14.0- 14.99	male	3	14.25	71.5	3.12	68.0	74.0	63.8, 79.3
	female	3	14.34	66.5	6.72	59.0	72.0	49.8, 83.2
	total	6	14.29	69.0	5.43	59.0	74.0	63.3, 74.7
15.0- 15.99	male	2	15.29	67.3	6.01	63.0	71.5	- -
	female	4	15.61	72.1	8.51	59.5	78.0	58.6, 85.7
	total	6	15.50	70.5	7.55	59.5	78.0	62.6, 78.4
16.0- 16.99	male	1	16.12	66.0	-	66.0	66.0	- -
	female	2	16.46	66.3	9.55	59.5	73.0	- -
	total	3	16.35	66.2	6.75	59.5	73.0	49.4, 82.9
17.0- 17.99	male	1	17.8	72.5	-	72.5	72.5	- -
	female	2	17.38	67.3	6.01	63.0	71.5	- -
	total	3	17.52	69.0	5.22	63.0	72.5	56.0, 82.0
19.0- 19.99	male	1	19.64	80.0	-	80.0	80.0	- -
	female	1	19.64	80.0	-	80.0	80.0	- -
	total	2	19.64	80.0	-	80.0	80.0	- -

Table 6.11 Length characteristics of age classes of male, female and total mussels sampled from the Magela Creek channel. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-	male	3	0.97	29.5	3.12	26.0	32.0	21.8, 37.3
0.99	total	3	0.97	29.5	3.12	26.0	32.0	21.8, 37.3
	male	109	1.55	39.4	3.98	28.0	51.0	38.6, 40.2
1.00-	female	104	1.46	40.2	4.03	32.0	54.5	39.4, 40.9
1.99	total	219	1.50	39.6	4.24	26.5	54.5	39.0, 40.1
	male	96	2.47	45.6	4.23	34.0	54.0	44.7, 46.4
2.00-	female	111	2.44	46.4	3.97	36.0	57.0	45.6, 47.1
2.99	total	211	2.46	45.9	4.10	34.0	57.0	45.4, 46.5
	male	94	3.55	49.5	3.29	40.0	56.0	48.9, 50.2
3.00-	female	72	3.52	50.3	4.29	40.0	59.5	49.3, 51.3
3.99	total	168	3.54	49.8	3.80	40.0	59.5	49.2, 50.4
	male	69	4.51	51.3	4.31	33.0	58.0	50.3, 52.3
4.00-	female	79	4.54	52.4	3.61	44.0	59.0	51.6, 53.2
4.99	total	149	4.53	51.9	3.97	33.0	59.0	51.2, 52.5
	male	64	5.56	53.8	4.12	45.0	65.0	52.8, 54.9
5.00-	female	64	5.51	54.1	3.83	43.5	63.0	53.1, 55.0
5.99	total	130	5.54	53.9	4.01	43.5	65.0	53.2, 54.6
	male	64	6.51	55.3	4.06	42.0	65.0	54.3, 56.4
6.00-	female	36	6.45	56.0	4.48	48.0	64.0	54.5, 57.5
6.99	total	100	6.49	55.6	4.20	42.0	65.0	54.7, 56.4
	male	41	7.50	56.2	3.65	47.0	62.0	55.0, 57.3
7.00-	female	29	7.54	57.4	4.18	51.0	66.0	55.9, 59.0
7.99	total	71	7.52	56.6	3.90	47.0	66.0	55.7, 57.6
	male	25	8.51	56.4	4.25	48.0	69.5	54.6, 58.2
8.00-	female	17	8.59	57.4	3.22	52.0	63.0	55.8, 59.1
8.99	total	42	8.54	56.8	3.86	48.0	69.5	55.6, 58.0
	male	19	9.57	57.4	4.46	51.0	67.0	55.3, 59.6
9.00-	female	14	9.47	59.1	3.17	53.0	64.0	57.3, 61.0
9.99-	total	33	9.53	58.2	4.00	51.0	67.0	56.8, 59.6
	male	3	10.30	55.7	4.93	50.0	59.0	43.4, 67.9
10.0-	female	11	10.40	58.9	3.85	54.5	66.0	56.3, 61.5
10.99	total	14	10.38	58.2	4.13	50.0	66.0	55.8, 60.6
	male	6	11.74	61.8	2.89	58.0	66.0	58.7, 64.8
11.0-	female	4	11.73	59.1	4.13	55.0	64.5	52.6, 65.7
11.99	total	10	11.73	60.7	3.49	55.0	66.0	58.2, 63.2
	male	2	12.46	57.0	2.83	55.0	59.0	- -
12.0-	female	-	-	-	-	-	-	- -
12.99	total	2	12.46	57.0	2.83	55.0	59.0	- -
	male	1	15.13	61.0	-	61.0	61.0	- -

Table 6.12 Length characteristics of age classes of male, female and total mussels sampled from Mudginberri billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	55	0.75	37.0	3.82	29.0	46.0	36.0, 38.0
	female	31	0.80	39.3	3.89	29.0	47.0	37.9, 40.7
	total	650	0.37	22.7	18.17	2.0	68.5	21.3, 24.1
1.00-1.99	male	22	1.36	45.0	5.97	31.0	59.0	42.4, 47.7
	female	29	1.30	45.8	6.01	33.0	65.0	43.5, 48.1
	male	194	1.37	44.9	6.16	20.5	66.0	44.1, 45.8
2.00-2.99	male	30	2.43	49.4	3.35	43.5	55.0	48.1, 50.6
	female	33	2.38	48.2	4.64	32.0	57.0	46.6, 49.9
	total	63	2.40	48.7	4.09	32.0	57.0	47.7, 49.8
3.00-3.99	male	38	3.43	52.1	3.45	44.0	58.0	51.0, 53.2
	female	38	3.48	53.8	4.33	45.0	64.0	52.3, 55.2
	total	76	3.45	52.9	3.97	44.0	64.0	52.0, 53.8
4.00-4.99	male	32	4.48	54.4	3.73	47.0	61.0	53.0, 55.7
	female	39	4.53	54.9	3.02	48.0	63.0	53.9, 55.9
	total	71	4.50	54.7	3.34	47.0	63.0	53.9, 55.4
5.00-5.99	male	49	5.42	55.1	2.68	49.5	61.5	54.3, 55.8
	female	47	5.46	55.5	4.00	48.0	64.0	54.4, 56.7
	total	96	5.44	55.3	3.38	48.0	64.0	54.6, 56.0
6.00-6.99	male	69	6.49	56.7	3.30	50.0	64.5	55.9, 57.5
	female	38	6.54	57.8	2.65	51.0	63.0	57.0, 58.7
	total	108	6.50	57.2	3.20	50.0	65.0	56.6, 57.8
7.00-7.99	male	73	7.53	57.8	3.32	51.0	66.0	57.0, 58.5
	female	69	7.43	58.9	3.68	49.0	67.0	58.1, 59.8
	total	142	7.48	58.3	3.53	49.0	67.0	57.8, 58.9
8.00-8.99	male	74	8.46	58.6	4.14	48.0	70.0	57.6, 59.6
	female	62	8.50	59.4	4.47	49.0	68.0	58.3, 60.6
	total	136	8.48	59.0	4.30	48.0	70.0	58.3, 59.7
9.00-9.99	male	49	9.50	59.3	4.90	39.0	69.0	57.9, 60.7
	female	42	9.38	58.3	3.92	48.0	66.5	57.1, 59.5
	total	91	9.45	58.9	4.48	39.0	69.0	57.9, 59.8
10.0-10.99	male	47	10.37	59.6	3.64	48.0	66.0	58.5, 60.7
	female	36	10.54	60.7	4.36	53.0	72.0	59.3, 62.2
	total	83	10.44	60.1	3.98	48.0	72.0	59.2, 61.0
11.0-11.99	male	25	11.50	61.5	4.23	53.5	69.0	59.7, 63.2
	female	35	11.50	61.4	4.45	51.0	68.0	59.9, 63.0
	total	60	11.50	61.5	4.32	51.0	69.0	60.3, 62.6
12.0-12.99	male	29	12.53	59.8	3.65	52.0	65.0	58.4, 61.2
	female	37	12.48	61.6	5.48	50.0	79.0	59.8, 63.5
	total	66	12.50	60.8	4.82	50.0	79.0	59.6, 61.8
13.0-13.99	male	31	13.47	61.4	5.20	55.0	82.0	59.5, 63.3
	female	40	13.53	61.7	4.11	51.0	72.0	60.2, 63.1
	total	71	13.50	61.5	4.58	51.0	82.0	60.4, 62.6
14.0-14.99	male	39	14.48	59.9	3.96	52.0	66.5	58.6, 61.1
	female	28	14.52	62.6	4.31	51.0	70.0	60.9, 64.2
	total	67	14.50	61.0	4.29	51.0	70.0	59.9, 62.0

Table 6.12 (Ctd)

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
15.0- 15.99	male	24	15.38	61.7	3.98	54.0	67.0	60.0, 63.4
	female	34	15.43	63.3	3.96	56.0	72.0	61.9, 64.6
	total	58	15.41	62.6	4.02	54.0	72.0	61.5, 63.7
16.0- 16.99	male	41	16.37	62.6	4.05	56.5	72.0	61.3, 63.9
	female	29	16.37	62.8	4.08	51.5	67.5	61.2, 64.3
	total	70	16.37	62.7	4.04	51.5	72.0	61.7, 63.6
17.0- 17.99	male	33	17.44	62.3	4.27	55.0	75.0	60.8, 63.8
	female	33	17.43	64.1	5.08	52.0	73.0	62.3, 65.9
	total	67	17.43	63.1	4.85	52.0	75.0	61.9, 64.2
18.0- 18.99	male	26	18.49	62.1	3.62	53.0	66.5	60.6, 63.6
	female	27	18.45	65.9	3.68	59.5	76.5	64.4, 67.4
	total	53	18.47	64.0	4.09	53.0	76.5	62.9, 65.2
19.0- 19.99	male	23	19.50	63.7	3.88	59.0	71.0	62.0, 65.4
	female	25	19.46	63.6	3.06	57.0	69.0	62.4, 64.9
	total	49	19.47	63.6	3.47	57.0	71.0	62.6, 64.6
20.0- 20.99	male	22	20.49	62.7	3.64	55.0	70.5	61.1, 64.3
	female	23	20.43	63.0	3.74	57.0	72.0	61.4, 64.6
	total	45	20.46	62.9	3.65	55.0	72.0	61.7, 64.0
21.0- 21.99	male	26	21.46	63.1	3.52	56.0	68.0	61.7, 64.6
	female	22	21.46	64.1	4.22	56.0	72.0	62.2, 66.0
	total	48	21.46	63.6	3.84	56.0	72.0	62.5, 64.7
22.0- 22.99	male	9	22.57	63.5	2.32	62.0	69.0	61.7, 65.3
	female	14	22.50	64.9	2.99	60.0	70.0	63.1, 66.6
	total	23	22.53	64.3	2.77	60.0	70.0	63.1, 65.5
23.0- 23.99	male	11	23.44	65.6	3.77	57.0	71.5	63.1, 68.1
	female	11	23.45	64.5	4.29	55.0	70.0	61.6, 67.3
	total	23	23.44	65.1	3.90	55.0	71.5	63.4, 66.8
24.0- 24.99	male	8	24.64	62.8	3.82	59.0	71.0	59.6, 66.0
	female	6	24.36	67.7	3.56	63.0	73.0	63.9, 71.4
	total	14	24.52	64.9	4.35	59.0	73.0	62.4, 67.4
25.0- 25.99	male	8	25.40	61.3	5.84	56.0	75.0	56.4, 66.1
	female	8	25.46	63.5	3.59	58.0	70.0	60.5, 66.5
	total	16	25.43	62.4	4.83	56.0	75.0	59.8, 65.0
26.0- 26.99	male	5	26.58	61.1	4.62	56.0	68.5	55.4, 66.8
	female	7	26.42	66.0	6.38	58.0	75.0	60.1, 71.9
	total	12	26.49	64.0	6.02	56.0	75.0	60.1, 67.8
27.0- 27.99	male	4	27.36	67.8	5.12	62.0	73.0	59.6, 75.9
	female	1	27.42	60.0	-	60.0	60.0	- -
	total	5	27.37	66.2	5.63	60.0	73.0	59.2, 73.2
28.0- 28.99	male	3	28.48	65.0	2.00	63.0	67.0	60.0, 70.0
	female	1	28.76	70.0	-	70.0	70.0	- -
	total	4	28.55	66.3	2.99	63.0	70.0	61.5, 71.0
29.0- 29.99	male	3	29.41	69.0	3.91	64.5	71.5	59.3, 78.7
	female	-	-	-	-	-	-	- -
	total	3	29.41	69.0	3.91	64.5	71.5	59.3, 78.7
32.0- 32.99	male	1	32.43	63.0	-	63.0	63.0	0
	female	-	-	-	-	-	-	- -
	total	1	32.43	63.0	-	63.0	63.0	0

Table 6.13 Length characteristics of age classes of male, female and total mussels sampled from Buffalo billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	4	0.78	33.5	8.73	24.5	44.5	19.6, 47.4
	female	5	0.78	31.1	2.38	32.5	38.5	33.2, 39.1
	total	174	0.30	12.2	9.32	2.5	44.5	10.8, 13.6
1.00-1.99	male	35	1.23	41.4	3.58	33.5	48.5	40.2, 42.6
	female	20	1.39	44.0	3.90	34.5	50.5	42.2, 45.9
	total	55	1.28	42.4	3.87	33.5	50.5	41.3, 43.4
2.00-2.99	male	18	2.30	46.4	2.22	42.0	50.5	45.3, 47.5
	female	26	2.36	47.9	3.70	41.5	55.5	46.4, 49.4
	total	44	2.33	47.3	3.24	41.5	55.5	46.3, 48.3
3.00-3.99	male	17	3.26	48.9	3.70	39.5	52.5	47.0, 50.8
	female	16	3.22	51.0	3.46	44.5	58.5	49.2, 52.8
	total	33	3.24	49.9	3.70	39.5	58.5	48.6, 51.2
4.00-4.99	male	20	4.19	52.4	3.48	47.5	58.0	50.8, 54.0
	female	18	4.25	52.7	3.61	43.0	57.0	50.9, 54.5
	total	38	4.22	52.5	3.50	43.0	58.0	51.4, 53.7
5.00-5.99	male	20	5.29	54.3	3.37	49.0	61.0	52.7, 55.9
	female	19	5.38	56.6	4.18	49.5	63.5	54.6, 58.6
	total	39	5.33	55.4	3.91	49.0	63.5	54.1, 56.7
6.00-6.99	male	35	6.39	56.6	4.90	47.5	73.0	55.0, 58.3
	female	30	6.38	56.7	5.15	48.0	71.0	54.7, 58.6
	total	65	6.38	56.7	4.98	47.5	73.0	55.4, 57.9
7.00-7.99	male	48	7.34	57.5	3.59	48.0	66.0	56.5, 58.6
	female	44	7.36	58.2	3.98	51.5	68.5	57.0, 59.4
	total	92	7.35	57.9	3.78	48.0	68.5	57.1, 58.6
8.00-8.99	male	46	8.35	59.3	4.47	51.0	70.0	58.0, 60.7
	female	30	8.34	59.4	3.43	52.0	67.0	58.1, 60.7
	total	76	8.35	59.3	4.07	51.0	70.0	58.4, 60.3
9.00-9.99	male	42	9.28	59.5	3.48	52.0	68.0	58.4, 60.5
	female	34	9.24	57.9	4.56	45.0	66.5	56.4, 59.5
	total	77	9.27	58.8	4.03	45.0	68.0	57.9, 59.7
10.0-10.99	male	30	10.42	61.1	3.55	54.5	68.0	59.8, 62.5
	female	33	10.32	60.2	5.14	49.0	70.0	58.4, 62.1
	total	63	10.37	60.7	4.44	49.0	70.0	59.5, 61.8
11.0-11.99	male	33	11.31	60.5	3.13	54.5	66.0	59.4, 61.6
	female	21	11.27	61.3	5.06	54.0	74.0	59.0, 63.6
	total	54	11.29	60.8	3.96	54.0	74.0	59.7, 61.9
12.0-12.99	male	20	12.29	60.9	5.31	51.0	74.5	58.5, 63.4
	female	22	12.30	60.2	3.66	53.0	66.5	58.6, 61.8
	total	42	12.30	60.6	4.48	51.0	74.5	59.2, 62.0
13.0-13.99	male	27	13.35	59.6	4.32	48.5	67.0	57.9, 61.3
	female	25	13.38	61.2	5.16	50.0	75.0	59.1, 63.4
	total	52	13.37	60.4	4.77	48.5	75.0	59.1, 61.7
14.0-14.99	male	15	14.25	60.2	2.67	56.0	66.0	58.8, 61.7
	female	19	14.31	60.5	4.60	53.0	69.0	58.3, 62.7
	total	34	14.28	60.4	3.80	53.0	69.0	59.0, 61.7
15.0-15.99	male	26	15.41	60.8	4.03	50.5	68.0	59.2, 62.4
	female	15	15.25	61.0	3.25	56.5	68.0	59.2, 62.8
	total	41	15.35	60.9	3.72	50.5	68.0	59.7, 62.0
16.0-16.99	male	26	16.30	61.9	4.04	50.0	68.0	60.3, 63.6
	female	18	16.35	62.4	4.35	55.5	70.0	60.2, 64.6
	total	44	16.32	62.1	4.12	50.0	70.0	60.9, 63.4

Table 6.13 (Ctd)

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
17.0-17.99	male	22	17.28	61.1	3.87	53.0	67.0	59.4, 62.8
	female	19	17.27	61.7	4.71	53.0	76.0	59.4, 64.0
	total	41	17.28	61.4	4.24	53.0	76.0	60.0, 62.7
18.0-18.99	male	27	18.33	60.7	4.27	49.0	67.5	59.0, 62.4
	female	17	18.40	63.0	3.99	55.0	68.5	60.9, 65.0
	total	44	18.36	61.6	4.27	49.0	68.5	60.3, 62.9
19.0-19.99	male	33	19.42	61.5	5.11	50.5	70.5	59.7, 63.3
	female	18	19.38	60.1	4.87	54.5	72.0	57.7, 62.5
	total	51	19.41	61.0	5.02	50.5	72.0	59.6, 62.4
20.0-20.99	male	23	20.31	61.1	6.38	53.0	83.5	58.3, 63.8
	female	29	20.31	62.8	5.55	53.0	81.0	60.7, 64.9
	total	52	20.31	62.0	5.93	53.0	83.5	60.4, 63.7
21.0-21.99	male	26	21.29	61.8	4.81	53.0	71.0	59.9, 63.8
	female	23	21.37	62.1	4.83	55.5	71.5	60.0, 64.2
	total	49	21.33	62.0	4.77	53.0	71.5	60.6, 63.3
22.0-22.99	male	20	22.39	58.6	4.19	51.5	67.5	56.6, 60.6
	female	22	22.41	63.9	5.31	51.5	73.5	61.5, 66.2
	total	42	22.40	61.4	5.46	51.5	73.5	59.7, 63.1
23.0-23.99	male	23	23.25	61.8	5.61	50.0	71.5	59.4, 64.3
	female	20	23.43	61.1	3.70	54.0	69.0	59.4, 62.8
	total	43	23.33	61.5	4.78	50.0	71.5	60.0, 63.0
24.0-24.99	male	28	24.39	61.7	5.09	49.0	69.0	59.7, 63.7
	female	14	24.5	62.6	3.09	59.0	69.0	60.8, 64.4
	total	42	24.43	62.0	4.50	49.0	69.0	60.6, 63.4
25.0-25.99	male	13	25.42	62.6	2.35	59.5	66.5	61.2, 64.0
	female	14	25.40	61.6	4.97	53.0	69.0	58.7, 64.4
	total	27	25.41	62.1	3.90	53.0	69.0	60.5, 63.6
26.0-26.99	male	11	26.35	63.4	4.23	56.5	69.0	60.6, 66.3
	female	10	26.33	60.3	4.76	53.0	67.5	56.9, 63.7
	total	21	26.34	61.9	4.65	53.0	69.0	59.8, 64.1
27.0-27.99	male	7	27.38	62.7	3.87	59.5	71.0	59.1, 66.3
	female	9	27.28	62.1	6.52	52.0	74.0	57.1, 67.1
	total	16	27.32	62.3	5.36	52.0	74.0	59.5, 65.2
28.0-28.99	male	10	28.38	61.4	4.31	55.0	67.0	58.3, 64.4
	female	10	28.21	60.7	5.71	50.5	69.5	56.6, 64.7
	total	20	28.30	61.0	4.94	50.5	69.5	58.7, 63.3
29.0-29.99	male	3	29.17	66.2	5.97	62.0	73.0	51.3, 81.0
	female	2	29.27	57.3	0.35	57.0	57.5	- -
	total	5	29.21	62.6	6.46	57.0	73.0	54.6, 70.6
30.0-30.99-	male	5	30.37	58.9	5.72	52.5	66.5	51.8, 66.0
	female	6	30.48	67.1	3.51	64.5	74.0	63.4, 70.8
	total	11	30.43	63.4	6.12	52.5	74.0	59.3, 67.5
31.0-31.99	male	3	31.45	66.7	4.51	62.0	71.0	55.5, 77.9
	female	1	31.78	64.0	-	64.0	64.0	- -
	total	4	31.54	66.0	3.92	62.0	71.0	59.8, 72.2
32.0-32.99	male	1	32.50	64.0	-	64.0	64.0	- -
	female	4	32.09	62.0	6.52	55.5	71.0	51.6, 72.4
	total	5	32.17	62.4	5.72	55.5	71.0	55.3, 69.5
33.0-33.99	male	1	33.04	63.5	-	63.5	63.5	- -
	female	1	33.50	64.0	-	64.0	64.0	- -
	total	2	33.27	63.8	0.35	63.5	64.0	- -
34.0-34.99	male	1	34.23	67.0	-	67.0	67.0	- -
	female	-	-	-	-	-	-	- -
	total	1	34.23	67.0	-	67.0	67.0	- -
35.0-35.99	male	2	35.37	59.8	4.60	56.5	63.0	- -
	female	-	-	-	-	-	-	- -
	total	2	35.37	59.8	4.60	56.5	63.0	- -

Table 6.14 Length characteristics of age classes of male, female and total mussels sampled from the Island billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	3	0.80	49.0	8.0	41.0	57.0	29.1, 68.9
	female	4	0.77	45.9	3.12	42.5	49.0	40.9, 50.8
	total	7	0.78	47.2	5.38	41.0	57.0	42.2, 52.2
1.00-1.99	male	44	1.39	51.3	5.72	42.0	61.0	49.5, 53.0
	female	43	1.38	52.5	5.04	43.0	66.0	50.9, 54.0
	total	87	1.38	51.9	5.39	42.0	66.0	50.7, 53.0
2.00-2.99	male	39	2.46	60.7	4.84	51.0	69.0	59.1, 62.2
	female	25	2.44	62.6	4.74	53.0	70.5	60.7, 64.6
	total	64	2.45	61.4	4.86	51.0	70.5	60.2, 62.7
3.00-3.99	male	46	3.51	65.5	4.14	53.5	75.0	64.3, 66.7
	female	46	3.38	66.1	5.07	50.0	74.0	64.6, 67.6
	total	92	3.45	65.8	4.61	50.0	75.0	64.8, 66.7
4.00-4.99	male	41	4.36	67.5	3.51	54.0	72.0	66.4, 68.7
	female	46	4.40	69.6	3.79	61.0	77.0	68.5, 70.8
	total	87	4.38	68.7	3.79	54.0	77.0	67.9, 69.5
5.00-5.99	male	69	5.48	72.5	5.19	58.0	87.5	71.3, 73.7
	female	62	5.46	73.0	4.94	55.0	83.0	71.8, 74.3
	total	133	5.46	72.7	5.04	55.0	87.5	71.9, 73.6
6.00-6.99	male	81	6.43	75.8	4.86	63.0	88.0	74.7, 76.9
	female	84	6.40	74.9	5.14	61.5	92.0	73.8, 76.1
	total	166	6.41	75.4	5.00	61.5	92.0	74.6, 76.1
7.00-7.99	male	51	7.40	78.8	5.94	60.0	94.0	77.1, 80.5
	female	49	7.48	76.3	4.60	60.0	89.0	74.9, 77.6
	total	100	7.44	77.6	5.45	60.0	94.0	76.5, 78.6
8.00-8.99	male	17	8.50	81.4	4.94	73.0	91.0	78.8, 83.9
	female	22	8.55	80.2	5.34	69.5	89.0	77.8, 82.6
	total	39	8.53	80.7	5.13	69.5	91.0	79.1, 82.4
9.00-9.99	male	19	9.39	78.8	6.66	66.0	90.0	75.6, 82.0
	female	11	9.50	80.5	4.99	69.0	86.0	77.1, 83.8
	total	30	9.43	79.4	6.06	66.0	90.0	77.1, 81.7
10.0-10.99	male	6	10.41	78.4	3.81	73.5	83.0	74.4, 82.4
	female	8	10.40	83.9	3.82	78.5	88.5	80.8, 87.1
	total	14	10.40	81.6	4.64	73.5	88.5	78.9, 84.3
11.0-11.99	male	11	11.36	85.3	3.43	79.0	90.0	83.0, 87.6
	female	8	11.61	86.8	5.76	79.5	95.0	82.0, 91.6
	total	19	11.47	85.9	4.48	79.0	95.0	83.8, 88.1
12.0-12.99	male	6	12.40	83.3	3.0	79.0	87.0	80.1, 86.4
	female	6	12.44	85.4	4.76	81.5	92.0	80.4, 90.4
	total	12	12.42	84.3	3.96	79.0	92.0	81.8, 86.9
13.0-13.99	male	6	13.70	87.8	4.43	82.0	95.0	83.2, 92.5
	female	1	13.74	84.5	-	84.5	84.5	- -
	total	7	13.70	87.4	4.24	82.0	95.0	84.8, 89.9
14.0-14.99	male	5	14.18	85.4	2.77	81.5	88.0	82.0, 88.8
	female	1	14.17	89.0	-	89.0	89.0	- -
	total	6	14.18	86.0	2.88	81.5	89.0	83.0, 89.0
15.0-15.99	male	2	15.71	88.8	0.35	88.5	89.0	- -
	female	1	15.32	79.0	-	79.0	79.0	- -
	total	3	15.58	85.5	5.63	79.0	89.0	71.5, 99.5
16.0-16.99	male	3	16.40	89.0	5.57	83.0	94.0	75.2,102.8
	female	-	-	-	-	-	-	- -
	total	3	16.4	89.0	5.57	83.0	94.0	75.2,102.8
17.0-17.99	male	1	17.41	96.0	-	96.0	96.0	- -
	female	1	17.18	91.5	-	91.5	91.5	- -
	total	2	17.30	93.8	3.18	91.5	96.0	- -
19.0-19.99	male	1	19.7	86.0	-	86.0	86.0	- -
	female	-	-	-	-	-	-	- -
	total	1	19.74	86.0	-	86.0	86.0	- -

Table 6.15 Length characteristics of age classes of male, female and total mussels sampled from the Hidden billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	1	0.08	48.0	-	48.0	48.0	- -
	female	-	-	-	-	-	-	- -
	total	1	0.08	48.0	-	48.0	48.0	- -
1.00-1.99	male	2	1.08	37.8	13.08	28.5	47.0	- -
	female	2	1.08	48.3	0.35	48.0	48.5	- -
	total	4	1.08	43.0	9.69	28.5	48.5	27.6, 58.4
2.00-2.99	male	5	2.08	54.7	3.03	50.5	58.0	50.9, 58.5
	female	3	2.08	57.0	2.00	55.0	59.0	52.0, 62.0
	total	8	2.08	55.6	2.80	50.5	59.0	53.2, 57.9
3.00-3.99	male	1	3.08	53.5	-	53.5	53.5	- -
	female	1	3.08	62.0	-	62.0	62.0	- -
	total	2	3.08	57.8	6.01	53.5	62.0	- -
4.00-4.99	male	1	4.08	71.5	-	71.5	71.5	- -
	female	3	4.08	67.0	6.24	62.0	74.0	51.5, 82.5
	total	4	4.08	68.1	5.57	62.0	74.0	59.3, 77.0
5.00-5.99	male	2	5.08	66.0	1.41	65.0	67.0	- -
	female	2	5.08	69.5	5.66	65.5	73.5	- -
	total	4	5.08	67.8	3.93	65.0	73.5	61.5, 74.0
6.00-6.99	male	2	6.08	64.3	0.35	64.0	64.5	- -
	female	3	6.08	68.2	7.65	63.5	77.0	49.2, 87.2
	total	5	6.08	66.6	5.82	63.5	77.0	59.4, 73.8
7.00-7.99	male	5	7.08	67.9	4.48	61.0	72.0	62.3, 73.5
	female	4	7.08	72.0	6.48	63.0	78.0	61.7, 82.3
	total	9	7.08	69.7	5.52	61.0	78.0	65.5, 74.0
8.00-8.99	male	2	8.08	79.3	1.77	78.0	80.5	- -
	female	5	8.08	71.1	5.07	66.0	78.5	64.8, 77.4
	total	7	8.08	73.4	5.78	66.0	80.5	68.1, 78.8
9.00-9.99	male	1	9.08	70.0	-	70.0	70.0	- -
	female	1	9.08	78.5	-	78.5	78.5	- -
	total	2	9.08	74.3	6.01	70.0	78.5	- -
10.0-10.99	male	1	10.08	71.0	-	71.0	71.0	- -
	female	-	-	-	-	-	-	- -
	total	1	10.08	71.0	-	71.0	71.0	- -
11.0-11.99	male	1	11.08	87.0	-	87.0	87.0	- -
	female	-	-	-	-	-	-	- -
	total	1	11.08	87.0	-	87.0	87.0	- -

Table 6.16 Length characteristics of age classes of male, female and total mussels sampled from JaJa billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
	male	-	-	-	-	-	-	- -
0.01–0.99	female	1	0.84	49.5	-	49.5	49.5	- -
	total	2	0.52	37.3	17.32	25.0	49.5	- -
	male	7	1.52	55.9	8.99	43.0	73.0	47.6, 64.2
1.00–1.99	female	7	1.31	48.3	2.86	44.5	53.0	45.7, 50.9
	total	14	1.41	52.1	7.51	43.0	73.0	47.7, 56.4
	male	8	2.38	54.7	2.17	52.0	58.5	52.9, 56.5
2.00–2.99	female	11	2.37	56.0	4.09	48.5	61.0	53.3, 58.8
	total	19	2.38	55.5	3.41	48.5	61.0	53.8, 57.1
	male	7	3.40	58.2	2.38	54.0	61.0	56.0, 60.4
3.00–3.99	female	4	3.40	59.8	4.27	57.0	66.0	53.0, 66.5
	total	11	3.40	58.8	3.08	54.0	66.0	55.7, 59.9
	male	10	4.31	64.2	2.93	60.5	69.0	62.1, 66.3
4.00–4.99	female	4	4.64	66.1	1.84	64.0	68.5	63.2, 69.1
	total	14	4.40	64.7	2.76	60.5	69.0	63.1, 66.3
	male	11	5.34	65.2	5.34	55.0	72.5	61.6, 68.8
5.00–5.99	female	9	5.38	66.0	3.78	57.0	69.0	63.1, 68.9
	total	20	5.36	65.6	4.60	55.0	72.5	63.4, 67.7
	male	20	6.48	68.6	5.32	57.0	79.0	66.1, 71.0
6.00–6.99	female	14	6.45	69.6	2.56	66.0	75.5	68.1, 71.1
	total	34	6.47	69.0	4.38	57.0	79.0	67.5, 70.5
	male	17	7.59	71.1	5.96	52.0	80.0	68.0, 74.1
7.00–7.99	female	24	7.43	71.9	4.62	64.0	82.5	70.0, 73.9
	total	41	7.50	71.6	5.16	52.0	82.5	69.9, 73.2
	male	17	8.42	74.2	3.21	68.0	80.0	72.6, 75.9
8.00–8.99	female	22	8.40	73.9	4.37	66.0	86.5	71.9, 75.8
	total	39	8.41	74.0	3.87	66.0	86.5	72.8, 75.3
	male	15	9.39	74.5	3.97	68.0	82.0	72.3, 76.7
9.00–9.99	female	14	9.36	74.4	3.88	68.0	79.0	72.1, 76.6
	total	29	9.38	74.4	3.86	68.0	82.0	72.9, 75.9
	male	6	10.32	74.3	2.80	71.0	79.0	71.4, 77.3
10.0–10.99	female	12	10.32	74.6	3.81	69.0	81.0	72.2, 77.1
	total	18	10.32	74.5	3.42	69.0	81.0	72.8, 76.2
	male	6	11.26	76.3	6.43	72.0	89.0	69.5, 83.0
11.0–11.99	female	14	11.38	75.5	4.55	67.0	82.0	72.9, 78.2
	total	20	11.34	75.8	5.01	67.0	89.0	73.4, 78.1

Table 6.16 (Ctd)

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
	male	11	12.31	78.3	4.68	69.5	84.0	75.1, 81.4
12.0-	female	7	12.46	78.6	6.54	68.5	86.0	72.6, 84.7
12.99	total	18	12.37	78.4	5.29	68.5	86.0	75.8, 81.1
	male	12	13.41	79.8	2.43	76.0	84.0	78.2, 81.3
13.0-	female	11	13.37	82.3	4.84	75.0	90.0	79.0, 85.5
13.99	total	23	13.39	81.0	3.91	75.0	90.0	79.3, 82.7
	male	4	14.41	84.4	1.80	83.0	87.0	81.5, 87.2
14.0-	female	8	14.36	81.3	1.28	79.0	83.0	80.2, 82.4
14.99	total	12	14.38	82.3	2.05	79.0	87.0	81.0, 83.6
	male	5	15.37	87.6	7.96	77.0	98.0	77.7, 97.5
15.0-	female	7	15.57	82.8	6.59	74.0	93.0	76.7, 88.9
15.99	total	13	15.47	84.6	6.99	74.0	98.0	80.4, 88.8
	male	7	16.29	84.5	6.28	73.5	91.0	78.7, 90.3
16.0-	female	5	16.38	80.3	2.49	77.0	83.0	77.2, 83.4
16.99	total	13	16.36	82.7	5.11	73.5	91.0	79.6, 85.8
	male	3	17.42	85.3	2.52	83.0	88.0	79.1, 91.6
17.0-	female	2	17.53	82.3	7.42	77.0	87.5	- -
17.99	total	5	17.46	84.1	4.45	77.0	88.0	78.6, 89.6
	male	3	18.63	87.2	11.75	75.5	99.0	58.0,116.4
18.0-	female	3	18.37	79.2	7.25	72.0	86.5	61.2, 97.2
18.99	total	6	18.50	83.2	9.77	72.0	99.0	72.9, 93.4
	male	1	19.24	85.0	-	85.0	85.0	- -
19.0-	female	-	-	-	-	-	-	- -
19.99	total	1	19.24	85.0	-	85.0	85.0	- -
	male	2	20.38	92.0	1.41	91.0	93.0	- -
20.0-	female	1	20.24	95.0	-	95.0	95.0	- -
20.99	total	3	20.33	93.0	2.00	91.0	95.0	88.0, 98.0
	male	1	21.52	95.0	-	95.0	95.0	- -
21.0-	female	-	-	-	-	-	-	- -
21.99	total	1	21.52	95.0	-	95.0	95.0	- -

Table 6.17 Length characteristics of age classes of male, female and total mussels sampled from Leichhardt billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	13	0.77	46.3	5.34	38.0	57.0	43.0, 49.5
	female	16	0.82	46.6	6.51	36.0	55.0	43.2, 50.1
	total	29	0.80	46.5	5.91	36.0	57.0	44.2, 48.7
1.00-1.99	male	27	1.54	55.4	5.93	44.0	68.0	53.1, 57.8
	female	20	1.62	56.3	5.28	44.0	66.0	53.8, 58.8
	total	48	1.56	55.4	6.13	38.0	68.0	53.7, 57.2
2.00-2.99	male	28	2.40	61.6	4.69	49.0	70.5	59.8, 63.5
	female	18	2.29	60.8	6.37	51.0	76.5	57.6, 64.0
	total	46	2.35	61.3	5.36	49.0	76.5	59.7, 62.9
3.00-3.99	male	19	3.37	64.3	5.43	53.0	78.0	61.7, 66.9
	female	12	3.43	64.6	4.58	58.0	75.0	61.7, 67.5
	total	31	3.39	64.4	5.04	53.0	78.0	62.6, 66.3
4.00-4.99	male	32	4.50	70.5	6.43	56.5	85.0	68.2, 72.8
	female	42	4.54	69.4	6.45	58.5	82.5	67.4, 71.4
	total	74	4.52	69.9	6.42	56.5	85.0	68.4, 71.4
5.00-5.99	male	68	5.55	73.8	5.55	58.5	87.0	72.5, 75.2
	female	90	5.46	74.7	6.13	58.5	88.0	73.5, 76.0
	total	158	5.50	74.3	5.88	58.5	88.0	73.4, 75.3
6.00-6.99	male	105	6.40	75.4	6.83	57.0	92.0	74.1, 76.7
	female	87	6.44	76.5	6.22	62.5	90.5	75.2, 77.8
	total	192	6.42	75.9	6.57	57.0	92.0	75.0, 76.8
7.00-7.99	male	108	7.44	77.7	6.66	61.0	93.0	76.4, 79.0
	female	59	7.37	78.2	6.99	62.5	89.0	76.4, 80.1
	total	168	7.41	77.9	6.76	61.0	93.0	76.9, 79.0
8.00-8.99	male	40	8.34	80.5	7.36	65.5	104.0	78.2, 82.9
	female	23	8.41	77.5	4.27	71.0	86.0	75.6, 79.3
	total	63	8.37	79.4	6.53	65.5	104.0	77.8, 81.1
9.00-9.99	male	17	9.23	86.6	6.47	77.0	97.5	83.2, 89.9
	female	11	9.28	81.1	5.44	70.5	92.0	77.4, 84.7
	total	28	9.25	84.4	6.57	70.5	97.5	81.9, 87.0
10.0-10.99	male	7	10.22	85.1	66.6	78.0	94.0	78.9, 91.2
	female	1	10.70	78.0	-	78.0	78.0	- -
	total	8	10.28	84.2	6.65	78.0	94.0	78.6, 89.8
11.0-11.9	male	4	11.41	84.5	3.32	80.0	88.0	79.2, 89.8
	female	1	11.22	91.0	-	91.0	91.0	- -
	total	5	11.38	85.8	4.09	80.0	91.0	80.7, 90.9
12.0-12.99	male	2	12.82	93.3	8.13	87.5	99.0	20.2,166.3
	female	1	12.20	77.5	-	77.5	77.5	- -
	total	3	12.61	88.0	10.76	77.5	99.0	61.3,114.7
17.0-17.99	male	-	-	-	-	-	-	- -
	female	1	17.27	96.0	-	96.0	96.0	- -
	total	1	17.27	96.0	-	96.0	96.0	- -

Table 6.18 Length characteristics of age classes of male, female and total mussels sampled from Jabiluka billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	6	0.96	40.0	6.84	32.0	51.0	32.8, 47.2
	female	2	0.86	46.5	7.78	41.0	52.0	- -
	total	8	0.93	41.6	7.15	32.0	52.0	35.7, 47.6
1.00-1.99	male	16	1.62	51.5	5.51	40.0	60.0	48.6, 54.5
	female	9	1.76	52.3	6.41	41.5	61.0	47.4, 57.2
	total	25	1.67	51.8	5.73	40.0	61.0	49.4, 54.2
2.00-2.99	male	34	2.45	57.5	4.42	47.0	67.0	56.0, 59.0
	female	25	2.62	56.4	4.98	46.5	64.0	54.3, 58.4
	total	59	2.52	57.0	4.66	46.5	67.0	55.8, 58.2
3.00-3.99	male	39	3.45	60.6	4.66	54.0	74.0	59.1, 62.1
	female	25	3.40	62.9	5.47	51.0	71.5	60.7, 65.2
	total	64	3.43	61.5	5.08	51.0	74.0	60.2, 62.8
4.00-4.99	male	46	4.51	64.5	5.48	56.0	79.0	62.9, 66.1
	female	31	4.55	66.2	5.64	52.0	77.0	64.1, 68.3
	total	78	4.52	65.2	5.55	52.0	79.0	64.0, 66.5
5.00-5.99	male	58	5.46	68.3	4.45	57.5	77.0	67.1, 69.4
	female	43	5.50	69.5	5.09	58.0	80.0	67.9, 71.0
	total	101	5.48	68.8	4.75	57.5	80.0	67.8, 69.7
6.00-6.99	male	68	6.42	71.3	4.39	63.5	83.0	70.2, 72.3
	female	62	6.52	71.1	5.17	60.5	83.5	69.8, 72.4
	total	131	6.47	71.2	4.74	60.5	83.5	70.4, 72.0
7.00-7.99	male	55	7.36	72.9	4.69	63.0	85.0	71.6, 74.2
	female	68	7.40	73.5	4.97	61.5	84.5	72.3, 74.7
	total	123	7.38	73.2	4.84	61.5	85.0	72.4, 74.1
8.00-8.99	male	37	8.45	75.0	4.67	64.5	85.0	73.5, 76.6
	female	30	8.35	75.6	4.71	63.0	82.5	73.8, 77.4
	total	68	8.40	75.4	4.74	63.0	85.0	74.3, 76.6
9.00-9.99	male	22	9.49	76.1	6.50	60.5	87.0	73.2, 79.0
	female	23	9.39	78.8	6.77	69.0	93.0	75.8, 81.7
	total	45	9.44	77.5	6.70	60.5	93.0	75.5, 79.5
10.0-10.99	male	17	10.35	80.0	5.46	73.0	94.0	77.2, 82.8
	female	12	10.40	78.2	4.26	71.0	87.0	75.5, 80.9
	total	29	10.37	79.3	5.00	71.0	94.0	77.4, 81.2
11.0-11.99	male	15	11.36	79.2	5.28	70.5	92.0	76.3, 82.2
	female	19	11.46	82.2	5.43	70.0	93.0	79.5, 84.8
	total	34	11.42	80.9	5.49	70.0	93.0	79.0, 82.8

Table 6.18 (Ctd)

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
12.0-12.99	male	14	12.42	83.5	3.92	75.0	90.0	81.2, 85.7
	female	7	12.36	80.6	4.79	72.0	86.0	76.2, 85.1
	total	21	12.40	82.5	4.32	72.0	90.0	80.6, 84.5
13.0-13.99	male	5	13.60	84.7	3.63	79.0	89.0	80.2, 89.2
	female	10	13.23	84.3	6.44	69.0	91.0	79.7, 88.9
	total	15	13.35	84.4	5.52	69.0	91.0	81.4, 87.5
14.0-14.99	male	4	14.59	85.0	8.60	75.0	94.0	71.3, 98.7
	female	4	14.15	84.9	5.51	77.5	90.0	76.1, 93.7
	total	8	14.37	84.9	6.69	75.0	94.0	79.4, 90.5
15.0-15.99	male	1	15.72	83.5	-	83.5	83.5	- -
	female	5	15.51	89.5	2.55	85.0	91.0	86.3, 92.7
	total	6	15.55	88.5	3.35	83.5	91.0	85.0, 92.0
16.0-16.99	male	2	16.60	95.5	0.71	95.0	96.0	- -
	female	3	16.44	89.7	1.04	88.5	90.5	87.1, 92.3
	total	5	16.50	92.0	3.30	88.5	96.0	87.9, 96.1
17.0-17.99	male	6	17.59	83.5	6.06	76.0	93.0	77.1, 89.9
	female	2	17.24	92.5	13.44	83.0	102.0	- -
	total	8	17.50	85.8	8.33	76.0	102.0	78.8, 92.7
18.0-18.99	male	4	18.31	81.0	6.80	75.0	88.5	70.2, 91.8
	female	4	18.36	86.8	5.56	83.0	95.0	77.9, 95.6
	total	8	18.34	83.9	6.52	75.0	95.0	78.4, 89.3
19.0-19.99	male	4	19.50	91.1	2.66	88.0	94.0	86.9, 95.4
	female	2	19.20	81.5	2.12	80.0	83.0	- -
	total	6	19.40	87.9	5.46	80.0	94.0	82.2, 93.7
20.0-20.99	male	2	20.35	85.0	2.83	83.0	87.0	- -
	female	2	20.24	90.8	3.89	88.0	93.5	- -
	total	4	20.30	87.9	4.33	83.0	93.5	81.0, 94.8
21.0-21.99	male	1	21.86	80.0	-	80.0	80.0	- -
	female	2	21.12	85.0	-	85.0	85.0	- -
	total	3	21.37	83.3	2.89	80.0	85.0	76.2, 90.5
22.0-22.99	male	1	22.72	88.0	-	88.0	88.0	- -
	female	1	22.20	93.0	-	93.0	93.0	- -
	total	2	22.46	90.5	3.54	88.0	93.0	- -
23.0-23.99	male	1	23.27	84.0	-	84.0	84.0	- -
	female	-	-	-	-	-	-	- -
	total	1	23.27	84.0	-	84.0	84.0	- -

Table 6.19 Length characteristics of age classes of male, female and total mussels sampled from Nankeen billabong. Total mussels includes males, females, unsexed individuals and hermaphrodites.

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
0.01-0.99	male	2	0.79	39.5	3.54	37.0	42.0	- -
	female	2	0.97	46.3	1.77	45.0	47.5	- -
	total	124	0.25	23.6	25.39	2.0	76.0	19.1, 28.1
1.00-1.99	male	29	1.51	45.7	7.01	33.5	56.0	43.0, 48.4
	female	50	1.49	47.9	7.58	34.0	72.5	45.7, 50.1
	total	98	1.49	46.3	7.90	21.0	72.5	44.7, 47.8
2.00-2.99	male	33	2.50	52.1	3.71	43.0	59.0	50.8, 53.4
	female	23	2.37	53.8	6.03	40.0	70.5	51.2, 56.4
	total	57	2.45	52.8	4.79	40.0	70.5	51.6, 54.1
3.00-3.99	male	26	3.52	57.3	5.55	45.0	75.5	55.1, 59.5
	female	21	3.50	57.4	3.78	48.0	61.0	55.7, 59.1
	total	48	3.52	57.4	4.74	45.0	75.5	56.0, 58.8
4.00-4.99	male	42	4.49	59.8	4.57	53.0	71.0	58.4, 61.2
	female	39	4.54	60.8	4.43	51.0	73.0	59.4, 62.2
	total	89	4.53	60.4	4.38	51.0	73.0	59.5, 61.3
5.00-5.99	male	49	5.52	61.9	4.89	54.0	81.0	60.5, 63.3
	female	44	5.53	63.0	5.09	53.5	75.5	61.4, 64.5
	total	108	5.51	62.1	4.76	53.5	81.0	61.2, 63.0
6.00-6.99	male	122	6.54	65.1	4.84	45.0	77.0	64.2, 66.0
	female	101	6.53	65.4	5.48	46.0	76.5	64.3, 66.5
	total	238	6.53	65.2	5.14	45.0	78.0	64.5, 65.9
7.00-7.99	male	142	7.50	65.9	4.72	52.5	81.0	65.1, 66.7
	female	120	7.50	66.7	4.64	56.5	85.0	65.9, 67.5
	total	278	7.50	66.2	4.64	52.5	85.0	65.7, 66.8
8.00-8.99	male	87	8.38	66.7	4.92	53.0	80.0	65.6, 67.7
	female	96	8.41	68.5	5.24	55.0	88.0	67.4, 69.5
	total	187	8.39	67.6	5.14	53.0	88.0	66.9, 68.8
9.00-9.99	male	67	9.44	67.7	5.24	57.0	79.0	66.4, 69.0
	female	66	9.38	68.0	5.53	53.5	82.0	66.6, 69.3
	total	133	9.41	67.8	5.37	53.5	82.0	66.9, 68.8
10.0-10.99	male	50	10.45	68.1	4.43	59.5	78.0	66.8, 69.4
	female	54	10.47	67.9	3.94	60.0	80.0	66.8, 69.0
	total	107	10.46	68.0	4.12	59.5	80.0	67.2, 68.8
11.0-11.99	male	45	11.44	67.8	4.12	59.0	77.0	66.6, 69.1
	female	44	11.49	70.1	4.93	60.0	82.0	68.6, 71.6
	total	106	11.50	68.5	4.66	59.0	82.0	67.6, 69.4

Table 6.19 (Ctd)

Age class	Sex	n	Mean age (years)	Mean length (mm)	S.D.	Minimum length (mm)	Maximum length (mm)	95% C.I. of mean (mm)
12.0-12.99	male	35	12.44	69.1	5.04	59.5	82.0	67.3, 70.8
	female	53	12.43	69.1	4.22	58.0	81.0	67.9, 70.2
	total	109	12.45	68.9	4.43	58.0	82.0	68.0, 69.7
13.0-13.99	male	39	13.41	68.4	4.28	61.0	79.0	67.0, 69.8
	female	24	13.47	70.3	5.80	60.0	81.0	67.8, 72.7
	total	97	13.45	69.2	4.58	60.0	81.0	68.3, 70.1
14.0-14.99	male	46	14.44	68.4	5.57	59.0	87.0	66.8, 70.1
	female	38	14.40	69.2	5.47	61.0	85.0	67.4, 71.0
	total	92	14.40	68.7	5.47	59.0	87.0	67.6, 69.9
15.0-15.99	male	19	15.39	68.1	3.97	60.5	75.0	66.2, 70.0
	female	21	15.38	70.0	5.21	62.0	81.0	67.6, 72.4
	total	46	15.41	69.3	4.54	60.5	81.0	68.0, 70.7
16.00-16.99	male	17	16.47	69.4	4.18	61.5	76.0	67.3, 71.6
	female	11	16.46	72.4	6.31	62.0	83.0	68.1, 76.6
	total	37	16.47	71.0	4.98	61.5	83.0	69.4, 72.7
17.0-17.99	male	15	17.42	68.2	4.25	62.5	76.0	65.8, 70.5
	female	8	17.46	71.9	2.84	66.5	75.0	69.5, 74.3
	total	28	17.44	69.2	4.11	62.5	76.0	67.6, 70.8
18.0-18.99	male	2	18.12	72.5	2.12	71.0	74.0	53.5, 91.6
	female	9	18.46	73.7	4.62	66.0	79.0	70.9, 74.1
	total	15	18.42	72.6	3.96	66.0	79.0	70.4, 74.8
19.0-19.99	male	5	19.34	71.6	7.12	65.0	80.5	62.8, 80.4
	female	2	19.25	76.3	8.84	70.0	82.5	- -
	total	15	19.43	73.2	6.18	65.0	82.5	69.8, 76.6
20.0-20.99	male	2	20.29	64.5	0.71	64.0	65.0	- -
	female	2	20.53	66.8	8.13	61.0	72.5	- -
	total	8	20.44	68.2	5.33	61.0	75.0	63.7, 72.7
21.0-21.99	male	1	21.74	79.0	-	79.0	79.0	- -
	female	1	21.09	79.0	-	79.0	79.0	- -
	total	2	21.42	79.0	-	79.0	79.0	- -

Table 6.20 The parameters of the von Bertalanffy growth equation (and 95% confidence intervals) computed from growth data between sexes and the sexes combined, for the different waterbodies of the Magela Creek.

Waterbody (code)	L_∞			K			t_o		
	males	females	sexes combined	males	females	sexes combined	males	females	sexes combined
Georgetown (2)	62.2 (61.4, 63.0)	63.7 (62.6, 64.9)	62.8 (62.3, 63.3)	0.331 (0.294, 0.369) *	0.243 (0.205, 0.280)	0.290 (0.261, 0.319)	-2.005 (-2.393, -1.618) *	-3.406 (-4.109, -2.703)	-2.539 (-2.792, -2.340)
Gulungul (7)	93.5 (51.2, 135.7)	68.3 (57.5, 79.1)	74.8 (64.2, 85.4)	0.076 (-0.023, 0.175)	0.218 (-0.040, 0.476)	0.161 (0.060, 0.262)	-7.731 (-14.220, -1.241)	-3.646 (-8.326, 1.035)	-4.182 (-6.327, -2.036)
Corndorl (9)	70.1 (66.2, 74.0)	71.3 (66.4, 76.1)	70.6 (67.6, 73.6)	0.153 (0.113, 0.192)	0.132 (0.092, 0.172)	0.143 (0.115, 0.171)	-4.155 (-5.433, -2.878)	-5.108 (-6.744, -3.472)	-4.587 (-5.596, -3.578)
Magela Creek channel (11)	58.3 (57.1, 59.5)	59.7 (58.2, 61.2)	58.9 (58.0, 59.8)	0.361 (0.303, 0.420)	0.328 (0.270, 0.386)	0.345 (0.303, 0.387)	-1.647 (-2.105, -1.190)	-2.022 (-2.554, -1.491)	-1.834 (-2.166, -1.502)
Mudginberri (12)	63.3 (62.6, 64.0)	64.6 (63.8, 65.3)	64.0 (63.5, 64.5)	0.183 (0.157, 0.209)	0.180 (0.154, 0.206)	0.180 (0.163, 0.197)	-5.774 (-6.947, -4.600)	-5.643 (-6.777, -4.510)	-5.746 (-6.287, -5.205)
Buffalo (14)	61.6 (61.1, 62.1)	62.1 (61.5, 62.7)	61.8 (61.4, 62.2)	0.270 (0.237, 0.303)	0.247 (0.207, 0.287)	0.263 (0.237, 0.289)	-2.885 (-3.499, -2.272)	-3.617 (-4.603, -2.631)	-3.113 (-3.639, -2.587)
Island (16)	88.7 (86.1, 91.3)	88.0 (84.7, 91.2)	88.5 (86.5, 90.5)	0.205 (0.174, 0.236)	0.201 (0.162, 0.239)	0.201 (0.177, 0.225)	-2.928 (-3.507, -2.348)	-3.339 (-4.095, -2.583)	-3.145 (-3.608, -2.682)
Hidden (17)	76.9 (65.0, 88.9)	73.7 (67.2, 80.1)	74.9 (69.1, 80.7)	0.302 (-0.004, 0.608)	0.404 (0.045, 0.764)	0.362 (0.134, 0.592)	-1.571 (-4.259, 1.116)	-1.574 (-4.017, 0.869)	-1.437 (-3.090, 0.215)
JaJa (22)	102.0 * (89.0, 115.0)	85.4 (82.1, 88.7)	91.7 (87.5, 95.9)	0.071 * (0.038, 0.103)	0.153 (0.118, 0.189)	0.107 (0.084, 0.130)	-9.213 (-12.685, -5.742)	-4.414 (-5.748, -3.080)	-6.455 (-7.952, -4.958)
Leichhardt (24)	95.7 (84.8, 106.5)	86.1 (81.0, 91.2)	90.2 (85.5, 94.9)	0.141 (0.077, 0.206)	0.233 (0.153, 0.313)	0.183 (0.134, 0.232)	-4.727 (-6.685, -2.768)	-2.892 (-4.193, -1.591)	-3.748 (-4.794, -2.702)
Jabiluka (26)	89.6 (86.5, 92.7)	92.2 (88.1, 96.3)	90.7 (88.2, 93.2)	0.142 (0.117, 0.167)	0.132 (0.103, 0.162)	0.138 (0.119, 0.157)	-4.589 (-5.584, -3.594)	-4.813 (-6.121, -3.506)	-4.650 (-5.436, -3.864)
Nankeen (29)	69.1 * (68.4, 69.8)	70.9 (70.0, 71.9)	70.0 (69.5, 70.5)	0.337 (0.297, 0.377)	0.281 (0.242, 0.319)	0.304 (0.279, 0.329)	-1.662 (-2.125, -1.200)	-2.508 (-3.095, -1.921)	-2.135 (-2.451, -1.819)

* overlap in the 95% confidence intervals between sexes.

Table 6.21 Seasonal measurements of surface chlorophyll a (arbitrary units) from different sites of Mudginberri billabong. Location of the sites is shown in Figure 3.1.

Site	Sampling Date				Mean chlorophyll concentration	Depth (m)
	Aug. 80	Nov. 80	Dec. 80	Jan. 81		
1	2.14	1.00	1.25	1.50	1.47	2.4
2	2.57	1.60	1.00	1.50	1.67	2.2
3	1.71	2.80	2.50	2.25	2.32	3.2
4	2.71	3.60	3.25	2.00	2.89	3.5
5	3.42	3.40	4.50	1.25	3.14	2.8

Table 6.22 Seasonal measurements of surface chlorophyll a ($\mu g/l$) from different sites of Buffalo billabong. Location of the sites is shown in Figure 3.1.

	Site									
	1	2	3	4	5	6	7	8	9	10
Date										
13/7/81	8.04	6.75	6.42	6.42	7.23	7.20	7.20	10.79	10.90	9.83
20/10/81	5.15	5.15	4.81	4.81	6.12	10.46	10.46	6.55	5.60	7.64
mean	6.60	5.95	5.62	5.62	6.68	8.83	8.83	8.67	8.25	8.74
Depth (m)	2.9	3.0	2.4	2.8	2.8	2.7	2.6	3.7	2.2	2.4

Table 6.23 Mean length (mm) and standard deviation (SD) of mussels in relation to depth and sampling transect in Georgetown billabong. Location of the transects is shown in Figure 3.1.

Depth (m)		Transect A	Transect B
0.0-0.49	mean	19.0	27.4
	SD	13.629	14.318
	n	131	41
0.5-0.99	mean	-	33.4
	SD	-	14.168
	n	-	122
1.0-1.49	mean	41.6	37.7
	SD	16.951	19.555
	n	378	519
1.5-1.99	mean	49.5	40.2
	SD	14.294	15.583
	n	957	1159
2.0-2.49	mean	50.7	46.4
	SD	10.883	13.826
	n	378	436
2.5-2.99	mean	53.0	-
	SD	8.413	-
	n	336	-
3.0-3.49	mean	51.1	-
	SD	9.556	-
	n	309	-

Table 6.24 Mean length (mm) and standard deviation (SD) of mussels in relation to depth in Gulungul billabong.

	Depth (m)					
	0.1	0.2	0.3	0.4	0.5	0.6
mean	0.0	0.0	51.1	49.9	53.1	66.3
SD	0.0	0.0	13.657	0.634	12.549	3.889
n	0	0	26	52	30	2

Table 6.25 Mean length (mm) and standard deviation (SD) of mussels in relation to depth and substrate in Corndorl billabong.

Depth (m)		Substrate		
		A	B	C
0.0-0.2	mean	61.7	58.2	64.5
	SD	10.017	4.324	7.188
	n	3	5	4
0.21-0.4	mean	56.3	57.6	61.0
	SD	9.468	5.482	9.403
	n	35	22	12
0.41-0.6	mean	58.3	55.5	53.0
	SD	6.434	6.897	3.256
	n	73	42	3
0.61-0.8	mean	57.2	53.9	56.3
	SD	6.040	6.378	8.483
	n	96	59	12
0.81-1.0	mean	56.1	52.6	-
	SD	7.465	7.901	-
	n	113	98	-
1.01-1.2	mean	55.5	43.2	-
	SD	9.058	12.637	-
	n	96	5	-
1.21-1.4	mean	53.6	-	-
	SD	7.371	-	-
	n	69	-	-
1.41-1.6	mean	54.3	-	-
	SD	6.544	-	-
	n	4	-	-

Key to substrates:

A. Very soft, organic silt and clay
B. Fine gravel with some silt and clay
C. Sand.

Table 6.26 Mean length (mm) and standard deviation (SD) of mussels in relation to depth and substrate in Mudginberri billabong.

Depth (m)		Substrate			
		A	B	C	D
0.0-0.9	mean	44.3	48.6	57.2	58.7
	SD	10.991	9.123	6.353	7.762
	n	29	10	11	9
1.0-1.9	mean	41.7	51.5	52.8	61.0
	SD	14.209	5.549	7.046	4.962
	n	7	75	90	17
2.0-2.9	mean	57.0	56.6	58.4	58.2
	SD	8.881	6.454	7.634	5.437
	n	114	168	111	49
3.0-3.9	mean	60.2	60.8	58.9	-
	SD	7.047	6.169	5.420	-
	n	165	121	52	-
4.0-4.9	mean	63.3	62.1	62.9	-
	SD	7.024	4.794	4.533	-
	n	52	17	15	-
5.0-5.9	mean	64.8	63.8	61.4	-
	SD	5.434	6.662	4.525	-
	n	13	24	11	-

Key to substrates:

A. Sand
B. Sand with a little silt and detritus
C. Sand with silt and detritus (soft)
D. Soft to stiff clay with rubble.

Table 6.27 Mean length (mm) and standard deviation (SD) of mussels in relation to depth and substrate in Buffalo billabong.

Depth (m)		substrate					
		A	B	C	E	F	G
0.0-0.9	mean	49.6	56.2	59.0	-	-	-
	SD	10.753	8.019	6.251	-	-	-
	n	4	8	3	-	-	-
1.0-1.9	mean	53.4	58.0	58.0	59.0	58.6	54.6
	SD	7.219	7.675	2.637	6.659	3.674	7.651
	n	33	50	9	20	20	12
2.0-2.9	mean	56.7	57.1	58.0	60.6	59.71	54.3
	SD	6.610	7.780	6.518	7.244	5.626	7.669
	n	303	302	142	103	51	58
3.0-3.9	mean	59.1	58.1	61.0	64.3	60.2	57.9
	SD	7.156	8.212	7.308	5.785	2.635	5.440
	n	315	141	145	17	43	24
4.0-4.9	mean	61.0	59.8	-	-	-	-
	SD	10.264	5.909	-	-	-	-
	n	8	4	-	-	-	-

Key to substrates:

A. Sand
B. Sand with a little silt and detritus
C. Sand with silt and detritus (soft)
E. Sand, silt and detritus (very soft)
F. Soft clay with some sand, silt and detritus
G. Soft silt, clay and fine detritus.

Table 6.28 Mean length (mm) and standard deviation (SD) of mussels in relation to depth in the floodplain billabongs.

Depth (m)		Billabong				
		Island	JaJa	Leichhardt	Jabiluka	Nankeen
0.0-0.9	mean	64.5	71.0	74.5	68.7	65.3
	SD	0.707	10.036	12.139	10.588	11.100
	n	2	59	207	21	452
1.0-1.9	mean	66.7	71.7	73.0	69.4	66.5
	SD	11.446	9.800	9.941	8.992	7.722
	n	52	192	328	43	564
2.0-2.9	mean	74.3	69.6	58.3	70.2	66.3
	SD	9.378	11.029	12.349	10.380	6.634
	n	38	33	92	26	95
3.0-3.0	mean	67.4	65.1	62.9	-	63.8
	SD	11.039	13.562	9.478	-	10.558
	n	37	13	22	-	17
4.0-4.9	mean	67.6	-	56.0	-	-
	SD	10.703	-	9.239	-	-
	n	8	-	14	-	-

Table 6.29 Linear and quadratic regression equations (with r^2 values and significance) describing the relationship between depth (X in metres) and mean length (Y in mm) of mussels in billabongs of the Magela Creek.

Billabong	Regression equation	r^2	significance
Georgetown	$Y = 19.198 + 20.748X - 3.381X^2$	0.993	**
Corndorl	$Y = 61.067 - 7.648X$	0.861	**
Mudginberri and Buffalo (pooled)	$Y = 6.326 \ln X + 52.022$	0.997	***
Floodplain (pooled)	$Y = 65.688 + 6.222X - 1.941X^2$	0.852	*

Table 6.30 Length characteristics of mussels recorded for the different waterbodies of the Magela Creek.

Billabong	Mean length (mm)	Standard deviation	Maximum length (mm)	Minimum length (mm)	n
Georgetown	43.3	17.46	77.5	3.0	4773
Gulungul	51.4	12.52	80.0	29.0	110
Corndorl	55.9	7.11	80.0	32.0	938
Magela Creek channel	49.5	7.33	69.5	26.0	1153
Mudginberri	54.2	15.27	82.0	2.0	5057
Buffalo	53.3	16.41	83.5	2.5	1518
Island	71.1	10.35	76.0	41.0	872
Hidden	64.7	10.95	87.0	28.5	48
JaJa	71.3	9.89	99.0	25.0	302
Leichhardt	71.8	11.56	104.0	36.0	968
Jabiluka	70.9	10.05	102.0	32.0	852
Nankeen	62.6	13.90	88.0	2.0	1967

Table 6.31 Mean age (years) and standard deviation (SD) of mussels in relation to depth and sampling transect in Georgetown billabong. Location of the transects is shown in Figure 3.1.

Depth (m)		Transect A	Transect B
0.0-0.49	mean	0.91	0.75
	SD	1.755	0.814
	n	129	40
0.5-0.99	mean	-	1.13
	SD	-	1.184
	n	-	106
1.0-1.49	mean	3.57	1.77
	SD	5.230	2.293
	n	218	562
1.5-1.99	mean	5.00	2.86
	SD	4.852	2.888
	n	434	675
2.0-2.49	mean	6.65	3.29
	SD	4.431	3.194
	n	211	323
2.5-2.99	mean	5.60	-
	SD	4.118	-
	n	201	-
3.0-3.49	mean	5.93	-
	SD	4.553	-
	n	210	-

Table 6.32 Mean age (years) and standard deviation (SD) of mussels in relation to depth and sampling sites in Mudginberri billabong. Location of the sites is shown in Figure 3.1.

	Site				
	1	2	3	4	5
mean	6.33	6.42	8.75	11.61	7.84
SD	5.241	5.995	8.694	8.084	6.064
n	446	493	580	425	430
depth (m)	2.4	2.2	3.2	3.5	2.8

Table 6.33 Mean age (years) and standard deviation (SD) of mussels in relation to depth and sampling sites in Buffalo billabong. Location of the sites is shown in Figure 3.1.

	Site									
	1	2	3	4	5	6	7	8	9	10
mean	13.91	14.61	10.28	13.91	12.19	13.46	12.46	10.57	9.57	9.94
SD	9.049	9.220	8.275	9.498	8.572	7.635	7.697	7.265	7.947	6.650
n	129	168	99	232	152	114	130	90	178	206
depth (m)	2.9	3.0	2.4	2.8	2.8	2.7	2.6	3.7	2.2	2.4

Table 6.34 Mean age (years) and standard deviation (SD) of mussels in relation to depth in the floodplain billabongs.

Depth (m)		Billabong				
		Island	JaJa	Leichhardt	Jabiluka	Nankeen
0.0-0.9	mean	2.95	8.58	5.44	6.82	6.96
	SD	0.057	4.324	2.531	3.387	4.229
	n	2	59	167	21	764
1.0-1.9	mean	4.44	8.67	6.45	6.87	9.76
	SD	2.631	4.410	2.323	2.659	4.080
	n	52	192	303	43	499
2.0-2.9	mean	7.18	9.00	6.28	8.66	9.34
	SD	2.927	4.047	1.665	5.758	4.097
	n	38	33	44	26	53
3.0-3.9	mean	5.55	8.26	5.63	-	-
	SD	2.974	2.510	2.011	-	-
	n	37	13	22	-	-
4.0-4.9	mean	5.31	-	6.15	-	-
	SD	2.475	-	1.414	-	-
	n	8	-	2	-	-

Table 6.35 Regression coefficients (±standard deviation) of logistic equations describing the relationship between depth and mean age of mussels on the two transects of Georgetown billabong. The equation is of the form:

$Y = A(1 + Be^{-KX})^{-1}$ where Y = mean age (years), X = depth (m).

TRANSECT	Regression coefficient		
	A	B	K
A	6.136 (±0.424)	13.987 (±13.850)	2.452 (±0.832)
B	4.306 (±0.924)	8.184 (±1.892)	1.494 (±0.391)

Table 6.36 Linear and quadratic regression equations (with r^2 values and significance) describing the relationship between depth (X in metres) and mean age (Y in years) of mussels in some billabongs of the Magela Creek.

Billabong	Regression equation	r^2	Significance
Mudginberri	$Y = -2.491 + 3.788X$	0.895	*
Buffalo	$Y = 5.575 + 6.747X$	0.884	***
Leichhardt	$Y = 3.452 + 3.206X - 0.801X^2$	0.941	**
Nankeen	$Y = 4.509 + 5.979X - 1.658X^2$	0.992	***

Table 6.37 Age characteristics of mussels recorded for the different waterbodies of the Magela Creek.

Billabong	Mean age	Standard deviation	Maximum age	Minimum age	n
Georgetown	3.31	3.910	27.07	0.07	3172
Gulungul	4.51	3.967	12.63	0.63	79
Corndorl	6.79	2.775	19.64	0.93	862
Magela Creek channel	4.33	2.476	15.13	0.97	1153
Mudginberri	7.89	7.271	32.43	0.01	2465
Buffalo	12.13	8.481	35.50	0.04	1501
Island	5.71	2.982	19.74	0.67	872
Hidden	5.28	2.798	11.08	0.08	48
JaJa	9.07	4.431	21.52	0.20	356
Leichhardt	5.83	2.276	17.27	0.22	855
Jabiluka	7.20	3.856	23.27	0.72	852
Nankeen	8.33	4.476	21.74	0.03	2022

Table 6.38 Numbers of juvenile (young-of-year) and adult mussels sampled from different sites in Mudginberri billabong. Location of the sites is shown in Figure 3.1.

Age Class	Site 1	2	3	4	5
juveniles	74	134	210	73	71
adults	851	850	933	822	1039

Table 6.39 Numbers of juvenile (young-of-year) and adult mussels sampled from different sites in Buffalo billabong. Location of the sites is shown in Figure 3.2.

Age Class	Site 1	2	3	4	5	6	7	8	9	10
juveniles	10	17	15	18	22	17	20	10	24	21
adults	133	172	100	232	153	116	131	91	179	208

Table 6.40 Numbers of juvenile (young-of-year) and adult mussels sampled from different depths in Nankeen billabong.

Age Class	Depth (m) 0.2	0.4	0.6	0.9	1.2	1.6	1.9	2.3
juveniles	22	11	14	27	7	1	3	1
adults	120	141	247	256	247	166	88	53

Table 6.42 Partial regression coefficients (and their significance) of the multiple linear regression equation describing the relationship between monthly discharges and age class strength of mussels in the floodplain billabongs.

Regression coefficient	(month)	Students t	Significance
0.1782	(-)	117.74	$P < 0.01$
-0.0017	(Dec)	-33.49	$P < 0.05$
0.0012	(Jan)	36.77	$P < 0.05$
0.0004	(Mar)	45.13	$P < 0.05$
0.0011	(Apr)	82.05	$P < 0.01$
-0.0017	(May)	-3.78	$P > 0.05$
0.0020	(Jun)	2.00	$P > 0.05$

Table 6.41 Regression and correlation coefficients of the significant linear regression equations describing the relationships ($P < 0.05$, unless indicated) between total discharge for the period and year class strength of mussels in the floodplain billabongs. (The equation is of the form:
$Y = mX + b$ where Y = year class strength (arcsin $\sqrt{}$ (Y in percent/100), radians) and X = discharge ($m^3 \times 10^{-6}$).)

Discharge Period	Regression coefficients		r^2 (percent)
	m	b	
Apr	0.0010	0.299	44.9
May	0.0279	0.255	56.7
Mar/Apr	0.0007	0.219	61.5
Apr/May	0.0010	0.296	47.3
May/Jun	0.0220	0.254	55.4
Feb/Mar/Apr	0.0005	0.174	64.0[1]
Mar/Apr/May	0.0007	0.217	62.7
Apr/May/Jun	0.0010	0.295	48.0
Jan/Feb/Mar/Apr	0.0004	0.182	60.7
Feb/Mar/Apr/May	0.0005	0.172	65.1[1]
Mar/Apr/May/Jun	0.0007	0.216	63.1
Dec/Jan/Feb/Mar/Apr	0.0003	0.200	51.0
Jan/Feb/Mar/Apr/May	0.0004	0.181	61.5
Feb/Mar/Apr/May/Jun	0.0005	0.171	65.5[1]
Dec/Jan/Feb/Mar/Apr/May/Jun	0.0003	0.198	52.1

[1] . $P < 0.01$

Table 6.43 Regression and correlation coefficients, and age ranges of the significant ($P < 0.05$) linear regression equations describing the relationship between age and the proportion of female mussels recorded in some billabongs of the Magela Creek. (The equation is of the form: $Y = mX + b$ where Y = Proportion of females within the particular age class (%) and X = age (years).)

Billabong	Linear regression coefficients		r^2	Age range (years)
	b	m		
Mudginberri	180.952	-5.260	0.536	23-30
Island	59.600	-1.537	0.306	4-20
JaJa	99.162	-3.180	0.357	11-22
Leichhardt	75.649	-4.360	0.477	4-13
Jabiluka	38.087	1.070	0.214	1-19

Table 6.44 Age specific survival (S) and instantaneous mortality (Z) rates of mussel populations in Mudginberri and Nankeen billabongs.

Age	Survival after each year from curves in Fig. 5.36. S		Instantaneous mortality rate Z	
	Mudginberri	Nankeen	Mudginberri	Nankeen
0	0.55	0.88	0.60	0.13
1	0.72	0.94	0.33	0.06
2	0.81	0.98	0.21	0.02
3	0.87	1.00	0.14	0.00
4	0.92	1.00	0.08	0.00
5	0.96	0.99	0.04	0.01
6	0.99	0.98	0.01	0.02
7	1.00	0.96	0.00	0.04
8	1.00	0.93	0.00	0.07
9	1.00	0.89	0.00	0.12
10	1.00	0.86	0.00	0.15
11	1.00	0.82	0.00	0.20
12	1.00	0.78	0.00	0.25
13	1.00	0.74	0.00	0.30
14	1.00	0.69	0.00	0.37
15	0.99	0.64	0.01	0.45
16	0.97	0.58	0.03	0.54
17	0.95	0.50	0.05	0.69
18	0.90	0.42	0.11	0.87
19	0.83	0.32	0.19	1.14
20	0.73	0.20	0.31	1.61
21	0.65	0.00	0.43	-
22	0.57*		0.56*	
23	0.57*		0.56*	
24	0.57*		0.56*	
25	0.57*		0.56*	
26	0.57*		0.56*	
27	0.57*		0.56*	
28	0.57*		0.56*	
29	0.57*		0.56*	
30	0.57*		0.56*	
31	0.57*		0.56*	
32	0.57*		0.56*	

*Estimate based on catch-curve analysis.

Table 7.1 Results of the linear regressions performed between each proportion of spermatogenic stage occurring at intervals in the testes of sectioned mussels (from selected billabongs), and the percent of gravid females found among all females examined at the same period and locality. (Both variables arcsine transformed.) Student t values of the slopes (and their significance) and correlation coefficients of the regressions are shown.

SPERMATOGENIC STAGE	BILLABONG					
	MUDGINBERRI		GEORGETOWN		NANKEEN	
	t	r^2	t	r^2	t	r^2
Spermatogonia	0.82	6.3	-0.03	0.1	-0.92	29.7
Sperm morulae	-1.66	21.7	-1.19	41.6	-0.18	1.5
Primary spermatocytes	1.84	25.3	0.54	12.6	0.83	25.6
Secondary spermatocytes	1.71	22.6	2.96	81.4	0.92	29.6
Spermatids	4.36**	65.5	1.18	40.9	3.40	85.3
Spermatozoa	-0.48	2.3	0.52	11.9	0.02	0.0
Empty	-2.44*	37.3	-1.20	41.8	-0.09	0.4
degrees of freedom	10		2		2	

* $P < 0.05$
** $P < 0.01$

Table 7.2 Mean number per ovarian follicle (N) and mean diameter (D) of primary oocytes found in the ovaries of sectioned mussels from selected waterbodies of the Magela Creek, in relation to time. 95 percent confidence intervals about the means are shown in brackets.

MONTH	WATERBODY							
	Georgetown		Magela Creek channel		Mudginberri		Nankeen	
	N	D	N	D	N	D	N	D
Jun (1980)	4.09 (3.09, 4.93)	87.7 (84.7, 90.7)	- -	- -	3.45 (2.06, 4.83)	95.2 (90.8, 99.6)	4.80 (2.93, 6.65)	100.7 (98.1, 103.4)
Jul	- -	- -	- -	- -	3.56 (2.49, 4.63)	91.2 (87.6, 94.8)	- -	- -
Aug	- -	- -	- -	- -	4.02 (2.03, 6.01)	96.3 92.3, 100.3)	- -	- -
Sept	3.08 (2.54, 3.62)	91.1 (87.9, 94.3)	- -	- -	4.39 (2.27, 6.51)	94.3 (90.9, 97.6)	5.54 (4.30, 6.79)	101.8 (98.8, 104.7)
Oct	- -	- -	- -	- -	4.95 (3.62, 6.28)	97.2 (94.3, 100.1)	- -	- -
Nov	- -	- -	4.36 (3.02, 5.70)	98.4 (94.9, 101.8)	5.79 (2.56, 9.01)	101.6 (98.0, 105.2)	- -	- -
Dec	3.44 (2.62, 4.25)	93.7 (90.1, 97.2)	6.62 (2.38, 10.85)	101.9 (98.2, 105.6)	5.42 (2.89, 7.94)	94.6 (91.4, 97.8)	4.35 (1.14, 7.57)	96.3 (92.9, 99.7)
Jan (1981)	- -	- -	6.22 (4.23, 8.22)	96.9 (93.4, 100.3)	4.86 (2.65, 7.07)	97.7 (94.5, 101.0)	- -	- -
Feb	- -	- -	- -	- -	3.57 (1.22, 5.91)	98.7 (95.2, 102.3)	- -	- -
Mar	4.48 (3.46, 5.50)	89.6 (87.0, 92.2)	- -	- -	4.57 (2.86, 6.28)	100.2 (97.0, 103.4)	3.55 (2.17, 4.94)	101.2 (98.4, 104.1)
Apr	- -	- -	- -	- -	4.26 (3.43, 5.08)	92.6 (89.8, 95.5)	- -	- -
May	- -	- -	- -	- -	4.85 (4.67, 5.04)	97.9 (94.2, 101.60)	- -	- -

Table 7.3 Numbers and percentages of hermaphrodites (H) detected by gonadal smears, in relation to the total number of mussels of each age class examined (N), from selected waterbodies of the Magela Creek.

	WATERBODY							
Age	Georgetown		Magela Creek channel		Mudginberri		Nankeen	
	N	H (%)	N	H (%)	N	H (%)	N	H (%)
0	14	–	3	–	89	3 (3.37)	4	–
1	292	2 (0.69)	217	4 (1.84)	51	–	79	–
2	217	-	207	-	63	-	57	1 (1.75)
3	213	1 (0.47)	166	-	76	-	48	1 (2.08)
4	150	1 (0.67)	149	1 (0.67)	71	-	81	-
5	113		130	2 (1.54)	96	-	94	1 (1.06)
6	108		100	-	108	1 (0.925)	224	1 (0.45)
7	115		71	1 (1.41)	142	-	262	-
8	103		42		136	-	184	1 (0.54)
9	109		33		91	-	133	-
10	51		14		83	-	107	3 (2.80)
11	44		10		60	-	90	1 (1.11)
12	40		2		66	-	88	
13	19		-		71	-	63	
14	35		-		67	-	84	
15	19		1		58	-	40	
16	9				70	-	28	
17	9				67	1 (1.49)	23	
18	7				53	-	11	
19	2				49	1 (2.04)	7	
20	1				45	-	4	
21	-				48	-	2	
22	2				23	-		
23	-				23	1 (4.35)		
24	-				14			
25	-				16			
26	-				12			
27	1				5			
28					4			
29					3			
30					-			
31					-			
32					1			
33					1			
Total	1673	4 (0.24)	1145	8 (0.70)	1761	7 (0.40)	1713	9 (0.53)

Table 7.4 Numbers of male (M) and female (F) hermaphrodites detected monthly by gonadal smears, from selected waterbodies of the Magela Creek. A total of 70 mussels from the billabongs and 50 mussels from the Magela Creek channel were examined each month.

	WATERBODY							
Month	Georgetown		Magela Creek channel		Mudginberri		Nankeen	
	M	F	M	F	M	F	M	F
JUN 1980	-	-	-	-	-	-	-	-
JUL	-	-	-	-	-	-	-	-
AUG	-	-	-	-	-	-	-	-
SEP	-	-	-	-	-	-	-	-
OCT	-	-	-	-	-	-	-	-
NOV	-	-	1	-	-	-	1	4*
DEC	-	-	-	1	-	1	-	-
JAN 1981	-	-	-	-	-	1	-	-
FEB	-	1	1	-	-	-	-	-
MAR	-	-	2	1	1	-	-	-
APR	1	-	-	-	-	-	-	-
MAY	-	-	-	-	1	-	-	-
JUN	-	1	-	-	-	-	1	-
JUL	-	-	-	-	-	-	-	-
AUG	-	-	-	-	-	-	-	-
SEP	-	-	-	1	-	-	1	-
OCT	-	-	1	-	-	1	-	-
NOV	-	-	-	-	-	-	-	-
DEC	-	-	-	-	-	-	-	1
JAN 1982	1	-	-	-	-	-	-	-
FEB	-	-	-	-	-	-	-	-
MAR	-	-	-	-	-	-	-	-
APR	-	-	-	-	-	-	-	1
MAY	-	-	-	-	-	-	-	-
TOTAL	2	2	5	3	2	3	3	6

* one brooding larvae.

Table 7.5 Nature and condition of the gonads and inner gills of hermaphrodites sectioned histologically from waterbodies of the Magela Creek.

Waterbody	Dominant visceral gonad	Sex as determined by inner gill morphology	Marsupial condition	Nature of follicles or tubules
Magela Creek channel	male (> 60%)	male	-	confined to discrete regions
"	male (> 80%)	male	-	"
Mudginberri	male (> 90%)	male	-	"
"	male (> 80%)*	male	-	"
"	male (> 90%)	female	brooding developing larvae	"
"	female (> 60%)	female	brooding mature larvae	interspersed

* ovarian follicles almost devoid of oocytes.

Table 7.6 Sex ratios (percentage of both males and females combined that are females) of mature mussels of all age classes and mature young of year mussels, examined from waterbodies of the Magela Creek. Mean length of mature young of year mussels (both males and females) is shown.

	total		young of year		
WATERBODY	no. of males and females examined	sex ratio (percent females)	no. of males and females examined	sex ratio (percent females)	mean length (mm)
Georgetown	1862	48.1	13	23.1	35.5
Gulungul	79	46.8	34	47.1	40.3
Corndorl	938	47.0	1	0.0	35.5
Magela Creek channel	1145	47.2	3	0.0	29.5
Mudginberri	1967	47.9	86	36.0	37.8
Buffalo	1336	46.0**	9	55.5	32.3
Island	872	47.9	7	57.1	47.5
JaJa	354	50.8	1	100.0	49.5
Leichhardt	855	44.8**	29	55.2	46.5
Jabiluka	852	45.9*	8	25.0	42.0
Nankeen	1886	48.3	4	50.0	42.9

* significant ($P < 0.05$) departure from 1:1 sex ratio

** very significant ($P < 0.01$) departure from 1:1 sex ratio.

Table 7.7 Sex ratios (percentage of both mature males and females combined that are females) of juvenile mussels from the Magela Creek waterbodies, in relation to size class of individuals examined. In brackets are the respective numbers examined of mature males and females combined, and individuals with immature (undifferentiated) gonads.

WATERBODY	Size class (mm)			
	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9
Georgetown	25 (4,3)	24 (21,3)	41 (64,1)	48 (162,0)
Gulungul	0 (1,0)	100 (2,0)	60 (10,0)	35 (17,0)
Corndorl	-	50 (10,0)	42 (12,0)	71 (17,0)
Magela Creek channel	0 (2,3)	39 (23,0)	45 (97,3)	49 (160,0)
Mudginberri	33 (3,2)	25 (20,4)	34 (41,3)	56 (54,0)
Buffalo	0 (1,9)	67 (3,3)	33 (18,2)	43 (42,0)
Island	-	-	-	27 (11,0)
JaJa	0 (0,1)	-	-	0 (2,0)
Leichhardt	-	-	80 (5,1)	22 (9,0)
Jabiluka	-	0 (1,0)	0 (2,0)	33 (6,0)
Nankeen	-	50 (6,0)	50 (8,1)	52 (21,0)

Table 7.8 Numbers of male and female mussels from selected waterbodies of the Magela Creek, infected monthly with cercarial trematodes. Infections detected by gonadal smears. A total of 70 mussels from the billabongs and 50 mussels from the Magela Creek channel, were examined each month. Corrected infection rates determined from histological observations.

	WATERBODY							
MONTH	Georgetown		Magela Creek channel		Mudginberri		Nankeen	
	M	F	M	F	M	F	M	F
JUN 1980	-	1	-	-	-	-	-	-
JUL	1	1	-	-	-	-	-	-
AUG	-	1	-	-	-	-	-	-
SEP	1	-	-	-	-	-	-	-
OCT	-	-	-	-	-	-	-	-
NOV	1	2	-	-	1	-	-	-
DEC	-	-	-	-	-	-	-	-
JAN 1981	-	-	1	-	-	1	1	-
FEB	-	1	-	-	-	1	-	-
MAR	-	-	-	-	-	-	-	1
APR	-	-	-	-	-	-	-	-
MAY	-	1	-	-	-	-	-	-
JUN	1	-	-	-	-	-	-	-
JUL	2	-	-	-	-	-	-	-
AUG	2	-	-	-	-	-	-	-
SEP	2	5	-	-	-	-	-	-
OCT	1	1	-	-	-	-	-	-
NOV	-	-	-	-	-	-	-	-
DEC	-	-	-	-	-	-	-	-
JAN 1982	-	-	-	-	-	-	-	1
FEB	-	1	-	-	1	1	-	-
MAR	1	2	-	-	-	-	1	-
APR	-	2	-	-	-	-	-	-
MAY	2	3	-	-	-	-	-	-
TOTAL	14	21	1	0	2	3	2	2
TOTAL NUMBER EXAMINED	1673		1145		1761		1713	
TOTAL PARASITISED	35		1		5		4	
PERCENT OF TOTAL	2.09		0.09		0.28		0.23	
(CORRECTED)	(3.49)		(0.15)		(0.47)		(0.39)	

Table 7.9 Nature of the gonads as determined by gonadal smears, of all young of year mussels below 30 mm in length examined from Mudginberri billabong during 1981.

Month	Age (years)	Total length (mm)	Sex
Sept. 1981	0.58	25.5	undifferentiated
"	"	27.0	"
"	"	29.0	male
"	"	30.0	undifferentiated
"	"	30.0	"
Oct. 1981	0.70	29.0	female
"	"	29.0	male

Table 7.10 Proportion and age of young of year mussels collected monthly from Mudginberri billabong during 1981, that had reached gonadal maturity (> 30 mm length) and first gravidity (> 40 mm length).

Month (1981)	Mean age (years)	Number of young of year	Proportion of length > 30 mm(%)	Proportion of length > 40 mm (%)
Feb	0.03	39	0.0	0.0
Mar	0.13	59	0.0	0.0
Apr	0.19	44	2.3	0.0
May	0.25	30	3.3	3.3
Jun	0.36	4	25.0	0.0
Jul	0.45	11	27.0	0.0
Aug	0.51	8	75.0	25.0
Sept	0.58	41	75.6	2.4
Oct	0.70	40	92.5	17.5
Nov	0.77	31	100.0	33.3
Dec	0.90	24	100.0	50.0

Table 7.11 Female young of year mussels examined from waterbodies of the Magela Creek, in relation to marsupial condition and mean length of gravid individuals. Minimum mean size at first gravidity (averaged over all waterbodies) used to estimate mean age at first spawning and brooding.

BILLABONG	Number of females examined	Empty marsupia (%)	PERCENTAGE WITH LARVAL STAGE			Mean length of females examined (mm)	Mean length of gravid females (mm)	Mean age at first spawning and brooding (years)
			Eggs and embryos (%)	Developing larvae (%)	Glochidia (%)			
Georgetown	3	100.0	0.0	0.0	0.0	33.7	-	1.4
Gulungul	16	18.8	37.5	12.5	31.3	39.4	39.0	0.8
Corndorl	-	-	-	-	-	-	-	1.5
Magela Creek channel	-	-	-	-	-	-	-	1.5
Mudginberri	31	41.9	16.1	12.9	29.0	39.3	41.0	0.8
Buffalo	5	100.0	0.0	0.0	0.0	31.1	-	1.2
Island	4	25.0	25.0	50.0	0.0	45.9	45.2	0.7
JaJa	1	0.0	0.0	0.0	100.0	49.5	49.5	0.6
Leichhardt	16	37.5	12.5	18.8	31.3	46.6	49.6	0.6
Jabiluka	2	50.0	0.0	0.0	50.0	46.5	41.0	0.8
Nankeen	2	50.0	0.0	0.0	50.0	46.3	45.0	1.0

Table 7.12 Data of marsupial condition of all female young of year mussels collected from Mudginberri billabong during September, October, and November 1981, used to determine size and age at first gravidity.

Month	Age (years)	Total length (mm)	Marsupial condition
Sept.	0.58	38.5	empty
"	0.58	39.0	eggs and embryos
"	"	39.5	"
"	"	40.0	empty
"	"	40.0	"
"	"	41.0	"
Oct.	0.70	36.5	empty
"	"	37.0	"
"	"	38.0	"
"	"	38.5	glochidia
"	"	41.0	developing larvae
Nov.	0.77	36.0	eggs and embryos
"	"	38.0	empty
"	"	40.0	glochidia
"	"	41.5	"
"	"	42.0	developing larvae
"	"	44.5	eggs and embryos
"	"	45.0	glochidia

Table 7.13 Linear and quadratic regression equations (with r^2 values and significance) describing the relationship between the percent of gravid females found among all females examined (arcsin $\sqrt{}$(Y in percent/100), radians) and age of mussels (X in years), in billabongs of the Magela Creek.

Billabong	Regression equation	R^2	Significance	Age range (years)
Cordorl	$Y = 0.984 - 0.0273X$	0.381	**	all ages
Mudginberri	$Y = 1.049 - 0.0078X$	0.172	*	"
Buffalo	$Y = 0.872 - 0.0110X$	0.318	***	"
Island	$Y = 1.027 - 0.0270X$	0.347	*	"
Leichhardt	$Y = 0.904 + 0.0330X - 0.0062X^2$	0.655	*	"
Jabiluka	$Y = 0.596 + 0.0317X - 0.0026X^2$	0.498	*	"
Nankeen	$Y = 0.740 - 0.0112X$	0.198	*	> 2.0

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 7.14 Partial regression coefficients (and their significance and coefficients of determination of the multiple linear regression equations describing the relationship between monthly larval production (percent of gravid female mussels found among all females examined) and various environmental variables, in billabongs of the Magela Creek. Equation is of the form: $Y = a + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$ where Y = larval production (arcsin $\sqrt{}$ (Y in percent/100), radians), a = constant, X_1 = ln dissolved oxygen, X_2 = chlorophyll, X_3 = turbidity, X_4 = time, X_5 = temperature and b_1 - b_5 are the respective regression coefficients of the independent variables.

BILLABONG		PARTIAL REGRESSION COEFFICIENT						r^2	DF
		constant	ln diss. oxygen (mg/l)	chloro. (µg/l)	turb. (NTU)	time (month)	temp. (°C)		
Georgetown	coeff.	-0.369	0.0625	0.0083	-0.0012	-0.0236	0.0458	0.723	21
	t value	-0.52	0.40	1.10	-2.29*	-1.66	2.24*		
Corndorl	coeff.	-2.570	0.0953	-0.0321	-0.0084	0.0519	0.1230	0.370	11
	t value	-1.30	0.65	-0.70	-1.94	0.79	1.72		
Mudginberri	coeff.	-0.818	-0.0525	-0.0045	0.0033	0.0296	0.0599		
	t value	-1.56	-0.28	-0.57	0.23	2.31*	3.48**	0.614	21
Island	coeff.	-2.110	0.1960	-0.0192	0.0562	0.0527	0.0870		
	t value	-1.83	3.33*	-1.45	1.38	2.36*	2.33*	0.828	11
JaJa	coeff.	-3.780	0.2620	-0.0004	-0.0106	0.1603	0.1269		
	t value	-3.68	6.88	-0.13	-4.65	6.08	3.83	0.995	1
Leichhardt	coeff.	-0.452	0.166	-0.0042	0.0569	-0.0099	0.0337		
	t value	-0.38	2.31*	-0.48	1.85	-0.27	0.80	0.575	11
Jabiluka	coeff.	0.081	0.0730	0.0145	0.0174	-0.0946	0.0131		
	t value	0.04	1.21	1.46	1.67	-1.36	0.21	0.695	11
Nankeen	coeff.	1.660	0.3110	-0.0008	0.0039	-0.0801	-0.0365		
	t value	2.07	5.64***	-0.14	2.26*	-3.11*	-1.35	0.734	21
Billabongs combined	coeff.	-0.874	0.2050	0.0040	-0.0019	0.0196	0.0475		
	t value	-2.36*	8.09***	1.28	-3.53***	2.14*	3.67***	0.387	150

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 7.15 Linear regression equations (with r^2 values and significance) describing the relationship between monthly larval production - the percent of gravid females found among all females examined (arcsin $\sqrt{}$ (Y in percent/100), radians), and various environmental variables (X), in billabongs of the Magela Creek.

Billabong	Regression equation	Independent variable	Significance	r^2
Georgetown	$Y = 0.973 - 0.002X$	turbidity (NTU)	$P < 0.001$	61.1
Mudginberri	$Y = -1.208 + 0.077X$	temperature (°C)	$P < 0.001$	47.9
Island	$Y = 0.598 + 0.301X$	(ln) dissolved oxygen (mg/l)	$P < 0.001$	61.0
JaJa	$Y = 0.511 + 0.327X$	"	$P < 0.05$	74.8
Leichhardt	$Y = 0.704 + 0.195X$	"	$P < 0.05$	30.2
Jabiluka	$Y = 0.453 + 0.142X$	"	$P < 0.10$	21.0
Nankeen	$Y = 0.259 + 0.344X$	"	$P < 0.001$	58.6

Table 7.16 Date of capture of fish examined for glochidial infection, from billabongs of the Magela Creek, in relation to the percent of gravid female mussels (found among all females) collected simultaneously.

BILLABONG	Date of capture	Percent of gravid female mussels
Georgetown	16/9/1980	11.9
"	29/10/1980	38.2
"	1/12/1980	27.3
"	24/4/1981	59.5
Corndorl	26/9/1980	52.6
"	29/10/1980	76.0
"	1/12/1980	84.0
"	23/9/1981	55.0
Gundur	15/8/1980	68.0
"	26/9/1980	79.0
"	1/12/1980	96.0
Mudginberri	2/12/1980	86.5
"	3/7/1981	46.9
"	27/11/1981	87.5
"	28/1/1982	66.7
"	3/2/1982	63.6
"	6/5/1982	50.0
Buffalo	2/12/1980	88.0
"	20/10/1981	83.5
Nankeen	24/2/1982	62.5

Table 7.17 Mean number per fish (and standard deviation) of encysted glochidia of _V_. _angasi_ found monthly upon the fins of the host, _Glossogobius giurus_, captured from Mudginberri billabong.

MONTH	Mean number of glochidia per fish	standard deviation	number of fish examined
March (1981)	6.25	4.54	20
April	6.81	5.44	16
May	3.40	4.20	20
June	2.75	2.36	20
July	1.70	2.25	20
August	4.50	4.38	12
September	6.01	3.67	5
October	7.09	2.74	5
November	7.42	2.30	5
December	6.29	4.50	3
January (1982)	1.48	2.01	10
February	0.82	1.32	10
March	0.45	0.52	11
April	5.64	5.94	11

Table 7.18 Mean number per fish of encysted glochidia of *V. angasi* found upon the various tissues of four host fish species, in relation to site and time of fish capture.

Fish species		Site of infection					Billabong (date)	Number of fish examined
		Internal surfaces			External surfaces			
Scientific name	Common name	mouth	opercula	gills	body surface	fins		
Ambassis spp.	perchlet	0.67	0.08	1.42	0.25	1.67	Georgetown (24/4/1981)	12
"	"	0.0	0.0	0.0	0.0	1.00	Gundur (26/9/1980)	2
"	"	0.17	0.0	3.50	0.67	1.33	Corndorl (1/12/1980)	6
Glossogobius giurus	flathead goby	1.05	1.30	19.05	0.30	6.35	Mudginberi (31/3/1981)	20
Oxyeleotris lineolatus	sleepy cod	0.0	0.0	2.00	0.0	1.00	Georgetown (24/4/1981)	1
Tandanus ater	eeltailed catfish	0.0	0.0	1.00	0.0	0.0	Georgetown (24/4/1981)	2
"	"	0.0	0.0	0.0	0.0	0.0	Gundur (26/9/1980)	4
"	"	0.0	0.0	2.33	0.0	0.0	Corndorl	4

Table 7.19 Natural infections of glochidia of *V. angasi* found upon the fins of fish species captured from various Magela Creek billabongs, in relation to the mean percent of gravid female mussels (found among all females) collected simultaneously. Incidence (% of fish infected = 'parasitised') and intensity (mean number of glochidia per infected fish = 'mean larvae') of infection are shown.

FISH SPECIES		BILLABONG						
		GEORGETOWN	CORNDORL	GUNDUR	MUDGINBERRI	BUFFALO	NANKEEN	AVERAGED OVERALL
	Percent of gravid female mussels	34.2	66.9	81.0	66.9	85.8	62.5	
Glossogobius giurus	examined	16	-	-	248*	-	-	264
	parasitised (%)	6.3	-	-	77.0	-	-	72.7
	mean larvae	1.00	-	-	4.14	-	-	4.13
Ambassis spp.	examined	72	60	72	5	-	-	209
	parasitised (%)	12.5	30.0	28.3	40.0	-	-	23.6
	mean larvae	2.56	1.94	2.27	2.50	-	-	2.21
Amniataba percoides	examined	-	13	19	9	21	-	62
	parasitised (%)	-	38.5	15.8	11.0	76.0	-	40.3
	mean larvae	-	4.40	1.00	4.00	2.56	-	2.80
Glossamia aprion	examined	7	40	32	13	-	-	92
	parasitised (%)	28.6	7.5	6.2	61.5	-	-	16.3
	mean larvae	1.50	2.67	1.5	3.6	-	-	2.85
Toxotes chatareus	examined	3	6	13	8	2	-	32
	parasitised (%)	67.0	0.0	46.2	25.0	0.0	-	31.3
	mean larvae	6.50	0.0	1.00	1.50	0.0	-	2.20
Oxyeleotris lineolatus	examined	10	6	3	1	-	-	20
	parasitised (%)	40.0	16.7	66.7	100.0	-	-	35.0
	mean larvae	1.75	2.00	2.50	2.00	-	-	2.00
Hexanematicthys spp.	examined	10	-	5	13	-	6	34
	parasitised (%)	0.0	-	0.0	23.1	-	33.3	14.7
	mean larvae	0.0	-	0.0	3.33	-	1.50	2.60
Nematalosa erebi	examined	39	-	2	18	13	-	72
	parasitised (%)	5.1	-	50.0	6.0	38.5	-	12.5
	mean larvae	1.00	-	4.00	1.00	1.20	-	1.44
Strongylura kreffti	examined	8	8	7	12	2	1	38
	parasitised (%)	25.0	0.0	0.0	0.0	0.0	100.0	7.9
	mean larvae	1.00	0.0	0.0	0.0	0.0	2.00	1.33
Melanotaenia splendida	examined	31	42	32	-	-	-	105
	parasitised (%)	12.9	7.1	0.0	-	-	-	6.7
	mean larvae	1.25	1.00	0.0	-	-	-	1.14
Mogurnda mogurnda	examined	2	2	1	1	-	-	6
	parasitised (%)	50.0	0.0	100.0	0.0	-	-	33.3
	mean larvae	2.00	0.0	1.00	0.0	-	-	1.50
Liza sp.	examined	-	-	1	-	-	-	1
	parasitised (%)	-	-	100.0	-	-	-	100
	mean larvae	-	-	2.0	-	-	-	2.00
Tandanus ater	examined	60	32	31	11	2	-	136
	parasitised (%)	1.60	3.1	3.2	0.0	0.0	-	2.2
	mean larvae	1.00	1.00	1.00	0.0	0.0	-	1.00
Lates calcarifer	examined	-	2	-	9	-	1	12
	parasitised (%)	-	50.0	-	0.0	-	100	17.0
	mean larvae	-	1.00	-	0.0	-	1.0	1.00
Denariusa bandata	examined	-	4	16	-	-	-	20
	parasitised (%)	-	25.0	0.0	-	-	-	5.0
	mean larvae	-	1.00	0.0	-	-	-	1.00
Craterocephalus stercusmuscarum	examined	-	-	28	6	-	-	34
	parasitised (%)	-	-	0.0	17.0	-	-	2.9
	mean larvae	-	-	0.0	2.00	-	-	2.00
Megalops cyprinoides	examined	1	-	-	5	-	8	14
	parasitised (%)	0.0	-	-	0.0	-	13.0	7.1
	mean larvae	0.0	-	-	0.0	-	1.00	1.00
Leiopotherapon unicolor	examined	1	4	1	-	-	-	6
	parasitised (%)	0.0	0.0	0.0	-	-	-	0.0
	mean larvae	0.0	0.0	0.0	-	-	-	0.0
Craterocephalus sp.	examined	-	-	-	-	2	-	2
	parasitised (%)	-	-	-	-	0.0	-	0.0
	mean larvae	-	-	-	-	0.0	-	0.0
Melanotaenia nigrans	examined	-	-	1	-	-	-	1
	parasitised (%)	-	-	0.0	-	-	-	0.0
	mean larvae	-	-	0.0	-	-	-	0.0
Porochilus rendahli	examined	2	-	-	2	-	-	4
	parasitised (%)	0.0	-	-	0.0	-	-	0.0
	mean larvae	0.0	-	-	0.0	-	-	0.0
Scleropages jardine	examined	-	-	-	1	-	6	7
	parasitised (%)	-	-	-	0.0	-	0.0	0.0
	mean larvae	-	-	-	0.0	-	0.0	0.0

* Collected monthly during 1981/1982.

Table 7.20 The host fish species of *Velesunio angasi* as determined by: natural infections found on field collected fish (F); and/or successful larval metamorphosis achieved in laboratory experiments (L). Feeding guilds of the fish species are also shown.

Fish species		Field (F) and/or laboratory (L) observation	Feeding guild
Scientific name	Common name		
Ambassis spp.	perchlet	F, L	microphagic carnivore
Glossogobius giurus	flathead goby	F, L	meiophagic carnivore
Glossamia aprion	mouth almighty	F	macrophagic carnivore
Amniataba percoides	banded grunter	F	meiophagic omnivore
Toxotes chatareus	archer fish	F	meiophagic insectivore
Oxyeleotris lineolatus	sleepy cod	F	macrophagic carnivore
Hexanematicthys spp.	forktailed catfish	F	macrophagic omnivore
Nematalosa erebi	bony bream	F	detritophagic /planktophagic
Strongylura kreffti	longtom	F	macrophagic piscivore/carnivore
Melanotaenia splendida	checkered rainbowfish	F, L	meiophagic omnivore
Mogurnda mogurnda	purple spotted gudgeon	F	meiophagic carnivore
Liza sp.	mullet	F	detritophagic /phytophagic
Tandanus ater	eeltailed catfish	F	meiophagic benthic carnivore
Lates calcarifer	barramundi	F, L	macrophagic piscivore/carnivore
Denariusa bandata	penny fish	F	meiophagic carnivore
Craterocephalus stercusmuscarum	speckled hardyhead	F	microphagic carnivore
Megalops cyprinoides	tarpon	F	macrophagic piscivore/carnivore
Leiopotherapon unicolor	spangled grunter	L	meiophagic omnivore
Hypseleotris compressus	northern carp gudgeon	L	microphagic carnivore

Table 8.1 Relative fractions of unicellular algae (with standard deviation), other unidentifiable organic material (detritus), and inorganic material found in the stomachs and intestines (where indicated) of mussels collected from selected billabongs of the Magela Creek, in relation to time of year.

		Stomach and Intestinal Content (percent)		
Billabong	DATE	Algae (SD)	Other organics	Inorganic
Georgetown	APR/1981	22.21 (5.42)	[77.8]	
	JUN/1982	14.34 (4.09)	51.7	34.0
	* "	-	-	31.6
	AUG/1981	1.72 (1.29)	61.8	36.5
	DEC/1981	3.70 (3.67)	59.2	37.1
	JAN/1982	7.10 (5.12)	48.2	44.7
Mudginberri	MAR/1981	6.34 (6.21)	[93.7]	
	JUN/1980	5.61 (3.81)	56.2	38.2
	* "	-	-	48.0
	JUN/1981	21.21 (6.53)	44.3	23.1
	AUG/1981	12.19 (4.77)	75.9	11.9
	* "	6.56 (4.83)	69.6	23.8
	DEC/1981	2.87 (2.25)	92.1	5.0
	JAN/1982	3.60 (1.30)	50.1	46.3
Nankeen	APR/1981	3.0 -	[97.0]	
	JUN/1981	27.44 (6.61)	[72.6]	
	AUG/1981	6.08 (2.66)	68.9	25.0
	DEC/1981	0.91 (1.56)	85.1	14.0
	JAN/1981	3.48 (2.87)	68.6	27.9
	* "	-	-	35.4

* intestinal content.
\- not determined.

Table 8.2 Relative fractions of the stomach contents (as mean percentages), and mean stomach and intestinal fullness of mussels from selected billabongs, in relation to time of year and prevailing environmental conditions.

		Stomach content (percent)			Stomach and intestinal fullness					
Billabong	DATE	Algae	Other Organics	Inorganics	Stomach (SD)	Intestine (SD)	n	Surface chlorophyll (μg/l)	Turbidity (NTU)	Dissolved oxygen (mg/l)
Georgetown	APR/1981	22.2	-	-	0.60 (0.69)	2.30 (0.96)	15	15.3	30.0	2.2
	JUN/1981	14.3	51.7	34.0	2.37 (1.14)	1.40 (0.39)	15	13.9	86.0	5.1
	AUG/1981	1.7	61.8	36.5	2.50 (1.60)	0.87 (0.58)	15	11.5	160.0	5.3
	DEC/1981	3.7	59.2	37.1	1.77 (1.18)	1.10 (0.28)	15	5.4	18.0	6.3
	JAN/1982	7.1	48.2	44.7	2.43 (1.39)	1.07 (0.42)	15	1.4	20.0	6.3
Mudginberri	MAR/1981	6.3	-	-	0.27 (0.32)	0.37 (0.52)	15	0.7	8.0	6.3
	JUN/1980	5.6	56.2	38.2	0.60 (0.47)	1.63 (0.35)	15	9.0	5.0	4.4
	JUN/1981	21.2	44.3	23.1	0.97 (0.88)	1.20 (0.68)	15	12.1	2.4	4.5
	AUG/1981	12.2	75.9	11.9	1.00 (0.75)	1.65 (0.53)	10	9.5	2.9	5.2
	DEC/1981	2.9	92.1	5.0	2.20 (1.10)	1.07 (0.32)	15	1.2	6.6	5.3
	JAN/1982	3.6	50.1	46.3	1.67 (1.08)	1.17 (0.70)	15	3.0	6.3	6.8
Nankeen	APR/1981	3.0	-	-	0.02 (0.11)	0.02 (0.11)	22	5.0	0.5	0.2
	JUN/1981	27.4	-	-	0.35 (0.52)	0.56 (0.53)	17	23.5	12.0	2.3
	AUG/1981	6.1	68.9	25.0	0.38 (0.52)	0.98 (0.49)	21	12.7	49.0	2.4
	DEC/1981	0.9	85.1	14.0	0.87 (0.88)	0.93 (0.32)	15	6.8	105.0	5.9
	JAN/1981	3.5	68.6	27.9	1.93 (1.29)	1.33 (0.62)	15	6.3	33.0	8.3

Table 8.3 Percentage composition of phytoplankton genera and other identifiable organic material, found in the stomachs of mussels sampled at different times of the year from Georgetown billabong. Values are means averaged over 10 individuals from each sampling period. Total numbers of phytoplankton species found among the stomach contents of the 10 individuals are given.

GENUS	DATE				
	APR 1981	JUN 1981	AUG 1981	DEC 1981	JAN 1982
Cl. DINOPHYCEAE					
Glenodinium	-	-	-	0.8	0.3
Peridinium	10.4	0.4	-	0.8	-
Cl. CHRYSOPHYCEAE					
Dinobryon	-	-	-	-	0.3
Cl. XANTHOPHYCEAE					
Anabaena	-	-	-	-	0.3
Centritractus	-	-	-	-	0.3
Microcystis	-	-	1.6	-	-
Ophiocytium	-	-	-	0.8	-
Cl. BACILLARIOPHYCEAE					
Unidentified A	-	-	-	2.8	0.6
Unidentified E	-	-	-	0.4	0.6
Unidentified F	-	-	-	0.4	-
Unidentified G	-	-	-	0.4	-
Unidentified H	-	-	-	-	0.4
Eunotia	-	-	1.2	0.4	-
Frustulia	-	-	0.4	-	0.3
Gomphonema	-	-	0.8	-	0.4
Pinnularia	-	-	-	0.4	-
Cl. EUGLENOPHYCEAE					
Euglena	1.6	1.2	-	5.2	1.7
Lepocinclis	16.8	8.2	1.2	-	4.1
Phacus	8.4	2.4	0.8	0.4	4.8
Strombomonas	0.8	-	-	0.4	-
Trachelomonas	48.2	81.0	83.6	34.0	61.2
Cl. CHLOROPHYCEAE					
O. Chlorococcales					
Ankistrodesmus	-	-	-	-	0.2
Crucigenia	-	-	-	0.4	2.2
Oocystis	2.4	3.2	0.4	-	0.3
Scenedesmus	-	-	-	0.4	0.3
Sphaerocystis	-	-	-	-	0.3
Tetraedron	-	-	-	-	0.4
O. Zygnematales					
Bambusina	-	-	-	0.8	-
Closterium	-	-	-	4.6	3.0
Cosmarium	5.8	0.8	0.4	5.8	1.3
Desmidium	-	-	-	2.4	1.0
Euastrum	0.4	-	-	2.4	0.7
Hyalotheca	-	-	-	0.4	0.3
Micrasterias	-	-	-	-	0.4
Netrium	-	-	-	0.4	-
Penium	-	-	-	1.2	1.3
Pleurotaenium	-	-	-	5.6	2.0
Sphaerozosma	-	0.4	-	-	-
Spirogyra	-	-	-	0.4	-
Staurastrum	4.6	0.4	0.8	17.2	7.5
Staurodesmus	-	0.4	-	0.4	0.7
Tetmemorus	-	-	-	-	0.4
Triploceras	-	-	-	-	0.3
O. Tetrasporales					
Gloeocystis	-	-	-	0.4	0.3
O. Volvocales					
Eudorina	-	-	-	-	1.4
Volvox	-	1.6	8.8	10.0	0.4
Allochthonous matter	-	-	-	4.8	11.5
Total number of species	35	17	14	66	86

Table 8.4 Percentage composition of phytoplankton genera and other identifiable organic material, found in the stomachs (and intestines where indicated) of mussels sampled at different times of the year from Mudginberri billabong. Values are means averaged over 10 individuals from each sampling period. Total numbers of phytoplankton species found among the stomach contents of the 10 individuals are given.

GENUS	DATE						
	JUN 1980	MAR 1981	JUN 1981	AUG 1981	AUG 1981*	DEC 1981	JAN 1982
Cl. DINOPHYCEAE							
Glenodinium	0.8	-	-	2.6	-	-	-
Peridinium	19.8	9.6	14.4	14.0	25.4	1.2	1.6
Cl. CHRYSOPHYCEAE							
Dinobryon	-	-	-	0.2	-	-	-
Cl. XANTHOPHYCEAE							
Anabaena	-	-	-	0.2	-	-	-
Certritractus	0.4	-	-	1.4	0.4	0.4	0.8
Microcystis	-	-	-	-	0.6	-	-
Ophiocytium	-	-	-	1.2	1.2	-	0.8
Cl. BACILLARIOPHYCEAE							
Unidentified sp.A	-	2.0	-	0.8	-	-	-
Unidentified sp.B	0.4	-	24.4	4.6	-	-	-
Unidentified sp.D	-	-	-	0.6	-	-	-
Unidentified sp.E	-	-	-	0.4	-	-	-
Eunotia	0.4	-	-	-	-	-	0.4
Frustulia	-	-	-	0.2	-	0.4	-
Cl. EUGLENOPHYCEAE							
Euglena	0.4	0.8	-	-	-	0.8	1.2
Lepocinclis	1.6	14.4	3.2	1.4	3.0	4.8	2.0
Phacus	2.8	3.6	0.8	1.2	0.8	3.6	0.4
Strombomonas	0.4	-	-	-	-	-	-
Trachelomonas	65.0	52.6	51.6	22.8	57.0	72.0	34.8
Cl. CHLOROPHYCEAE							
O. Chlorococcales							
Botrycoccus	0.4	-	-	-	-	-	-
Coelastrum	-	-	-	0.2	-	-	-
Coenochloris	-	-	-	9.0	1.6	0.4	-
Crucigenia	-	-	-	0.2	-	-	-
Oocystis	-	4.8	0.8	6.2	0.6	-	1.6
Scenedesmus	0.4	0.4	-	0.6	0.8	2.0	-
Sphaerocystis	-	0.4	-	0.2	-	-	-
Tetrastrum	-	-	-	0.2	-	-	-
O. Zygnematales							
Actinotaenium	-	-	-	0.2	-	-	-
Closterium	0.8	0.4	-	0.8	-	0.4	4.8
Cosmarium	2.0	2.8	-	3.6	0.6	5.2	10.8
Desmidium	-	-	0.2	0.2	-	1.2	1.6
Docidium	-	-	-	-	-	-	0.4
Euastrum	0.8	0.4	-	-	0.4	-	3.2
Penium	-	-	-	0.2	-	-	-
Pleurotaenium	0.4	-	0.4	-	0.2	0.4	6.4
Staurastrum	1.6	1.6	0.4	0.2	0.4	5.6	11.8
Staurodesmus	0.4	0.4	-	0.2	-	0.4	0.4
Xanthidium	-	0.8	-	-	-	-	-
O. Tetrasporales							
Gloeocystis	-	-	1.2	25.8	6.6	-	0.4
O. Volvocales							
Eudorina	-	-	-	0.6	-	-	-
Volvox	1.2	4.4	1.6	0.2	0.4	1.2	16.0
Allochthonous matter	-	-	-	-	-	-	-
Total number of species	28	31	14	52	23	34	52

* intestinal contents.

Table 8.5 Percentage composition of phytoplankton genera and other identifiable organic material, found in the stomachs of mussels sampled at different times of the year from Nankeen billabong. Values are means averaged over 10 individuals from each sampling period. Total numbers of phytoplankton species found among the stomach contents of the 10 individuals are given.

GENUS	DATE				
	APR 1981	JUNE 1981	AUG 1981	DEC 1981	JAN 1982
Cl. DINOPHYCEAE					
Peridinium	-	3.2	-	0.4	-
Cl. XANTHOPHYCEAE					
Microcystis	-	-	-	0.4	-
Ophiocytium	-	-	-	0.4	-
Cl. BACILLARIOPHYCEAE					
Unidentified sp. A	-	-	-	-	1.8
Unidentified sp. B	-	-	-	-	0.2
Unidentified sp. C	-	-	-	-	0.4
Navicula	-	-	-	-	0.2
Cl. EUGLENOPHYCEAE					
Euglena	-	0.4	2.0	8.4	0.4
Lepocinclis	2.0	2.0	7.2	12.6	-
Phacus	-	0.8	3.6	8.9	1.4
Strombomonas	-	-	0.4	0.4	-
Trachelomonas	92.0	93.6	86.4	49.9	2.0
Cl. CHLOROPHYCEAE					
O. Chlorococcales					
Coelastrum	-	-	-	0.4	-
Crucigenia	-	-	-	1.6	0.6
Dimorphococcus	-	-	-	1.6	-
Oocystis	2.0	-	-	1.2	0.4
Scenedesmus	-	-	-	1.2	1.2
Stigeoclonium	-	-	-	0.4	-
O. Zygnematales					
Closterium	-	-	-	0.8	0.8
Cosmarium	2.0	-	-	2.9	79.0
Desmidium	-	-	-	0.8	1.4
Euastrum	-	-	-	0.4	-
Penium	-	-	-	-	0.6
Pleurotaenium	-	-	0.4	-	0.4
Sphaerozosma	2.0	-	-	-	-
Staurastrum	-	-	-	0.8	7.0
Staurodesmus	-	-	-	0.4	0.2
Triploceras	-	-	-	1.2	-
Xanthidium	-	-	-	-	0.4
O. Tetrasporales					
Gloeocystis	-	-	-	-	0.2
Paulschulzia	-	-	-	-	0.2
O. Volvocales					
Eudorina	-	-	-	-	0.6
Volvox	-	-	-	4.8	0.4
Allochthonous matter	-	-	-	-	1.0
Total number of species	7	10	12	42	41

Table 8.6 Percentage composition of phytoplankton genera found in the stomachs of mussels collected from Mudginberri billabong on 15 June 1980, in relation to the number of days (out of 11) from 24 June to 4 July 1980, over which genera were present among the plankton of the billabong waters. The number of phytoplankton species of each genus recorded in the plankton and stomachs of mussels is indicated in brackets. Stomach values are means averaged over 10 individuals. Plankton data from Kessell and Tyler (1983).

GENUS	SOURCE	
	PLANKTON	STOMACH
Cl. CYANOPHYCEAE		
Aphanocapsa	3 (1)	-
Gomphosphaeria	4 (1)	-
Merismopedia	3 (1)	-
Oscillatoria	1 (1)	-
Spirulina	1 (1)	-
Cl. DINOPHYCEAE		
Glenodinium	1 (1)	0.8 (1)
Peridinium	11 (5)	19.8 (2)
Cl. CHRYSOPHYCEAE		
Dinobryon	8 (1)	-
Mallomonas	6 (2)	-
Synura	1 (1)	-
Cl. XANTHOPHYCEAE		
Centritractus	8 (1)	0.4 (1)
Cl. BACILLARIOPHYCEAE		
Asterionella	11* (1)	-
Eunotia	7 (1)	0.4 (1)
Frustulia	2 (1)	-
Gomphonema	1 (1)	-
Melosira	7 (1)	-
Nitzschia	4 (1)	-
Rhizosolenia	9 (1)	-
Unidentified sp.B	-	0.4 (1)
Cl. CHLOROMONADOPHYCEAE		
Chloromonad flagellate	6 (1)	-
Cl. EUGLENOPHYCEAE		
Euglena	8 (4)	0.4 (1)
Lepocinclis	1 (1)	1.6 (1)
Phacus	11 (4)	2.8 (2)
Strombomonas	4 (1)	0.4 (1)
Trachelomonas	11 (5)	65.0 (3)
Cl. CHLOROPHYCEAE		
O. Chlorococcales		
Ankistrodesmus	4 (1)	-
Botryococcus	4 (1)	0.4 (1)
Coelastrum	2 (1)	-
Crucigenia	3 (1)	-
Distyosphaerium	7 (1)	-
Kirchneriella	9 (2)	-
Micractinium	1 (1)	-
Oocystis	1 (1)	-
Scenedesmus	11 (5)	0.4 (1)
Selenastrum	1 (1)	-
Tetraedron	9 (2)	-
O. Zygnemateles		
Closterium	2 (2)	0.8 (2)
Cosmarium	7 (4)	2.0 (1)
Desmidium	1 (1)	-
Euastrum	3 (3)	0.8 (2)
Hyalotheca	1 (1)	-
Micrasterias	1 (1)	-
Netrium	1 (1)	-
Pleurotaenium	1 (1)	0.4 (1)
Sphaerozosma	4 (1)	-
Staurastrum	9 (6)	1.6 (3)
Staurodesmus	4 (2)	0.4 (1)
Xanthidium	1 (1)	-
O. Tetrasporales		
Gloeocystis	1 (3)	-
O. Volvocales		
Volvox	-	1.2 (1)
Total number of species	81	27

* dominant taxon.

Table 8.7 Regression and correlation coefficients of the linear log-log transformed equations describing the relationship between dry and wet weight of mussels (all seasons) from the Magela Creek waterbodies, for sexes separate and combined. Equation is of the form: $\ln DW = b + m \ln FW$ where DW = dry weight (g), FW = flesh (or wet) weight (g). Levels of significant differences between the slopes and intercepts of the equations derived for each sex (as shown by analysis of covariance testing) are indicated.

WATERBODY		n	regression and correlation coefficient		
			b	m	r^2
Georgetown	male	660	-2.107	1.151	0.935
	female	599	-2.086	1.142	0.930
	total	1267	-2.089	1.142	0.936
Corndorl	male	223	-1.966	1.054	0.912
	female	181	-1.898	1.003	0.863
	total	404	-1.937	1.032	0.891
Magela Creek channel	male	370	-1.883	1.053	0.844
	female	312	-1.919	1.089	0.875
	total	690	-1.928	1.089	0.866
Mudginberri	male	688	-2.167***	1.175	0.901
	female	648	-2.079	1.148	0.892
	total	1340	-2.130	1.165	0.897
Buffalo	male	136	-2.150	1.099	0.882
	female	121	-2.179	1.082	0.860
	total	257	-2.159	1.088	0.868
Island	male	205	-1.980	1.146	0.979
	female	206	-2.121	1.180	0.961
	total	412	-2.057	1.165	0.969
JaJa	male	173	-1.919	1.124	0.945
	female	180	-1.793	1.072	0.952
	total	353	-1.861	1.100	0.955
Leichhardt	male	217	-2.001	1.143	0.959
	female	186	-1.895	1.103	0.962
	total	403	-1.950	1.124	0.960
Jabiluka	male	216	-2.061	1.105	0.889
	female	191	-2.171	1.157	0.884
	total	410	-2.125	1.134	0.887
Nankeen	male	636	-2.016	1.150	0.885
	female	628	-1.984	1.151	0.934
	total	1274	-1.996	1.148	0.913

*** $P < 0.001$.

Table 8.8 Regression and correlation coefficients of the linear log-log transformed equations describing the relationship between dry weight and length of mussels (all seasons) from the Magela Creek waterbodies, for sexes separate and combined. Equation is of the form: $\ln DW = a + b \ln L$ where DW = dry weight (g), L = shell length (mm). Levels of significant differences between the slopes and intercepts of the equations derived for each sex (as shown by analysis of covariance testing) are indicated.

BILLABONG	Regression and correlation coefficient		Sex		
			male	female	combined
Georgetown	a	***	-12.428	-11.820	-12.159
	b	*	3.083	2.908	3.004
	r^2		0.837	0.794	0.821
	n		658	598	267
Corndorl	a		-11.401	-11.203	-11.311
	b		2.800	2.746	2.776
	r^2		0.761	0.771	0.764
	n		223	181	404
Magela Creek channel	a		-13.026	-13.439	-13.465
	b		3.274	3.368	3.380
	r^2		0.766	0.812	0.798
	n		371	312	691
Mudginberri	a		-13.773	-13.187	-13.464
	b		3.421	3.264	3.339
	r^2		0.801	0.801	0.803
	n		685	646	1335
Buffalo	a		-14.789	-13.658	-14.187
	b		3.635	3.340	3.478
	r^2		0.816	0.751	0.780
	n		136	121	257
Island	a	***	-13.190	-13.538	-13.404
	b		3.363	3.426	3.403
	r^2		0.881	0.855	0.866
	n		205	206	412
JaJa	a		-13.252	-12.952	-13.311
	b		3.346	3.278	3.361
	r^2		0.806	0.833	0.842
	n		171	180	353
Leichhardt	a		-12.544	-13.244	-12.851
	b		3.183	3.346	3.255
	r^2		0.853	0.868	0.860
	n		217	186	403
Jabiluka	a		-9.729	-10.730	-10.295
	b		2.458	2.701	2.595
	r^2		0.704	0.755	0.731
	n		216	191	410
Nankeen	a	***	-10.879	-11.896	-11.488
	b	*	2.739	2.966	2.876
	r^2		0.658	0.765	0.715
	n		640	628	1278
Total	a		-	-	-13.704
	b		-	-	3.412
	r^2		-	-	0.862
	n		-	-	6804

* $P < 0.05$
*** $P < 0.001$

Table 8.9 Partial regression coefficients (and their significance) and coefficients of determination of the multiple linear regression equations describing the relationship between mean monthly condition of mussels and various environmental variables, in billabongs of the Magela Creek. Equation is of the form: $Y = a + b_1X_1 + b_2X_2 + b_3X_3 + b_4x_4 + b_5X_5$ where Y = condition (K), a = constant, X_1 = ln dissolved oxygen, X_2 = ln chlorophyll, X_3 = ln turbidity, X_4 = time, X_5 = temperature and b_1-b_5 are the respective regression coefficients of the independent variables.

BILLABONG		PARTIAL REGRESSION COEFFICIENT						r^2	DF
		constant	ln diss. oxygen (mg/l)	ln chloro. (μg/l)	ln turb. (NTU)	time (month)	temp. (°C)		
Georgetown	coeff.	0.787	0.1400	0.0055	0.0762	-0.0256	-0.0071	45.2	20
	t value	1.68	1.41	0.18	3.34**	-2.80*	-0.56		
Corndorl	coeff.	0.442	0.0377	-0.0626	-0.0498	0.0255	0.0154	33.2	10
	t value	1.03	1.00	-0.84	-1.40	1.76	0.86		
Mudginberri	coeff.	1.644	-0.0400	0.0376	0.0166	0.0143	-0.0281	48.8	21
	t value	5.17***	-0.36	1.73	0.44	2.02	-2.84**		
Island	coeff.	0.517	0.0208	0.0613	0.1505	-0.0098	0.0203	27.4	10
	t value	0.75	0.66	0.96	1.68	-0.65	0.94		
JaJa	coeff.	5.931	0.1390	-0.0958	-0.2977	0.1462	-0.1769	98.1	1
	t value	5.69	3.41	-1.70	-4.54	4.68	-5.03		
Leichhardt	coeff.	0.003	0.0095	0.1184	-0.0508	0.0063	0.0352	51.2	10
	t value	0.0	0.32	1.35	-0.62	0.29	1.53		
Jabiluka	coeff.	0.182	0.0289	0.1200	-0.0378	0.0063	0.0209	78.1	9
	t value	0.47	1.84	3.05*	-0.54	0.27	1.58		
Nankeen	coeff.	1.862	0.0126	0.0205	0.0456	-0.0088	-0.0345	56.4	21
	t value	3.83***	0.38	0.54	1.89	-0.68	-2.12*		
Billabongs combined	coeff.	0.884	0.0146	0.0682	-0.0166	0.0079	-0.0003	13.1	145
	t value	3.76***	0.94	3.43***	-1.37	1.31	-0.03		

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

Table 8.10 Linear regression equations (with r^2 values and significance) describing the relationship between mean monthly condition of mussels, K (Y), and chlorophyll concentration (X in µg/l), in billabongs of the Magela Creek. The significance of other linear regressions describing the relationship between (a) mean monthly condition (Y) and turbidity (lnX), and (b) monthly chlorophyll (lnY) and turbidity (lnX), in the billabongs is also shown.

Billabong	Regression equation	r^2	P	Significance (P) of other regressions	
				Condition(Y) /log turbidity(X)	log chlorophyll(Y) log turbidity(X)
Georgetown	-	-	N.S.	*	*
Mudginberri	Y=0.869+0.0556X	0.251	**	N.S.	N.S.
Leichhardt	Y=1.038+0.0824X	0.313	*	*	**
Jabiluka	Y=0.793+0.0907X	0.624	***	**	***
Nankeen	Y=0.811+0.0996X	0.291	**	***	**
billabongs combined	Y=0.896+0.0725X	0.112	***	N.S.	***

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

Table 8.11 Linear and quadratic regression equations (with r^2 values and significance) describing the relationship between mean condition of mussels, K (Y), and age of mussels (X in years), in billabongs of the Magela Creek.

Billabong	Regression equation	r^2	significance
Georgetown	$1.052 - 0.016X$	0.776	***
Corndorl	$1.034 - 0.023X$	0.847	***
Mudginberri	$0.937 + 0.012X - 0.0005X^2$	0.331	**
Buffalo	$0.768 + 0.005X$	0.237	**
Island	$1.280 + 0.031X - 0.0029X^2$	0.354	*
JaJa	$1.027 + 0.057X - 0.0031X^2$	0.482	***
Leichhardt	$1.334 - 0.019X$	0.554	**
Jabiluka	$1.279 - 0.055X + 0.0015X^2$	0.846	**
Nankeen	$1.137 - 0.013X$	0.458	***

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 8.12 Mean shell free, dry weight (g/m^2) and standard deviation (SD) of mussels in relation to depth and substrate in Georgetown billabong.

Depth (m)		substrate			
		A	B	C	D
0.0-0.9	mean	14.511	7.203	14.451	2.858
	SD	7.916	2.809	14.111	4.369
	n	15	12	21	6
1.0-1.9	mean	8.970	9.004	-	-
	SD	4.052	4.920	-	-
	n	9	21	-	-

Key to substrates:

A. Soft silt and clay
B. Sand with a little silt, clay and detritus
C. Silt, clay and detritus with some sand
D. Friable organic mud.

Table 8.13 Mean shell free, dry weight (g/m²) and standard deviation (SD) of mussels in relation to depth in Gulungul billabong.

	Depth (m)					
	0.1	0.2	0.3	0.4	0.5	0.6
mean	0.0	0.0	0.664	1.265	1.967	2.791
SD	0.0	0.0	0.926	1.014	1.537	2.007
n	19	40	31	26	13	10

Table 8.14 Mean shell free, dry weight (g/0.25m²) and standard deviation (SD) of mussels in relation to depth and substrate in Corndorl billabong.

Depth (m)		substrate		
		A	B	C
0.00-0.2	mean	0.155	0.980	1.319
	SD	0.439	1.399	1.038
	n	23	5	4
0.21-0.4	mean	0.768	2.651	2.596
	SD	1.018	2.538	2.317
	n	43	8	6
0.41-0.6	mean	2.091	7.403	0.374
	SD	2.686	5.072	0.748
	n	35	5	4
0.61-0.8	mean	3.704	12.619	2.907
	SD	2.989	9.006	1.403
	n	30	10	6
0.81-1.0	mean	4.241	15.130	-
	SD	3.757	9.292	-
	n	24	5	-
1.01-1.2	mean	3.617	2.452	-
	SD	2.234	1.953	-
	n	24	7	-
1.21-1.4	mean	2.317	-	-
	SD	1.608	-	-
	n	24	-	-
1.41-1.6	mean	0.511	-	-
	SD	0.731	-	-
	n	5	-	-

Key to substrates:

A. Very soft, organic silt and clay
B. Fine gravel with some silt and clay
C. Sand.

Table 8.15 Mean shell free, dry weight (g/0.25m²) and standard deviation (SD) of mussels in relation to depth and substrate in Mudginberri billabong.

Depth (m)		substrate			
		A	B	C	D
0.0-0.9	mean	0.219	0.724	2.413	0.857
	SD	2.104	0.594	2.046	0.840
	n	13	5	5	4
1.0-1.9	mean	0.299	3.056	4.062	6.495
	SD	0.523	2.424	2.836	4.033
	n	12	19	19	5
2.0-2.9	mean	2.044	7.789	5.313	9.424
	SD	2.341	4.932	6.570	7.647
	n	63	23	25	6
3.0-3.9	mean	4.691	10.123	5.643	-
	SD	5.550	5.352	3.155	-
	n	46	16	11	-
4.0-4.9	mean	6.660	8.024	5.519	-
	SD	3.533	5.109	1.678	-
	n	12	3	4	-
5.0-5.9	mean	5.314	4.743	1.363	-
	SD	2.097	2.535	1.110	-
	n	4	2	11	-

Key to substrates:

A. Sand
B. Sand with a little silt and detritus
C. Sand with silt and detritus (soft)
D. Soft to stiff clay with rubble.

Table 8.16 Mean shell free, dry weight ($g/0.25m^2$) and standard deviation (SD) of mussels in relation to depth and substrate in Buffalo billabong.

Depth (m)		substrate					
		A	B	C	E	F	G
0.0-0.9	mean	0.352	1.928	1.423	-	-	-
	SD	0.610	0.500	1.161	-	-	-
	n	8	5	3	-	-	-
1.0-1.9	mean	4.308	6.853	1.881	1.252	5.667	2.827
	SD	2.442	4.265	0.962	1.154	3.154	1.969
	n	10	3	8	10	4	4
2.0-2.9	mean	4.872	5.286	4.513	3.317	10.979	7.744
	SD	3.500	2.983	3.929	2.455	9.401	3.920
	n	66	54	31	37	5	6
3.0-3.9	mean	5.416	4.630	4.525	3.372	9.314	4.633
	SD	3.645	2.451	3.327	3.043	6.723	2.568
	n	61	31	38	7	5	5
4.0-4.9	mean	1.119	4.302	-	-	-	-
	SD	0.966	3.784	-	-	-	-
	n	4	5	-	-	-	-

Key to substrates:

A. Sand
B. Sand with a little silt and detritus
C. Sand with silt and detritus (soft)
E. Sand, silt and detritus (very soft)
F. Soft clay with some sand, silt and detritus
G. Soft silt, clay and fine detritus.

Table 8.17 Mean shell free, dry weight (g/m²) and standard deviation (SD) of mussels in relation to depth and substrate in Leichhardt billabong.

Depth (m)		substrate		
		A	B	C
0.0-0.9	mean	26.208	0.0	-
	SD	36.905	0.0	-
	n	28	1	-
1.0-1.9	mean	33.596	0.0	-
	SD	21.311	0.0	-
	n	31	4	-
2.0-2.9	mean	7.991	0.445	0.366
	SD	16.342	1.335	0.625
	n	19	10	9
3.0-3.9	mean	2.114	0.0	0.0
	SD	3.056	0.0	0.0
	n	6	27	2
4.0-4.9	mean	0.522	-	0.0
	SD	1.651	-	0.0
	n	4	-	1

Key to substrates;

A. Soft, coarse silt and clay
B. Silt and unconsolidated plant debris
C. Extremely compacted grey clay.

Table 8.18 Mean shell free, dry weight (g/m²) and standard deviation (SD) of mussels in relation to depth in the floodplain billabongs.

Depth (m)		Billabong			
		Island	JaJa	Jabiluka	Nankeen
0.0-0.9	mean	0.128	14.547	1.174	31.804
	SD	0.520	8.975	4.675	14.496
	n	34	12	37	41
1.0-1.9	mean	3.925	22.540	3.611	39.638
	SD	9.788	13.604	13.692	55.712
	n	36	26	25	37
2.0-2.9	mean	7.484	8.372	1.318	6.358
	SD	10.584	6.117	5.965	4.594
	n	19	11	43	29
3.0-3.9	mean	2.862	1.685	0.0	1.135
	SD	3.579	0.975	0.0	0.306
	n	36	7	38	28
4.0-4.9	mean	1.304	-	0.0	-
	SD	1.987	-	0.0	-
	n	17	-	9	-

Table 8.19 Mean shell free, dry weight (g/0.25m^2) and standard deviation (SD) of mussels in relation to depth and stations sampled in Nankeen billabong.

Station		Depth (m)			
		0.0-0.9	1.0-1.9	2.0-2.9	3.0-3.9
1	mean	4.355	4.342	1.594	0.211
	SD	11.337	12.440	6.734	3.263
	n	68	51	21	11
2	mean	9.104	14.947	2.260	0.715
	SD	7.463	16.374	1.973	1.387
	n	11	11	11	11
3	mean	6.356	7.525	0.877	0.0
	SD	8.299	7.179	1.674	0.0
	n	11	11	11	11
4	mean	16.801	14.968	1.757	0.362
	SD	15.577	17.535	1.896	0.661
	n	11	11	11	11
5	mean	6.782	6.875	2.456	0.167
	SD	7.128	9.375	5.902	0.553
	n	11	11	11	11
6	mean	14.300	13.483	1.016	0.0
	SD	14.623	11.812	1.767	0.0
	n	11	11	11	11
7	mean	3.882	6.964	0.888	0.239
	SD	4.173	7.486	1.465	0.794
	n	11	11	11	11
8	mean	12.791	21.784	4.274	1.144
	SD	17.687	16.048	4.287	1.493
	n	11	11	11	11
9	mean	1.616	3.751	0.177	0.0
	SD	2.009	4.180	0.613	0.0
	n	11	11	11	11
10	mean	3.524	4.456	0.596	0.0
	SD	6.418	7.611	0.907	0.0
	n	11	11	11	11
Mean East Bank	mean	4.598	5.891	1.198	0.102
	SD	2.081	1.715	0.863	0.121
	n	112	95	65	55
Mean West Bank	mean	11.304	13.928	1.981	0.444
	SD	5.167	6.200	1.434	0.491
	n	55	55	55	55

Table 8.20 Step by step computations used to calculate annual production, biomass, and turnover (P/B) ratios of age classes of mussels in Georgetown billabong. (Following the procedure of Lewandowski and Stanczykowska, 1975.)

Age (years)	Density (numbers/ m^2) n	Biomass of one individual (shell free dry weight) (g) b	Increase of the biomass of one individual per year (g) Δb	Average biomass (g/m^2) $B = n.b$	Production per year (g/m^2) $P = n.\Delta b$	P/B
0.5	0.383	0.266	0.266	0.102	0.102	1.000
1.5	0.230	0.434	0.168	0.100	0.039	0.386
2.5	0.174	0.597	0.163	0.104	0.028	0.273
3.5	0.127	0.743	0.146	0.094	0.019	0.196
4.5	0.193	0.866	0.123	0.167	0.024	0.142
5.5	0.304	0.966	0.101	0.293	0.031	0.104
6.5	0.549	1.047	0.080	0.575	0.044	0.077
7.5	0.647	1.109	0.063	0.717	0.041	0.057
8.5	0.552	1.158	0.049	0.639	0.027	0.042
9.5	0.356	1.195	0.037	0.426	0.013	0.031
10.5	0.280	1.224	0.028	0.342	0.008	0.023
11.5	0.256	1.245	0.022	0.319	0.006	0.017
12.5	0.280	1.261	0.016	0.353	0.005	0.013
13.5	0.248	1.274	0.012	0.316	0.003	0.010
14.5	0.243	1.283	0.009	0.312	0.002	0.007
15.5	0.111	1.290	0.007	0.143	0.001	0.005
16.5	0.100	1.295	0.005	0.130	0.001	0.004
17.5	0.066	1.299	0.004	0.086	0.000	0.003
18.5	0.048	1.302	0.003	0.062	0.000	0.002
19.5	0.032	1.304	0.002	0.041	0.000	0.002
20.5	0.026	1.306	0.002	0.035	0.000	0.001
21.5	0.005	1.307	0.001	0.007	0.000	0.001
Total	13.358	-	-	5.363	0.394	0.073

Table 8.21 Step by step computations used to calculate annual production, biomass, and turnover (P/B) ratios of age classes of mussels in Mudginberri billabong. (Following the procedure of Lewandowski and Stanczykowska, 1975.)

Age (years)	Density (numbers/ m^2) n	Biomass of one individual (shell free dry weight) (g) b	Increase of the biomass of one individual per year (g) Δb	Average biomass (g/m^2) $B = n.b$	Production per year (g/m^2) $P = n.\Delta b$	P/B
0.5	1.518	0.411	0.411	0.625	0.625	1.000
1.5	0.533	0.531	0.120	0.283	0.064	0.225
2.5	0.425	0.648	0.117	0.276	0.050	0.181
3.5	0.505	0.759	0.111	0.383	0.056	0.146
4.5	0.469	0.861	0.102	0.404	0.048	0.119
5.5	0.668	0.954	0.093	0.637	0.062	0.097
6.5	0.721	1.036	0.082	0.747	0.059	0.080
7.5	0.919	1.109	0.073	1.019	0.067	0.065
8.5	0.881	1.172	0.063	1.032	0.056	0.054
9.5	0.605	1.227	0.055	0.742	0.033	0.045
10.5	0.558	1.274	0.047	0.710	0.026	0.037
11.5	0.409	1.314	0.040	0.537	0.017	0.031
12.5	0.414	1.348	0.034	0.558	0.014	0.026
13.5	0.453	1.377	0.029	0.624	0.013	0.021
14.5	0.431	1.402	0.025	0.604	0.011	0.018
15.5	0.417	1.423	0.021	0.593	0.009	0.015
16.5	0.461	1.440	0.018	0.664	0.008	0.012
17.5	0.422	1.455	0.015	0.615	0.006	0.010
18.5	0.351	1.468	0.012	0.515	0.004	0.009
19.5	0.326	1.478	0.011	0.482	0.003	0.007
20.5	0.320	1.487	0.009	0.476	0.003	0.006
21.5	0.318	1.494	0.007	0.474	0.002	0.005
22.5	0.146	1.500	0.006	0.220	0.001	0.004
23.5	0.171	1.506	0.005	0.258	0.001	0.003
24.5	0.083	1.510	0.004	0.125	0.000	0.003
25.5	0.091	1.514	0.004	0.138	0.000	0.002
26.5	0.077	1.517	0.003	0.117	0.000	0.002
27.5	0.039	1.519	0.003	0.059	0.000	0.002
28.5	0.030	1.521	0.002	0.046	0.000	0.001
29.5	0.019	1.523	0.002	0.029	0.000	0.001
30.5	0.000	1.524	0.002	0.000	0.000	0.000
31.5	0.000	1.526	0.001	0.000	0.000	0.000
32.5	0.008	1.527	0.001	0.013	0.000	0.001
Total	12.788	-	-	14.005	1.239	0.088

Table 8.22 Step by step computations used to calculate annual production, biomass, and turnover (P/B) ratios of age classes of mussels in Leichhardt billabong. (Following the procedure of Lewandowski and Stanczykowska, 1975.)

Age (years)	Density (numbers/ m^2) n	Biomass of one individual (shell free dry weight) (g) b	Increase of the biomass of one individual per year (g) Δb	Average biomass (g/m^2) $B = n.b$	Production per year (g/m^2) $P = n.\Delta b$	P/B
0.5	0.144	0.815	0.815	0.117	0.117	1.000
1.5	0.228	1.257	0.441	0.287	0.101	0.351
2.5	0.228	1.732	0.476	0.395	0.109	0.275
3.5	0.154	2.213	0.481	0.340	0.074	0.217
4.5	0.367	2.679	0.466	0.983	0.171	0.174
5.5	0.783	3.115	0.436	2.440	0.342	0.140
6.5	0.952	3.514	0.399	3.344	0.380	0.114
7.5	0.833	3.872	0.358	3.224	0.298	0.093
8.5	0.312	4.189	0.317	1.308	0.099	0.076
9.5	0.139	4.466	0.277	0.620	0.039	0.062
10.5	0.040	4.707	0.240	0.187	0.010	0.051
11.5	0.025	4.914	0.207	0.122	0.005	0.042
12.5	0.015	5.091	0.177	0.076	0.003	0.035
13.5	0.005	5.242	0.151	0.026	0.001	0.029
Total	4.223	-	-	13.469	1.748	0.130

Table 8.23 Step by step computations used to calculate annual production, biomass, and turnover (P/B) ratios of age classes of mussels in Nankeen billabong. (Following the procedure of Lewandowski and Stanczykowska, 1975.)

Age (years)	Density (numbers/ m^2) n	Biomass of one individual (shell free dry weight) (g) b	Increase of the biomass of one individual per year (g) Δb	Average biomass (g/m^2) $B = n.b$	Production per year (g/m^2) $P = n.\Delta b$	P/B
0.5	0.751	0.378	0.378	0.284	0.284	1.000
1.5	0.451	0.658	0.280	0.296	0.126	0.425
2.5	0.342	0.933	0.275	0.319	0.094	0.295
3.5	0.249	1.178	0.245	0.293	0.061	0.208
4.5	0.378	1.383	0.205	0.523	0.078	0.148
5.5	0.596	1.548	0.165	0.922	0.099	0.107
6.5	1.077	1.678	0.130	1.808	0.140	0.077
7.5	1.269	1.778	0.100	2.256	0.127	0.056
8.5	1.083	1.855	0.076	2.008	0.083	0.041
9.5	0.699	1.912	0.058	1.337	0.040	0.030
10.5	0.549	1.956	0.043	1.074	0.024	0.022
11.5	0.502	1.988	0.032	0.999	0.016	0.016
12.5	0.549	2.012	0.024	1.105	0.013	0.012
13.5	0.487	2.030	0.018	0.988	0.009	0.009
14.5	0.477	2.043	0.013	0.974	0.006	0.007
15.5	0.218	2.053	0.010	0.447	0.002	0.005
16.5	0.197	2.060	0.007	0.406	0.001	0.004
17.5	0.130	2.066	0.005	0.268	0.001	0.003
18.5	0.093	2.070	0.004	0.193	0.000	0.002
19.5	0.062	2.073	0.003	0.129	0.000	0.001
20.5	0.052	2.075	0.002	0.108	0.000	0.001
21.5	0.010	2.076	0.002	0.022	0.000	0.001
Total	10.219	-	-	17.065	1.205	0.071

OFR 38

THE BIOLOGY AND ECOLOGY OF VELESUNIO ANGASI (BIVALVIA: HYRIIDAE) IN THE MAGELA CREEK, NORTHERN TERRITORY

Part 4 (Figures)

prepared by

C.L. Humphrey and R.D. Simpson
University of New England, Armidale, NSW

October 1985

The Supervising Scientist for the Alligator Rivers Region manages the Alligator Rivers Region Research Institute, which conducts, co-ordinates and integrates research relating the effects on the environment of uranium mining in the Alligator Rivers Region.

Supervising Scientist for the Alligator Rivers Region

THE BIOLOGY AND ECOLOGY OF *VELESUNIO ANGASI* (BIVALVIA: HYRIIDAE) IN THE MAGELLA CREEK, NORTHERN TERRITORY

PART IV
(FIGURES)

C.L. HUMPHREY AND R.D. SIMPSON

Department of Zoology,
University of New England,
Armidale, NSW

Report to the Office of the Supervising Scientist
October, 1985

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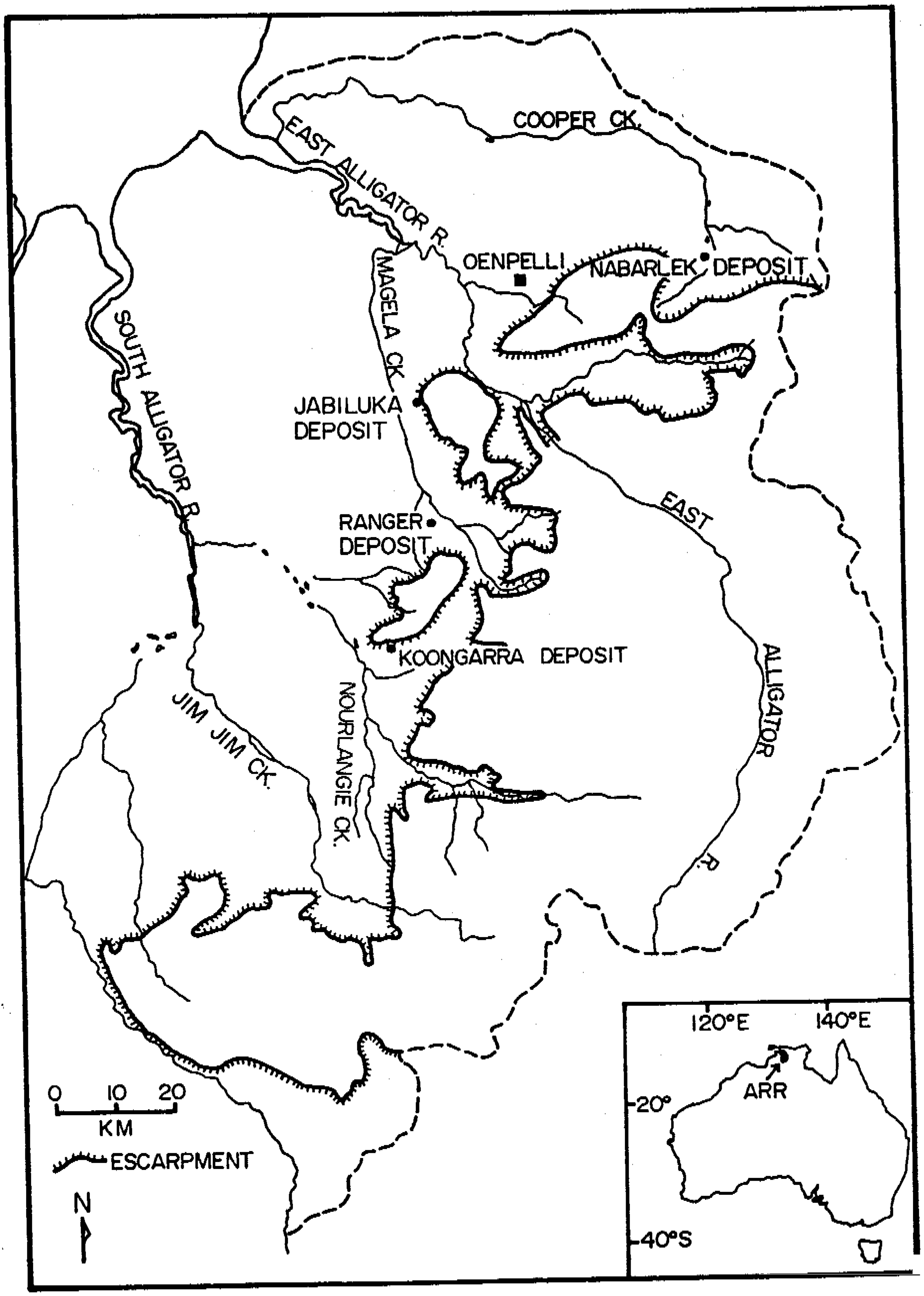


Figure 2.1 Map showing the Alligator Rivers Region (ARR), its principal drainage systems and the important uranium deposits of the Region. Inset shows the location of the ARR in relation to Australia.

Figure 2.2 Average and seasonal distribution of rainfall at Jabiru from 1971/72 to the present study period.

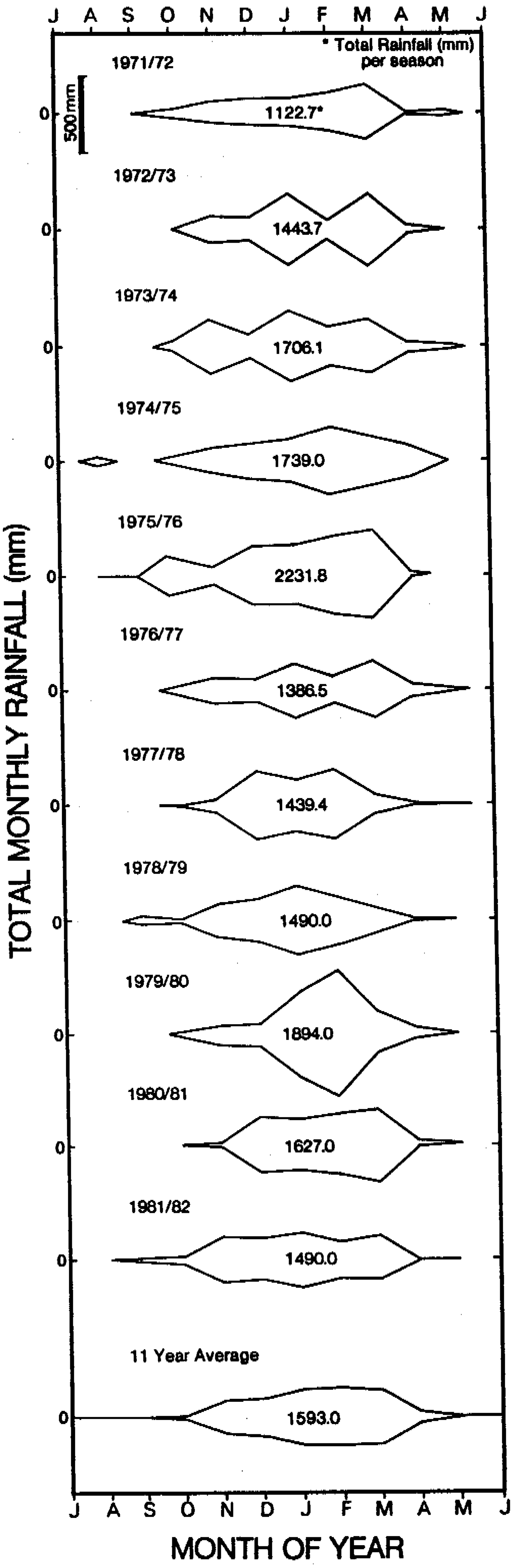
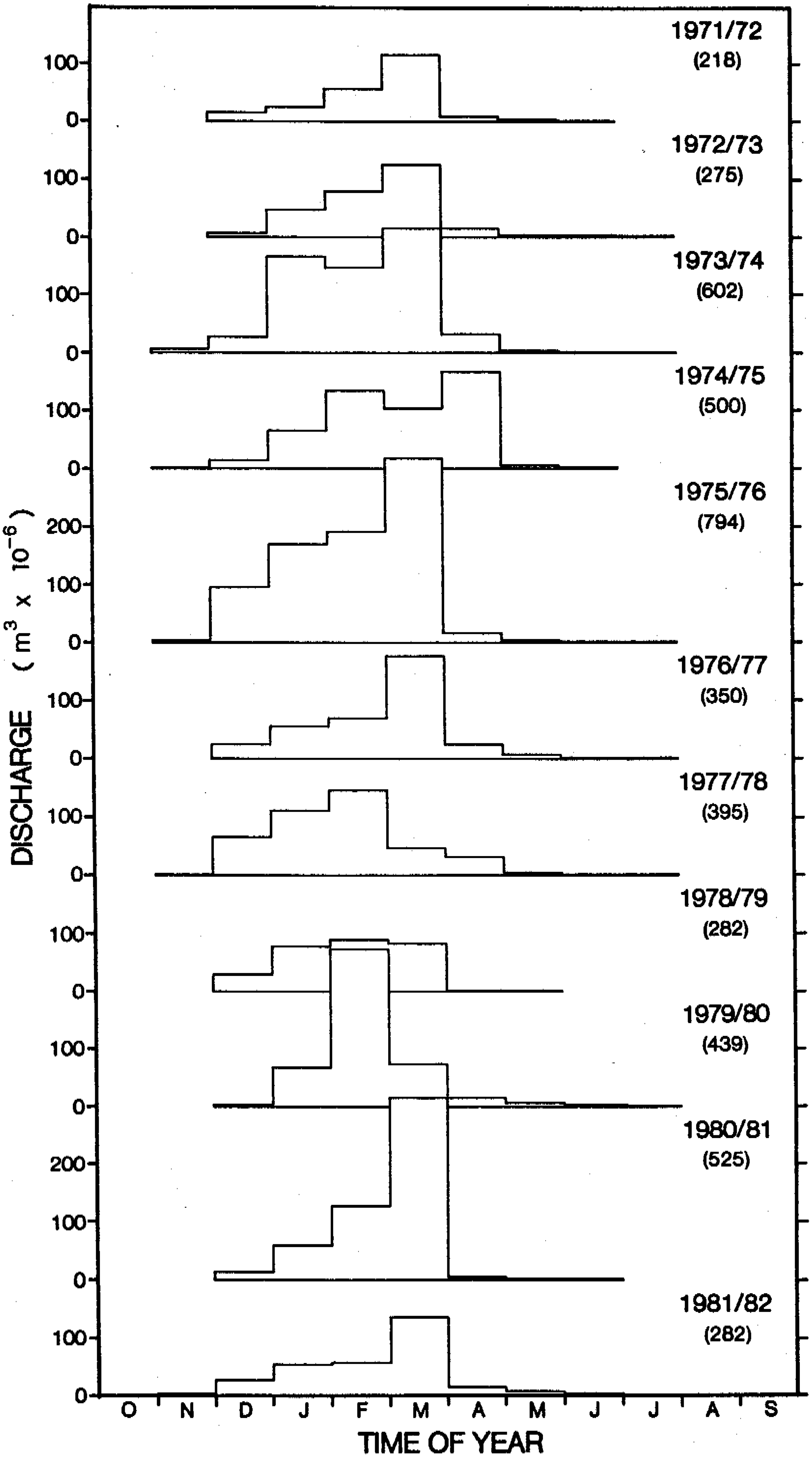

J A S O N D J F M A M J
* Total Rainfall (mm) per season
500 mm
1971/72
1122.7*
1972/73
1443.7
1973/74
1706.1
1974/75
1739.0
1975/76
2231.8
1976/77
1386.5
1977/78
1439.4
1978/79
1490.0
1979/80
1894.0
1980/81
1627.0
1981/82
1490.0
11 Year Average
1593.0
0
TOTAL MONTHLY RAINFALL (mm)
J A S O N D J F M A M J
MONTH OF YEAR

Figure 2.3 Seasonal discharge in the Magela Creek measured at GS821009 (below Jabiru) from 1971/72 to the present study period. Total discharge for the Wet season is figured in brackets.


1971/72
(218)
1972/73
(275)
1973/74
(602)
1974/75
(500)
1975/76
(794)
1976/77
(350)
1977/78
(395)
1978/79
(282)
1979/80
(439)
1980/81
(525)
1981/82
(282)
100
0
200
DISCHARGE ($m^3 \times 10^{-6}$)
O
N
D
J
F
M
A
M
J
J
A
S
TIME OF YEAR

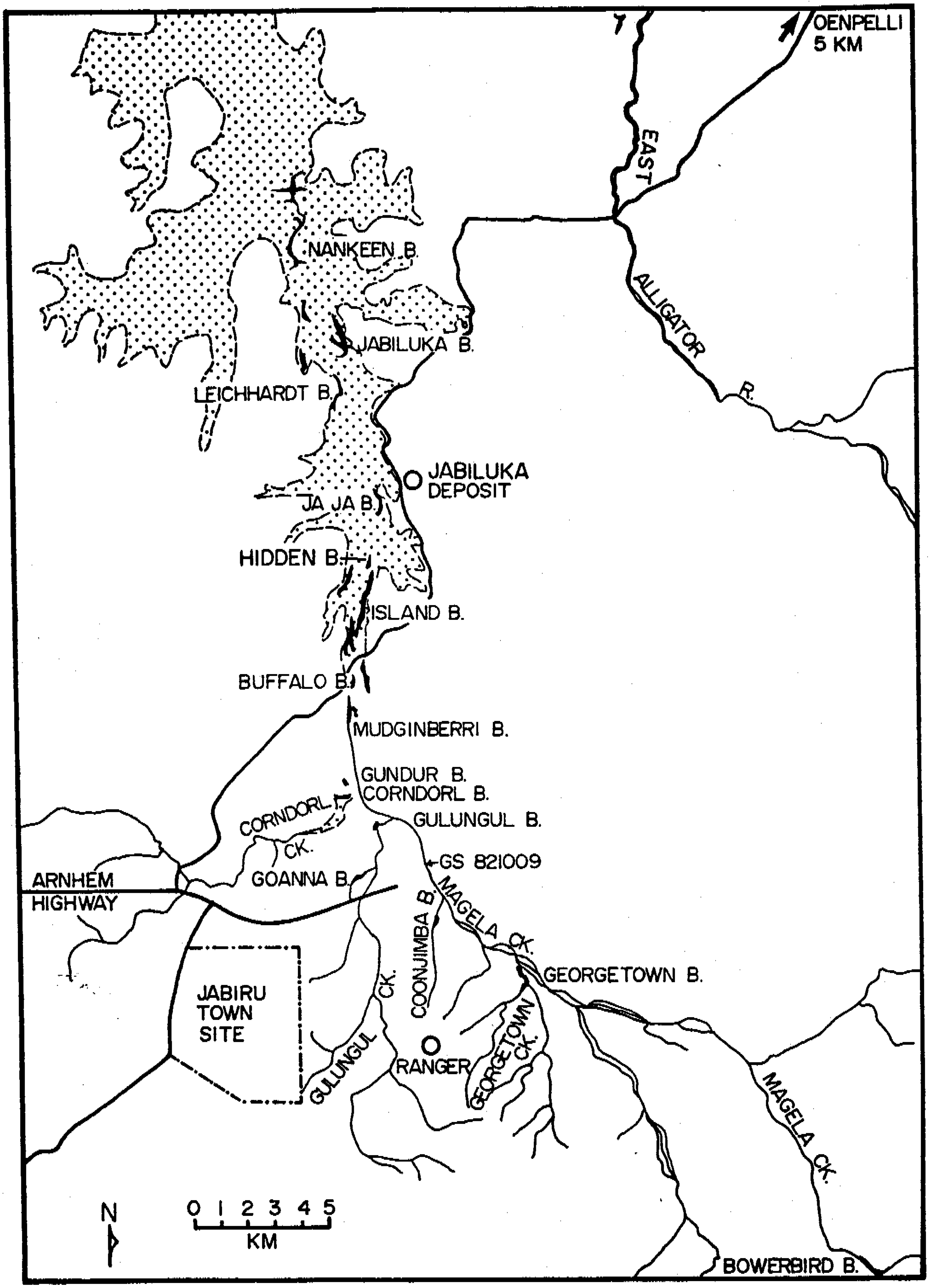
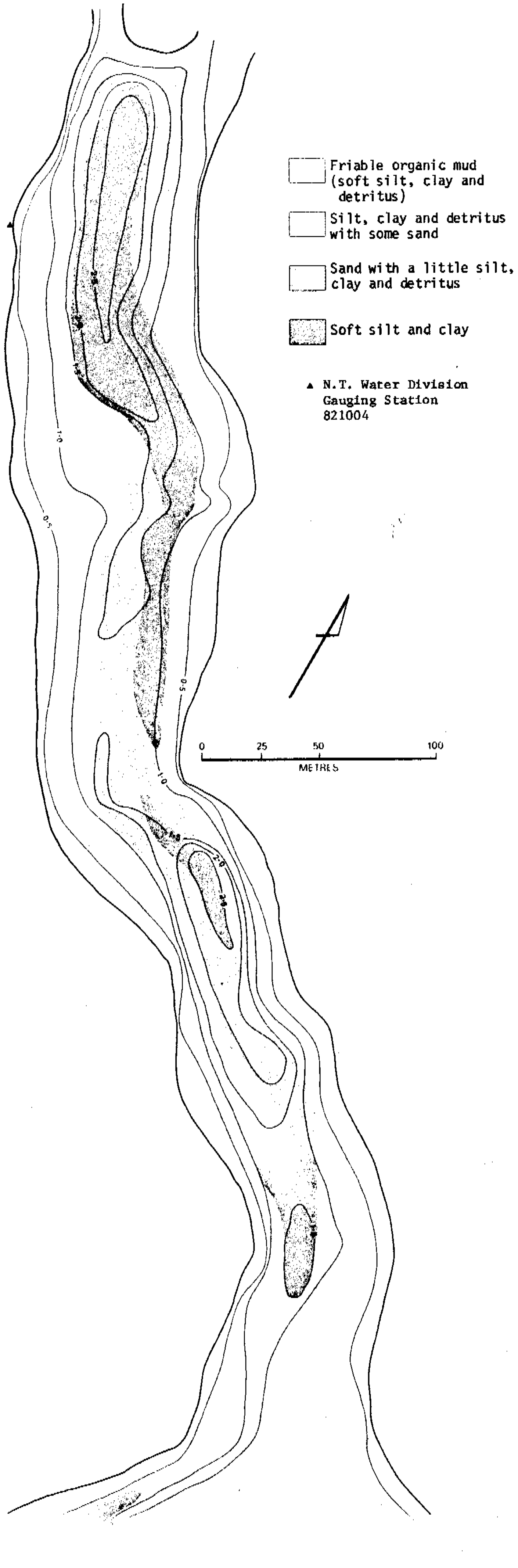


Figure 2.4 Map showing the Magela Creek, the location of the billabongs sampled and the floodplain (indicated by the hatched region).

Figure 2.5 Bathymetric map of Georgetown billabong in relation to the major bottom sediments observed during the study period. Map is drawn for a gauge height of 2.0 m (February, 1982).


Friable organic mud (soft silt, clay and detritus)
Silt, clay and detritus with some sand
Sand with a little silt, clay and detritus
Soft silt and clay
▲ N.T. Water Division Gauging Station 821004
0
25
50
100
METRES
0·5
1·0
1·5
2·0
2·5

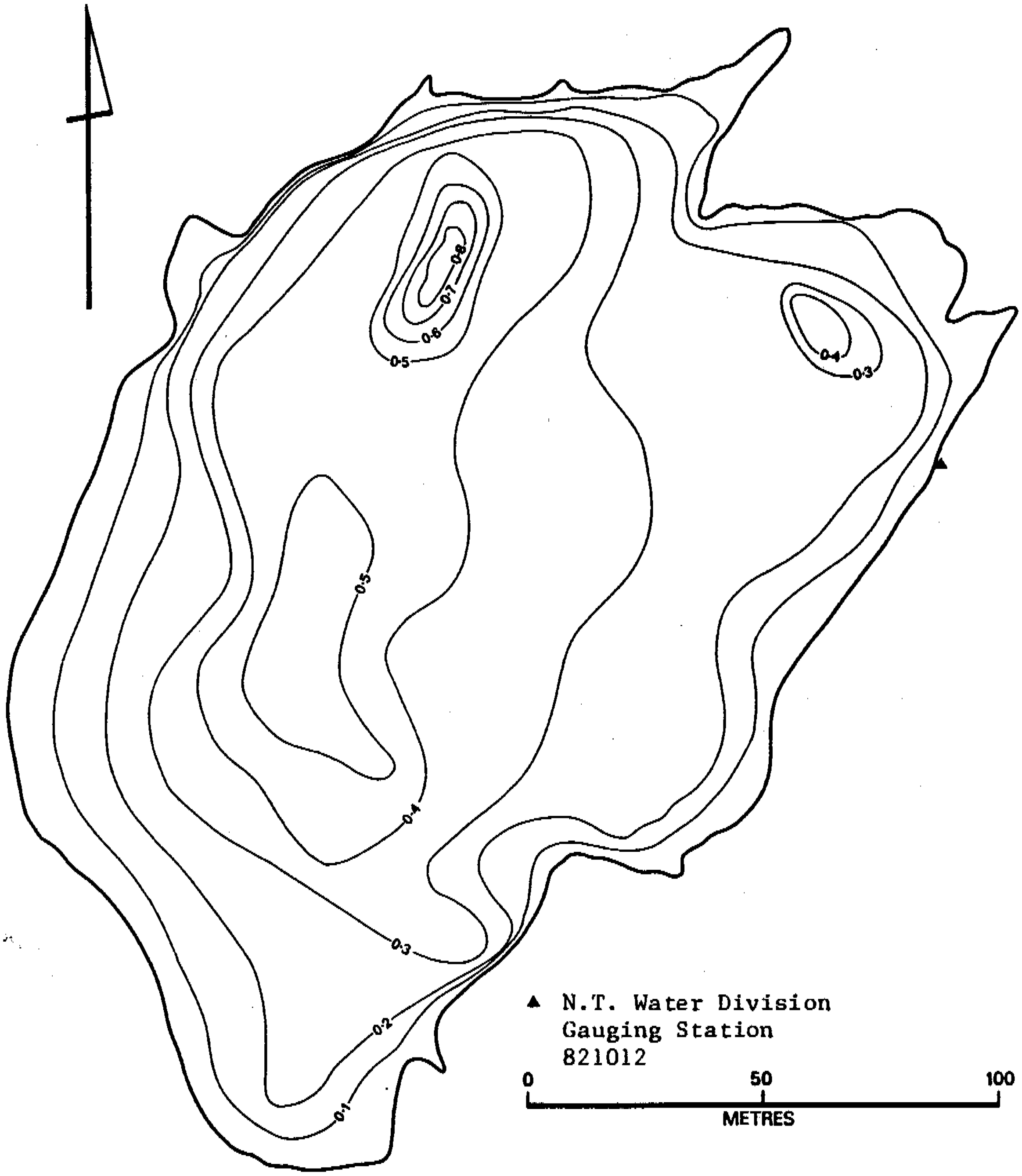


Figure 2.6 Bathymetric map of Gulungul billabong. Map is drawn for a gauge height of 0.84 m (4 November, 1981).

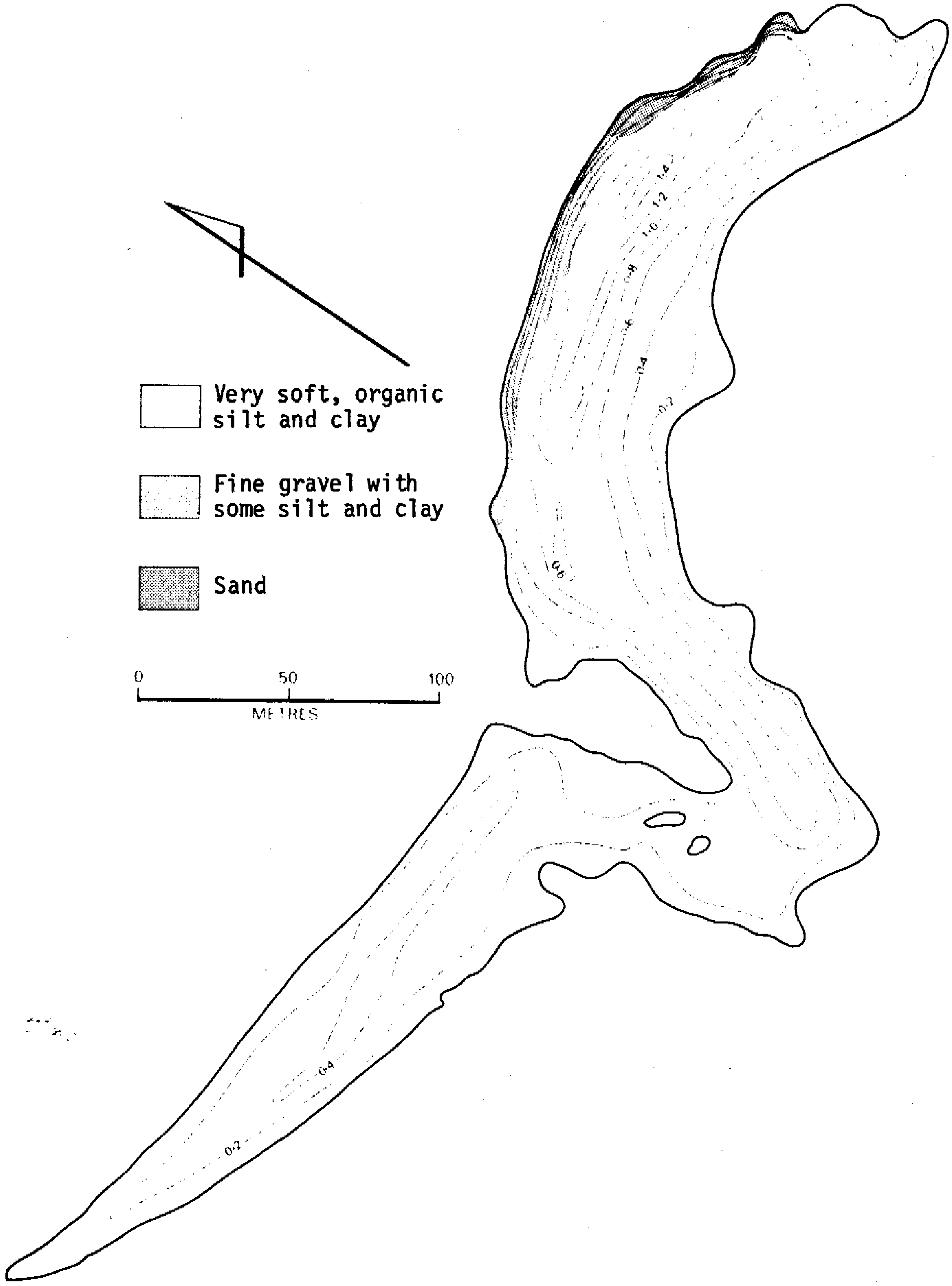


Figure 2.7 Bathymetric map of Corndorl billabong in relation to the major bottom sediments observed during the study period. Map is drawn for a gauge height of 1.05 m (12 October, 1980).

Figure 2.8 Bathymetric map of Mudginberri billabong in relation to the major bottom sediments observed during the study period. Map is drawn for a gauge height of 7.96 m (1 September, 1980).

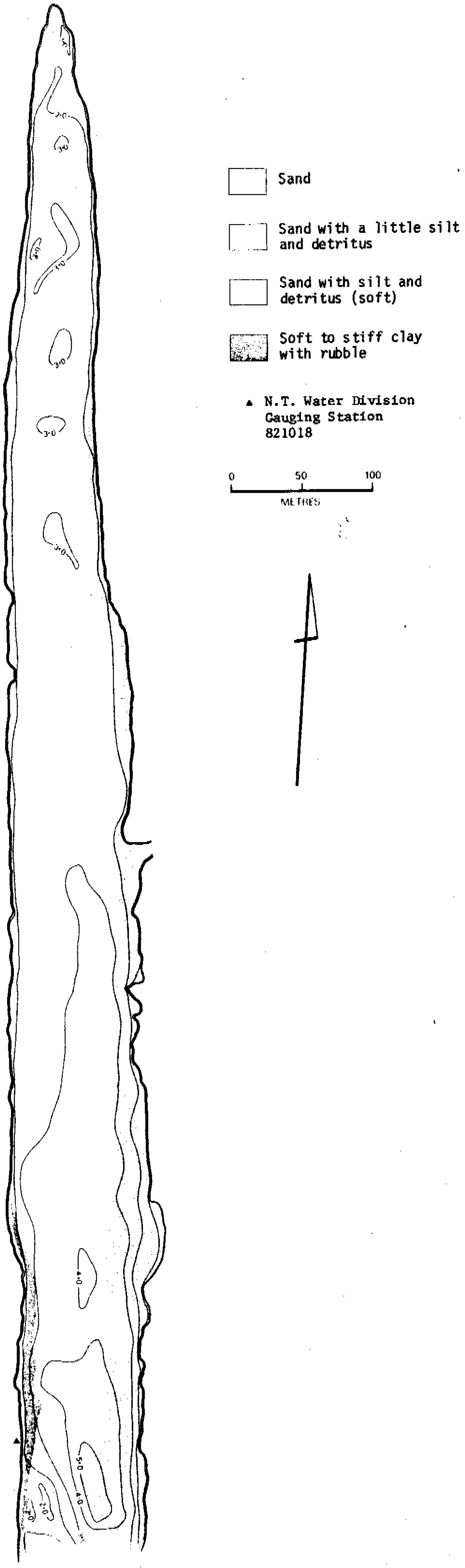

Sand
Sand with a little silt and detritus
Sand with silt and detritus (soft)
Soft to stiff clay with rubble
▲ N.T. Water Division Gauging Station 821018
0
50
100
METRES
1·0
2·0
3·0
4·0
5·0

Figure 2.9 Bathymetric map of Buffalo billabong in relation to the major bottom sediments observed during the study period. Map is drawn for a gauge height of 2.35 m (2 August, 1980).

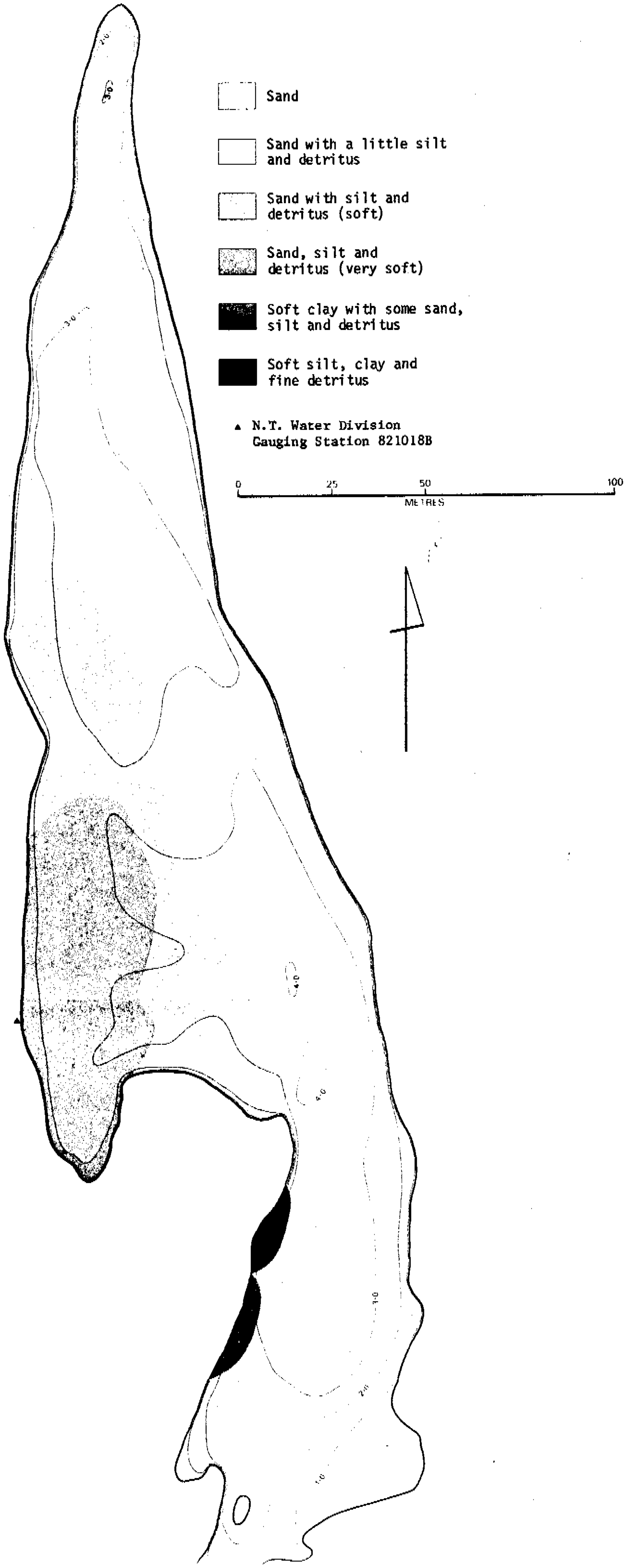

Sand
Sand with a little silt and detritus
Sand with silt and detritus (soft)
Sand, silt and detritus (very soft)
Soft clay with some sand, silt and detritus
Soft silt, clay and fine detritus
▲ N.T. Water Division Gauging Station 821018B
0
25
50
100
METRES
2·0
3·0
3·0
4·0
4·0
3·0
2·0
1·0

Figure 2.10 Bathymetric map of Island billabong. Map is drawn for a gauge height of 1.05 m (1 November, 1981).

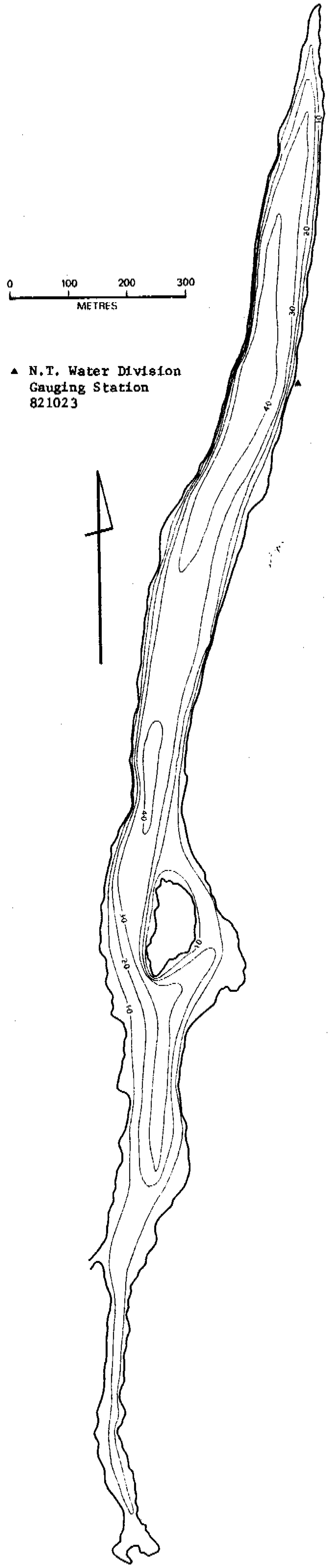

0
100
200
300
METRES
▲ N.T. Water Division
Gauging Station
821023
10
20
30
40
40
30
20
10
10

Figure 2.11 Bathymetric map of JaJa billabong. Map is drawn for a gauge height of 2.84 m AHD (6 November, 1979 - JaJa Extension (nth); 25 November, 1980 - JaJa billabong). (Source - Pancontinental Mining Limited, 1981.)

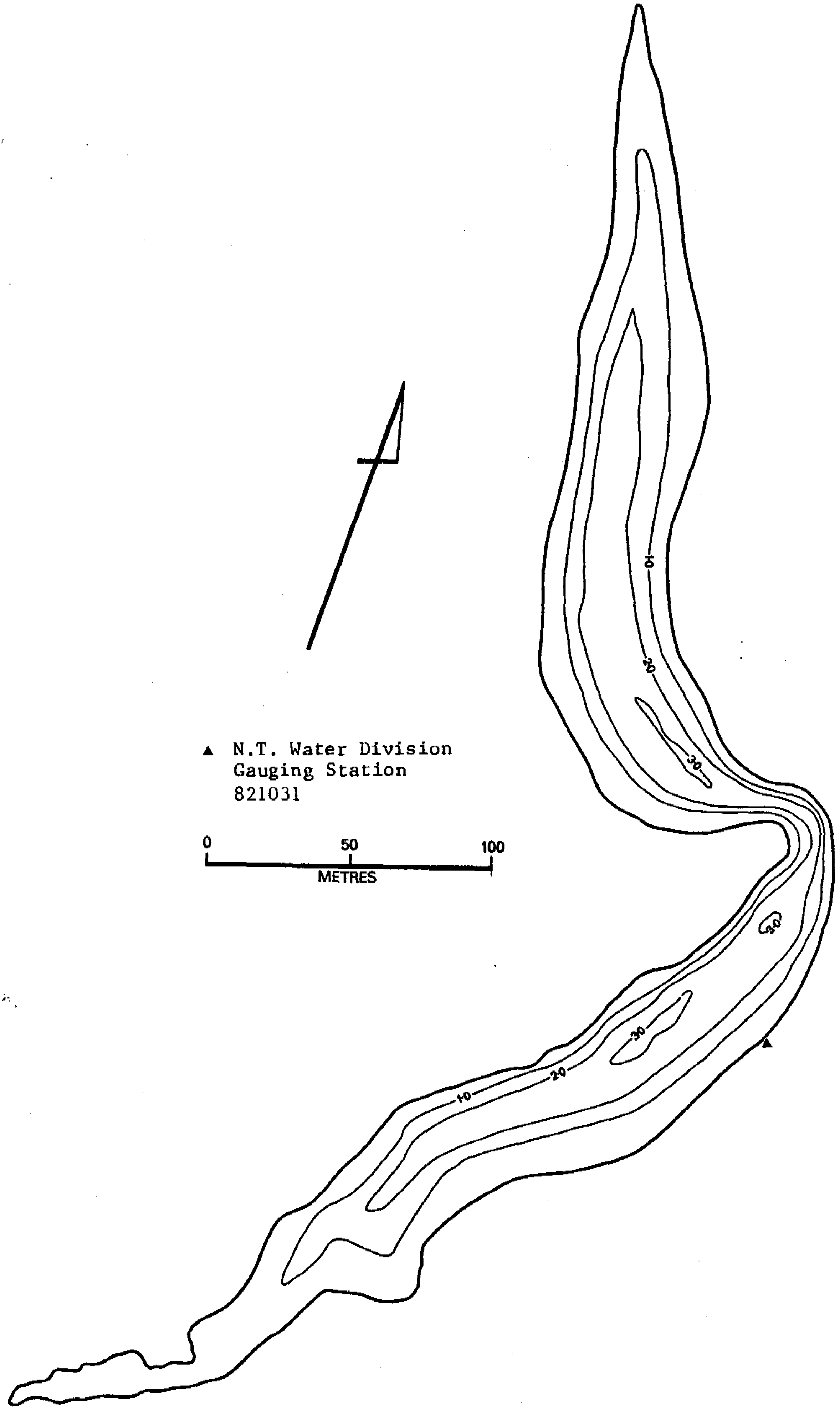

▲ N.T. Water Division
Gauging Station
821031
0
50
100
METRES
1·0
2·0
3·0
3·0
3·0
1·0
2·0

Figure 2.12 Bathymetric map of Leichhardt billabong in relation to the major bottom sediments observed during the study period. Map is drawn for a gauge height of 2.35 m (1 November, 1981).

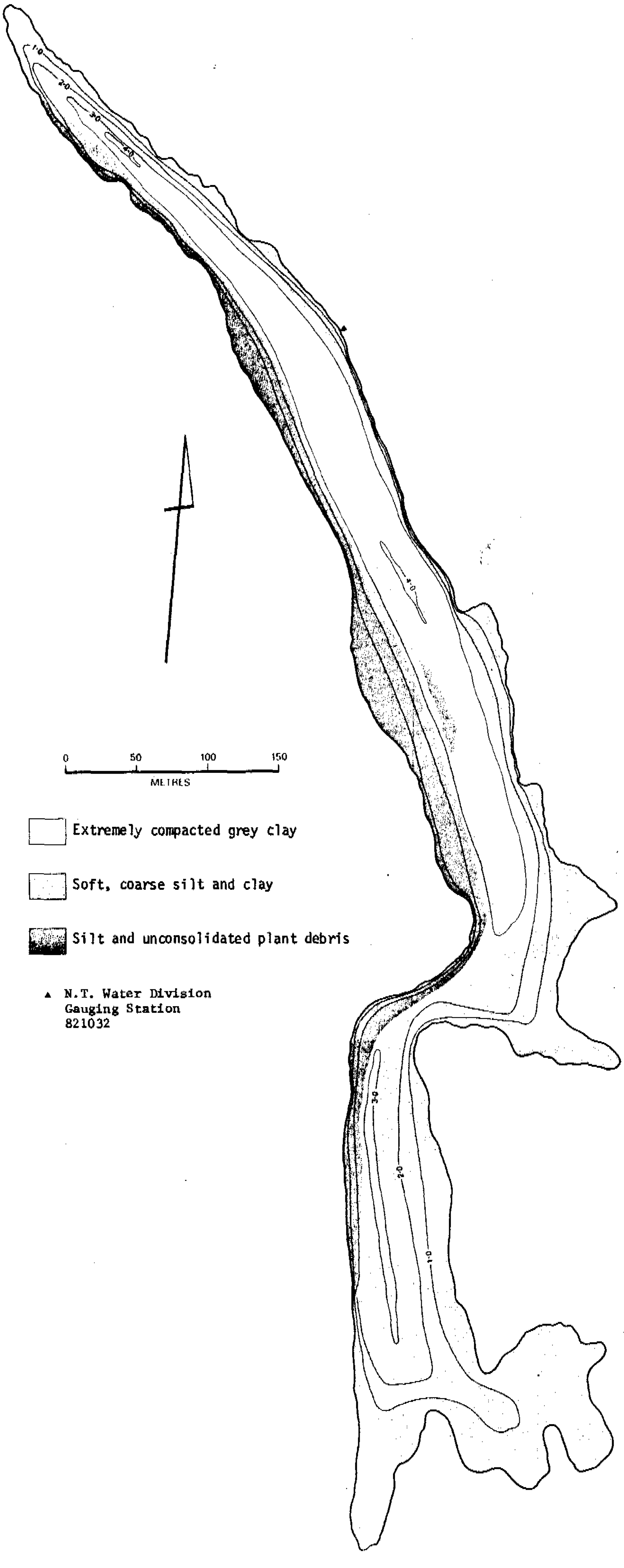
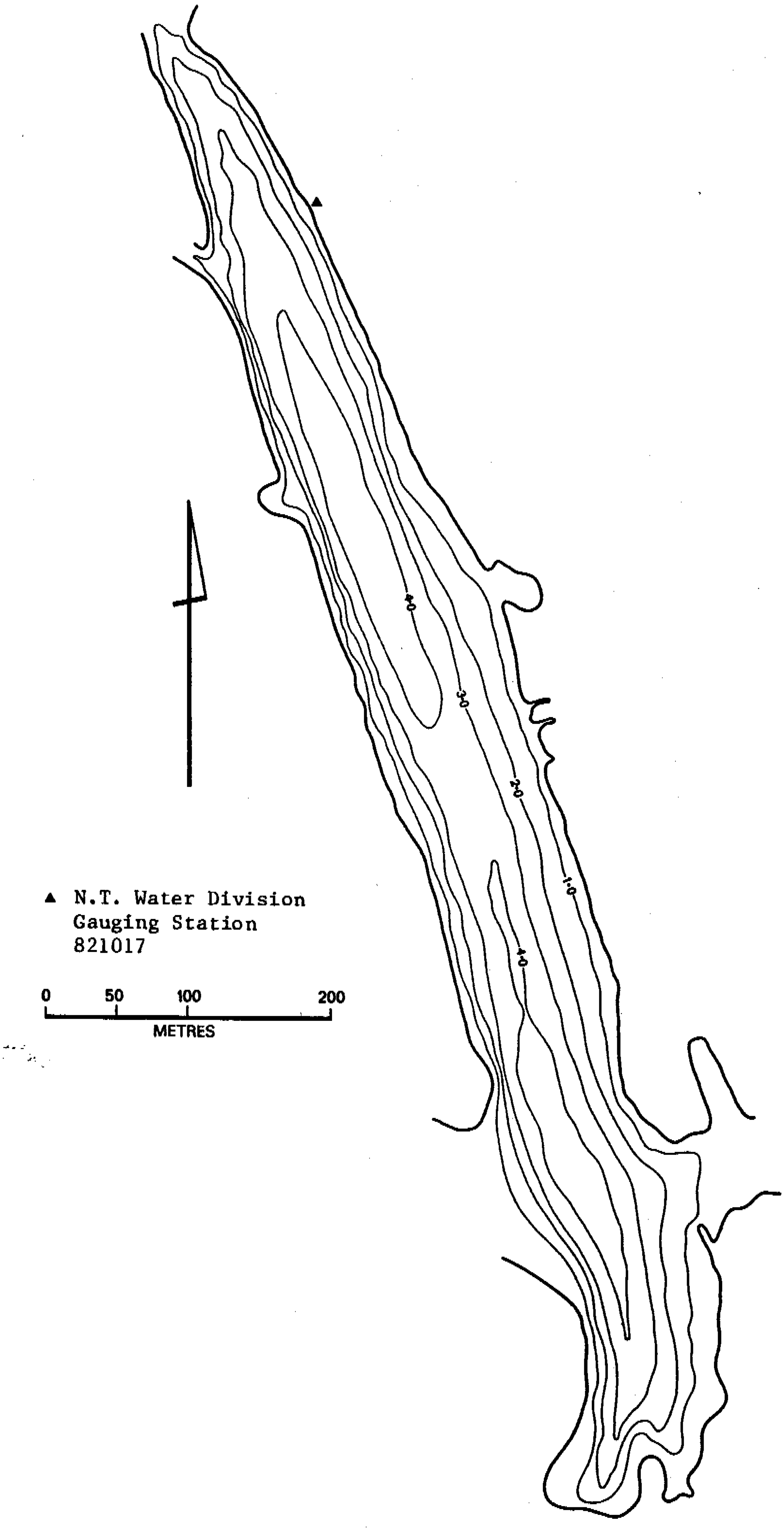

1·0
2·0
3·0
4·0
4·0
3·0
2·0
1·0
0
50
100
150
METRES
Extremely compacted grey clay
Soft, coarse silt and clay
Silt and unconsolidated plant debris
▲ N.T. Water Division
Gauging Station
821032

Figure 2.13 Bathymetric map of Jabiluka billabong. Map is drawn for a gauge height of 3.70 m AHD (17 August, 1979). (Source - Pancontinental Mining Limited, 1981.)



▲ N.T. Water Division
Gauging Station
821017

Figure 2.14 Bathymetric map of Nankeen billabong. Map is drawn for a gauge height of 2.70 m (1 November, 1981).

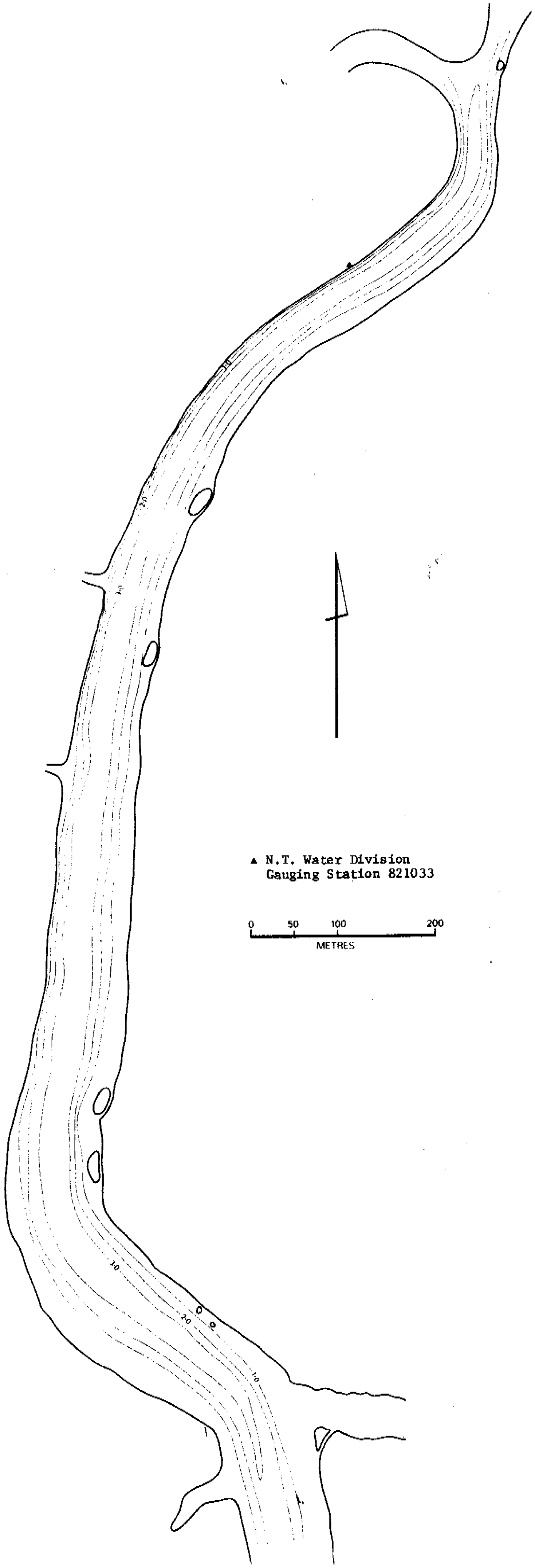

▲ N.T. Water Division
Gauging Station 821033
0
50
100
200
METRES
10
20
10
20
10

Figure 2.15 Stream flow rates recorded through Mudginberri billabong on 30 January, 1982 (gauge height of 9.92 m). Isovels in metres/sec.

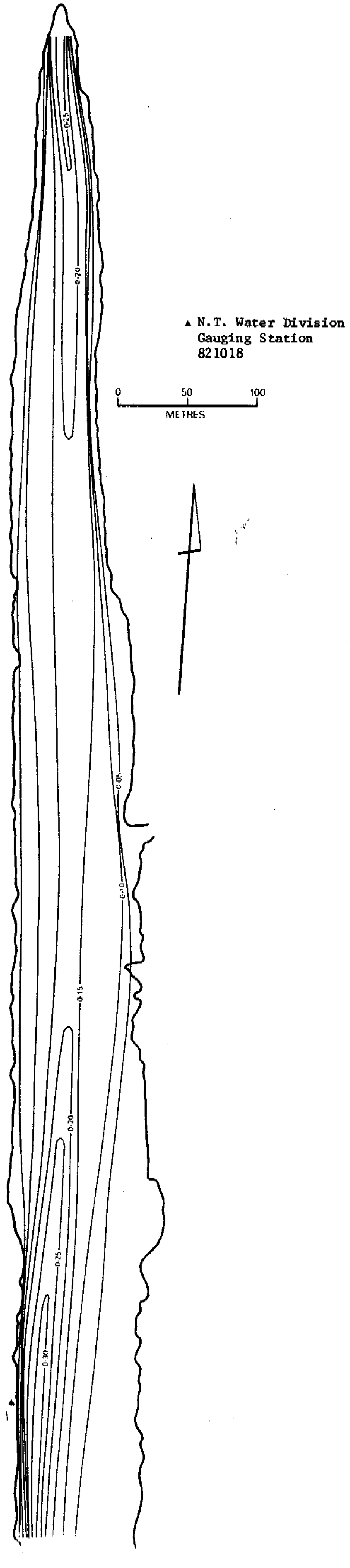
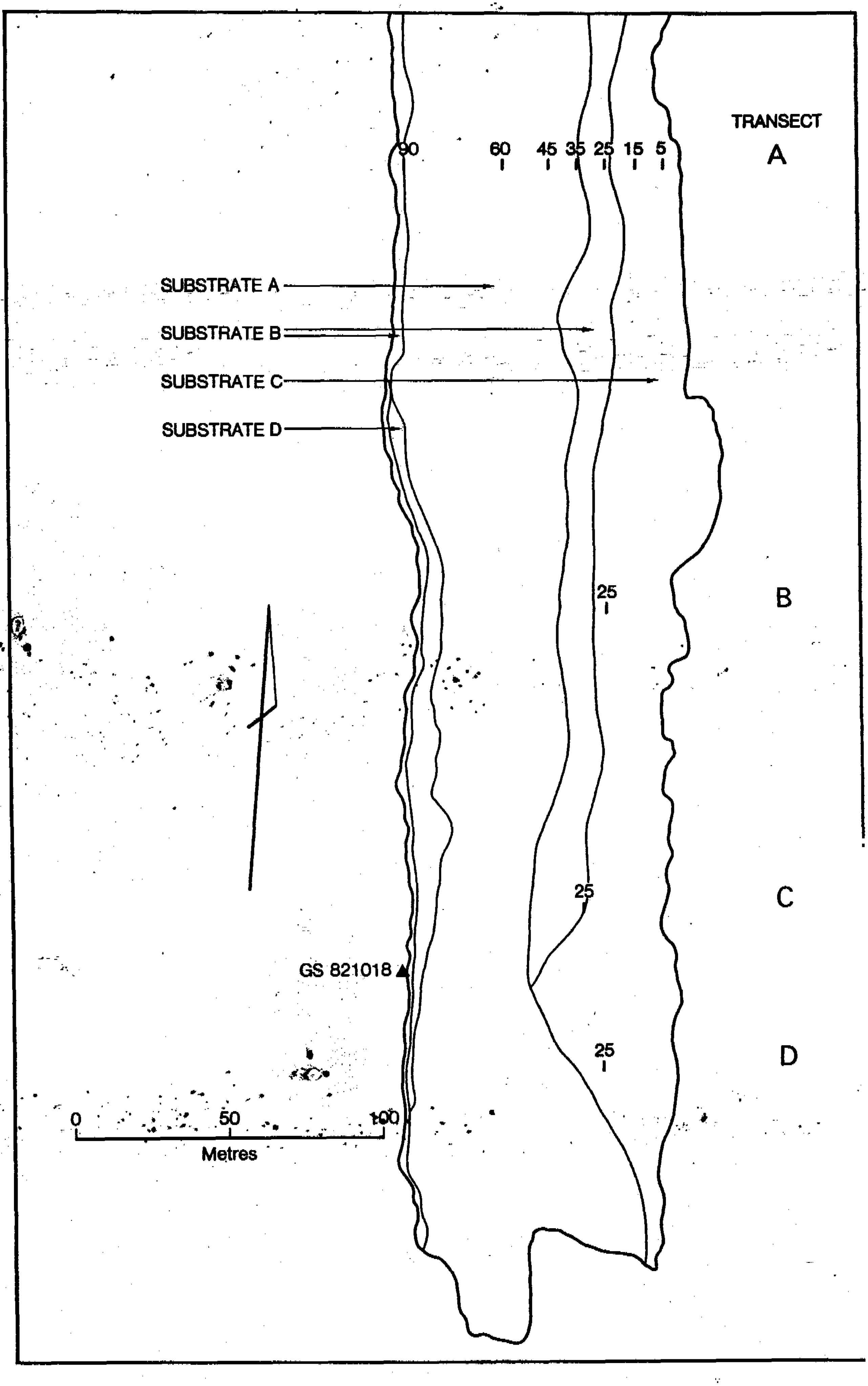
▲ N.T. Water Division
Gauging Station
821018
0
50
100
METRES
0·15
0·20
0·05
0·10
0·15
0·20
0·25
0·30

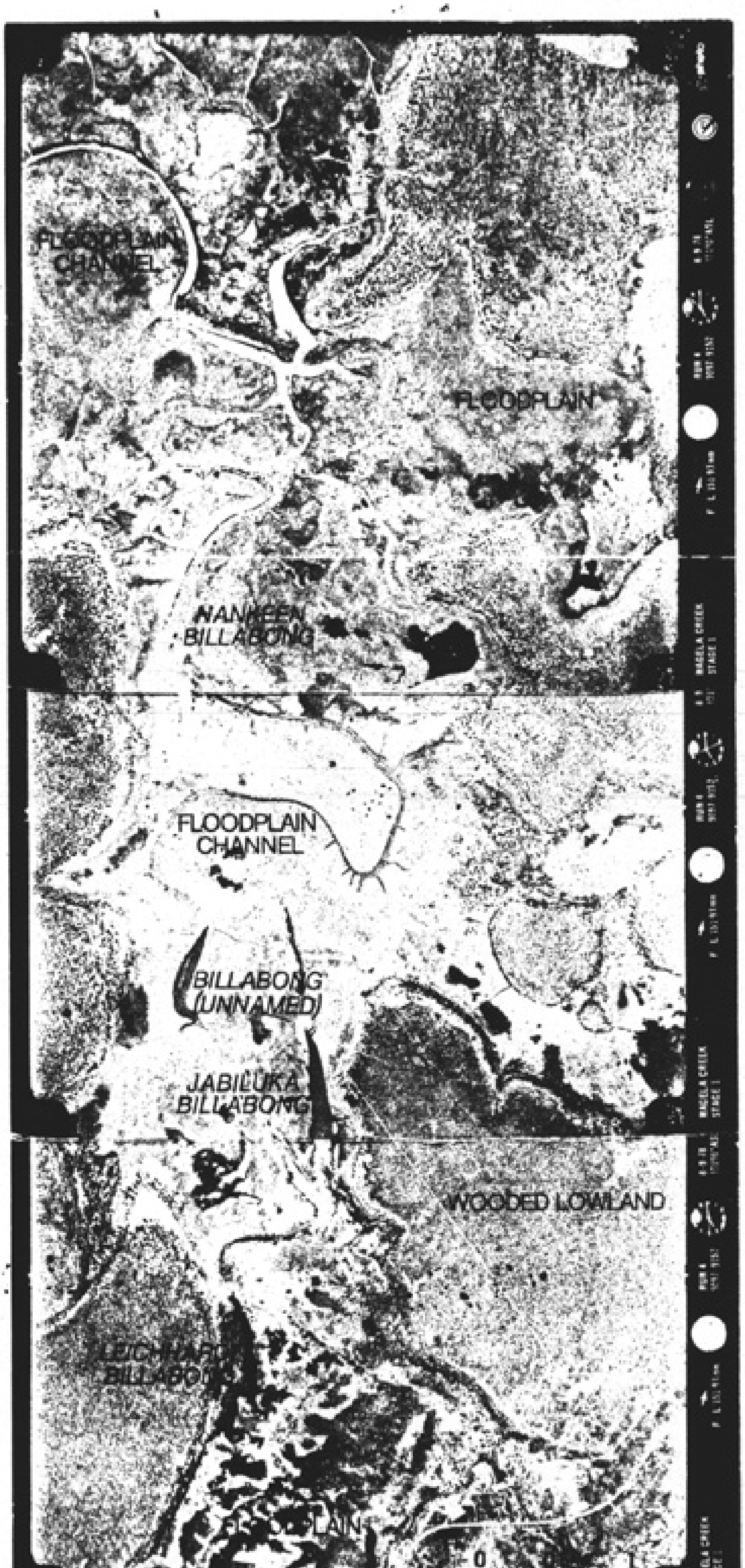
Figure 2.16 Map of Mudginberri billabong (south end) showing the sites sampled for sediment analyses in October 1980. Numbers across the transects refer to the respective distances, right to left (metres) at which sediments were sampled. (See Table 5.4 for key to substrates.)

Figure 2.16 Map of Mudginberri billabong (south end) showing the sites sampled for sediment analyses in October 1980. Numbers across the transects refer to the respective distances, right to left (metres) at which sediments were sampled. (See Table 5.4 for key to substrates.)



TRANSECT
A
90
60
45
35
25
15
5
SUBSTRATE A
SUBSTRATE B
SUBSTRATE C
SUBSTRATE D
25
B
25
C
GS 821018
25
D
0
50
100
Metres

Figure 2.17 Aerial photograph of Magela Creek floodplain north of JaJa billabong, showing the floodplain billabongs and channels, and surrounding wooded lowlands.


FLOODPLAIN CHANNEL
FLOODPLAIN
NANKEEN BILLABONG
FLOODPLAIN CHANNEL
BILLABONG (UNNAMED)
JABILUKA BILLABONG
WOODED LOWLAND
LEICHHARDT BILLABONG
FLOODPLAIN
0

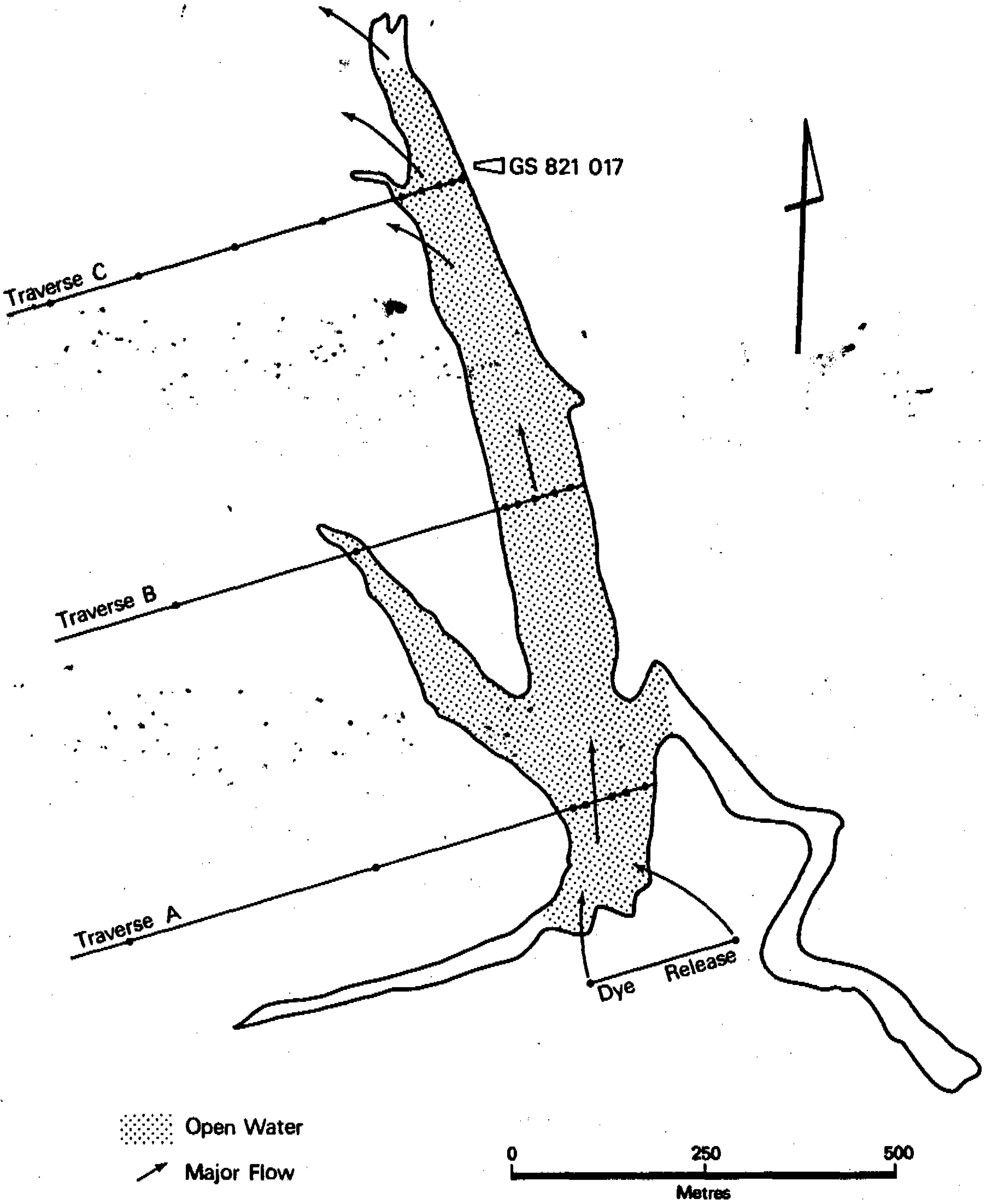
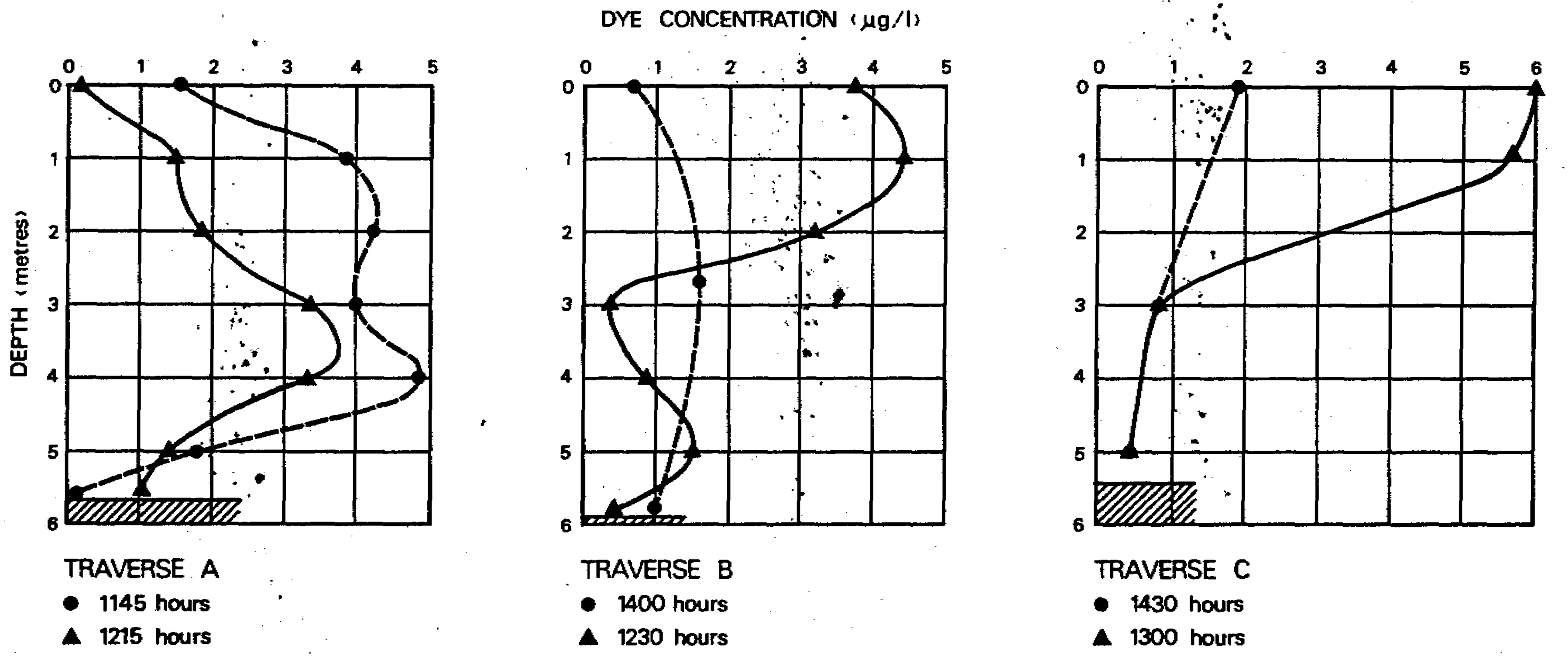


Figure 2.18 Location of the sampling sites (points on the traverses) in Jabiluka billabong, 20th February, 1979, at which fluorometric samples of dye were taken, for studies of flow characteristics leading into the billabong. (Source - N.T. Dept. Transport and Works, Water Division, 1980.)

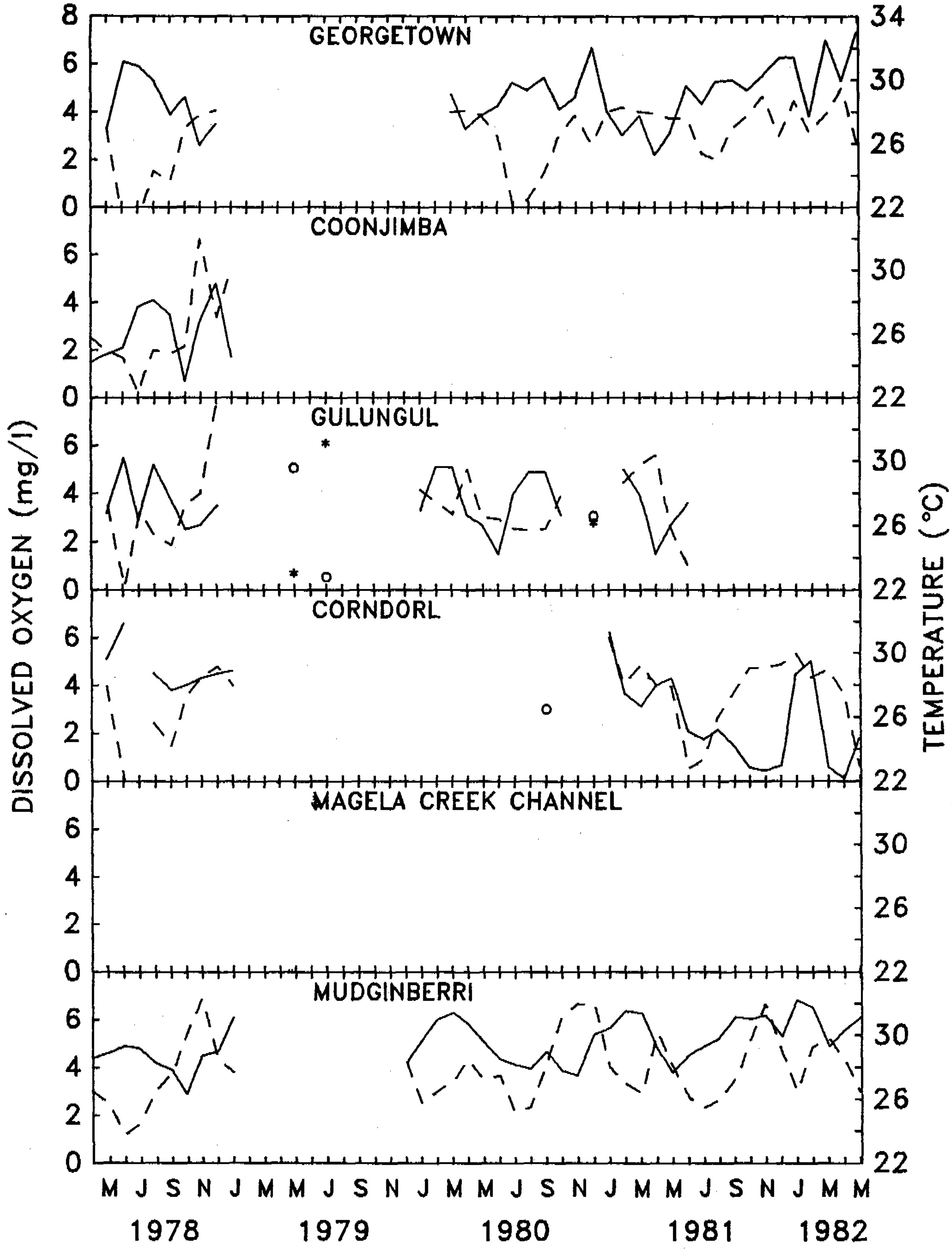
Figure 2.19 Dye concentrations recorded in flow studies, across the traverses in Jabiluka billabong in relation to depth and time. (Traverses are shown in Figure 2.18.)



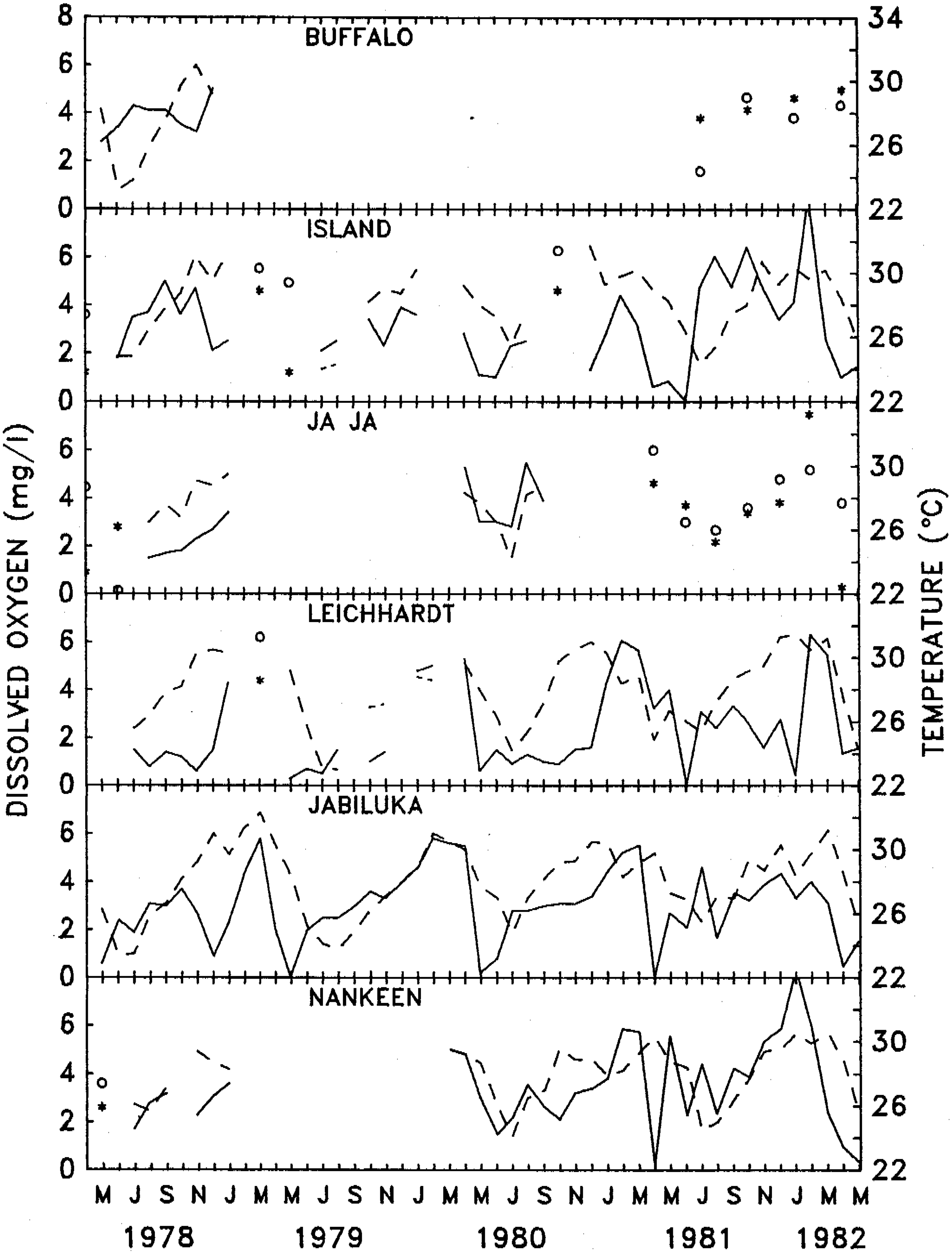
Figures 2.20 and 2.21 Seasonal changes in bottom dissolved oxygen concentration (solid line) and water temperature (dotted line) recorded over a four year period (1978 to 1982) in the Magela Creek billabongs. Asterisks and open circles indicate isolated dissolved oxygen and temperature readings respectively.

Values for Georgetown downstream to Mudginberri billabong are shown in Figure 2.20 while values for Buffalo downstream to Nankeen billabong are shown in Figure 2.21.

2.20

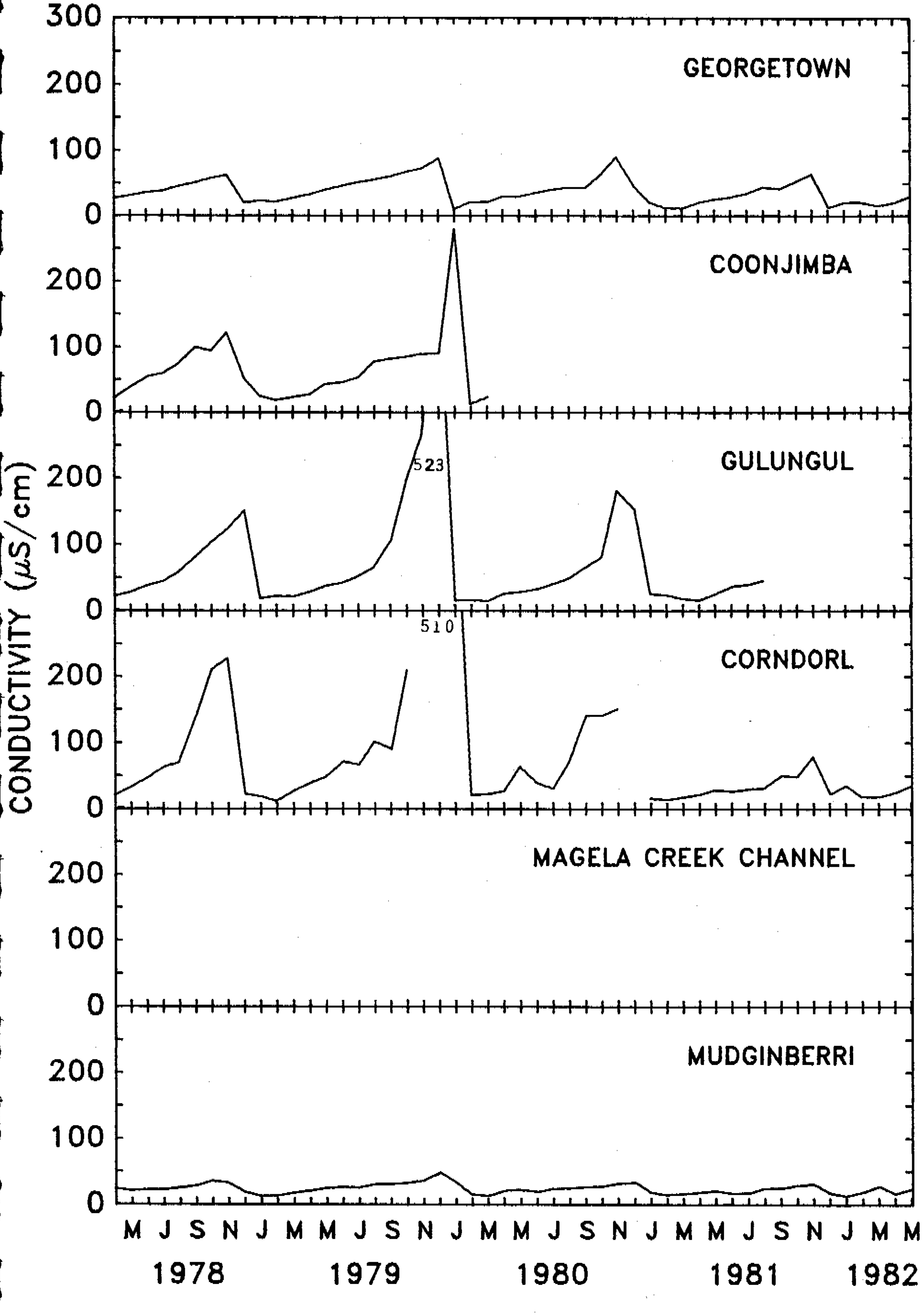

GEORGETOWN
COONJIMBA
GULUNGUL
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
DISSOLVED OXYGEN (mg/l)
TEMPERATURE (°C)
0
2
4
6
8
22
26
30
34
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

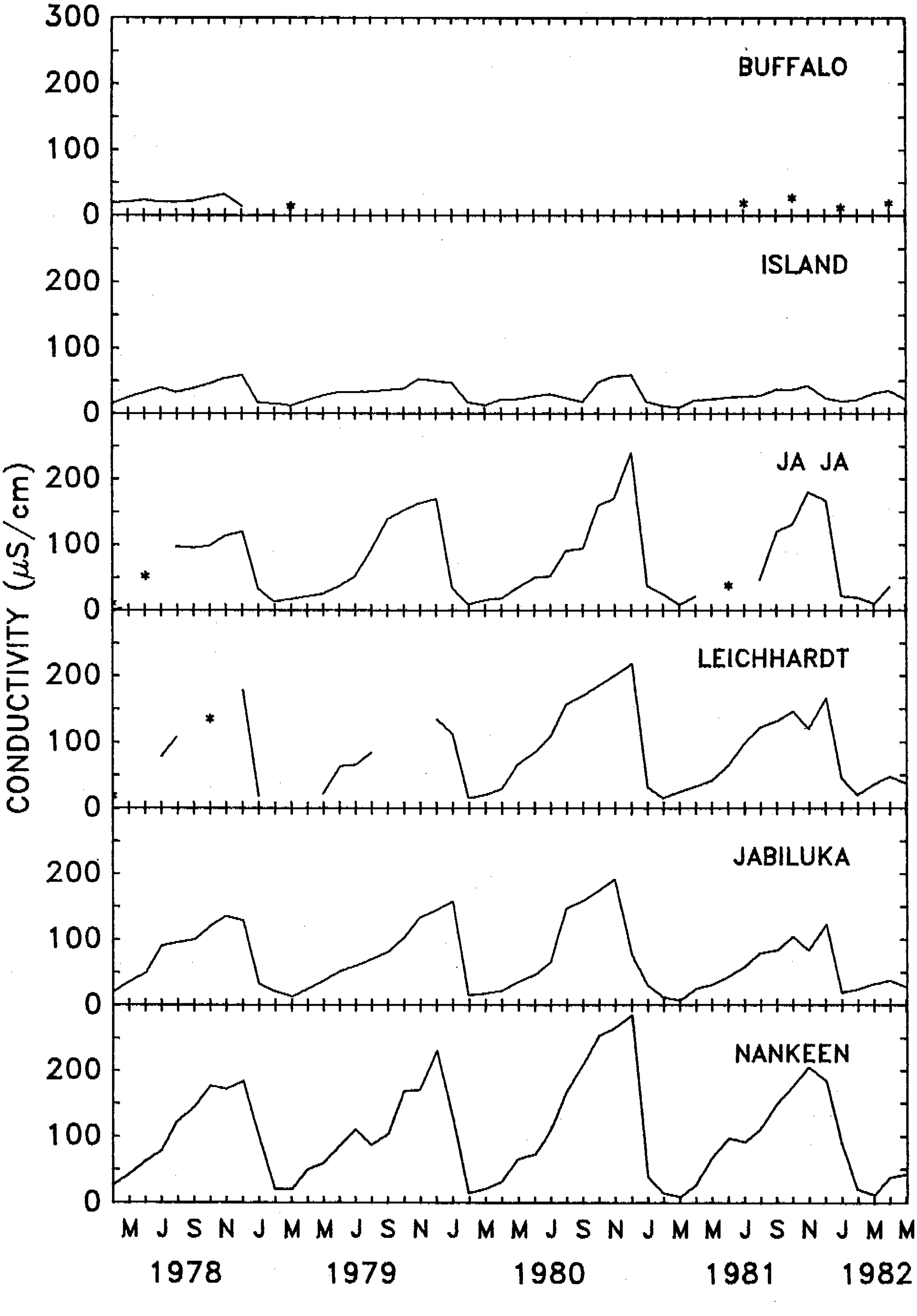
2.51


BUFFALO
ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
DISSOLVED OXYGEN (mg/l)
TEMPERATURE (°C)
0
2
4
6
8
22
26
30
34
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

Figures 2.22 and 2.23 Seasonal changes in surface conductivity recorded over a four year period in the Magela Creek billabongs. Asterisks indicate isolated readings.

Values for Georgetown downstream to Mudginberri billabong are shown in Figure 2.22 while values for Buffalo downstream to Nankeen billabong are shown in Figure 2.23.

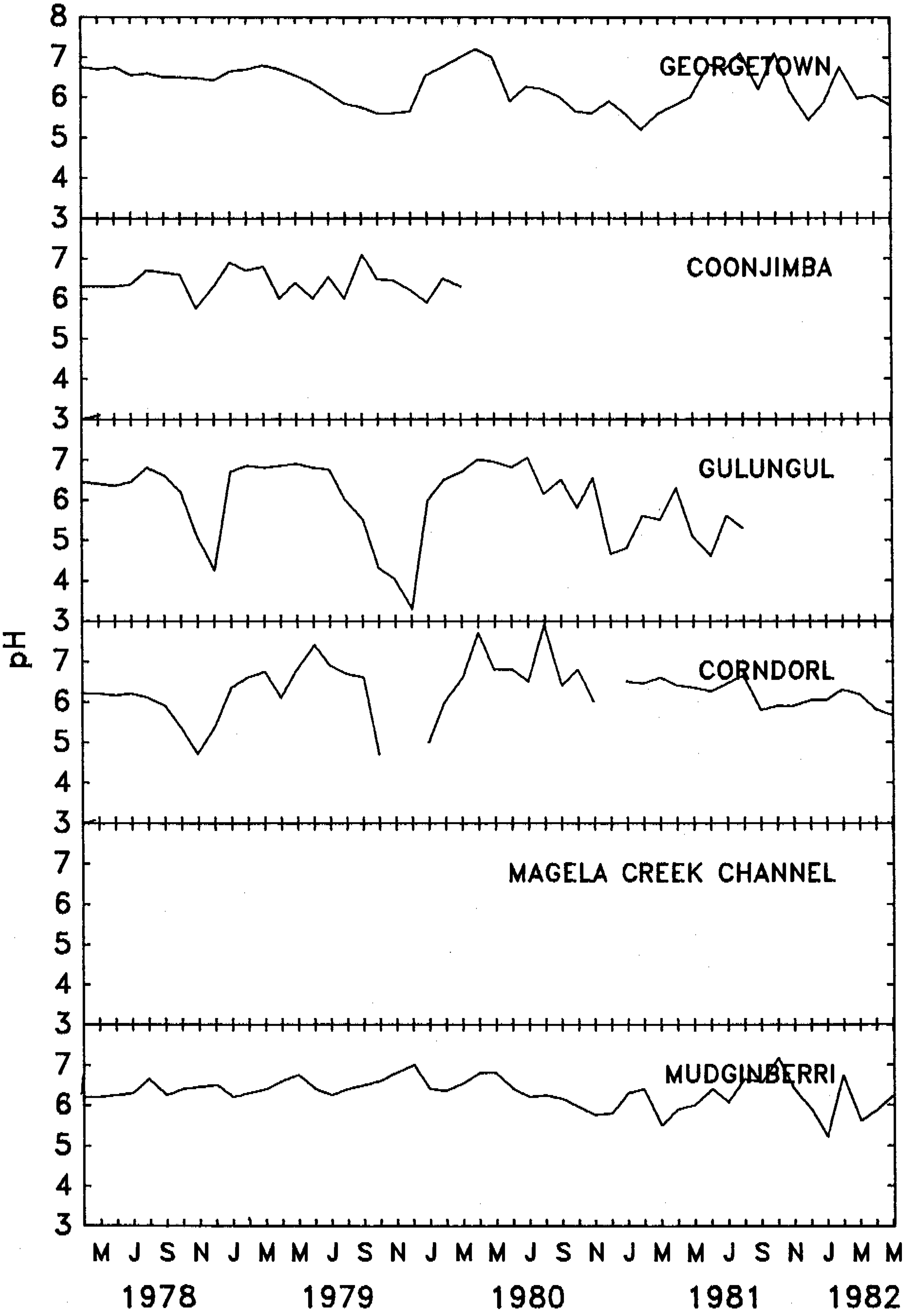

CONDUCTIVITY (µS/cm)
300
200
100
0
GEORGETOWN
COONJIMBA
GULUNGUL
523
CORNDORL
510
MAGELA CREEK CHANNEL
MUDGINBERRI
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982


CONDUCTIVITY (µS/cm)
BUFFALO
ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
300
200
100
0
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

Figures 2.24 and 2.25 Seasonal changes in surface pH recorded over a four year period in the Magela Creek billabongs. Asterisks indicate isolated readings.

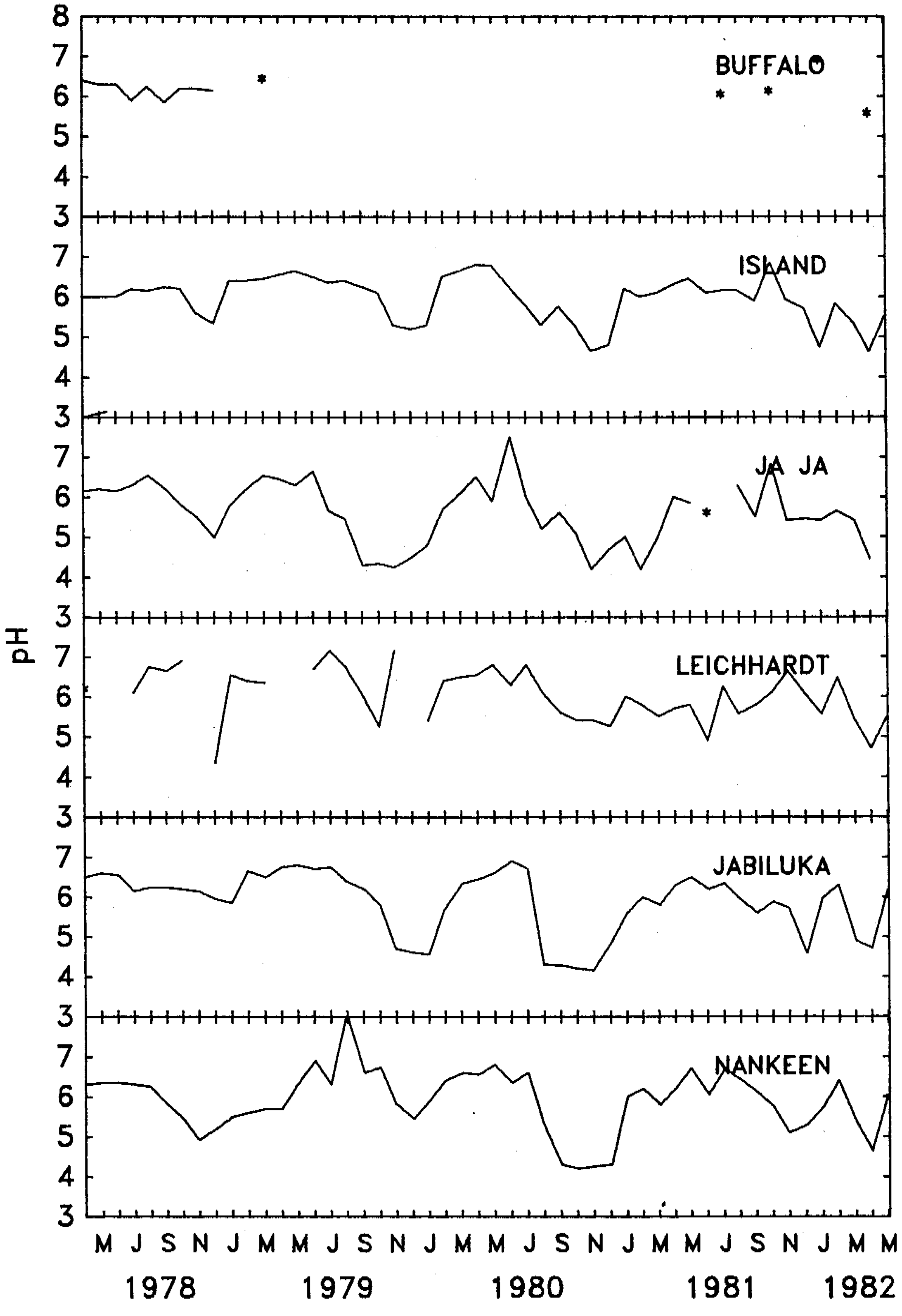
Values for Georgetown downstream to Mudginberri billabong are shown in Figure 2.24 while values for Buffalo downstream to Nankeen billabong are shown in Figure 2.25.

2.04



GEORGETOWN
COONJIMBA
GULUNGUL
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
pH
8
7
6
5
4
3
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

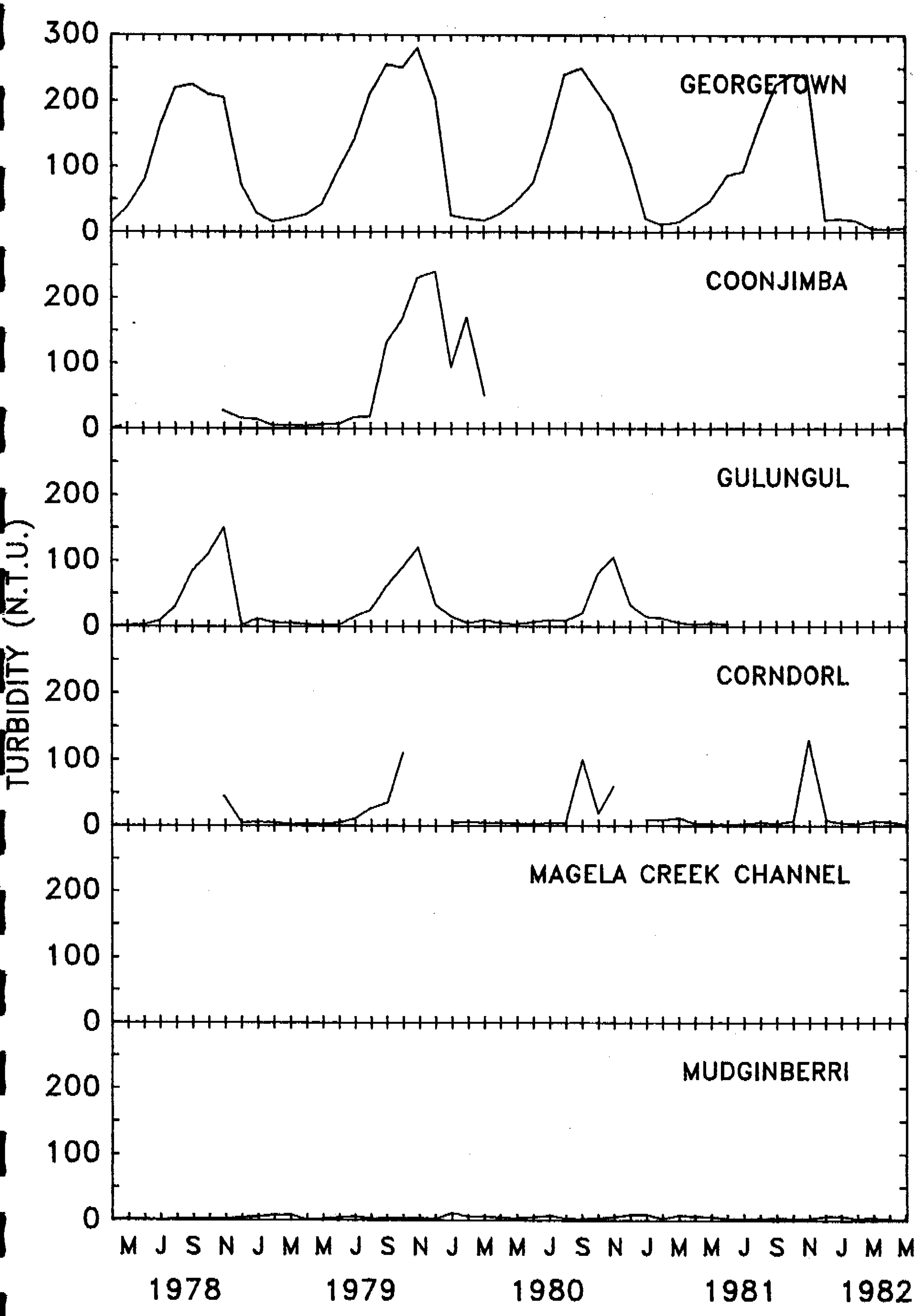
2.28

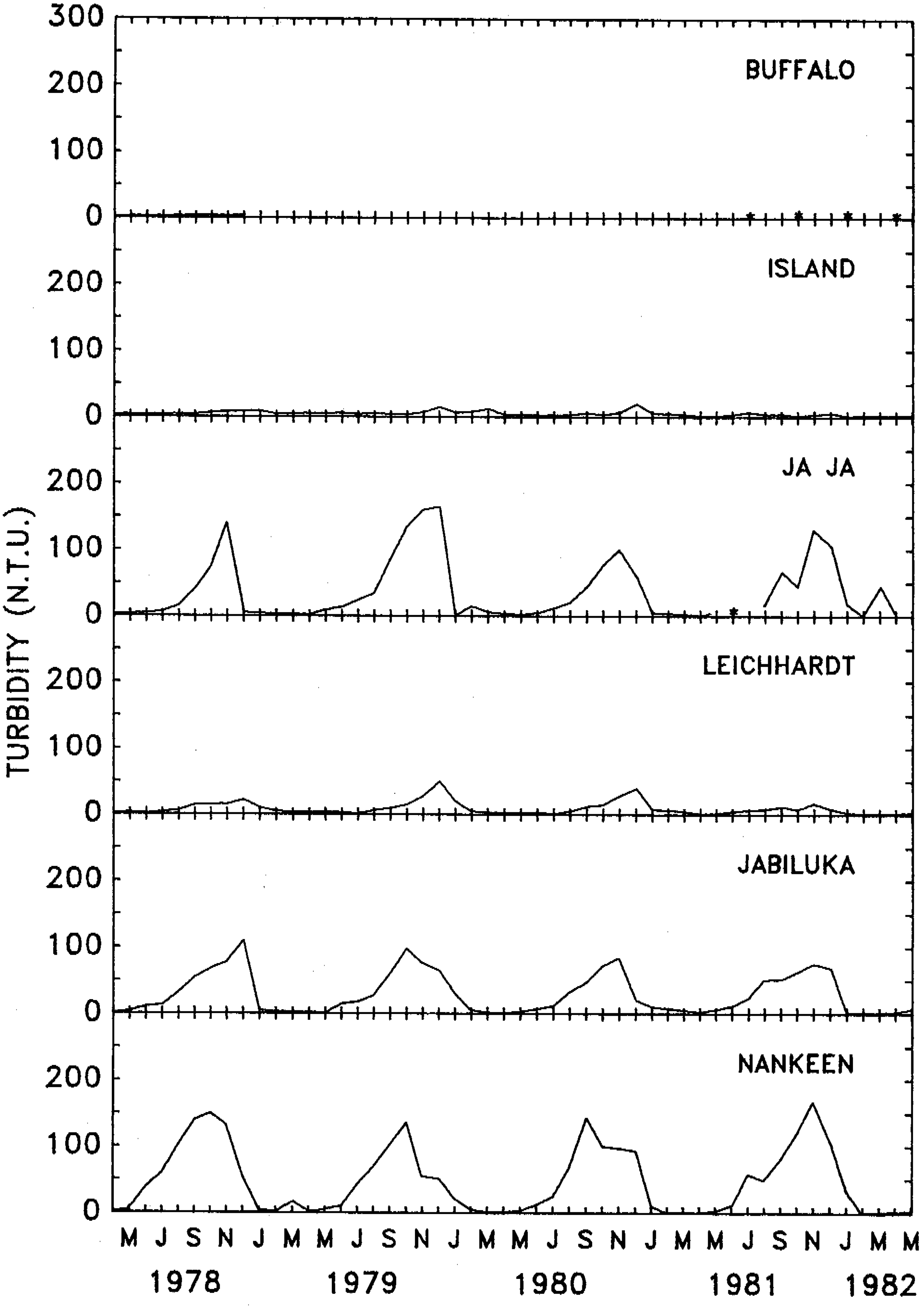


BUFFALO
ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
pH
8
7
6
5
4
3
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

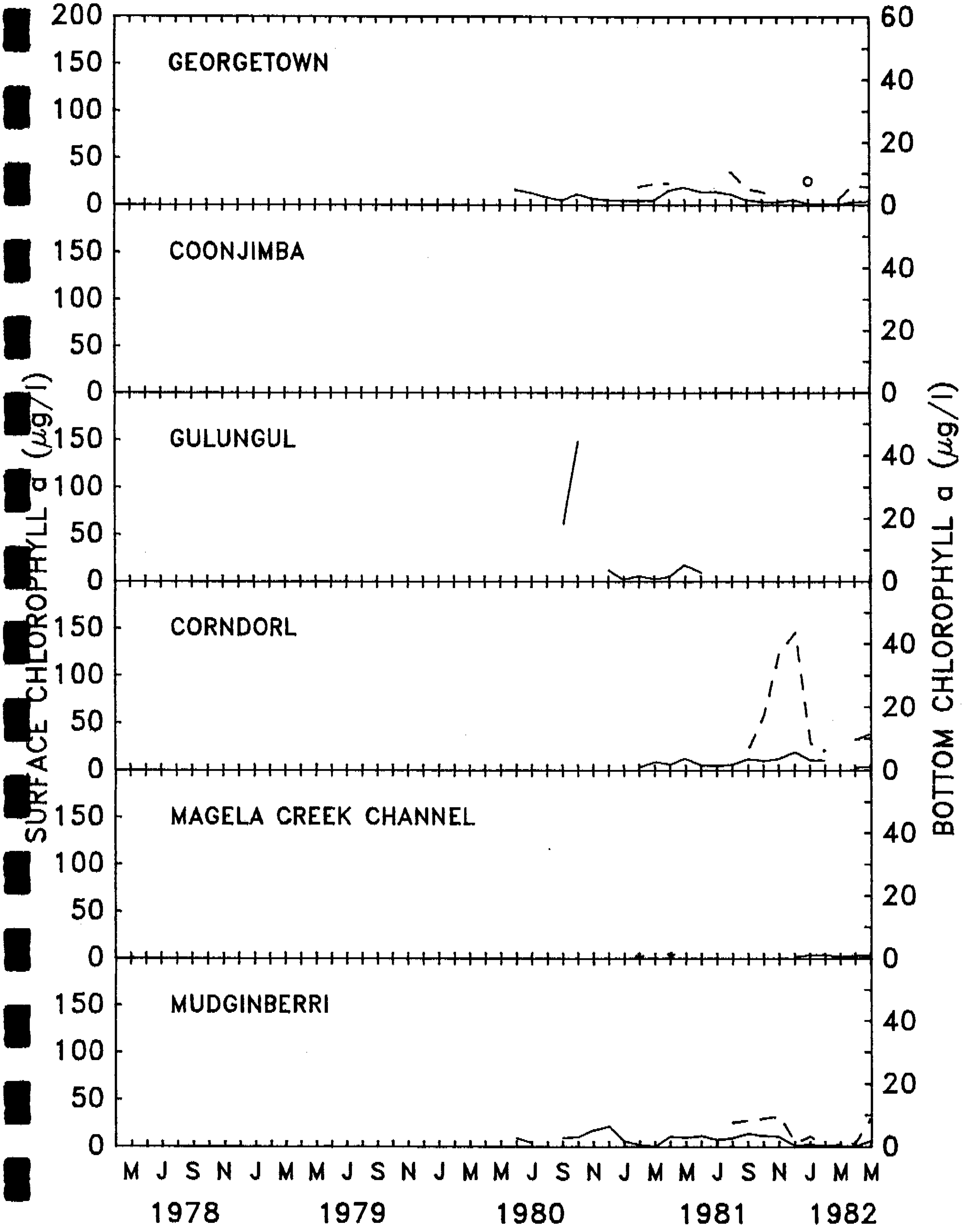
Figures 2.26 and 2.27 Seasonal changes in surface turbidity recorded over a four year period in the Magela Creek billabongs. Asterisks indicate isolated readings.

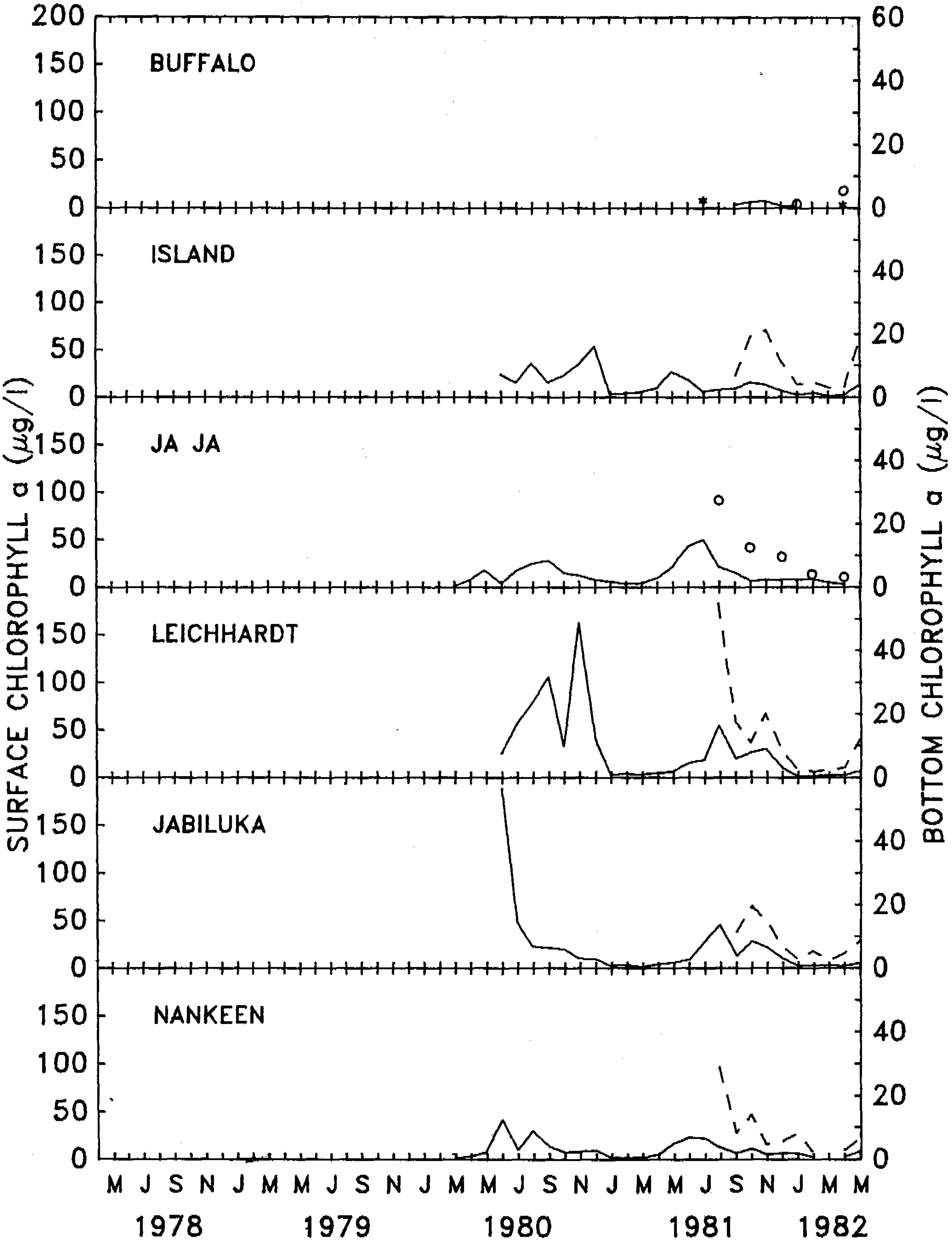
Values for Georgetown downstream to Mudginberri billabong are shown in Figure 2.26 while values for Buffalo downstream to Nankeen billabong are shown in Figure 2.27.


TURBIDITY (N.T.U.)
300
200
100
0
GEORGETOWN
COONJIMBA
GULUNGUL
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982


BUFFALO
ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
TURBIDITY (N.T.U.)
300
200
100
0
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

Figures 2.28 and 2.29 Seasonal changes in surface (solid line) and bottom (dotted line) chlorophyll concentrations recorded over a two year period in the Magela Creek billabongs. Asterisks and open circles indicate isolated surface and bottom chlorophyll readings respectively.


GEORGETOWN
COONJIMBA
GULUNGUL
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
SURFACE CHLOROPHYLL a (μg/l)
BOTTOM CHLOROPHYLL a (μg/l)
200
150
100
50
0
60
40
20
0
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982


BUFFALO
ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
SURFACE CHLOROPHYLL a (μg/l)
BOTTOM CHLOROPHYLL a (μg/l)
200
150
100
50
0
60
40
20
M J S N J M M J S N J M M J S N J M M J S N J M M
1978
1979
1980
1981
1982

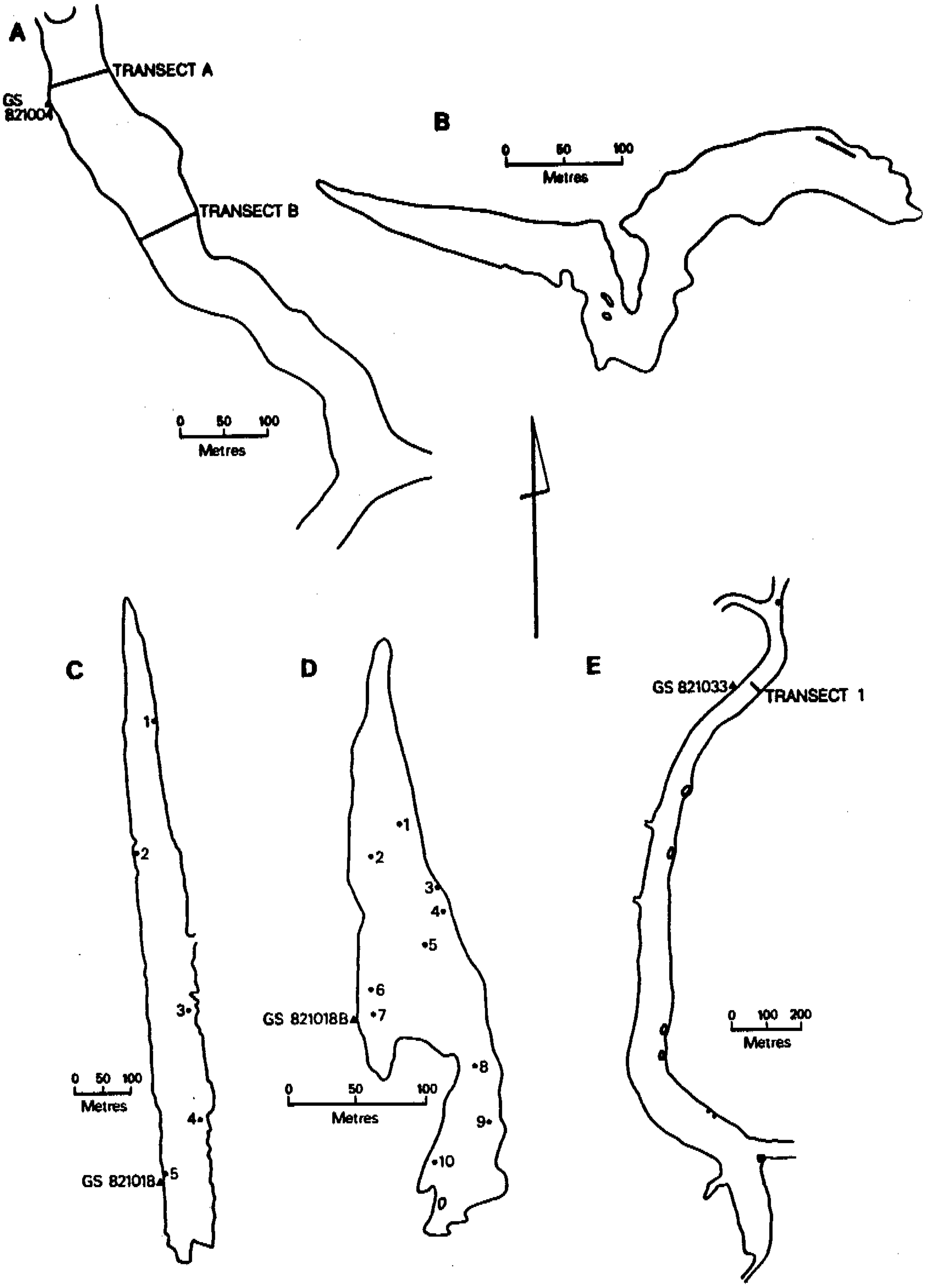


Figure 3.1 Maps of A) Georgetown, B) Corndorl, C) Mudginberri, D) Buffalo and E) Nankeen billabongs, showing the routine transects and sites at which mussels were collected during the study. Sites are indicated by numbered points or in Corndorl billabong, by the solid bar.

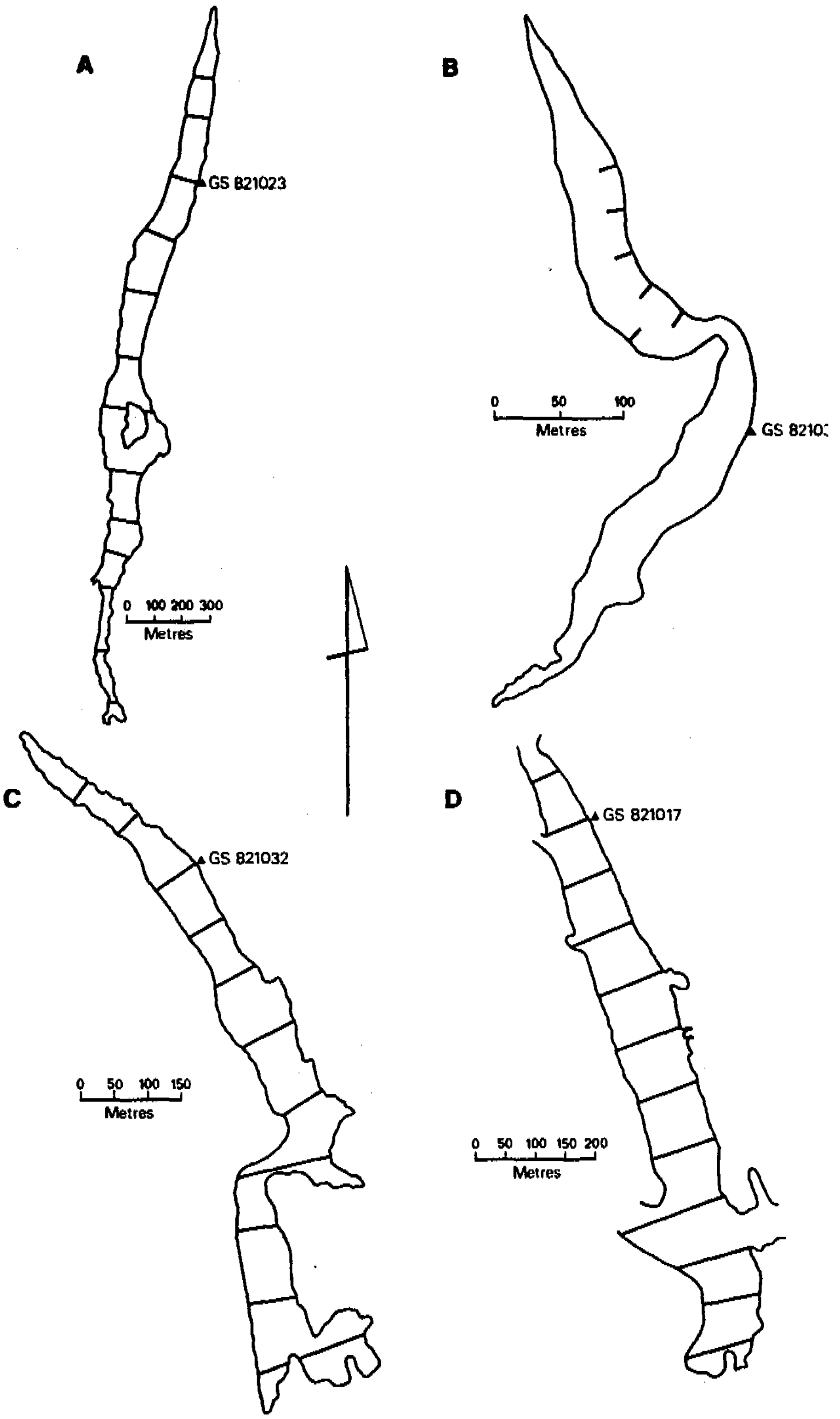


Figure 3.2 Maps of A) Island, B) JaJa, C) Leichhardt and D) Jabiluka billabongs, showing the transects across which samples of mussels were collected during the study.

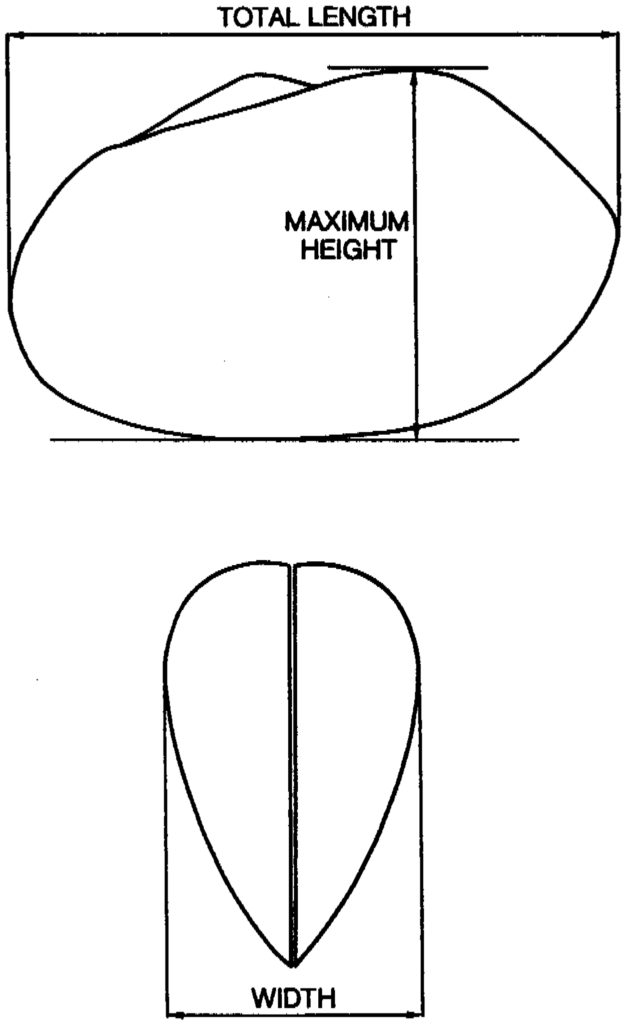
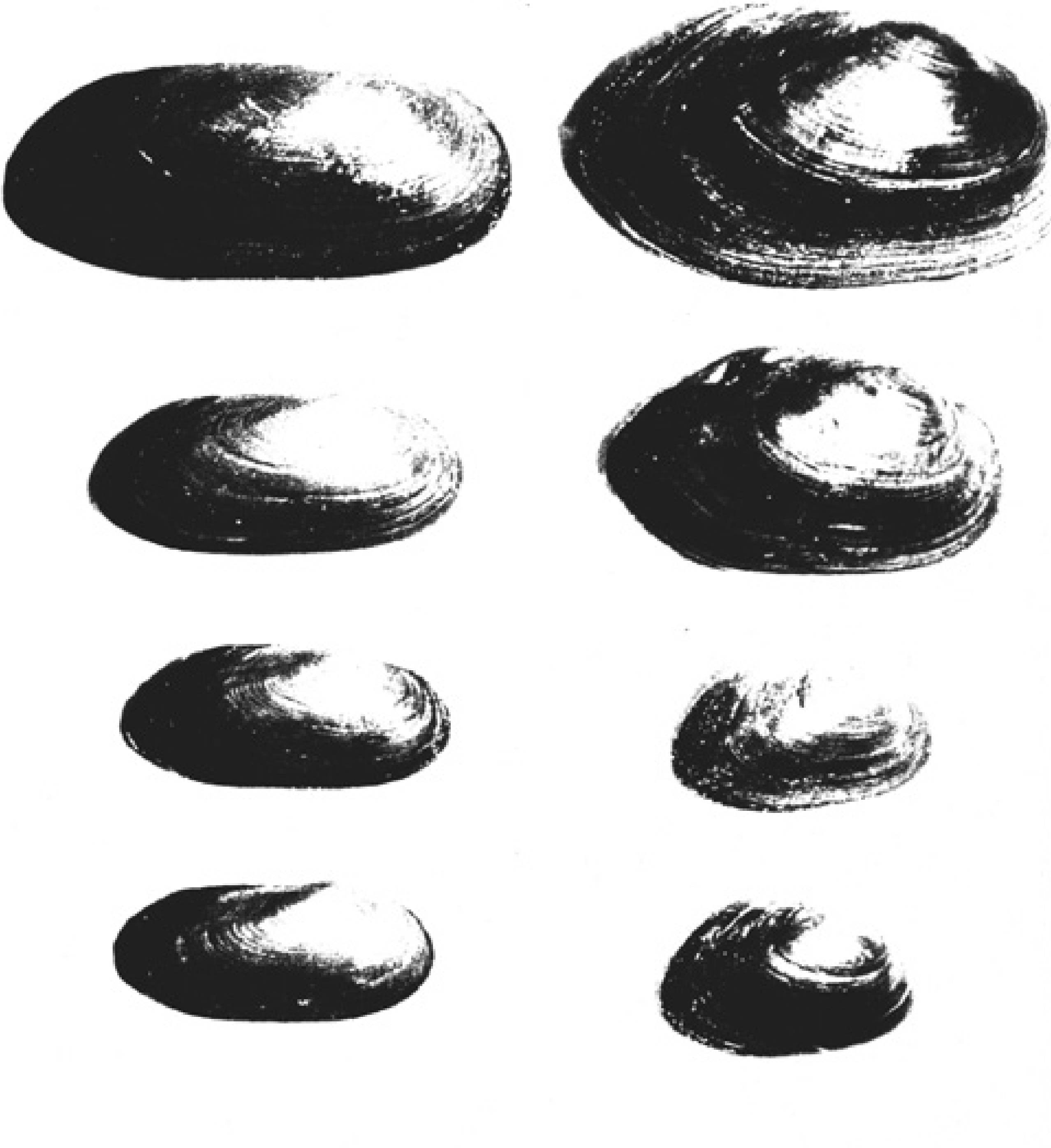


Figure 3.3 Mussel shells (upper figure: internal view of a right valve and lower figure: intact valves) showing the measurements used to specify size of *Velesunio angasi*.

Figure 4.1 Typical juvenile *Velesunio angasi* from billabongs of the Magela Creek (right hand side), and juvenile *V. wilsonii* from Corella River, Mary Kathleen (Queensland) (left hand side). Scale bar 1 cm.



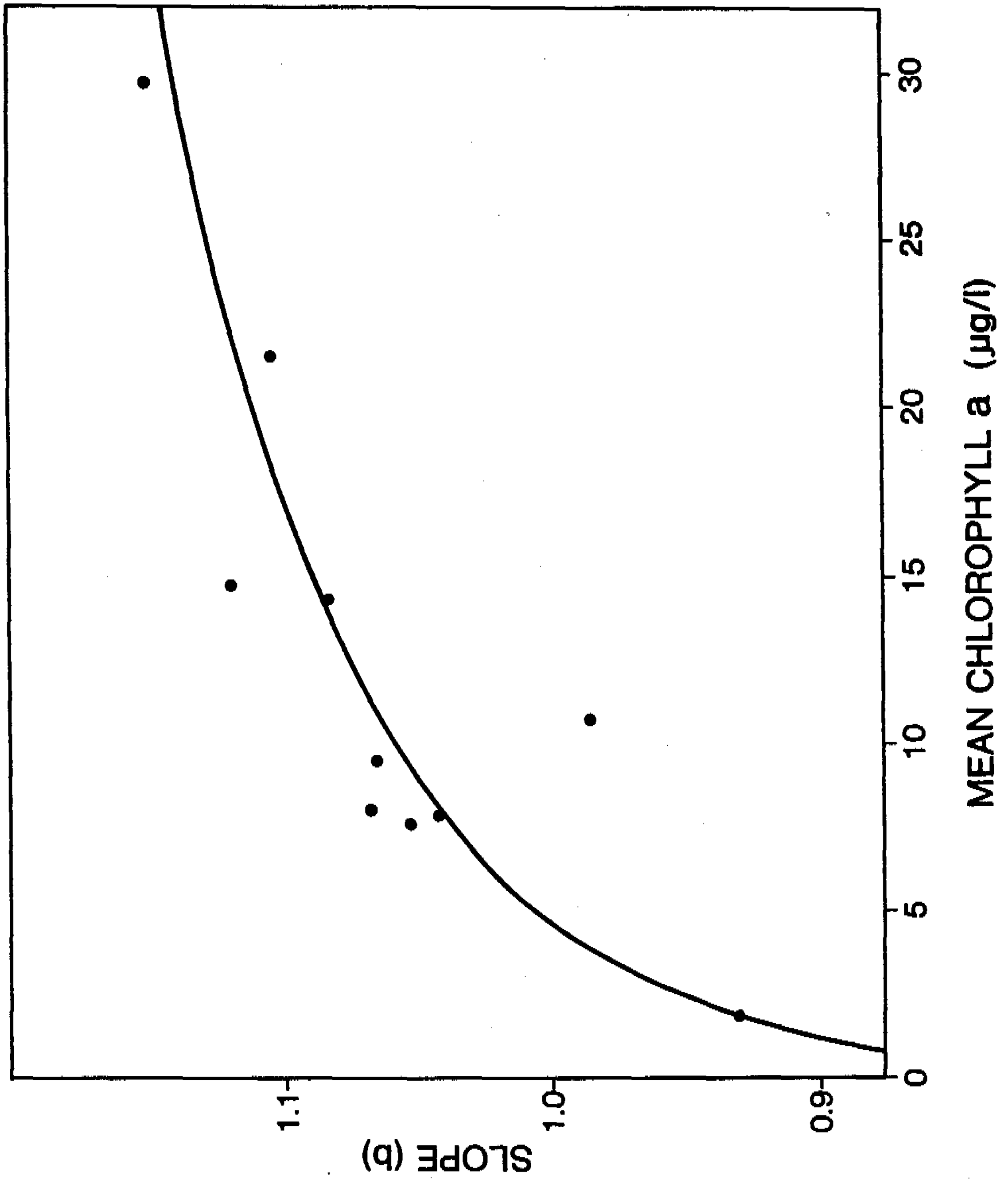


Figure 4.2 Logarithmic relationship between relative shell height (as indicated by slope b, of the allometric regression equation between shell length and height) of mussel populations between different billabongs of the Magela Creek, and mean chlorophyll a concentration of the surface waters averaged over the seasons.

Fitted regression equation is:

$$Y = 0.887 + 0.0753 \ln X \quad (P < 0.001,\ r^2 = 0.769)$$

where Y = slope (b) of the allometric equation for relative height of the combined sexes, and X = mean chlorophyll a concentration averaged over the seasons (µg/l).

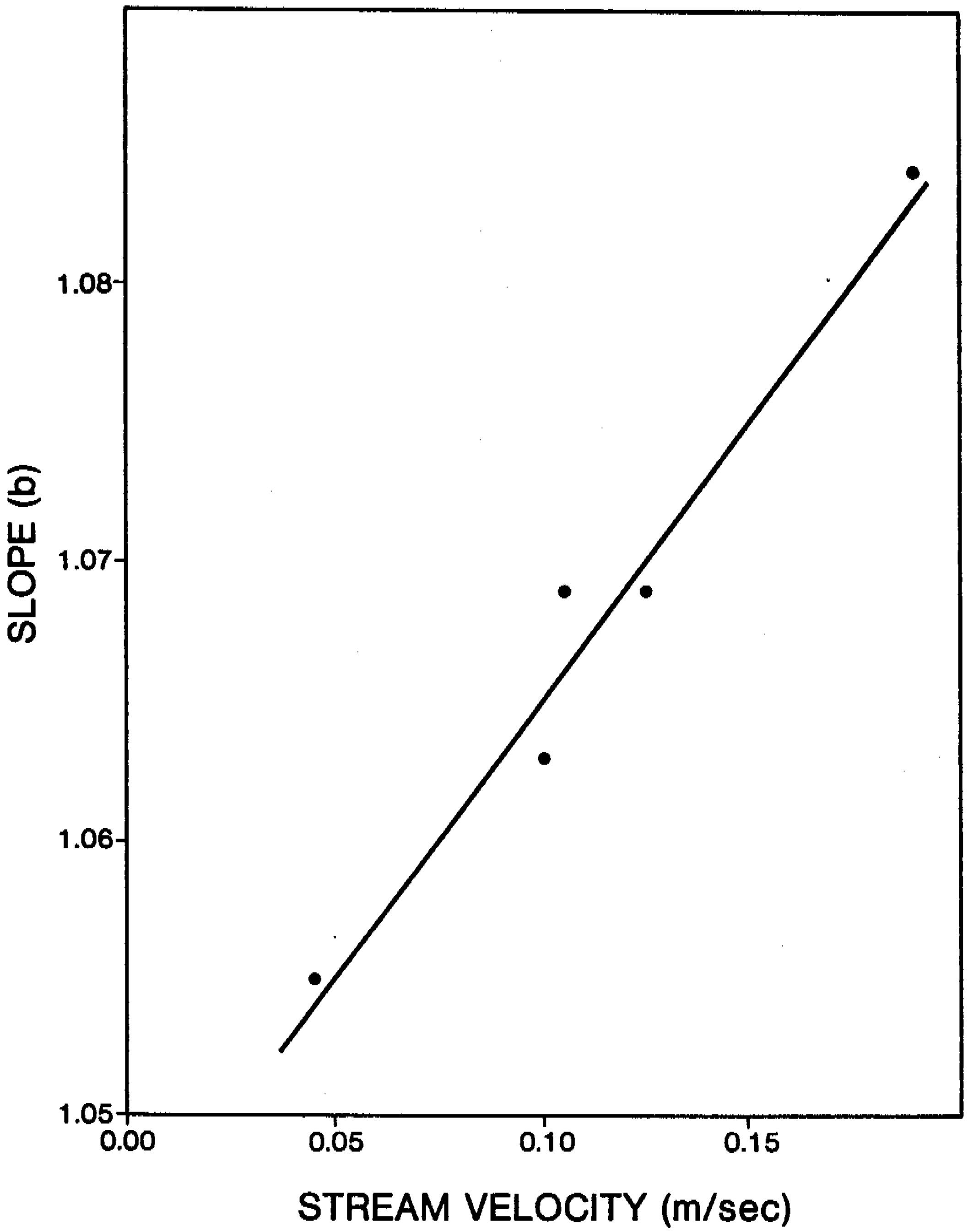


Figure 4.3 Linear relationship between relative shell height (as indicated by slope b, of the allometric regression equation between shell length and height) of mussels between sites of Mudginberri billabong, and Wet season stream velocity measured on 30 January, 1982 (see Figure 2.15).

Fitted regression equation is:

$$Y = 1.045 + 0.199X \qquad (P < 0.01,\ r^2 = 0.969)$$

where Y = slope (b) of the allometric equation for relative height of the combined sexes, and X = stream velocity (m/sec).

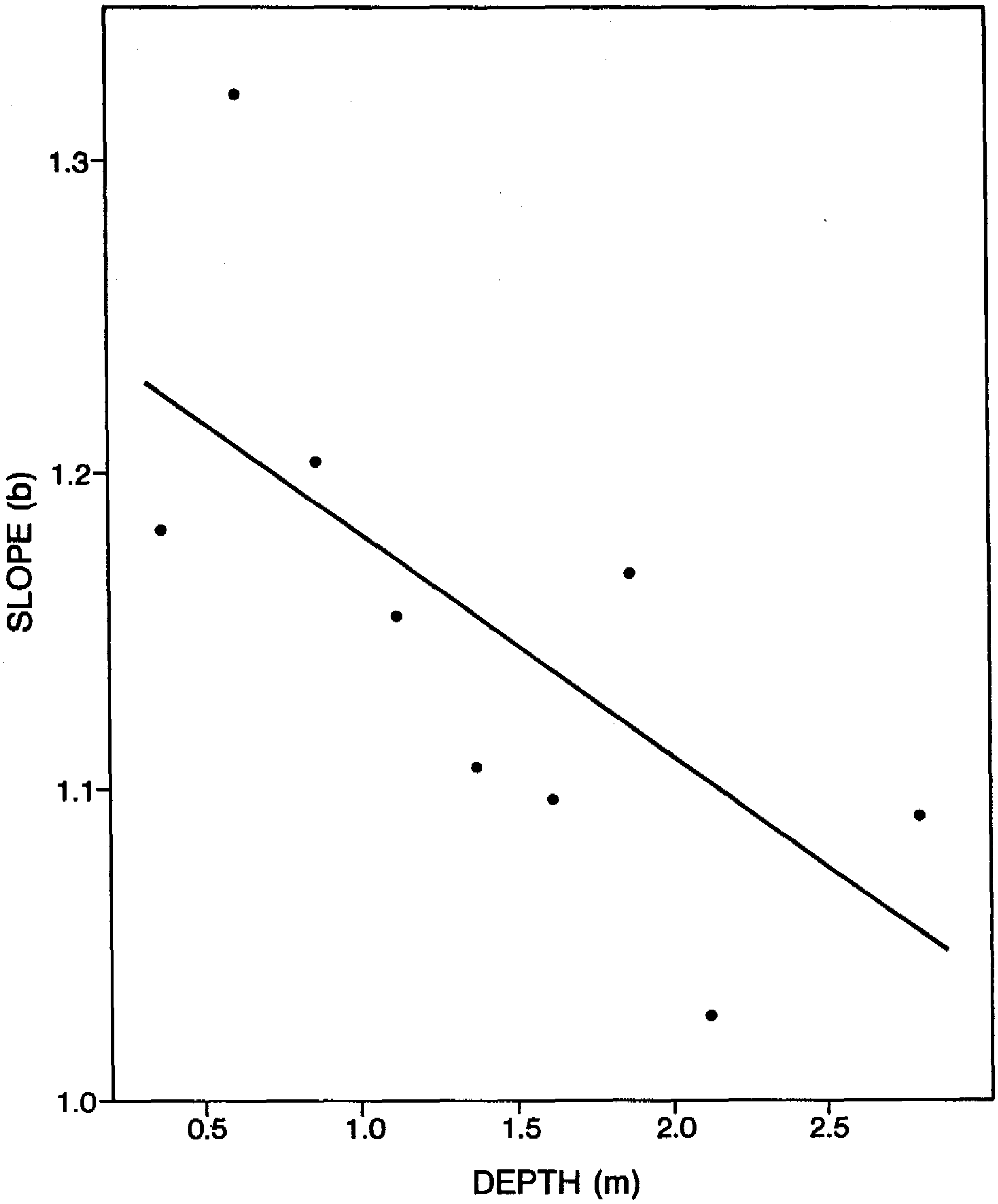


Figure 4.4 Linear relationship between relative shell height (as indicated by slope b, of the allometric regression equation between shell length and height) of mussels and depth in Leichhardt billabong.

Fitted regression equation is:

$$Y = 1.252 - 0.071X \qquad (P < 0.05,\ r^2 = 0.475)$$

where Y = slope (b) of the allometric equation for relative height of the combined sexes, and X = depth (m).

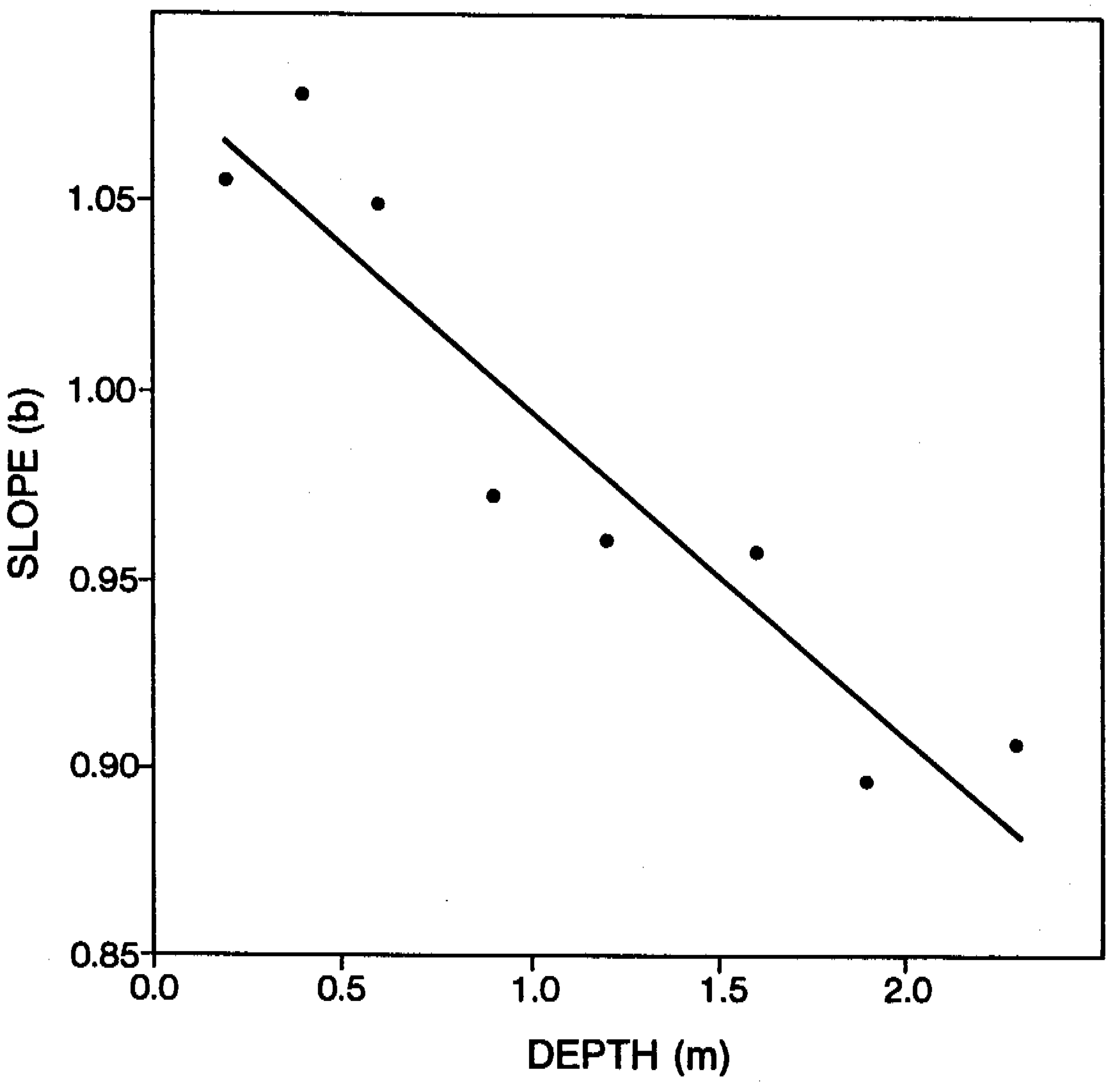


Figure 4.5 Linear relationship between relative shell height (as indicated by slope b, of the allometric regression equation between shell length and height) of mussels and depth in Nankeen billabong.

Fitted regression equation is:

$$Y = 1.084 - 0.0867X \quad (P < 0.001,\ r^2 = 0.882)$$

where Y = slope (b) of the allometric equation for relative height of the combined sexes, and X = depth (m).

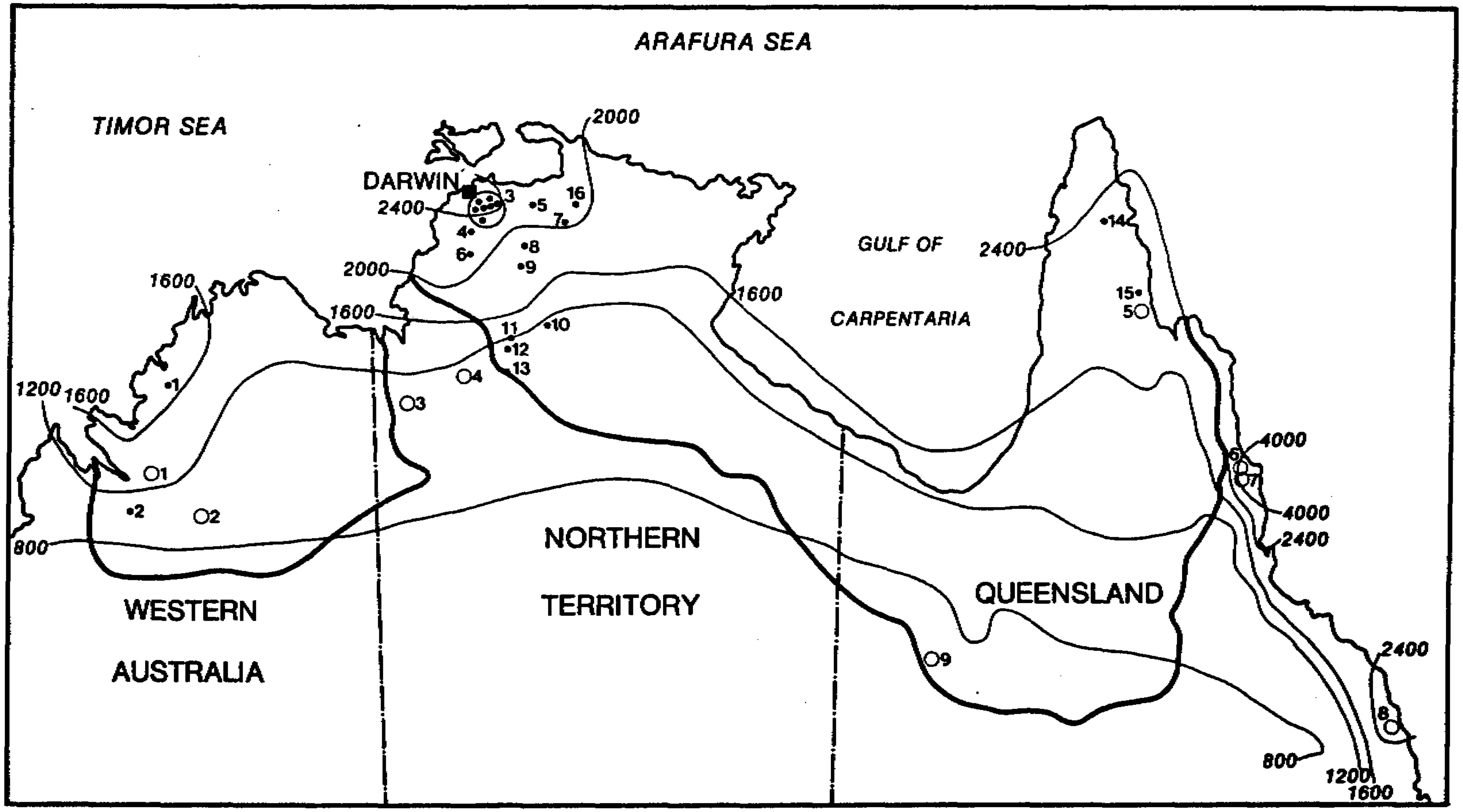


Figure 4.6 Map of northern Australia showing locations at which small (< 40 mm, length) *Velesunio angasi* (solid circles) and *V. wilsonii* (open circles) were collected for analysis of relative shell height. Records are from the Australian Museum (Sydney).

The numbers about the symbols are codes to the locations and are given in Table 4.8.

Geographical range of *V. angasi* shown by solid lines; mean annual rainfall (mm) indicated by finer isohyets.

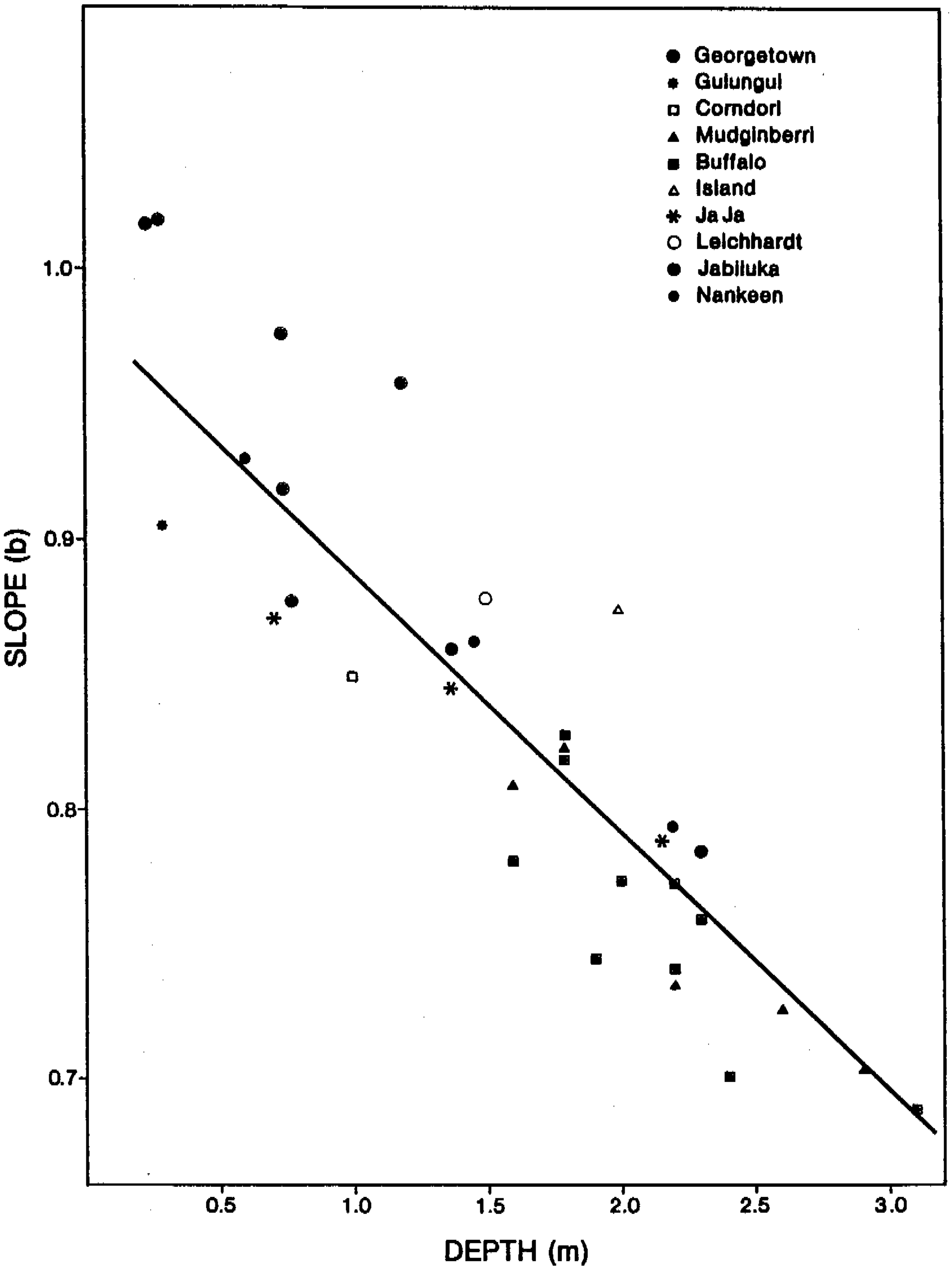


Figure 4.7 Linear relationship between obesity (as indicated by slope b, of the allometric regression equation between shell length and width) of mussel populations within and between different billabongs of the Magela Creek, and water depth.

Fitted regression equation is:

$$Y = 0.986 - 0.097X \quad (P < 0.001, r^2 = 0.801)$$

where Y = slope (b) of the allometric equation for obesity of the combined sexes, and X = depth (m).

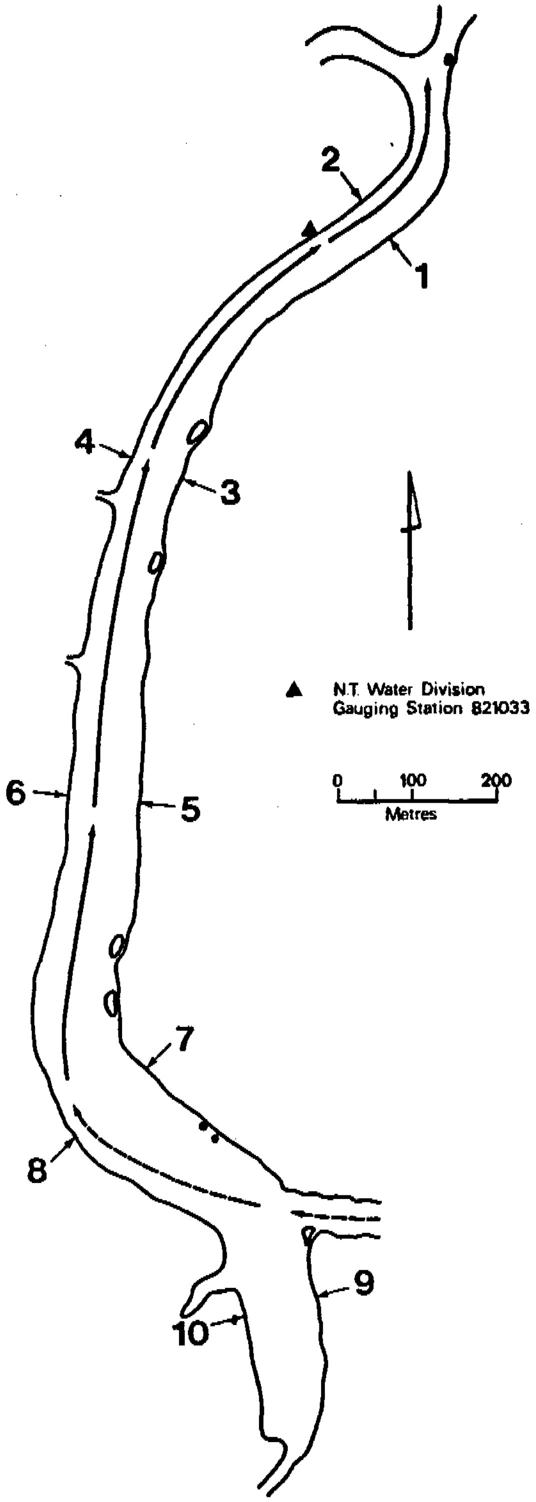


Figure 5.1 The 10 stations sampled in Nankeen billabong at which population densities of mussels were measured.

The solid and unbroken arrows show the observed pathway of flow through the billabong during the Wet season. The broken arrows indicate an hypothesised path of water entry into the billabong during the Wet.

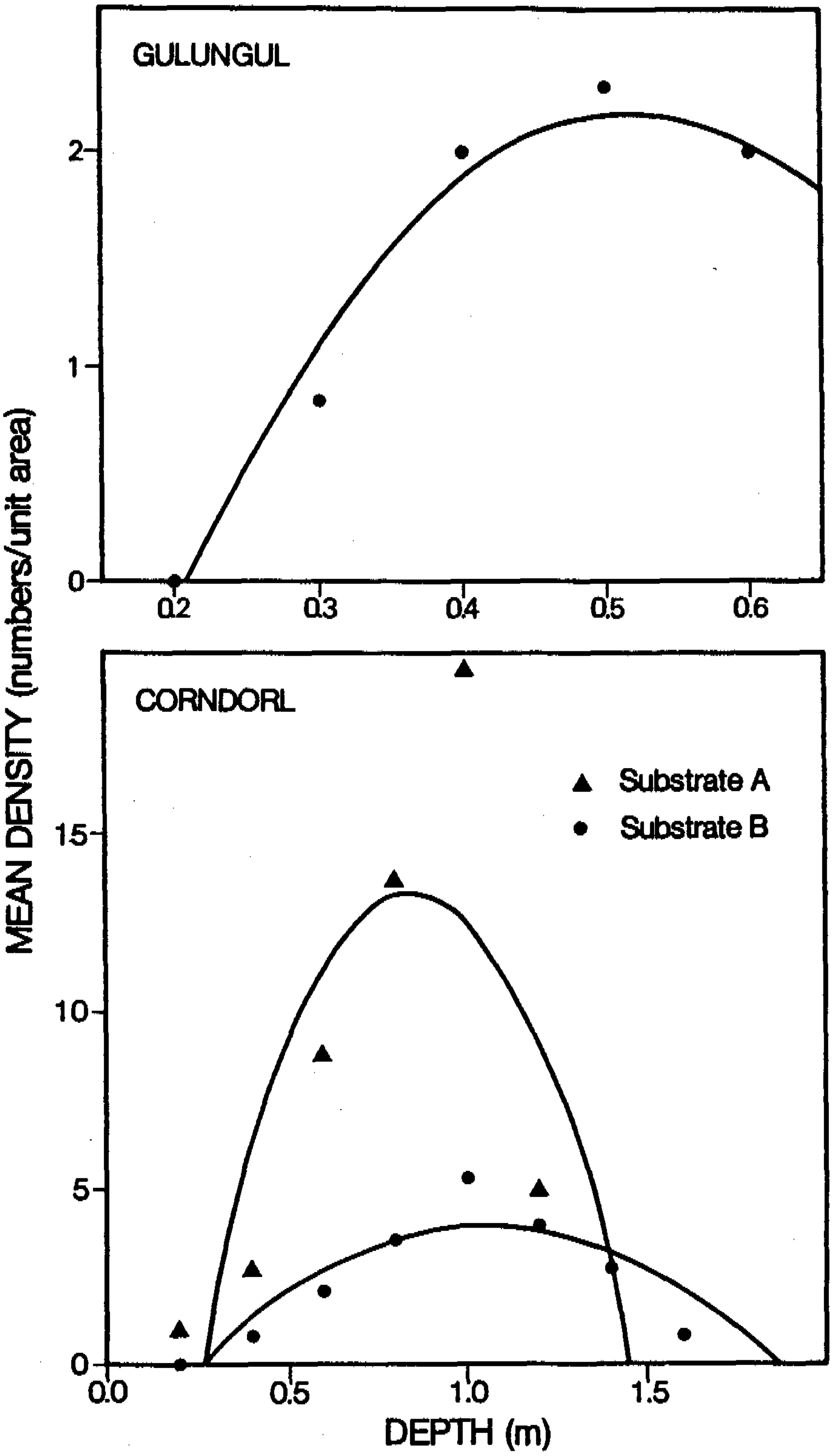


Figure 5.2 Quadratic relationships between depth and density of mussels in the backflow billabongs. For Corndorl billabong the relationships on the different substrates are shown.

Fitted regression lines are of the form:

$Y = a + bX + cX^2$
(where Y = density, X = depth) and are described in Table 5.11.

Key to the substrate types in Corndorl billabong is shown in Table 5.3.

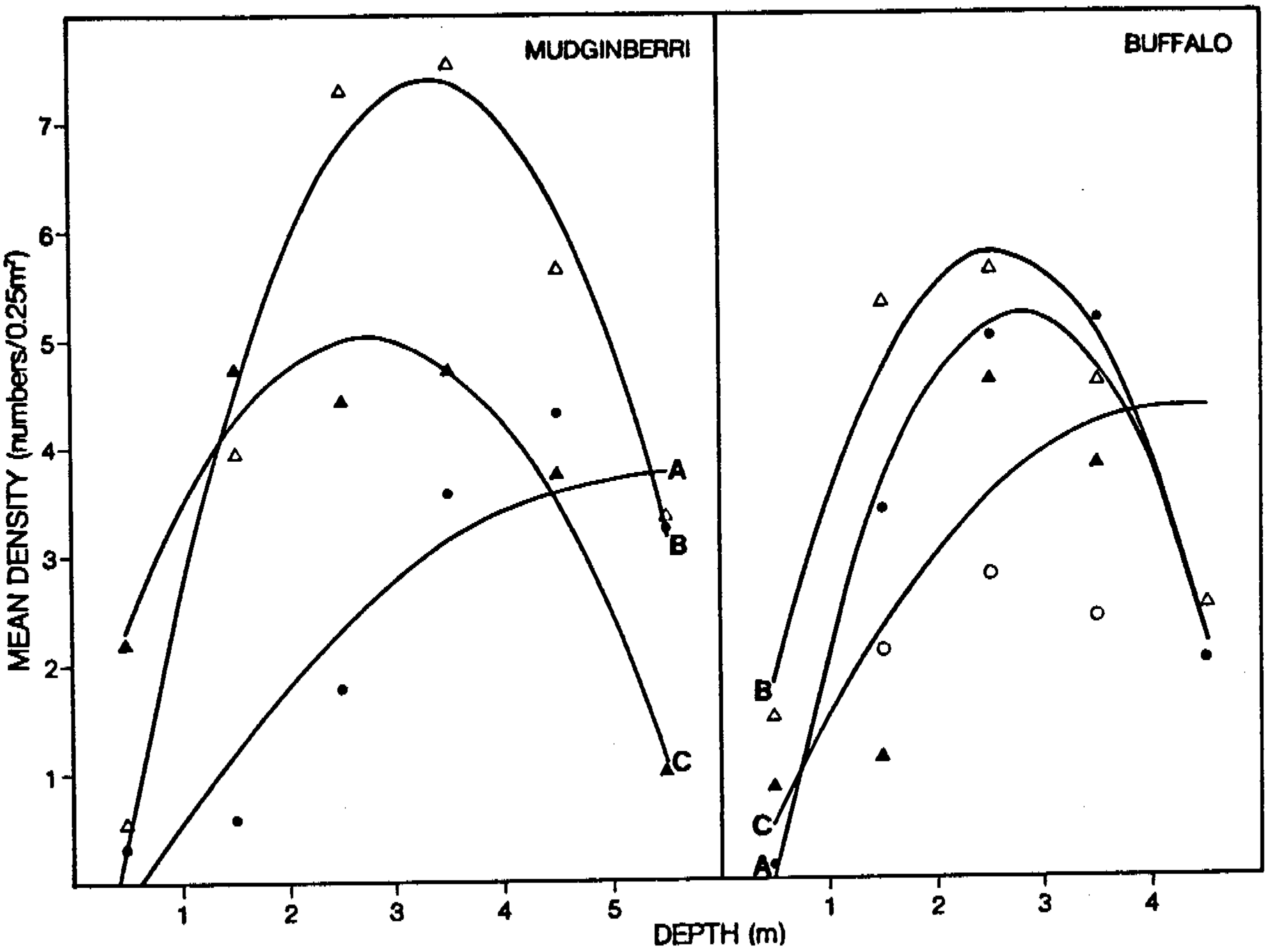


Figure 5.3 Quadratic relationships between depth and density of mussels on the different substrates of the channel billabongs.

Fitted regression lines are of the form:

$Y = a + bX + cX^2$

(where Y = density, X = depth) and are described in Table 5.11.

Solid circles - substrate A; open triangles - substrate B; solid triangles - substrate C; and open circles - substrate E.

Keys to the substrate types are shown in Table 5.4 (Mudginberri) and Table 5.5 (Buffalo).

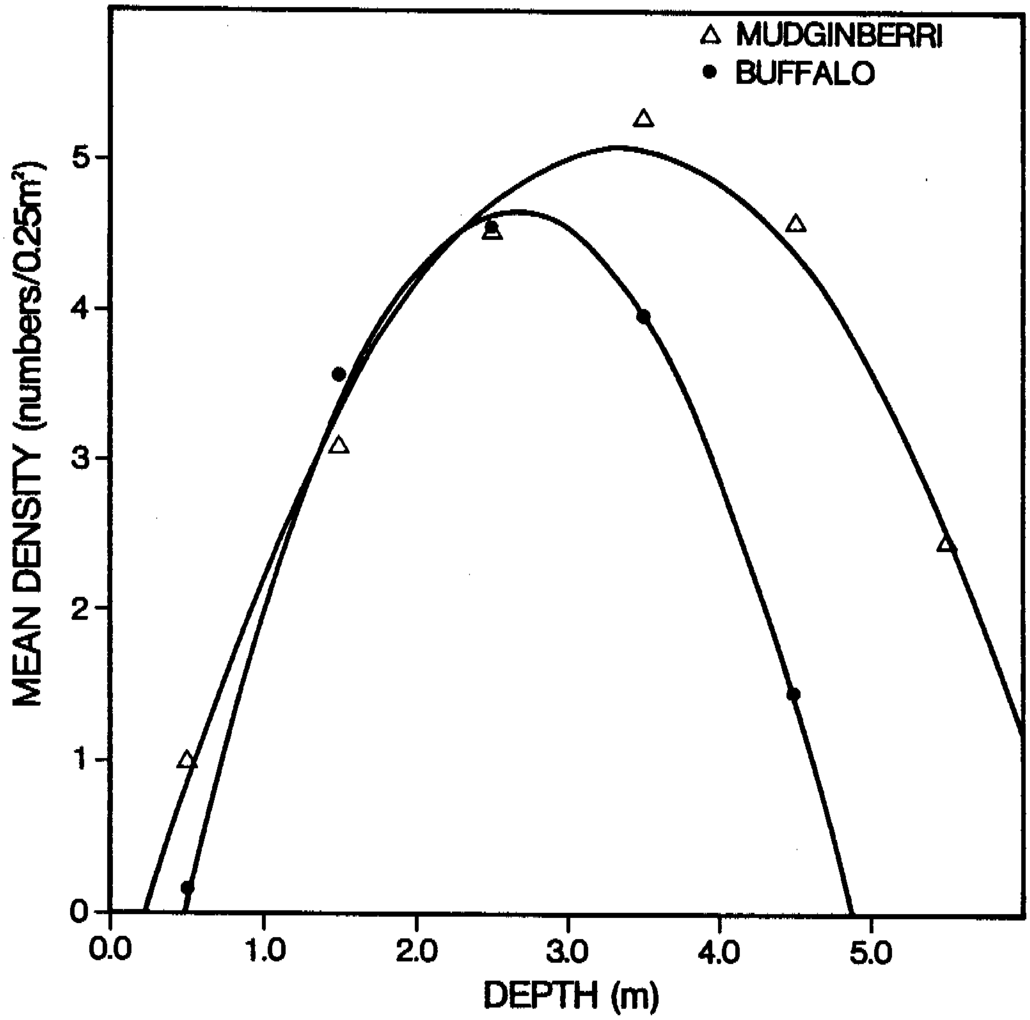


Figure 5.4 Quadratic relationships between depth and density of mussels in the channel billabongs.

Fitted regression lines are of the form:

$Y = a + bX + cX^2$

(where Y = density, X = depth) and are described in Table 5.11.

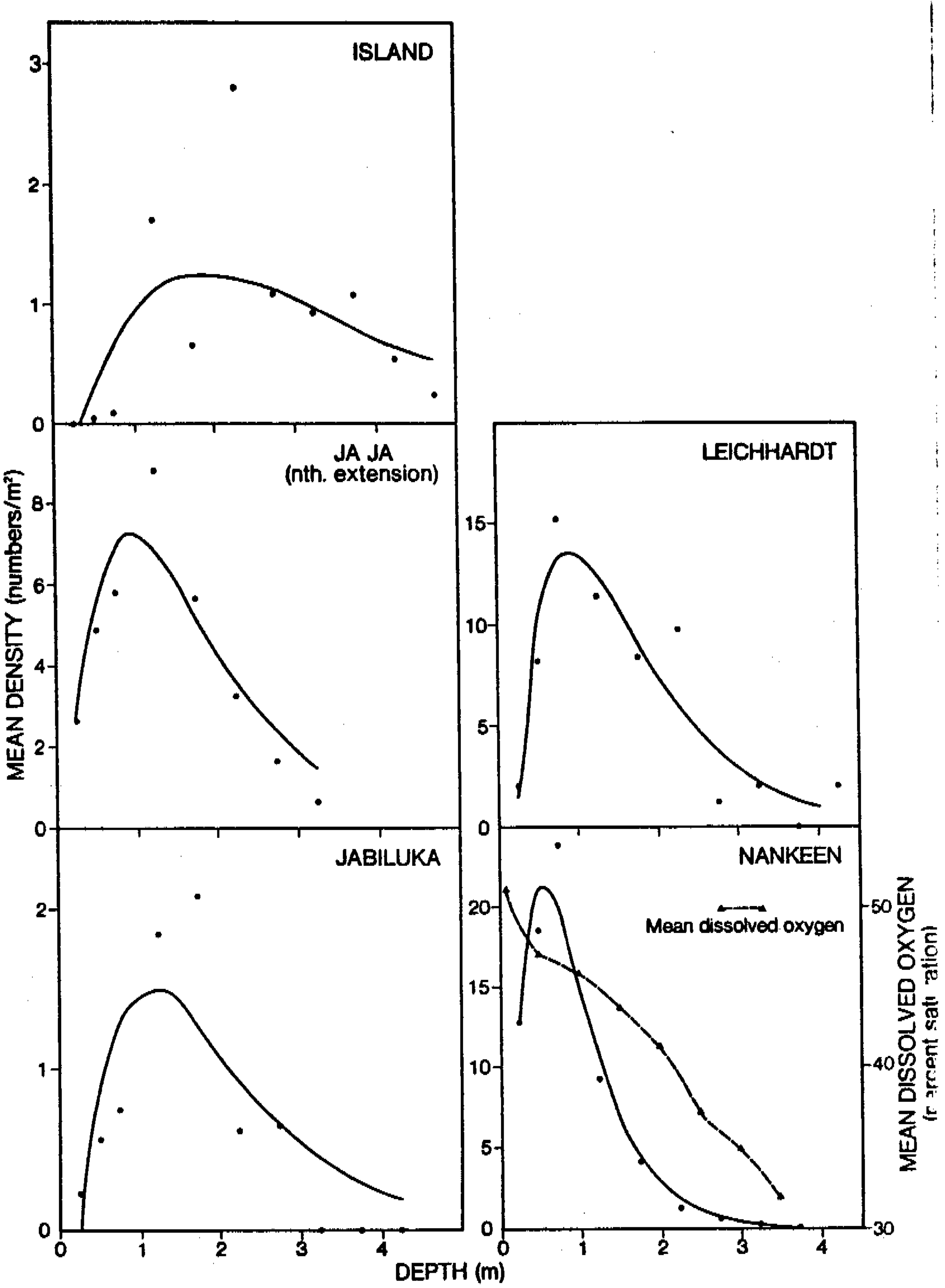


Figure 5.5 Exponential relationships between depths and density of mussels in the floodplain billabongs.

Fitted regression lines are of the form:

$$Y = Ae^{-\alpha x} - Be^{-\beta x}$$

(where Y = density, X = depth) and are described in Table 5.12.

Mean dissolved oxygen concentration is also plotted against depth for Nankeen billabong.

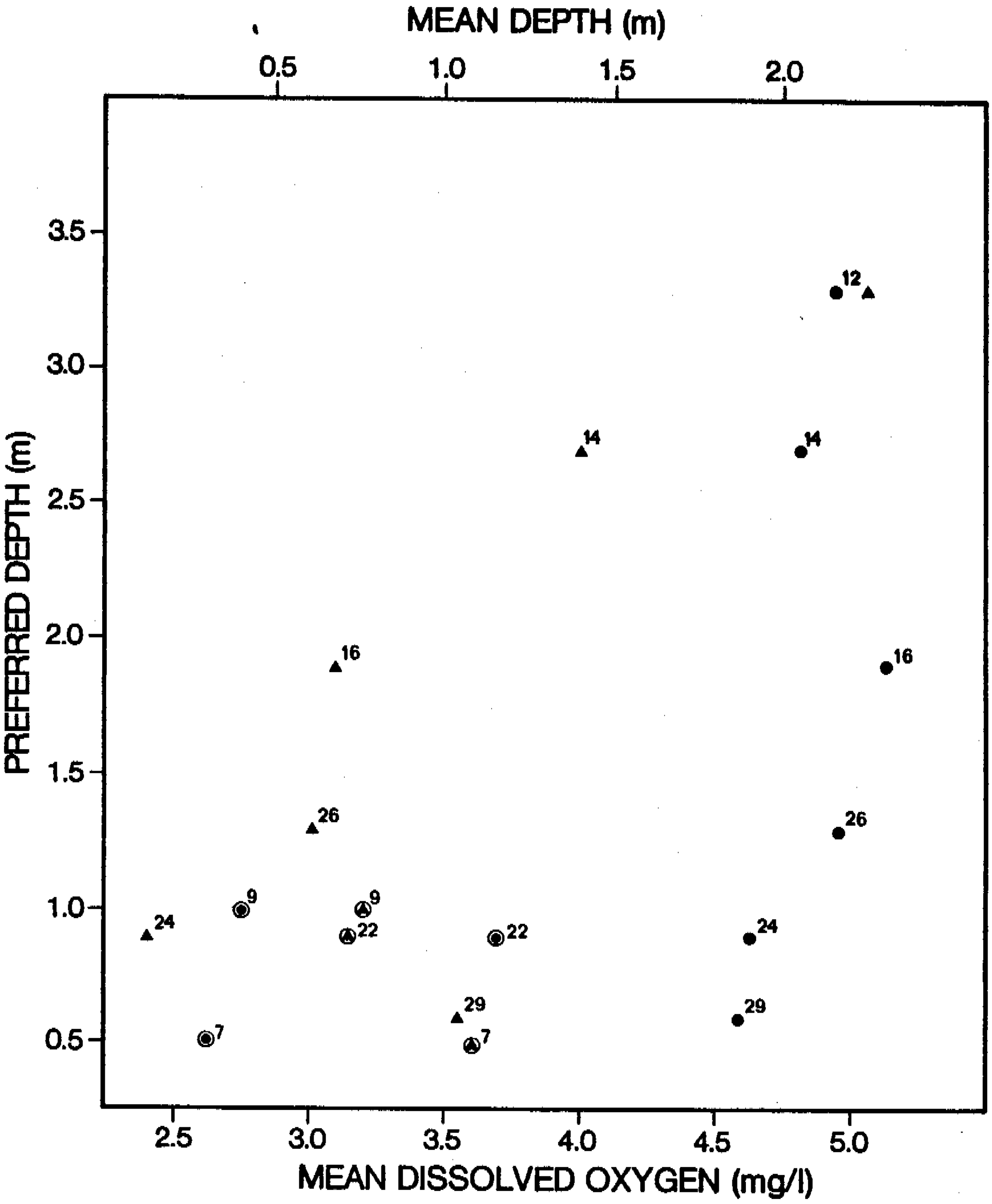


Figure 5.6 Preferred depth of mussels in relation to mean billabong depth (circles) and mean dissolved oxygen concentration (triangles) in the Magela Creek billabongs.

The numbers about the symbols are codes to the billabongs and are given in Table 5.13.

Unencircled symbols are billabongs lying on the mainstream channel of Wet season flow of the Magela Creek, while encircled symbols are billabongs lying off the main flow path of the creek.

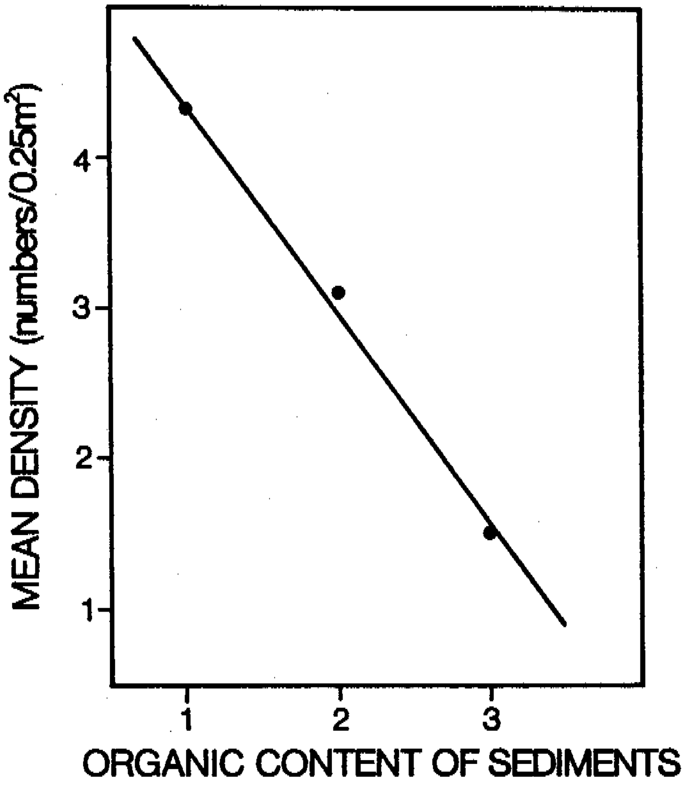


Figure 5.7 Linear relationship between mean density of mussels and organic content of the sediments in the channel billabongs (Mudginberri and Buffalo).

Sediments 1, 2 and 3 correspond to sediments B, C and E respectively, keyed in Table 5.5.

Fitted regression equation is:

$$Y = 5.783 - 1.400X \ (P < 0.10, \ r^2 = 0.993)$$

where Y = mean density (numbers/0.25 m^2) and X = organic content of sediments (arbitrarily ranked).

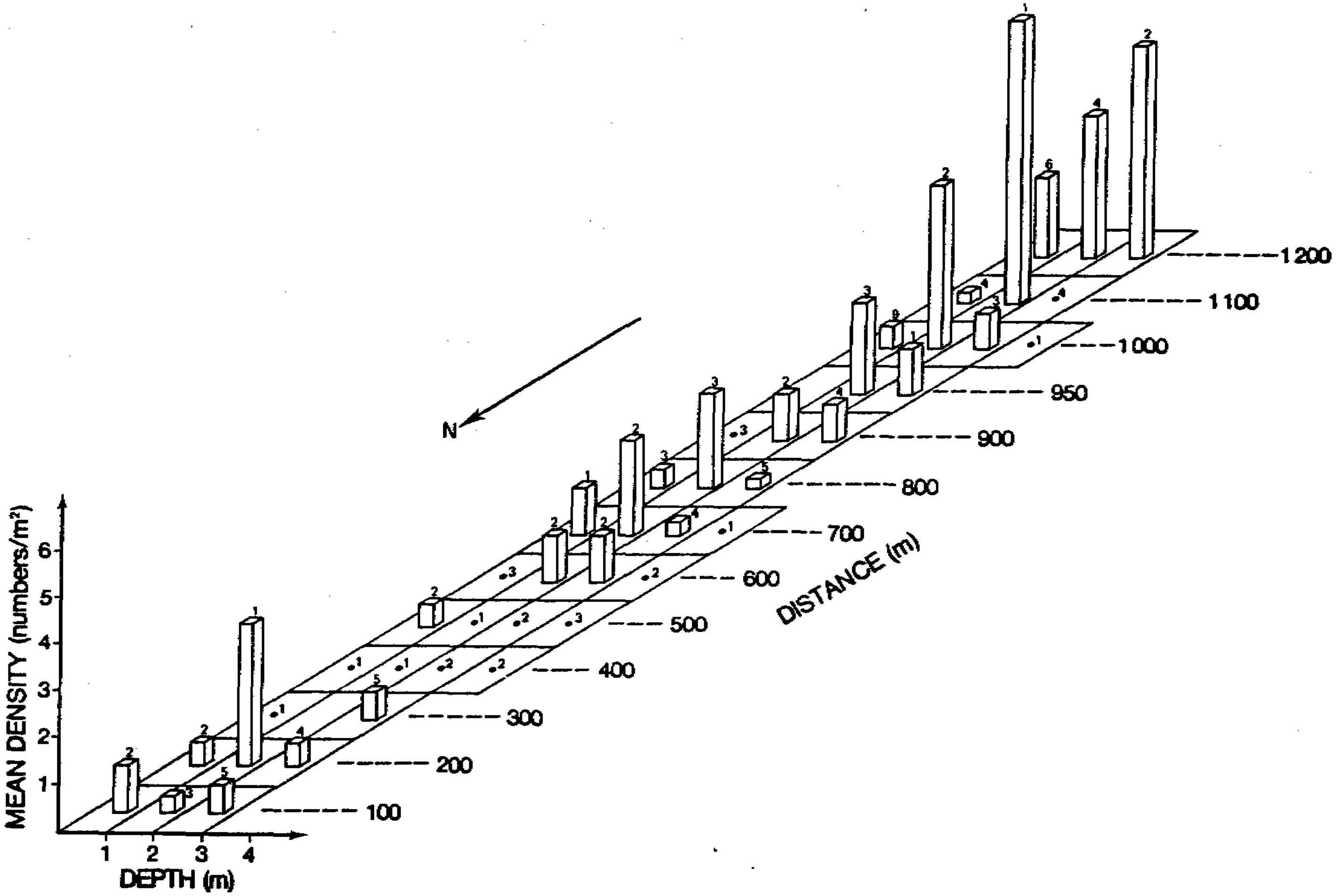


Figure 5.8 Mean density of mussels in Jabiluka billabong in relation to depth, and distance along the billabong. Points indicate zero density, and numbers about the points and histograms are the sample sizes (numbers of m² sampled).

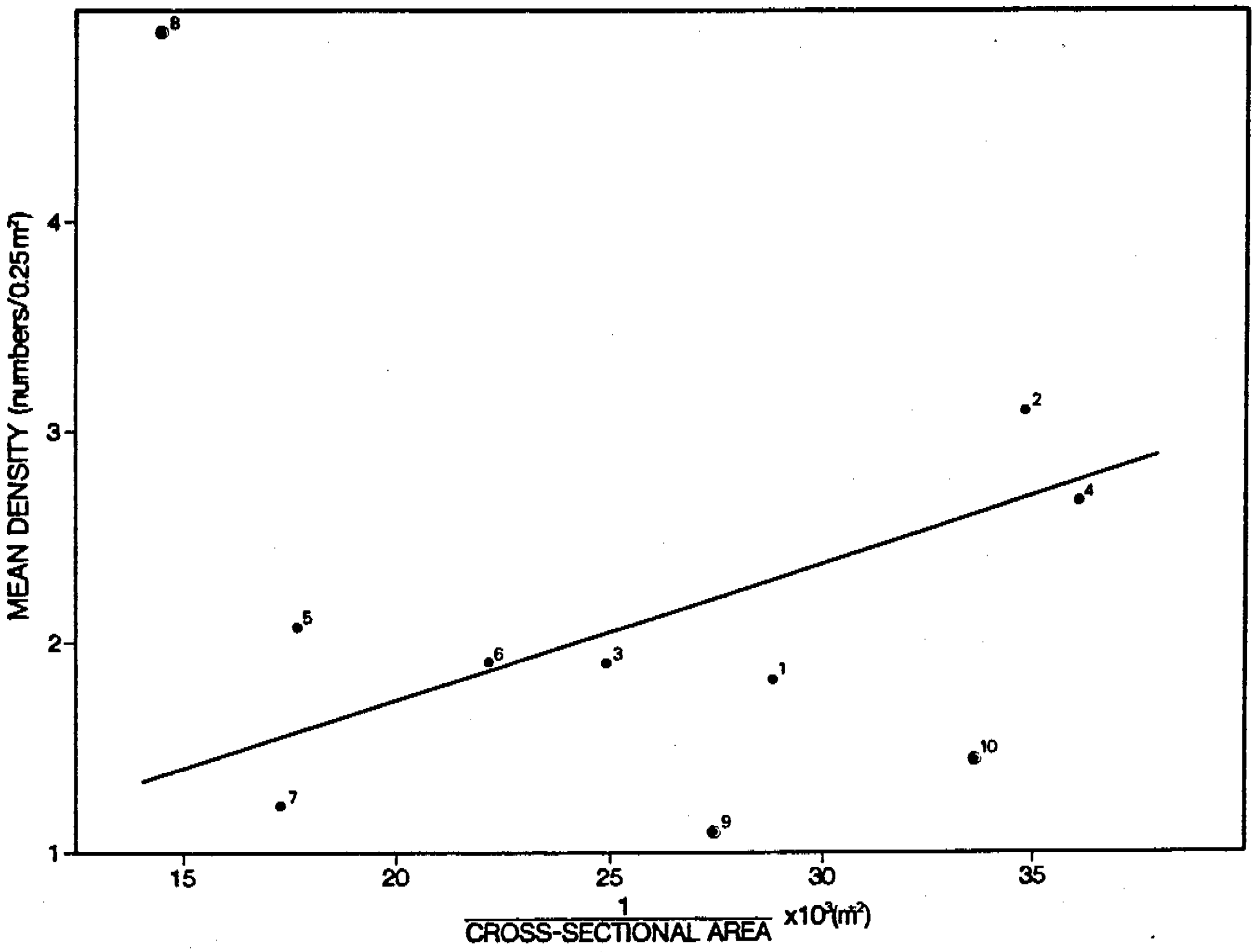


Figure 5.9 Linear relationship between mean density of mussels and cross-sectional area of billabong at the various stations at which densities were measured in Nankeen billabong. Numbers about the points are the station numbers whose locality are shown in Figure 5.1. Encircled points were not included in the regression analysis.

The linear regression equation is:

$$Y = 0.422 + 65.274X \qquad (P < 0.05,\ r^2 = 0.658)$$

where Y = mean density (numbers/m^2) and X = 1/cross-sectional area (m^{-2}).

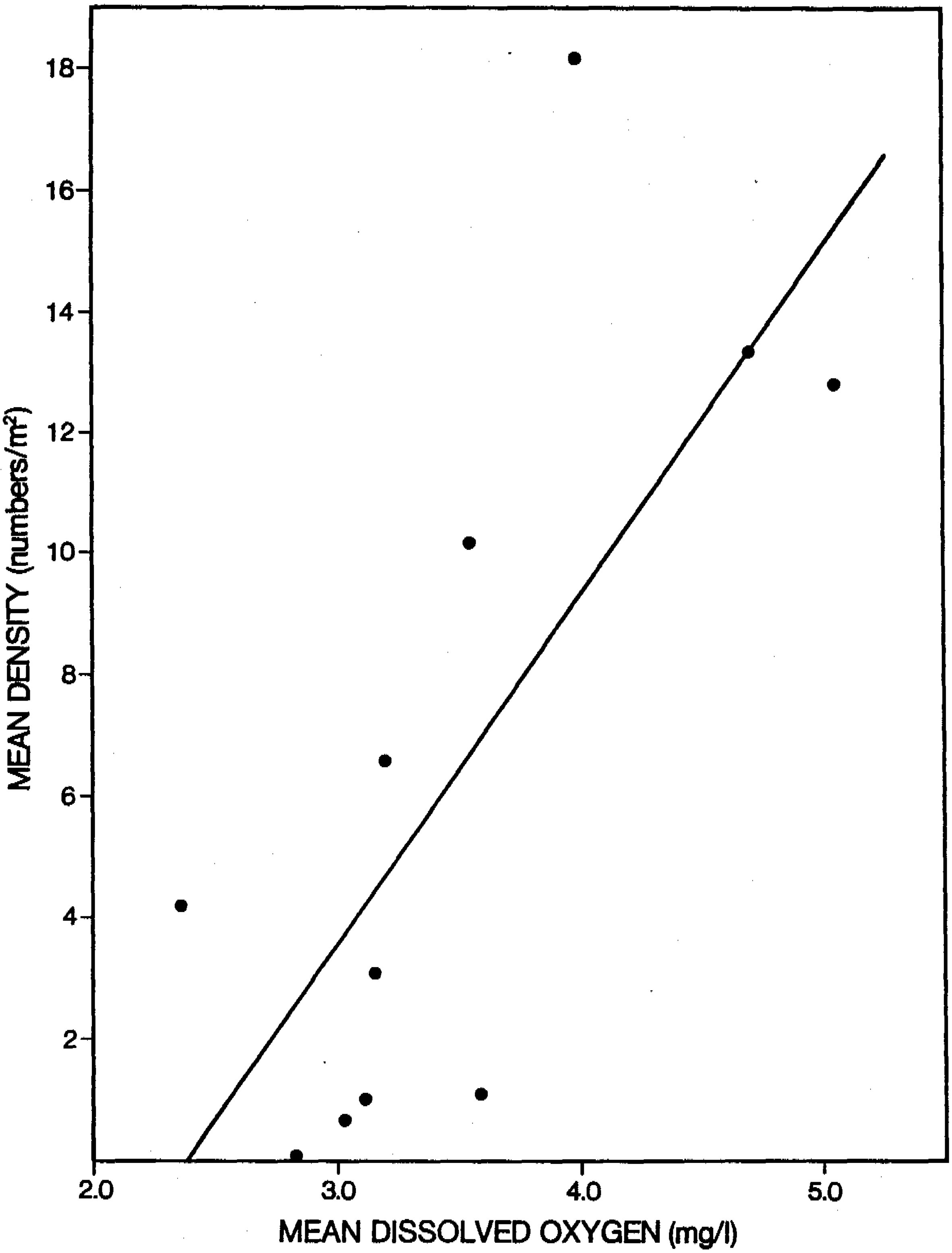


Figure 5.10 Linear relationship between mean density of mussels and mean dissolved oxygen concentration in the Magela Creek billabongs.

Fitted regression equation is:

$Y = -13.518 + 5.702X$ ($P < 0.01$, $r^2 = 0.540$)

where Y = mean density (numbers/m²) and X = mean dissolved oxygen concentration (mg/l).

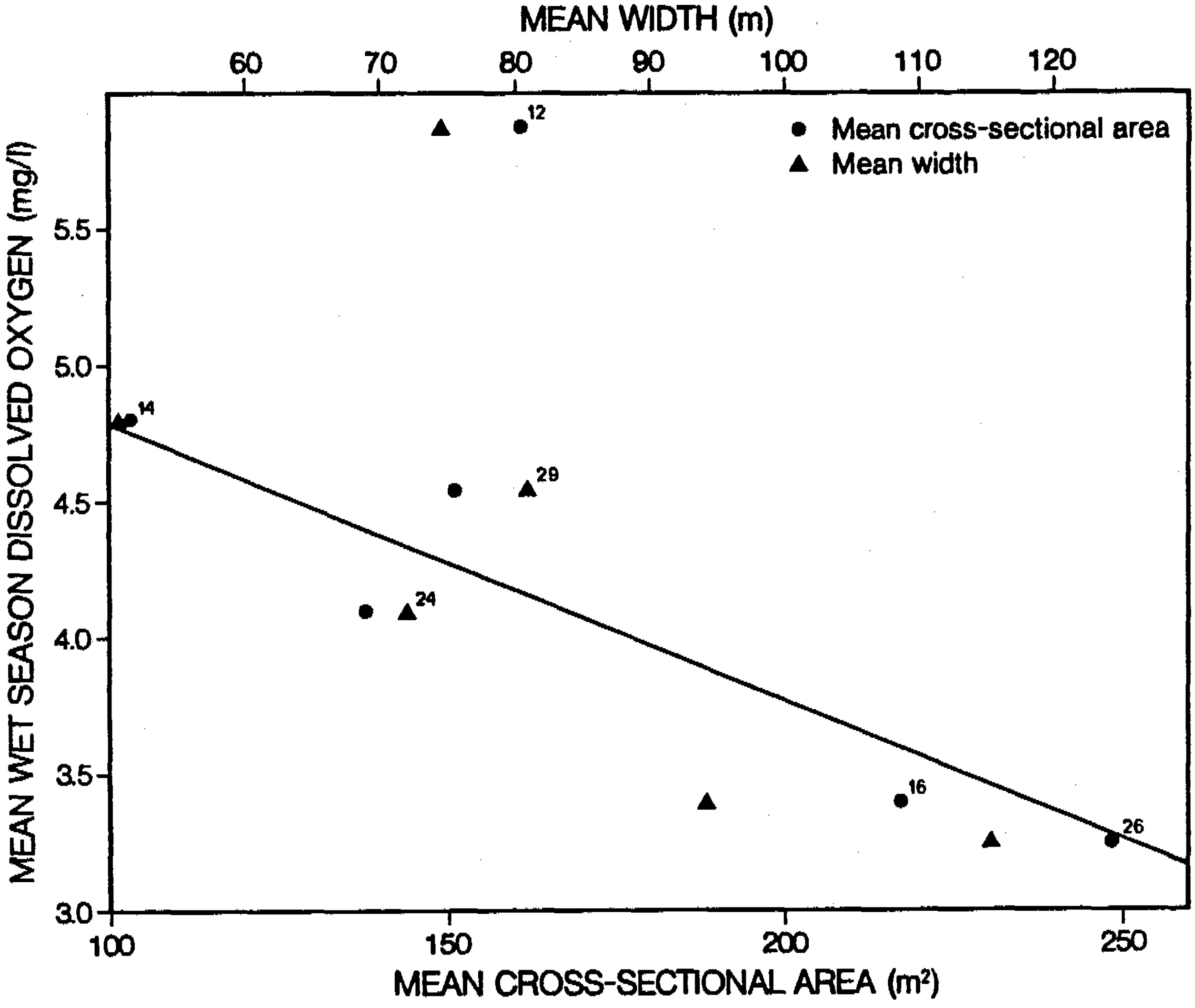


Figure 5.11 Mean Wet season dissolved oxygen concentration in relation to mean cross-sectional area and mean width, of billabongs lying on the mainstream channel of flow of the Magela Creek.

The numbers about the symbols are codes to the billabongs and are shown in Table 5.13.

The fitted line is the linear relationship between mean Wet season dissolved oxygen concentration and cross-sectional area of billabongs. The linear regression equation is:

$$Y = 5.785 - 0.01X \ (P < 0.05, r^2 = 0.891)$$

where Y = mean Wet season dissolved oxygen concentration (mg/l) and X = mean cross-sectional area (m^2).

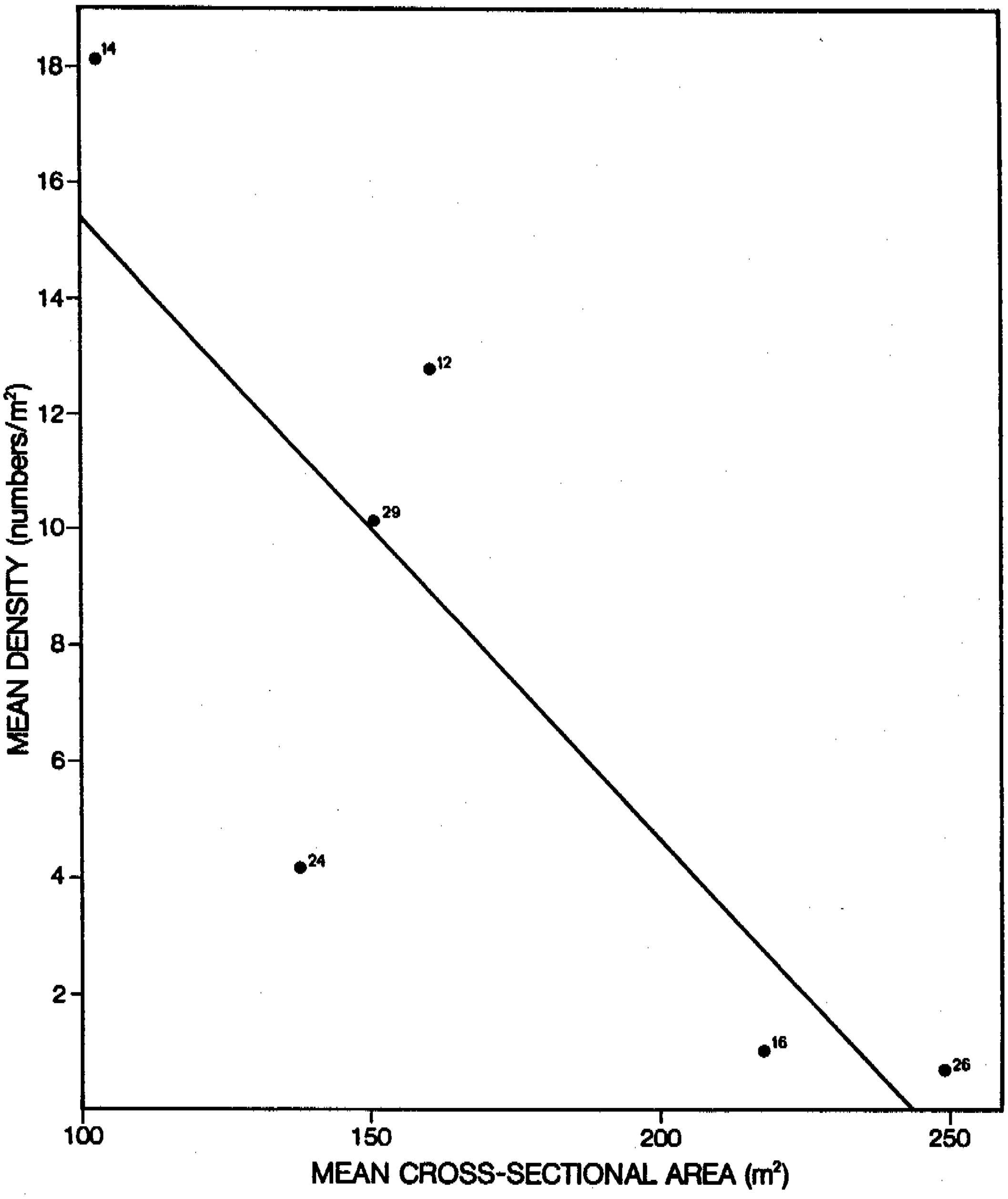


Figure 5.12 Linear relationship between mean density of mussels and cross-sectional area of billabongs lying on the mainstream channel of flow of the Magela Creek.

The numbers about the symbols are codes to the billabongs and are given in Table 5.13.

Fitted regression equation is:

$$Y = 26.094 - 0.107X \qquad (P < 0.05,\ r^2 = 0.676)$$

where Y = mean density (numbers/m²) and X = mean cross-sectional area (m²).

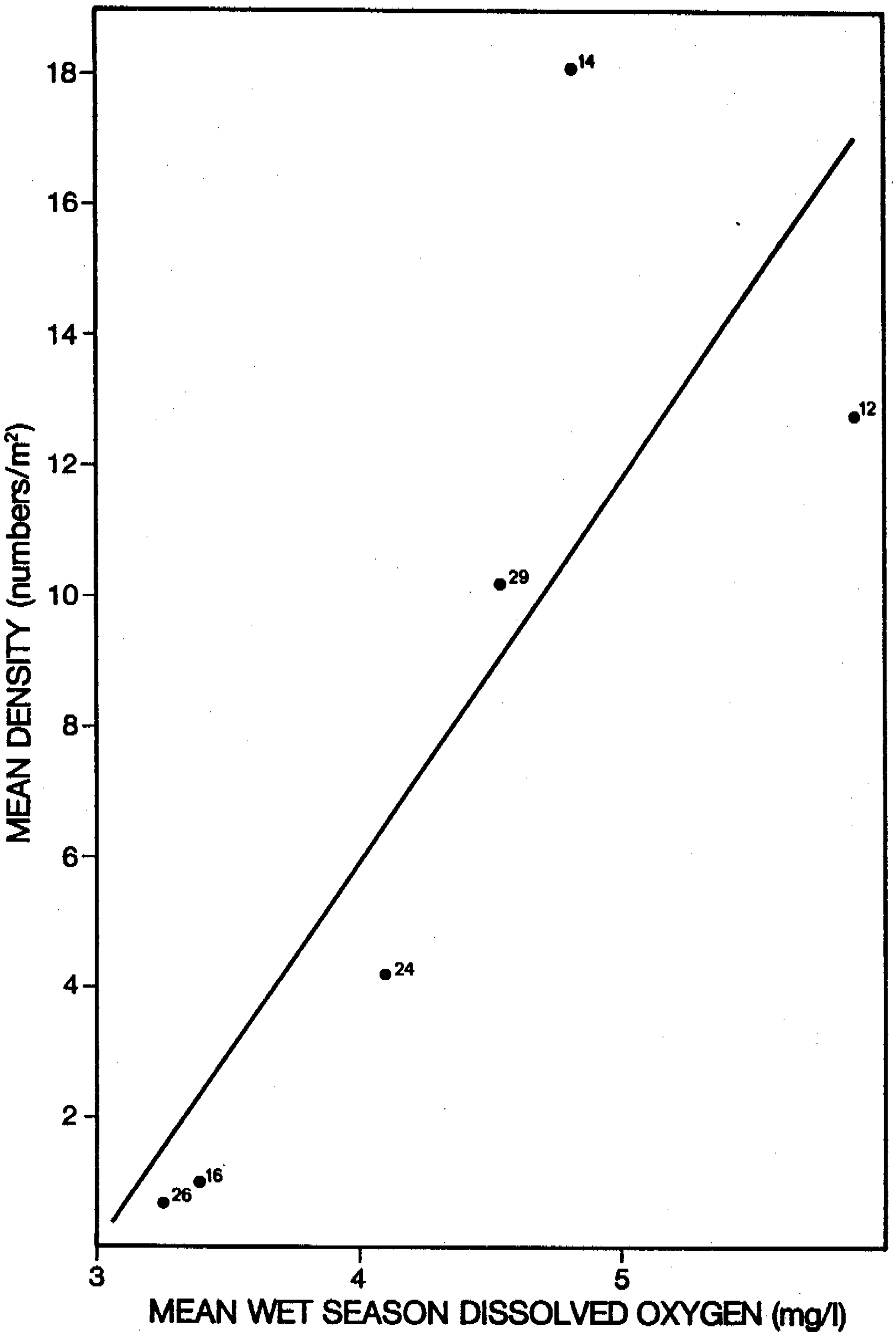


Figure 5.13 Linear relationship between mean density of mussels and mean Wet season dissolved oxygen concentration of billabongs lying on the mainstream channel of flow of the Magela Creek.

The numbers about the symbols are codes to the billabongs and are given in Table 5.13.

Fitted regression equation is:

$$Y = -17.745 + 5.913X \qquad (P < 0.05,\ r^2 = 0.669)$$

where Y = mean density (numbers/m^2) and X = mean Wet season dissolved oxygen concentration (mg/l).

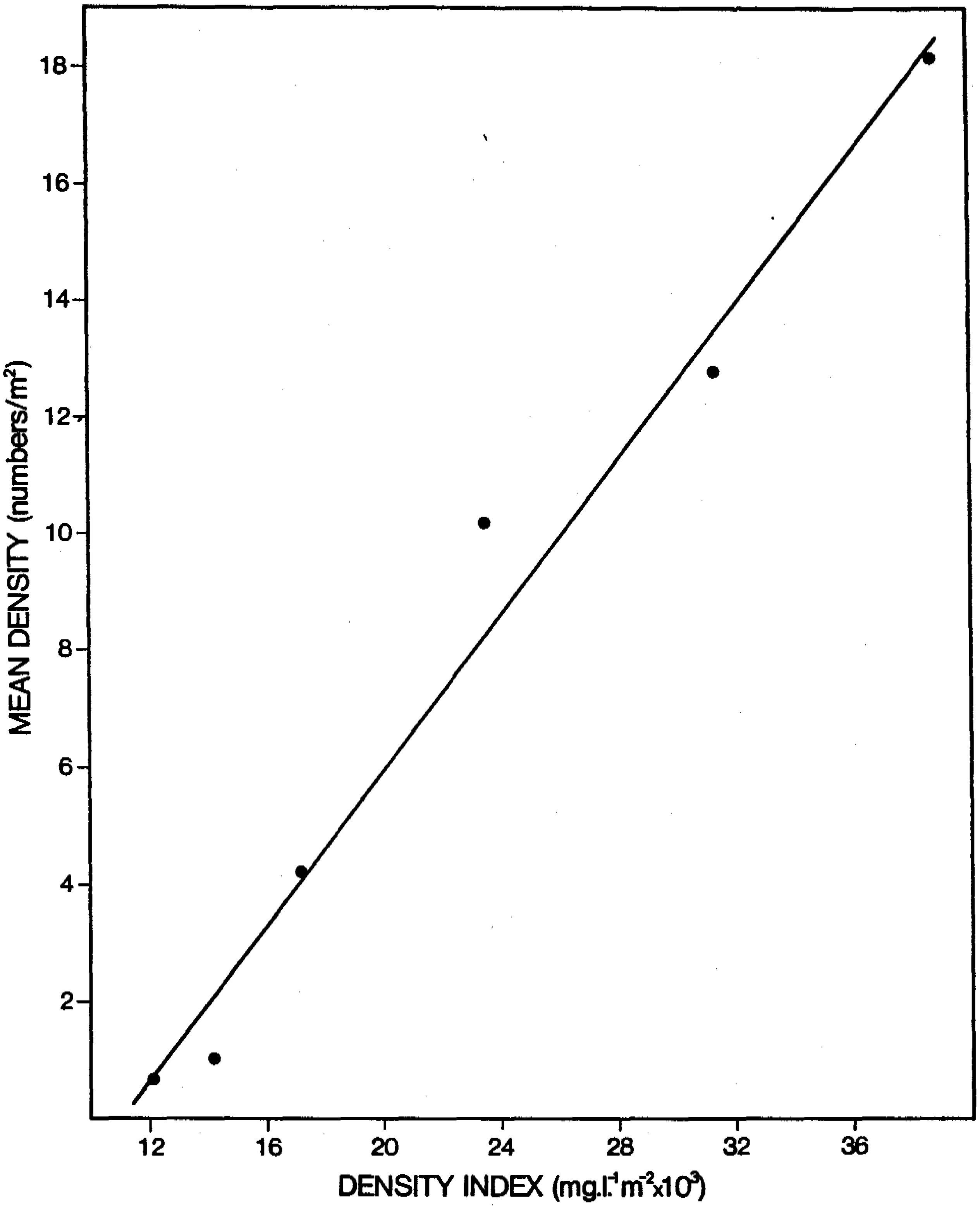


Figure 5.14 Linear relationship between mean density of mussels and density index of billabongs lying on the mainstream channel of flow of the Magela Creek.

Fitted regression equation is:

$$Y = -7.325 + 663.98X \quad (P < 0.001,\ r^2 = 0.978)$$

where Y = mean density (numbers/m^2)

$$\text{and } X = \frac{\text{mean dissolved oxygen concentration}}{\text{mean billabong cross-sectional area}}$$

(mg.l^{-1}.m^{-2}).

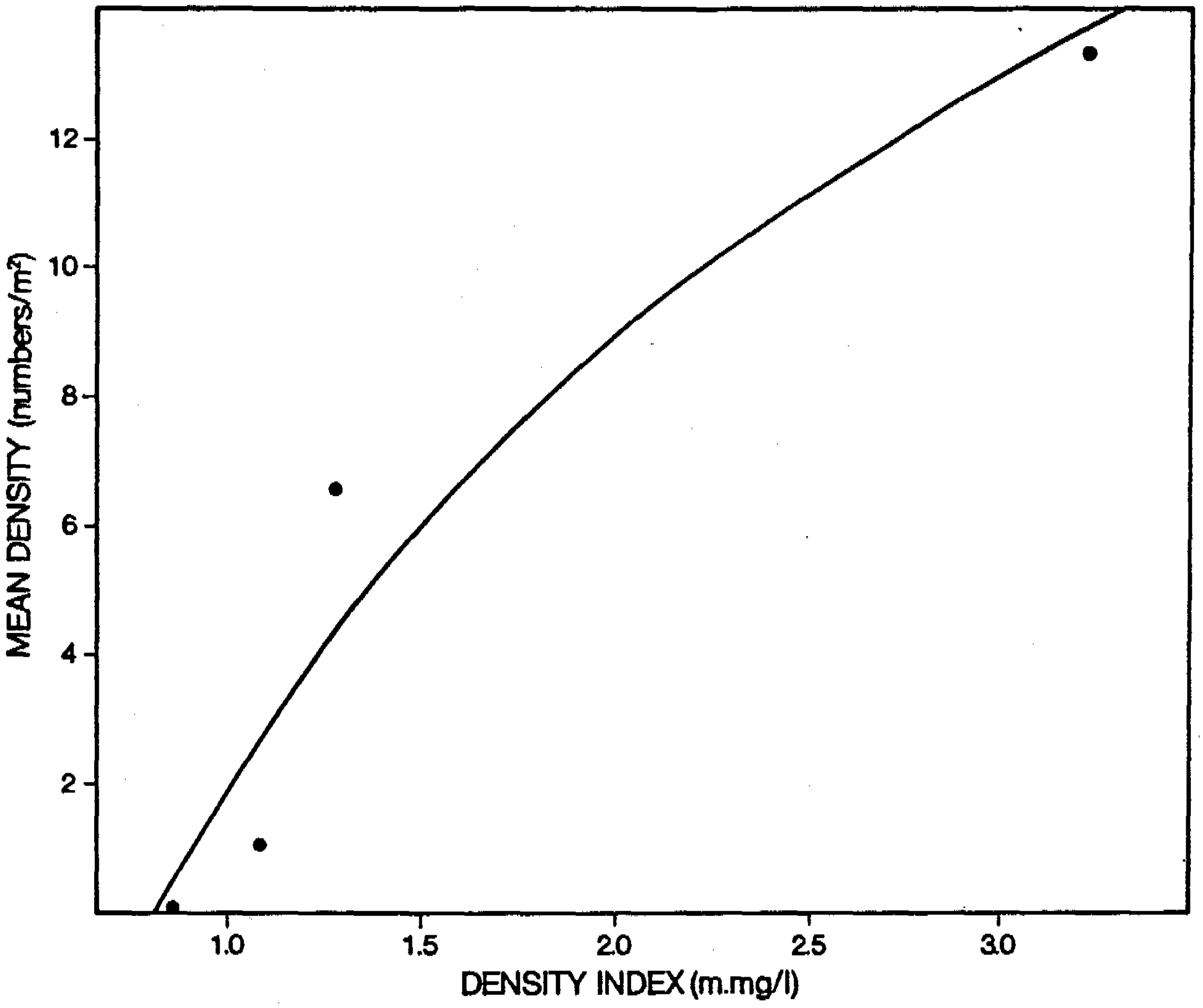


Figure 5.15 Logarithmic relationship between mean density of mussels and density index of backflow billabongs of the Magela Creek.

Fitted regression equation is:

$Y = 10.034 \ln X + 1.987$ ($P < 0.05$, $r^2 = 0.932$)

where Y = mean density (numbers/m^2)
and X = mean dissolved concentration x mean billabong depth (m.mg/l).

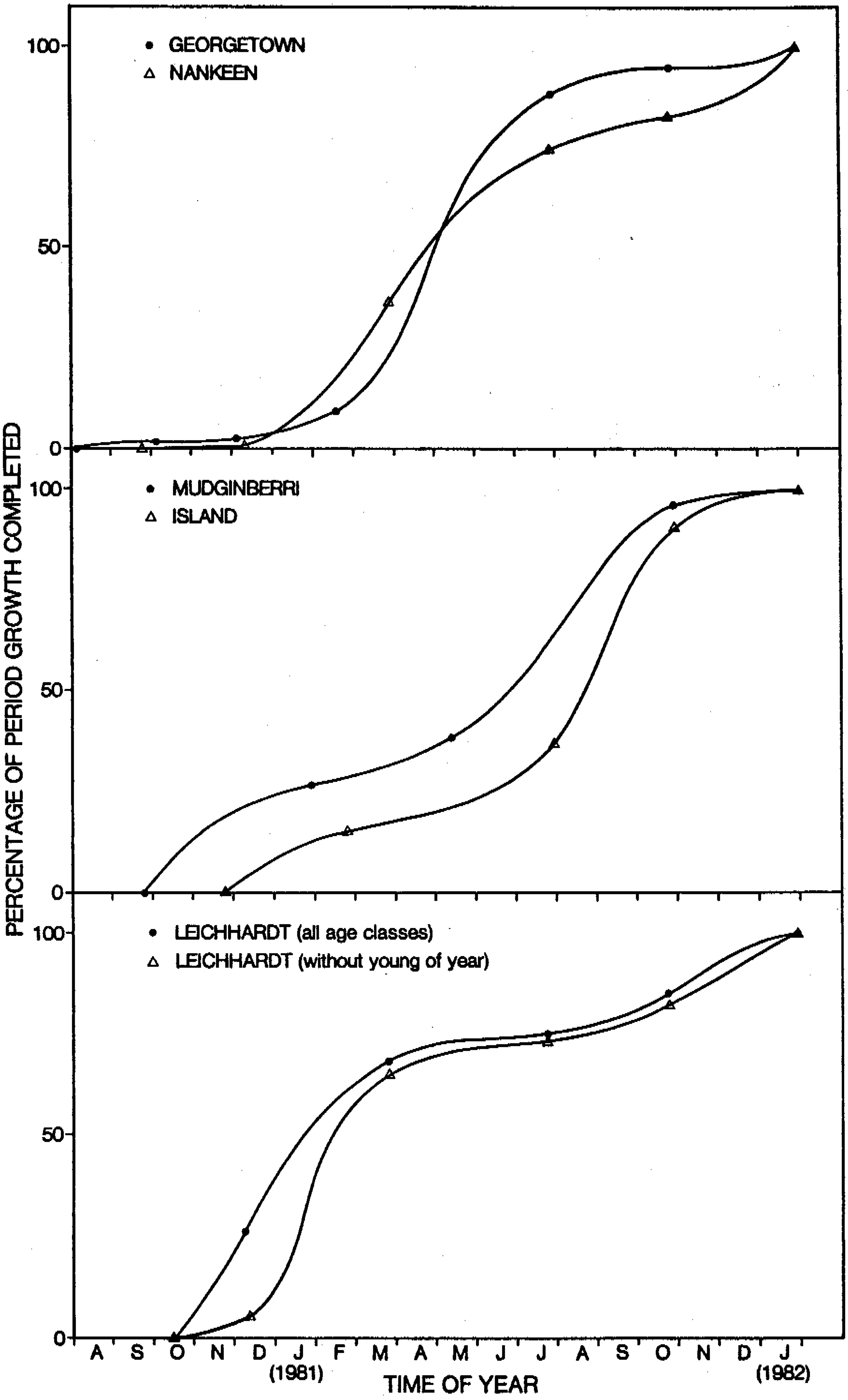


Figure 6.1 Seasonal growth of marked mussels in some Magela Creek billabongs, expressed as percentage of the growth completed over an 18 month period. Lines fitted by eye.

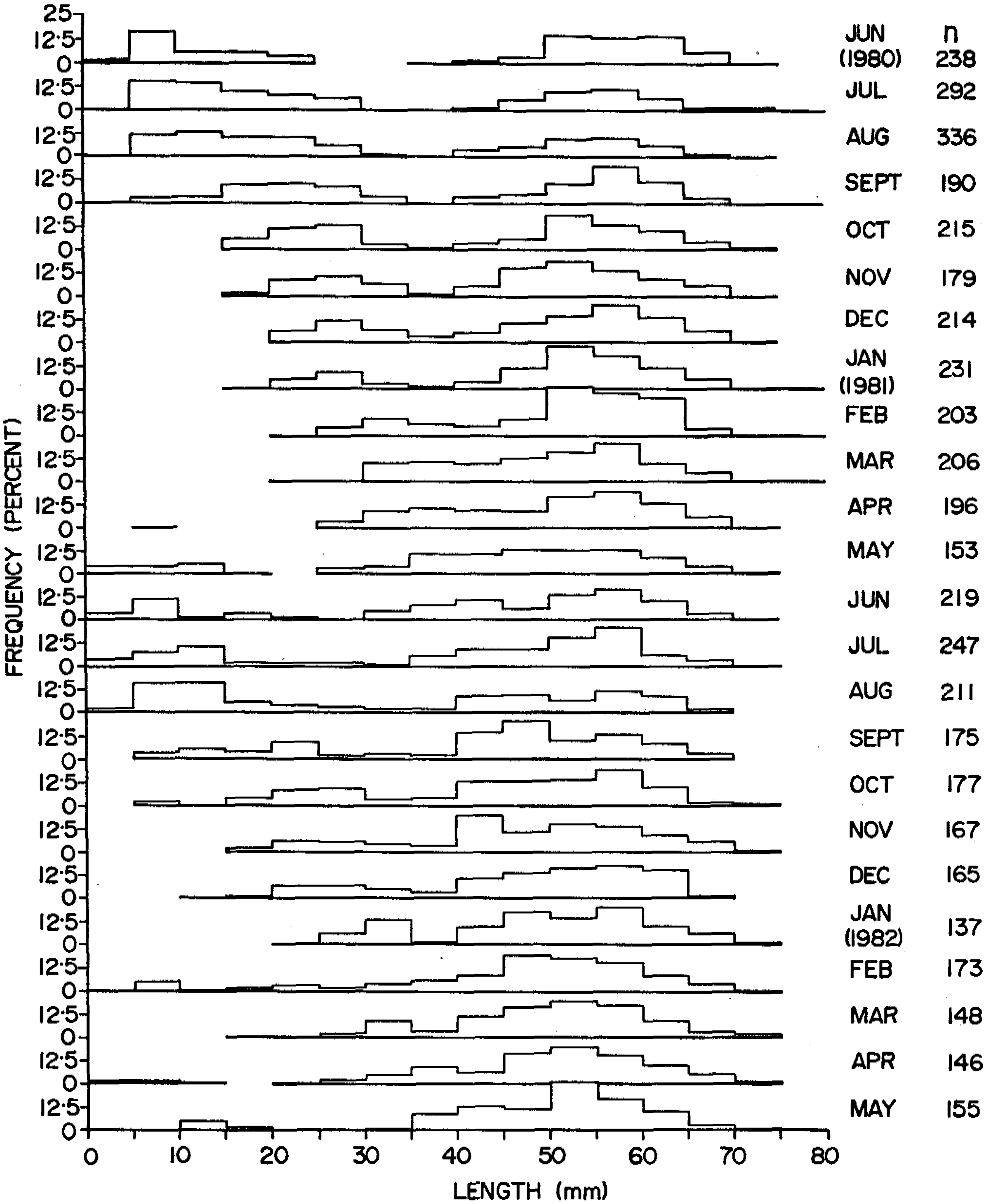


Figure 6.2 Monthly frequency distributions of lengths of mussels in Georgetown billabong sampled over the study period.

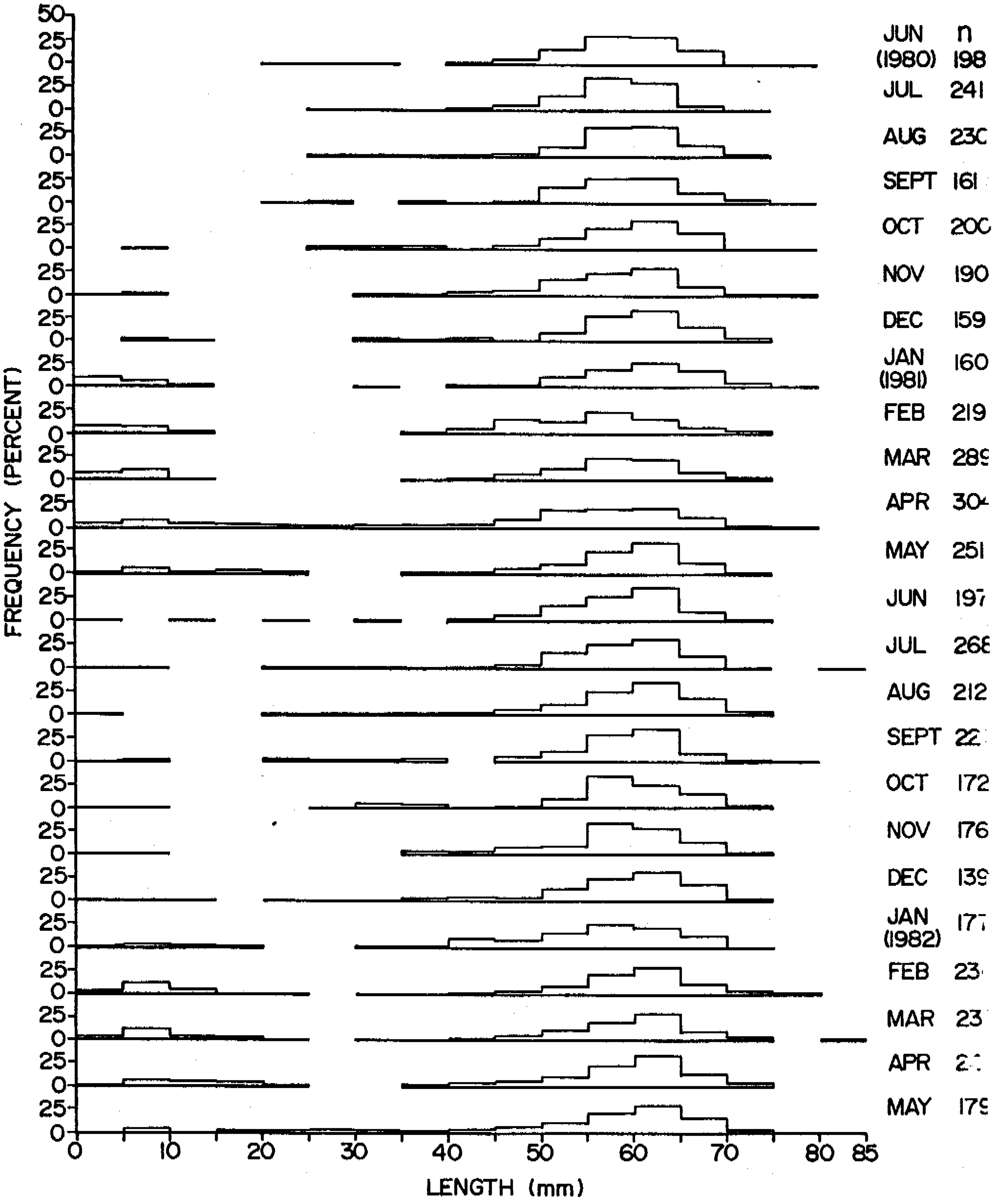


Figure 6.3 Monthly frequency distributions of lengths of mussels in Mudginberri billabong sampled over the study period.

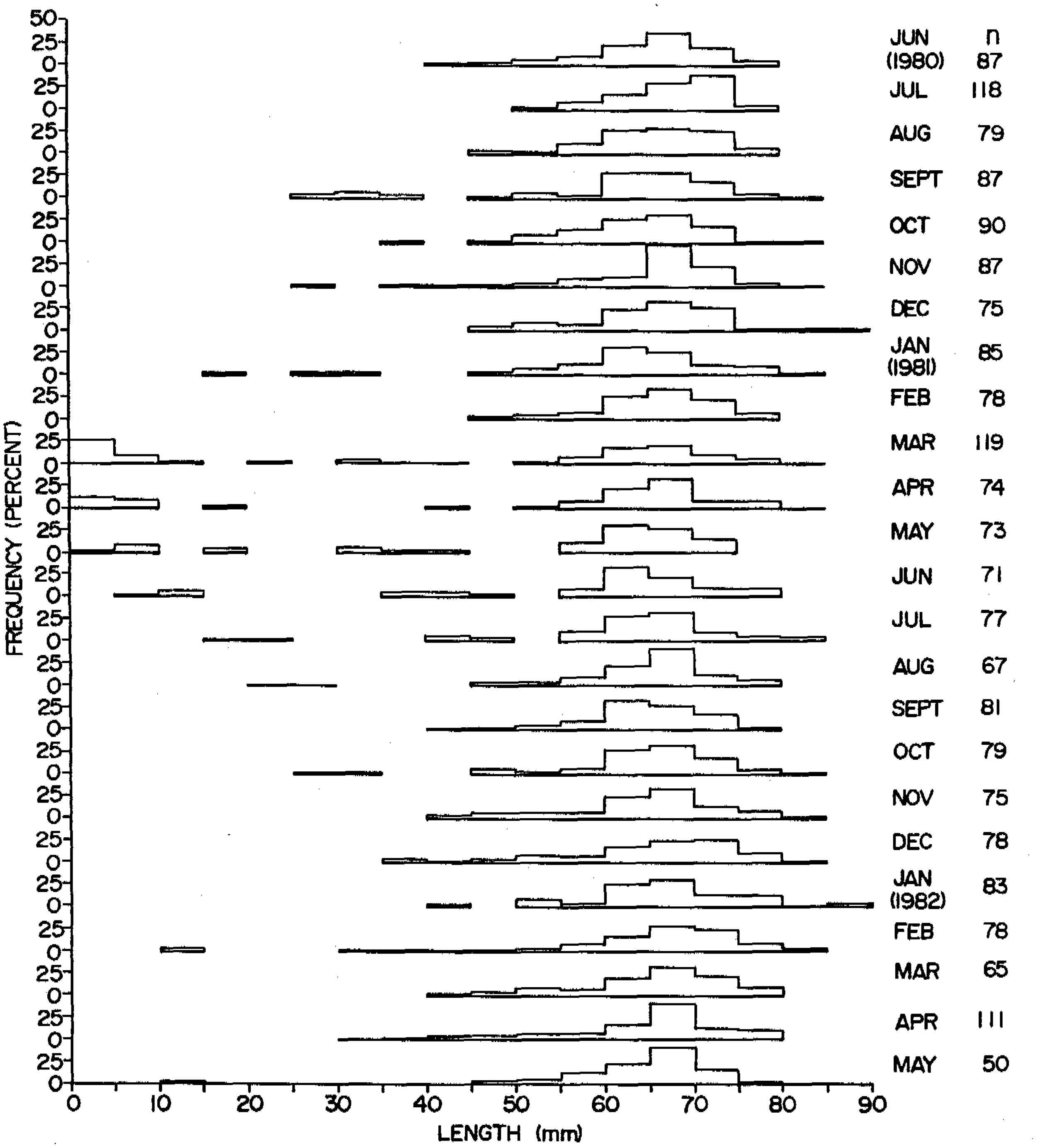


Figure 6.4 Monthly frequency distributions of lengths of mussels in Nankeen billabong sampled over the study period.

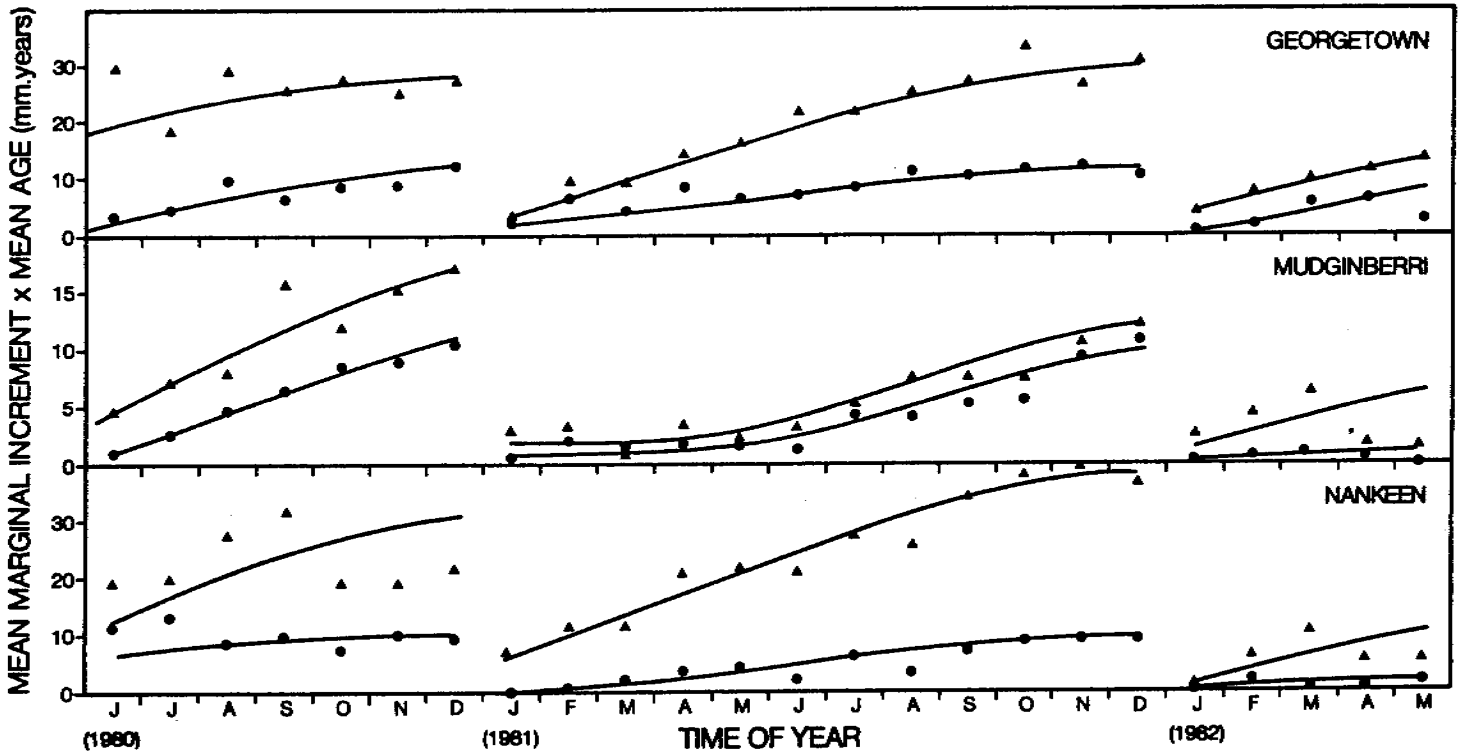


Figure 6.5 Growth beyond the last formed annulus on shells of mussels from Georgetown, Mudginberri and Nankeen billabongs, plotted against time of year. Points are mean values plotted according to appropriate age divisions (different symbols) and standardised for age by multiplying the mean marginal increments by the mean age of mussels used in the particular age division.

The age divisions are represented:

triangles 0.0 - 4.99 years
circles 5.0 - 9.99 years.

Lines fitted by eye.

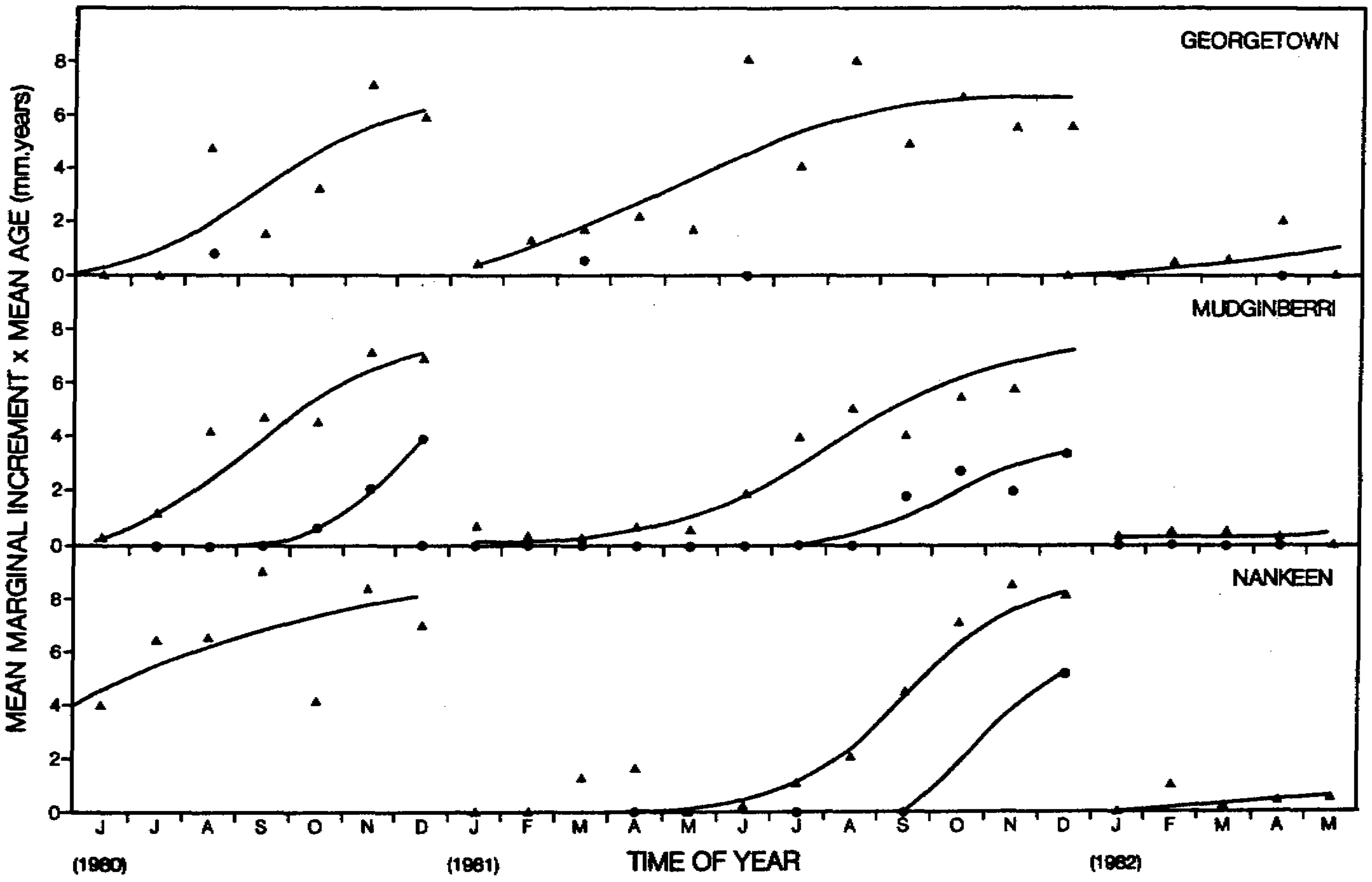


Figure 6.6 Growth beyond the last formed annulus on shells of mussels from Georgetown, Mudginberri and Nankeen billabongs, plotted against time of year. Points are mean values plotted according to appropriate age divisions (different symbols) and standardised for age by multiplying the mean marginal increments by the mean age of mussels used in the particular age division.

The age divisions are represented:

triangles 10.0 - 19.99 years
circles > 19.99 years.

Lines fitted by eye.

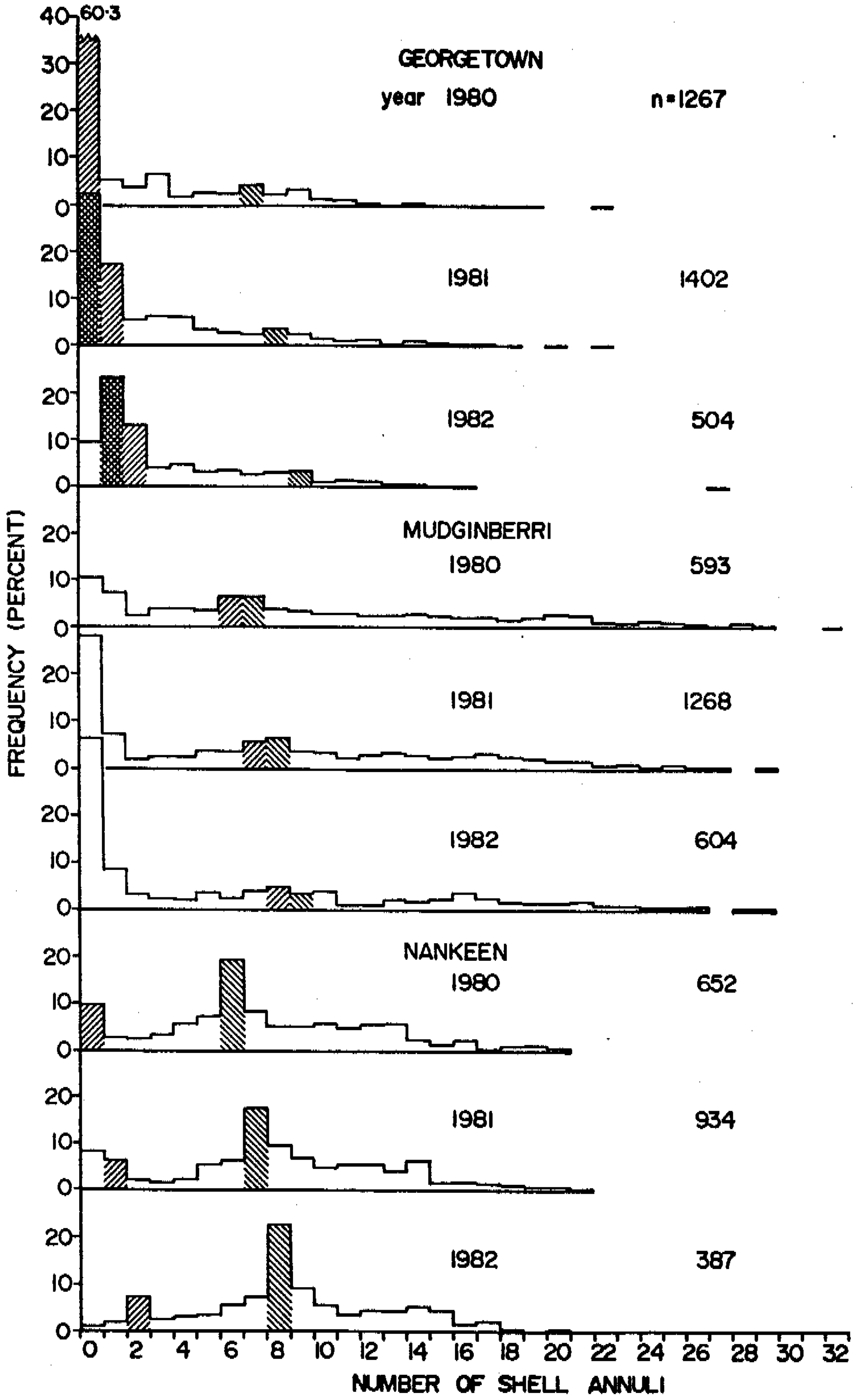


Figure 6.7 The age structures of mussel populations from Georgetown, Mudginberri and Nankeen billabongs, plotted according to number of shell annuli and between the three successive years of sampling. The respective hatched histograms are dominant year classes that appear as successively older age classes in progressive sampling years.

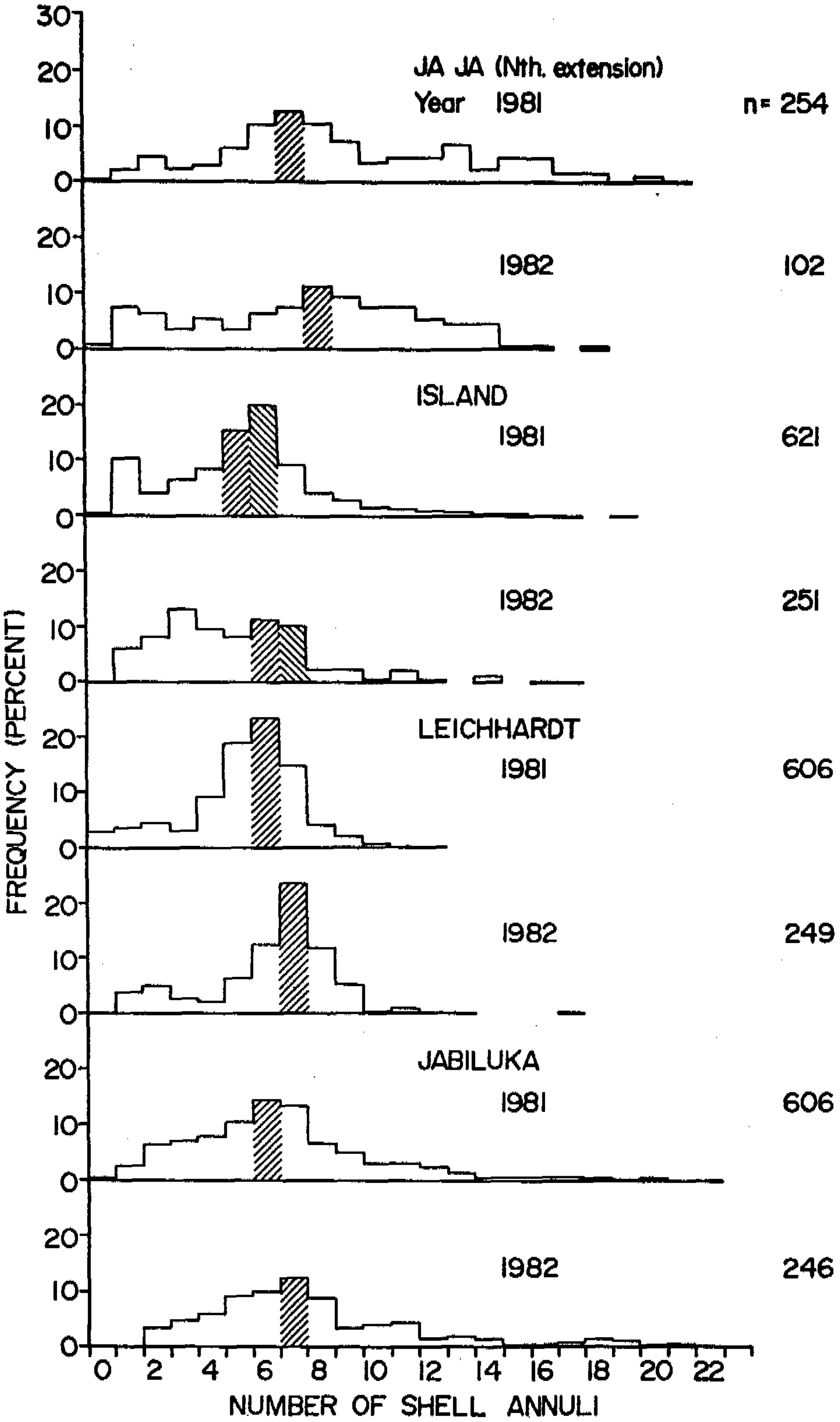


Figure 6.8 The age structures of mussel populations from the floodplain billabongs, plotted according to number of shell annuli and between the two successive years of sampling. The respective hatched histograms are dominant year classes that appear as successively older age classes in progressive sampling years.

Figure 6.9 Growth in length of mussels from Georgetown, Mudginberri and Nankeen billabongs as determined by recovery of marked individuals. The instantaneous growth rate $(\frac{l_2 - l_1}{t_2 - t_1})$ is plotted and regressed against the mean length of mussels $(\frac{l_1 + l_2}{2})$ where l_1, l_2 are the lengths at times t_1, t_2 respectively, for the conditions:

A. All age classes, adult (circled points) and juvenile young-of-year (triangles) mussels are included in the regression;
B. Adult mussels (circled points) only are included in the regression.

The resulting linear regression lines are:

Georgetown A. $Y = 49.86 - 0.770X$ ($r^2 = 0.745$)
B. $Y = 28.35 - 0.403X$ ($r^2 = 0.514$)

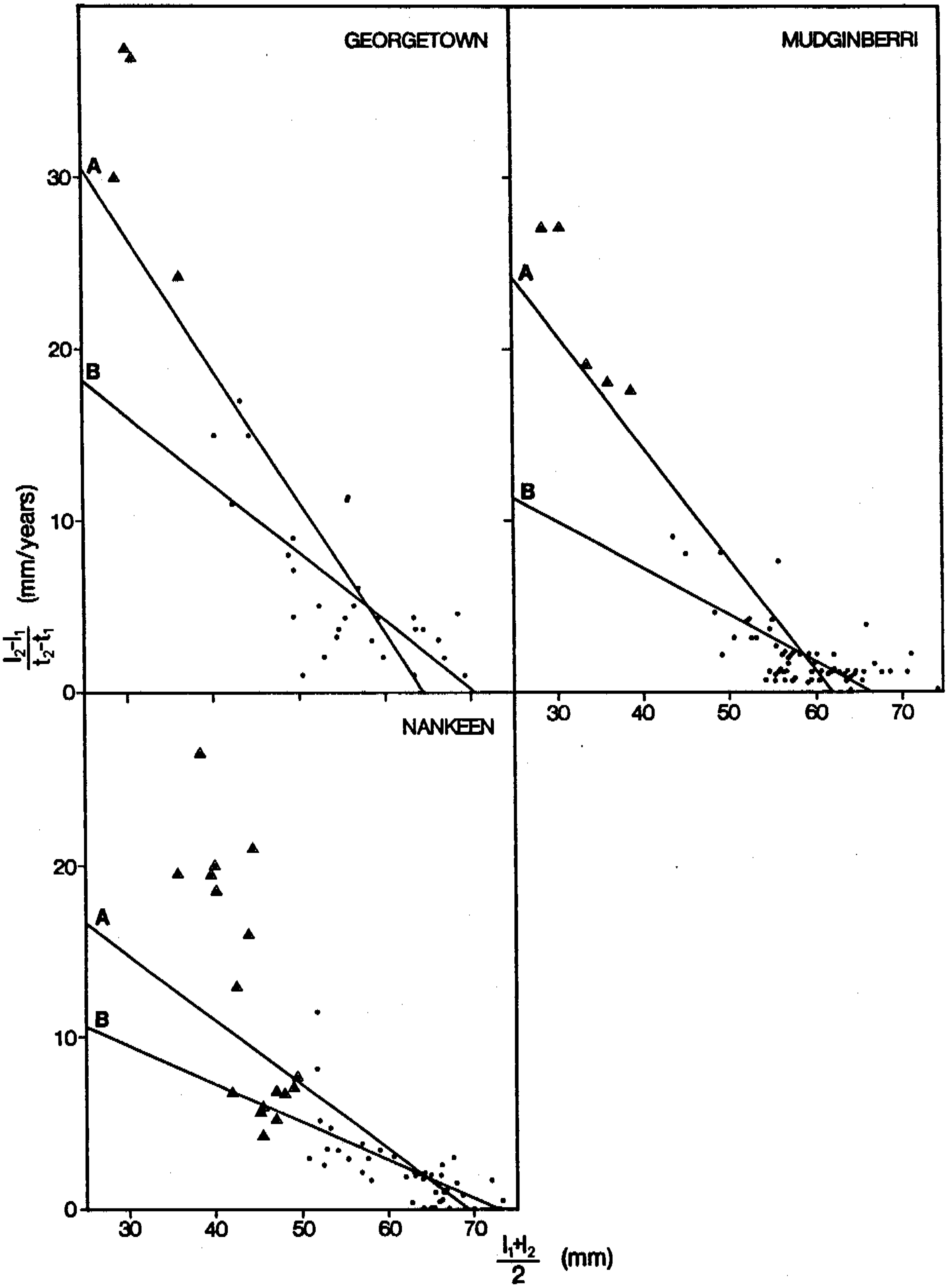
Mudginberri A. $Y = 40.71 - 0.662X$ ($r^2 = 0.834$)
B. $Y = 18.04 - 0.274X$ ($r^2 = 0.429$)

Nankeen A. $Y = 26.28 - 0.379X$ ($r^2 = 0.672$)
B. $Y = 16.11 - 0.222X$ ($r^2 = 0.518$),

where Y = instantaneous growth rate and X = mean length of mussels over the time period.

The intercept on the X-axis and the slope of the regression line provide estimates of L_∞ and -K respectively, constants of the von Bertalanffy growth equation.

6.9



GEORGETOWN
MUDGINBERRI
NANKEEN
A
B
$\frac{l_2-l_1}{t_2-t_1}$ (mm/years)
0
10
20
30
40
50
60
70
$\frac{l_1+l_2}{2}$ (mm)

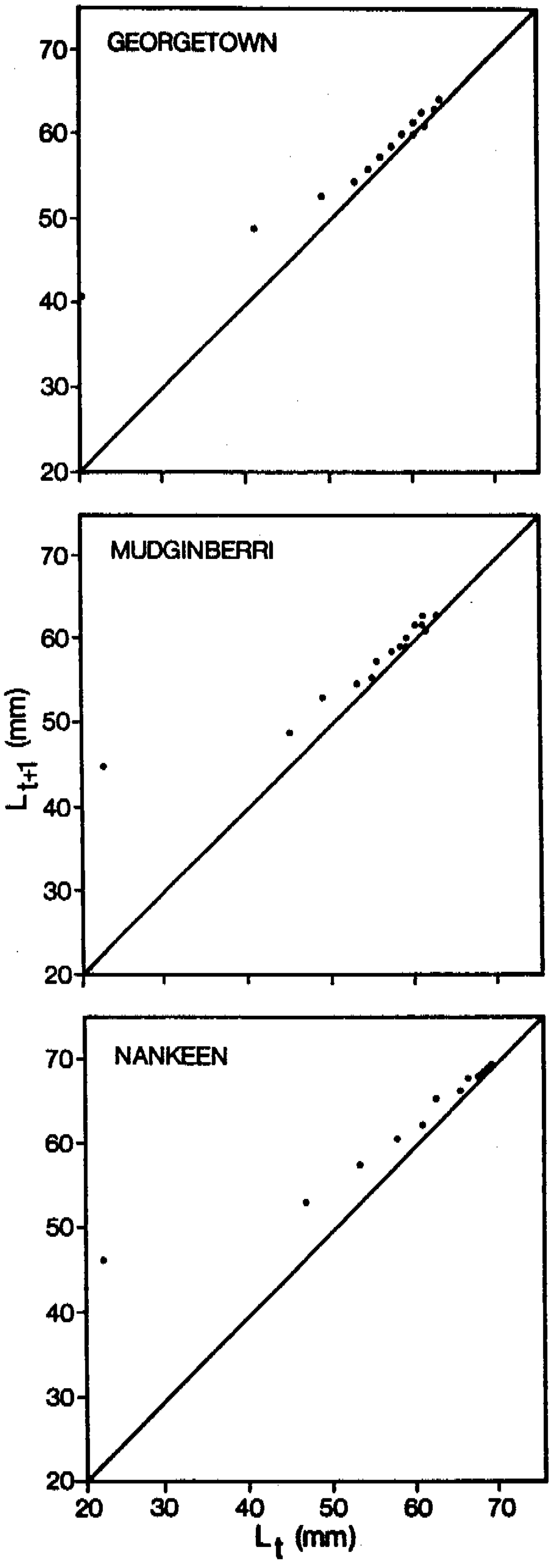
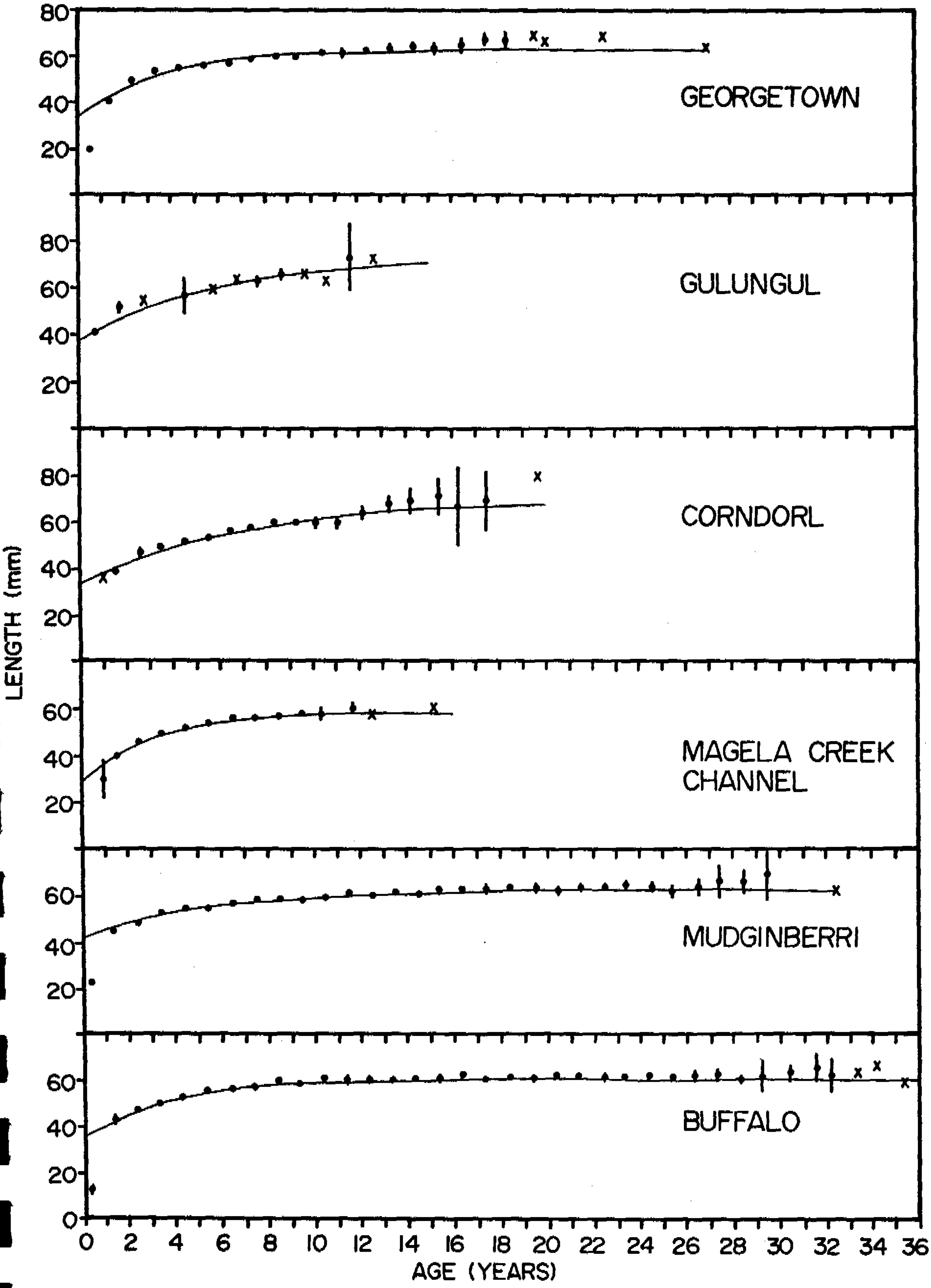


Figure 6.10 Walford plots of mean lengths at consecutive ages from age data determined by shell annuli, of mussel populations in Georgetown, Mudginberri and Nankeen billabongs.

Figures 6.11 and 6.12 Growth in length of mussels in the Magela Creek waterbodies. Circled points (n > 2) and crosses (n < 2) are mean lengths at each age and vertical lines (for n > 2) indicate 95 per cent confidence limits of the mean. Lines are fitted using the von Bertalanffy growth equation and are described in Table 6.20.

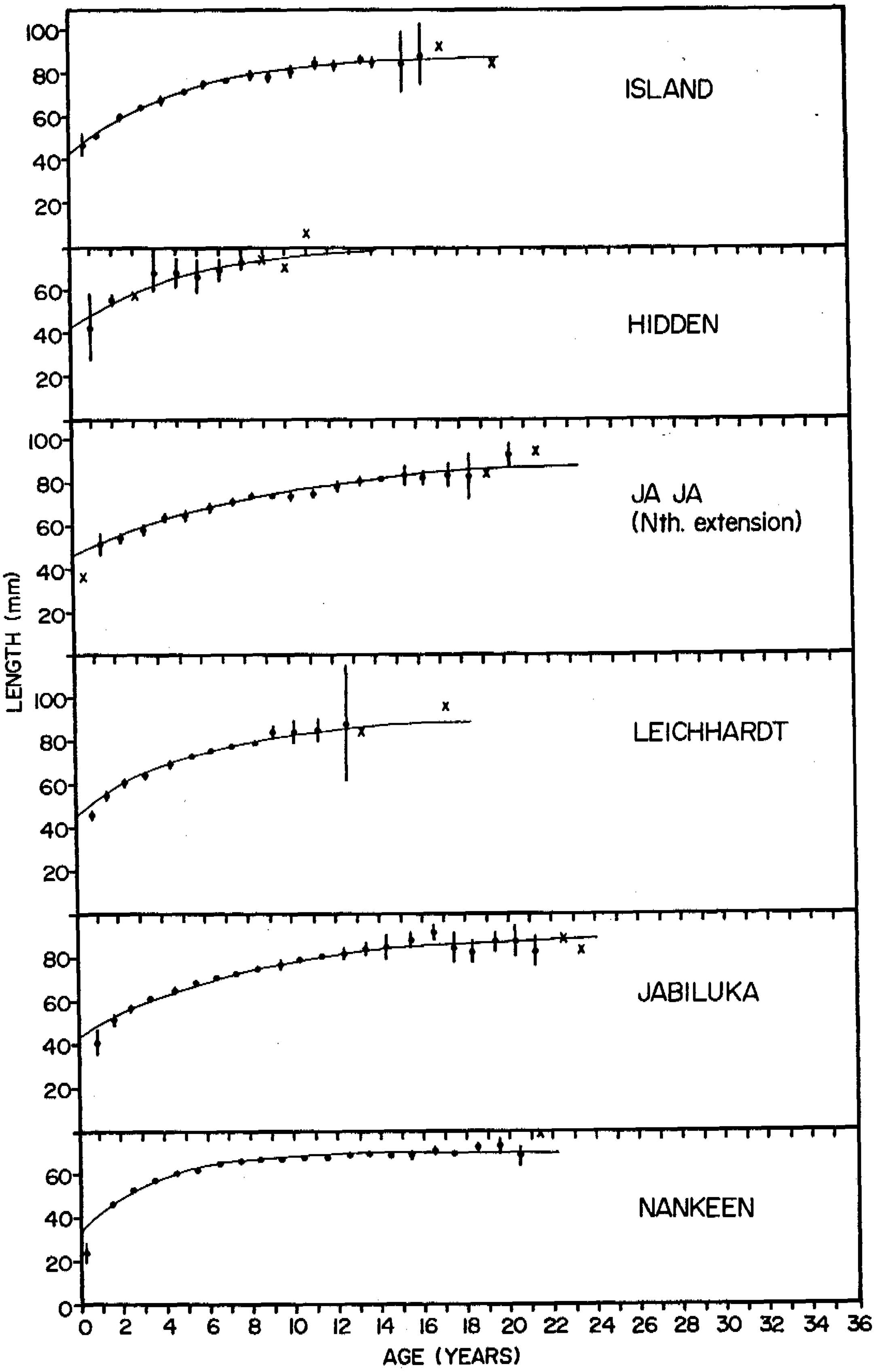
Growth curves for populations from Georgetown downstream to Buffalo billabong are shown in Figure 6.11 while those from Island downstream to Nankeen are shown in Figure 6.12.

6.11



GEORGETOWN
GULUNGUL
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
BUFFALO
LENGTH (mm)
AGE (YEARS)
0
20
40
60
80
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36

6.12



ISLAND
HIDDEN
JA JA
(Nth. extension)
LEICHHARDT
JABILUKA
NANKEEN
LENGTH (mm)
AGE (YEARS)
0
20
40
60
80
100
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36

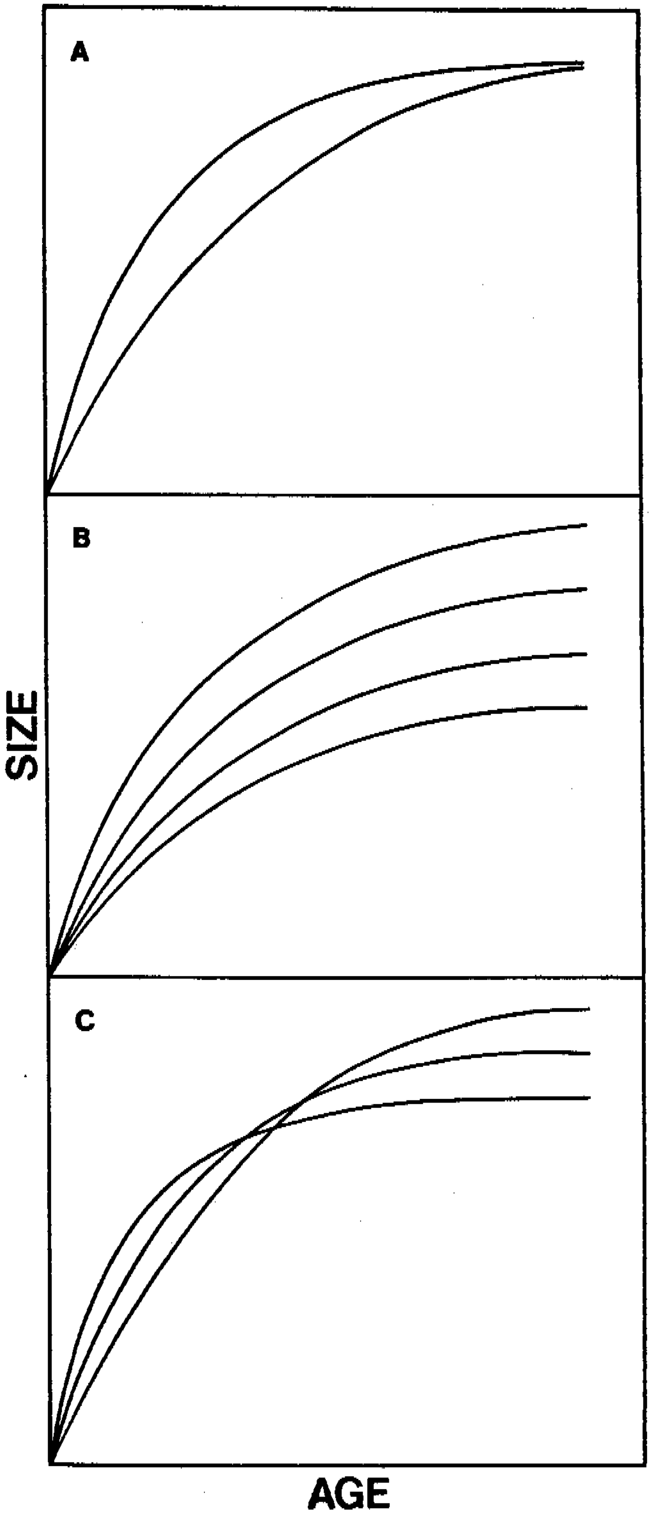


Figure 6.13 Hypothetical growth curve comparisons (Types A, B and C) of size for given ages among mussel populations within, and of different waterbodies of the Magela Creek.

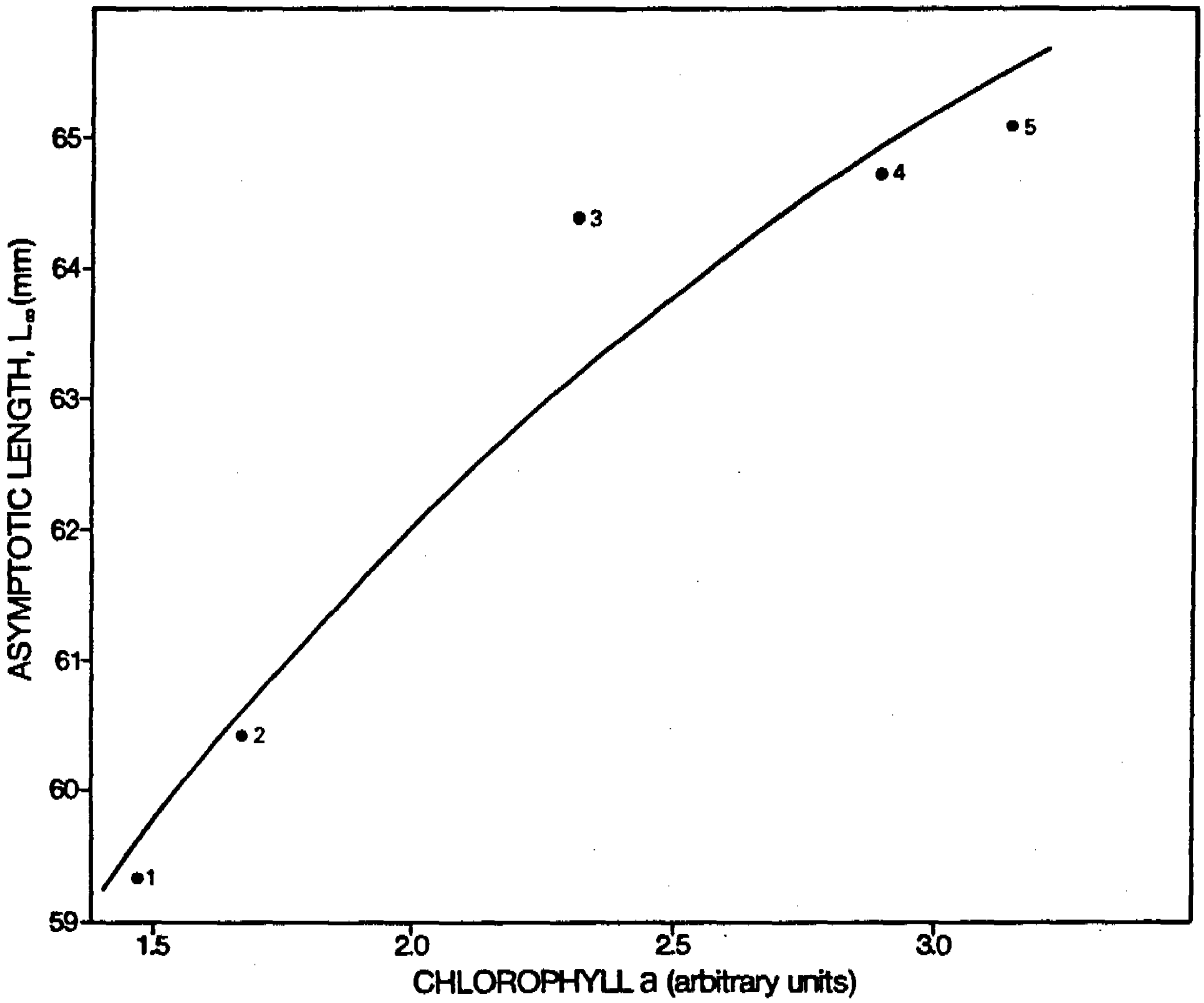


Figure 6.14 Logarithmic relationship between asymptotic length (L_∞ of the von Bertalanffy growth equation) of mussel populations and mean chlorophyll a concentrations at different sites in Mudginberri billabong. Numbers about the points are the site locations and are shown in Figure 3.1.

Fitted regression equation is:

$$Y = 7.861 \ln X + 56.589 \quad (P < 0.01, r^2 = 0.938)$$

where Y = asymptotic length (mm), and X = mean chlorophyll a concentration (arbitrary units).

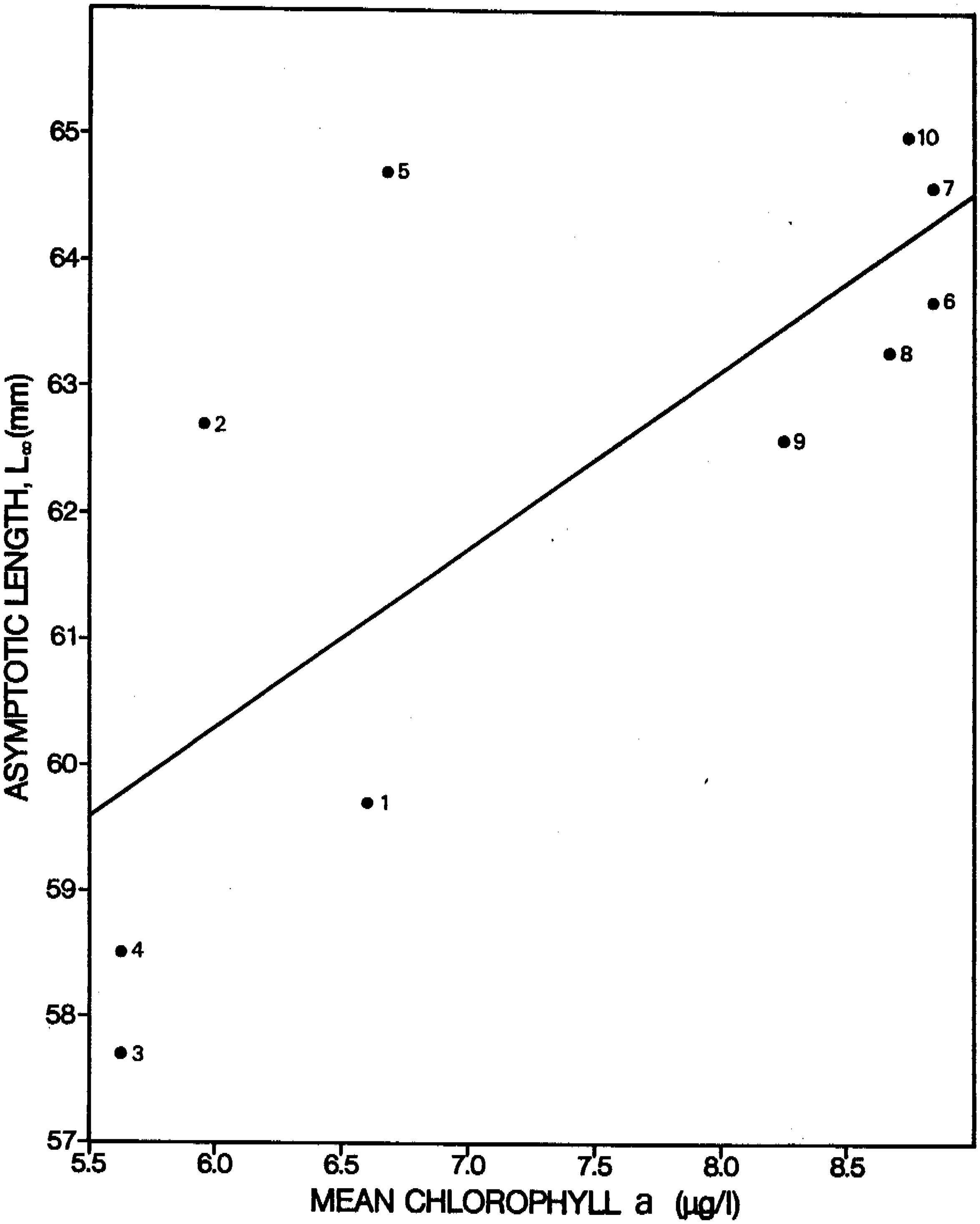


Figure 6.15 Linear relationship between asymptotic length (L_∞ of the von Bertalanffy growth equation) of mussel populations and mean chlorophyll a concentrations at different sites in Buffalo billabong. Numbers about the points are the site locations and are shown in Figure 3.1.

Fitted regression equation is:

$$Y = 1.412X + 51.833 \quad (P < 0.05,\ r^2 = 0.556)$$

where Y = asymptotic length (mm), and X = mean chlorophyll a concentration (µg/l).

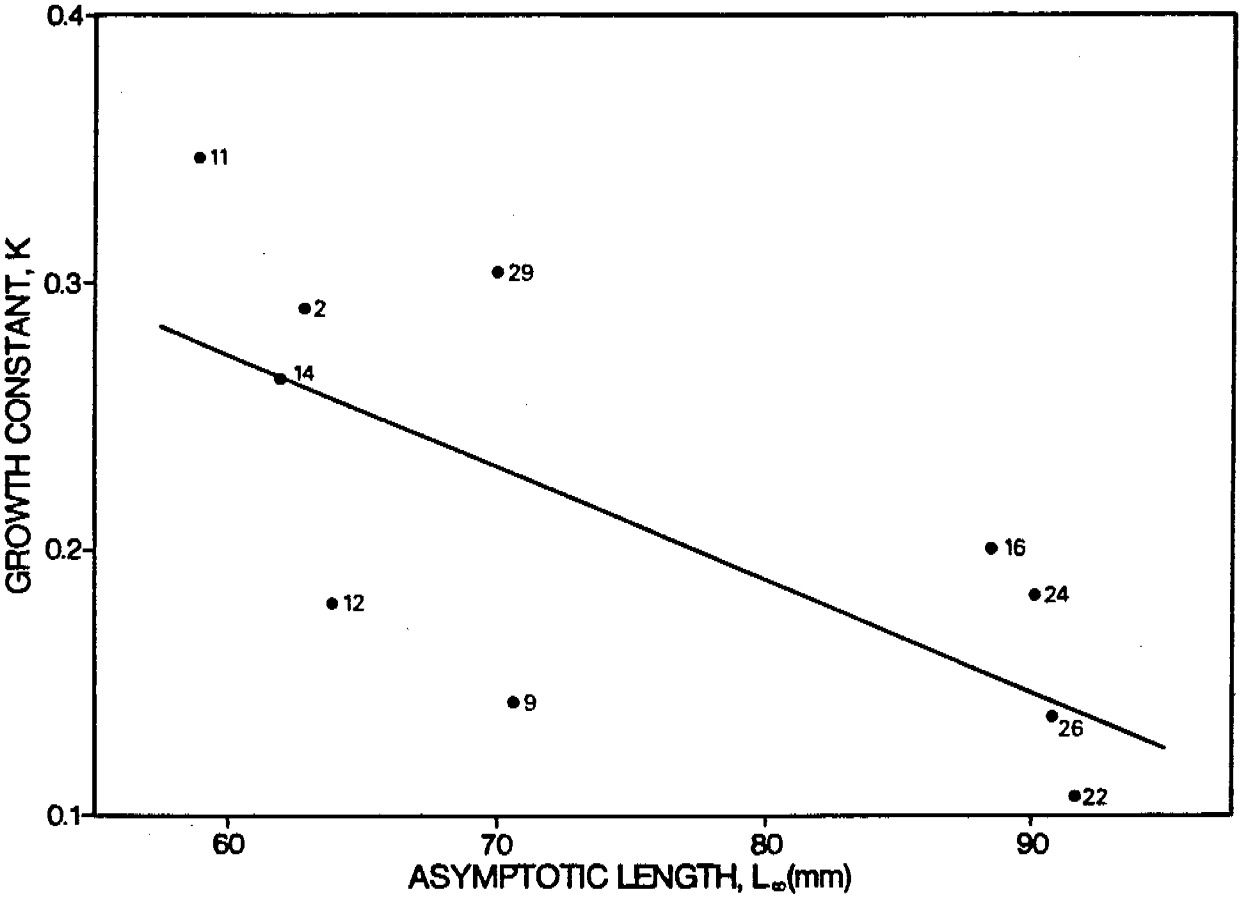


Figure 6.16 Linear relationship between asymptotic length (L_∞) and the growth constant (K) of the von Bertalanffy growth equation, calculated for mussel populations among different waterbodies of the Magela Creek. Numbers about the points are waterbody codes and are given in Table 6.20.

Fitted regression equation is:

$$Y = 0.525 - 0.0042X \qquad (P < 0.05,\ r^2 = 0.523)$$

where Y = asymptotic length, L_∞ (mm) and X = growth constant, K.

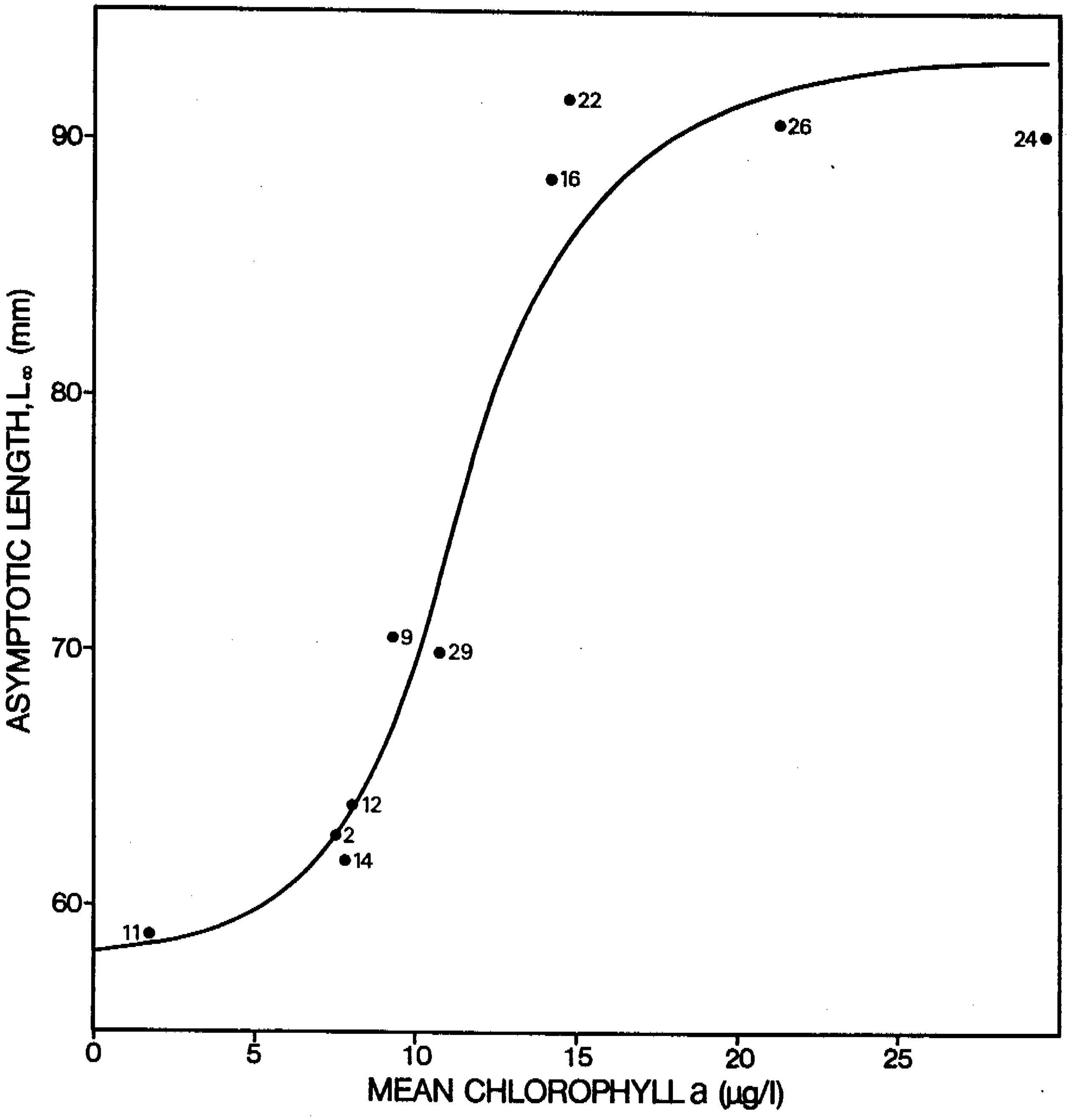


Figure 6.17 Asymptotic-type relationship between asymptotic length (L_∞) of the von Bertalanffy growth equation plotted for mussel populations among different waterbodies of the Magela Creek, and mean chlorophyll a concentration of the surface waters averaged over the seasons. Numbers about the points are waterbody codes and are given in Table 6.20.
Curve fitted by eye.

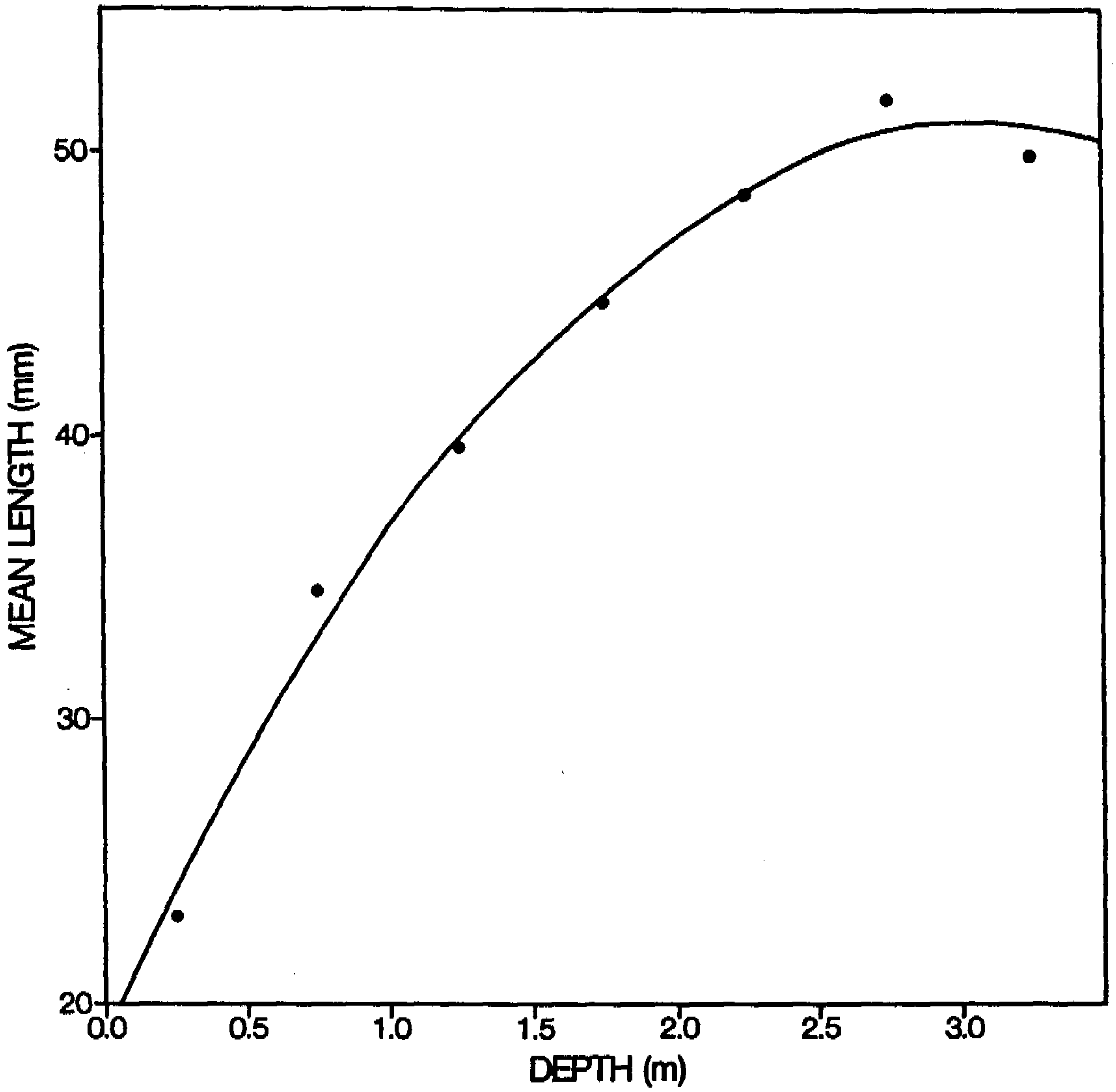


Figure 6.18 Quadratic relationship between depth and mean length of mussels in Georgetown billabong.

Fitted regression equation is of the form:
$Y = a + bX + CX^2$ (where Y = mean length and X = depth) and is described in Table 6.29.

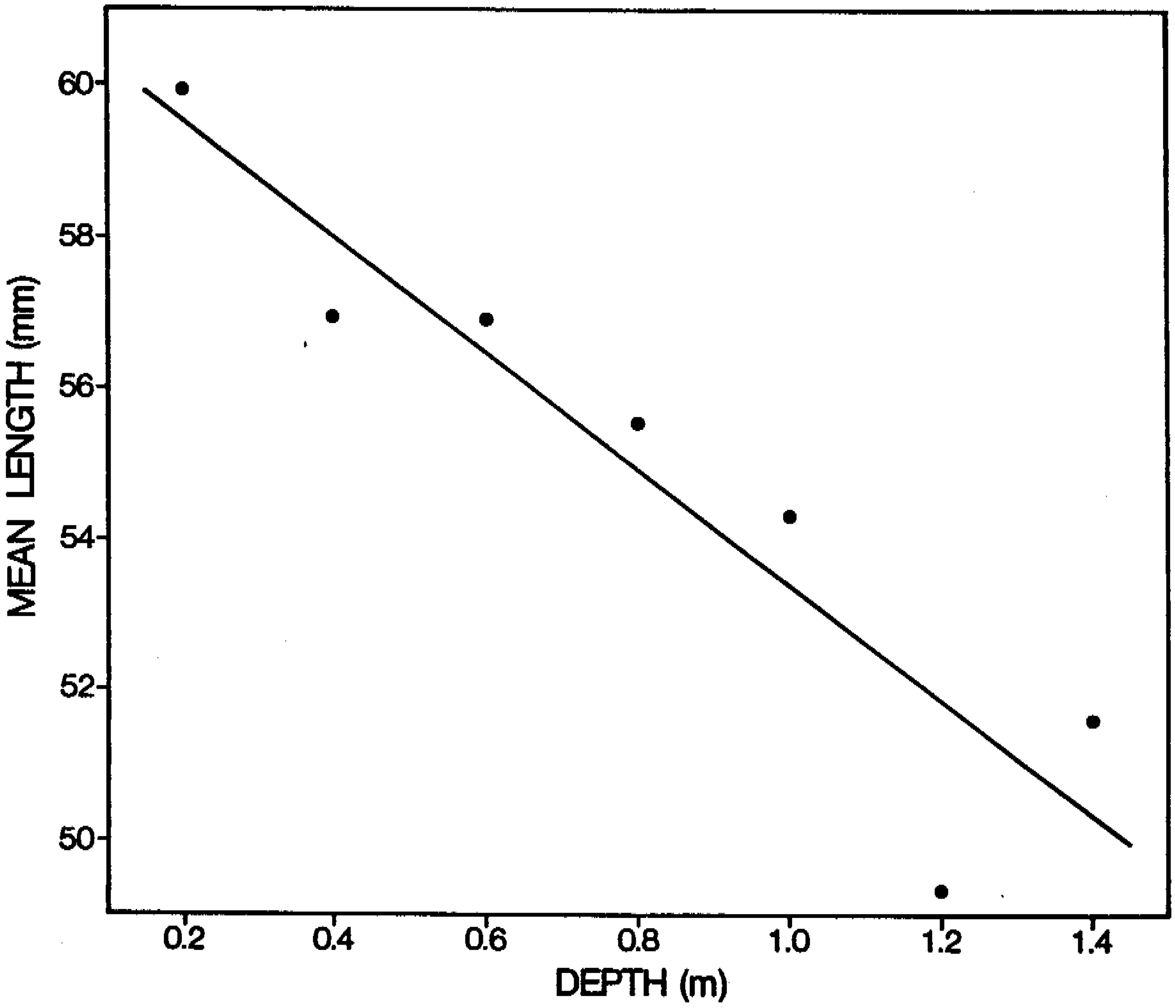


Figure 6.19 Linear relationship between depth and mean length of mussels in Corndorl billabong.

Fitted regression equation is of the form:
Y = a + bX (where Y = mean length and X = depth) and is described in Table 6.29.

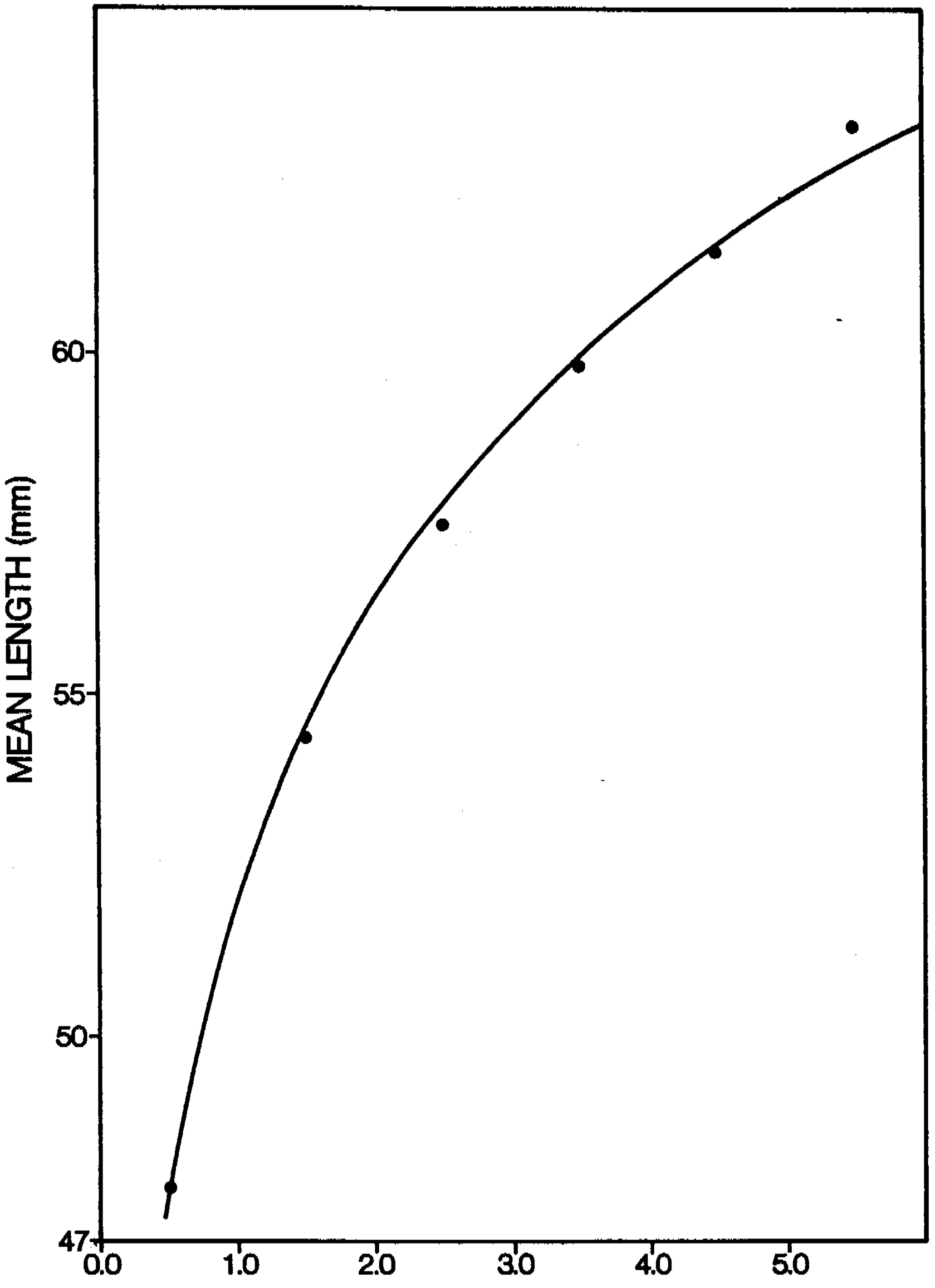


Figure 6.20 Logarithmic relationship between depth and mean length of mussels in the channel billabongs (Mudginberri and Buffalo).

Fitted regression equation is of the form:
Y = alnX + b (where Y = mean length and X = depth) and is described in Table 6.29.

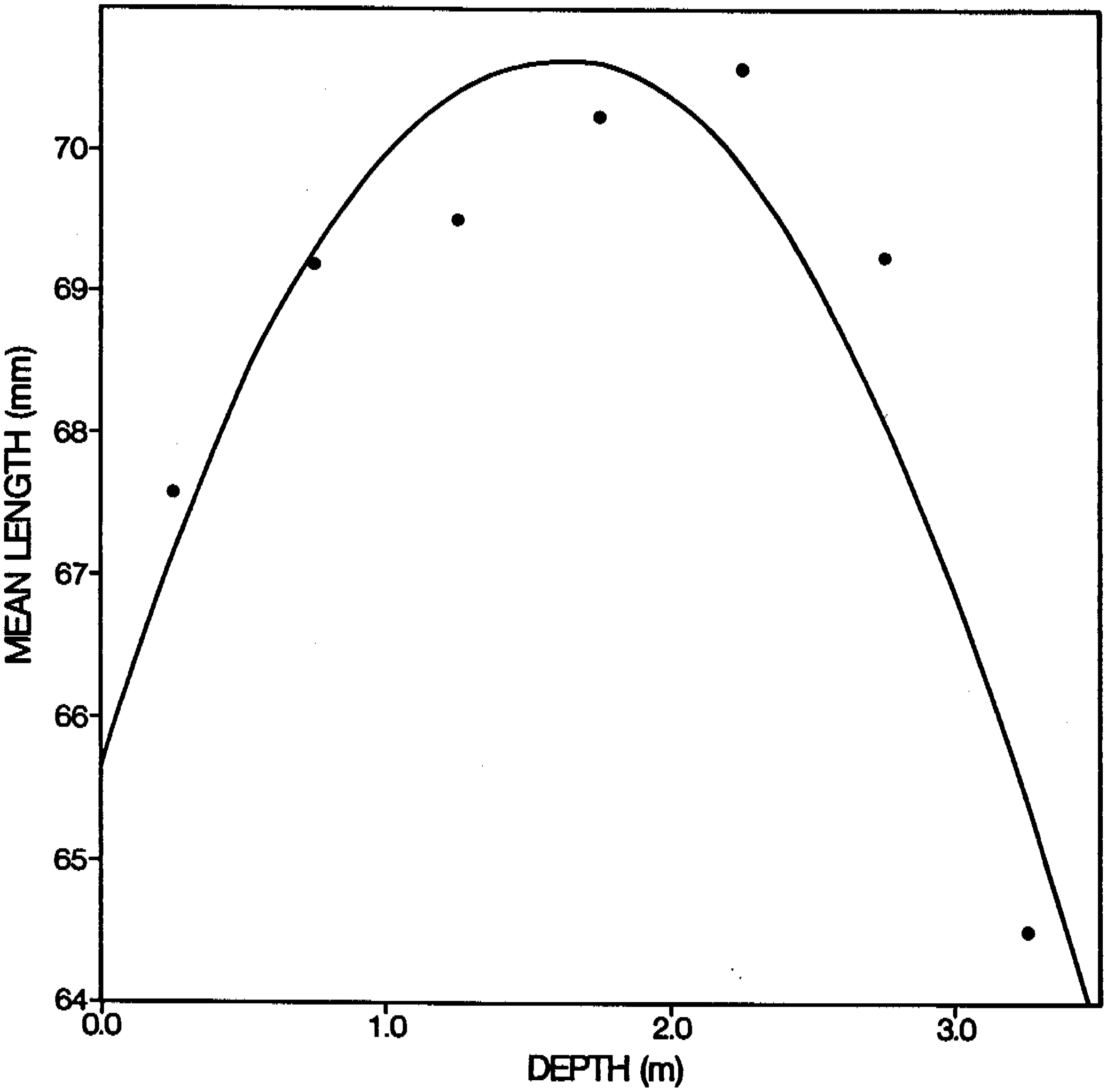


Figure 6.21 Quadratic relationship between depth and mean length of mussels in the floodplain billabongs.

Fitted regression equation is of the form:
$Y = a + bX + CX^2$ (where Y = mean length and X = depth) and is described in Table 6.29.

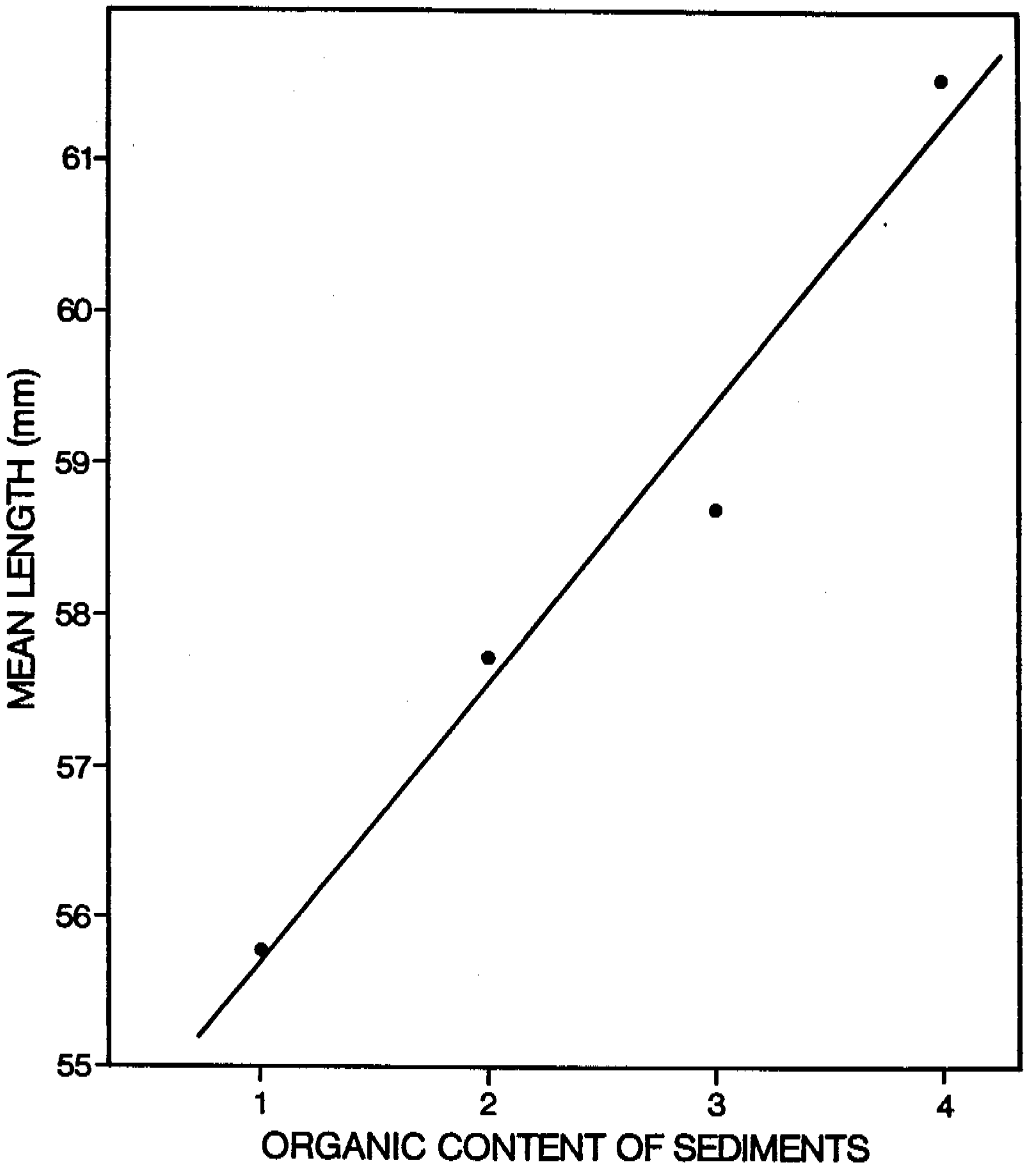


Figure 6.22 Linear relationship between mean length of mussels and organic content of the sediments in the channel billabongs (Mudginberri and Buffalo).

Sediments 1, 2, 3 and 4 correspond to sediments A, B, C and E respectively, keyed in Table 6.27.

Fitted regression equation is:

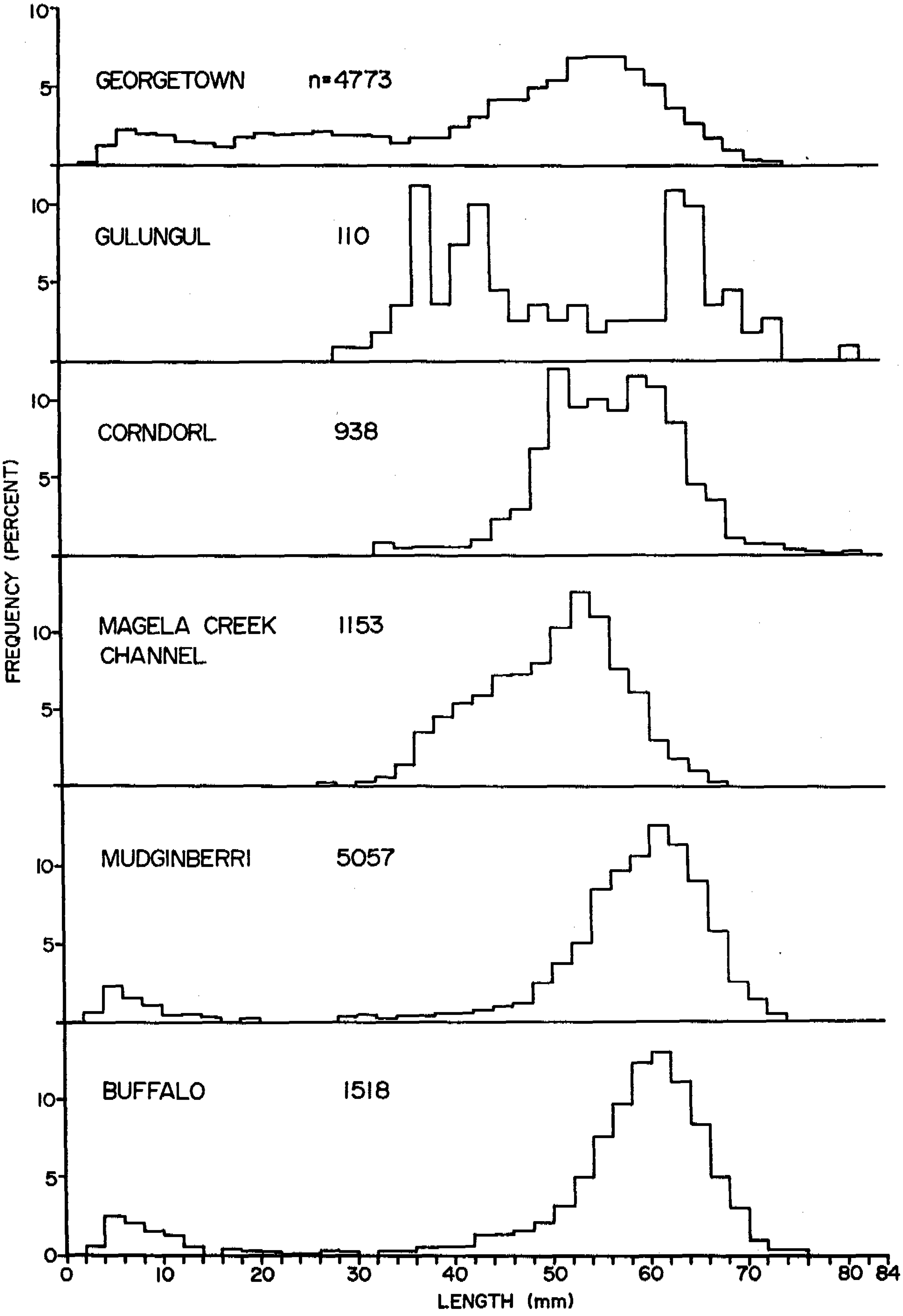
$Y = 53.885 - 1.829X$ $(P < 0.05, r^2 = 0.962)$

where Y = mean length (mm) and X = organic content of sediments (arbitrarily ranked).

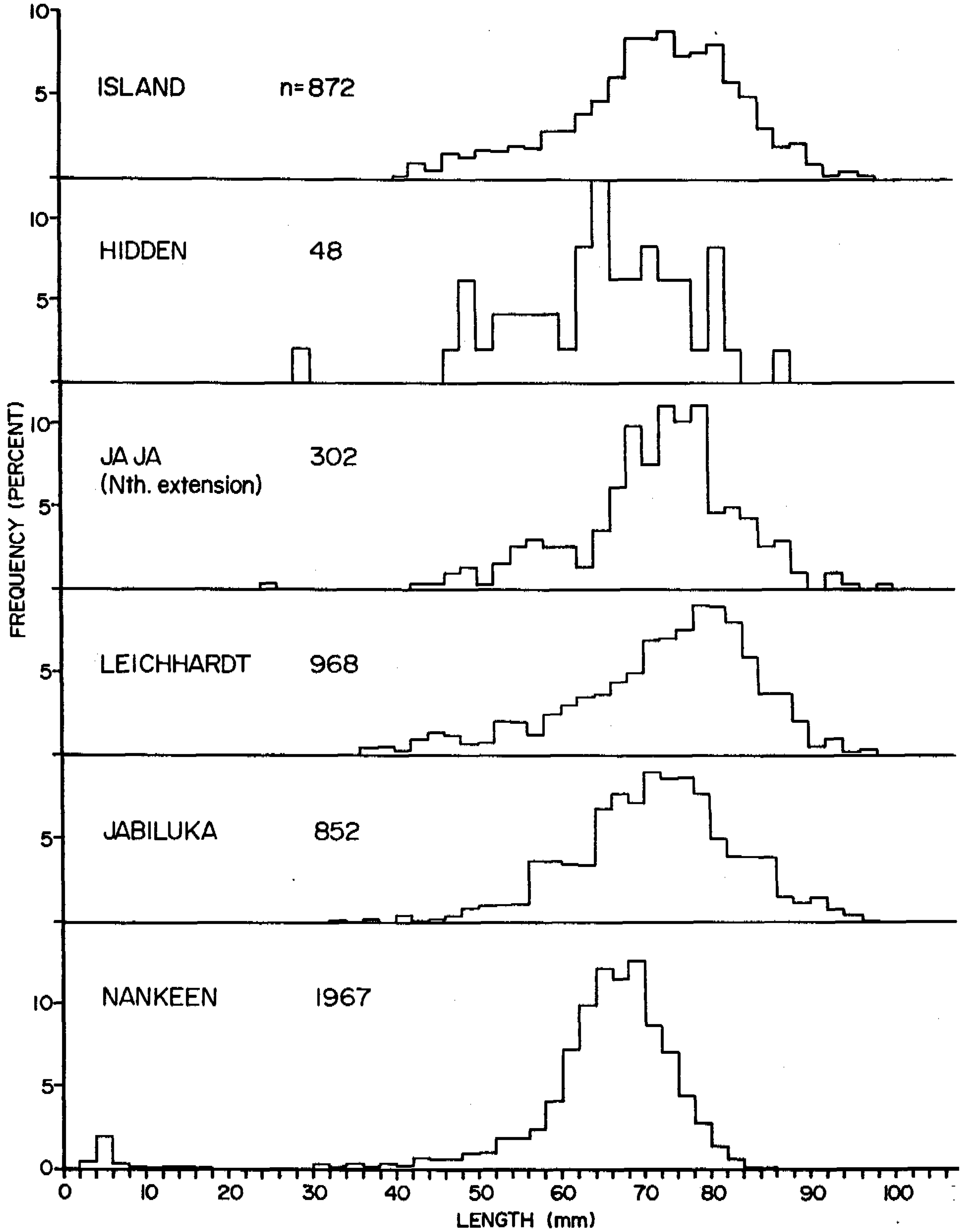
Figures 6.23 and 6.24 Length frequency distributions of mussels from the Magela Creek waterbodies sampled over the study period.

Distributions for populations from Georgetown downstream to Buffalo billabong are shown in Figure 6.23 while those from Island downstream to Nankeen are shown in Figure 6.24.

Fig 6.23


GEORGETOWN n=4773
GULUNGUL 110
CORNDORL 938
MAGELA CREEK CHANNEL 1153
MUDGINBERRI 5057
BUFFALO 1518
FREQUENCY (PERCENT)
0
5
10
LENGTH (mm)
0
10
20
30
40
50
60
70
80
84

6.24



ISLAND n=872
HIDDEN 48
JA JA (Nth. extension) 302
LEICHHARDT 968
JABILUKA 852
NANKEEN 1967
FREQUENCY (PERCENT)
10
5
0
0 10 20 30 40 50 60 70 80 90 100
LENGTH (mm)

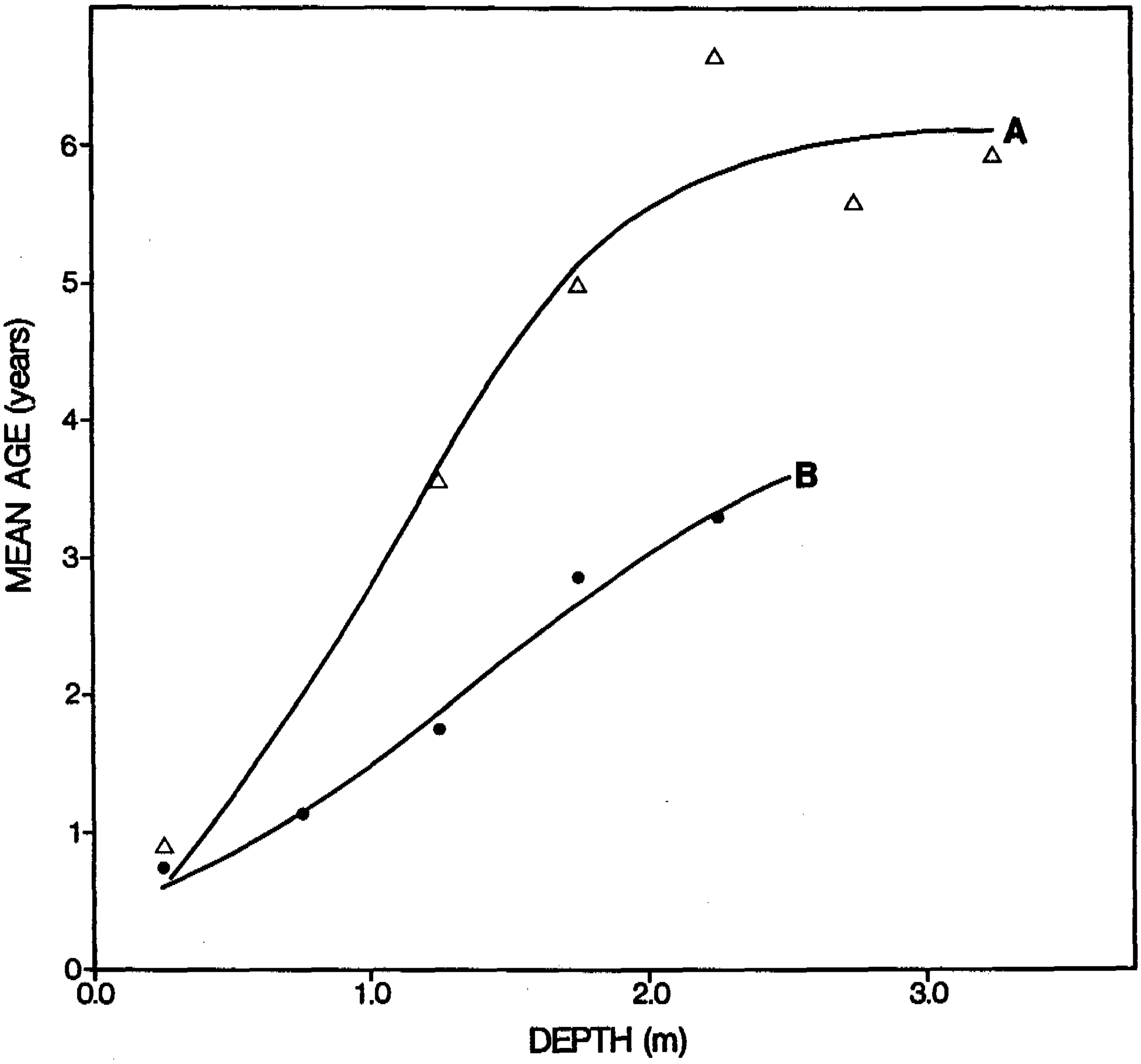


Figure 6.25 Logistic relationships between depth and mean age of mussels on the two sampling transects (A and B) of Georgetown billabong. Location of the transects is shown in Figure 3.1.

Fitted functions are of the form: $Y = A(1 + Be^{-kx})^{-1}$ (where Y = mean age and X = depth) and are described in Table 6.35.

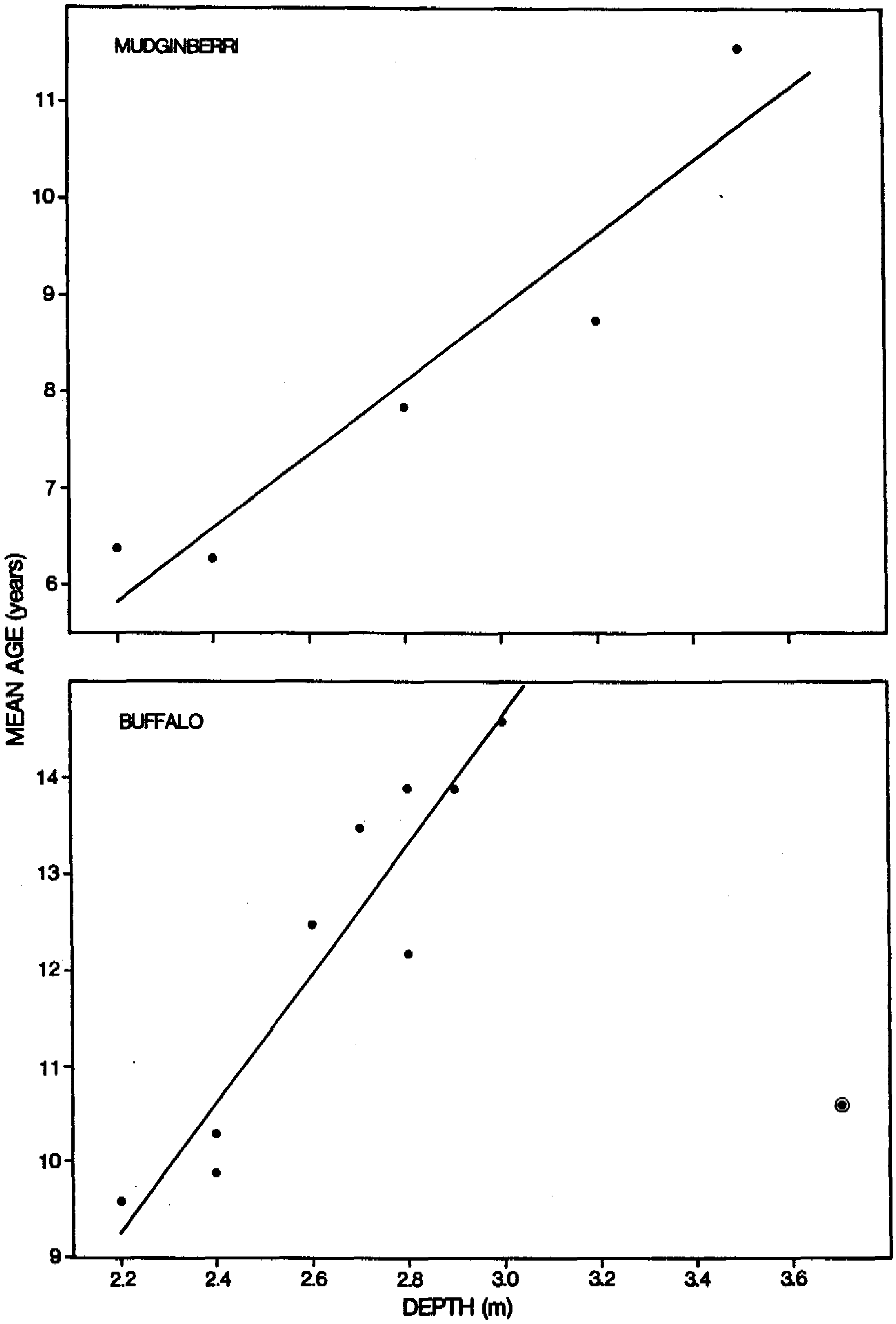


Figure 6.26 Linear relationships between depth and mean age of mussels in the channel billabongs, Mudginberri and Buffalo.

Fitted regression equations are of the form:
$Y = a + bX$ (where Y = mean age and X = depth) and are described in Table 6.36. The encircled point in Buffalo was not included in the regression analysis of the data from that billabong.

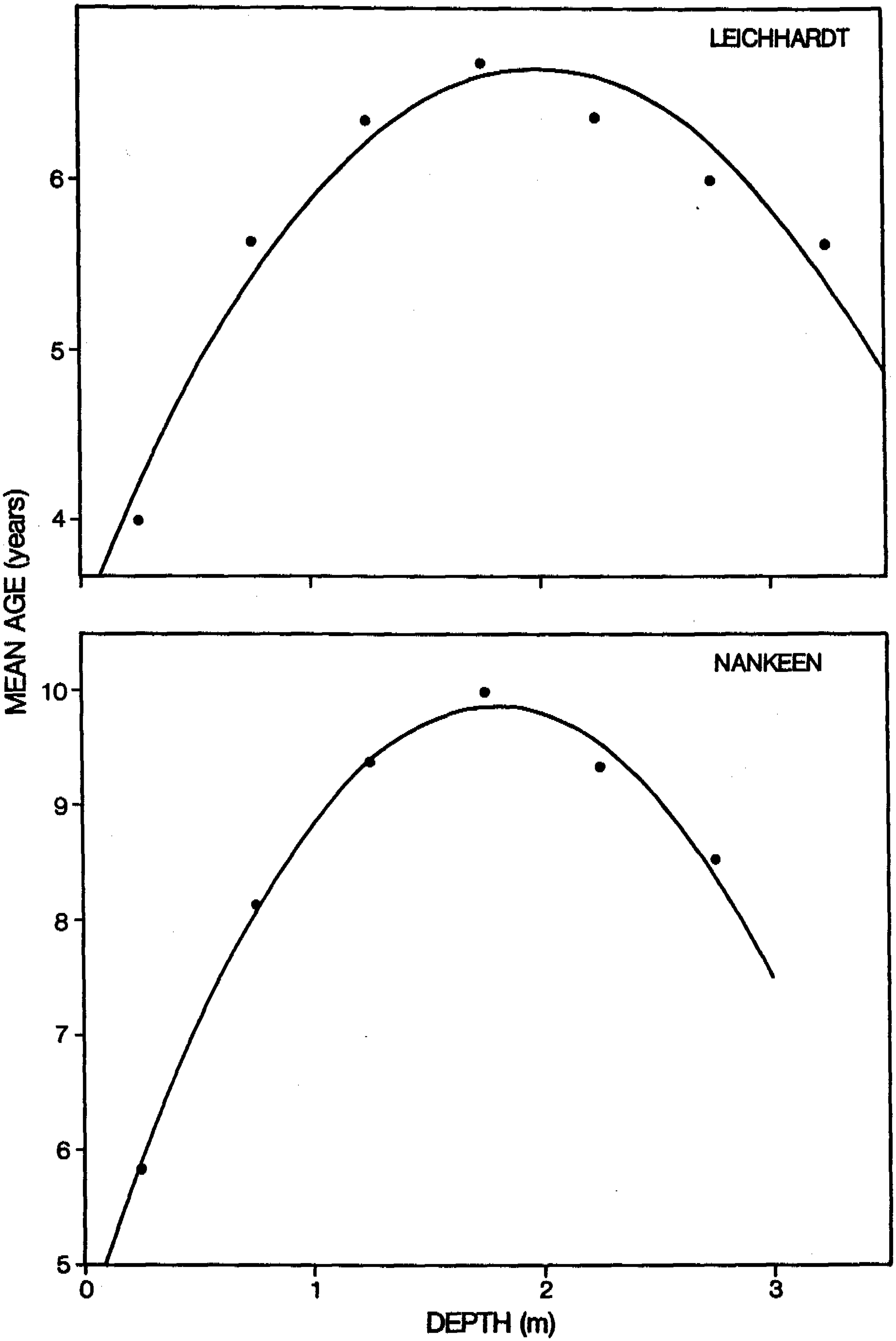


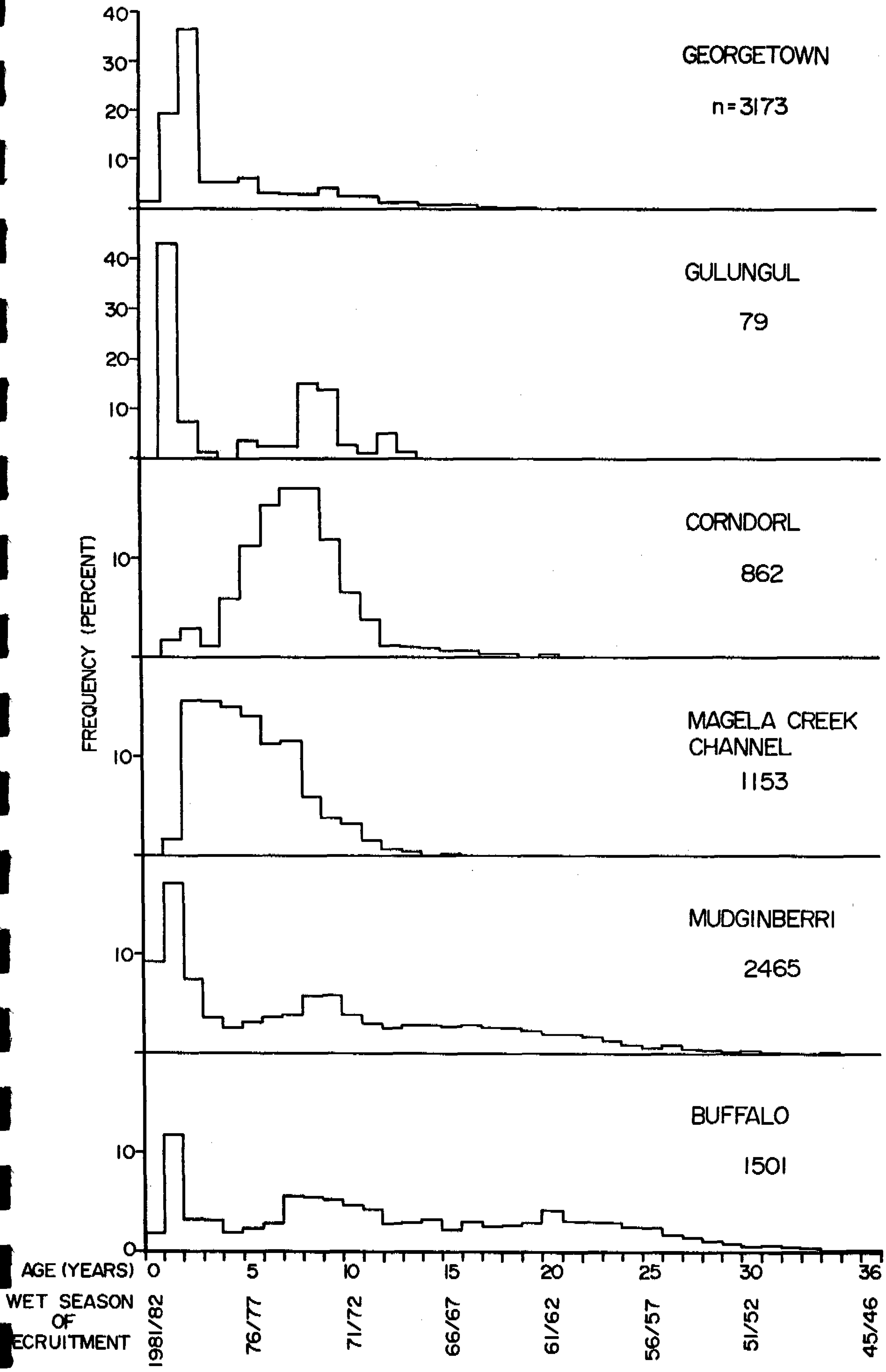
Figure 6.27 Quadratic relationships between depth and mean age of mussels in the floodplain billabongs, Leichhardt and Nankeen.

Fitted regression equations are of the form:
$Y = a + bX + CX^2$ (where Y = mean age and X = depth) and are described in Table 6.36.

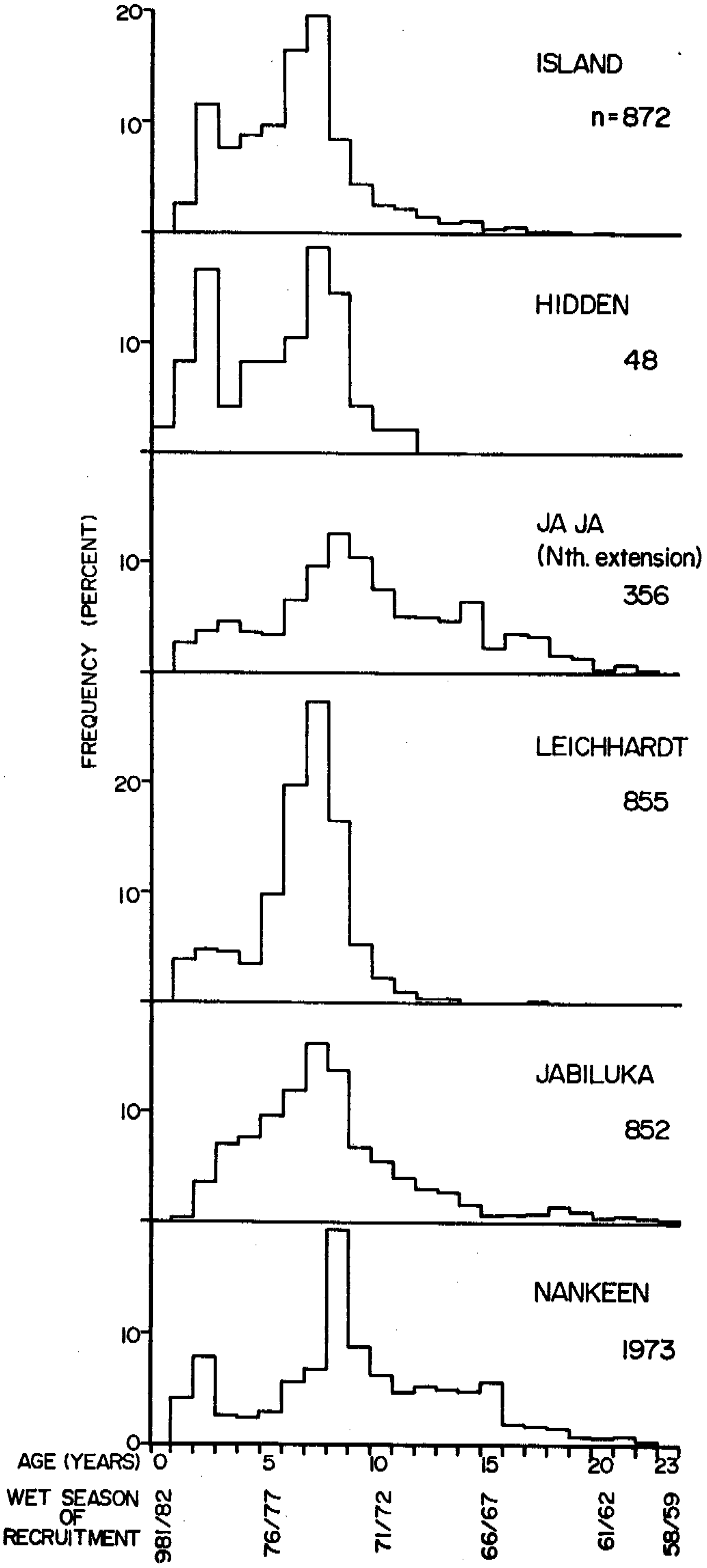
Figures 6.28 and 6.29 Age structure of mussel populations from the Magela Creek waterbodies in relation to year of recruitment of the age classes.

Age distributions for populations from Georgetown downstream to Buffalo billabong are shown in Figure 6.28 while those from Island downstream to Nankeen are shown in Figure 6.29.

6.28


GEORGETOWN
n=3173
GULUNGUL
79
CORNDORL
862
MAGELA CREEK CHANNEL
1153
MUDGINBERRI
2465
BUFFALO
1501
FREQUENCY (PERCENT)
40
30
20
10
0
AGE (YEARS)
0
5
10
15
20
25
30
36
WET SEASON OF ECRUITMENT
1981/82
76/77
71/72
66/67
61/62
56/57
51/52
45/46

6.29


ISLAND
n=872
HIDDEN
48
JA JA
(Nth. extension)
356
LEICHHARDT
855
JABILUKA
852
NANKEEN
1973
FREQUENCY (PERCENT)
20
10
0
AGE (YEARS)
0
5
10
15
20
23
WET SEASON OF RECRUITMENT
1981/82
76/77
71/72
66/67
61/62
58/59

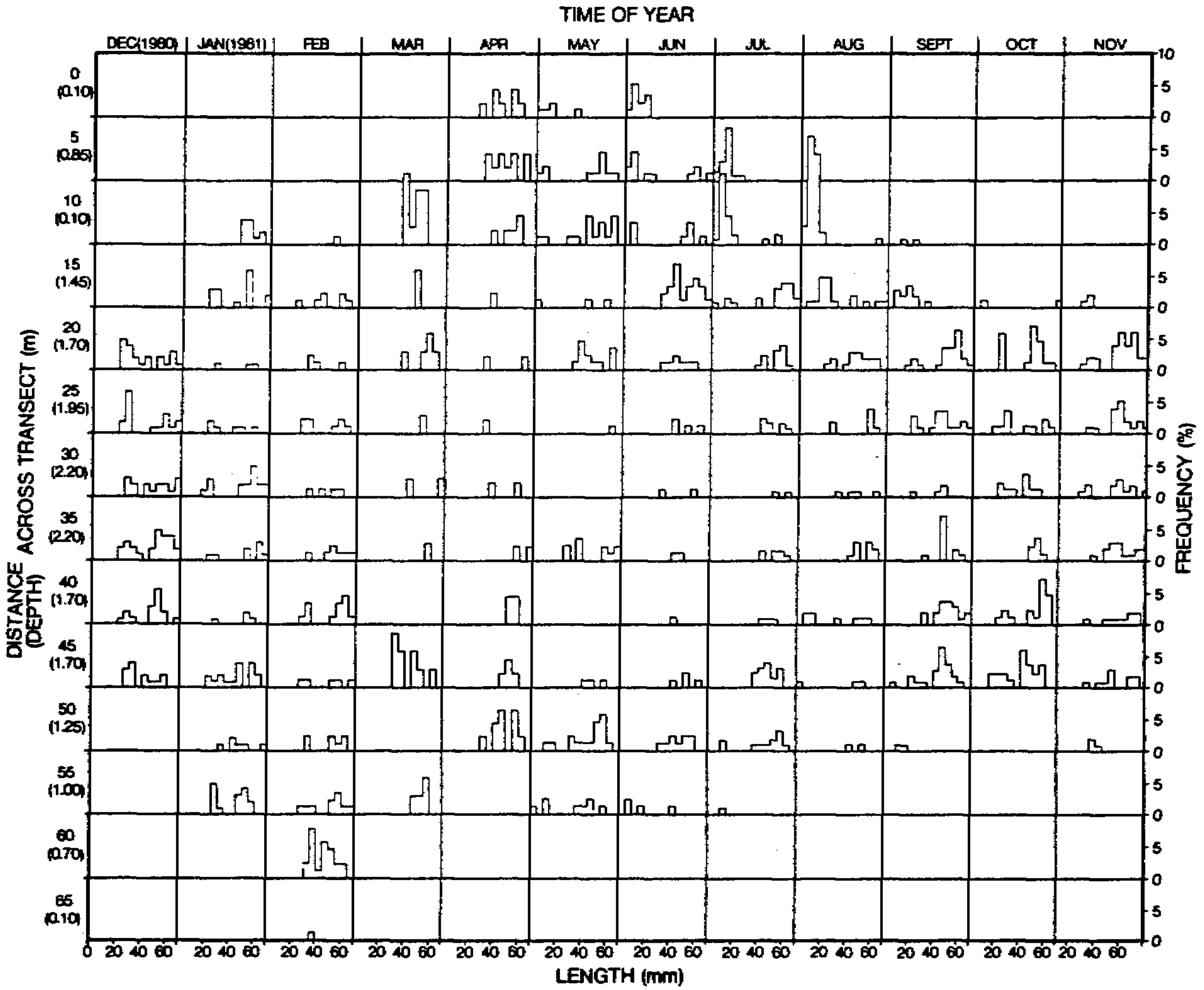


Figure 6.30 Spatial and seasonal changes in size frequency distributions of mussels along sampling transect B of Georgetown billabong. Location of the transect is shown in Figure 3.1.

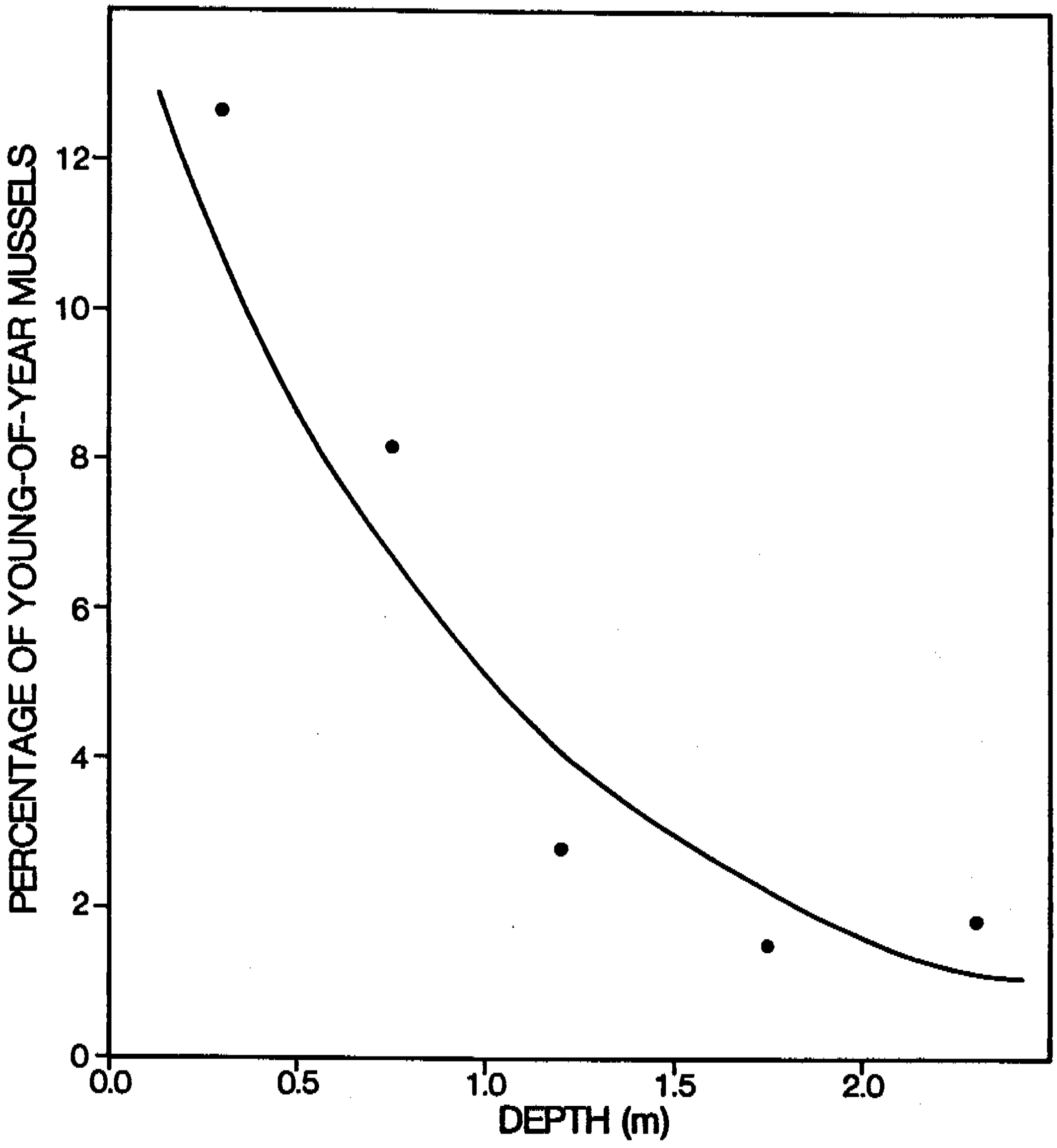


Figure 6.31 Exponential relationship between depth and the proportion of juvenile, young-of-year mussels in Nankeen billabong.

Fitted regression equation is:

$Y = 100(1-EXP(0.158EXP(-1.097X)))$ ($P < 0.05$, $r^2 = 0.846$)

where Y = proportion of young-of-year mussels (percent), and X = depth (m).

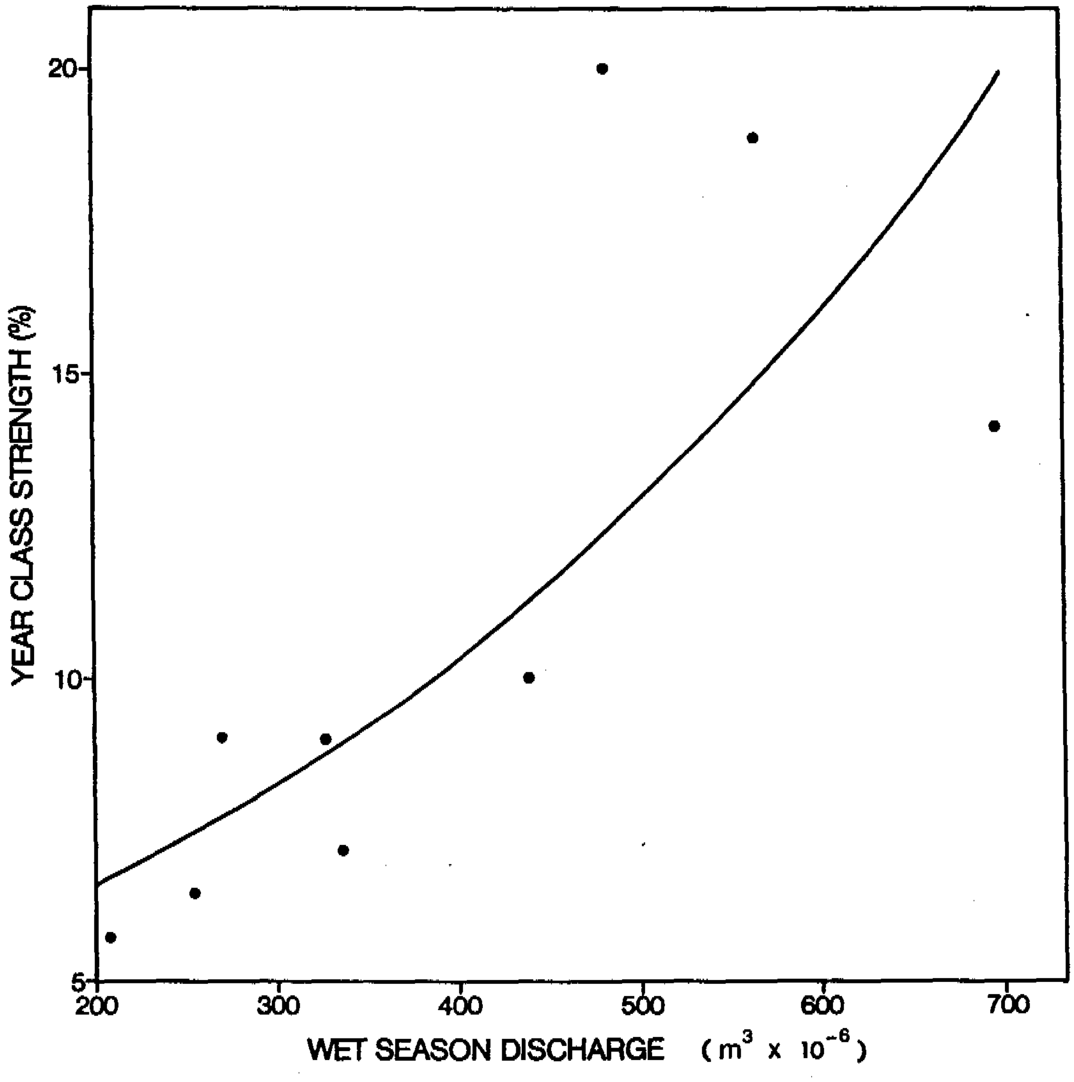


Figure 6.32 Exponential relationship between year class strength of mussels in the floodplain billabongs and Wet season discharge at GS821009 on the Magela Creek.

Fitted regression equation is:

$Y = 100(1-EXP(-0.043EXP(0.00234X)))$ ($P < 0.01$, $r^2 = 0.653$)

where Y = Year class strength (percent), and X = total discharge for the period January to May ($m^3 \times 10^{-6}$).

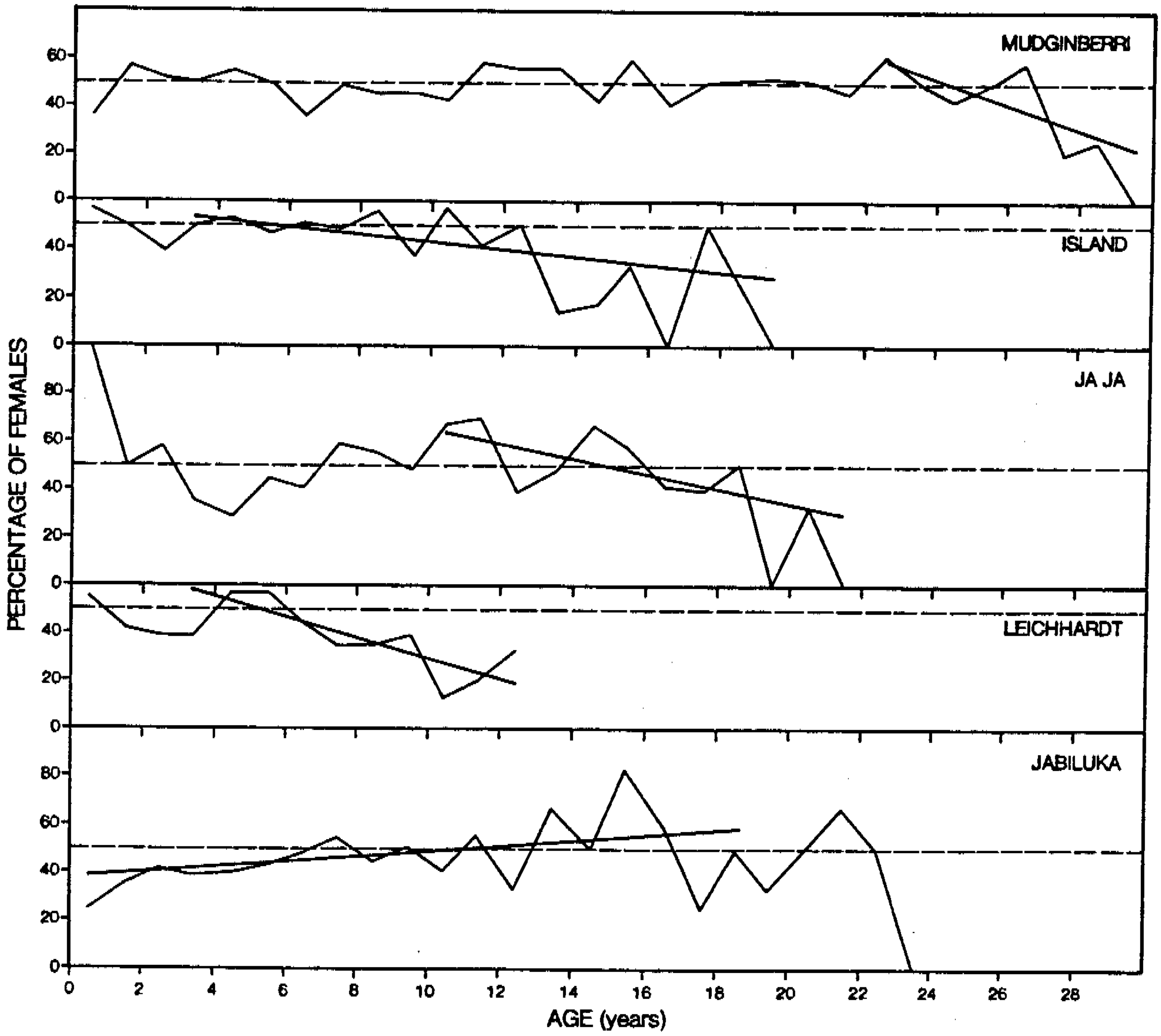


Figure 6.33 Relationships between sex ratio (percent of females) and age of mussels, in billabongs of the Magela Creek. Fitted lines represent the age classes over which significant linear correlations were found between sex ratio and age.

The linear equations are of the form:
Y = mX + b (where Y = percentage of females within a particular age class and X = age) and are described in Table 6.43.

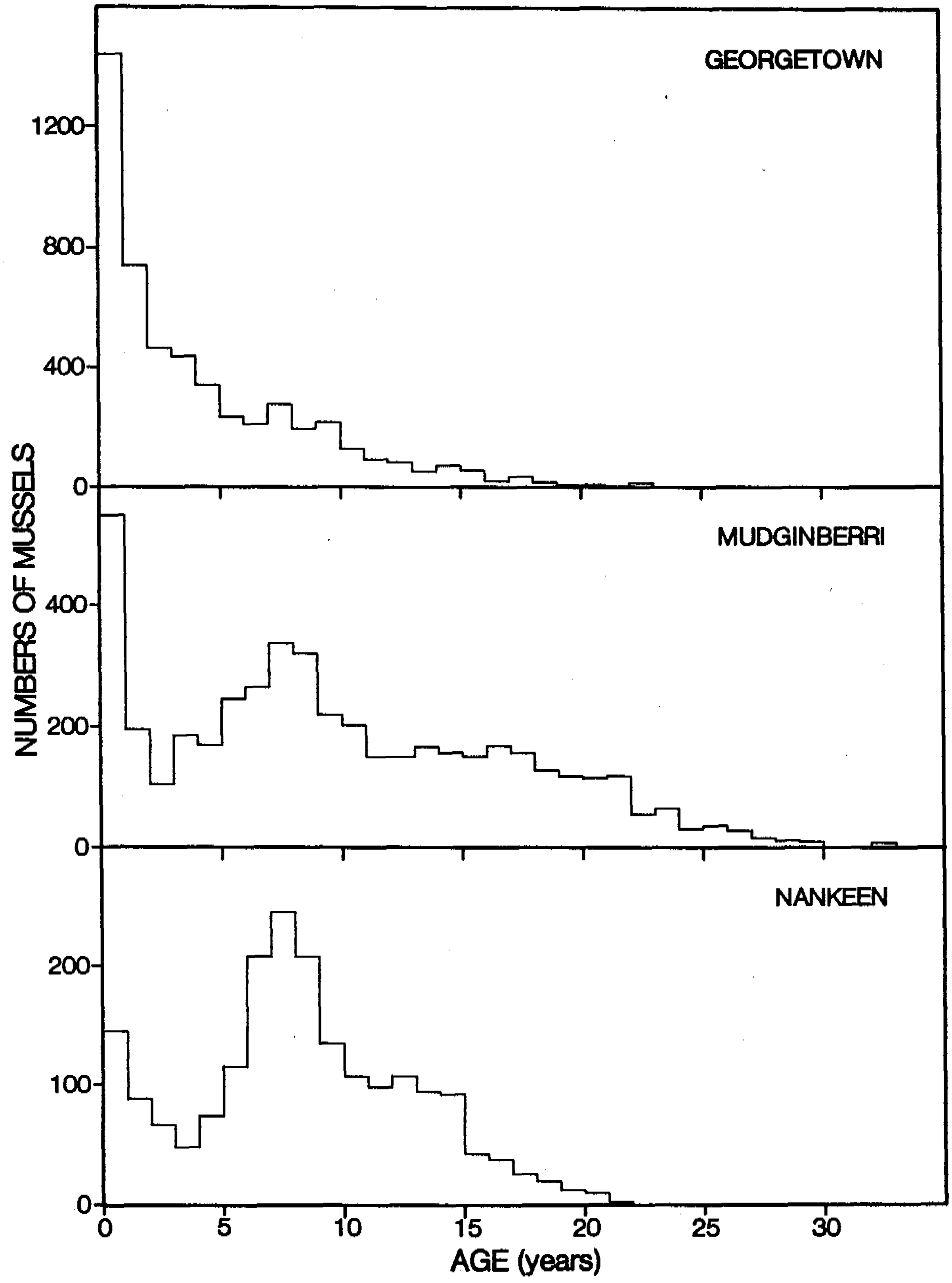


Figure 6.34 Age structures of mussel populations from Georgetown, Mudginberri and Nankeen billabongs. The numbers of mussels within specific age classes collected over the study period are pooled without regard for the year of recruitment.

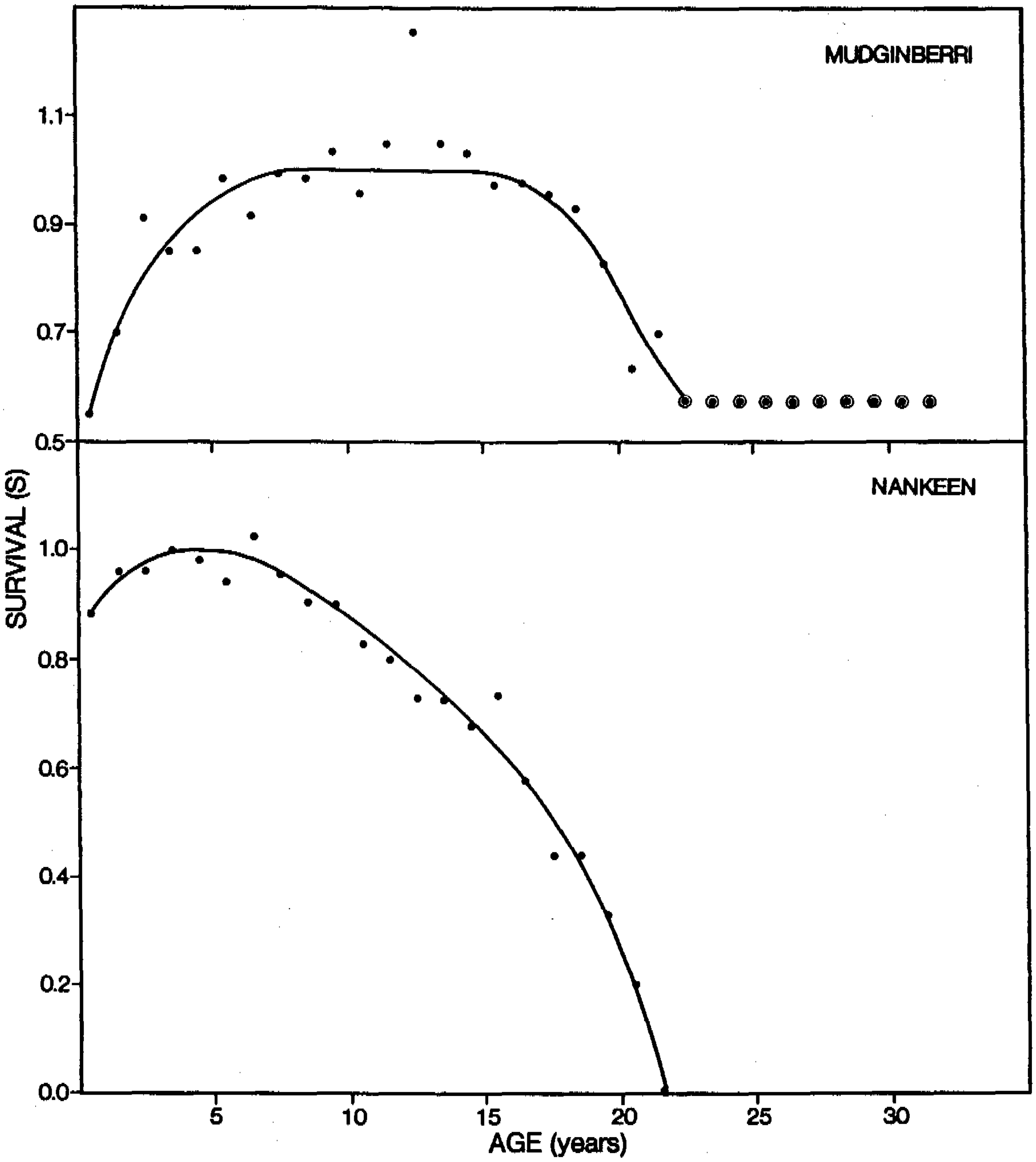


Figure 6.35 Annual, age-specific survival rates (S) in the mussel populations from Mudginberri and Nankeen billabongs, calculated from comparison of abundance of individual year-classes at successive ages. The survival values encircled in Mudginberri were calculated from catch curve analysis.

Smoothed lines are fitted by eye.

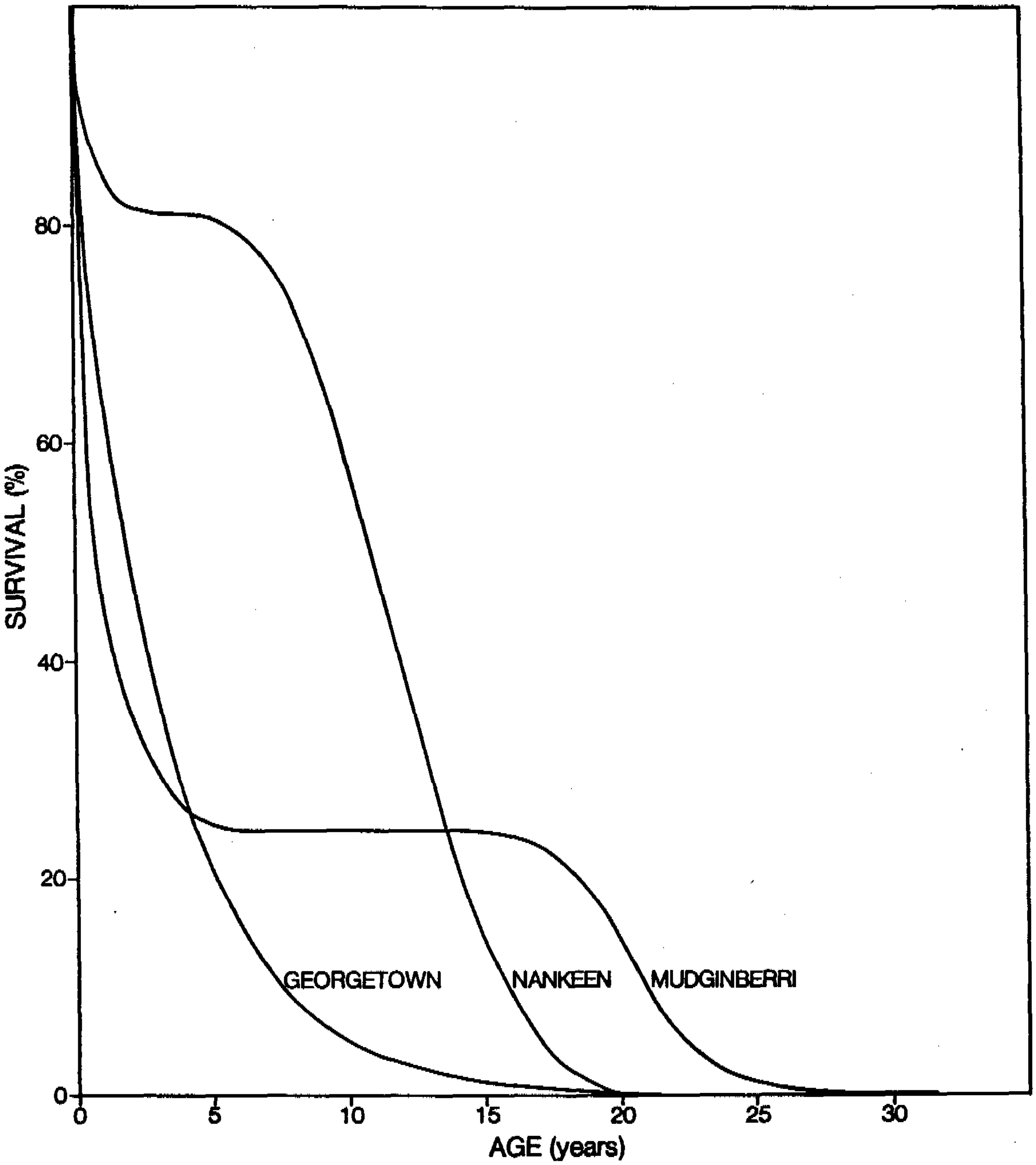


Figure 6.36 Survivorship curves predicted from survival estimates, for regular recruitment of mussels in Georgetown, Mudginberri and Nankeen billabongs.

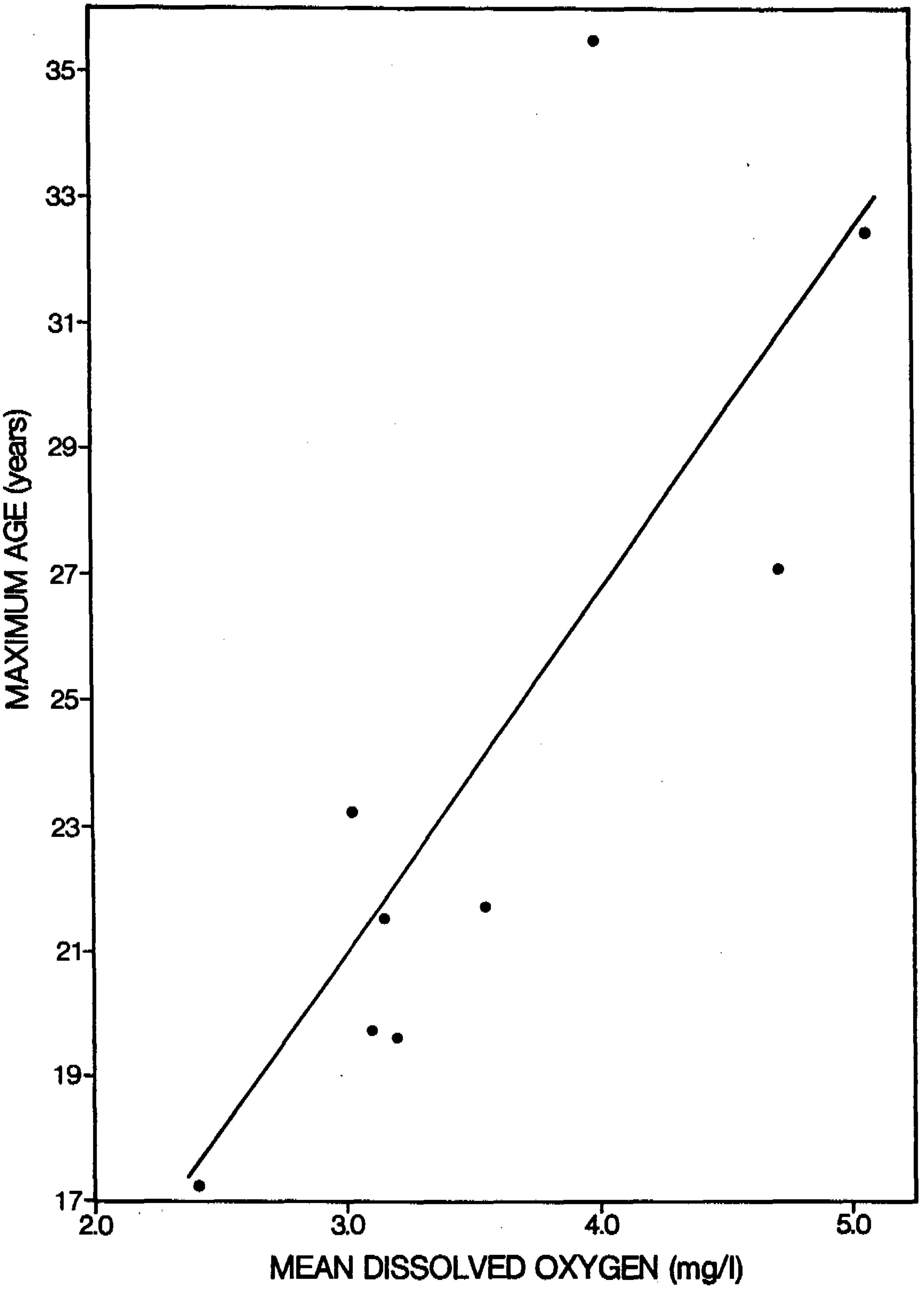


Figure 6.37 Linear relationship between maximum age of mussels recorded and mean dissolved oxygen concentration in permanent waterbodies of the Magela Creek.

Fitted regression equation is:

$$Y = 3.695 + 5.741X \quad (P < 0.05, r^2 = 0.636)$$

where Y = maximum age (years) and X = mean dissolved oxygen (mg/l).

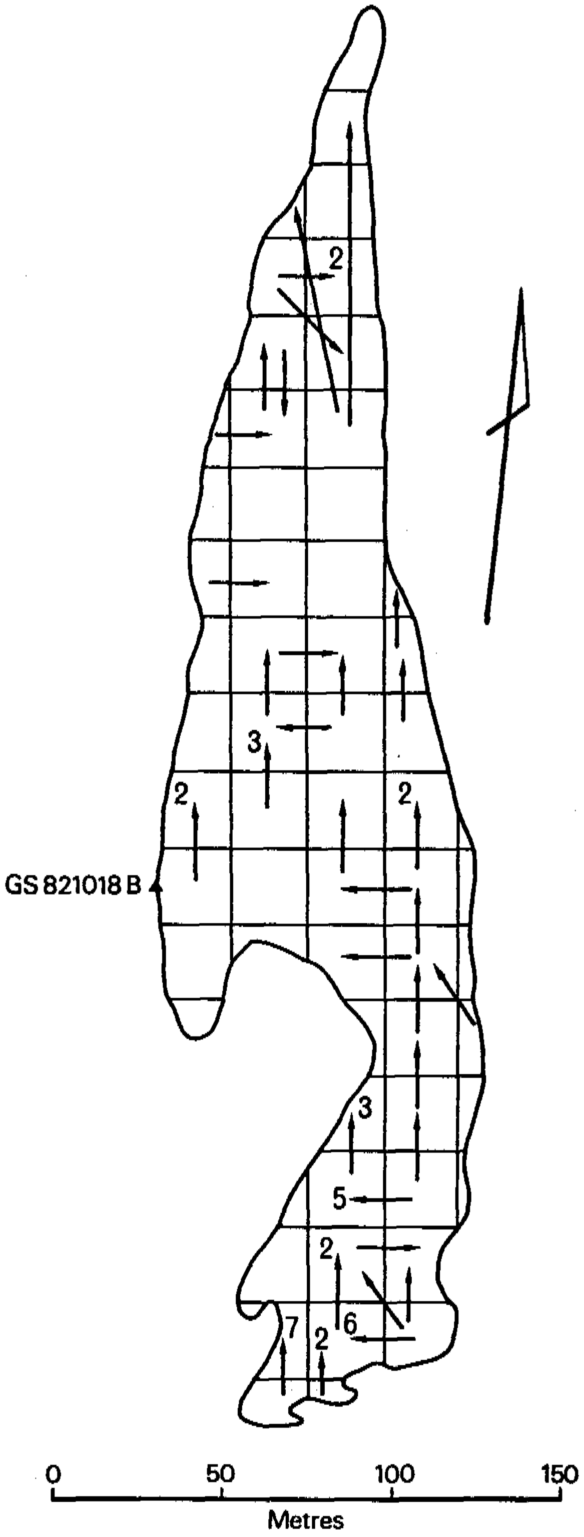


Figure 6.38 Map of Buffalo billabong showing movements of mussels over a one year period. Arrows indicate the direction of movement of mussels out of the quadrats. Unnumbered arrows are individual movements, and numbered arrows are the numbers of mussels that were recorded to have moved in the specific direction out of the quadrats.

Figure 7.1 Photomicrograph of seminiferous tubules and parasitised gonads of *V. angasi*.

A. Tubules of inactive testes (low power), showing predominance of stages characteristic of atypical spermatogenesis - spermatogonia, spermatozoa and especially sperm morulae. (Testes of aestivating Creek mussel, collected November 1980.) Scale bar 200 µm.

B. Tubules of active testes (low power), showing stages characteristic of typical spermatogenesis - spermatocytes, spermatids and much spermatozoa. (Testes of mussel collected from Georgetown billabong, March 1981.) Scale bar 200 µm.

C. Tubule of inactive testes (high power), showing predominance of stages characteristic of atypical spermatogenesis. (Same testes as A.) Scale bar 50 µm.

D. Tubule of active testes (high power), showing stages characteristic of typical spermatogenesis. (Same testes as B.) Scale bar 50 µm.

E. Section of gonads (low power), almost completely sterilised by heavy infection of cercarial trematodes. Cercarial sporocysts are shown. (Ovaries of mussel collected from Mudginberri billabong, February 1981.) Scale bar 200 µm.

Abbreviations

csp, cercarial sporocyst
psp, primary spermatocyte
sg, spermatogonia
sm, sperm morulae
ssp, secondary spermatocyte
st, spermatid
sz, spermatozoa.

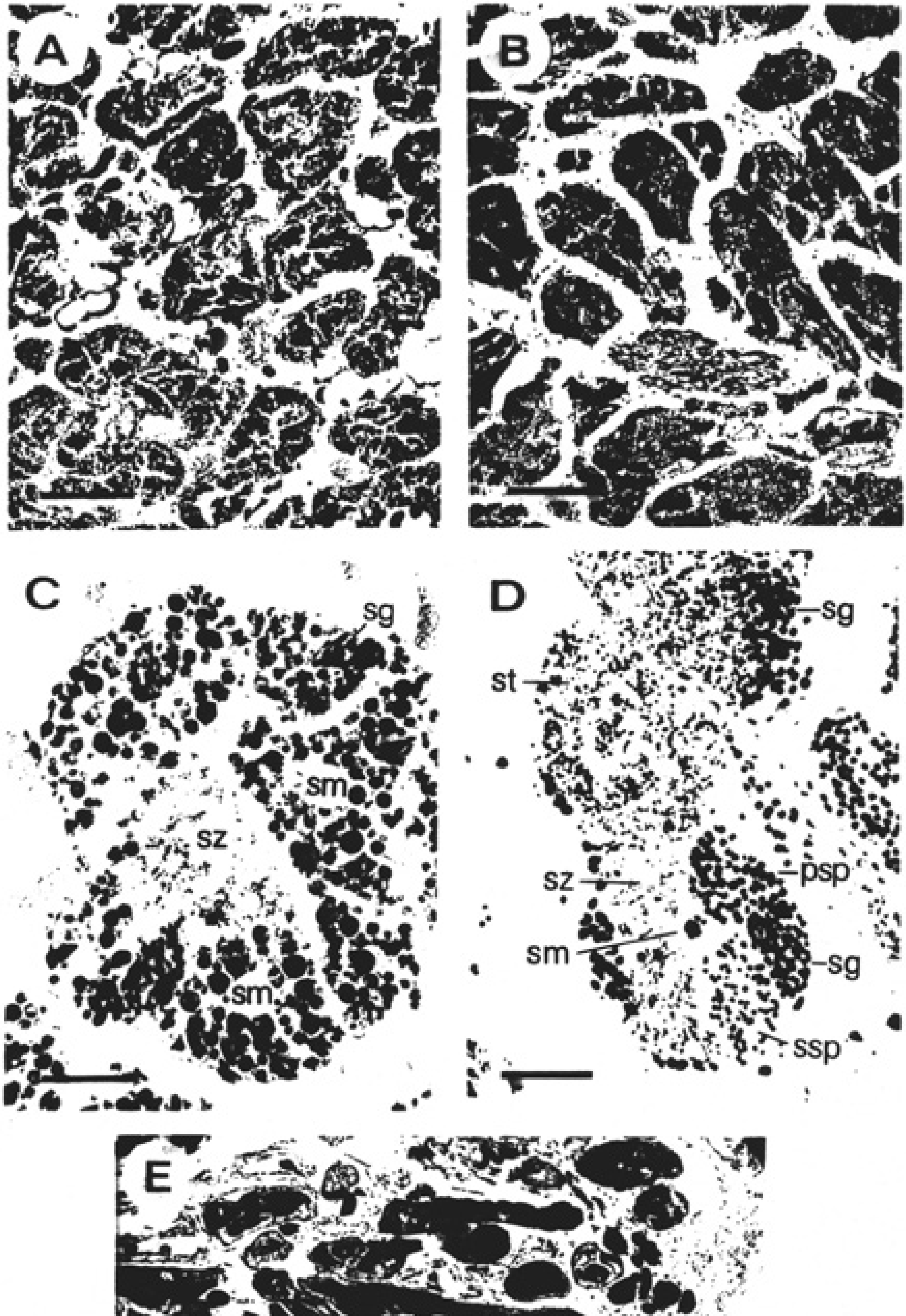

A
B
C
sg
sm
sz
sm
D
sg
st
sz
sm
psp
sg
ssp
E
ssp

Figure 7.2 Photomicrograph of ovarian follicles and hermaphroditic gonads of V. angasi.

A. Follicles of inactive ovaries (low power), showing their empty appearance with relatively few primary oocytes. (Ovaries of mussel collected from Georgetown billabong, September 1980.) Scale bar 500 µm.

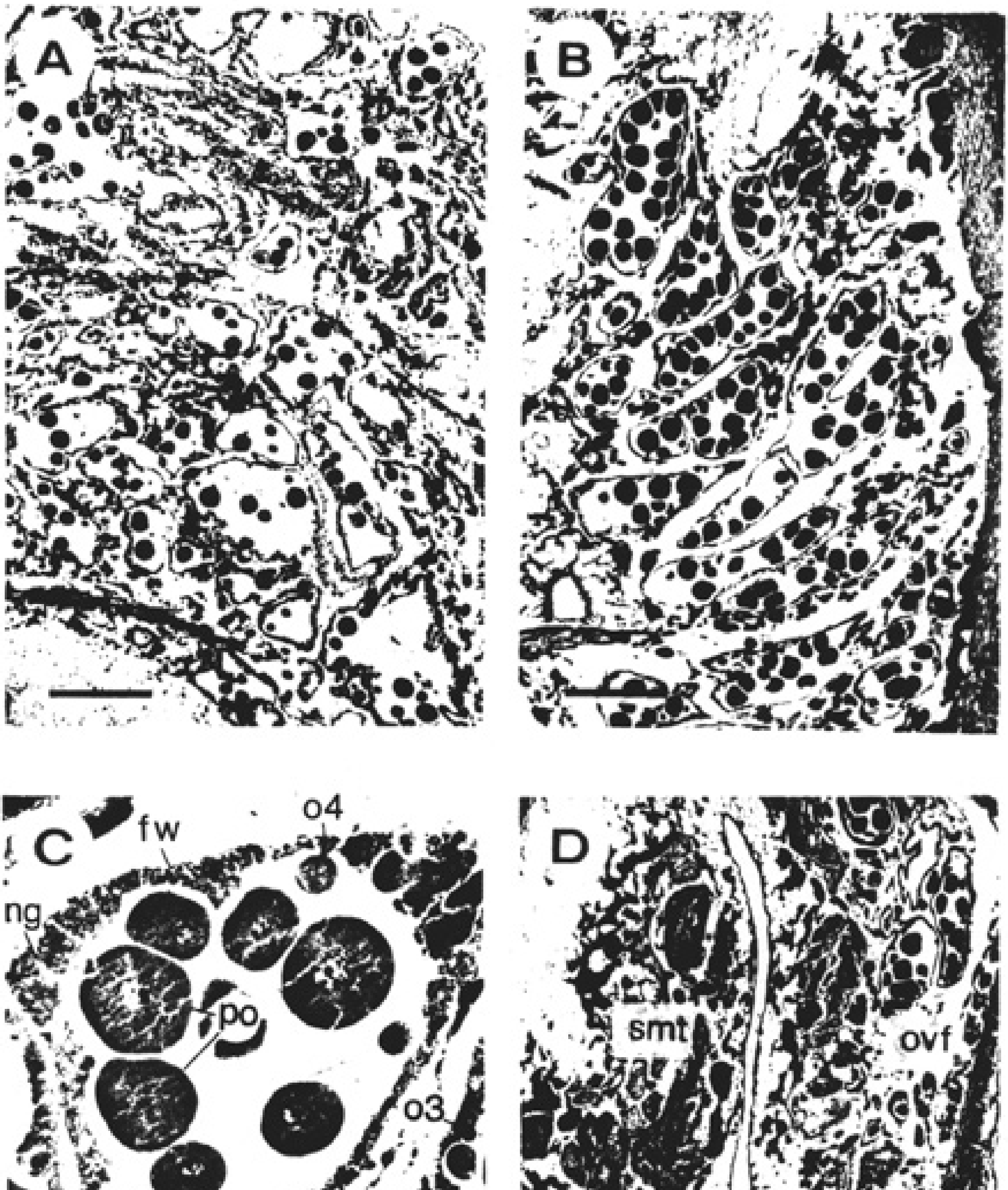
B. Follicles of active ovaries (low power), showing presence of large numbers of primary oocytes. (Ovaries of mussel collected from Mudginberri billabong, November 1980.) Scale bar 500 µm.

C. Follicles of active ovaries (high power), showing vitellogenic stages of oocyte maturation. (Ovaries of aestivating Creek mussel, collected December 1980.) Scale bar 50 µm.

D. Section of male hermaphrodite (low power), showing predominance of testicular tissue, and discrete ovarian follicles and testicular tubules confined to distinct regions of the gonad. (Gonads of mussel collected from Mudginberri billabong, December 1980.) Scale bar 500 µm.

Abbreviations

fw,	follicle wall
ng,	nutritive granules
o3,	oocyte 3
o4,	oocyte 4
ovf,	ovarian follicle
po,	primary oocyte
smt,	seminiferous tubule.


A
B
C
fw
o4
ng
po
o3
o3
o4
po
D
smt
ovf
smt

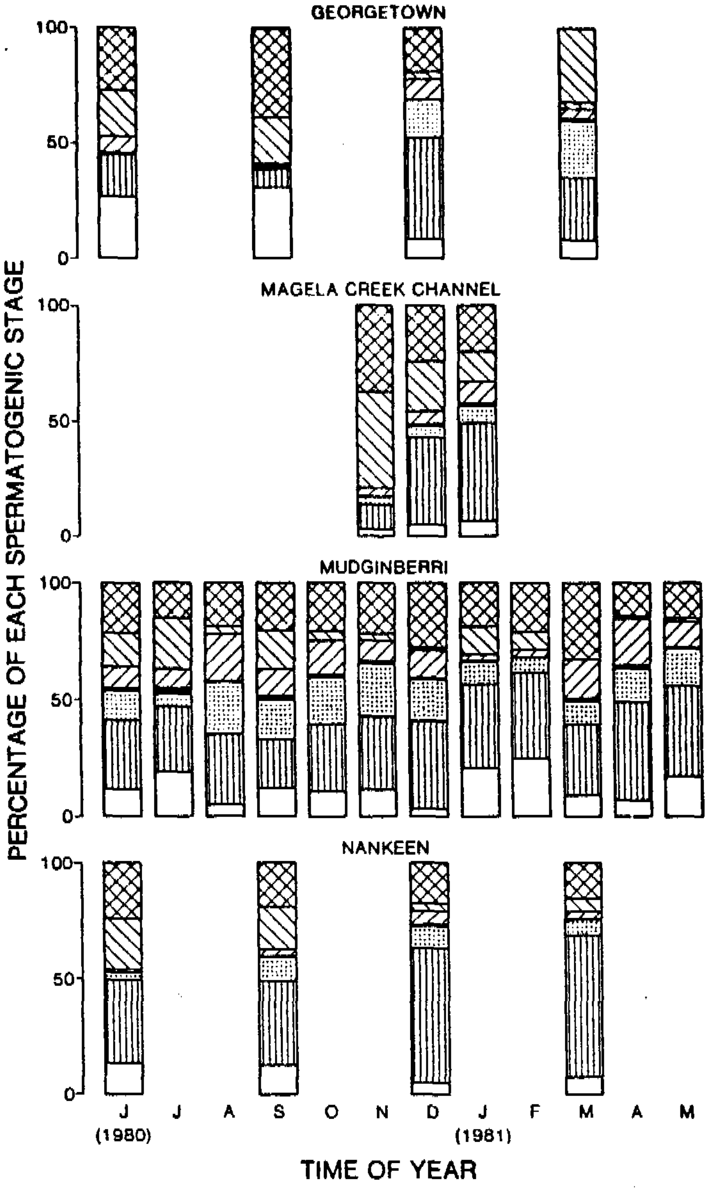


Figure 7.3 Relative proportions of spermatogenic stages found seasonally in the testes of mussels from selected Magela Creek waterbodies.

Key to spermatogenic stages:

- ▦ spermatogonia
- ▧ sperm morulae
- ▨ primary spermatocytes
- ■ secondary spermatocytes
- ░ spermatids
- ▥ spermatozoa
- □ empty

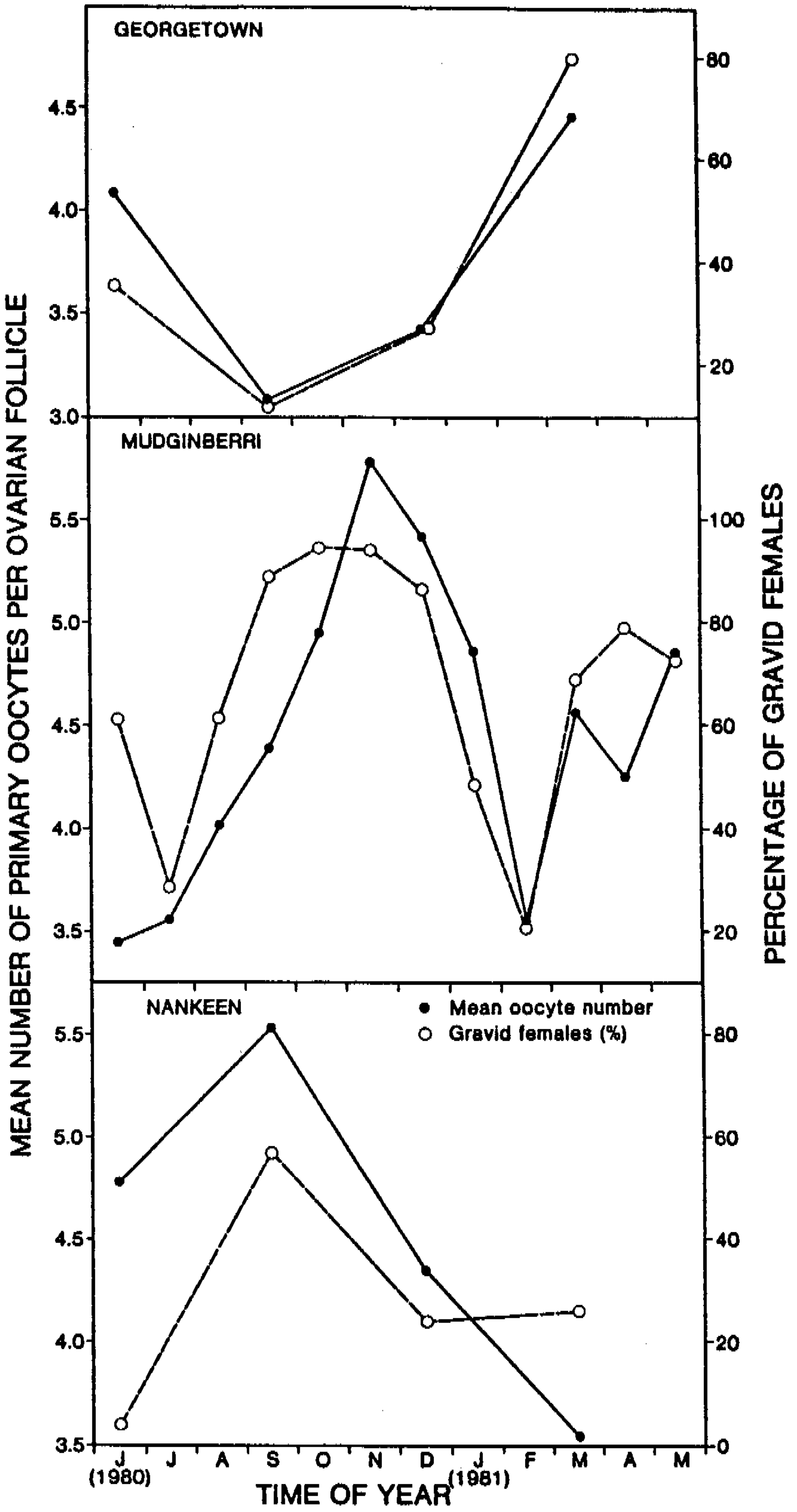


Figure 7.4 (a) Mean numbers of primary oocytes per ovarian follicle in the ovaries of sectioned female mussels, and (b) the percent of gravid females among all females examined, found seasonally in selected billabongs of the Magela Creek.

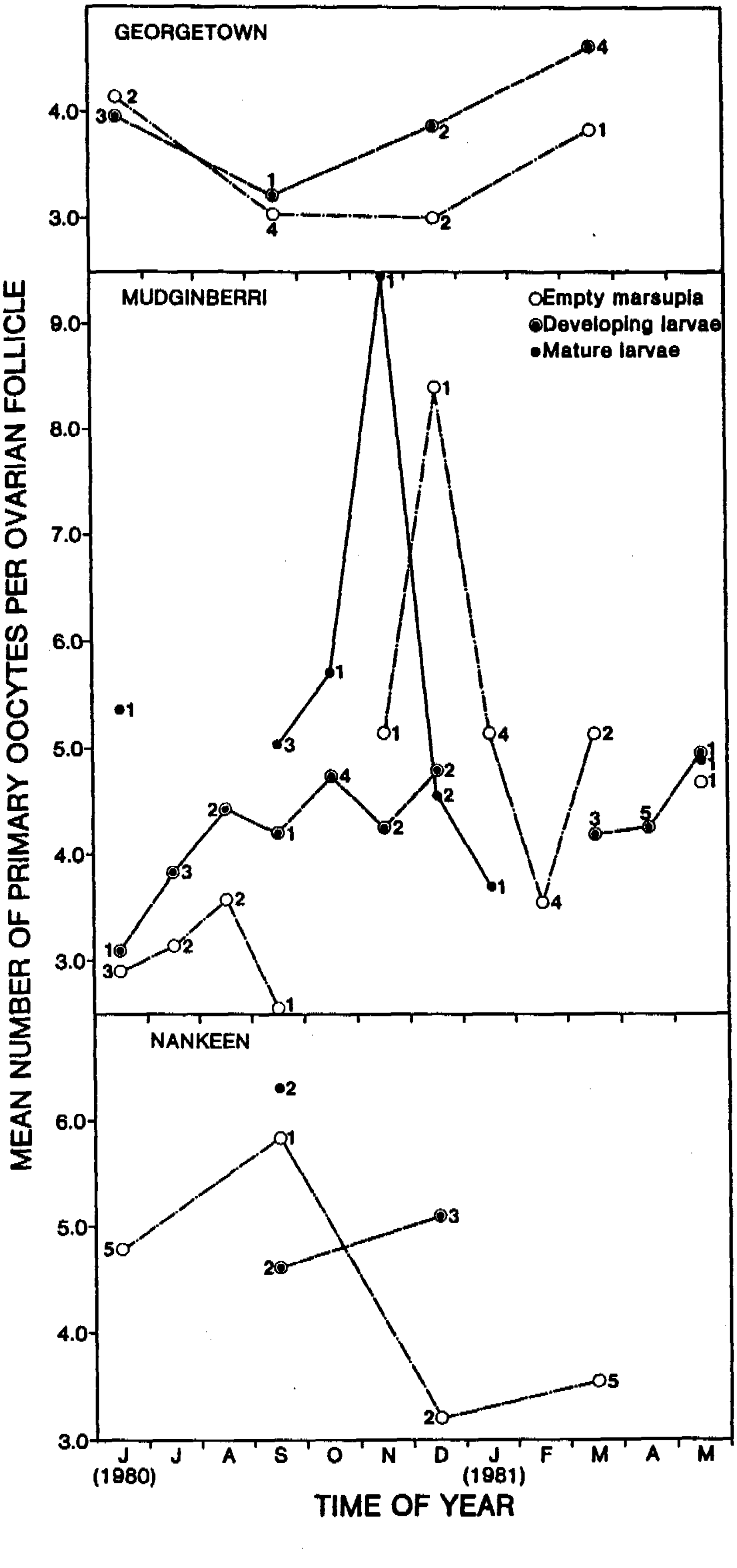


Figure 7.5 Mean numbers of primary oocytes per ovarian follicle in the ovaries of sectioned female mussels (a) with empty marsupia, (b) bearing developing larvae in the marsupia, and (c) bearing mature larvae in the marsupia, found seasonally in selected billabongs of the Magela Creek. Numbers about the symbols are the numbers of individual mussels sectioned.

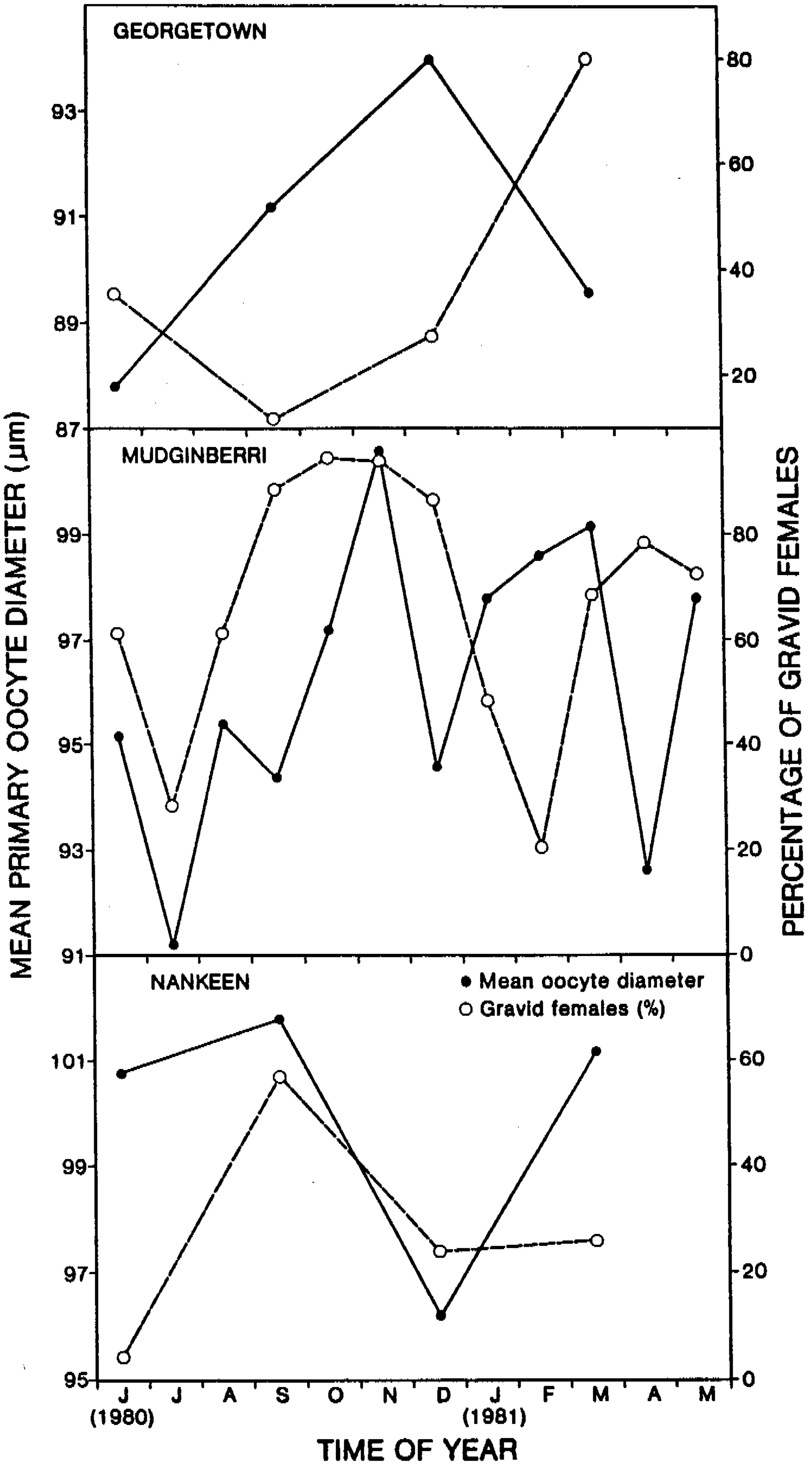


Figure 7.6 (a) Mean diameter of primary oocytes in the ovaries of sectioned female mussels, and (b) the percent of gravid females among all females examined, found seasonally in selected billabongs of the Magela Creek.

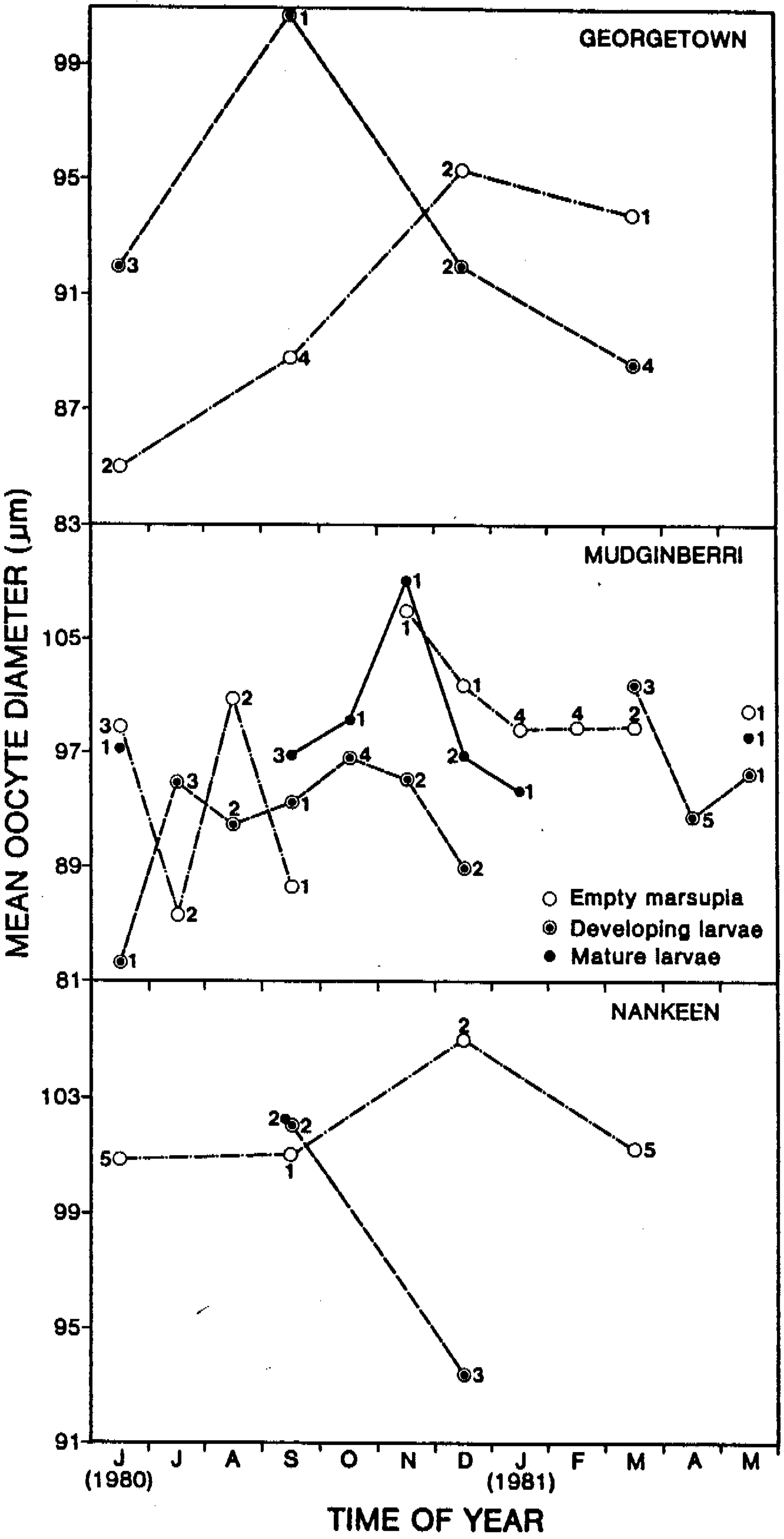


Figure 7.7 Mean diameter of primary oocytes in the ovaries of sectioned female mussels (a) with empty marsupia, (b) bearing developing larvae in the marsupia, and (c) bearing mature larvae in the marsupia, found seasonally in selected billabongs of the Magela Creek. Numbers about the symbols are the numbers of individual mussels sectioned.

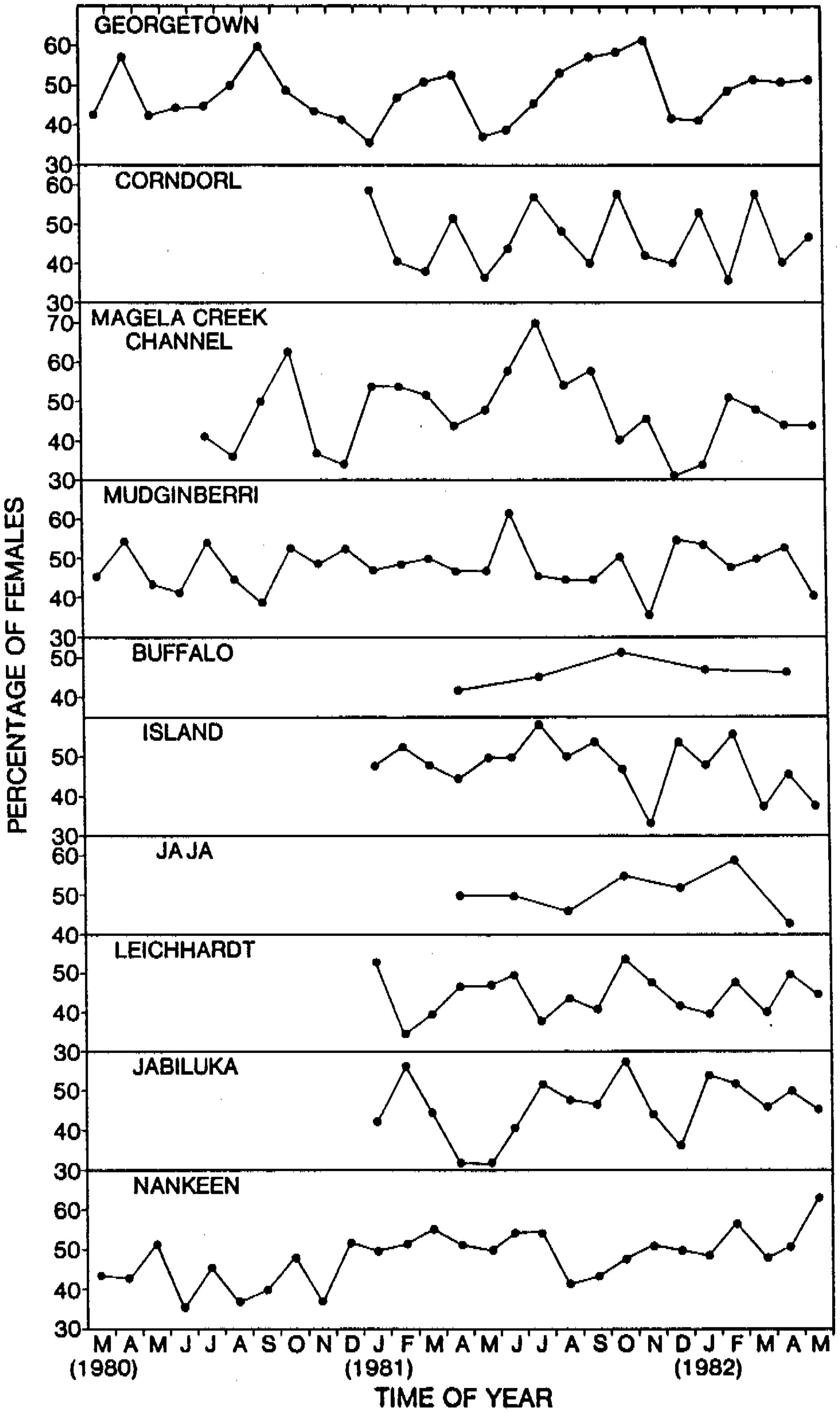
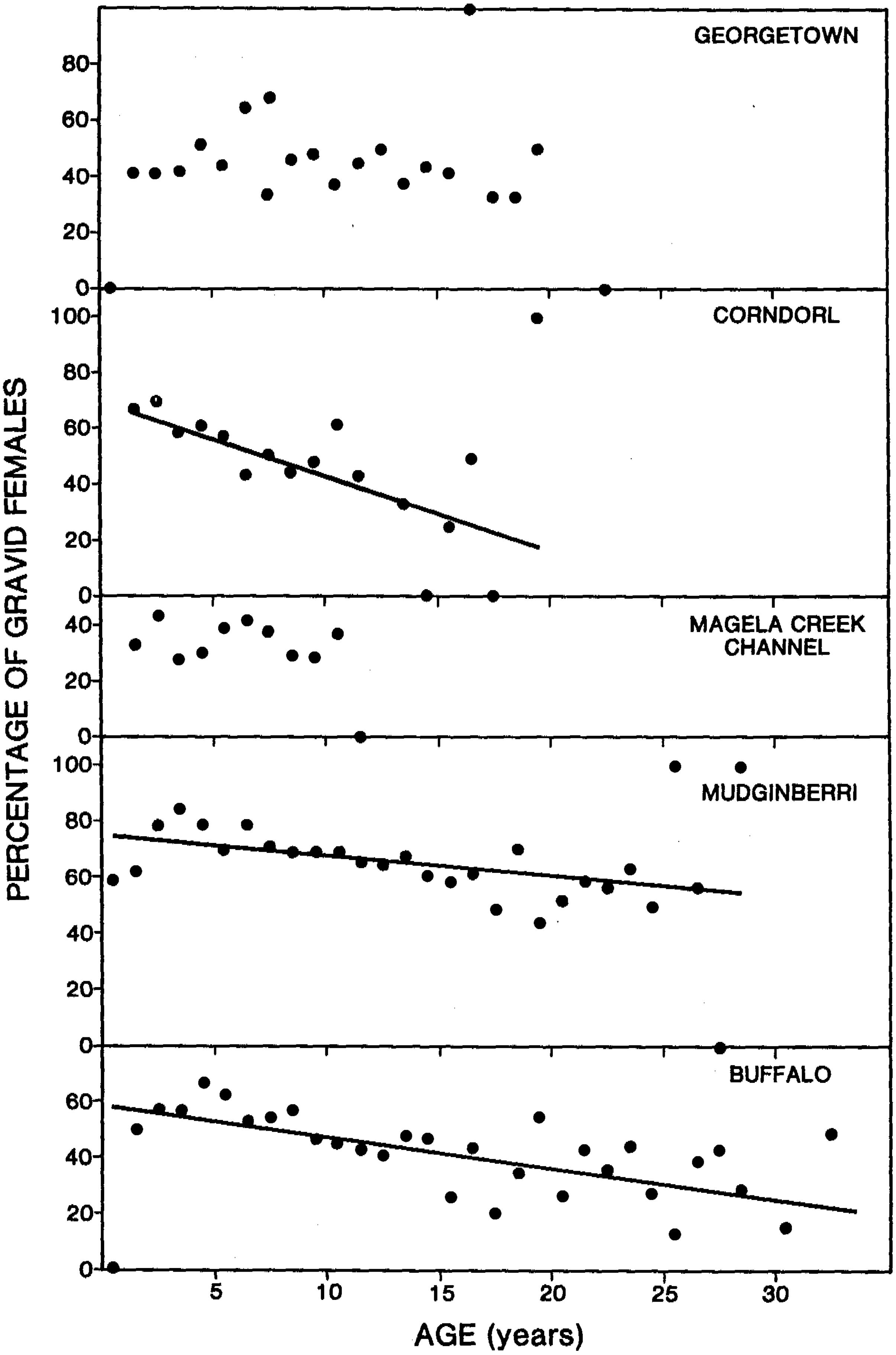


Figure 7.8 Proportion of female mussels as a percent of the total number of mussels examined monthly (all sexes) in the Magela Creek waterbodies. 50 mussels were examined each month in all waterbodies except Georgetown, Mudginberri and Nankeen billabongs (70 mussels).

Figures 7.9 and 7.10 Relationships between proportion of gravid females as a percent of the total number of females examined and age of mussels, in waterbodies of the Magela Creek. Fitted lines represent the age classes over which significant linear or quadratic correlations were found between percent of gravid females and age. The regression equations are described in Table 7.13.

Relationships for Georgetown downstream to Buffalo billabong are shown in Figure 7.9 while relationships for Island downstream to Nankeen billabong are shown in Figure 7.10.


GEORGETOWN
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
BUFFALO
PERCENTAGE OF GRAVID FEMALES
AGE (years)
0
20
40
60
80
100
5
10
15
20
25
30

7.10

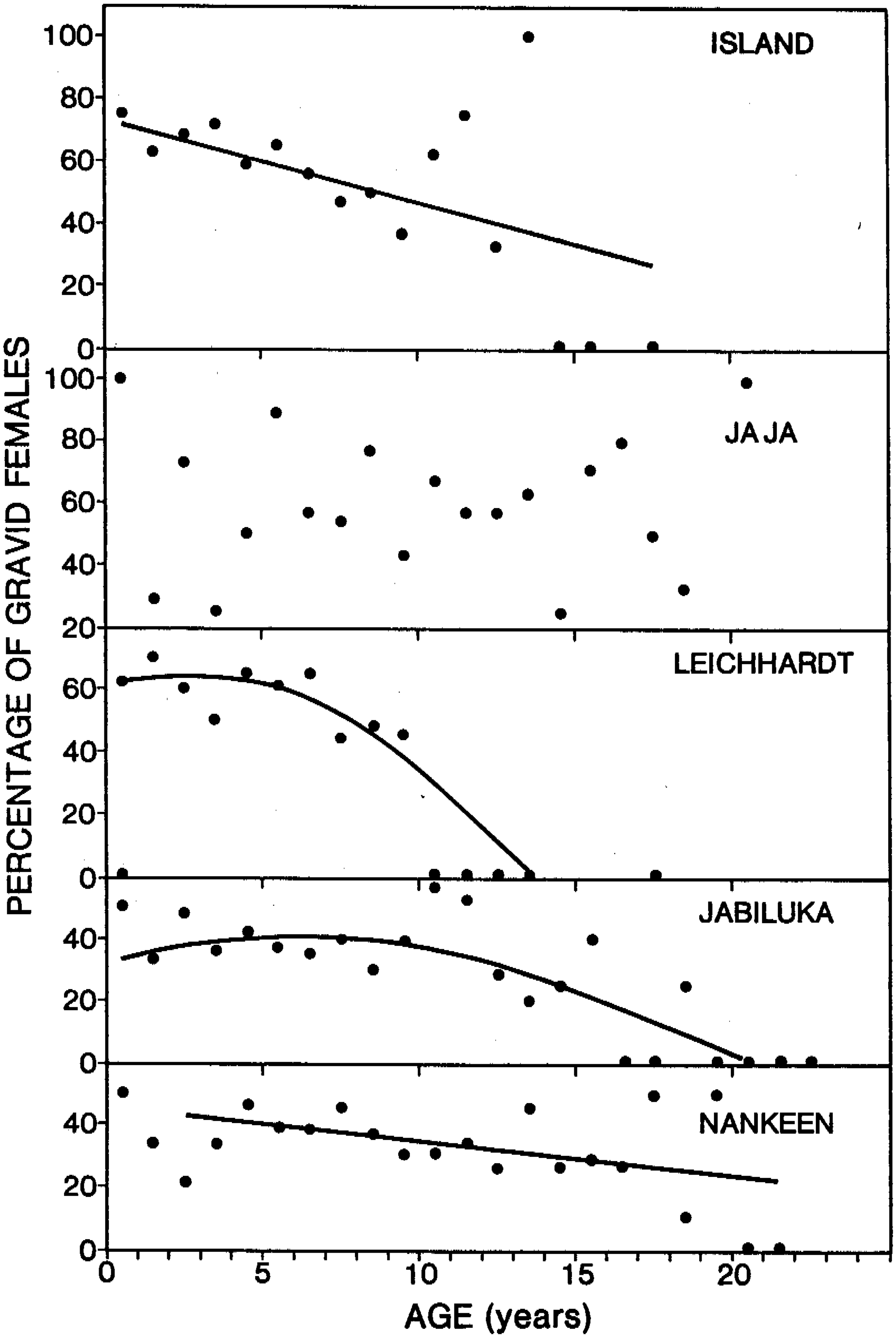

ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
PERCENTAGE OF GRAVID FEMALES
AGE (years)
0
5
10
15
20
100
80
60
40
20
0

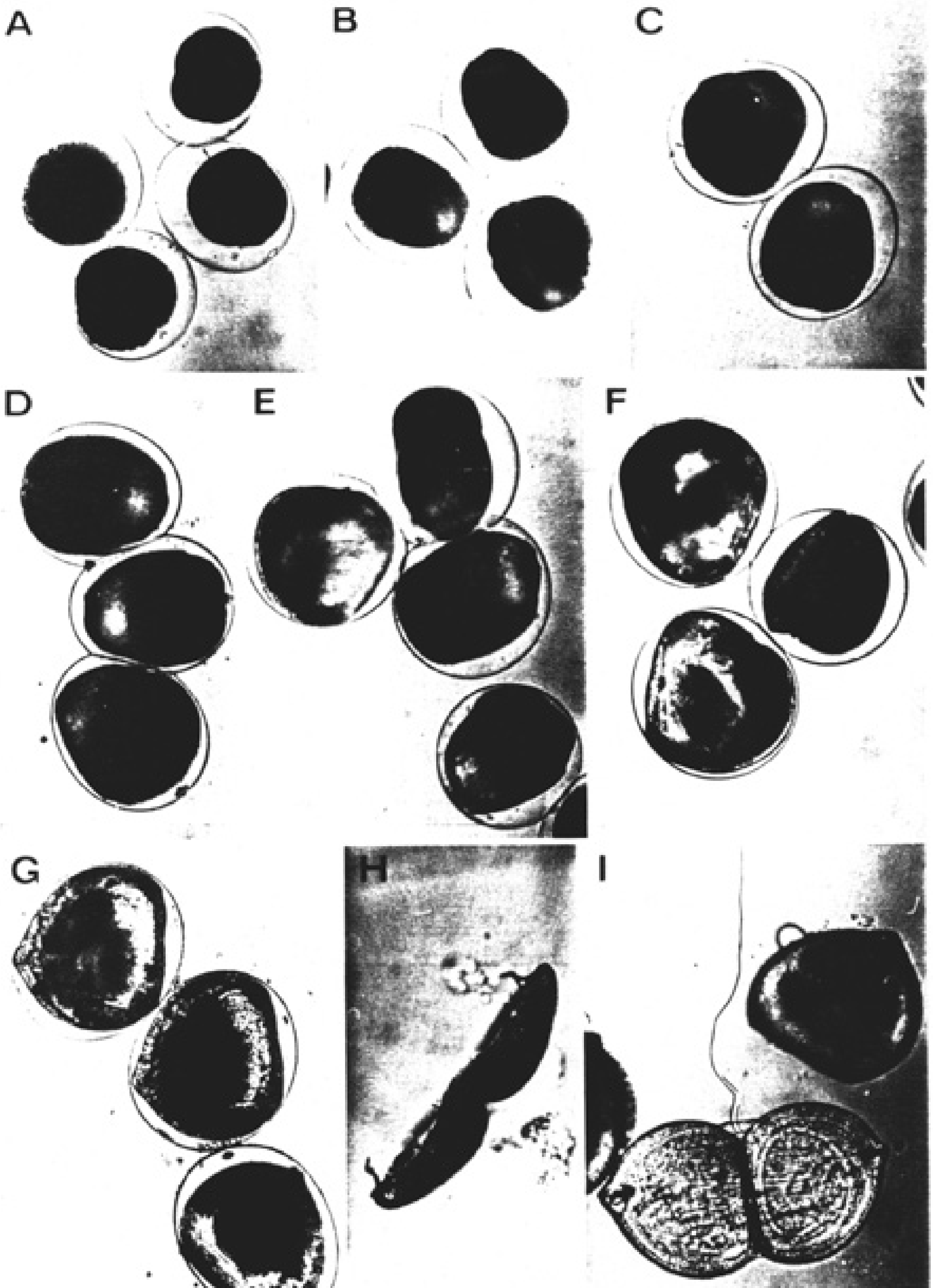
Figure 7.11 Photomicrograph of stages of larval development of *V. angasi*.

A-C. 'Early larvae' - early spheroid (A) to more advanced elliptical (B and C) mass of cells enclosed within vitelline membrane.

D-F. 'Developing larvae' - adductor muscle present as cross band of striated tissue within centres of larvae; slight invagination of larval mantle evident in more advanced stages (the right-most larva in F).

G-I. 'Glochidia' - invagination of larval mantle and formation of larval shell. Early glochidia untoothed, with shell margins not partitioned fully, and enclosed in vitelline membrane (G); mature glochidia free of vitelline membrane, toothed (H), and with larval thread (I).

Scale bar 200 µm.


A
B
C
D
E
F
G
H
I

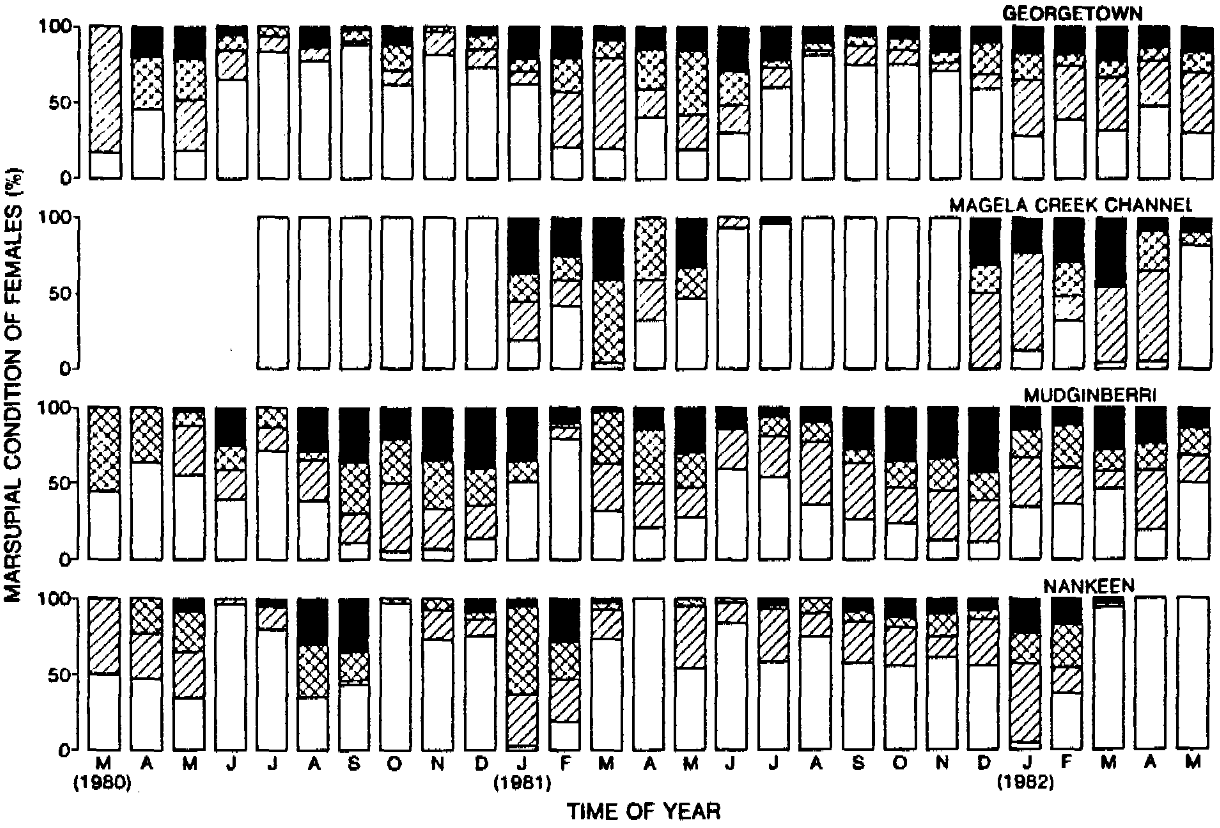


Figure 7.12 Relative proportions of the various marsupial appearances found monthly among female mussels from selected Magela Creek waterbodies, over a 27 month period.

Key to marsupial condition:

□ empty marsupia

▨ with early larvae

▩ with developing larvae

■ with glochidia

Figures 7.13 and 7.14 Relative proportions of the various marsupial appearances found monthly among female mussels from waterbodies of the Magela Creek.

Monthly marsupial appearances for females from Georgetown downstream to Buffalo billabong are shown in Figure 7.13, while appearances for females from the floodplain billabongs, Island downstream to Nankeen billabong, are shown in Figure 7.14.

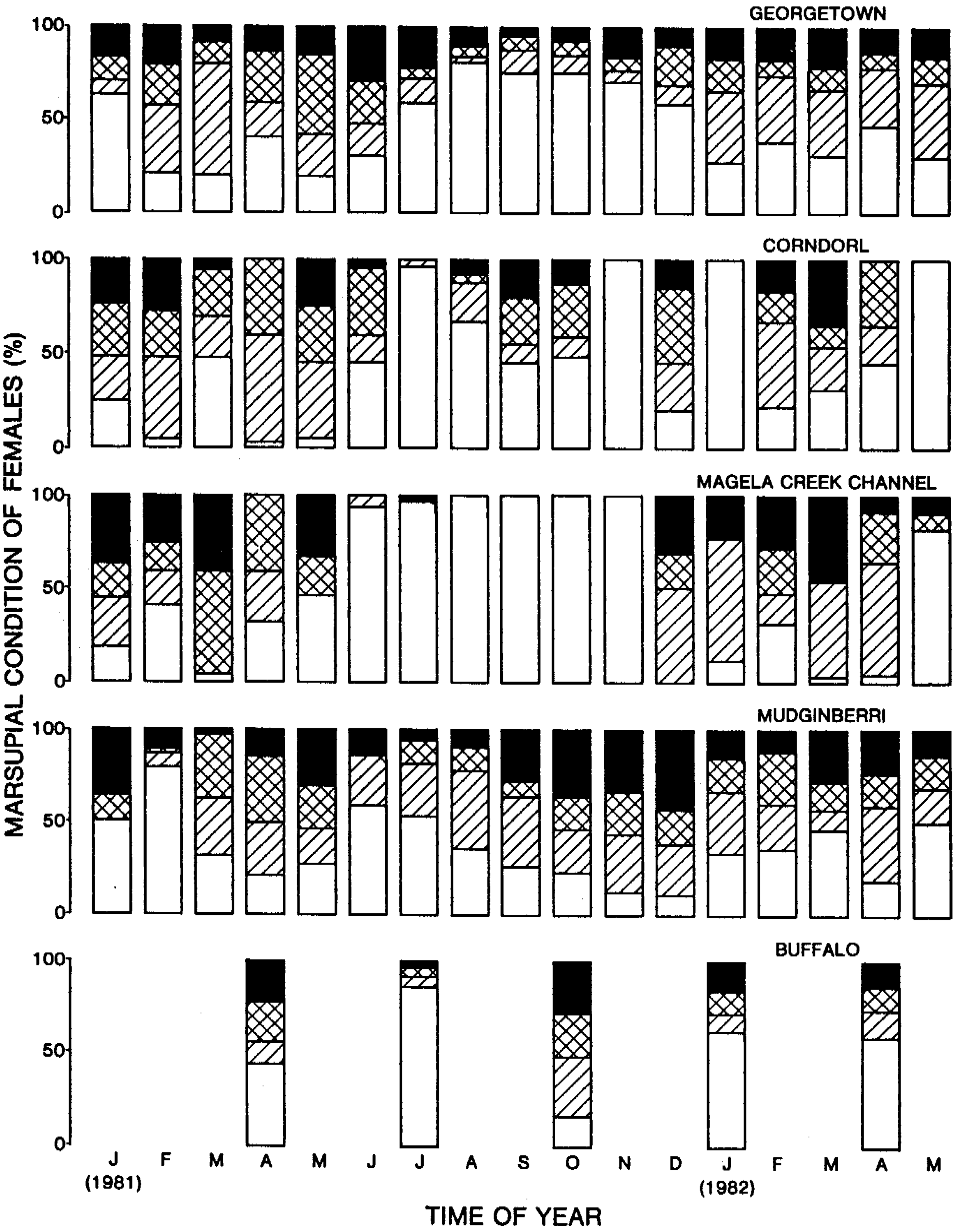
Key to marsupial condition:

□ empty marsupia

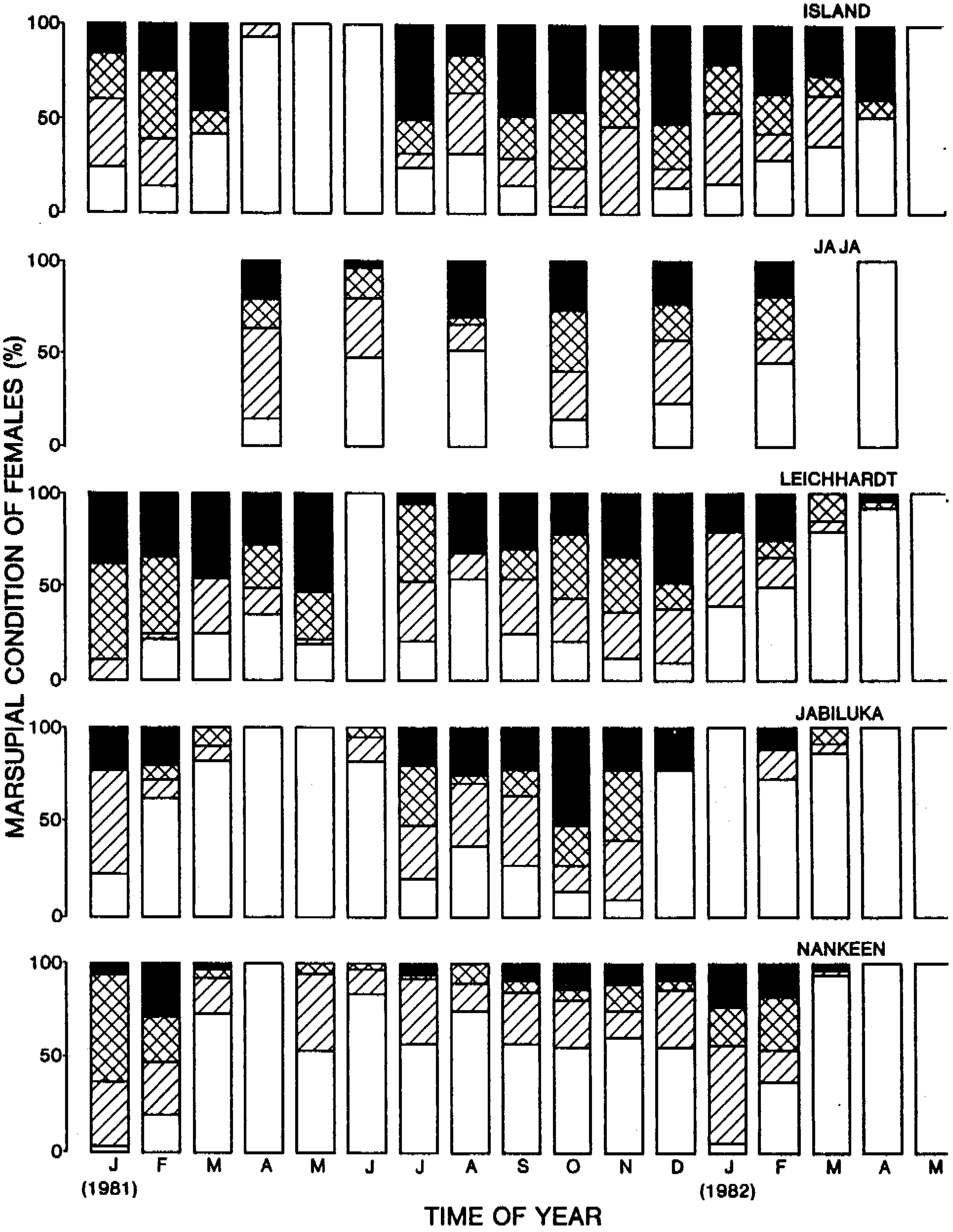
▨ with early larvae

▦ with developing larvae

■ with glochidia


GEORGETOWN
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
BUFFALO
100
50
0
MARSUPIAL CONDITION OF FEMALES (%)
J
(1981)
F
M
A
M
J
J
A
S
O
N
D
J
(1982)
F
M
A
M
TIME OF YEAR

7.14


ISLAND
JA JA
LEICHHARDT
JABILUKA
NANKEEN
MARSUPIAL CONDITION OF FEMALES (%)
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
(1981)
(1982)
TIME OF YEAR

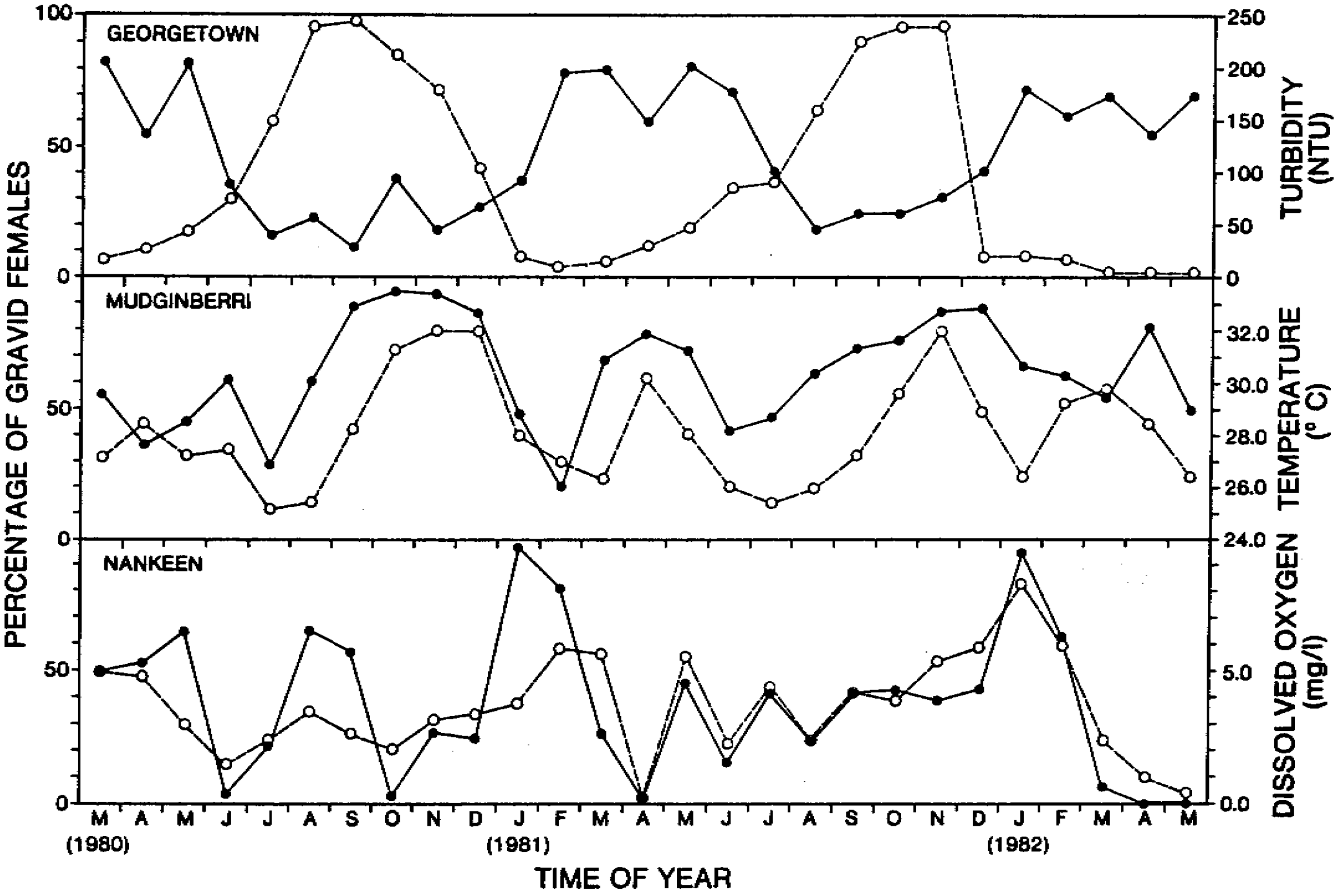


Figure 7.15 Monthly plots of the percent of gravid female mussels found among all females examined (solid circles), in relation to various environmental variables (open circles) recorded over a 27 month period in selected Magela Creek billabongs.

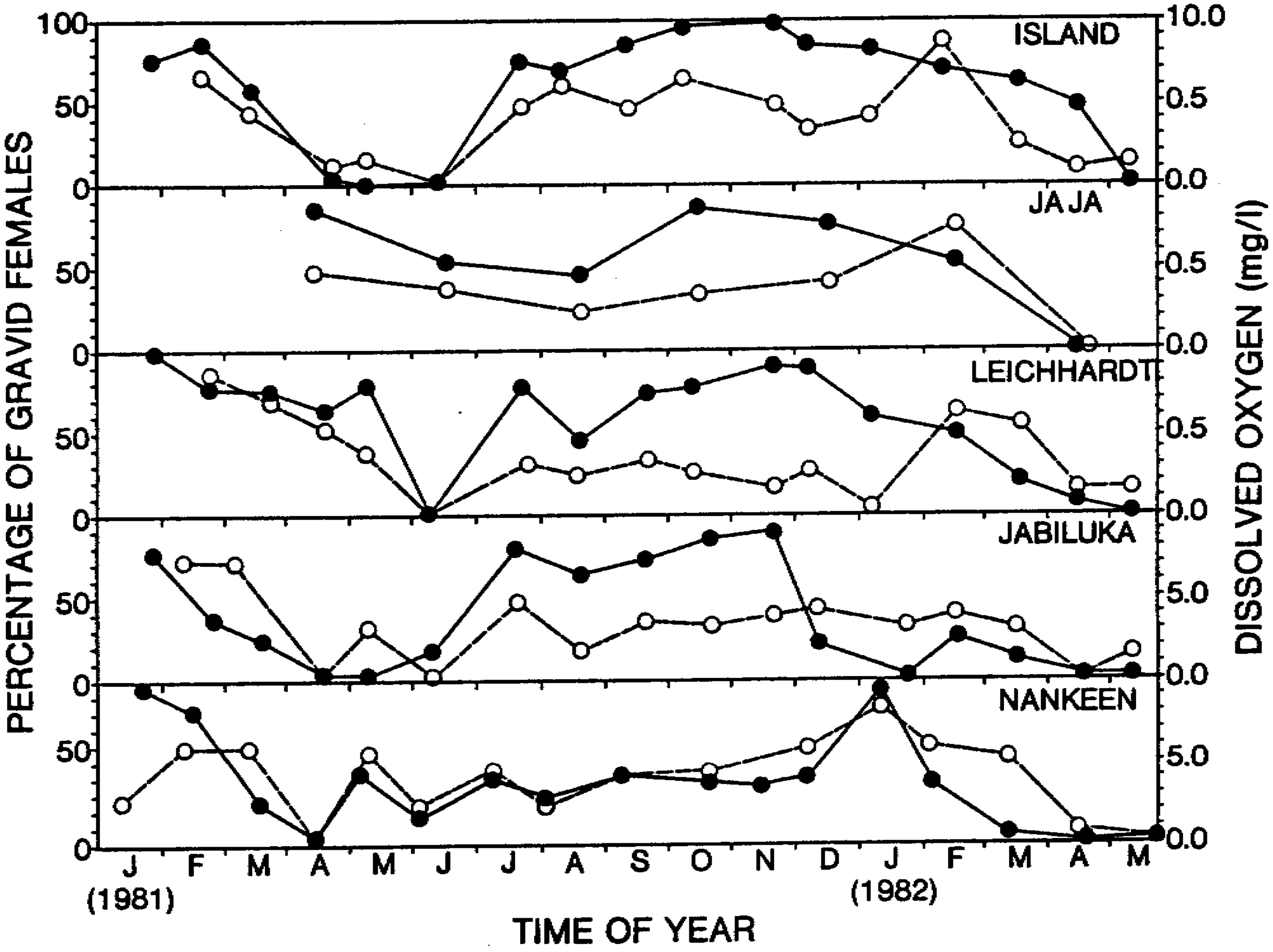


Figure 7.16 Monthly (or bimonthly) plots of the percent of gravid female mussels found among all females examined (solid circles), in relation to dissolved oxygen concentration of the bottom waters (open circles) in floodplain billabongs of the Magela Creek.

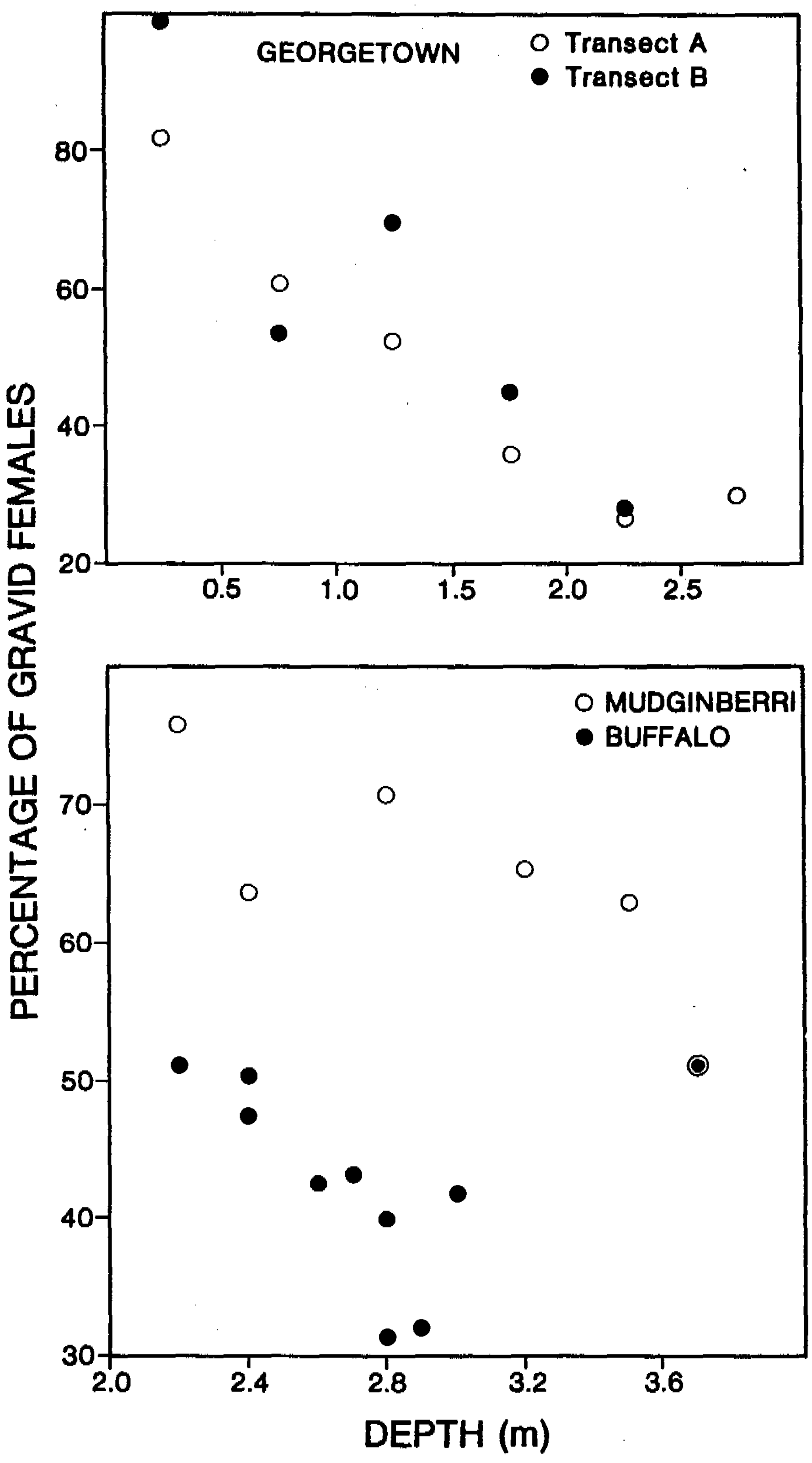


Figure 7.17 Plots of the percent of gravid female mussels found among all females examined over the study period, in relation to depth and/or sampling location in Georgetown billabong and the channel billabongs, Mudginberri and Buffalo. (The significance of the encircled point in Buffalo billabong is explained in section 6.5.3.1.)

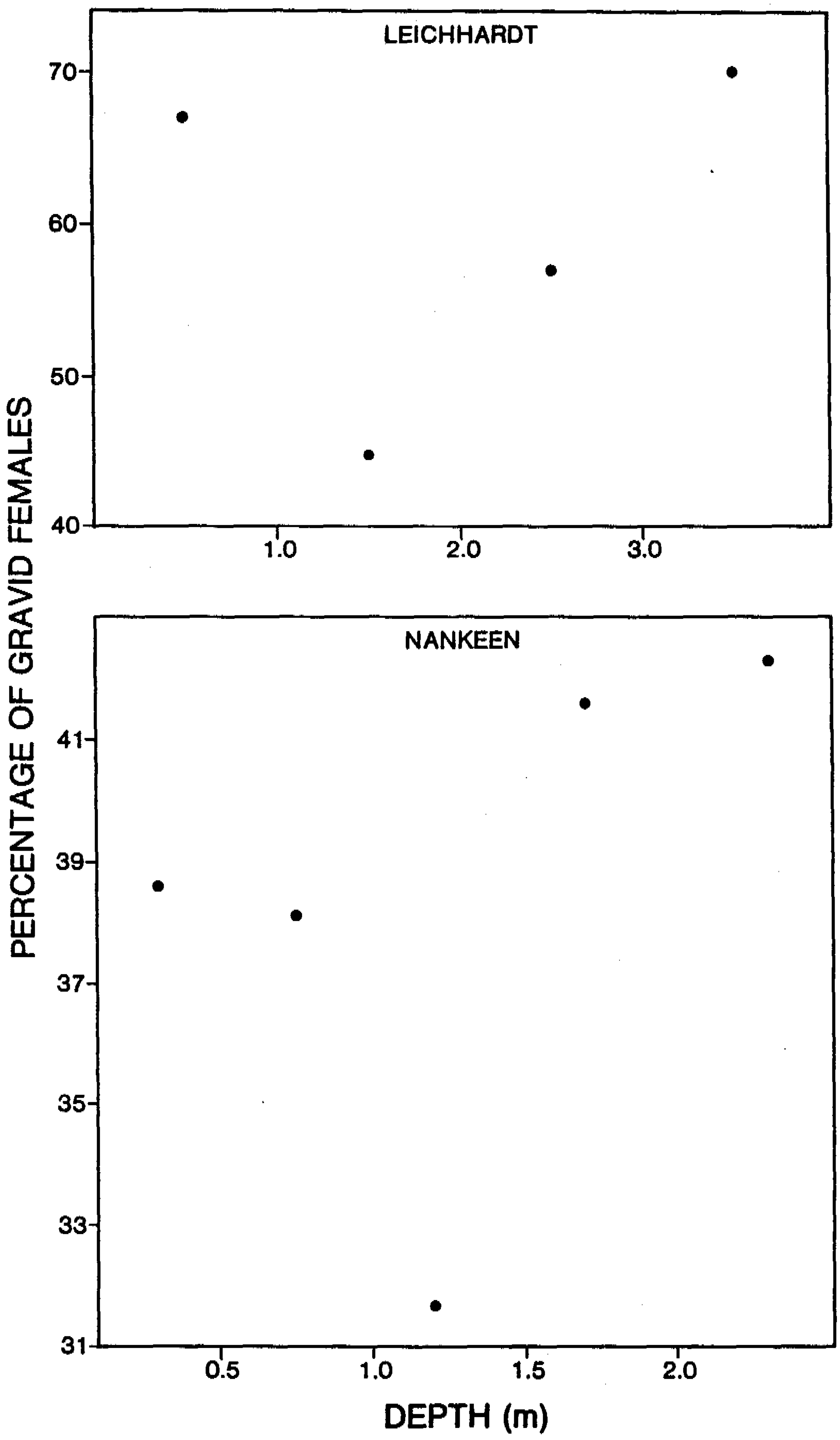


Figure 7.18 Plots of the percent of gravid female mussels found among all females examined over the study period, in relation to depth in the floodplain billabongs, Leichhardt and Nankeen.

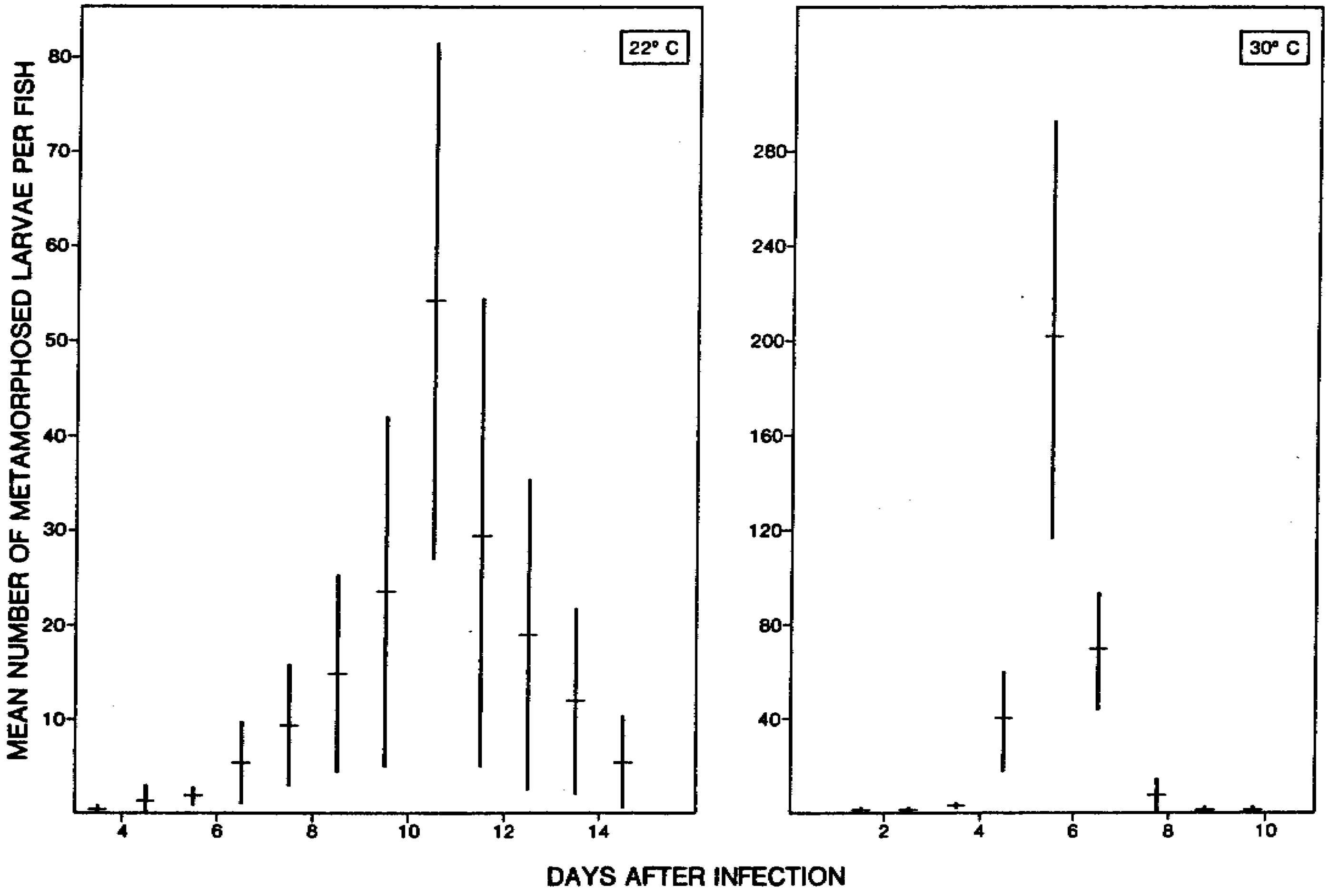


Figure 7.19 Mean numbers of newly metamorphosed juveniles of *V. angasi* per each laboratory infected *Glossogobius giurus*, found at daily intervals subsequent to initial infection at different temperatures. 95 percent confidence intervals about the means are indicated by vertical lines.

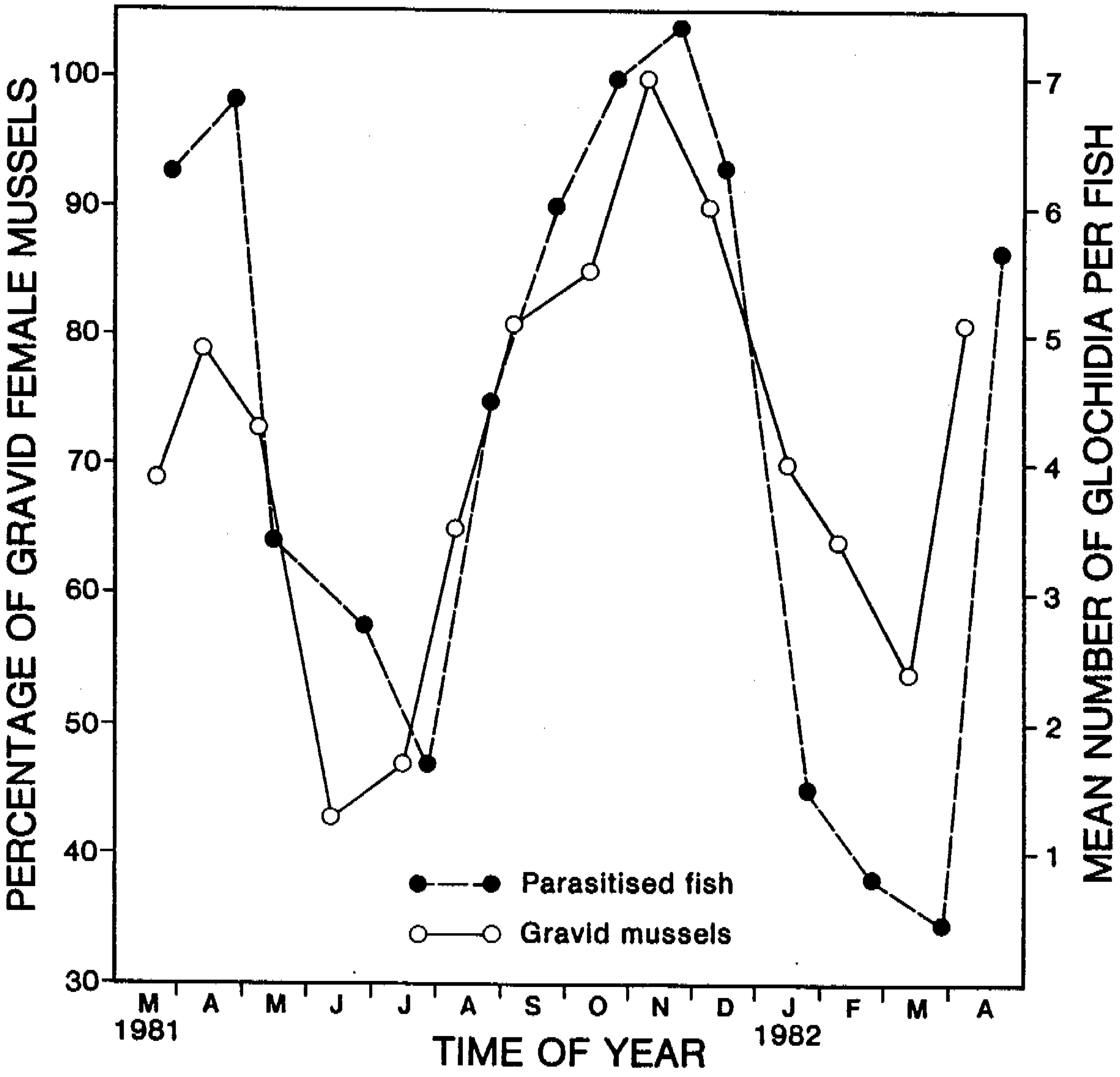


Figure 7.20 Monthly plots of the mean number of glochidia observed upon the fins of individual Glossogobius giurus from Mudginberri billabong, in relation to the percent of gravid female mussels found simultaneously among the females examined.

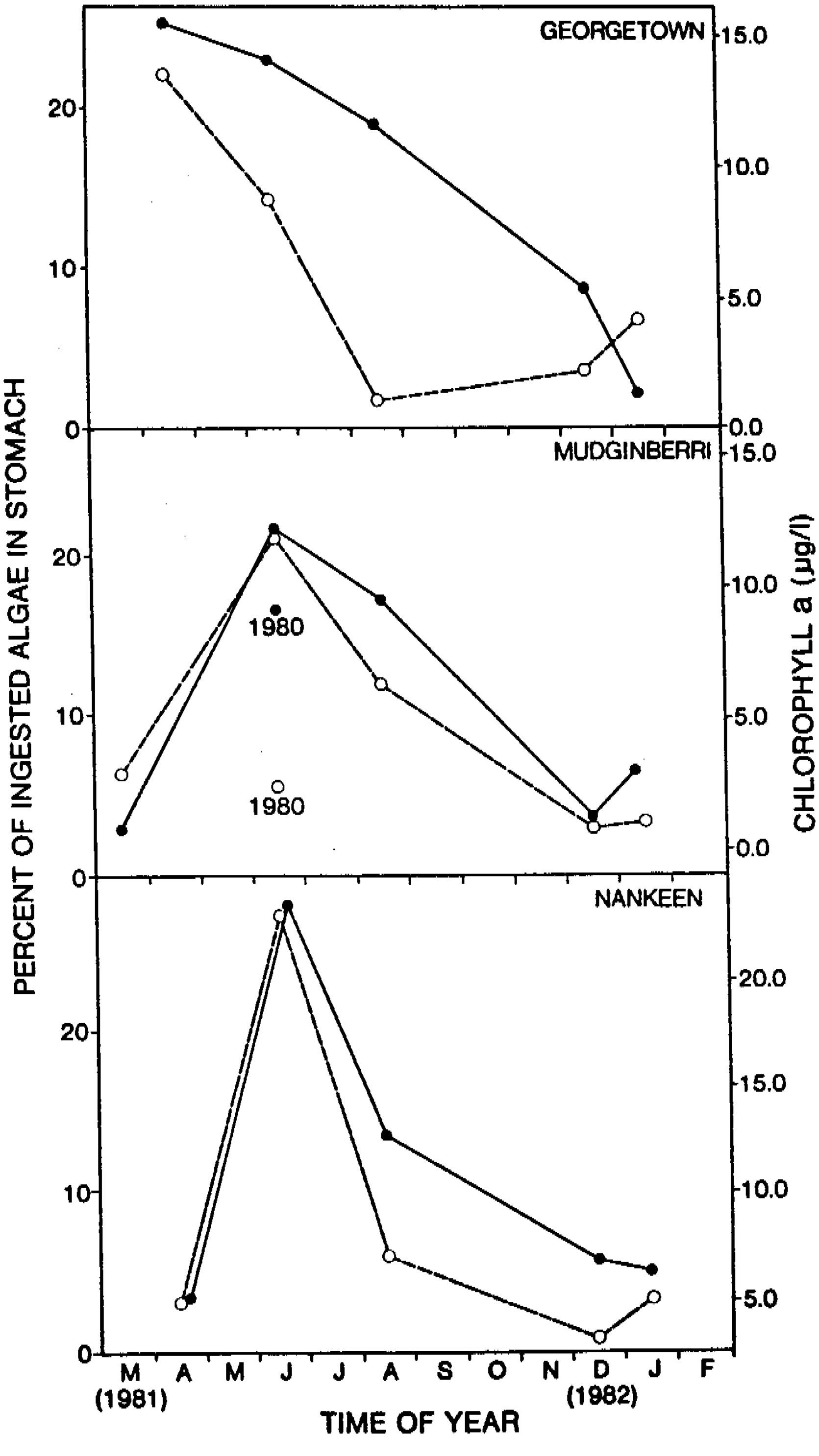


Figure 8.1 (a) Mean percentage of algae found seasonally among the stomach contents of mussels (open circles) and (b) algal abundance (as chlorophyll a concentration) measured simultaneously in the waters (solid circles), from selected billabongs of the Magela Creek.

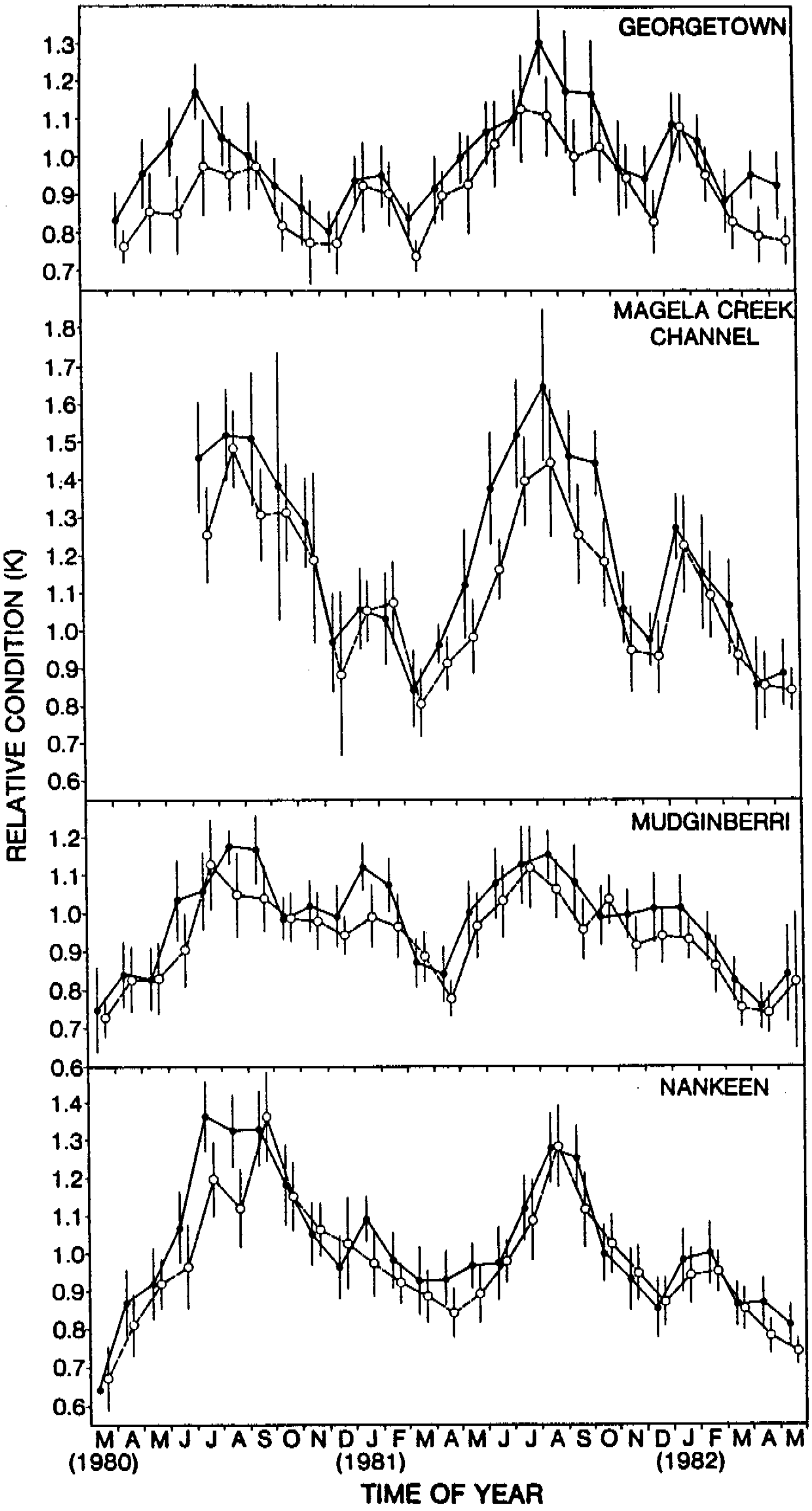


Figure 8.2 Mean relative condition (K) of male (solid circles) and female (open circles) mussels, measured monthly in selected waterbodies of the Magela Creek. 95 percent confidence intervals about the means are indicated by vertical lines.

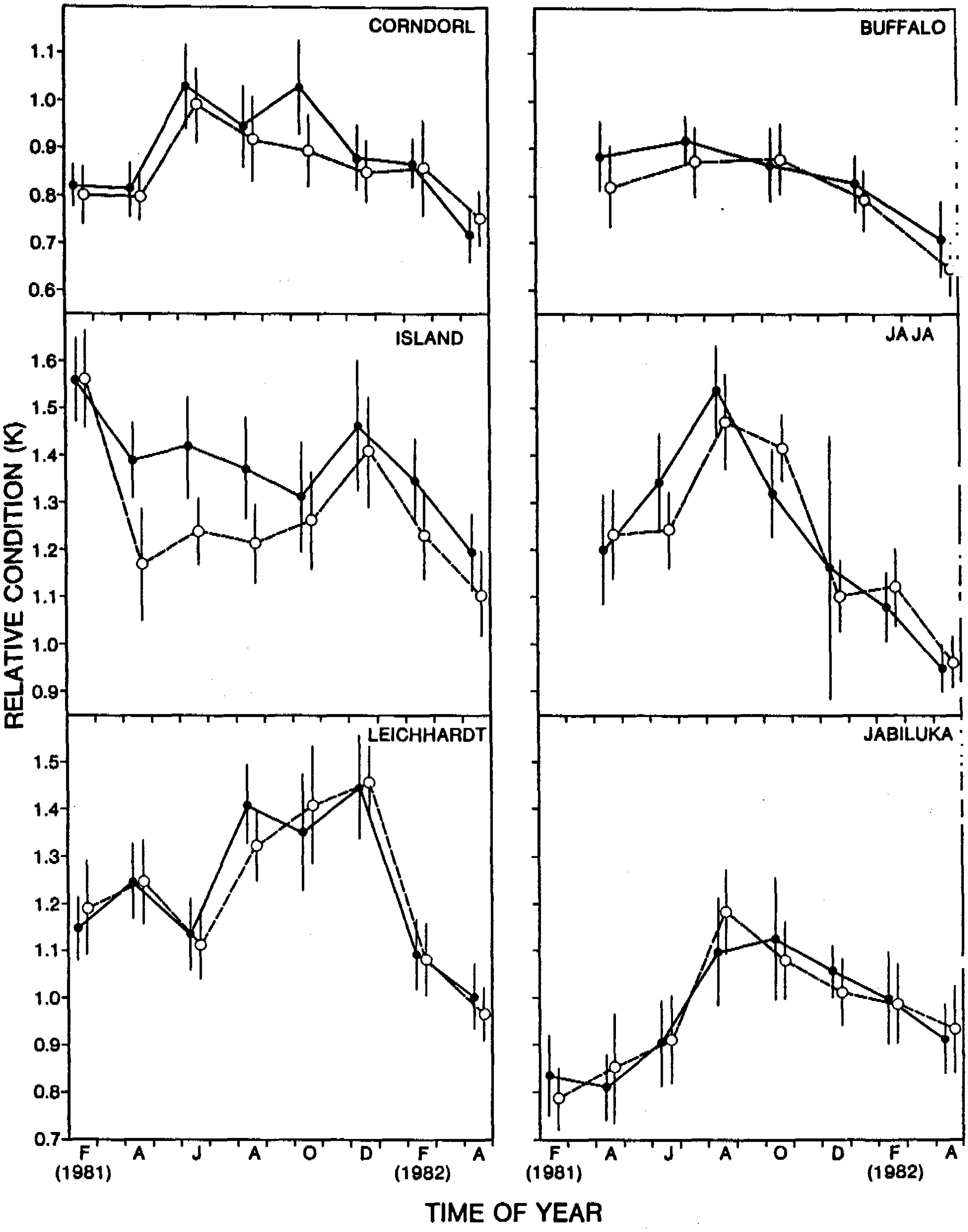


Figure 8.3 Mean relative condition (K) of male (solid circles) and female (open circles) mussels, measured seasonally in billabongs of the Magela Creek. 95 percent confidence intervals about the means are indicated by vertical lines.

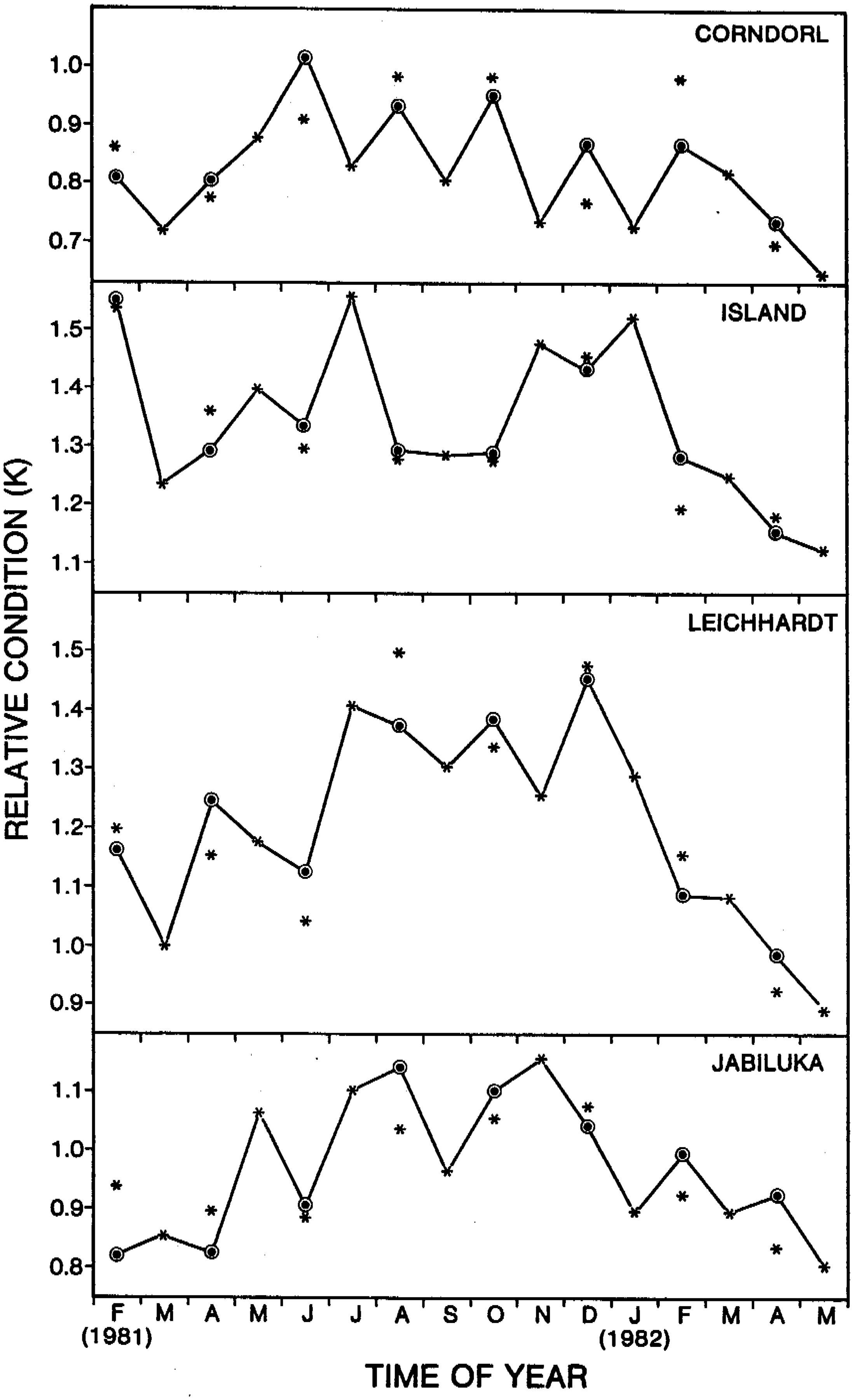


Figure 8.4 Mean relative condition (K) of mussels measured seasonally (sexes combined) in selected billabongs, as calculated using actual dry weights (encircled points), or using a conversion of wet to dry weight (asterisks).

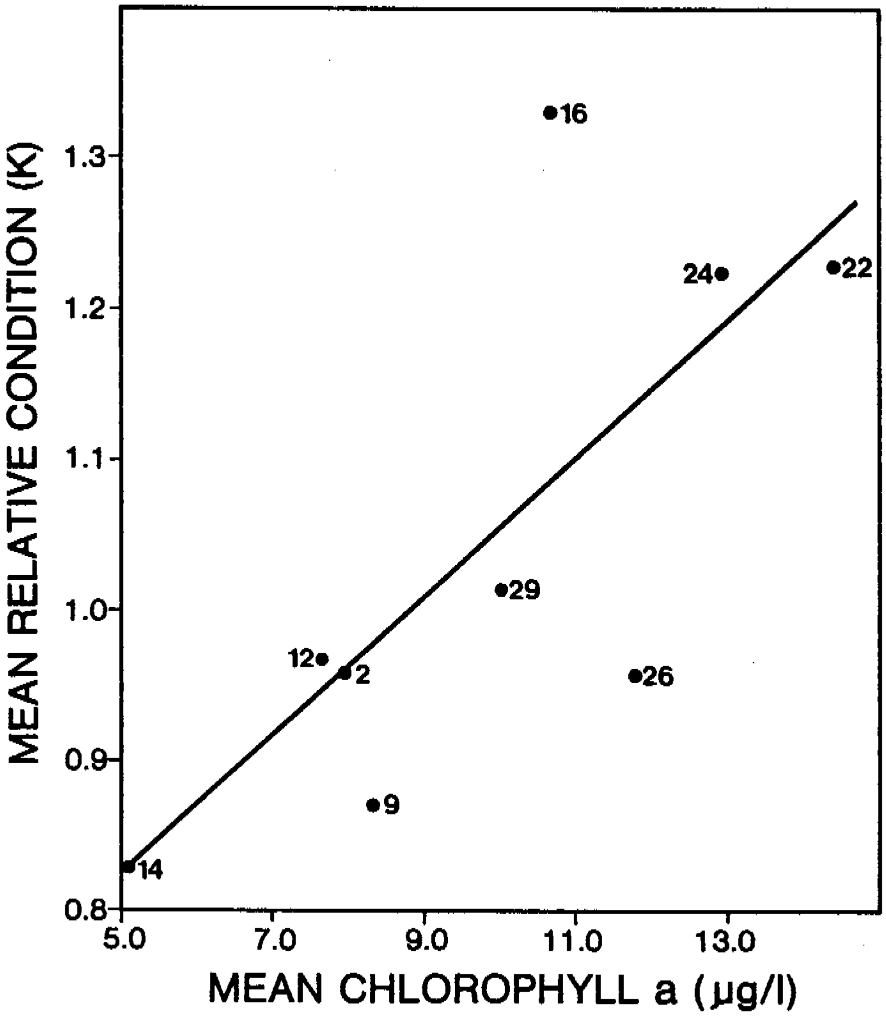


Figure 8.5 Linear relationship between mean condition (K) of mussels and mean chlorophyll concentration, averaged over the seasons, in billabongs of the Magela Creek.

Fitted regression equation is:

$$Y = 0.595 + 0.046X \qquad (P < 0.05,\ r^2 = 0.575)$$

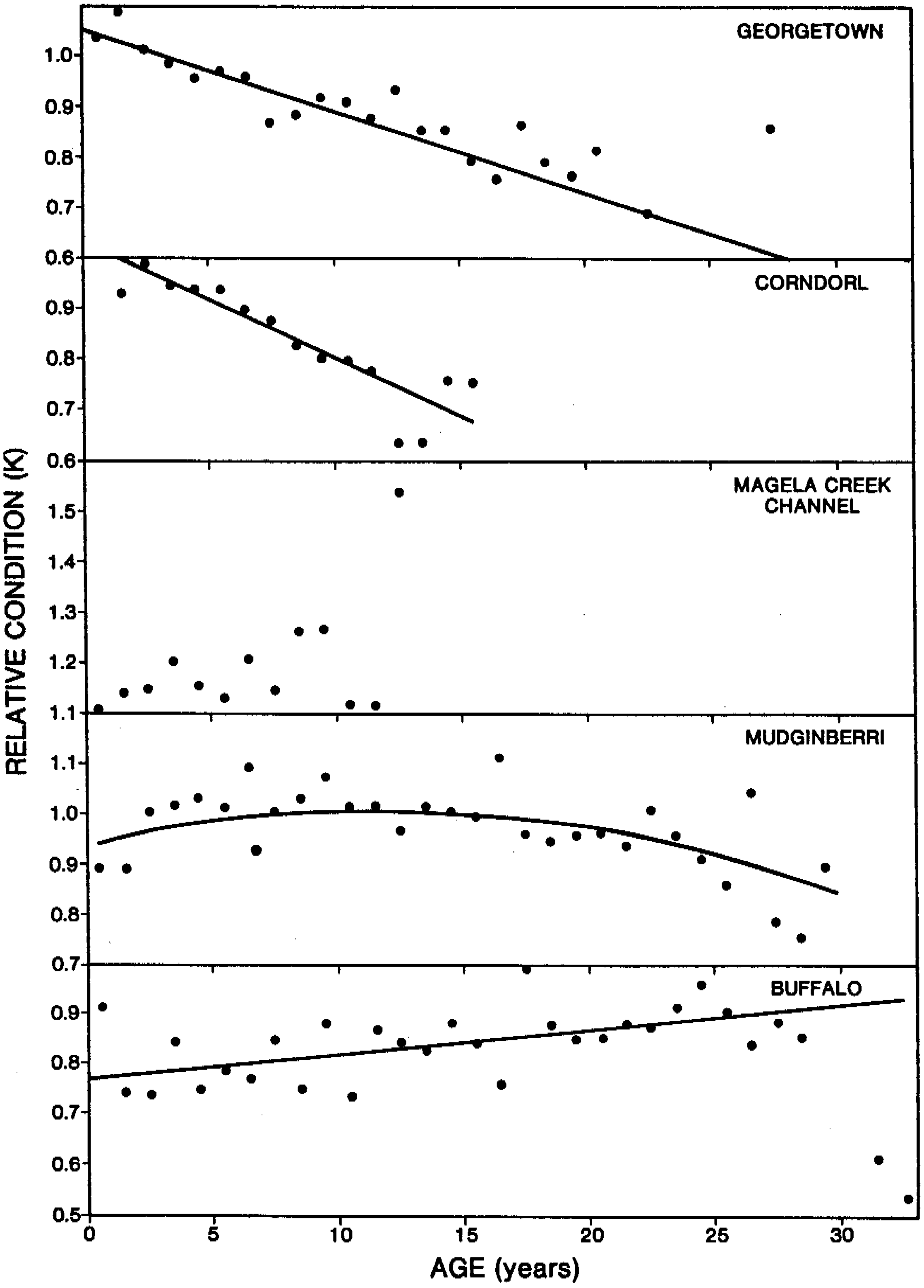
where Y = mean relative condition and X = mean chlorophyll concentration (µg/l).

Numbers about the symbols, are billabong codes referred to in the text (also explained in Table 6.20).

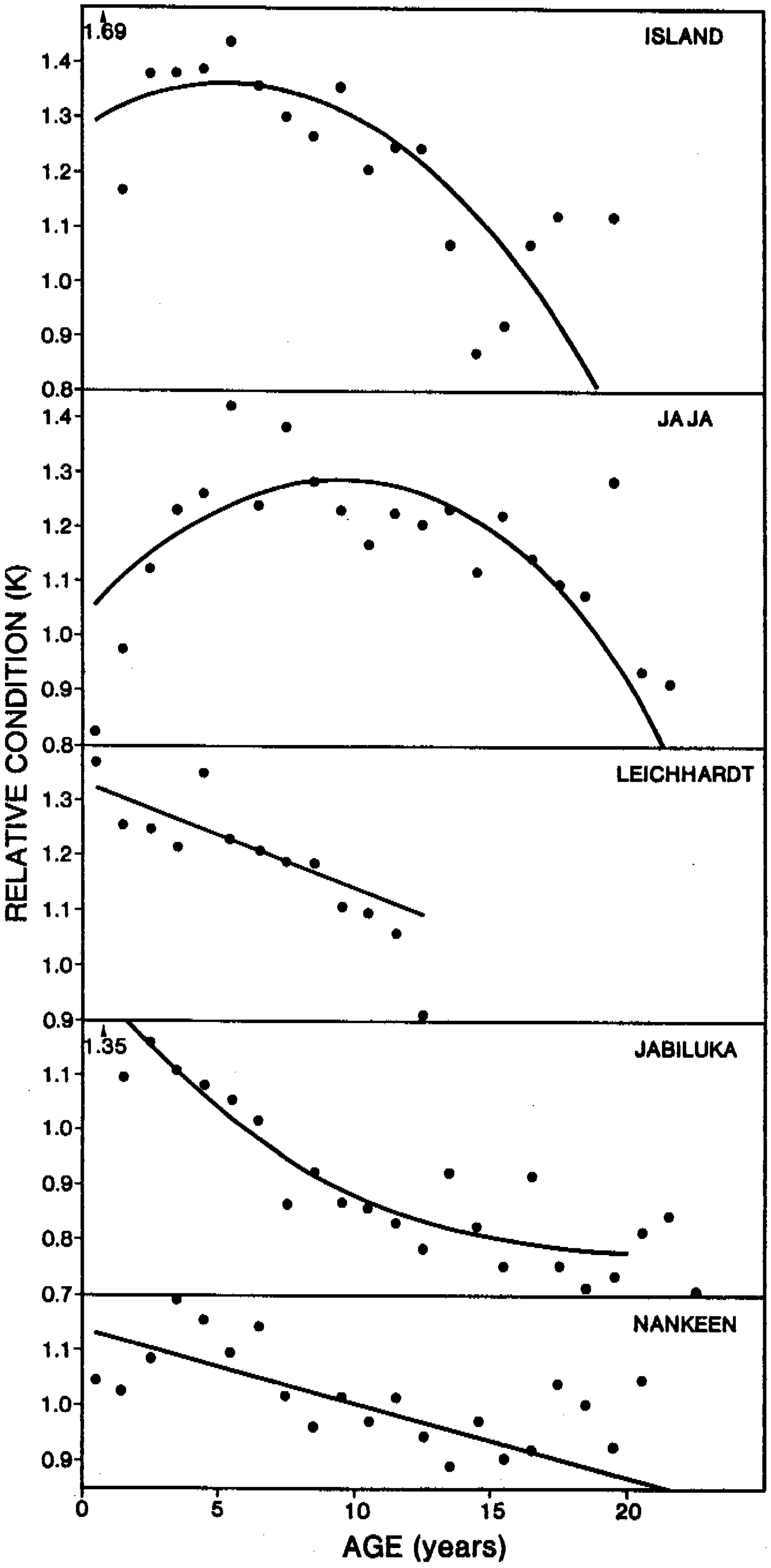
Figures 8.6 and 8.7 Relationships between mean condition (K) of mussels (sexes combined) and age of mussels, in waterbodies of the Magela Creek. Fitted lines represent the age classes over which significant linear or quadratic correlations were found between mean condition and age. The regression equations are described in Table 8.11.

Relationships for Georgetown downstream to Buffalo billabong are shown in Figure 8.6, while relationships for Island downstream to Nankeen billabong are shown in Figure 8.7.

8.6


GEORGETOWN
CORNDORL
MAGELA CREEK CHANNEL
MUDGINBERRI
BUFFALO
RELATIVE CONDITION (K)
AGE (years)
1.0
0.9
0.8
0.7
0.6
0.9
0.8
0.7
0.6
1.5
1.4
1.3
1.2
1.1
1.1
1.0
0.9
0.8
0.7
0.9
0.8
0.7
0.6
0.5
0
5
10
15
20
25
30

7.4



ISLAND
1.69
JA JA
LEICHHARDT
JABILUKA
1.35
NANKEEN
RELATIVE CONDITION (K)
AGE (years)
0
5
10
15
20
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7

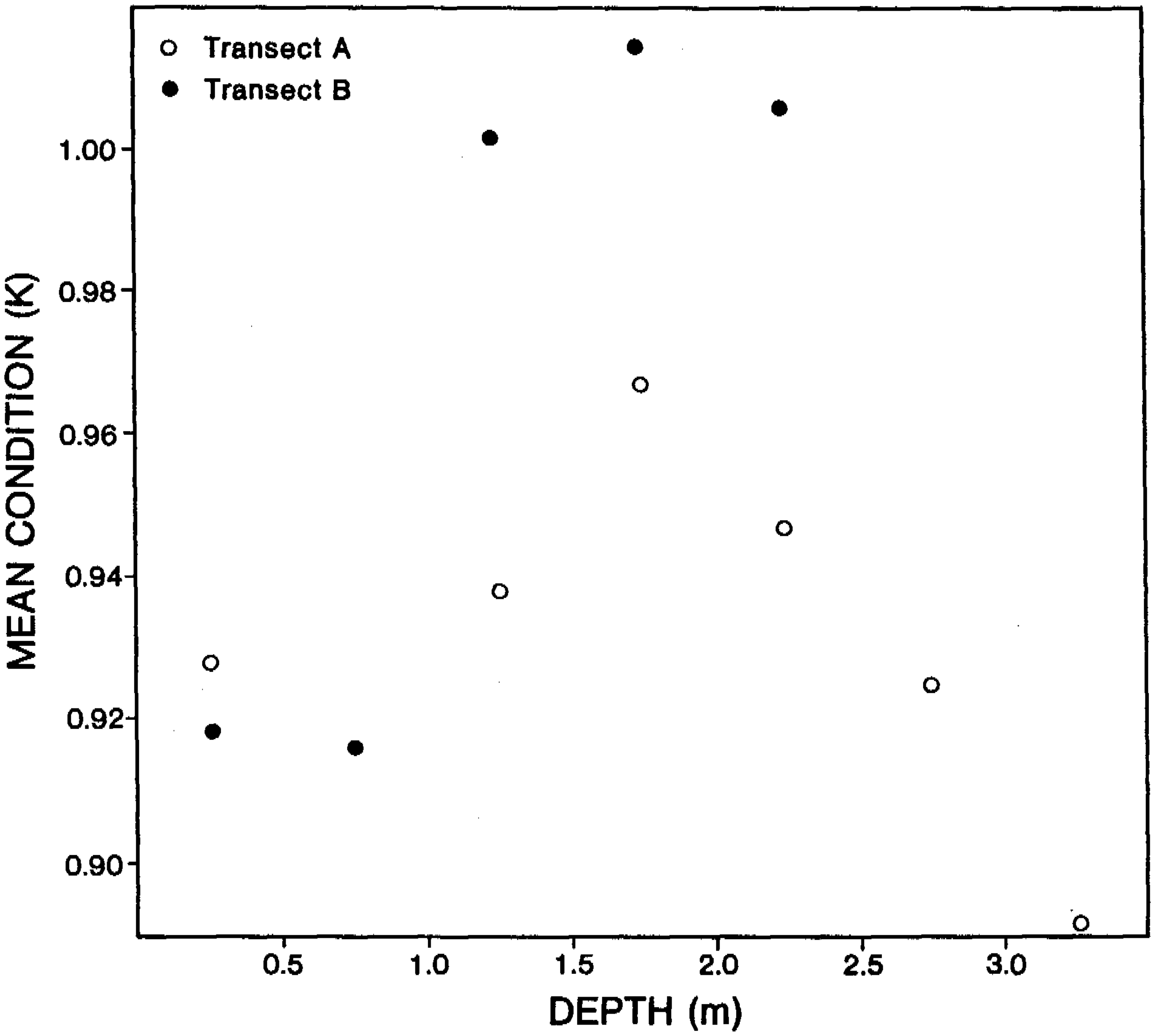


Figure 8.8 Plots of mean condition (K) of mussels averaged over the study period, in relation to depth and sampling transect in Georgetown billabong.

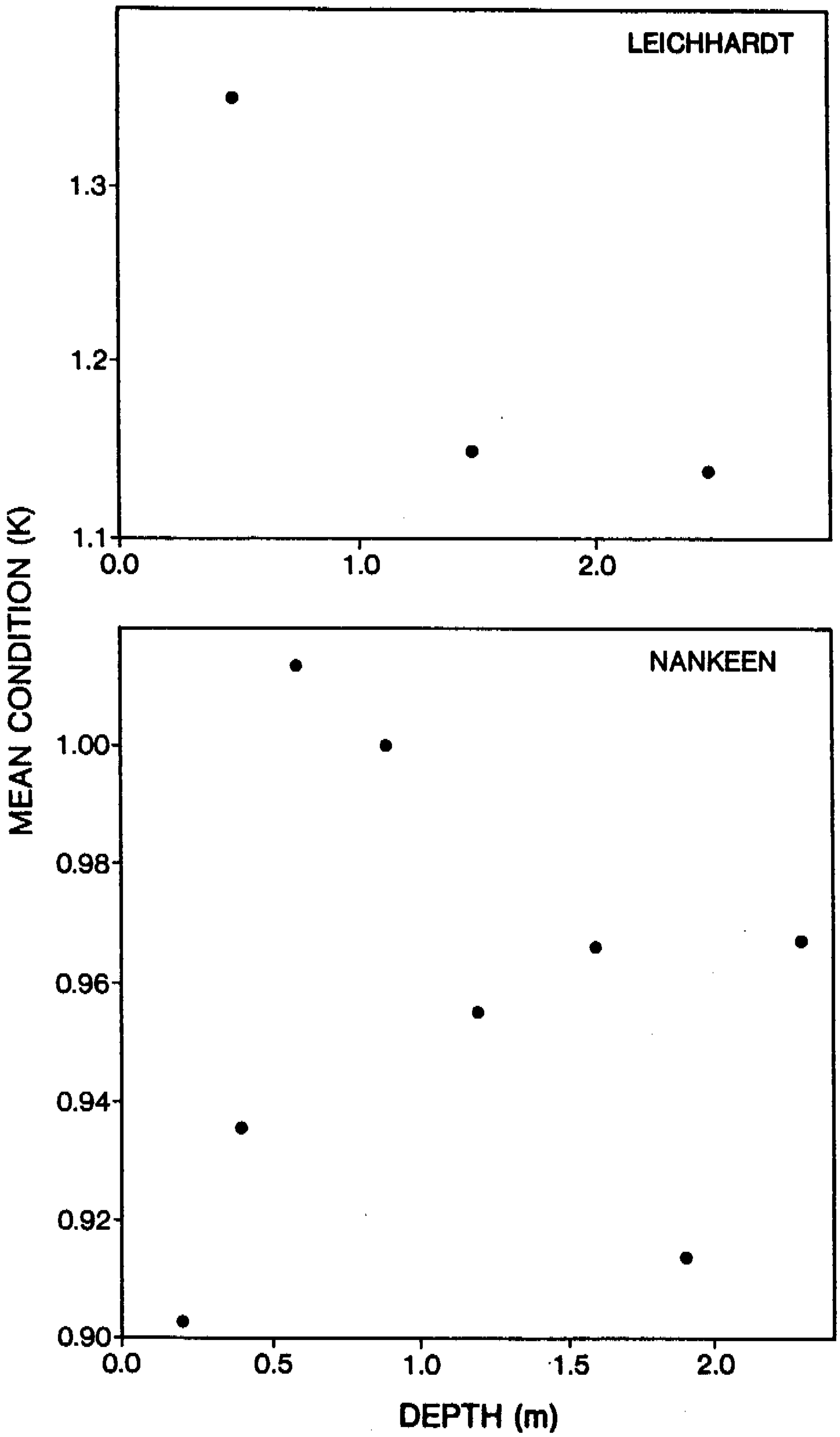


Figure 8.9 Plots of mean condition (K) of mussels averaged over the study period, in relation to depth in the floodplain billabongs, Leichhardt and Nankeen.

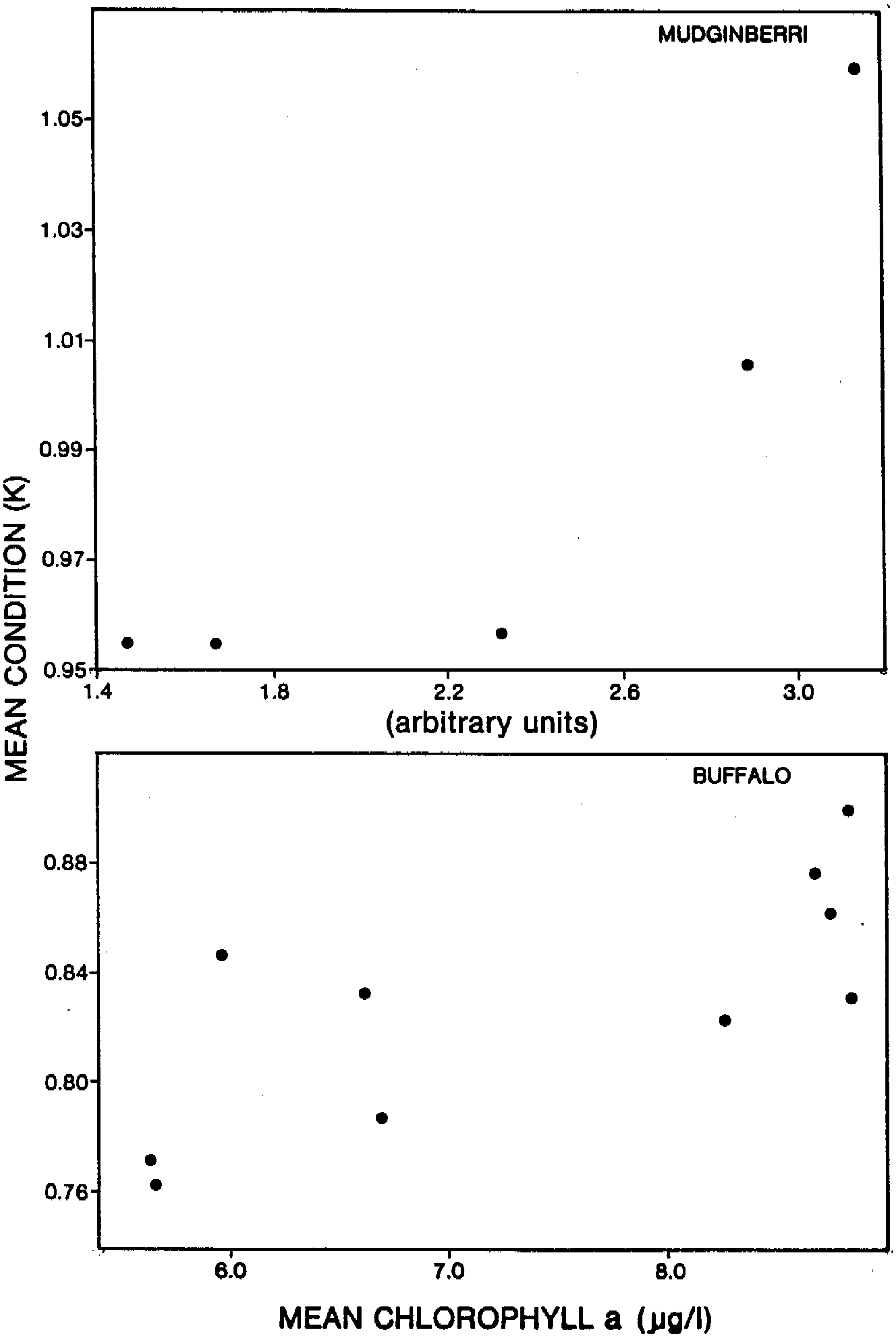


Figure 8.10 Relationship between mean condition (K) of mussels averaged over the study period and mean chlorophyll concentration, among sampling sites of the channel billabongs, Mudginberri and Buffalo.