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The macroinvertebrate colonisation of the tropical, seasonally-inundated, Magela Creek floodplain

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THE MACROINVERTEBRATE COLONISATION OF THE TROPICAL, SEASONALLY-INUNDATED, MAGELA CREEK FLOODPLAIN

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Abstract

This study examined the colonisation of the Magela Creek floodplain by aquatic macroinvertebrates. The Magela Creek floodplain is located in Northern Australia which has a tropical, monsoonal climate. During the Wet-season, floodplain waters cover an area of over 150 km^2. As the Dry-season progresses, water recedes forming several large permanent billabongs. The permanent billabongs, floodplain soils and the aerial stages of aquatic insects were identified as the likely sources of colonising fauna. The taxa occurring in each one of these sources, at the end of the Dry-season, was determined. The floodplain soil fauna was examined by taking soil cores from five locations along a transect adjacent to Djabiluka and Island billabongs. The cores were artificially wetted and the emerging fauna identified. Aerial insects were sampled using Malaise traps.

After floodplain inundation, the colonising fauna was collected along the same transects used for the soil fauna determination. Samples were collected from the Island site on days 1, 4, 7, 14 and 21 after inundation. Samples from the Djabiluka site were collected on days 3, 9, 17 and 24 after inundation. Due to time constraints only one location from the Island transect and four locations along the Djabiluka transect could be examined. Changes in taxon richness and relative abundance of the colonising fauna with time and distance from the billabongs was examined using an ANOVA on the results of a principal coordinates analysis.

The Oribatida, Oligochaeta, Chironomidae and Nematoda were the most important taxa in colonisation. Within the Chironomidae, all locations at the Djabiluka site became dominated by the genera *Chironomus* and *Parachironomus*. The success of *Chironomus* was attributed to a combination of high fecundity, adaptations to low oxygen conditions, and competitive superiority. The source of *Parachironomus* was attributed to dispersal of larvae from the billabongs, rather than egg-laying by flying adults, as a result of age determinations on colonising individuals. Sources of colonisation for *Chironomus* were probably from the billabongs, as well as, rain-pools present on the floodplain prior to inundation. During early inundation, one location at both Island and Djabiluka transects closely resembled the billabong chironomid fauna. This was probably due to remnant pools at each of these two locations. The oribatid fauna was dominated by the species *Trhypochthoniellus* sp. This species was found in both the floodplain soils and the permanent billabongs, and has an asexual mode of reproduction. While asexual reproduction may be an adaptation to an aquatic life-style, it is likely that this species is pre-adapted to such an environment by its asexual ancestry.

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1. INTRODUCTION

1.1 The importance of floodplain habitats

A floodplain can be defined as "areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physicochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic assemblage structures" (Junk *et al.*, 1989; p.112). In Australia, floodplains are important feeding and breeding grounds for water fowl (Jaensch *et al.*, 1995). Surveys of Magpie Geese of wetlands in the Northern Territory have found populations at times in the order of three million birds (Bayliss and Yeomans, 1990).

Floodplains also play an important role in fish production. Many fish found in the main channels of rivers rely directly or indirectly on the primary production of the linked floodplain habitat (Junk *et al.*, 1989). Most fisheries in large river/floodplain systems are dominated by species that colonise the floodplain habitat seasonally (Junk *et al.*, 1989). Furthermore, many species time their spawning to occur at the beginning of rising flood waters so as to utilise the abundant food and shelter provided by the floodplains (Welcomme, 1985; Bayley, 1988).

Floodplain habitats are also important for invertebrates. Temporary waters regardless of the geographic region, seasonal flooding regime, substrate type, water chemistry or vegetation type, show higher densities but lower taxonomic diversity of aquatic invertebrates compared to permanently-inundated habitats (Neckles *et al.*, 1990). This has important implications on the rest of the floodplain biota, as large populations of aquatic invertebrates often provide the necessary cue for some species of water fowl to begin nesting as they provide the source of protein for egg production and growth in juveniles (Maher and Carpenter, 1984). The macroinvertebrate fauna also provide an important source of food for fish and thus are partly responsible for the high productivity in these areas. The macroinvertebrate fauna can even have direct impacts on humans. The relatively still waters of many tropical floodplains can give rise to high densities of mosquitoes and midges that can become a nuisance in nearby human settlements (Ali, 1980a; 1980b) and in some cases spread arboviruses and malaria (Mattingly, 1969).

Over the last several years there has been growing international awareness of the importance of wetlands, including floodplains (Finlayson, 1995). This awareness coupled with the high rate of wetland degradation and loss has resulted in the formulation of international

conventions such as the "Ramsar" 1971 Convention on Wetlands of International Interest, which aims to produce guidelines on the wise use and conservation of these habitats. Fundamental to these aims is the requirement of good scientific knowledge on the patterns and processes important in these systems. Despite this requirement little information exists. For floodplains important questions that need answering relate to the role of flooding and drying in stimulating and regulating key ecosystem processes (Lake, 1995). It appears that invertebrates play a key role in at least the trophic structure of the floodplain ecosystem, thus their response to flooding has important implications for the other inhabitants.

1.2 Sources of colonisation

If floodplain habitat is important to the aquatic invertebrate community, what are the mechanisms by which colonisation of the floodplain takes place? Most of the work on the colonisation of temporary aquatic habitats has been based on creeks and streams, the majority of which has been carried out in Northern Hemisphere. Few studies have examined the process of colonisation with respect to floodplain systems.

Comparisons of the floodplain environment with that of other aquatic environments, such as lakes and rivers, are complicated by floodplains showing characteristics of both during its existence (Junk *et al.*, 1989). A floodplain after the water level has stopped rising is often considered to represent a standing water environment such as a lake. Conversely, the filling stage of a floodplain is more comparable to a flowing water environment, such as a river. Given that floodplain colonisation occurs during the filling stage, the extension of work on colonisation sources derived from studies on rivers and streams seems applicable to the floodplain environment.

Williams and Hynes (1976) based on their own work and reviews of the work of several other authors (Müller, 1954, Waters, 1964; Cairns *et al.*, 1971) recognised four main potential sources of recolonisation of denuded areas of a temporary stream bed. These sources were drift and/or migration from permanent water elsewhere in the system; vertical migration from within the substrate and oviposition by aerial stages of aquatic insects.

1.2.1 Permanent waters

The most obvious source of colonisers of temporary aquatic habitats is from permanent bodies of water within or adjacent to the system being considered. Colonisation from these sources can occur in one of two ways depending on the location of the permanent water relative to the newly-inundated habitat; these being downstream drift or upstream migration by the aquatic phase of the organism.

Downstream drift

Downstream drift is an important aspect of life for many aquatic invertebrates (Cellot, 1996). Studies on the colonisation of newly formed habitats within permanently flowing rivers have found drift to be an important source of immigration. Most of the taxa that are well known for being the first colonisers of newly-formed habitats, such as species of Baetidae, Simuliidae and Chironomidae (Hynes, 1975; Hemphill & Cooper, 1983; McArthur & Barnes, 1985; Matthaei *et al.*, 1996) are known to dominate stream drift (Waters, 1972; personal observation). This pathway can also be applied to temporary systems where organisms from permanent upstream sources can recolonise newly-inundated habitat by drifting down with flood waters. If the level of flood disturbance is high enough, these waters can carry with them other species that rarely or never occur in the drift (Anderson & Lehmkuhl, 1968; Corkum *et al.*, 1977).

Although downstream drift is an important source of colonisation in permanent streams, some have suggested that this pathway is less important in temporary streams (Gray & Fisher, 1981). This observation appears to be supported by other studies on temporary freshwater systems (Larimore *et al.*, 1959; Harrison, 1966; Williams, 1977; Fisher *et al.*, 1982; McArthur & Barnes, 1985; Smith & Pearson, 1987; Boulton, 1989; Carl, 1989; Morrison, 1990). One exception is a recent study of recolonisation in Magela Creek, Northern Territory (Paltridge *et al.*, 1992), in which drift from permanent upstream sources was the most important source of colonisers. Although, most studies suggest that downstream drift is not the main colonisation pathway in temporary systems, few authors doubt its importance. For example, Gray and Fisher (1981) found that while few taxa were derived from drift, this source contributed the highest number of individuals during a study of the colonising invertebrate fauna of a temporary desert stream in Arizona.

Upstream migration

Some aquatic insects can migrate more than 12 km upstream within a period of just four weeks, indicating that migration upstream into temporary habitats from permanent downstream sources is possible over large distances (Gore, 1977). As with drift, upstream migration has not been seen as an important colonisation pathway for most taxa in temporary systems (Harrison, 1966; Williams, 1977; Fisher, 1982; McArthur & Barnes, 1985; Smith & Pearson, 1987; Boulton, 1989; Carl, 1989; Morrison, 1990). None-the-less, like downstream drift, it has been shown to contribute large numbers of individuals of certain taxa in some streams (Gray & Fisher, 1981).

Based on the reports of upstream migration of the immature stages of other aquatic insects, Gore (1977) suggested aquatic insects can detect favourable changes in upstream environments (such as newly available habitat) and will then attempt to invade it. However, Bird & Hynes (1981) found that upstream movement could not be significantly differentiated from lateral movement and concluded that upstream migration was the result of random movement and changes of density in the benthos (the faunal assemblage living at the interface of the water and substrate). This study was performed in a permanent stream where selection for directed migration may not have been strong. Benzie (1984) agreed that benthic invertebrate movements may result more from random foraging behaviour than distinct dispersal behaviour, but acknowledges that certain species may have mass movements at restricted periods in their life cycle and that these movements could be restricted in direction.

1.2.2 Vertical migration upwards from within the substrate

The movement of invertebrates up from within the substrate into the water column has been identified as the major source of colonisation in some temporary waters (Williams, 1977; Morrison, 1990; Boulton, 1989). The importance of this pathway is due to the ability of many taxa to survive in the dry soils of temporary aquatic habitats and to emerge once the soil is wetted. Survival in the soils during the dry phase can be achieved in several ways. Certain gastropods and isopods have impermeable shells which can be closed tightly to prevent water loss. Enclosed within such a shell, adults and juveniles can withstand many months of desiccation, as well as anaerobic conditions and high temperatures (Williams, 1985). Other groups of invertebrates can survive long dry periods in the soil as larvae which have undergone a form of arrested development or diapause. Perhaps the most striking example of this strategy is seen in the chironomid *Polypedilum vanderplankii* (Hinton) which is found in temporary

pools in Africa. The larvae of this species can withstand desiccation for more than ten years and in this condition survives exposure to temperatures above 100°C and to -270°C. When conditions become suitable again hydration is rapid and the larvae resume activity within several days of rewetting (Hinton, 1960). This strategy, called cryptobiosis, has also been found in several other groups of invertebrates including nematodes, rotifers and tardigrades (Williams, 1985). Some species of chironomid can also survive drought conditions by constructing cocoons which probably help the larvae to avoid excessive water loss (Grodhaus, 1980). Other invertebrates can also survive in temporary waters by means of eggs that are resistant to drying (Williams, 1985), these include some species of odonates and many mosquitoes, especially of the genus *Aedes* (Gullan and Cranston, 1994).

1.2.3 Aerial stages of aquatic insects

Colonisation from aerial sources can be a significant pathway for colonising temporary habitats (Harrison, 1966; Fisher *et al.*, 1982; Smith & Pearson, 1987; Carl, 1989). In a study on post-flood colonisation pathways of a temporary desert stream, Gray & Fisher (1981) found that aerial recolonisation accounted for nearly two-thirds of the total recolonising taxa. A study examining the annual cycles of macro-invertebrates of a temporary river in southern Ghana (Hynes, 1975) attributed the early appearance of tiny Simuliidae larvae to eggs laid by adults flying in after the resumption of flow. Morrison (1990) noted also the appearance of early life stages of Plecoptera, Trichoptera and Diptera larvae within a month of refilling of several drought-stricken streams in central Scotland. Since many species of Trichoptera had flight periods lasting several months, Morrison suggested that eggs laid by flying adults, as water levels rose, could have been responsible for the appearance of these early life stages but acknowledged that survival of eggs or young larvae within the dry sediments could have been responsible.

1.3 Isolating colonisation sources for specific species - the role of instar determination

An objective of any aquatic colonisation project is to determine from what source(s) a particular coloniser is derived. Certain sources of colonisation can be detected or rejected by establishing the age of larvae. For example, a species that colonises a newly-formed aquatic environment via oviposition by flying adults would appear in the new habitat as very young individuals

because they have emerged from eggs. Therefore, the ability to determine the age structure of a population can be useful tool.

External growth in insects is discontinuous due to the presence of thickly sclerotized cuticle which prevents the outward growth of the body underneath it. For an insect to increase in size, it must first shed its existing cuticle. The insect then expands its body such that the newly forming cuticle is enlarged before it hardens. This ensures the new cuticle is large enough to accommodate the next period of body growth. Between the periodic shedding of the cuticle there is little or no apparent increase in size of these sclerotized regions. An inter-moult period called an instar (Gullan and Cranston, 1994).

It was first noted by Dyar in 1890 (Daly, 1974) that the increase in size of an insect between instars is relatively constant in some species, particularly in those that have few instars (Hughes, 1974). Dyar showed that the size of the sclerotized head capsule in 28 species of lepidopteran larvae (Butterflies) increased by a ratio in the range of 1.3 to 1.7 between successive instars. This lead to the formation of Dyar's rule which states that: *postmoult size/pre moult size (or moult increment) = constant*. Subsequent work has found similar patterns of growth in other insect orders.

If a species conforms to Dyar's rule then it is possible, by examining the size distribution of a sclerotized structure, to determine the size range of each instar. Once a range can be allocated to a given instar it is then possible to assign each individual of that species to an instar.

It is not always possible to see every instar represented in a sample from a population. For example, the Chironomidae (non-biting midges) have four larval instars, the first of which is planktonic. The planktonic larva then moults into a second instar as soon as it settles on the substrate. As a result, first instar chironomid larvae are rarely found in samples taken from the substrate.

1.4 Importance of source

The literature reveals that aerial and vertical migration up from the substrate are the most significant sources of colonisation in temporary systems. In most studies only one of these pathways predominates. Why does aerial colonisation dominate in some systems and vertical migration in others? Aerial sources are most significant in habitats with a sandy substrate (Harrison, 1966; Fisher, 1982; Carl, 1989) and vertical migration in areas where the particle size of the substrate is larger (Williams, 1977; Morrison, 1990; Boulton, 1989). Possibly, the sandy

substrate is unstable (Mackay, 1992), particularly if the resumption of flow is characterised by rapid changes in water velocity or high levels of water velocity making this habitat unsuitable as a refuge.

The significance of any one source is obviously affected by the specific environmental conditions of the aquatic system being considered. Thus, understanding the basic structure and physicochemistry of the main habitats in a system can be used to generate hypotheses on the likely sources and contribution of each source to colonisation.

1.5 Site description

Due to the rapid rate of loss and degradation of wetland habitats on a world-wide basis, it is often difficult to collect data from a truly undisturbed system. In the wet/dry tropics of Australia there are large areas of natural floodplain systems that have remained in pristine condition due to the low population densities of humans and the recognition, and incorporation, of such areas into national parks of World Heritage status. Magela Creek is a seasonally-flowing tributary of the East Alligator River, located within Kakadu National Park, Northern Territory (Fig. 1). This region of Australian has a tropical monsoonal climate and receives an average rainfall of 1250mm, the majority of which falls during the wet season between the months of November and March (McDonald & McAlpine, 1991). The catchment includes several habitat types, including sandstone escarpment, lowland forest and floodplain.

The floodplain becomes inundated shortly after the onset of the Wet-season, with waters typically covering over 150 km^2 (Williams, 1979). Flood waters then recede during the dry months, leaving several large permanent billabongs that are formed by water pooling in remnants of the creek channel (Brown *et al.*, 1983). Soil conditions on the floodplain, particularly during the Dry-season, are harsh. Soils are rich with organic material deposited during the Wet-season floods (Hart *et al.*, 1987). The soils are also rich in sulphates which cause soil pH to be highly acidic (East *et al.*, 1992). In more open areas the soils are baked by the intense heat of the sun.

Given this set of environmental conditions it is possible to generate some hypotheses on the likely sources of colonisation within the Magela Creek floodplain system. The permanent billabongs both on the floodplain and upstream in the creek channel proper are likely to contribute some colonising aquatic fauna via drift or migration. The dry floodplain soils provides a source of vertical upwards migration in this system. The issue of the stability of the

soil, in how it is likely to affect the significance of this source, is not such an issue for the floodplain soils which are well compacted and thus more stable than sand. The harshness of the soil will presumably affect the fauna. Given the highly acidic nature of the soil one would predict the associated fauna to show relatively low diversity. Furthermore, adding water to this stressful system is predicted to give rise to a stressful aquatic environment that is unlike the permanent billabongs and this should be reflected in the colonising and early pioneering fauna.

2. MATERIALS & METHODS

2.1 Sources of colonisation

To determine the faunal composition of each source of colonisation, each potential Dry-season source was identified and studied. Three main sources were recognised; the permanent billabongs, floodplain soils and aerial stages of aquatic insects.

2.1.1 Permanent billabongs

Three billabongs within the Magela Creek system were chosen: Island, Djabiluka and Mudginberri (Fig. 1). Djabiluka and Island billabongs are situated on the lower and upper floodplain, respectively, while Mudginberri billabong is located within the Magela Creek channel, upstream from the floodplain.

Within each billabong, two habitat types were recognised. The littoral zone, constitutes the shallow waters of billabongs which contain very dense populations of aquatic vascular plants (macrophytes). Samples from this zone were taken using a 250 μm mesh sweep net. Five replicate samples were taken from the littoral zone of each billabong. Each replicate consisted of 10 sweeps of the net through the water at a given location. The location of each replicate was determined in a randomised manner.

The second habitat type was the profundal zone, which comprises deep water where light penetration is insufficient to promote the growth of macrophytes. Due to the depth of the water an airlift sampler was used. An airlift sampler consists of a compressor that pumps air into an 80 mm wide piece of PVC tubing that can be varied in length. The displacement of water as the air rises up the length of tubing, causes water and sediment to be drawn up and expelled from the non-submerged portion, where it can be collected in a 250 μm mesh net. A steel rake attachment at the end of the intake ensures that the sediment is sufficiently disturbed. A sample was collected by dragging the airlift sampler from a boat over a 1 metre strip of habitat. It was necessary to sieve some samples on site, using a 500 μm mesh sieve, to reduce the volume of the sample by removing fine silt.

An attempt was made to take five replicate samples from the profundal zone of each billabong. The location of each replicate was decided in a randomised manner. Only 3 replicates were taken at Djabiluka due to boat engine failure, part way through sampling.

In the field, profundal and littoral samples were stored in an ice-chest to minimise any decomposition of the sampled fauna due to the high ambient air temperatures.

Upon returning to the laboratory, samples were passed through a stack consisting of two sieves of 8 mm and 250 μm mesh size. The organic material retained by the 8 mm sieve was carefully washed to dislodge any invertebrates clinging to the material, which was then discarded. The fraction retained by the 250 μm sieve was retained for sorting (the extraction of macroinvertebrates). The removal of more bulky material was necessary to facilitate easier subsampling and sorting of the samples. All samples were subsampled to a fraction that enabled 200 animals to be picked. This figure of 200 animals was chosen as it is considered the optimal number required for an accurate representation of most species of macroinvertebrates present in the sample (MRHI, 1994). Subsampling, using a Geosplitter®, reduces the original sample to a manageable fraction that can be expediently identified. Identification of animals to the lowest taxonomic level, usually species, were made by Ruth O'Connor and Lisa Thurtell of ERISS.

Previous studies have suggested that the profundal zone in the billabongs have low species diversity and abundance (Marchant, 1982). Given the time constraints of the project, the ERISS staff concentrated on the littoral zone samples since these contained a richer fauna. Two profundal samples from Djabiluka were examined, one in its entirety and a second only partially, to confirm that the samples conformed to previous expectations.

2.1.2 Floodplain soils

2.1.2.1 Soil rewetting experiment

In the field

A 300 metre long transect was measured out from the edge of Djabiluka billabong. The placement of the transect had been predetermined by its position relative to other water bodies in the area, the severity of soil damage due to feral pig routing and ease of access in the Wet-season. Locations were marked off at 20, 60, 120, 200 and 300m from the start of the transect, at the edge of the billabong. At each location, a 1 m^2 quadrat was laid out. Within the quadrat, various parameters of the habitat were described. These included an estimate of the percentage of live and dead plant cover, the maximum vegetation height, an estimate of the percentage canopy cover, the depth of litter - if present - and a description of the plant species present.

Two cores of soil were then taken from within the quadrat, with the second being taken 50 cm from the first. Each core covered an area 15 cm^2 and a depth of 10 cm. A third core, of

similar dimensions, was then taken half way between the other two. The bottom 3 cm of this core was shaved off and placed in a plastic bag, which was sealed and placed on ice for transport back to the laboratory. This soil was to be used to obtain a measurement of the soil moisture and pH at each location on the transect.

The above-mentioned sampling protocol was used also at Island billabong; however, the dimensions and spatial arrangement of the transect differed from Djabiluka due to the presence of another water body located approximately 250 m from the edge of the billabong. If the end of the transect was too close to this second water body, then colonisation at the distal portion of the transect could be influence by this other source rather than the billabong. For this reason the transect was shortened to 100m with locations marked at 10, 20, 30, 60 and 100m from the edge of Island billabong.

In the laboratory

With 20 samples to be wetted it was not practical to start inundation simultaneously, as examining all the samples in a single day would not have been possible, due to the time required to look at each one. Instead the starting of the rewetting process was staggered over four days. The samples used to start the rewetting experiment on each day were selected at random. Each sample was placed into a 4 L ice-cream container to which 2 L of distilled water was added. Each container was then placed inside a clear plastic bag, which was sealed, to prevent any contamination of the samples by other organisms. The samples were then allocated a random position on a workbench. Every second day the samples were repositioned randomly to minimise any positional effects and the dissolved oxygen (DO) measured using a Hach (model 16046) Portable Dissolved Oxygen Meter. If the DO of a sample dropped below $1 mg.L^{-1}$ the water was changed by pouring off the surface water through a 63 μm mesh sieve. The retained fraction was then washed back into the sample with 2 litres of fresh distilled water.

Samples were examined on days 1, 3, 7, 14 and 21 with day 0 being the time of the addition of distilled water. On each of the five days the soil was slightly agitated and the water then poured through a 250 μm mesh sieve. The contents of the sieve was live sorted under a stereo dissecting microscope and the number of organisms recorded. After sorting, both the original water and the organisms were returned to the containers holding the soil. On the final day of the experiment (day 21) the animals were preserved in 80% ethanol, for more detailed identification. Organisms were identified to as low a taxonomic level as possible, but in most cases it was only possible to identify classes and orders of macroinvertebrates during the live

sorting. In a few cases some family level identifications were possible on the more familiar taxa.

During the experiment any shed pupal and larval skins, as well as emerged adults, were collected. These were identified in combination with the preserved animals on day 21 to produce a taxon list from each location, which gave higher taxonomic resolution than the list derived from the live sorting.

2.1.2.2 Soil physicochemistry

Soil Moisture

For each soil moisture sample, 40 grams of soil was weighed and placed into an open foil tray of known weight. The combined weight of the soil and container was weighed. Each container was then placed into a drying oven at 107°C. The containers with soil were re-weighed every couple of days then replaced in the oven. Once a constant weight had been reached this was recorded as the dry soil weight. The percentage moisture content of the soil, at each location on the transect, was determined using the procedure outlined by Rayment and Higginson (1992).

Soil pH

The soil pH at each location along the transect was determined following the procedures described by Rayment and Higginson (1992). The soil used in the soil moisture analysis was used as the source of oven-dried soil for the pH analysis. The oven-dried soil was mixed with distilled water at a ratio of 1:5 w/w. The pH of the soil/water mixture was determined using an Orion Ionalyzer (model 720A) pH meter in combination with an Orion Ross Sure-flow combination electrode (model 8165).

Soil temperature

Surface and sub-surface soil temperature measurements were taken at each location along both transects. Temperatures were taken using a standard mercury bulb thermometer. To take these measurements, each transect was visited at the hottest period of the day, such that differences in the surface and sub-surface measurements would be at a maximum. This was necessary to determine whether the sub-surface soil may be providing a temperature related refuge from the high surface soil temperatures experienced during the day.

2.1.3 Aerial sources

Malaise traps (Upton, 1991) were used to determine what flying adult stages of aquatic insects were present at the time of floodplain inundation. A Malaise trap is an intercept trap with no lure. This has advantages in a study of localised sources of colonisation, since light traps can attract animals from up to several kilometres away, making it difficult to associate animals with a specific locality. One malaise trap was set at Island billabong, the other at Buffalo, a small billabong adjacent to Mudginberri billabong (Fig. 1). It was originally intended to set the trap at Mudginberri billabong, since this was a sampled billabong, but this would have be too accessible to the public making it susceptible to vandalism.

Each trap was positioned at the edge of the billabong, in an open area. The traps were emptied weekly from the time of setting up (28/11/96) until a few days before floodplain inundation (27/12/97). After the last sample had been collected, the last two weeks of samples collected prior to flooding were examined. Although only the last two samples were used, it was necessary to begin collecting samples in late November as the start of flooding can occur anytime from December onwards.

Adult insects, known to have aquatic stages as part of their life history, were separated from the terrestrial insect component of the sample and identified to species. The identification of adult chironomids was based on males even though females are the ovipositing sex and therefore the sex that contributes to colonisation. Unfortunately too little is known about the taxonomy of most females to make identifications possible. Males can act as a surrogate for the presence of gravid females since both sexes are synchronised due to the short life of adults of little more than a few days (Armitage *et al.*, 1995). The data obtained from this method was used to produce a presence/absence list of species at each site.

2.2 Sampling following floodplain inundation

2.2.1 Macroinvertebrate sampling

Following inundation of the floodplain, identical transects to the soil survey were used at both Djabiluka and Island billabongs to sample the colonising fauna. Samples were collected from each of the five locations along each transect. An attempt was made to sample on days 1, 3, 7, 14 and 21, as for the soil rewetting experiments so that any trends in colonisation could be

related to the results of the soil rewetting experiments. It was not always possible to collect on these days as the timing of sampling was largely dependant on the availability of supporting staff and transport. As a result, samples were collected from the Island site on days 1, 4, 7, 14, and 21 and from the Djabiluka site on days 3, 9, 17, and 24 after inundation.

Samples were collected using one of two methods. At locations on the transect where the water depth was less than 1.5 m and the submerged vegetation not too dense, a 250 μm mesh sweep net was used. Each sample was collected by sweeping the net through the water ten times. With each sweep an attempt was made to disturb the sediment and vegetation - if present - so as to dislodge any animals. In areas where the water depth exceeded 1.5 m a suction sampler, consisting of a hand-operated water pump with a long hose attached to the inlet, was used to take samples from the lower section of the water column and the sediment. To use the suction sampler effectively, particularly in areas with dense vegetation, the inlet of the suction pump was attached to the end of an iron reinforcing rod, which was used to puncture the thick root mass of grass and disturb the sediment enough to suspend any animals into the water column. At any one location, five minor samples were taken within an area of 1 m^2 and combined to make up the single sample from that location. Each minor sample was collected by ramming the reinforcing rod up and down, through the water column, until it became well lodged in the substrate, indicating that the root mass, if present, had been broken up and the substrate sufficiently disturbed.

Samples were processed using the same method as the billabong samples with a stack of two sieves and subsampling to approximately 200 animals. During the sorting stage it became apparent that not all samples could be examined due to time constraints imposed by a late start to the Wet-season. As a result it was decided to exclude the 20m location at Island and the 60m location from Djabiluka. These locations were chosen as it was felt that even with their removal the remaining four locations at each site still gave a good coverage of the two transects. The macroinvertebrates in the remaining samples were identified to species. With the exception of the Chironomidae and Oribatida mites, species level identifications were impossible for most taxa due to the early stages of development and physical condition of many of the animals collected. During the identification phase of the study it became apparent that there would not be enough time to examine all of the sorted samples. Rather than excluding more samples from both sites, it was decided to focus on a single site. Djabiluka was chosen since the interpretation of results would be less likely to be confounded by problematic factors that were apparent at Island. These factors included inundation of some locations by pre-Wet-season flooding (this is described in detail in section 3.2.1) and the use of more than one sampling technique between

locations. After the identifications had been made on the macroinvertebrates from the four locations at the Djabiluka transect, the assemblage at each one of these locations was examined to verify there was no obvious faunal transition between the 20m and 120m location that would necessitate the inclusion of the 60m location.

To complicate matters further, the macroinvertebrates from the sample that was collected on day3 at the 20m location at Djabiluka went missing in the postal service. When it was finally recovered there was not sufficient time left to identify all the animals. As a result only the Chironomidae were identified. The rest of the sample was scanned to determine if it differed greatly from any of the other samples already examined.

To prevent any confusion, a list of the samples that were used in the subsequent analysis and the sampling technique used to collect each sample can be found in table 1.

For the Chironomidae the similarity of the assemblage at each location was compared using a similarity index:

$$\text{Similarity index} = \frac{2C}{A + B}$$

Where A = number of species in sample A; B = number of species in sample B; and C = number of species common to both.

The mean similarity of samples at both the Djabiluka and Island sites and the two sites combined was calculated.

The head capsule length (HCL) of the two dominant species of *Chironomus* (*Chironomus* sp.2 and *Chironomus* sp.5) and the single dominant species of *Parachironomus* (*Parachironomus* sp.1) were measured. For each species a distribution of HCL was constructed from which the size range of the different instars was determined. For species in which it was not possible to accurately determine instars, the distribution of HCL was divided into three relative age classes (Early, Middle, and Late), based on the assumption that size is proportional to age.

Each individual of a species was then assigned to a particular instar or age class, which enabled the relative composition of instars or age class for each location and each sampling time to be determined.

2.2.2 Water quality measurements

Water samples were collected at each location on the transect during each floodplain sampling trip. Samples were collected by filling a 60mL Nalgene® bottle 30 cm under the water surface. Bottles were capped under water, placed in a bucket of water to prevent temperature fluctuations, and returned to the laboratory for analysis of pH and conductivity. pH measurements were taken with a Metrohm (model 682) Titroprocessor using a Metrohm (model 6.0210.100) pH combination electrode. Conductivity measurements were taken with a Metrohm (model E518) Conductometer using a Activon (model AECP221) electrode. The depth of the water at each location was measured to the nearest 5 cm. Measurements of dissolved oxygen (DO) were also taken. Due to equipment failure it was not possible to use the same portable DO meter on all occasions and in one case it was not possible to obtain any DO measurements. As a result a total of three different dissolved oxygen meters were used over the course of floodplain sampling (Table 2). While it is desirable to take DO readings from near the bottom of the water column, as macroinvertebrate samples where collected from the substrate, incorrect advice on the operation of the DO meters resulted in all measurements being taken at a depth of 10cm, with the exception of the Hydrolab® (Table 2). In an attempt to standardise against differences in readings between meters, a DO measurement was taken using all three models of a single sample of distilled water.

2.3 Analysis

2.3.1 Sources of colonisation

Data collected from the potential sources of colonisation were used to obtain a list of taxa present in the billabongs, floodplain soils and the aerial adult stages of aquatic insects. This data was used to determine which of these sources were important for groups of taxa found during the post-inundation survey work.

2.3.2 Floodplain colonisation

Data collected from the post-inundation phase of the project consisted of both the presence/absence and relative composition of taxa. Relative composition is a measure of the percentage composition of each taxon in a sample. Total measures of abundance were not used due to the low level of comparability across samples as a result of the non-quantitative nature of sample collection. Since many taxa appeared in only one or two of the samples examined, the data matrix had to be compressed for statistical analysis. Rather than arbitrarily setting a level and discarding taxa, an attempt was made to aggregate animals on a biological basis. Animals that occurred in two or less samples and could not be readily combined with another taxonomic group in any meaningful way were eliminated from the data matrix (details of how taxa were grouped can be found in table 3).

To test for any changes in the number of taxa (or diversity) over time, two indices of diversity were used; Taxon richness and Simpson's index:

Taxon Richness = total number of taxa

$$\text{Simpson's index} = \frac{1}{\sum(n_i / N)^2}$$

Where n_i = the number of individuals of a specific taxon and N = the total number of animals in all taxa combined

Taxon richness is a count of the number of taxa present at a given location. Simpson's index involves the number of taxa present but also takes into account the relative abundance of each taxon. This index gives greater weight to those animals that are abundant and is less likely to be confounded by the presence of rare taxa. An Analysis of Variance (ANOVA) was used to determine whether there were any significant changes over time at the Djabiluka site using both these indices.

In order to detect any changes in taxa composition over time, or with distance from the edge of the billabong, a multivariate technique was used. A Principal Coordinates Analysis (PCO) was used on both the presence/absence and relative abundance data. The similarity of

taxa between samples was calculated using the Jaccard's index for the presence/absence data and the ecological index for the relative abundance data:

$$\text{Jaccard} = \frac{a}{a + b - c}$$

Where a = number of taxa in sample A; b = number of taxa in sample B; c = number of taxa common to both samples.

$$\text{Ecological} = \frac{1 - |x_i - x_j|}{\text{range}}$$

Where x_i = proportion of the ith taxon in first sample; x_j = proportion of the jth taxon in second sample.

In the calculations of both these indices any 0-0 matches were ignored.

The first three dimensions of the PCO were subjected to an ANOVA to test for significant differences between locations and collection times. The PCO was performed on the statistical software package Genstat 5 (©1994, Lawes Agricultural Trust).

Histograms were constructed, showing broad taxonomic composition of samples. These histograms were derived from the condensed data set used for the PCO and used to identify important groups of taxa in floodplain colonisation.

For the Chironomidae, an ANOVA was used to test for changes in the percentage composition of the genus *Chironomus* and *Parachironomus* over time at the Djabiluka site. ANOVAs were performed using Microsoft Excel Version 8 (© 1997, Microsoft Corporation). To determine whether there were any similarities in the presence and relative abundance of chironomid species between samples, a PCO identical to that used on the whole floodplain fauna was performed using Genstat 5. Changes in diversity over time were also examined by calculating Jaccard and Ecological indices which were subjected to ANOVA. The chironomid data used in this analysis was derived from the data matrix used for the original PCO. Analysis of the Chironomidae was necessary due to the importance of this group in colonisation. While other taxa were found to be important, only the chironomids showed high enough taxon diversity to potentially show changes in the assemblage over time.

3. RESULTS

3.1 Sources of colonisation

3.1.1 Permanent billabongs

A total of 185 taxa were recorded across the three billabongs during the survey at the end of the Dry-season. Comparing the mean number of individuals of each taxon from the littoral zone across billabongs, Mudginberri tends to have fewer individuals on a per taxon basis than Island and Djabiluka billabongs (Table 4). At Island and Djabiluka billabongs several taxa are particularly abundant, notably oribatid mites, Chironomidae, Ceratopogonidae, Anisoptera (including the family Libellulidae), Dytiscidae, Hydrophilidae, Corixidae and Pleidae. The Naididae (Oligochaete worms) were also abundant in the littoral zone of Djabiluka billabong.

Within the Chironomidae, the subfamilies Tanypodinae and Orthocladiinae were well represented, as were several genera of the Chironominae (*Polypedilum* and *Tanytarsus*; Figure 2). Two other noteworthy genera are *Chironomus* and *Parachironomus* due to their importance in floodplain colonisation. One species of *Chironomus*, *Chironomus* sp.2, was present only in a single sample from the littoral zone of Djabiluka billabong (Appendix A). *Parachironomus* was more widespread having representatives in all three billabongs, but its abundance in any one billabong was low (Table 4).

The oribatid mites were not identified to species by the staff of ERISS; however, by examining the oribatids from several replicates from each billabong, I was able to establish that one species, *Trhypochthoniellus* sp., dominated, representing 86% of the Oribatida fauna in Island billabong (based on the mean of 3 replicate samples) and 72% of the oribatid fauna in Djabiluka billabong (based on the mean of 2 replicate samples).

3.1.2 Soil rewetting data

3.1.2.1 Physicochemistry of floodplain soils and vegetation survey

Soil pH and temperature were taken during this study in order to explain any spatial trends found in the emerging soil fauna. Examination of the spatial distribution of soil fauna was subsequently decided to be beyond the scope of this study, given the inherent time constraints.

Furthermore, the nature of the data precluded such an examination. This makes the soil pH and temperature measurements largely redundant. Therefore, they will not be discussed any further.

The soil moisture content appears to increase with increasing distance at both Island (Fig. 3) and Djabiluka (Fig. 4) billabongs. At both sites, only the most distal point on the transect (100m at Island and 300m at Djabiluka) was supersaturated, indicating that there was free water in the soil.

At Island billabong the section of the transect containing the 60m and 100m locations was dominated by a tall, dense, monoculture of para grass (*Urochloa mutica*), which is a weed species. The other three locations contained sparser stands of para grass, covered in a layer of litter consisting of the leaves of the tree *Melaleuca* spp. (Table 5). The Djabiluka vegetation transect was very different to that of Island. Here the floodplain is very open and the edge of billabong lacks *Melaleuca* spp. The first two locations on the transect (20m and 60m) were dominated by tall para grass, the remainder being a more diverse assemblage of shorter grass and herbaceous species. The 300m location on the transect was unusual in having very little vegetation (Table 6).

3.1.2.2 The macroinvertebrate soil fauna

There are no distinct trends in either abundance or diversity among the taxonomic groups observed due to the patchy nature of the data. None-the-less, the abundance data shows that the Acarina (mites) and Nematoda are numerically the most important taxa (Table 7). It was not possible to determine the taxonomic composition of the Acarina found during the experiment, as specimens could not be mounted for identification since they were being kept alive. In hind sight, it appears that the majority of Acarina belonged to the species *Trhypochthoniellus* sp.

The presence/absence data show Nematoda and the mite *Trhypochthoniellus* sp. to be ubiquitous across all locations (Table 8). Oligochaetes, as well as several aquatic Diptera (flies) and Coleoptera (beetles) are present. The Ceratopogonidae (Diptera) were found only at the 300m location at Djabiluka and the Tabanidae (Diptera) only at the 100m location at Island. Chironomidae were found at both these location as well as at the 20m and 200m locations on the Djabiluka transect. Two genera of Chironomidae, *Polypedilum* and *Nanocladius*, were identified as being present from the shed pupal skins and/or emerged adults found during the experiment.

3.1.3 Malaise traps

During the two weeks prior to inundation, the samples of aerial insects collected from both Island and Buffalo billabongs were dominated by adult chironomids and the occasional odonate (Table 9). No Ephemeroptera (mayflies) or Trichoptera (caddis-flies) were found despite their presence as immature stages in the billabongs (section 3.1.1). Within the Chironomidae, species belonging to the subfamilies Chironominae and Tanypodinae were collected. No representatives of the subfamily Orthocladiinae were collected. Buffalo had the largest number of chironomid species as well as several genera that were not found at Island. Within the Chironominae, two genera, *Chironomus* and *Parachironomus*, are worthy of attention due to their dominance in the post-inundation, floodplain samples (section 3.2.3.2.2). While three species of *Parachironomus* were found, there was a distinct absence of *Chironomus* at both sites.

3.2 Post-inundation Floodplain data

3.2.1 Description of flooding and vegetation response

The first monsoonal rain event of the 96/97 wet season began sometime during the first and second week of December, with rain falling mostly in the escarpment which drains into the Magela system. The first flood waters reached the Magela Creek crossing on the 13/12/96 which is several hundred metres down stream from Mudginberri billabong (Fig. 1). Normally, it takes a few days for the upper floodplain to become inundated once the flood waters reach the creek crossing (Chris Humphrey, personal communication). On this occasion, flow subsided shortly after the crossing was reached. It was not until a follow-up monsoonal rain event in late December, that enough water had entered the system to cause Island billabong to overflow and start the process of floodplain inundation. This unusual pattern of flooding had some unexpected affects on the Island billabong site which should be mentioned before any description of the floodplain data.

Part of the Island transect followed a boat track that leads from Island billabong to Leichhardt billabong. A slight levee at the start of the boat track, located approximately fifty metres from the start of the transect, had been bulldozed to facilitate boat access. Ease of access was an important factor in locating the transect. Since the billabong filled much more slowly than usual, water began to move up the boat track and spill out on the distal portion of

the transect. Four days prior to floodwaters breaking the levee and inundating the whole site, water had covered the 100m location and had reached the 60m location, and two days later the water level had risen to the 40m mark. The levee bank proper was not breached until approximately 24 hours later, inundating the whole site.

The inundation of the Djabiluka transect was not observed directly. However, based on discussions with people familiar with the pattern of inundation, flooding is assumed to have occurred within a day or two after Island billabong had filled, and commenced from the end of the transect closest to the billabong. The vegetation response to flooding at Djabiluka was quite dramatic. On day 3 of inundation, there was little emergent vegetation, but, by day 9 the emergent grass was so dense as to seriously impede the movement of the boat and sampling.

Following flooding at the Island site there was rapid growth of para grass in areas were it had dominated. In contrast, those areas at Djabiluka that had been dominated by para grass at the end of the Dry-season were completely replaced by the grass *Panicum palidofolium*. The remaining areas where para grass had not been present was dominated by a finer leafed species of *Panicum*.

3.2.2 Physicochemistry of floodplain waters

The water level at both sites slowly dropped after the initial inundation (Fig. 5 and Fig. 6), then increased a second time as a result of water from a third monsoonal rain event. The conductivity at both sites varied inversely with water depth, with highest conductivity occurring during the period of low water level (Fig. 7 and Fig. 8). All water conductivity measurements are considered very low (Hart, 1974), nearing deionised water in quality. The pH tended to remain fairly constant across both sites, with only slight deviations being detected in samples on day 1 at Island (Fig. 9) and at 120m on day 24 at Djabiluka (Fig. 10). The concentration of dissolved oxygen (DO) in the water (Fig. 11 and Fig. 12) appears to reflect the water level at the time of sampling, with low DO during periods of low water level. Measurements are absent for Djabiluka day 3 due to equipment malfunction and those taken on day 9 were determined *in situ* using a Hydrolab® multi-probe meter that gave higher readings than other DO meters used in this project (Table 2). Furthermore, meter readings were approximately 80 cm deeper than for other meters.

3.2.3 The macroinvertebrate data

3.2.3.1 General description

The total number of macroinvertebrates picked from each subsample (a fraction of the main sample) ranged from 171 to 278 with a mean of 207. The mean total number of animals in a sample, based on extrapolation from the subsample, was 1341, with a range of 467 to 3440. All taxa were identified to species level except for the Prostigmata mites, Nematoda (round worms), Oligochaeta (worms), Turbellaria (flat worms) and very small or damaged Hemiptera (bugs), Diptera (flies), Ephemeroptera (mayflies) and Trichoptera (caddisflies). The total number of taxa recognised from floodplain collections was 129, with 59 taxa appearing in two or less samples. On any one sampling occasion the number of taxa collected in a sample was low, with a mean of 33 taxa (range 23 - 44) from the Island floodplain site and 20 taxa (range 11 - 29) at the Djabiluka floodplain site.

The ANOVA performed on the taxon richness index showed no significant difference over time [Table 10(a)]. Likewise, no significant difference in the Simpson's index could be found over time [Table 10(b)]. This suggests that there is no increase in taxon diversity over time at the Djabiluka site. It was not possible to include the Island data in this analysis since the days on which the samples were collected did not correspond to the collection days at Djabiluka.

Although the first three dimensions of the PCO were examined, only the first two dimensions revealed any information for both the presence/absence data and the relative abundance data. As a result only the first two dimensions have been illustrated (Fig. 13 and Fig. 14). Samples collected at similar times or distances from the billabong do not cluster in the ordinations derived from the PCO (Fig. 13 and Fig. 14), suggesting that there are no trends across time or with distance. This is confirmed by the results of the ANOVAs on the first two dimensions for both the presence/absence and relative abundance data [Table 10(c-f)]. It is interesting to note that the ordination derived from the PCO of the presence/absence data shows clustering of the samples collected from the Island site, the 300m location on day 3 at Djabiluka and the 20m location on day 9 at Djabiluka (Fig. 13). This pattern is also observable to a lesser extent in the relative abundance data (Fig. 14).

The relative abundance of the floodplain invertebrate fauna when placed into broad taxonomic groupings reveals four important groups; the Oribatida (mites), Naididae (Oligochaeta), and to a lesser extent, Chironomidae and Nematoda (Fig. 15). Other common groups in the billabong samples, such as the Odonata, Dytiscidae, Corixidae and

Ceratopogonidae represented only small fractions of the colonising fauna, despite their abundance in the permanent billabongs. Inspection of the day 3 sample from the 20m location at Djabiluka appeared to confirm these findings.

The broad taxonomic groupings reveal also a decline in the oribatid fauna and an increase in the Naididae at the Island site and at the 120m location at Djabiluka (Fig. 15). This is not a general trend, given its absence at other Djabiluka locations. This trend was apparent during the sorting of other samples collected from Island, that were not included in the final analysis, due to time constraints. It is therefore not possible to quantify this trend without examining the other Island samples.

3.2.3.2 Chironomid data

3.2.3.2.1 General description

The total number of chironomid taxa found during floodplain sampling was 55, with an average of 12 (range 4 - 20) taxa per sample at Island and 6 (range 0 - 12) taxa per sample at Djabiluka. Although many taxa were present, 26 (47%) of taxa appeared in a single sample and 13 (24%) in only two samples. Thus, most samples contained a few taxa that were common to all samples and a large number of rare taxa that only appeared once or twice. This results in low similarity indices for chironomid taxon richness between samples (Table 11).

The ANOVA performed on taxon richness and Simpson's index showed no significant differences [Table 12(a-b)], suggesting no change in taxon diversity over time. Similarly to the floodplain macroinvertebrate assemblage, an ANOVA on the first two dimensions of the PCO for both the chironomid presence/absence and relative abundance data failed to reveal any significant differences over time or with distance from the billabong [Table 12(c-f)]. This result is reflected by the PCO ordinations on both these data sets (Fig. 16 and Fig. 17)

3.2.3.2.2 Species composition

From the onset of flooding at Island billabong, the chironomid assemblage has reasonable representation of species of the subfamily Tanypodinae and Orthocladiinae and the genera *Tanytarsus* and *Parachironomus*. These proportions of Tanypodinae, Orthocladiinae, and *Tanytarsus* remain relatively constant over time (Fig. 18).

In contrast, at Djabiluka there are changes in the chironomid assemblage at each sampling location (Fig. 18). During early inundation, at the 120m and 200m locations, the chironomid assemblage is fairly depauperate, with no animals on day 3 at 200m and only two animals at 120m. This differs from day 3 samples collected at 20m and 300m at Djabiluka, in which samples of the chironomid assemblage appears to be more complex due to reasonable representation of members of the subfamilies Tanypodinae and Orthocladiinae and the genus *Tanytarsus* - a condition resembling that of the chironomid assemblage at the Island site. This similarity between the chironomid assemblage on all sampling occasions at the Island site and the earliest samples collected at the 20m and 300m locations at Djabiluka is reflected in the PCO ordinations for the chironomid assemblage presence/absence and relative abundance data (Fig. 16 and Fig. 17).

Despite the obvious differences in the chironomid assemblage during the early stages of inundation at the Djabiluka site, there appears to be a common trend. At the conclusion of observations, no matter what the starting condition, there is a distinct trend towards an assemblage dominated by species of *Chironomus* and *Parachironomus* (refer to lines linking columns in Fig. 18). The ANOVA on the relative composition of these two genera show that that there is a significant increase in the composition of *Chironomus* over time [Table 13(a)], but no significant increase occurs in the composition of *Parachironomus* [Table 13(b)]. Even though the analysis does not support the notion of an increase in *Parachironomus* over time, its numerical importance in most of the samples is undoubted (Fig. 18).

3.2.3.2.3 Instar determination

The distribution of head capsule length (HCL) for the dominant species of *Parachironomus*, *P.* sp.1, shows three distinct clusters (Fig. 19). The calculated Dyar's constant, based on the mean HCL for each of these clusters, falls within the range predicted for a species that conforms to the rule (Fig. 19). Based on this clustering and assigning each individual of *Parachironomus* sp.1 to an instar, third and fourth instar larvae obviously dominate the samples from day 3 onwards (Fig. 20). Second instar larvae were found only on day 9 of inundation. Examination of the instar distribution across different locations on the Djabiluka transect show third and fourth instar larvae dominate (Fig. 21).

The distribution of HCL for the two dominant species of *Chironomus*, *C.* sp.2 and *C.* sp.5, does not show such a clear cut clustering (Fig. 22 and Fig. 23). For both species the data could

be construed as forming five clusters rather than three (c.f. *Parachironomus* sp.1). The spread within these clusters is also markedly greater than found in *Parachironomus* sp.1. This high degree of variability and number of clusters makes it impossible to accurately assign instars to individuals or to accurately calculate Dyar's constant. Instead individuals were assigned to early, middle and late age classes. For *Chironomus* sp.2, a single larva of late age dominates the first sample (Fig. 24). On day 9 there is a large proportion of early individuals as well as a few late animals. Between days 8 and 24, there are changes in the numbers of early, middle and late age classes, but no distinct trend can be discerned. When different locations are compared by pooling the data from each of the four days, there are generally large proportions of early instars, but they do not monopolise any one location (Fig. 25). For *Chironomus* sp.5, no individuals were present on day 3. On day 9 all three age categories were present and remained present for the rest of the sampling period (Fig. 26). Although the composition of these three relative age categories varied over time, at no stage do early aged individuals have a monopoly. When differences between locations were compared, middle and late instars dominated with the exception of the 200m location (Fig. 27).

3.2.3.3 Oribatida data

In numerical terms the Oribatida represent the most important group of the colonising macroinvertebrate fauna. In all samples they represent a significant proportion of the assemblage and in most cases they dominated (Fig. 15). A total of 15 species were recognised, of which only 7 occurred in more than two samples (Table 3). When the relative abundance of the 7 species, used in the floodplain analysis, is examined it is apparent that all samples are dominated by the species *Trhypochthoniellus* sp. (Fig. 28)

4. DISCUSSION

4.1 Problems of interpretation

4.1.1 Sampling technique

The Magela Creek floodplain macroinvertebrate assemblage during the first four weeks of inundation is dominated by four taxonomic groups; the Oribatida mites, Oligochaeta, Chironomidae and Nematoda. Although other taxa occurred, these were infrequent across samples and in very low numbers. These minor taxa were important in the littoral fauna of the permanent billabongs, thus, one would expect a reasonable representation of these animals on the floodplain. Investigations of colonisation of a new reservoir in Ontario, showed a dominance of the exact same four groups that occurred in the current study (Paterson and Fernando, 1970). As in this study many of the minor colonising fauna were found to be dominant in the littoral zone. They concluded that this was the result of bias in the sampling technique, which used an Ekman grab, that collects samples from the surface of the substrate. It was concluded that the grab was inefficient for large mobile species, such as adult and some juvenile Coleoptera (Beetles) and Hemiptera (Bugs).

Although an Ekman grab was not used in the current study, the situation may be analogous. A suction sampler is designed for the removal of the surface layer of the substrate and is thus biased already towards those animals that live at the interface of water and sediment. While there was an attempt to sample animals from higher up in the water column, by moving the intake up and down, this would have sampled at most 40 cm above the surface of the substrate. Therefore, one should keep in mind that any generalisations to emerge in this study should be restricted to the benthic macroinvertebrate assemblage, rather than the floodplain macroinvertebrate assemblage as a whole.

Another problem with the sampling technique is that it does not allow direct quantitative comparisons between samples. It is common for studies of colonisation to examine the changes in abundance of taxa, or the whole assemblage, over time. A requirement for making such comparisons of abundance is that the sampling technique must be quantitative. It is difficult to take quantitative samples using a suction sampler at the best of times. One technique to overcome this problem is to limit a sample to a set volume of water; however, this is itself, problematic. For example, if the compaction of the sediment varies, some samples would contain less sediment than others, possibly leading to a lower abundance of sediment-dwelling

fauna in some samples. Since there are problems associated with any collection technique, one cannot claim all results void, otherwise it would be impossible to gain any data. However, I feel that sampling conditions on the Magela floodplain had higher than acceptable problems that justifies not using any data on abundance.

Further problems can be attributed to the very dense vegetation associated with the inundated floodplain. First, it was not possible to sample by pumping a set volume of water, because dense vegetation resulted in a thick root mass that covered the substrate. As a result the amount of effort in obtaining a sample varied across locations. If a set volume of water was used then some samples may have differed in the amount of benthos habitat sampled, which in turn could have affected the numbers of animals captured. Second, the dense vegetation encountered were all grasses with long, leaf blades that readily broke off during sampling and clogged the suction sampler intake. This caused further variations in the flow of water and amount of material collected, thus invalidating any comparisons between samples. Despite the problem with abundance comparisons, it is still possible to focus on the presence of taxa and the relative abundance (or composition) of taxa across samples. This works on the assumption that the assemblage at a given location was sampled in a random manner.

4.1.2 Natural variation

The use of presence/absence data and relative composition data is not without its problems. The most common problem associated with monitoring changes over any temporal and/or spatial scale is that of variability. Common causes of variability are environmental heterogeneity and the degree to which benthic invertebrates aggregate (Norris and Georges, 1986). Such variability results in a dilemma for the researcher: is a change in taxa present, relative composition, or abundance due to a biological reason or simply the effects of a highly variable environment. One solution to the problem is to collect replicate samples (Norris and Georges, 1993). This raises the new problem of how many replicates are required to account for the natural variability in a system. Since collecting and sorting samples is a time-consuming process, the collection of large numbers of replicate samples is not desirable. One approach is to calculate the minimum number of replicates required based on the variability of data obtained from a pilot study. By using the following formula it is possible to calculate the minimum number of replicates (n) required:

$$n = \frac{S^2}{Y^2} \frac{1}{D^2}$$

Where S^2 is an estimate of the variance of measurements at the site or time in question; Y^2 is an estimate of the mean value of the measurements; and D is the desired level of precision (Norris and Georges, 1986).

This study clearly lacks replication which suggests that the lack of any detectable change in the floodplain assemblage, as a whole, could be the result of natural variation masking a true trend. Using the above equation, a minimum of 9 replicates, for a level of precision of 10%, would be required to eliminate the effects of variability. The collection and analysis of nine replicates was not possible given the time constraints imposed on this project. Before the reader confines him or herself into believing that any results in this study cannot be sufficiently separated from the effects of natural variation, I should point out that this study is not without any form of replication.

Whether there is adequate replication in this project is dependant on how one looks at the data. Clearly there is no replicate transect for the Djabiluka site. However, if one considers the observed change in the composition of the chironomid assemblage at the Djabiluka site, towards one dominated by *Chironomus* and *Parachironomus*, then the context of the situation changes. Now one is considering whether at any point along the transect at Djabiluka there is a change towards such an assemblage. The unit of interest has shifted away from the transect, to any point along the transect. Since four locations on the transect were used we now have four replicates. Thus, one can be more confident about such a claim.

The inclusion of the island site in the analysis was to provide some form of replication of the Djabiluka transect. The faunal assemblage at the Island site is clearly very different from the Djabiluka site as a whole. There are a great may differences between the two sites in terms of the pattern of inundation, location on the floodplain (upper versus lower) and vegetation. Given that one location only was used from Island it is difficult to know whether colonisation at Island is typically different from Djabiluka or whether colonisation at Island is similar to Djabiluka accept at the 100m location, due to some unique factor (refer to section 4.4.3.2 for a possible explanation). This question can only be addressed by examining the other samples collected at the Island site.

4.1.3 Temporal variation

So far I have only discussed natural variation on a spatial scale without any real mention of temporal variation. Just as spatial replication is needed in a broad based community study, it is equally important to have temporal replication. From the results it is clear that one can make some claims about the colonisation of the Magela Creek floodplain. For example, the chironomid assemblage of the floodplain adjacent to Djabiluka billabong becomes dominated by *Chironomus* and *Parachironomus*; but how typical is this of colonisation? Are these observations typical of the colonisation process in general or just a freak occurrence due to a unique set of environmental conditions particular to this year's Wet-season? Given that this study was conducted during a single season, it is impossible to provide answers for such questions. This doesn't make the study any less important, as this work provides a set of testable hypotheses that can be used in future studies of this floodplain system.

4.2 General discussion

The general composition of the floodplain macroinvertebrate fauna found in this study and an explanation on why certain taxa were rare has already been alluded to in section 4.1.1. To reiterate there were four major groups found in this study; the Oribatida, Oligochaeta (predominantly Naididae), Chironomidae and Nematoda. Since these four groups accounted for such a large proportion of the samples, I wish to concentrate the rest of the discussion on these four taxa.

4.3 Oligochaeta and Nematoda

The contribution of the Oligochaeta and Nematoda to any discussion on colonisation is limited, due to the lack of taxonomic resolution for these organisms. Identification of the nematodes to a taxonomic level lower than phylum, is not possible without the use of special preservation techniques, that were not used in this study. Furthermore, the numbers of animals in a sample are only approximate as the nematodes in this study were very small and difficult to extract from the samples.

There was a potential for species level identifications with the oligochaetes, but this was severely hampered by the tendency of these animals to fragment during collection and

subsampling. Families were identified and three genera could be confidently named, but given the large proportion of unidentifiable Naididae, it would be rather difficult to detect any changes across time or locations. One observation that does stand out is the large proportion of Naididae compared to the Tubificidae. Species of Tubificidae are well known for their tolerance of low oxygen and polluted conditions (Williams, 1980). Given the high organic load of the floodplain soils one would expect low oxygen conditions to be a frequent occurrence (McLachlan, 1974b). Under such conditions one would expect tubificids to be reasonably successful. One possible explanation for the apparent success of Naididae and the rarity of Tubificidae in the few weeks after inundation comes from the work of Juget and Lafont (1994). Analysis of the species traits of several oligochaete families occurring in the Upper Rhône River and its floodplain, in France, found that species of Naididae possess the traits of good colonisers. These traits include having many reproductive cycles per year, short generation times, asexual reproduction by budding off the parent, and exhibiting generalist feeding preferences. This contrasts with other families (including Tubificidae) that have longer generation times, mostly reproduce sexually and have more specialised feeding preferences. Therefore it is possible that the predominance of Naididae on the Magela floodplain during the first few weeks of inundation could be due to their life-history which predisposes them to being good colonisers, in contrast with species of Tubificidae.

4.4 Chironomidae

4.4.1 Dominance of *Chironomus*

While a number of taxa were able to colonise the floodplain benthos, during the first four weeks of inundation, only the chironomids showed any detectable changes over time. This is not an isolated case. Many studies that examine invertebrate colonisation of temporary, standing water habitats note the importance of the chironomids in the early stages of colonisation (McLachlan, 1970; Paterson and Fernando, 1970; McLachlan, 1974a, 1974b; Cantrell and McLachlan, 1977; Maher and Carpenter, 1984). In a study of colonisation of a marsh habitat in Canada, chironomids were the only group of macroinvertebrates to show any detectable change in response to flooding (Murkin and Kadlec, 1986). Species of the genus *Chironomus* have been identified in all of these studies as being the most important during early inundation. There are several potential reasons as to why species of *Chironomus* are such successful colonisers; these being high fecundity, the possession of physiological and behavioural adaptations to low oxygen

conditions, differential predation and/or competitive superiority during the early stages of inundation.

Fecundity

Chironomids typically lay their eggs in batches, consisting of 20 to 30 eggs in smaller species, up to several thousand in larger species (Nolte, 1993). Since the number of eggs produced is related to the size of the species, large species such as those of *Chironomus*, tend to be highly fecund. Typically, chironomid females only produce a single egg mass (or batch of eggs). However, studies on the reproductive system of *Chironomus plumosus*, a species that is frequently cited as a primary coloniser in temperate still-water habitats in the Northern hemisphere, have shown this species capable of laying up to three egg masses (Wensler and Rempel, 1962). Even more impressive is the finding that the Australian species, *Chironomus tepperi*, can produce up to six egg masses (Martin and Porter, 1977). While it is not known whether such reproductive traits are present in the species of *Chironomus* occurring in this study, there is some possibility that high fecundity could be a contributing factor to their success. This is clearly an area that requires further research.

Low oxygen conditions

Habitats such as floodplains or wetlands, which contain soils enriched with organic matter, are often subjected to problems of low concentrations of dissolved oxygen or even anoxia (McLachlan, 1974b). It is the ability of species of *Chironomus* to exploit such habitats that is the most frequently-cited reason for the early dominance of this genus (McLachlan, 1970; Murkin and Kadlec, 1986). Since species of *Chironomus* generally live in the soft sediments of lakes and wetlands, which experience periods of low oxygen or anoxia, they have developed both physiological and behavioural traits that enable them to survive. Many species of *Chironomus* construct tube-like retreats in the sediments from where they feed on detritus. In low oxygen conditions the entrance of the tubes are raised to a height, above the sediment surface, which avoids the most oxygen-depleted layer of water. In experiments using *Chironomus plumosus*, Konstantinov (1971) observed that the height of the tube entrance was modified by the inhabitant such that an oxygen concentration of 0.7-0.9 $mg.L^{-1}$ was maintained at the mouth of the tube. Furthermore, if oxygen concentrations continued to fall, larvae would undulate their bodies, which created a flow of water through the tubes, which helped to remove oxygen depleted water from the retreat and replace it with fresh water.

Among the physiological adaptations to low oxygen conditions is the possession of haemoglobin, which can be found in all species of the subfamily Chironominae (including *Chironomus*) and some members of the subfamily Tanypodinae. Chironomid haemoglobin has a high affinity for oxygen and can be readily saturated when fresh water passes through the tubes as a result of body undulations (Konstantinov. 1971). Another physiological adaptation is the ability to survive conditions of anoxia for periods of up to several weeks, by converting stored glycogen into energy (Augenfeld, 1967). The ability to survive anoxic conditions is dependant on the amount of stored glycogen which is in turn proportional to the body size of the animal. While all members of the Chironominae subfamily contain glycogen, only the largest species would have sufficient stores to survive any significant period of anoxia. Thus smaller species of Chironominae, such as those belonging to *Tanytarsus*, cannot survive anoxic conditions (Augenfeld, 1967).

Measurements of dissolved oxygen taken during floodplain sampling failed to show any signs of anoxia, but low oxygen conditions were detected at the Djabiluka site (Fig. 12). It is quite possible that anoxic conditions were present at some stage during this study but were not detected. Most dissolved oxygen (DO) measurements were taken in the top 10cm of the water column, with the exception of day 9 when the Hydrolab® was used. The oxygen probe on the Hydrolab was located approximately 80cm below the water surface. This could be partly responsible for the lower oxygen readings obtained on this day. Even at greater depths it may not have been possible to detect anoxia. Oxygen consumption within the sediment can create a sharp gradient of reducing oxygen concentration in the few millimetres or centimetres above the sediment surface (Int Panis *et al.*, 1995). Without precise control over the depth at which DO measurements are taken it may be impossible to determine whether anoxic conditions exist in the benthos. There may also have been very high diurnal variation due to the dense vegetation. Photosynthesis during the day would cause DO levels to rise, while at night plant respiration would cause the DO level to drop, perhaps to very low concentrations (Westlake *et al.*, 1980). Since floodplain water samples were collected late in the morning, it may not have been possible to detect anoxia. Circumstantial evidence for the presence of anoxic conditions comes from the observation that the sediment from some samples, particularly late in the study, had a strong odour of hydrogen sulphide which is produce by the breakdown of organic material in an oxygen free environment (Gross, 1990).

Differential predation

Chironomids are prey for a wide variety of invertebrates (Crosby, 1975; Reynoldson and Sefton, 1976; Davies *et al.*, 1979; Johnson, 1985; Soluk and Clifford, 1985; Hill, 1988; Peckarsky *et al.*, 1990), including other chironomids (Jones, 1974). Amongst chironomids, those that do not live in fixed retreats tend to be the most susceptible to predation. In species that live in fixed retreats, those that spend the greatest proportion of their time engaged in activities out side of the retreat are most susceptible (Brown *et al.*, 1980; Hershey and Dodson, 1985; Hershey, 1987). Species of *Chironomus* typically live in fixed retreats, however, the contribution of differential predation to the success of the taxon would be minimal, given the very low abundance of odonates, dytiscids, and other predatory invertebrates in the samples. The impact of fish predation on chironomid larvae is probably low also. At the end of the Dry-season the fish populations in the permanent billabongs are usually in a state of decline as fish kills are a common occurrence due to poor water quality (Brown *et al.*, 1983). Following inundation, fish disperse out onto the vast area of the floodplain. The resulting low densities of fish and the dense vegetation of the floodplain, which could provide a refuge (Marchant, 1982), make it seem unlikely that fish predation would have a significant impact on chironomid numbers.

Competition

Lastly, the overall success of *Chironomus* during the early stages of floodplain colonisation could be due to the successful outcome of interspecific competition. When larvae of *Chironomus plumosus* were added to cylinders containing the benthic fauna from a Polish lake, a marked reduction was observed in the number of *Tanytarsus gregarius* and *Cladotanytarsus mancus* (Kajak *et al.*, 1968). In a newly-flooded lake in England, competition between *C. plumosus* and *T. gregarius* was ascribed to physical disturbance caused by the tube-building activities of *C. plumosus* which caused *T. gregarius* to leave their own tubes (Cantrell and McLachlan, 1977). The size of the larvae, rather than the species concerned, was found to be the critical determining factor in the outcome of competition for space. Since *C. plumosus* is considerably longer than the largest *T. gregarius* larvae, competition resulted in the success of *C. plumosus*.

The success of *Chironomus* as an early coloniser is probably not a result of competitive superiority alone. *Chironomus* is often referred to as a "fugitive" taxon (a term first used by Hutchinson, 1951), as although they quickly invade newly-formed habitats and build up large populations, in the long term they are poor competitors (Kajak, 1964), and consequently become replaced by other mud dwellers (Paterson and Fernando, 1970; Cantrell and McLachlan, 1977).

Such claims seem to contradict the notion of the competitive superiority of the genus. The most likely scenario in this system is that species of *Chironomus* are superior competitors during the periods of greatest environmental instability, such as shortly after inundation, due to the various aspects of its biology previously mentioned. As the system stabilises, it loses its superiority, giving away to a more diverse assemblage, except perhaps in areas that experience low oxygen conditions.

As a final cautionary note, most of the work on *Chironomus* discussed here has been performed on Northern hemisphere species and one or two tropical species from Central Africa. Whether direct comparison can be made between these species and the species of *Chironomus* that dominate the Magela floodplain remains to be seen, due to the lack of work on tropical Australian species.

4.4.2 Dominance of *Parachironomus*

While it is possible to speculate as to why *Chironomus* is so successful, its coexistence with *Parachironomus* is less than clear. Knowledge on the biology and life history of *Parachironomus* is virtually non-existent (Peter Cranston, personal communication). Of the four species known to occur in the Kakadu region only two have been reared from larvae to adults. The remaining two species are known only from the pupal stage of the life cycle (Cranston, 1996). Typically where *Parachironomus* is found, the taxon usually constitutes a small proportion of the chironomid assemblage (O'Connor *et al.*, unpublished data), which makes their codominance on the Magela floodplain even more surprising. Although, little is known on the biology, it is unlikely that their presence is due to the possession of similar traits to *Chironomus* (Peter Cranston, personal communication).

Several explanations come to mind, some of which can be tested against evidence gained through this study. The most obvious explanation is the lack of direct competition between these two taxa. Whether this separation between taxa is due to different microhabitat or trophic requirements is impossible to ascertain given the lack of knowledge on *Parachironomus*. A second explanation is that *Parachironomus* may not be successfully coexisting with *Chironomus*, but its abundance was being buffered by *en mass* egg laying. The reasoning for such a line of thinking is a result of the numerical dominance of *Parachironomus* in the Malaise trap samples. If this was the case, then one would expect earlier larval stages (2nd instars) to dominate during early inundation and remain dominant over time, rather than seeing a population, derived from a synchronised egg-laying, aging with time (i.e. a shift in dominance

towards 3rd and then 4th instars). Since the instar determination work performed on the dominant species of *Parachironomus* did not show the early and continued dominance of 2nd instars, one can easily discount this explanation as the cause of *Parachironomus*' success. Clearly, this study can document only the dominance of this group in the colonisation of the Magela Creek floodplain for this particular Wet-season. The question as to the cause of its success or whether this is typical of colonisation on this floodplain remains to be answered.

4.4.3 Sources of colonisation

4.4.3.1 *Chironomus* and *Parachironomus*

Given the numerical dominance of *Chironomus* and *Parachironomus* in floodplain colonisation, at the Djabiluka site, it is important to determine the sources of colonisation for these taxa. Species of *Parachironomus* were identified in both the billabongs and the malaise trap samples. Although there is no direct evidence that the species collected in the malaise traps are identical to those found on the floodplain, the fact that species out of the four species known from Kakadu were found in both habitats suggests they are the same species. However, as already alluded to in the previous section (see section 4.4.2), colonisation from aerial sources seems unlikely, due to the lack of 2nd instars throughout this study. This would suggest that most of the colonisation was occurring by animals that have either migrated and/or been flushed out of the billabong. While this seems the most likely source, it would be inappropriate to completely rule out the floodplain soils as a source of colonisation. There is a possibility that *Parachironomus* was present in the soils, since larvae found during the soil-rewetting experiment could not be identified past family due to the live-sorting technique used. Furthermore, the soil may not have been sufficiently disturbed during live sorting to reveal the presence of sediment-dwelling chironomids. The lack of information on the biology of *Parachironomus* means it is not known if this taxon is likely to show adaptiveness to surviving in the floodplain soils during the Dry-season. Since only *Polypedilum* and *Nanocladius* were identified through the use of shed pupal skins and/or emerged adults, during the rewetting experiment, it is unlikely that *Parachironomus* was present (table 8).

The source of colonisation for species of *Chironomus* is not clear since the genus was absent from the Malaise trap samples, floodplain soils and only one species, *Chironomus* sp.2, was found in very low numbers in a single sample from the littoral zone of Djabiluka billabong. One possibility is that gravid females are flying in from areas outside the study site as adult

chironomids have been shown to make wind-assisted dispersal flights, in some instances, of up to several hundred kilometres (Holzapfel and Perkins, 1969). As with *Parachironomus* it is impossible to exclude the floodplain soils, but the absence of pupal skins and emerged adults from the soil, and lack of reports of drought resistance in this genus, suggests that they were not present. As with *Parachironomus*, an examination of the distribution of instars should narrow down the likely source. If ovipositing adults are the primary source, one would expect early (2nd) instars to predominate initially, followed by a shift with time towards later instars. If the animals are derived from billabongs, one would expect a higher proportion of later instars (3rd and 4th) at the outset. Alas, the distribution of head capsule length (HCL) in the two predominant species of *Chironomus* in this study (*Chironomus* sp.2 and *Chironomus* sp.5) did not lend itself to instar determination. While there is some clustering of HCL it is unlikely that these represent instars for two reasons. First, there is too much spread in each cluster, far higher than can be considered normal (Peter Cranston, personal communication). Second, in both species there appears to be five distinct clusters, which might be considered instars (Fig. 22 and Fig. 23). Since chironomids are known to have four instars the clustering cannot be considered indicative of instars of a single species.

The difficulty in identifying instars for these two species of *Chironomus* could indicate that each species is a composite of several species, which is causing the large variation in HCL, or it could be that the amount of variation in HCL was higher than expected. The former is probably the more likely explanation (Peter Cranston, personal communication). So where does this leave *Chironomus* in terms of sources of colonisation? Although direct instar determination on the two species of *Chironomus* is not feasible, we can still get a feel for instar composition if we use the relative age classes. In both species there is insufficient dominance of young individuals, to suggest that oviposition by adults is the main source of colonists.

This leaves the permanent billabongs as the other main source. The rarity of *Chironomus* in the permanent billabongs is a little surprising. Certainly this genus has the reputation of containing "fugitive species" that make poor competitors in well developed communities, which would lead one to expect this taxon to be present in low numbers. However, a survey the littoral chironomid fauna of seven billabongs within the creek channel proportion of the system at the end of the 1995 Dry-season revealed low, but significant, numbers of *Chironomus* (O'Connor *et al.*, unpublished data). The higher abundance of the genus in the upstream billabongs sampled in 1995 can be interpreted in one of two ways. Either the fauna in these billabongs are substantially different to the floodplain billabongs, or the abiotic and/or biotic conditions differed between the late Dry-seasons of 1995 and 1996. Marchant (1982) suggested that

Djabiluka billabong has a similar littoral fauna to the billabongs upstream of the floodplain, pointing towards a temporal explanation for the low abundance of *Chironomus*, rather than differences between floodplain and upstream billabongs *per se*. Another possibility is that the high tolerance of low oxygen conditions shown by *Chironomus* may enable it to inhabit the profundal zone of Djabiluka billabong which was not sufficiently explored in this study.

Rain-formed pools on the floodplain, that were not studied in this project, could also have been a source of these animals. Towards the end of the Dry-season, localised thunderstorms increase in frequency in the build up to the Wet-season, giving rise to numerous small bodies of water on the floodplain. These pools may provide the necessary conditions for species of *Chironomus* to persist until the start of Wet-season flooding, providing sources of larvae during colonisation. A pre-Wet-season visual survey of one such pool revealed large chironomid larvae, possibly of *Chironomus* due to their size (personal observation). However, the transects used in this study were selected to reduce the influence of such temporary sources of colonisation by minimising the distance between the transect and these pools.

4.4.3.2 Remnant standing water populations

Significant numbers of Tanypodinae, Orthocladiinae and the tribe Tanytarsini (Chironominae) are quite characteristic of chironomid assemblages in standing waters from a number of environments ranging from the Nearctic to the Tropics (Table 14). The billabongs sampled in this project concur with such findings, by having reasonable representation by the Tanypodinae, Orthocladiinae and Tanytarsini (which includes the genus *Tanytarsus*; Fig. 2). It is interesting that the chironomid assemblage at the 100m location at Island and the 20m (day3 and Day 9) and 300m (day3) locations at Djabiluka also bear some resemblance to a permanent standing water assemblage (Fig. 18).

Species of Tanypodinae and Orthocladiinae are regarded as being typical of standing-water communities (Rosenberg *et al.*, 1984) and not early colonisers. Since these floodplain samples resemble the standing water communities in the billabongs, it is important to try to understand what might be the underlying cause of this observation. One possibility is that the chironomid assemblage at these locations are the remnants of a standing water assemblage prior to inundation. At the 100m location at Island and the 300m location at Djabiluka there could have been a standing pool of water towards the end of the Dry-season, which may have persisted long enough for a typical standing water assemblage to develop. Some circumstantial evidence

makes this a reasonable assumption: the pooling of water near the 100m location at Island, due to pre-flooding inundation along the boat track, indicates a natural depression in which water might collect (refer to description of inundation in section 3.2.1). Observations at the 300m location at Djabiluka at the time of soil sampling suggested this location had once been a pool of standing water, due to the lack of vegetation so prevalent at other locations on the transect (Table 6) and its location in a slight depression. The presence of supersaturated soil at Island 100m and Djabiluka 300m, as revealed by the soil physicochemistry analysis, shows that there was free water present, which adds further weight to the argument.

The presence of supersaturated soils could also provide the means by which the remnant pool assemblage survives until inundation by floodwaters. One would expect some support for this notion from the soil rewetting experiments. The presence of Chironomidae and Tabanidae larvae in the soil at the 100m location at Island could represent animals that survived in the supersaturated soil (Table 8). This is certainly not conclusive as there is the obvious possibility the chironomids emerged from a desiccation-resistant cocoon (Grodhaus, 1980). Desiccation-resistant cocoons may also have been responsible for finding chironomids in the subsaturated soils at the 20m and 200m locations at Djabiluka. The presence of Tabanids is not necessarily indicative of an aquatic environment as larvae of the subfamily Panginiinae live in damp soil and mud (Williams, 1980). Ceratopogonidae at the 300m location at Djabiluka, provides more substantial evidence for the survival of aquatic larvae in the supersaturated soil, since there is no published literature to suggest drought resistant species occur in this family. Further circumstantial evidence to the existence of remnant pools was the observation of a number of rain-formed pools on the otherwise dry floodplain in early October (as discussed in section 4.4.3.1).

The evidence suggests that there could be a fourth source of colonisation; the supersaturated soils that are remnants of rain-formed pools. As to why the chironomid communities at the two locations just discussed (Island 100m and Djabiluka 300m) then diverge over time, shifting towards dominance by *Chironomus* and *Parachironomus* at Djabiluka, is not easy to ascertain. Clearly there are some major differences between sites with respect to the vegetation, distance from nearest billabong and pattern of flooding, but whether these factors would influence the success of *Chironomus* and *Parachironomus* will not be clear without further investigation.

The source of the putative standing water assemblage at the 20m location at Djabiluka is probably derived from a different source. The proximity of this location to the permanent billabong, makes it likely that the fauna is a result of dispersal of billabong taxa out into the

floodplain. The use of a 250 μm mesh sweep net on day 3 could also have been responsible for the similarity of the sample to the billabong littoral samples, since this technique is more likely to collect animals from higher up in the water column, including the vegetation, when compared to the suction sampler. If a different habitat was being sampled by the sweep net then one would expect subsequent samples collected from the 20m location to differ. Identifying changes in fauna, as a result of a change in sampling technique, could be hindered by the natural transformation of the assemblage due to the colonisation process. Given that there is a similarity in the species present in the sample collected on day 9 at the 20m location (Fig. 16), which was collected using the suction sampler, I would suggest that differing sampling technique is not responsible for the likeness of the day 3 sample to samples collected from the littoral zone of Djabiluka billabong.

4.5 Oribatida

4.5.1 Life history

There are some aspects of Oribatida life history pertinent to this study on aquatic colonisation. *Trhypochthoniellus* sp. belongs to the cohort Desmonomata which are considered "primitive". The Desmonomata represent something of a biological anomaly as most of the families and some superfamilies occurring in this cohort (including the Trhypochthoniidae) are entirely parthenogenetic, that is they possess the ability to produce offspring from unfertilised eggs (Norton *et al.*, 1992). Thus one can be reasonably certain that *Trhypochthoniellus* sp. is a parthenogen. The fact that this species is so prominent raises some interesting questions which relate to assumptions about the habitat requirements and ecological consequences of being parthenogenetic.

It is a commonly held belief that the occurrence of parthenogenesis can be correlated with certain biotic and abiotic conditions in the environment. Modern evolutionary theory suggests that genetic variability is important in communities that are biologically complex due to the coevolutionary struggle of individuals against parasites, predators and competitors. Since sexually reproducing animals have a more flexible genome, through recombination, than parthenogenetic animals, they can adapt more easily to such pressures (Norton and Palmer, 1991). Conversely, parthenogens, due to their low genetic variability might be expected to occur in biologically simple habitats. Ecosystems tend to be more biologically complex under benign physical conditions and more simple when subjected to unstable physical conditions

(Odum, 1983). This has been proposed as an explanation to parthenogenetic organisms being found commonly in patchy habitats, freshwater, and especially newly formed environments or disclimax habitats (sites kept underdeveloped by frequent disturbance), such as soil subjected to annual flooding (Norton and Palmer, 1991).

Parthenogens have also been theorised to have certain advantages in colonisation of newly formed habitats. Such advantages include not having to find a mate; all offspring are capable of reproducing (i.e. there is no cost associated with having to produce males which don't produce any offspring on their own [Ridley, 1993]); and have high fecundity since they need not waste resources in activities such as finding mates and courtship. It was the very high correlation between the occurrence of parthenogens and the freshwater environment that led research to look for a more direct, and simple, underlying cause, than that suggested by ecological theory (Norton and Palmer, 1991). It was thought that perhaps the normal mating behaviour of oribatid mites was not effective in a freshwater environment. The fact that sexual freshwater species of mites have atypical methods of reproduction has been suggested as supporting such a notion (Norton and Palmer, 1991). Normal mating behaviour, in sexual species of oribatid mites, involves the male depositing numerous, freestanding, packets of sperm (spermatophores) which are then picked up by the female without the male being present; there is no direct interaction between the sexes during reproduction. Simple explanations of why freshwater environments hinder may hinder sexual reproduction, such as osmotic differences affecting free-standing spermatophores or problems of communication between sexes, seem unlikely since this method of sexual reproduction is used quite successfully by many Hydracarina (freshwater Prostigmata) mites (Norton and Palmer, 1991). None-the-less, major lineages in the Hydracarina show a distinct trend towards closer association of the sexes and rapid sperm transfer, suggesting that there may be some inherent disadvantage of sexual reproduction in freshwater (Norton and Palmer, 1991). For example Mitchell (1958) found that free-standing spermatophores of *Hydryphantes ruber* had a functional lifespan of only a few minutes. Thus there may still be some advantages of being parthenogenetic in a freshwater environment.

The presence of the parthenogenetic *Trhypochthoniellus* sp. during the early stages of inundation on the Magela floodplain can be understood through modern ecological theory and the possibility of reproductive advantages. However, if one examines the geographical distribution and biology of parthenogenetic species of Oribatida, we see a very different picture. Many parthenogenetic oribatids are found in unstable habitats, but so are many sexually reproducing species. For example, parthenogenetic species occur in abundance at high latitudes

and altitudes, which are typically considered unstable environments, but so do many sexual species of oribatid mite (Norton and Palmer, 1991).

The theory that an asexual lifestyle makes for a good coloniser due to the ability to quickly increase the size of a population appears inapplicable to the Desmonomata. Most species have generation times of one to two years and females usually produce about 50 eggs in a lifetime, giving them very low fecundity. This coupled with the fact that most species are slow moving and have no special means of dispersal predicts these animals to be poor colonisers in the conventional sense (Palmer and Norton, 1992).

Although parthenogenesis may have some adaptive value in freshwater, the dominance of a parthenogenetic oribatid mite in floodplain colonisation is probably unrelated to its mode of reproduction and the relative stability of the habitat. Rather than *Trhypochthoniellus* sp. being adapted to an aquatic lifestyle by being parthenogenetic, it is more likely that this species, and other aquatic Desmonomata, are pre-adapted to such an environment. Unlike most parthenogens, the Desmonomata have no close relatives that reproduce sexually (Palmer and Norton, 1992) with many families and even superfamilies contain no sexual species at all. This is particularly puzzling from an evolutionary view point as asexuality is believed by many to be an evolutionary dead-end. Given the theoretical short life of parthenogenetic species on an evolutionary time scale, due to genetic inflexibility and the accumulation of deleterious genes, it is argued that higher taxonomic groups of parthenogens could not evolve. Yet it is impossible to believe that all the asexual species and genera within completely asexual families could have arisen independently. The only valid conclusion is that the radiation of the Desmonomata occurred sometime after sexual reproduction was lost. The amazingly successful radiation of these species, given their supposedly short evolutionary lives, is impressive to say the least. The family Trhypochthoniidae, is known from Jurassic fossils (Krivolutsky and Druk, 1986), and biogeographical evidence suggests that the origins of the extant species, *Mucronothrus nasalis*, predates the break up of Pangea some 200 million years ago.

Thus, the dominance of *Trhypochthoniellus* sp. in floodplain colonisation is probably not due to any advantage of parthenogenesis in colonisation or the fact that the seasonally inundated floodplain is an unstable and thus biologically simple system. It appears that parthenogenesis is a residual of an asexual ancestry that may preadapt this species to an aquatic or at least semi-aquatic lifestyle.

4.5.2 Sources of colonisation

The Oribatida are known to have aquatic species, but there are also many terrestrial species that inhabit periodically flooded soils (Beck, 1972). While it is not unusual to find terrestrial invertebrates in colonisation projects, they don't usually persist for very long with most species being in some state of decomposition when found (Mark Harvey, personal communication), which can make them easy to identify. This may not be so straight forward with the Oribatida, in which the metabolic rate is very slow, which could enable terrestrial species to persist in flooded conditions for some time (Matthew Colloff, personal communication). The only real way of determining whether an oribatid shows adaptiveness for an aquatic life style is to study the autecology of the species involved. Where this is not possible one must look for the presence of aquatic species within the same taxon and signs that it may be feeding or reproducing in such an environment. This is certainly not a problem for *Hydrozetes* which are considered exclusively aquatic (Krivolutsky and Druk, 1986).

Given that *Trhypochthoniellus* sp. was found to dominate the oribatid billabong assemblage and has known aquatic relatives (Norton and Palmer, 1991) we can assume that it shows adaptiveness for an aquatic life style. This does not conclusively prove this species to be fully aquatic due to the presence of *Trhypochthoniellus* sp. in the floodplain soils. The presence of this species in the floodplain soils can be interpreted in several ways. This species could be equally adapted to a terrestrial lifestyle which would enable the species to exists in both environments. Unfortunately there is no literature to test the validity of such a statement. Another interpretation of the animal's presence in the floodplain soils, is that individuals are stranded in the soil as the floodwaters recede. The ability to become dormant during undesirable conditions has been documented in some oribatid species (Norton, 1994). If *Trhypochthoniellus* sp. has such an ability, it could remain dormant until the next cycle of inundation. While these interpretations are completely speculative it does propose some interesting questions for future research. If this species does turn out to be equally adapted to both environments, does it inhabit the terrestrial habitat by choice or is its presence in the soil a result of the individuals inability to track the receding floodwaters?

4.6 Future research

This study raises many questions about colonisation of the Magela floodplain that cannot be answered without further study. Directions for future research have been eluded to throughout this discussion, so for the sake of brevity, only the most important will be outlined here.

The issue requiring most attention is that of spatial and temporal variability. Do the observed trends in the macroinvertebrate assemblage on the floodplain at Djabiluka truly reflect colonisation at this site or the floodplain in general? Since there are obvious differences in upper and lower floodplain habitats (Djabiluka *c.f.* Island) I would suggest focussing attention on the lower floodplain, using the findings of this study to generate hypotheses for testing.

The low abundance of *Chironomus* in permanent billabong samples (*c.f.* 1995/96 late Dry-season) and the importance of *Parachironomus*, considered to be a minor taxon in most studies, raises the question of how typical are these observations to colonisation in other years. The volume of water entering the system is variable from year to year, having affects on the number of waterholes present and the level of water left in the permanent billabongs during the Dry-season (Finlayson *et al.*, 1989). Perhaps these conditions alter the faunal composition of these sources of colonisation.

Finely divided habitats are known to support more species than more coarsely divided habitats (Tokeshi, 1994). On this assumption, one would expect the floodplain vegetation to support a more diverse fauna compared with the sediment-dwelling fauna, as suggested by the billabong littoral zone samples. Thus, studies of the vegetation-dwelling invertebrate assemblage will probably reveal a very different story to colonisation, perhaps due to greater effects of competition as a result of greater taxon diversity.

Finally, what happens to the benthic invertebrate community as the season progresses? A study of feeding groups would be useful in answering such a question. During these early stages of inundation one would expect detritus feeding taxa, such as *Chironomus* and naidid worms, to dominate given the high organic content of the soil. Is there a trend with time towards invertebrates that utilise the decaying plant material likely to result from the prolific floodplain vegetation as the season progresses? and do predators ever play a significant role in this habitat?

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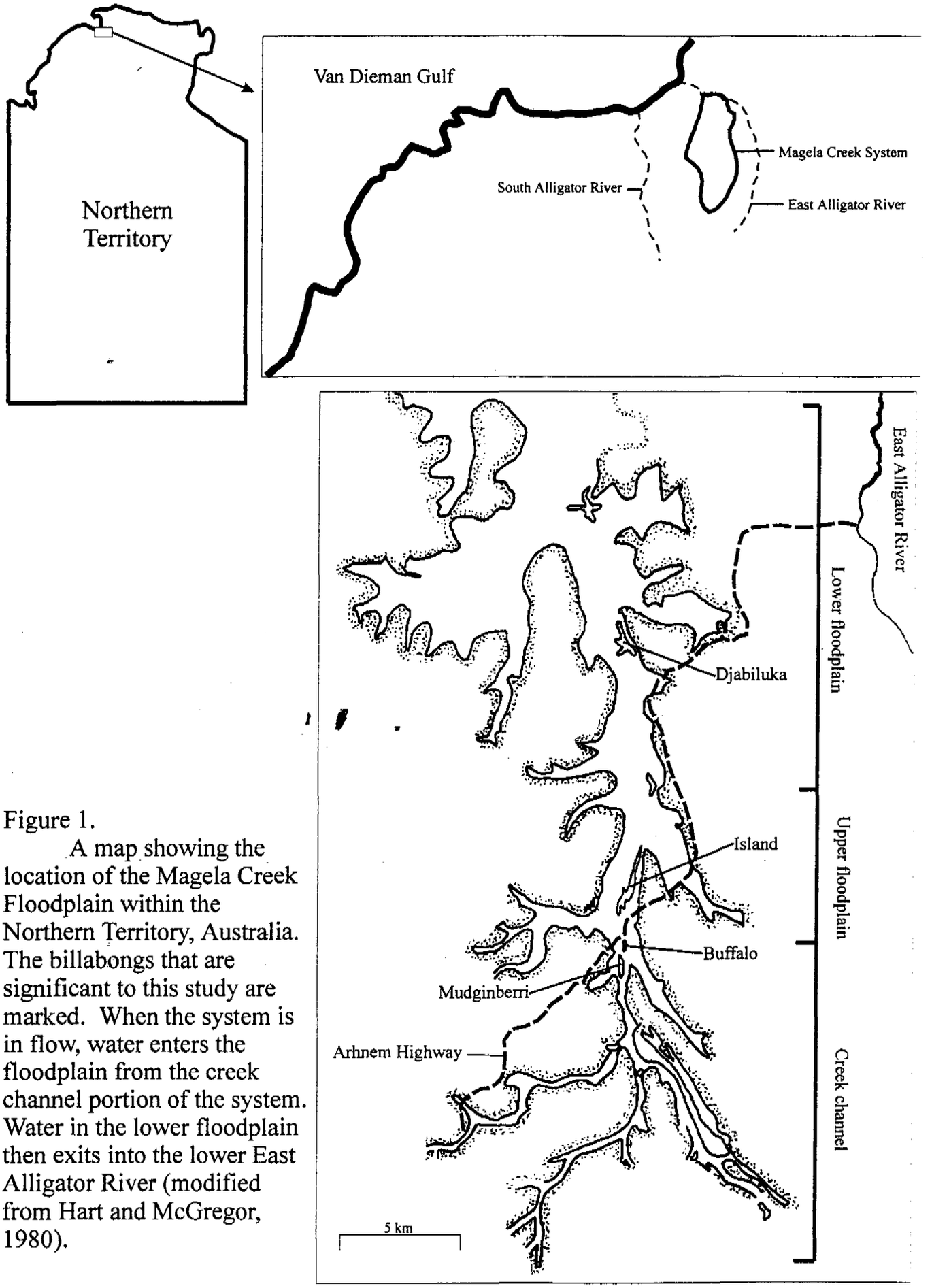
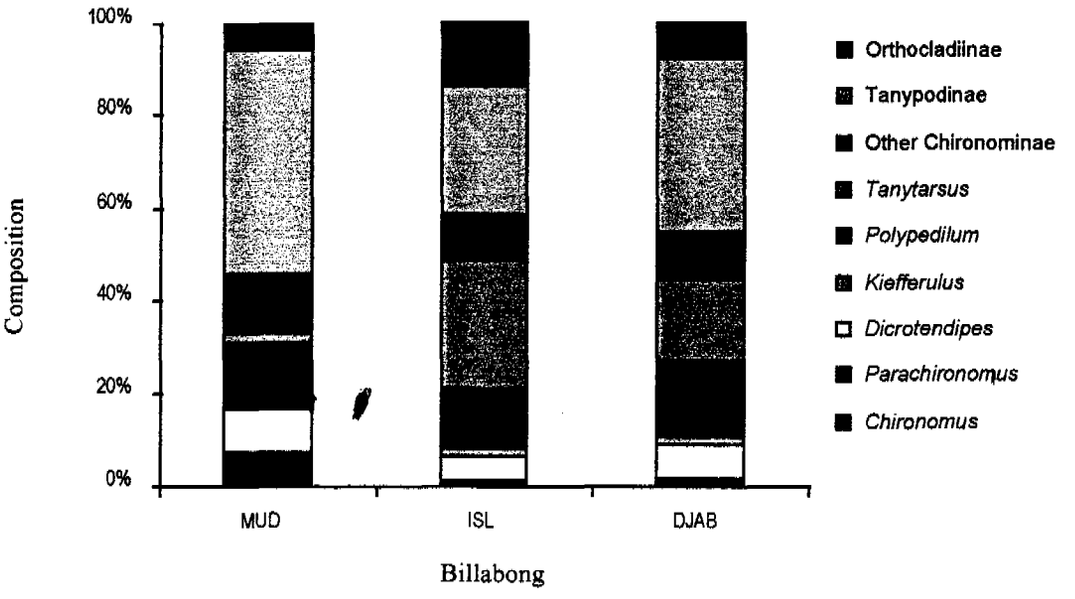


Figure 1.

A map showing the location of the Magela Creek Floodplain within the Northern Territory, Australia. The billabongs that are significant to this study are marked. When the system is in flow, water enters the floodplain from the creek channel portion of the system. Water in the lower floodplain then exits into the lower East Alligator River (modified from Hart and McGregor, 1980).

Figure 2 The composition of the larval chironomid community in Mudginberri (MUD), Island (ISL) and Djabiluka (DJAB) billabongs at the end of the Dry-season.



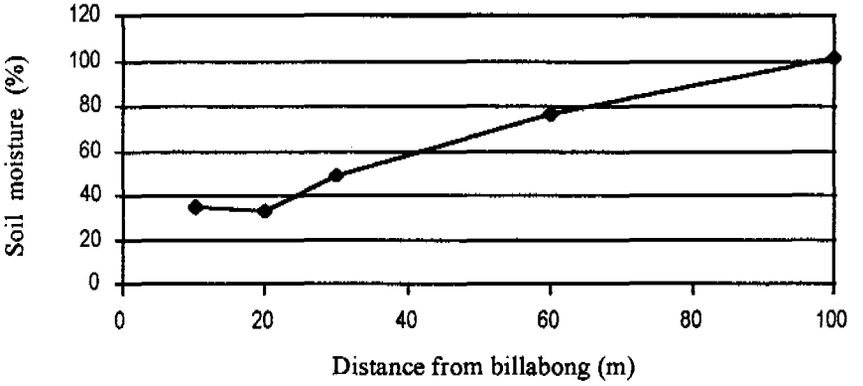


Figure 3 Percentage soil moisture at each location along the 100m transect at Island billabong. Measurements were taken at the end of the Dry-season. A moisture content of greater than 100% indicates supersaturated conditions.

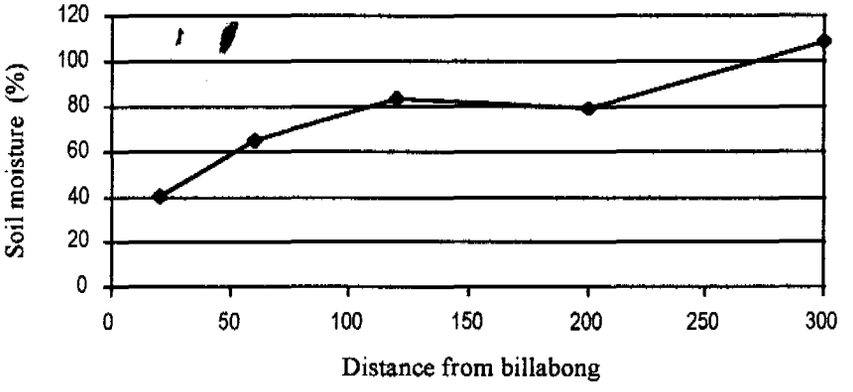


Figure 4 Percentage soil moisture at each location along the 300m transect at Djabiluka Billabong. Measurements were taken at the end of the Dry-season. A moisture content of greater than 100% indicates that the soil is supersaturated.

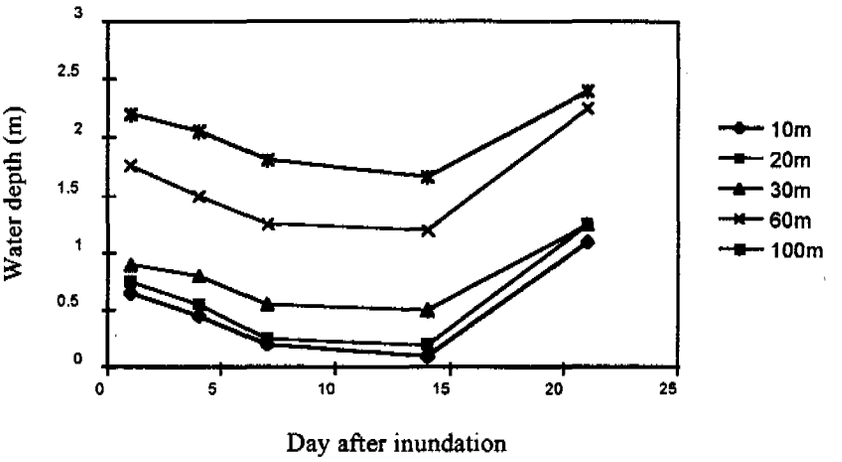


Figure 5 The depth of the water at each location sampled on the floodplain adjacent to Island billabong.

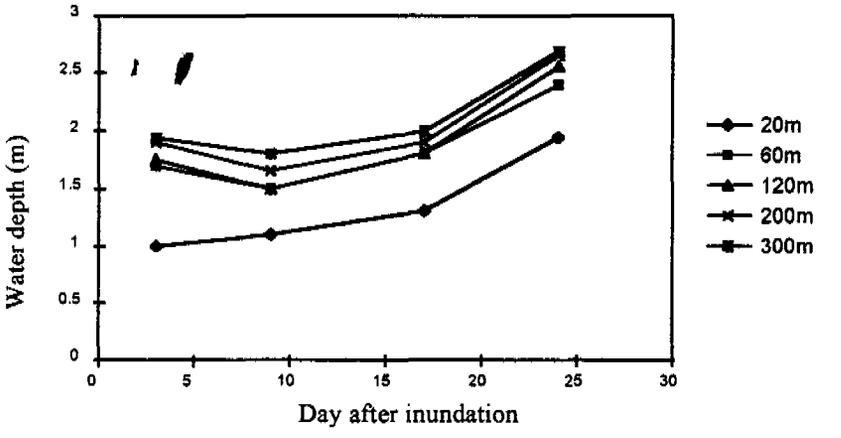


Figure 6 The depth of water at each location sampled on the floodplain adjacent to Djabiluka billabong.

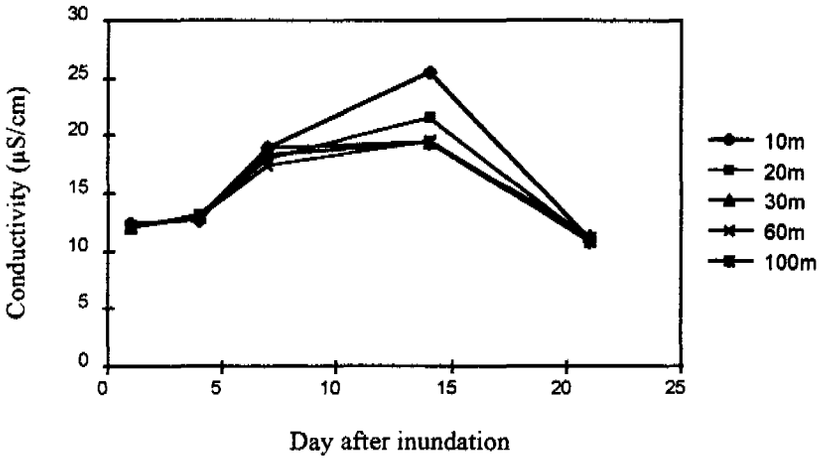


Figure 7 The conductivity of the water, at a depth of 30cm, for each location sampled on the floodplain adjacent to Island billabong.

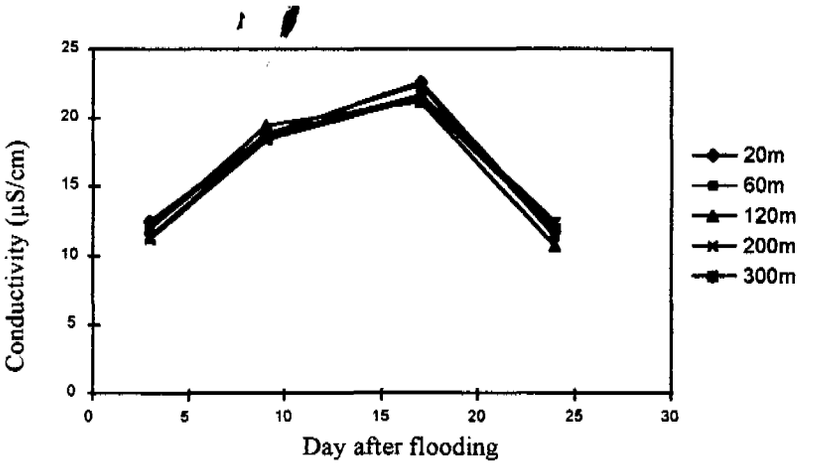


Figure 8 The conductivity of the water, at a depth of 30cm, for each location sampled on the floodplain adjacent to Djabiluka billabong.

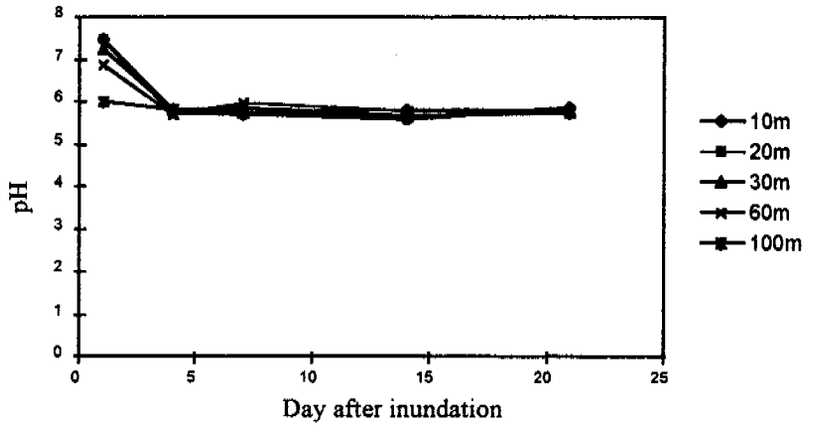


Figure 9 The pH of the water, at a depth of 30cm, for each location sampled on the floodplain adjacent to Island billabong.

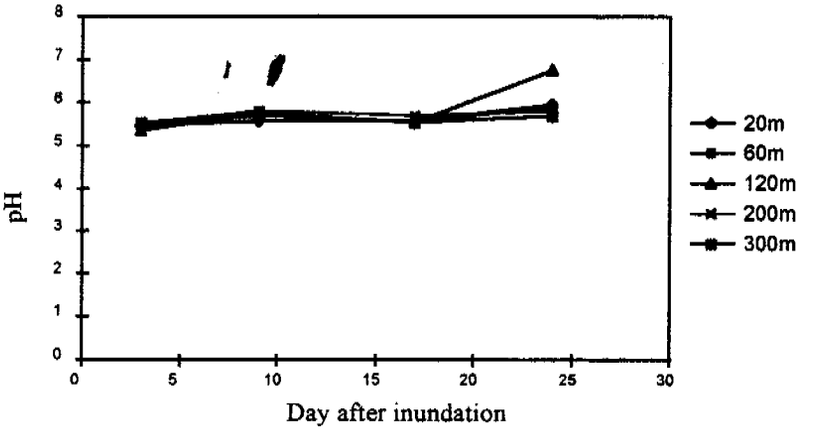


Figure 10 The pH of the water, at a depth of 30cm, for each location sampled on the floodplain adjacent to Djabiluka billabong.

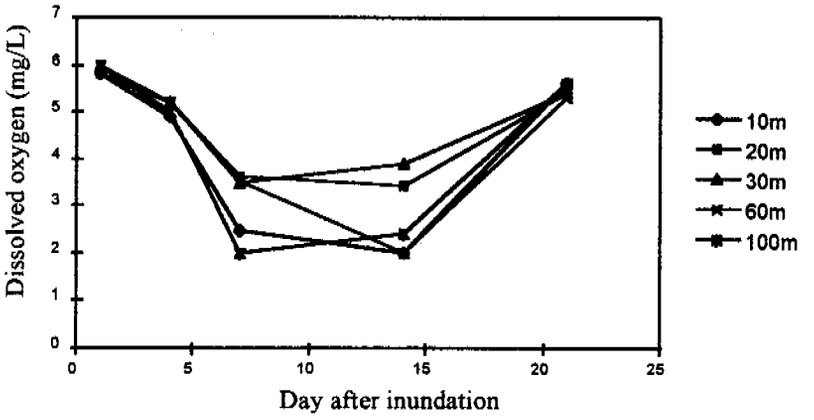


Figure 11 The concentration of dissolved oxygen, at a depth of 10cm, for each location sampled on the floodplain adjacent to Island billabong.

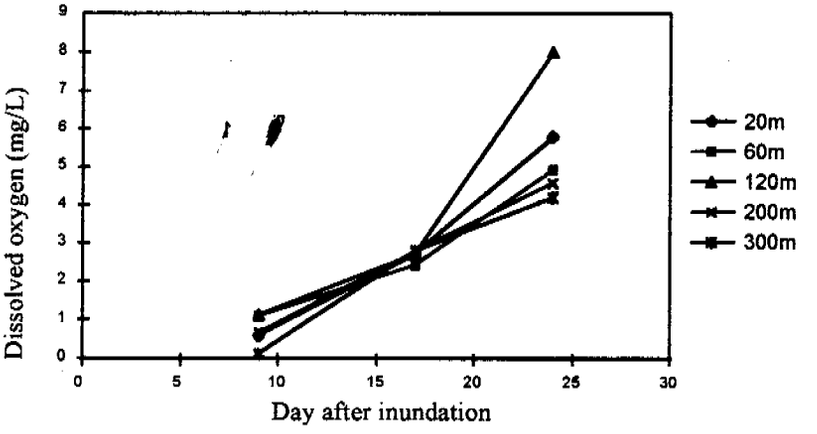


Figure 12 The concentration of dissolved oxygen, at a depth of 10cm, for each location sampled on the floodplain adjacent to Djabiluka billabong. The measurements on day 3 were taken at a depth of approx. 80cm.

Figure 13 First two dimensions of Principal Coordinates Analysis (PCO) ordination (Jaccard similarity), of the presence/absence data for the floodplain macroinvertebrate assemblage. Numbers indicate post-inundation sampling day.

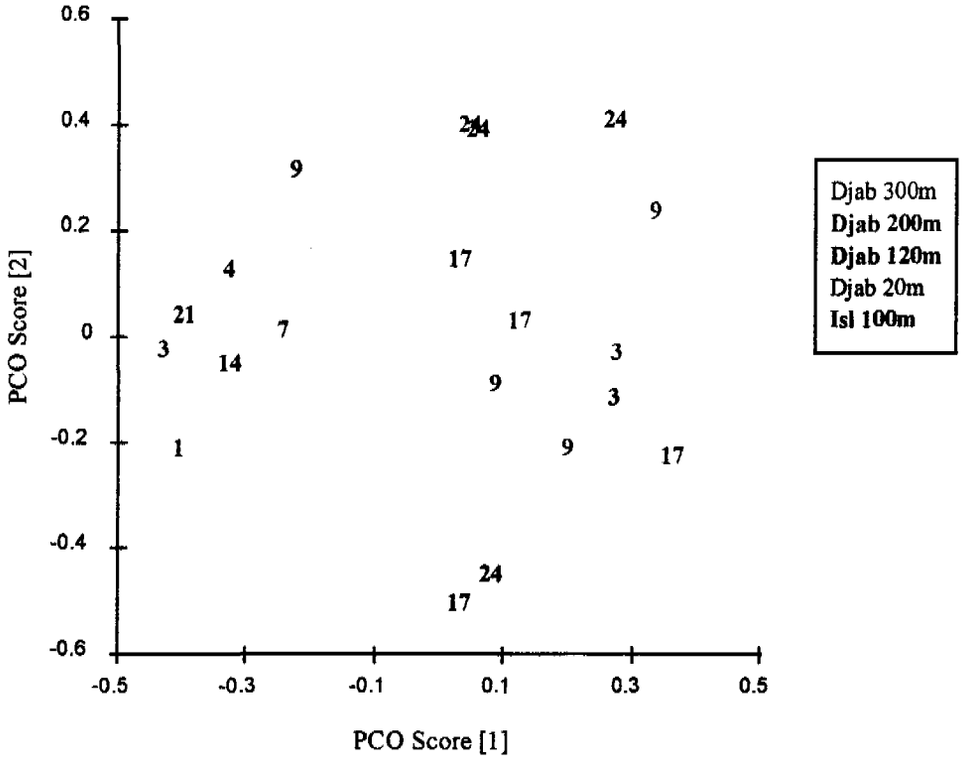
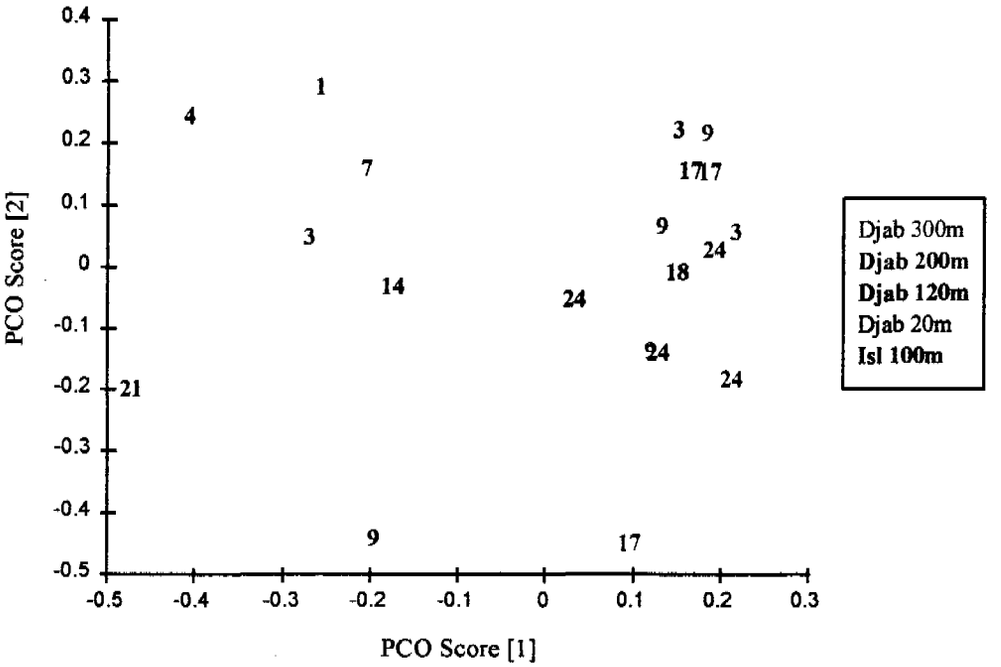


Figure 14 First two dimensions of Principal Coordinates Analysis (PCO) ordination (Ecological similarity), of the relative abundance data for the floodplain macroinvertebrate assemblage. Numbers indicate post-inundation sampling day.



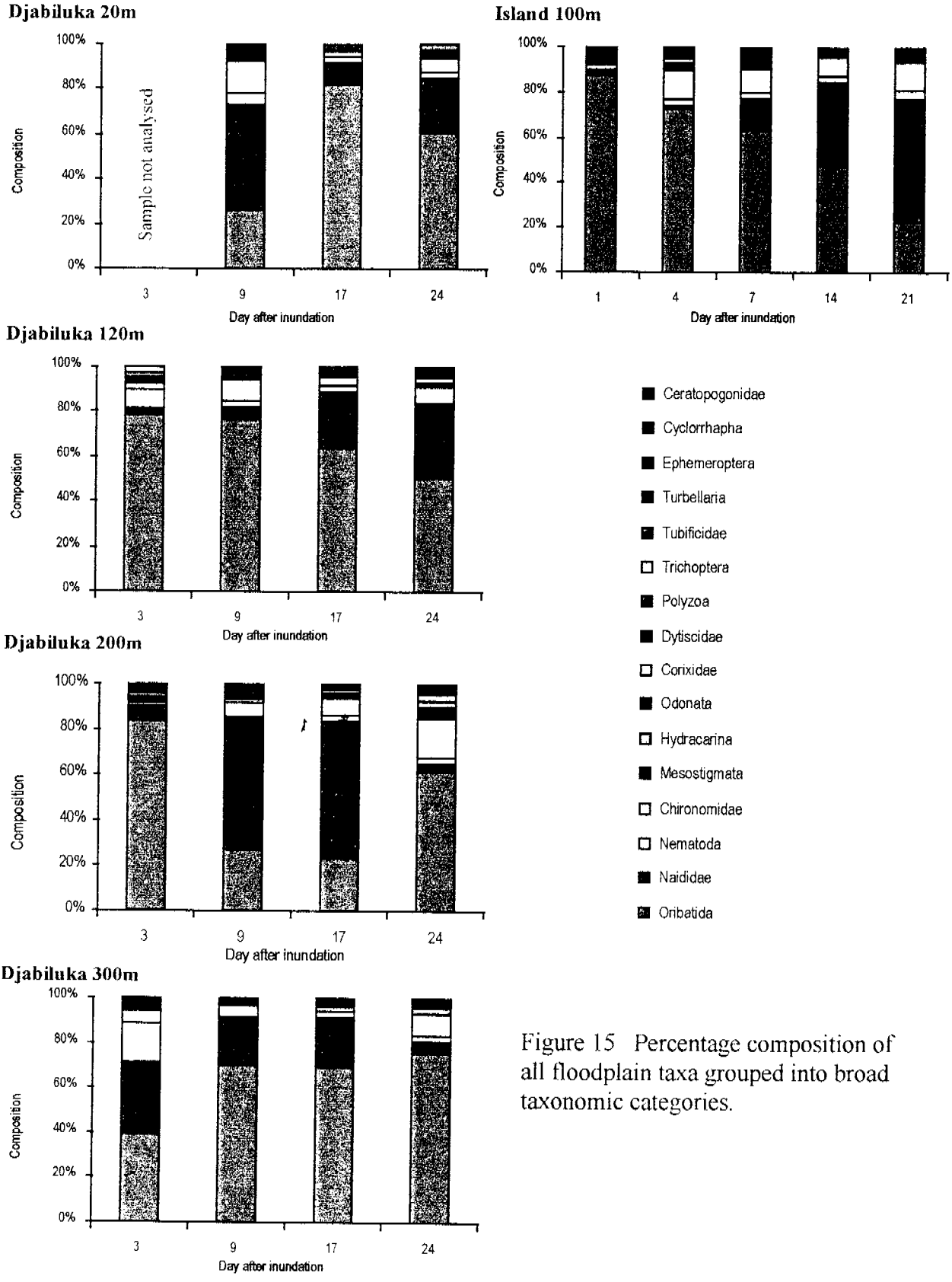


Figure 15 Percentage composition of all floodplain taxa grouped into broad taxonomic categories.

Figure 16 First two dimensions of Principal Coordinates Analysis ordination (Jaccard similarity), of the presence/absence data for the floodplain chironomid assemblage. Numbers indicate the post-inundation sampling day.

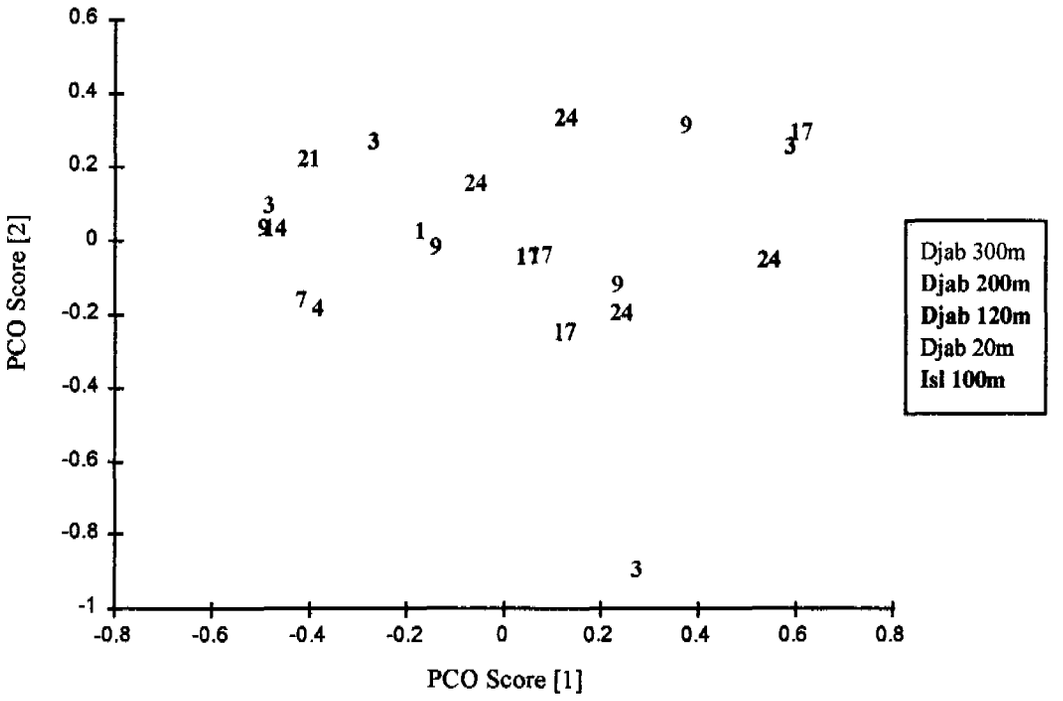
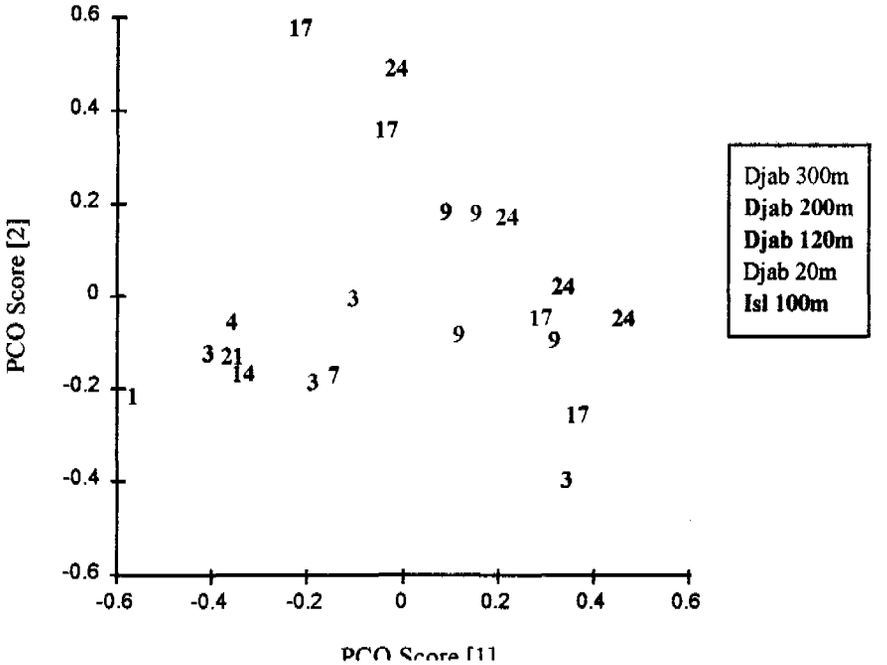


Figure 17 First two dimensions of Principal Coordinates Analysis ordination (Ecological similarity), of the relative abundance data for the floodplain chironomid assemblage. Numbers indicate the post-inundation sampling day.



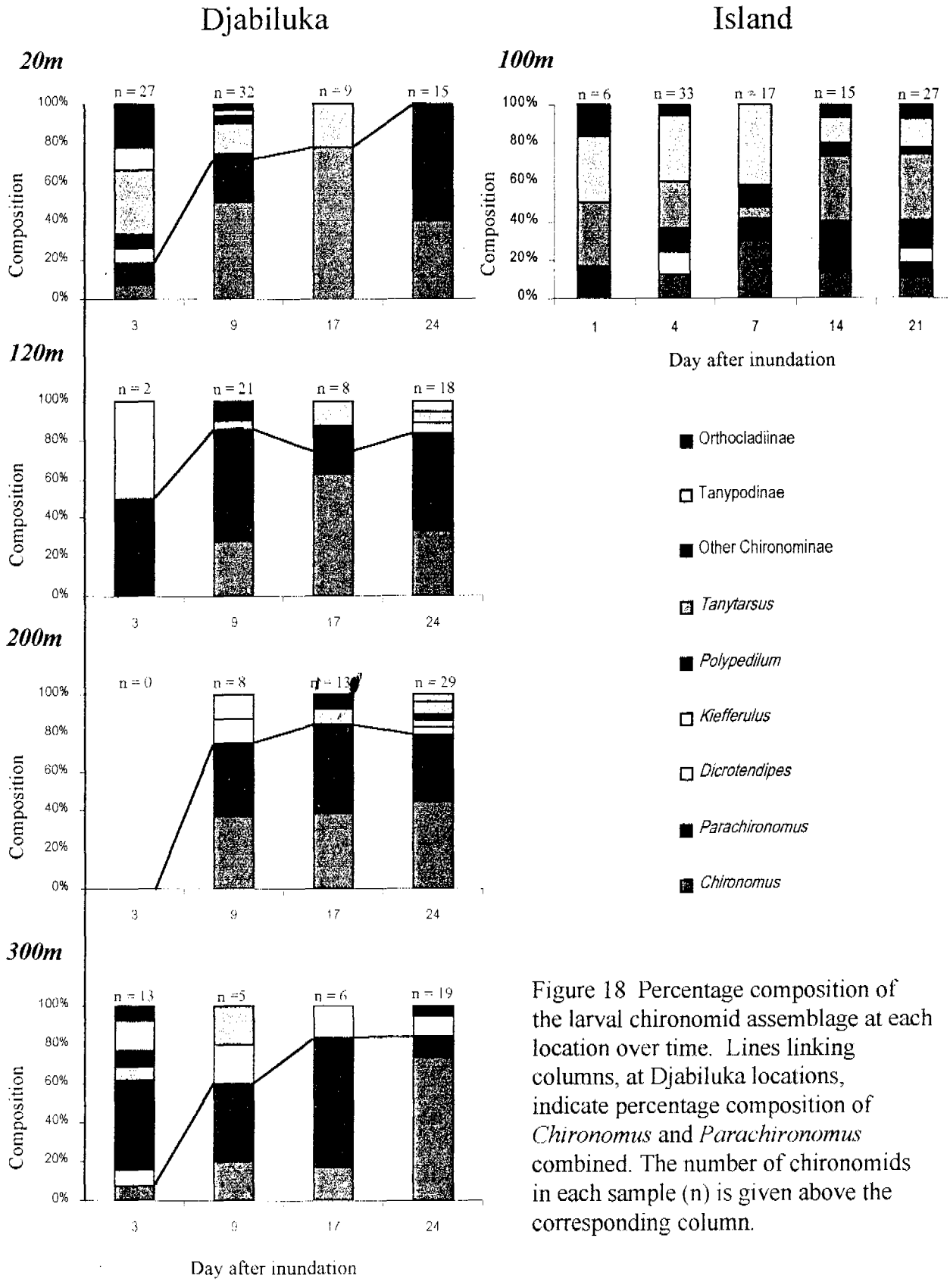


Figure 18 Percentage composition of the larval chironomid assemblage at each location over time. Lines linking columns, at Djabiluka locations, indicate percentage composition of *Chironomus* and *Parachironomus* combined. The number of chironomids in each sample (n) is given above the corresponding column.

Figure 19 The distribution of head capsule length for *Parachironomus* sp.1 derived from individuals that were collected during floodplain sampling at Island and Djabiluka sites. The distribution has been divided into three sections, each of which represents a single instar, denoted in roman numerals. Dyar's constant between successive instars is also given.

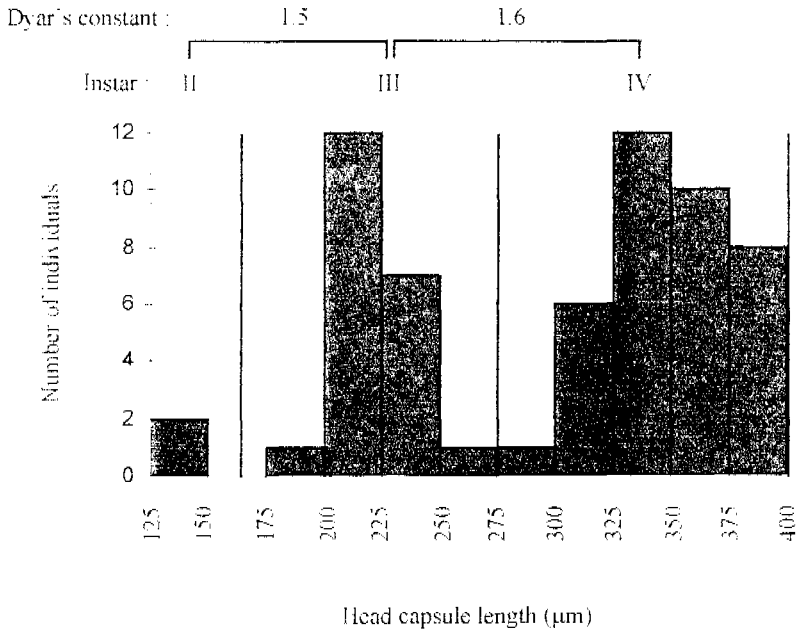


Figure 20 Composition of each developmental stage (instar), for larval *Parachironomus* sp.1, over time at the Djabiluka floodplain site. The composition for each day of sampling was created by summing the individuals collected from each location (20m, 120m, 200m and 300m).

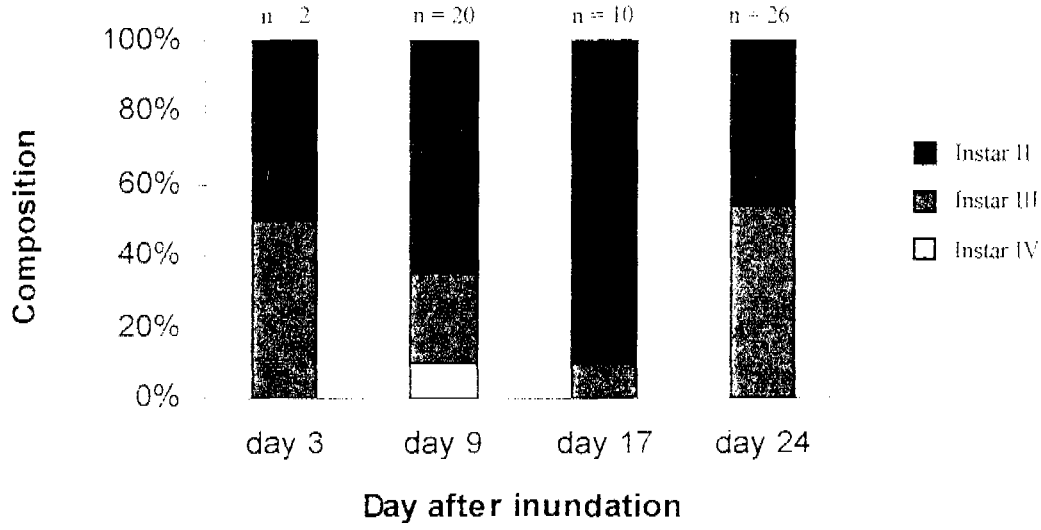


Figure 21 Composition of each developmental stage (instar), for larval *Parachironomus* sp. 1, at each location along the Djabiluka transect. The composition for each location was created by summing all the individuals collected on each day of sampling at that location.

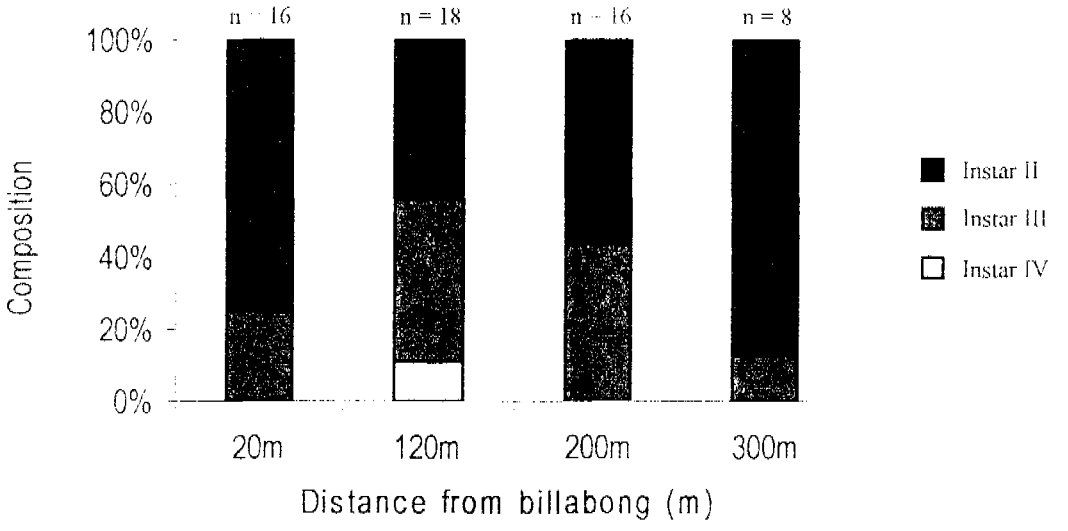


Figure 22 The distribution of head capsule length for *Chironomus* sp.2 derived from individuals collected during floodplain sampling at both Island and Djabiluka sites. The distribution has been divided into three sections (Early, Middle and Late), each representing a relative age class.

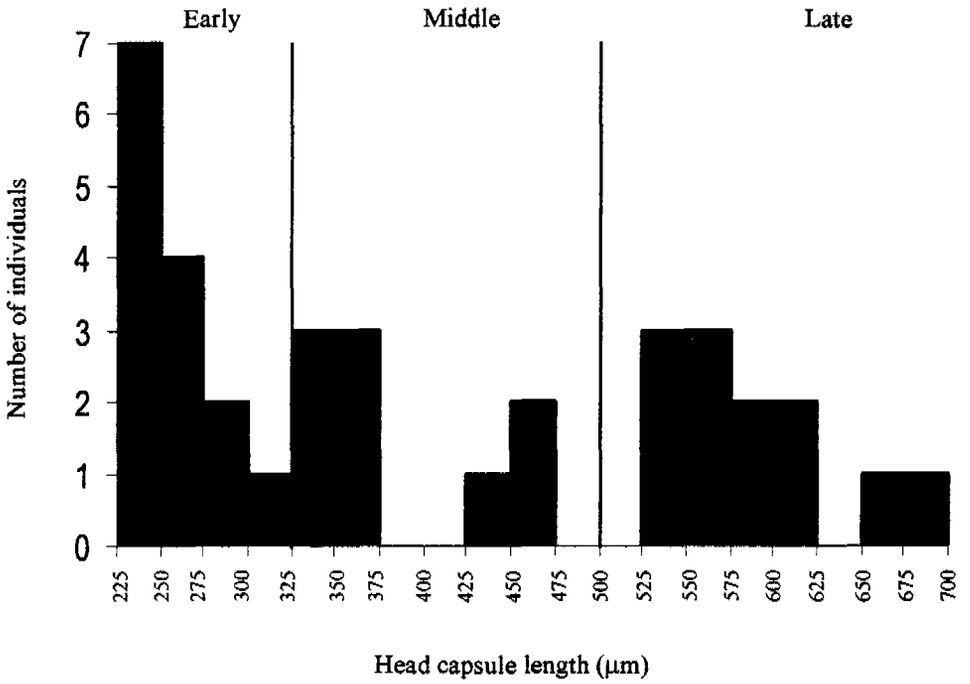


Figure 23 The distribution of head capsule length for *Chironomus* sp.5 derived from individuals collected during floodplain sampling at both Island and Djabiluka sites. The distribution has been divided into three sections (Early, Middle and Late), each of which represents a relative age class.

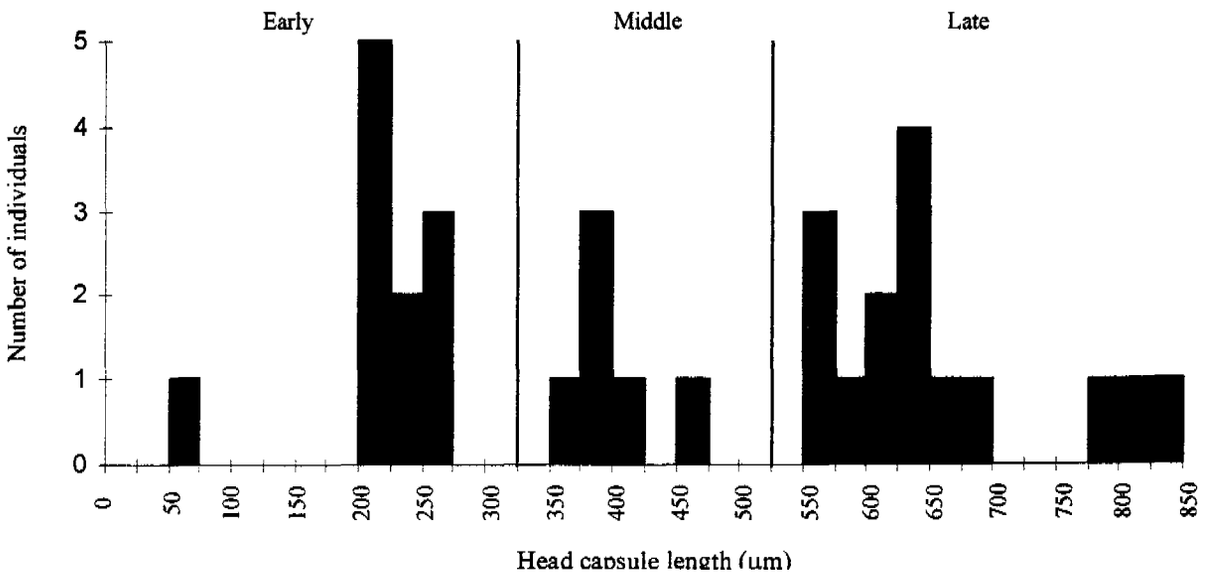


Figure 24 The composition of each relative age class (Early, Middle, Late), for *Chironomus* sp.2, across time at the Djabiluka floodplain site. The composition for each day of sampling was created by summing the individuals collected from each location (20m, 120m, 200m, 300m).

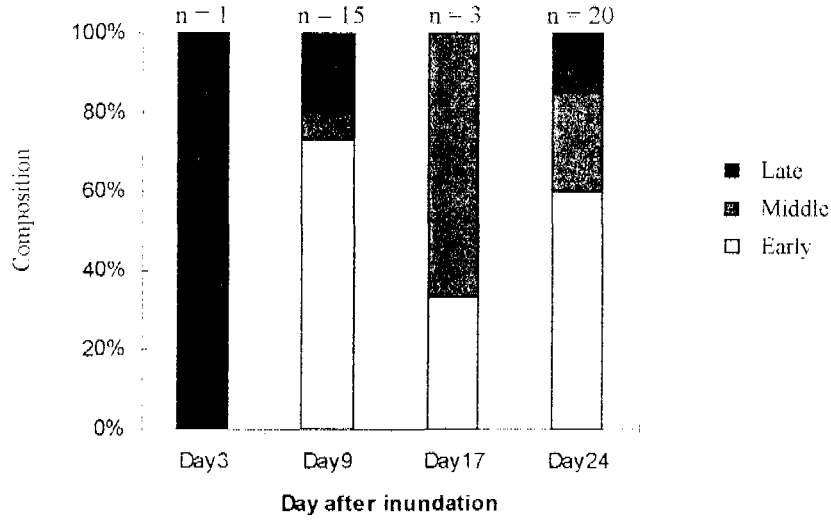


Figure 25 The composition of each relative age class for *Chironomus* sp.2 with distance from the edge of Djabiluka billabong. The composition at each distance (location) was created by summing all the individuals collected over the four collection periods (days 3, 9, 17 and 24).

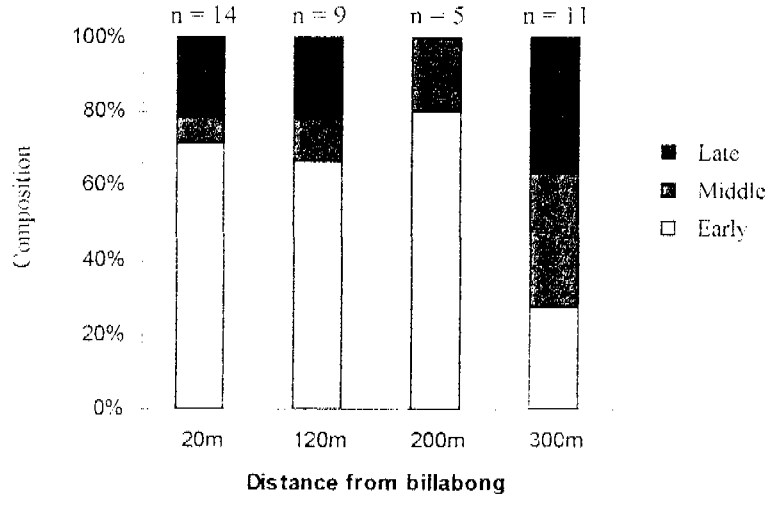


Figure 26 The composition of each relative age class (Early, Middle, Late), for *Chironomus* sp.5, across time at the Djabiluka floodplain site. The composition for each day of sampling was created by summing the individuals collected from each location (distance from the billabong 20m, 120m, 200m, 300m).

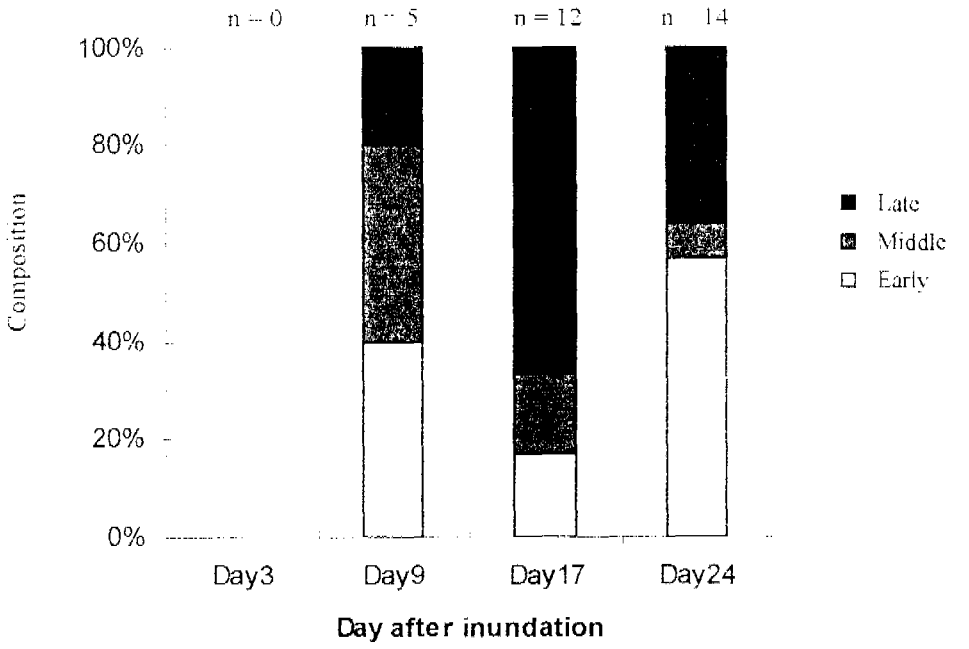
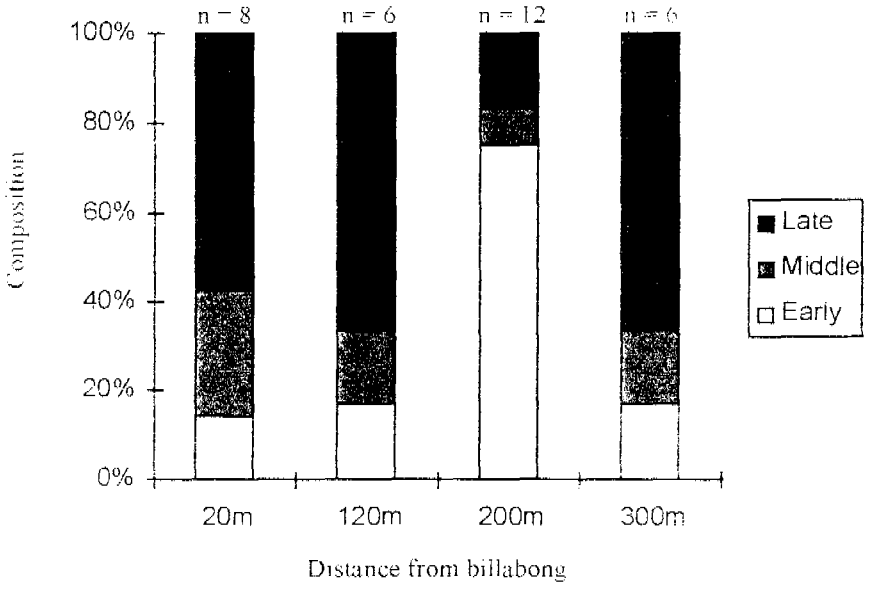


Figure 27 The composition of each relative age class (Early, Middle, Late), for *Chironomus* sp.5, with distance from the edge of Djabiluka billabong. The composition at each distance (location) was created by summing all the individuals collected over the four collection periods (days 3, 9, 17 and 24).



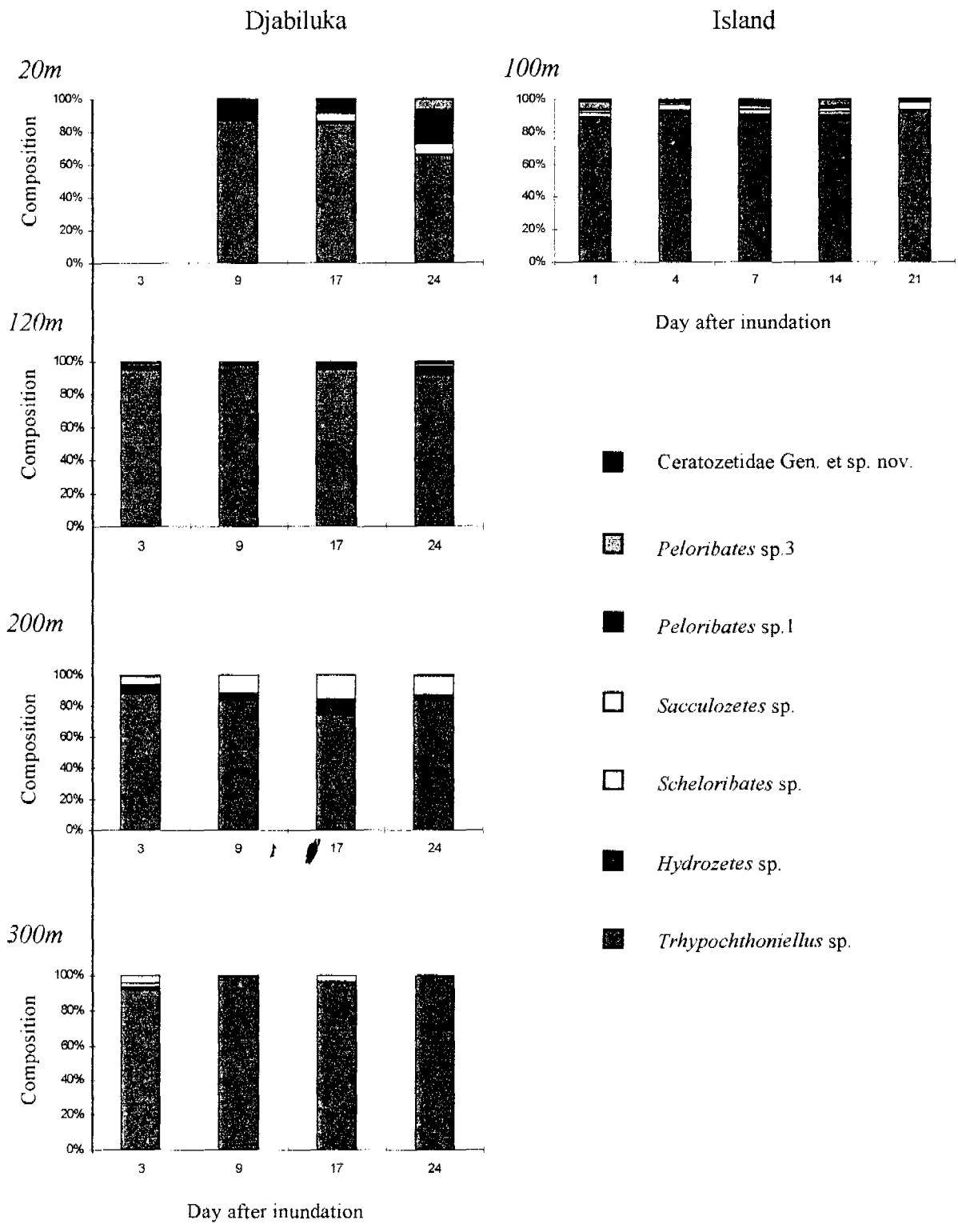


Figure 28 The percentage composition of the Oribatida assemblage at each location over time. Only those species that were used in the data analysis are included. Any oribatid species that was not present in more than two samples have been excluded.

Table 1 The samples that were used in the final analysis. All samples were collected with a suction sampler, except where indicated.

Location	Days after inundation				
Island 100m	1	4	7	14	21
Djabiluka 20m	3*§	9	17	24	
Djabiluka 120m	3	9	17	24	
Djabiluka 200m	3	9	17	24	
Djabiluka 300m	3	9	17	24	

* Only the chironomids were examined in this sample.

§ Sample was collected using a 250 µm mesh sweep net.

Table 2 The dissolved oxygen meters used during the floodplain sampling phase of the study. Listed is the depth at which measurements were taken, a dissolved oxygen (DO) measurement of a sample of distilled water (used to compare meters), and the samples taken using each meter.

Meter	Probe depth	DO distilled water ($mg.L^{-1}$)	Samples
Hydrolab	≈ 80cm	8.65	Djabiluka day9
Hanna (HI9143)	10cm	7.47	Island day7
Hach (16046)	10cm	7.3	All other samples

Table 3 (this table is continued on pages 71 - 73)

A taxon list for the floodplain macroinvertebrates. All insects in this list are juveniles (nymphs or larvae) except where otherwise stated. Adult insects are denoted by (A) following the taxon name. Insect pupa are denoted by (P) following the taxon name. Numbers given in this table represent the number of individuals in each sample. Due to delayed receipt and time constraints, the Chironomidae was the only group examined in the sample collected from Djabiluka 20m day3. The use of the term indeterminate, indicates that lower taxonomic identification was not possible due to the individuals being either damaged or not sufficiently developed.

The small symbol following the taxon name provides information as to how the taxon was used in the principle coordinates analysis (PCO):
X = taxon was discarded from data set for PCO
1..34 = taxon was merged into one of the broader taxonomic units below for PCO

1. Ephemeroptera
2. Ceratopogonidae
3. Other Chironominae
4. Orthocladiinae
5. *Chironomus*
6. *Dicrotendipes*
7. *Kiefferulus*
8. *Parachironomus*
9. *Polypedilum*
10. Tanypodinae
11. *Tanytarsus*
12. Odonata
13. Corixidae
14. Dytiscidae
15. Naididae
16. *Pristina*
17. *Pristinella*
18. *Stylaria*
19. Nematoda
20. Unionicolidae
21. non-unionicolids
22. Mesostigmata
23. *Scheleribates* sp.
24. *Sacculozetes* sp.
25. *Hydrozetes* sp.
26. *Trhypochthoniellus* sp.
27. *Peloribates* sp.1
28. *Peloribates* sp.3
29. Ceratozetidae Gen. et sp. nov.
30. Polyzoa
31. Trichoptera
32. Tubificidae
33. Turbellaria
34. Cyclorrhapha

Some common names of listed taxonomic groups:
Platyhelminthes - flatworms; Nematoda - round worms; Gastropoda - snails; Oligochaeta - worms; Arachnida - spiders & mites (only mites represented in this study); Diptera - flies; Chironomidae - non-biting midges; Ceratopogonidae - biting midges; Ephemeroptera - mayflies; Odonata - dragonflies & damselflies; Trichoptera - caddisflies; Coleoptera - beetles; Hemiptera - true bugs; Corixidae - water boatmen; Hymenoptera - wasps.

Phylum	Class	Order (Suborder)	Family (subfamily)	Taxon	Data analysis	Djabiluka 20m day3	Djabiluka 20m day9	Djabiluka 20m day17	Djabiluka 20m day24	Djabiluka 120m day3	Djabiluka 120m day9	Djabiluka 120m day17	Djabiluka 120m day24	Djabiluka 200m day3	Djabiluka 200m day9	Djabiluka 200m day17	Djabiluka 200m day24	Djabiluka 300m day3	Djabiluka 300m day9	Djabiluka 300m day17	Djabiluka 300m day24	Island 100m day1	Island 100m day4	Island 100m day7	Island 100m day14	Island 100m day21
Polyzoa				Polyzoa	X	-	8	8	0	0	0	0	0	16	0	0	0	0	0	0	0	0	4	1	0	0
Platyhelminthes	Turbellaria			Turbellaria	33	-	16	0	0	0	8	0	5	8	21	0	4	0	16	11	11	0	4	0	0	0
Nematoda				Nematoda	19	-	80	24	43	76	48	16	0	8	91	16	12	160	176	32	32	0	12	3	32	75
Mollusca	Gastropoda			Gastrapoda	X	-	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	32	11
Annelida	Hirudinea			Hirudinea	X	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
	Oligochaeta		Enchytraeidae	Enchytraeidae	X	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
			Haplotaxidae	Haplotaxidae	X	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
			Naididae	Naididae indeterminate	15	-	496	144	523	8	96	440	352	200	752	512	0	267	704	491	117	12	8	23	1152	811
				Pristina spp.	16	-	184	0	0	0	0	8	16	0	5	5	0	21	16	0	0	0	0	0	16	235
				Pristinella spp.	17	-	24	0	0	0	0	0	5	0	0	0	0	5	0	0	11	0	0	0	0	0
				Stylaria spp.	18	-	80	8	11	0	8	48	5	8	16	48	0	0	0	11	0	0	4	0	48	107
			Tubificidae	Tubificidae	32	-	0	0	53	0	8	0	0	0	0	0	0	11	0	0	0	0	0	1	0	21
Arthropoda	Crustacea		Atyidae	Atyidae	X	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
	Arachnida	Acarina																								
		(Prostigmata)	Anisitsiellidae	Anisitsiellidae	21	-	0	0	0	8	8	0	0	24	11	0	0	0	0	0	0	0	0	0	0	0
			Arrenuridae	Arrenuridae	21	-	0	0	0	0	0	8	5	8	0	0	0	0	0	0	0	0	0	0	0	0
			Hydrophantidae	Hydrophantidae	21	-	16	0	0	0	0	0	5	8	0	0	0	0	0	0	0	0	4	0	0	0
			Limnesidae	Limnesidae	21	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
			Unionicolidae	Unionicolidae	20	-	0	0	0	16	0	0	0	8	11	0	12	0	0	11	11	12	8	3	16	11
		(Oribatida)	?Mycobatidae	*Sacculozetes* sp.	24	-	0	0	0	4	0	8	11	8	0	0	4	16	0	0	0	8	12	2	32	0
			Ceratozetidae	Ceratozetidae Gen. et sp. nov.	29	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	8	5	0	11
			Ceratozetidae	*Zetommius* sp.	X	-	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			Galumnidae	*Galumna* sp.	X	-	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0
			Haplozetidae	*Peloribates* sp.1	27	-	16	136	288	0	0	0	0	8	0	0	0	0	0	0	0	4	4	0	16	0
			Haplozetidae	*Peloribates* sp.2	X	-	0	16	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			Haplozetidae	*Peloribates* sp.3	28	-	0	0	85	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	64	0
			Hydrozetidae	*Hydrozetes* sp.	25	-	40	16	11	12	8	48	32	96	16	21	12	5	0	0	0	4	0	3	48	0
			Oppidae	*Multioppia* sp.	X	-	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
			Oripodidae	*Scheloribates* sp.	23	-	0	56	75	12	16	0	5	104	43	32	52	5	0	53	0	16	24	3	32	21
			Trhypochthoniidae	*Trhypochthoniellus* sp.	26	-	376	1040	853	588	1360	1088	517	1656	304	160	360	331	2416	1440	1536	500	640	86	1296	448
		(Mesostigmata)		Mesostigmata sp.1	22	-	16	0	11	0	48	56	11	16	5	37	44	0	0	32	32	0	8	3	96	21
				Mesostigmata sp.2	22	-	0	0	0	20	8	0	0	16	0	0	0	0	0	0	0	8	4	0	0	0
				Mesostigmata sp.3	22	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Arthropoda	Insecta	Diptera	Chironomidae																							
			(Tanypodinae)	*Ablabesmyia hilli*	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21
				Ablabesmyia indeterminate	10	16	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
				Larsia sp.	10	8	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	8	16	5	0	0
				Paramerina "dark head"	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
				Paramerina parva	10	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	4	0	0	0
				Procladius "goanna".	10	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	16	2	32	0
				Tanypodinae (small tooth on proleg)	10	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	8	0	0	11
				Tanypus sp.	10	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			(Orthocladiinae)	*Corynoneura* sp.	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11

	Nanocladius sp.	4	0	0	0	0	0	8	0	0	0	0	0	0	5	0	0	0	4	4	0	0	11
	Parakiefferiella sp.	4	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
	Parametriocnemus sp. (Adult)	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Thienemanniella indeterminate (P.)	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
(Chironominae)	*Chironomus sp.2*	5	0	88	8	32	0	24	8	27	0	16	5	16	5	16	0	85	0	16	3	16	21
	Chironomus sp.2 (P.)	5	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Chironomus sp.A	5	0	24	16	21	0	0	0	5	0	0	0	4	0	0	0	0	0	0	1	0	0
	Chironomus indeterminate (P.)	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
	Chironomus sp.5	5	16	16	32	11	0	24	24	0	0	0	21	32	0	0	11	53	0	0	1	16	11
	Cladopelma sp.	3	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
	Conochironomus sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
	Dicrotendipes ?lindae	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Dicrotendipes jobetus	6	0	0	0	0	0	0	0	0	0	5	0	4	0	0	0	0	0	4	0	0	0
	Dicrotendipes jonmartinae & ?sarinae	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Dicrotendipes K1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
	Dicrotendipes K4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Dicrotendipes pelechloris	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
	Harnishia sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
	Kiefferulus "tinctus"	7	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0
	Kiefferulus (K1) tumidus	7	0	0	0	0	0	0	0	5	0	0	0	0	0	0	11	0	0	0	0	0	11
	Kiefferulus ?intertinctus	7	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Kiefferulus martinii	7	0	0	0	0	4	0	0	0	0	0	0	4	5	0	0	0	0	0	0	0	11
	Kiefferulus martinii (P.)	7	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Parachironomus (sp.2) *K1*	8	16	0	0	0	4	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Parachironomus K2 (P.)	8	0	0	0	0	0	8	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
	Parachironomus sp.1	8	8	56	0	96	0	72	8	43	0	16	32	36	0	32	43	21	4	0	0	32	21
	Parachironomus sp.3	8	0	0	0	0	0	8	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
	Polypedilum convexum	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
	Polypedilum indeterminate	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Polypedilum indeterminate (A.)	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
	Polypedilum K1	9	0	8	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
	Polypedilum K3	9	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	11	0	0	0	0	0
	Polypedilum nubifer	9	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
	Polypedilum orestitrophus	9	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	16	0
	Polypedilum seorsus	9	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	12	2	0	11
	Polypedilum vespertinus (M2)	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Polypedilum watsoni	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Rheotanytarsus indeterminate	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Stempellinella sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
	Tantarsus ?K12	11	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Tanytarsus (K6) bispinosis	11	24	8	8	0	0	0	8	5	0	0	0	4	0	16	0	0	8	0	1	48	21
	Tanytarsus ?(K6) bispinosis	11	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Tanytarsus B1	11	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
	Tanytarsus fuscithorax	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	11
	Tanytarsus indeterminate	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Tanytarsus indeterminate (A.)	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
	Tanytarsus K10	11	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
	Tanytarsus K12	11	40	16	0	0	0	0	0	0	0	0	5	0	5	0	0	0	0	20	0	0	11
	Tanytarsus manlyensis	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
	Tanytarsus richardsi	11	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	11
	Zavrelella marmorata	3	0	0	0	0	0	8	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Ceratopogonidae	Ceratopogonidae	2	-	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	16	11

		Ceratopogonidae (P.)	2	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0
	Drosophilidae	*Unknown puparium*	34	-	0	0	0	0	0	0	5	16	0	5	0	0	0	0	11	0	0	0	0	0	0
	Ephydridae	Ephydridae	34	-	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
	Helcomyzidae	Helcomyzidae	34	-	8	0	0	0	0	0	0	0	5	0	8	0	0	0	0	0	0	0	1	0	0
	Muscidae	Muscidae sp.	34	-	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	Baetidae	Baetidae indeterminate	1	-	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	8	0	0	11
		Cloeon fluviatile	1	-	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Caenidae	Caenidae indeterminate	1	-	16	0	0	0	0	8	0	0	0	0	0	5	0	0	0	0	4	0	0	0	0
		Tasmanocoensis arcuata	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Odonata	Libellulidae	*Brachydiplax denticauda*	12	-	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
		Libellulidae indeterminate	12	-	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	4	8	0	0	11
		Rhyothemis graphiptera	12	-	0	0	0	0	0	0	0	0	0	0	0	0	16	11	0	0	0	0	0	0	0
	Corduliidae	*Hemicordulia intermedia*	12	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
		Hemicordulia tau	12	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
	Coenagrionidae	Coenagrionidae indeterminate	12	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	11
Trichoptera	?	Trichoptera indeterminate	31	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	16	0
	Ecnomidae	*Ecnomina* sp.	31	-	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ecnomus sp.	31	-	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hydroptilidae	*Acritoptila* sp.	31	-	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	Curculionidae	Curculionidae sp.	X	-	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
	Dytiscidae	*Bidessus* sp.	14	-	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	4	0	0	0
		Hyphydrus sp.	14	-	0	0	0	0	0	0	0	0	0	0	4	5	0	0	0	0	0	8	0	0	0
		Laccophilus sp.	14	-	0	0	21	0	0	0	0	0	0	0	0	0	0	0	11	0	4	2	0	0	0
	Noteridae	Noteridae sp.	X	-	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemiptera	Belostomatidae	Belostomatidae sp.	X	-	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Corixidae	Corixidae sp.	13	-	8	0	0	0	0	0	32	0	0	11	36	0	0	0	43	0	4	0	0	0	11
	Notonectidae	Notonectidae sp.	X	-	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Velidae	Velidae sp.	X	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0
Hymenoptera		Hymenoptera sp.	X	-	0	0	0	0	0	0	0	0	5	5	0	0	0	0	0	0	0	0	0	0	0

Table 4 Mean number of taxa in samples from the littoral zones of Mudginberri (MUD), Island (ISL), and Djabiluka (DJAB) billabongs at the end of the Dry-season. Those taxa important in the discussion on floodplain colonisation are indicated in bold type. Indeterminate taxa are individuals that could not be identified to a lower taxonomic level due to physical damage or underdevelopment of the animal.

Phylum	Class	Order (Suborder)	Family (Subfamily)	Taxon	MUD	ISL	DJAB
Nematoda				Nematoda	16	0	112
Mollusca	Gastropoda			Gastropoda	10	32	96
			Naididae	**Naididae**	**60**	**79**	**179**
				Pristina spp.	0	0	64
				Pristinella spp.	0	0	0
				Stylaria spp.	0	0	0
			Tubificidae	Tubificidae	15	0	64
Arthropoda	Crustacea		Atyidae	Atyidae	31	89	76
			Palaemonidae	Palaemonidae	15	28	48
	Acarina			Acarina indeterminate	58	16	48
		Prostigmata	Arrenuridae	Arrenuridae	0	128	56
			Hydrachnidae	Hydrachnidae	0	8	0
			Hydrophantidae	Hydrophantidae	16	32	32
			Limnesidae	Limnesidae	8	0	0
			Mideopsidae	Mideopsidae	126	0	0
			Oxidae	Oxidae	20	8	0
			Unionicolidae	Unionicolidae	102	30	43
		Oribatida		**Oribatida indeterminate**	**33**	**731**	**1781**
Arthropoda	Insecta	Diptera	Chironomidae	Chironomidae indeterminate (L)	34	19	72
				Chironomidae indeterminate (P)	56	56	112
				Chironomidae unidentified	80	0	64
			(Tanypodinae)	*Ablabesmyia hilli*	8	8	0
				Ablabesmyia notabilis	13	32	16
				Clinotanypus crux	4	16	0
				Larsia albiceps	**98**	**210**	**249**
				Paramarina parva	34	0	0
				Procladius paludicola	15	28	68
				Tanypodinae indeterminate	32	102	99
				Tanypus indeterminate	0	0	48
				***Thienemannyia* indeterminate**	**5**	**226**	**416**
			(Orthocladiinae)	*Nanocladius* indeterminate	12	0	128
				Orthocladinae	8	0	0
				***Parakiefferiella* indeterminate**	**4**	**316**	**44**
				?Parametriocnemus nr.ornaticornis	0	0	16
			(Chironominae)	Chironominae indeterminate	15	56	40
				***Chironomus* sp.2**	**0**	**0**	**16**
				Cladotanytarsus indeterminate	12	106	32
				Dicrotendipes septemmaculatus	0	0	0
				Dicrotendipes indeterminate	13	20	59
				Dicrotendipes jobetus	28	36	120
				Dicrotendipes ?flexus	0	64	0
				Kiefferulus indeterminate	0	32	32
				Kiefferulus tinctus	0	12	0
				***Parachironomus* indeterminate**	**16**	**0**	**0**
				***Parachironomus* K1**	**0**	**0**	**16**
				***Parachironomus* K2**	**16**	**16**	**0**
				Paratanytarsus indeterminate	9	0	0
				Polypedilum (Pentapedilum) convexu	**8**	**193**	**86**
				Polypedilum (Pentapedilum) K1	0	20	64
				Polypedilum (Pentapedilum) leei	**38**	**14**	**204**
				Polypedilum (Polypedilum) scorsus	4	0	0
				Polypedilum indeterminate	12	64	48
				Rheotanytarsus indeterminate	0	24	64
				Stenochironomus watsoni	4	0	0
				Strictochironomus indeterminate	8	0	0

		Tanytarsus indeterminate	4	126	116
		Tanytarsus K10	0	160	0
		Tanytarsus K12	0	100	52
		Tanytarsus manleyensis	**4**	**247**	**250**
		?Xenochironomus indeterminate	0	16	0
		Zavreliella marmorata	8	19	112
	Ceratopogonidae	**Ceratopogonidae**	**29**	**362**	**189**
		Ceratopogonidae (P.)	5	35	53
	Chaoboridae	Chaoboridae	0	0	16
	Culicidae	Culicidae (L)	6	56	160
		Culicidae (P)	0	25	32
	Stratiomyidae	Stratiomyidae	0	0	24
	Tipulidae	Tipulidae (L)	0	0	32
		Tipulidae (P)	0	0	32
Ephemeroptera	Baetidae	Baetidae indeterminate	28	20	44
		Centroptilum indeterminate	4	0	0
		Cloeon fluviatile	8	0	0
	Caenidae	Caenidae indeterminate	0	0	0
		Tasmanocoenis arcuata	0	0	0
		Tasmanocoenis sp.E	0	0	0
		Tasmanocoenis sp.H	0	0	0
		Tasmanocoenis sp.J	0	0	0
		Tasmanocoenis indeterminate	0	0	0
		Wundacaenis dostini	0	0	0
	Leptophlebiidae	Leptophlebiidae indeterminate	16	0	0
Odonata					
(Anisoptera)	**Anisoptera**	**Anisoptera indeterminate**	**20**	**288**	**472**
(Zygoptera)	Zygoptera	Zygoptera indeterminate	28	98	64
	Libellulidae	*Aethriamanta nymphaea*	0	0	16
		Hydrobasileus brevistylus	0	16	0
		Libellulidae indeterminate	**6**	**135**	**176**
		Macrodiplax cora	0	0	0
		Nannodiplax rubra	16	48	16
		Neurothemis indeterminate	0	0	64
		Nannophya pygmaea	0	64	0
		Nannophya indeterminate	0	0	32
		Rhodothemis lieftincki	4	16	72
	Corduliidae	Corduliidae indeterminate	0	0	0
		Hemicordulia tau	0	0	0
	Coenagrionidae	Coenagrionidae indeterminate	21	103	150
		Austroagrion exclamationis	0	16	0
		Austrocnemis maccullochi	10	32	48
		Agriocnemus pygmaea	0	0	96
		Ischnura indeterminate	0	0	32
		Pseudagrion microcephalum	4	8	0
		Pseudagrion indeterminate	4	0	0
		Xanthagrion erythroneurum	8	0	0
	Protoneuridae	*Nososticta* indeterminate	4	0	0
	Gomphidae	*Austrogomphus mjobergi*	12	0	0
		Austrogomphus indeterminate	0	16	0
		Gomphidae indeterminate	28	32	0
		Ictinogomphus australis	0	8	0
	Aeshnidae	Aeshnidae indeterminate	0	8	0
Trichoptera	Ecnomidae	Ecnomidae indeterminate	5	0	0
		Ecnomia indeterminate	8	0	0
		Ecnomus indeterminate	8	0	0
	Hydroptilidae	*Hellyethira ramosa*	4	0	0
		Hellyethira indeterminate	8	0	0
		Hydroptilidae indeterminate	31	40	80
		Orthotrichia indeterminate	23	24	0
		Orthotrichia indeterminate (P)	8	0	0
	Leptoceridae	Leptoceridae indeterminate	54	0	32
		Leptorussa OSS1L	8	0	0
		Oecetis epekeina	0	0	32
		Oecetis indeterminate	41	20	109
		Triplectides ciuskus	4	0	0
		Triplectides helvolus	0	0	16

Coleoptera	Chrysomelidae	OSS1A (A)	0	0	32
		OSS1L	0	0	64
		OSS2A (A)	0	0	16
		Donacia OSS3A (A)	0	0	144
	Curculionidae	OSS1L	4	0	0
		OSS5A (A)	0	48	40
		Curculionidae indeterminate	4	0	16
	Dytiscidae	*Clypeodytes bifasciatus*	0	16	53
		OSS7L	16	0	0
		OSS23A (A)	4	0	0
		Hyphydrus OSS2L	0	16	0
		Hyphydrus OSS5L	0	0	16
		***Hyphydrus* indeterminate**	**8**	**0**	**192**
		Hydroglyphus godeffroyi	**0**	**0**	**269**
		Hydrovatus fasciatus	0	0	32
		Laccophylus clarki	0	0	16
		Laccophylus transversalis	0	0	32
		Megaporus rufa	0	0	16
	Elmidae	*Austrolimnius* indeterminate	17	0	0
	Gyrinidae	*Dineutus neohollandicus*	0	16	0
	Hydraenidae	*Hydraena* OSS1A (A)	0	0	16
		Hydraenidae indeterminate	0	0	32
	Hydrophilidae	*Amphiops queenslandicus*	0	20	64
		Berosus australiae	0	0	80
		Enochrus desertícola	**0**	**0**	**208**
		Hydrochus OSS3A (A)	4	0	16
		Hydrochus OSS4A (A)	10	0	171
		Hydrochus OSS5A (A)	10	0	0
		Helochares foveicollus (A)	0	0	32
		Hydrobiomorpha microspina	0	16	0
		OSS2L	7	16	56
		OSS15A (A)	0	0	56
		OSS16A (A)	0	0	16
		Hydrophilidae indeterminate	0	0	64
		Paracymus pygmaeus	0	16	0
		Paranacaena horni	0	0	48
	Noteridae	*Hydrocophus subfasciatus*	0	20	0
		OSS1L	0	0	32
	Staphylinidae	OSS6A (A)	4	0	0
Hemiptera	Belostomatidae	*Diplonychus* OSS1A (A)	0	0	32
	Belostomatidae	*Diplonychus* OSS2N	8	0	32
	Corixidae	**Corixidae indeterminate**	**0**	**8**	**256**
	Corixidae	*Micronecta micra*	0	0	144
	Corixidae	*Micronecta* indeterminate (A)	4	0	0
	Corixidae	*Micronecta* indeterminate	16	0	192
	Gerridae	OSS4N	10	0	0
	Hebridae	*Hebrus nourlangiei*	0	48	0
	Mesoveliidae	OSS1A (A)	10	0	0
	Mesoveliidae	OSS2N	16	0	64
	Mesoveliidae	OSS3N	0	32	24
	Mesoveliidae	Mesoveliidae indeterminate	0	64	32
	Naucoridae	*Naucoris rhizomatus*	0	16	0
	Naucoridae	*Naucoris* indeterminate	0	0	64
	Nepidae	*Ranatra* indeterminate (A)	0	0	32
	Nepidae	*Ranatra* indeterminate	64	0	0
	Notonectidae	*Enithares* indeterminate	4	0	0
	Notonectidae	Notonectidae indeterminate	16	0	0
	Pleidae	***Plea* indeterminate (A)**	**11**	**0**	**944**
	Pleidae	***Plea* indeterminate**	**8**	**12**	**496**
	Veliidae	OSS4N	24	0	16
	Veliidae	OSS5N	10	0	0
	Veliidae	Veliidae indeterminate	12	0	0
Lepidoptera	Pyralidae	OSS2L	0	40	32
	Pyralidae	Pyralidae indeterminate	8	16	80

Table 5 Habitat description within a $1m^2$ quadrat at each location along the transect at Island billabong.

Distance from billabong	10m	20m	30m	60m	100m
% live cover	80	90	60	100	100
% dead cover	20	10	40	0	0
% bare ground	0	0	0	0	0
% litter coverage	100	100	100	0	0
Litter depth	5	5	2	10	10
Max. vegetation height (cm)	80	70	90	110	120
Canopy cover†	2	4	1	0	0
Plant species present	para grass	para grass *Melaleuca*	para grass *Pseudoraphis*	para grass	para grass

† Canopy cover has the following units; 0 = 0%; 1 = 0-25%; 2 = 25-50%; 3 = 50-75%; 4 = 75-100%.

Table 6 Habitat description within a $1m^2$ quadrat at each location along the transect at Djabiluka billabong.

Distance from billabong	20m	60m	120m	200m	300m
% live cover	100	100	95	95	5
% dead cover	0	0	0	0	0
% bare ground	0	0	5*	5*	95
% litter coverage	0	0	0	0	0
Litter depth	0	0	0	0	0
Max. vegetation height (cm)	70	120	2	2	1
Canopy cover†	0	0	0	0	0
Species present	para grass	*Pseudoraphis* para grass	*Nymphoides* *Cynodon* *Glinus oppositifolius* *?Hymenachne* *Eleocharis* sp. *Persecaria*	*Glinus oppositifolius* *Nymphoides* *Cynodon* *Pseudoraphis* *Eleocharis* sp.	*Nymphoides* *?Cynodon* *Hymenachne*

* Bare ground due to damage caused by pig routing activity

† Canopy cover has the following units; 0 = 0%; 1 = 0-25%; 2 = 25-50%; 3 = 50-75%; 4 = 75-100%.

Table 7 The number of individuals of each taxon appearing during the soil rewetting experiment. All insects in this table are immature (either larvae or nymphs) unless otherwise indicated: (P.) = pupae; (P.Ex.) = shed pupal skin; (A.) = Adult.

					Island 100m										Djabiluka 20m										Djabiluka 60m									
				Day	1		3		7		14		21		1		3		7		14		21		1		3		7		14		21	
				Replicate	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Phylum	Class	Order	Family	Taxon																														
Platyhelminthes	Turbellaria			Turbellaria																							1		8	3	4	3		
Rotifera				Rotifera												7				3	3	57						1		1	4	2		
Nematoda				Nematoda	1	1			3	2			1			7		3	1	4		2			6	31	17	19	7	32	6	9	38	
Annelida	Oligochaeta			Oligochaeta											1				1							1								
Arthropoda	Arachnida	Acarina		Acarina	2	8	12	2	17	28	15	12	39	7	1	3	2	1	1	2			10		7	3	8	5	10	9	11	1	25	
	Insecta	Diptera	Ceratopogonidae	Ceratopogonidae																														
				Ceratopogonidae (P.)																														
				Ceratopogonidae (P.Ex.)																														
				Ceratopogonidae (A.)																														
			Chironomidae	Chironomidae	1						1								1															
				Chironomidae (P.)																														
				Chironomidae (P.Ex.)							3		2																					
				Chironomidae (A.)							1																							
			Tabanidae	?Tabanidae							1																							
		Coleoptera	Dytiscidae	Dytiscidae																1														
			Gyrinidae	Gyrinidae											1																			
			Hydrophilidae	Hydrophilidae (A.)																						1								
		Hemiptera	Velidae	Vellidae		1	2	1	2	1	2		1																				

Table 7 (continued)

					Djabiluka 120m										Djabiluka 200m										Djabiluka 300m									
				Day	1		3		7		14		21		1		3		7		14		21		1		3		7		14		21	
				Replicate	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Phylum	Class	Order	Family	Taxon																														
Platyhelminthes	Turbellaria			Turbellaria																											1			
Rotifera				Rotifera						1	4						1	2	1	5		7								1				
Nematoda				Nematoda	25	31	18	34	5	36	4	6	4	7	26	16	10	8	15	6	1	3			60	13	44	25	53	17	15	9	9	3
Annelida	Oligochaeta			Oligochaeta									1		2					1					5							2		
Arthropoda	Arachnida	Acarina		Acarina						1			1		4	6				1	2	3	17	21							3	1	3	1
	Insecta	Diptera	Ceratopogonidae	Ceratopogonidae (L.)																								1						
				Ceratopogonidae (P.)																											1			
				Ceratopogonidae (P.Ex.)																											1			
				Ceratopogonidae (A.)																											1			
			Chironomidae	Chironomidae (L.)																														
				Chironomidae (P.)																														
				Chironomidae (P.Ex.)																											1			
				Chironomidae (A.)																	1													
			Tabanidae	?Tabanidae																														
		Coleoptera	Dytiscidae	Dytiscidae (L.)											1	2																		
			Gyrinidae	Gyrinidae (L.)																														
			Hydrophilidae	Hydrophilidae (A.)																														
		Hemiptera	Velidae	Vellidae																														

Table 8 Shows the presence of taxa from the soil at each location. This data is based on identifications made using shed pupal and larval skins. Identifications were also made using the preserve animals from the final day of the rewetting experiment (day 21). This method enabled greater taxonomic penetration than the live sorting technique. Indeterminate taxa are individuals that could not be identified to a lower taxonomic level due to physical damage or underdevelopment of the animal.

Phylum	Class	Order	Family	Taxon	Island 100m	Djabiluka 20m	Djabiluka 60m	Djabiluka 120m	Djabiluka 200m	Djabiluka 300m
Platyhelminthes	Turbellaria			Turbellaria			+		+	+
Rotifera				Rotifera		+	+	+	+	+
Nematoda				Nematoda	+	+	+	+	+	+
Annelida	Oligochaeta			Oligochaete			+	+	+	+
				Naididae				+	+	+
				Dero						+
Arthropoda	Arachnida	Acarina		Mesostigmata sp.1	+	+	+			
				Mesostigmata sp.2					+	
				Scheloribates sp.						+
				Sacculozetes sp.	+					
				Hydrozetes sp.	+	+				
				Trhypochthoniellus sp.	+	+	+	+	+	+
				Unionicolidae	+					+
	Insecta	Diptera	Ceratopogonidae	Ceratopogonidae						+
			Chironomidae	Chironomidae indeterminate	+	+			+	
				Polypedilum K4	+					
				Polypedilum ?K4	+					
				Nanocladius sp.					+	+
			Tabanidae	?Tabanidae	+					
		Coleoptera	Dytiscidae	?Dytiscidae (L)					+	
			Gyrinidae	Gyrinidae (L)		+				
			Hydrophilidae	Hydrophilidae (A)			+			
		Hemiptera	Velidae	Velidae	+					

Table 9 List of aerial insects, known to have aquatic larval stages, collected in Malaise traps two weeks prior to floodplain inundation. The Chironomidae are grouped by subfamily and the Odonata by family. As well as showing those taxa present at the two trapping locations (Buffalo and Island billabongs), those taxa that were found in floodplain samples are also depicted. (+) indicates the presence of the taxon at a site. (?) indicates that the species concerned could be the same as a species present in the floodplain samples, but insufficient information exists to directly link the adult with the larvae.

	Buffalo	Island	Floodplain
CHIRONOMIDAE			
Chironominae			
Cryptochironomus		+	
Dicrotendipes pelechloris	+		+
Harnischia complex	+	+	+
Kiefferulus tumidus	+		?
Parachironomus type A	+		?
Parachironomus type B	+		?
Parachironomus type C	+		?
Polypedilum convexum	+		+
Polypedilum species A	+	+	?
Polypedilum species B		+	?
Polypedilum species C		+	?
Rheotanytarsus trivittatus	+		
Stenochironomus ?watsoni	+		
Xenochironomus sp.A	+		
Tanypodinae			
Procladius (*?goanna*)	+		+
Tanytarsus sp.		+	+
Pentaneurini	+		?
Ablabesmyia notabilis	+		?
Larsia	+		+
ODONATA			
Coenagrionidae			
Austroagrion exclamationis		+	
Ceriagrion aeruginosum	+		
Libellulidae			
Brachydiplex denticauda	+		+
Diplecodes trivialis	+	+	
Nannodiplax rubra		+	

Table 10 Results of the ANOVAs performed on the floodplain macroinvertebrate assemblage. Where applicable the data set and similarity index used are listed in brackets. *M.S.* = Mean Squares, *df* =degrees of freedom.

(a) ANOVA taxon richness

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	49.85	3	16.62	1.10	0.389
Residual	165.75	11	15.07		
Total	215.60	14			

(b) ANOVA Simpson's index

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.02549	3	0.0085	0.35	0.789
Residual	0.26579	11	0.02416		
Total	0.29	14			

(c) ANOVA first dimension of PCO (presence/absence data; Jaccard similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.01876	3	0.00625	0.11	0.951
Residual	0.60915	11	0.05538		
Total	0.62792	14			

(d) ANOVA second dimension of PCO (presence/absence data; Jaccard similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.23798	3	0.07933	0.88	0.479
Residual	0.98754	11	0.08978		
Total	1.22552	14			

(e) ANOVA first dimension of PCO (relative abundance data; Ecological similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.03693	2	0.01231	0.54	0.668
Residual	0.25307	11	0.02301		
Total	0.29	14			

(f) ANOVA second dimension of PCO (relative abundance data; Ecological similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.07874	3	0.02625	0.54	0.664
Residual	0.53345	11	0.0485		
Total	0.61219	14			

Table 11 Mean similarity of the chironomid taxa present in pair wise comparisons of samples from each site.

Site	Mean similarity index
Island	29%
Djabiluka	27%
Island and Djabiluka combined	27%

Table 12 Results of the ANOVAs performed on the larval chironomid assemblage at the Djabiluka site. Where applicable the data set and similarity index used are listed in brackets. *M.S.* = Mean Squares, *df* =degrees of freedom.

(a) ANOVA taxon richness richness

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	6.687	3	2.229	0.45	0.723
Residual	59.75	12	4.979		
Total	66.438	15			

(b) ANOVA Simpson's index

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.08142	3	0.02714	2.13	0.154
Residual	0.13984	11	0.01271		
Total	0.21557	14			

(c) ANOVA first dimension of PCO (presence/absence data; Jaccard similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.17	3	0.0567	0.44	0.731
Residual	1.5604	12	0.13		
Total	1.7304	15			

(d) ANOVA second dimension of PCO (presence/absence data; Jaccard similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.0448	3	0.0149	0.13	0.938
Residual	1.3404	12	0.1117		
Total	1.3852	15			

(e) ANOVA first dimension of PCO (relative abundance data; Ecological similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.25675	3	0.08558	1.52	0.261
Residual	0.6776	12	0.05647		
Total	0.93435	15			

(f) ANOVA second dimension of PCO (relative abundance data; Ecological similarity)

Source of Variation	*SS*	*df*	*MS*	*v.r.*	*P-value*
Time	0.3015	3	0.1005	1.61	0.238
Residual	0.748	12	0.06233		
Total	1.0495	15			

Table 13 Results of the ANOVAs on the relative abundance of *Chironomus* and *Parachironomus* in the Djabiluka floodplain chironomid assemblage over time. *M.S.* = Mean Squares, *df* = degrees of freedom.

(a) *Chironomus*

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*
Between Groups	0.5297	3	0.1766	5.7758	0.0111
Within Groups	0.3669	12	0.0306		
Total	0.8966	15			

(b) *Parachironomus*

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*
Between Groups	0.148	3	0.0493	0.9096	0.4653
Within Groups	0.6509	12	0.0542		
Total	0.799	15			

Table 14 Percentage composition of the major subgroups of the Chironomidae from the littoral zones of selected reservoirs (modified from Rosenberg *et al*., 1984).

Reservoir and location	Tanypodinae	Orthocladiinae	Chironomini	Tanytarsini
Southern Indian Lake, *Manitoba*	13	18	40	29
Beaver, *Arkansas*	35	7	58	<1
Kempton Park East, *Texas*	52	9	9	30
Eglwys Nunydd, *South Wales*	50	5	17	28
Lakes Vissavesi and Venetjärvi, *Finland*	24	22	54	<1
Lake Blåsjön, *Sweden*	1	31	<1	68
Friedenheim Farm Dam, *East Transvaal*	27	23	43	7
Lake Volta, *Ghana*	0.5	0	91	8.5

Appendix A Abundance of each taxon from the littoral (L) and profundal (P) zone of Mudginberri, Island and Djabiluka billabongs. All insects are immature (larvae or nymphs) unless otherwise indicated.

Phylum	Class	Order	Family (subfamily)	Taxon	Mudginberri					Island					Djabiluka					
					L	L	L	L	L	L	L	L	L	L	P	L	L	L	L	L
					1	2	3	4	5	1	2	3	4	5	3	1	2	3	4	5
Nematoda				Nematoda	16			16							20	128			96	
Mollusca	Gastropoda			Gastropoda	16		4	16	4		32	48	16			64	96		96	128
			Naididae	Naididae		48	152	24	16	28		160	16	112		12	321		128	256
				Pristina spp.											8				64	
				Pristinella spp.																
				Stylaria spp.																
			Tubificidae	Tubificidae	32	4	8								4				64	
Arthropoda	Crustacea		Atyidae	Atyidae	80	4			8	173	96	64	16	96	144	64		176	32	32
			Palaemonidae	Palaemonidae	32	12	4		12	8		48								48
	Acarina			Acarina indeterminate	48	148	4	32					16				64			32
		Prostigmata	Arrenuridae	Arrenuridae							128							80	32	
			Hydrachnidae	Hydrachnidae										8						
			Hydrophantidae	Hydrophantidae		8		24			32	32					32		32	
			Limnesidae	Limnesidae					8											
			Mideopsidae	Mideopsidae		204		48												
			Oxidae	Oxidae		36			4	8										
			Unionicolidae	Unionicolidae	256	64	16	96	76		64	16	32	8	924			48	64	16
		Oribatida		Oribatida indeterminate*	16	52		32			800	32	1360		4			48	3514	
Arthropoda	Insecta	Diptera	Chironomidae	Chironomidae indeterminate		12		56		8			16	32		64		32	128	64
				Chironomidae indeterminate (Pupa)			56	88	24	17	96	48	64				128	80	160	80
				Chironomidae unidentified	80											64				
			(Tanypodinae)	*Ablabesmyia hilli*				8		8					4					
				Ablabesmyia notabilis		24	8	8				32			8			16		
				Clinotanypus crux			4						16							
				Larsia albiceps	80	160	116	120	16	116	768	16	16	136	8	256	256	192	319	224
				Paramarina parva	64	4														
				Procladius paludicola		28	8	8		25		32			104	128	32	64		48
				Tanypodinae indeterminate		64	8	24			160	64	160	24	20	64	32	48	288	64
				Tanypus indeterminate											4	64		32		
				Thienemannyia indeterminate		8	4		4	25	704	160	128	112		577	160	336	927	80
			(Orthocladinae)	*Nanocladius* indeterminate	16			8							44	128				
				Orthocladinae				8												
				Parakiefferiella indeterminate			4			25	608				8	64		48	32	32
				?Parametriocnemus nr.ornaticornis														16		
			(Chironominae)	Chironominae indeterminate	16	12		16			96			16	32			48		32
				Chironomus sp.2														16		
				Cladotanytarsus indeterminate		16	8			8	384	16		16	12			32		
				Dicrotendipes septemmaculatus											4					
				Dicrotendipes indeterminate		8	8	24			32			8	32	64		80		32
				Dicrotendipes jobetus	32	8	32	40		17	64		32	32	220	128	32	176		144
				Dicrotendipes ?flexus									64							

		Kiefferulus indeterminate							32							32			
		Kiefferulus tinctus					8		16			28							
		Parachironomus indeterminate	16									24							
		Parachironomus K1																	16
		Parachironomus K2	16				17		16	16	16	56							
		Paratanytarsus indeterminate	16	4		8													
		Polypedilum (Pentapedilum) convexum		8	8		33		352				64	64	112	128	64		
		Polypedilum (Pentapedilum) K1					8	32				4		64					
		Polypedilum (Pentapedilum) leei		24	52		17		16		8	8	449	288	48		32		
		Polypedilum (Polypedilum) seorsus		4	4							8							
		Polypedilum indeterminate		16		8	17		112			8			64	32	48		
		Rheotanytarsus indeterminate					17	32			24	12		64					
		Stenochironomus watsoni			4														
		Strictochironomus indeterminate		8															
		Tanytarsus indeterminate		4				384	32	80	8	40		64	48	224	128		
		Tanytarsus K10						160											
		Tanytarsus K12						192			8	220	64		32	96	16		
		Tanytarsus manleyensis		4	4		41	832	112	224	24		256	96	32	415	448		
		?*Xenochironomus* indeterminate								16		4							
		Zavreliella marmorata		8			17	32	16	16	16		192		128	96	32		
	Ceratopogonidae	Ceratopogonidae		48	16	32	20	8	1568	96	48	88		513	192	16	192	32	
		Ceratopogonidae (Pupa)		4	4	8	4	8	64			32		64	32		64		
	Chaoboridae	Chaoboridae										8						16	
	Culicidae	Culicidae		8	4				96			16					160		
		Culicidae (Pupa)						25				12		32					
	Stratiomyidae	Stratiomyidae													32			16	
	Tipulidae	Tipulidae													32				
		Tipulidae (Pupa)														32			
Ephemeroptera	Baetidae	Baetidae indeterminate	16	44	20	32		8	32				64	32	48	32			
		Centroptilum indeterminate					4												
		Cloeon fluviatile		8	8														
	Caenidae	Caenidae indeterminate																	
		Tasmanocoenis arcuata																	
		Tasmanocoenis sp.E																	
		Tasmanocoenis sp.H																	
		Tasmanocoenis sp.J																	
		Tasmanocoenis indeterminate																	
		Wundacaenis dostini																	
	Leptophlebiidae	Leptophlebiidae indeterminate	16																
Odonata	Libellulidae	*Aethriamanta nymphaea*																	16
		Hydrobasileus brevistylus								16									
		Libellulidae indeterminate		8	4			74	128	144	288	40		128		144	288	144	
		Macrodiplax cora										4							
		Nannodiplax rubra	16								48								16
		Neurothemis indeterminate											64						
		Nannophya pygmaea									64								
		Nannophya indeterminate													32				
		Rhodothemis lieftincki		4							16				112	32			
	Corduliidae	Corduliidae indeterminate																	

		Hemicordulia tau																
	Coenagrionidae	Coenagrionidae indeterminate	48	16	12	24	4	25	192	112	48	136	8	64	32	32	383	240
		Austroagrion exclamationis										16						
		Austrocnemis macculiochi		12		8			32				4		64	64	32	32
		Agriocnemus pygmaea													96			
		Ischnura indeterminate															32	
		Pseudagrion microcephalum		4			4					8	48					
		Pseudagrion indeterminate			4													
		Xanthagrion erythroneurum			8													
	Protoneuridae	*Nososcticta* indeterminate		4														
	Zygoptera	Zygoptera indeterminate	64	4		16		25	224	32	112		52	64	96	32	64	64
	Gomphidae	*Austrogomphus mjobergi*		12														
		Austrogomphus indeterminate								16								
		Gomphidae indeterminate					28		32									
		Ictinogomphus australis										8						
	Aeshnidae	Aeshnidae indeterminate						8										
	Anisoptera	Anisoptera indeterminate	32		4	24		306	480	192	448	16		833		64	863	128
Trichoptera	Ecnomidae	Ecnomidae indeterminate		4	4	8							16					
		Ecnomia indeterminate		8														
		Ecnomus indeterminate			8		8											
	Hydroptilidae	*Hellyethira ramosa*		4														
		Hellyethira indeterminate				8												
		Hydroptilidae indeterminate	48	4		40			64	16				128			32	
		Orthotrichia indeterminate	48	8	4	32					32	16						
		Orthotrichia indeterminate (Pupa)				8												
	Leptoceridae	Leptoceridae indeterminate	224	12	4	24	8										32	
		Leptorussa OSS1L		8														
		Oecetis epekeina													32			
		Oecetis indeterminate		88	4	40	32	8	32				8	64	128	208	96	48
		Triplectides ciuskus		4														
		Triplectides helvolus														16		
Coleoptera	Chrysomelidae	OSS1A (Adult)													32	16		48
		OSS1L												64				
		OSS2A (Adult)														16		
		Donacia OSS3A (Adult)														144		
	Curculionidae	OSS1L		4														
		OSS5A (Adult)								48							64	16
		Curculionidae indeterminate			4											16		
	Dytiscidae	*Clypeodytes bifasciatus*								16				64		64	32	
		OSS7L	16															
		OSS23A (Adult)			4													
		Hyphydrus OSS2L									16							
		Hyphydrus OSS5L																16
		Hyphydrus indeterminate				8											192	
		Hydroglyphus godeffroyi												64	32	656	479	112
		Hydrovatus fasciatus															32	
		Laccophylus clarki																16
		Laccophylus transversalis														32		
		Megaporus rufa														16		

	Elmidae	*Austrolimnius* indeterminate	32			16	4													
	Gyrinidae	*Dineutus neohollandicus*								16										
	Hydraenidae	*Hydraena* OSS1A (Adult)														16				
		Hydraenidae indeterminate														32				
	Hydrophilidae	*Amphiops queenslandicus*						25		16							64			
		Berosus australiae														80				
		Enochrus deserticola														208				
		Hydrochus OSS3A (Adult)			4											16				
		Hydrochus OSS4A (Adult)		12		8								128		192	192			
		Hydrochus OSS5A (Adult)	16	8	8	16	4													
		Helochares foveicollus (Adult)														32				
		Hydrobiomorpha microspina									16									
		OSS2L		8	4		8			16							64	48		
		OSS15A (Adult)															64	48		
		OSS16A (Adult)																16		
		Hydrophilidae indeterminate												64						
		Paracymus pygmaeus										16								
		Paranacaena horni														48				
	Noteridae	*Hydrocophus subfasciatus*						8		32										
		OSS1L															32			
	Staphylinidae	OSS6A (Adult)					4													
Hemiptera	Belostomatidae	*Diplonychus* OSS1A (Adult)															32			
	Belostomatidae	*Diplonychus* OSS2N				8										32				
	Corixidae	Corixidae indeterminate						8					12	256						
	Corixidae	*Micronecta micra*														144				
	Corixidae	*Micronecta* indeterminate (Adult)					4													
	Corixidae	*Micronecta* indeterminate	16													192				
	Gerridae	OSS4N		4	16															
	Hebridae	*Hebrus nourlangiei*									48									
	Mesovellidae	OSS1A (Adult)			4	16														
	Mesoveliidae	OSS2N	16											64						
	Mesoveliidae	OSS3N							32							16		32		
	Mesoveliidae	Mesoveliidae indeterminate							64								32			
	Naucoridae	*Naucoris rhizomatus*									16									
	Naucoridae	*Naucoris* indeterminate												64						
	Nepidae	*Ranatra* indeterminate (Adult)													32					
	Nepidae	*Ranatra* indeterminate	64																	
	Notonectidae	*Enithares* indeterminate		4																
	Notonectidae	Notonectidae indeterminate	16																	
	Pleidae	*Plea* indeterminate (Adult)	16		8	8								897			990			
	Pleidae	*Plea* indeterminate		8						16		8			415	688		384		
	Veliidae	OSS4N				24										16				
	Veliidae	OSS5N	16		4															
	Veliidae	Veliidae indeterminate		12																
Lepidoptera	Pyralidae	OSS2L						17	64						32					
	Pyralidae	Pyralidae indeterminate				8					16				32	32	32	224		