4 Discussion

4.1 Size composition

Because freshwater fish characteristically display a considerable range of growth rates, depending on conditions such as food, space, numbers, competition and water temperature, a particular species does not necessarily achieve a specific maximum size (Weatherley & Roger 1978). In tropical waters, which have prevailing high temperatures, fish generally grow faster, mature younger, and have a shorter life span than fish in temperate waters (Lowe-McConnell 1975). Tropical fish species do, however, display a wide range of sizes, growth rates and life spans.[243] Certain adaptive characteristics (eg high efficiency as a predator, ability to avoid predators and to swim long distances) enable some species to grow rapidly and attain a large size. Other species remain small, their chances of survival improved by their ability to exploit foods not used by larger species,[244] to avoid predators within dense cover,[245] and to enter well-differentiated communities.

In communities of floodplain fishes in the seasonal tropics, a species may have an advantage if it can reproduce at a small size and early age (Lowe-McConnell 1975). Many smaller species living in such environments mature within a year — or larger ones within two years — enabling the fish to spawn in the next or next but one flood season. There is thus a high turnover in populations, and the results of 'good' or 'bad' spawning years (influenced by, for example, the extent of flooding, physical and chemical conditions, and also biotic factors) are rapidly reflected in catches. These seasonal fish populations in floodplain areas thus have high proportions of young-of-the-year, and the dynamic system of interacting variables results in large fluctuations in fish numbers both seasonally and annually.

Relative sizes of fish species

The mean lengths and weights of all species measured during the present study are shown in ranked order in figures 169a and b, respectively. From these data (particularly the mean weights) the fish species were grouped by size into small, medium, large and very large species.

The small species (mean lengths generally less than 50 mm LCF or TL and weights generally less than 2 g) were mainly members of the families Atherinidae, Ambassidae, Gobiidae, Eleotrididae (except for *O. lineolata*) and Melanotaeniidae. Most members of these families were carnivorous (except the melanotaeniids and *P. tenellus,* which were omnivorous). The atherinids and ambassids frequently exploited microcrustaceans from the middle of the water column, while the more predatory eleotrids and gobiids were bottom-water dwellers.

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[243] Peters (1983) has subsequently discussed the profound ecological consequences of body size, and Welcomme (1995) has highlighted the greater vulnerability of riverine fish taxa with large body size.

[244] Pusey et al (1995) examined the feeding ecology of freshwater fishes in two rivers of the Australian wet tropics. Five trophic guilds were recognised, and substantial discrimination between guilds on the basis of body size was observed. Small fishes (< 5 gm body weight) consumed a variety of insect larvae and small terrestrial insects. The diet of the large fish was characterised by the presence of large aquatic invertebrates and fish. A third group of intermediate sized fish (10–20 gm), which included the 0+ age class of three species of larger fish, also consumed aquatic invertebrates, but only a small proportion of terrestrial invertebrates.

[245] Bishop (1987) examined the dynamics of freshwater fish communities in the Alligator Rivers Region. Clear evidence was revealed that small species were better adapted than large species to shallower and more heavily vegetated areas.

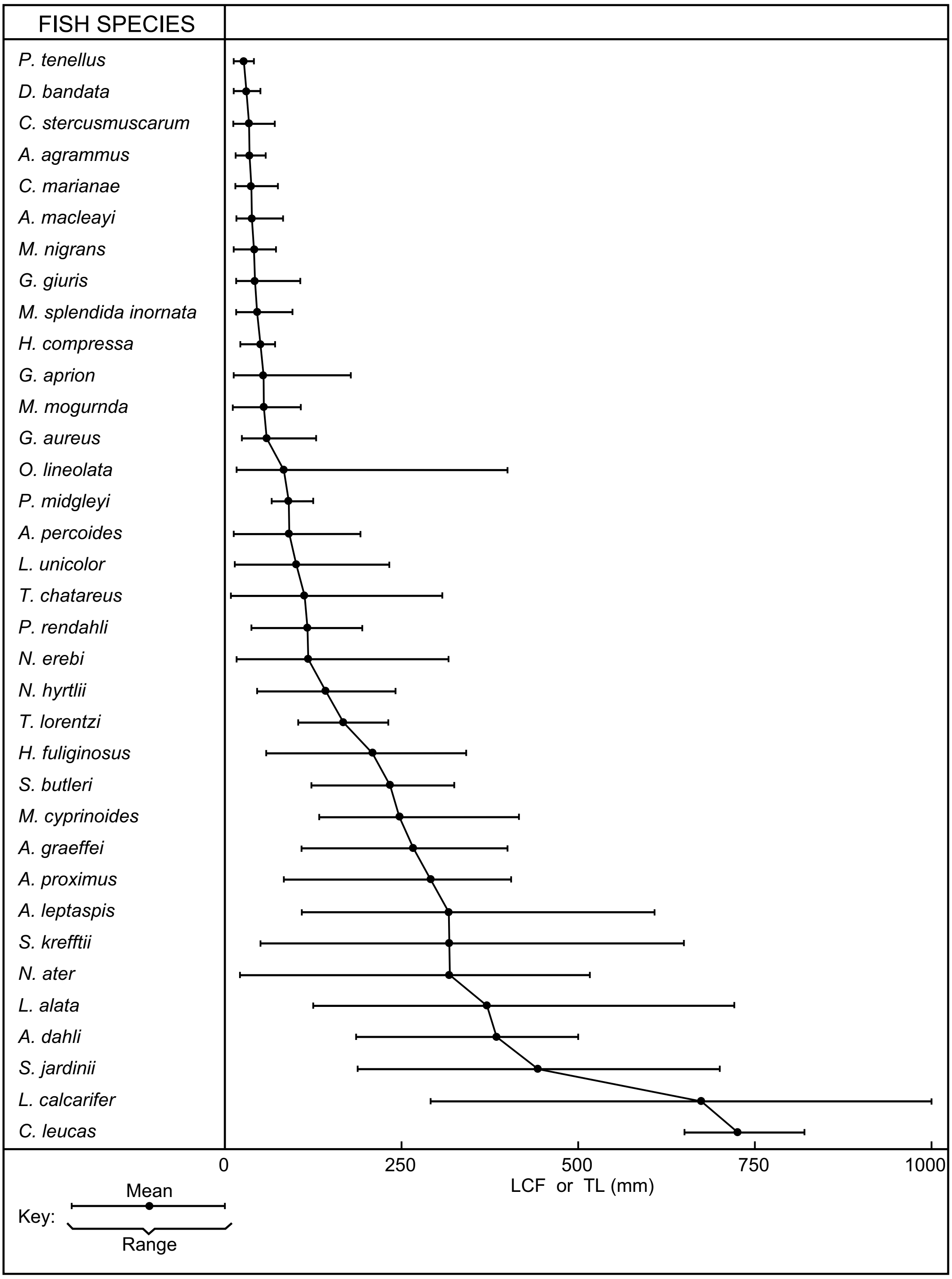

Figure 169a Ranked order of mean lengths of all species measured in the present study

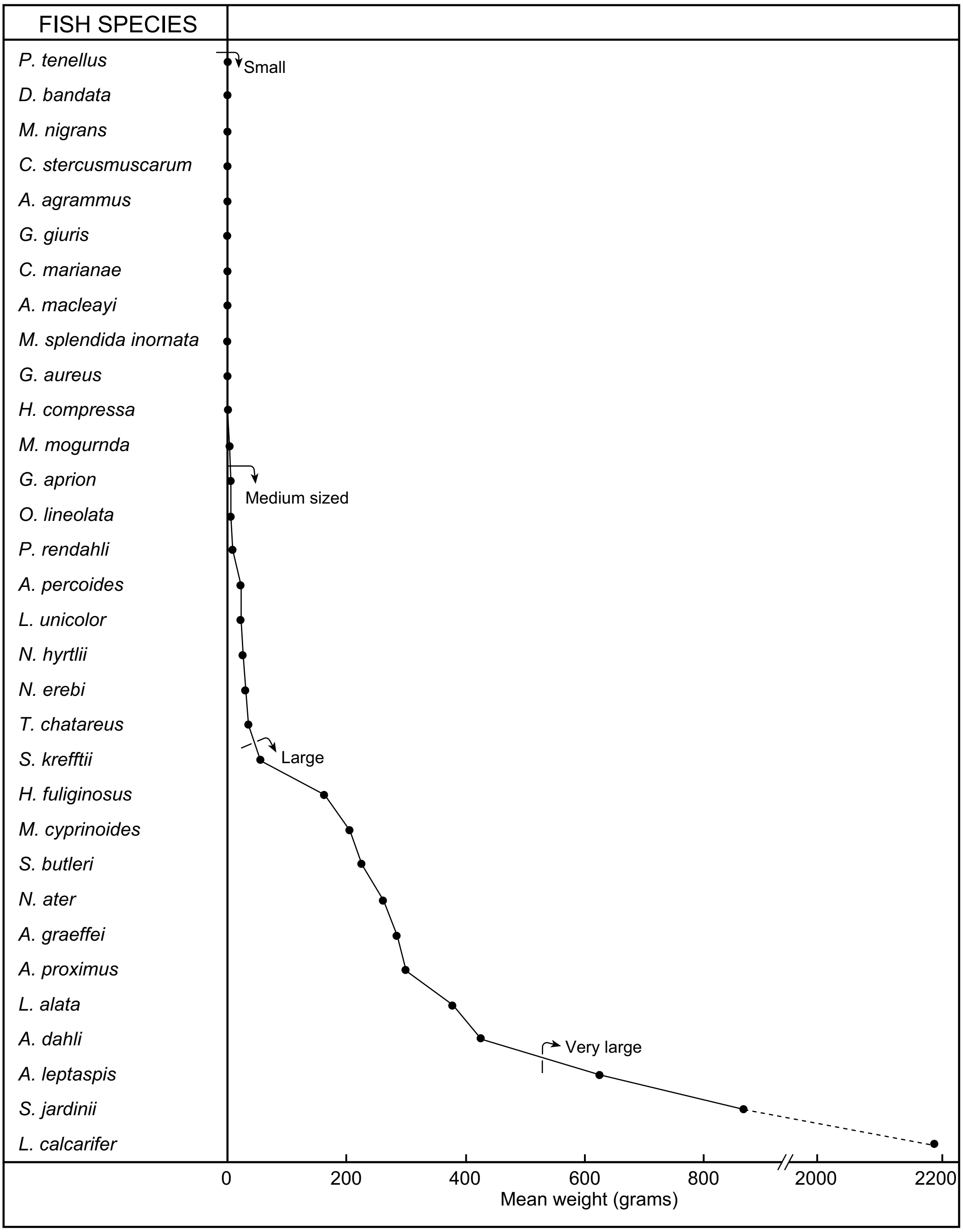

Figure 169b Ranked order of mean weights of all species measured in the present study

Medium-sized species (mean lengths and weights greater than the small species but less than 200 mm LCF or TL and 30 g) were *G. aprion*, the two small plotosid species (*P. rendahli* and *N. hyrtlii*), the smaller terapontids (*P. midgleyi*, *L. unicolor* and *A. percoides*), *O. lineolata, N. erebi* and *T. chatareus*. Although the last three species frequently grow to over 300 mm, their populations are usually dominated by young-of-the-year, which in turn correlates with their high fecundity. The feeding habits of all of these medium-sized fish species vary and in some cases are quite specialised (eg *P. midgleyi* and *T. chatareus*). *G. aprion, L. unicolor* and *O. lineolata* were piscivorous.

Large species were those with mean lengths greater than the medium-sized species and mean weights of less than 500 g. (Mean weight was the preferred variable, as it gives a better multi-dimensional perspective of size.) These included *S. krefftii*, the larger terapontids (*H. fuliginosus* and *S. butleri*), the larger plotosids (*N. ater* and *A. dahli*), *M. cyprinoides*, *L. alata* and two ariid catfishes (*A. graeffei* and *A. proximus*).

The two ariid catfishes might have been considered as very large species if more specimens had been collected in other seasons. The large species were mostly captured in deeper and more permanent waterbodies. Their feeding habits were varied; however, two were piscivores (*S. krefftii* and *M. cyprinoides*).

Very large species (mean weights greater than 500 g) were *A. leptaspis*, *S. jardinii*, *L. calcarifer*, and from estuarine upper reach habitats, *C. leucas*. These species were usually found in deeper and more permanent waterbodies. Their feeding habits varied, but at least three of the species were piscivorous.

Although the largest sizes of most species recorded were less than those reported in the published literature, individuals of five species (*S. butleri*, *T. lorentzi*, *A. dahli*, *N. ater* and *P. rendahli*) exceeded the published record lengths.

Methods

The small-sized and some medium-sized species were usually captured by seine net (SA, SZ, etc); some medium-sized and the large and very large species were usually captured by gillnet (GN and BN).

The two standard methods (SA and GN) caught the same species when large adult specimens of small and medium-sized species were captured by small-mesh gillnets, and small juvenile specimens of large and very large species were captured by seine nets. Fish of a considerable range of sizes were observed under water in clear escarpment streams.

The very small juveniles of primarily small fish species were caught only in seine nets that had become clogged with hydrophytes and filamentous algae, which reduced the effective mesh size. Very large species frequently escaped from monofilament gillnets (GN) during sets, as they were strong enough to break free from the entangling meshes. Some species (eg *H. fuliginosus* and *S. jardinii*) appeared to avoid gillnets set in clear waters, for few of them were caught, even though they were observed to be relatively abundant at such sites. The mesh selectivity of seine nets and gillnets frequently resulted in length-frequency peaks that were due to selectivity rather than real size trends (eg for *S. krefftii*).

After completing fish fauna surveys in the Finniss River (Northern Territory, Rum Jungle ex-uranium mining catchment), Jeffree and Williams (1975) concluded that spotlighting and poisoning tended to sample the same species, whereas gillnetting tended not to. The database of the present study should be examined to determine the size and species selectivity of each method, particularly gillnetting, so that comparison can be made with the study of Jeffree and Williams.

Size structure of samples

It was difficult to classify some species (eg *S. krefftii*) into adult and juvenile size groups because of apparent sexual differences in the lengths at first sexual maturity. Length-frequency analyses by separate sexes are thus required before such species can be assigned to the correct size grouping. Of the species for which there was enough biological information, fairly equal proportions were classified into the following three juvenile–adult dominance groups: skewed towards juveniles; approximately equal numbers of juveniles and adults; and skewed towards adults.

Nine species had length-frequency distributions skewed towards juvenile sizes. No small species were found in this group, as the mesh of the seine nets was generally too large to catch many of their juveniles. Three of the four very large species are in this group, as well as two catadromous species (*L. calcarifer* and *M. cyprinoides*) and several species with high fecundities (*N. erebi*, *T. chatareus* and *O. lineolata*). *Scleropages jardinii* and *N. ater,* which are also in this group, are particularly long at first maturation. The mortality of adult *G. aprion* is apparently high after it attains its LFM.

Eight fish species had fairly equal numbers of juveniles and adults. This group comprised only small species. Evidently, the LFM of most of these species coincided approximately with the mesh selectivity of the 10 mm mesh seine net (SA). This may reflect mesh-selectivity bias in the calculation of LFM or a high turnover of populations in the study area or both.

Nine species had length-frequency distributions skewed towards adult sizes, which could be because the juveniles grow quickly, the adults live longer, or both. In this group were small species (*M. splendida inornata*, *A. macleayi* and *H. compressa*) that have smaller LFM than the other species captured by seine net. Four species (*A. leptaspis*, *A. dahli*, *S. butleri* and possibly *P. midgleyi*) were also included in this group as their juveniles were seldom found abundantly (in some cases not at all), and therefore a greater number of adults than juveniles were captured in the samples. Male *A. leptaspis* buccally incubate their young until they attain 50 to 80 mm LCF; this fact, and the apparently fast growth of large juveniles, may explain the rarity of smaller juveniles of this species in the samples. The juveniles of *P. rendahli*, *L. unicolor* and *A. percoides* also grow rapidly, which may account for juveniles being present for only short periods during the year.

Habitats occupied by adult and juvenile size-groups

Lowe-McConnell (1975) suggested that young stages of many fish species often live in different biotopes from those of the parent fish. Many species move up rivers to spawn, and the newly hatched young often remain either upstream (where they may be more likely to escape predation by larger fishes) or in floodplain pools (although many of them may perish when the pools dry up, or fall prey to birds or the predatory fishes that frequent these pools).

For each species, habitats were defined as primary (the habitat where the species was most abundant) and secondary (where it was next most abundant). Primary and secondary habitats in which smaller juveniles, larger juveniles/smaller adults, and larger adults of some fish species were captured in the study area are shown in table 150. (The three size-groups above were considered as larger juveniles — smaller adults of some species occupied different habitats from smaller juveniles and larger adults.)

Table 150 Primary and secondary habitats in which smaller juveniles, larger juveniles/small adults and larger adults of various fish species were captured

	Smaller juveniles		Larger juveniles/smaller adults		Larger adults	
Habitat	Primary	Secondary	Primary	Secondary	Primary	Secondary
Escarpment mainchannel waterbody	*H. fuliginosus*	*C. marianae* *A. percoides* *G. giuris*	*H. fuliginosus* *P. midgleyi*	*C. marianae*	*H. fuliginosus* *S. butleri* *P. midgleyi* *T. chatareus*	*S. jardinii* *C. marianae* *A. percoides* *L. unicolor* *G. giuris*
Escarpment perennial stream	*M. nigrans* *P. midgleyi*	*H. fuliginosus* *S. butleri* *M. mogurnda*	*S. jardinii* *N. hyrtlii* *M. nigrans*	*H. fuliginosus* *L. unicolor* *P. midgleyi*	*M. nigrans*	*H. fuliginosus* *P. midgleyi* *M. mogurnda*
Lowland sandy creekbed	*M. splendida inornata* *C. marianae* *L. unicolor* *S. butleri* *M. mogurnda*	*N. hyrtlii* *S. krefftii* *M. nigrans*	*C. marianae* *P. tenellus* *A. percoides* *M. mogurnda*	*N. erebi* *N. ater* *S. krefftii* *C. stercusmuscarum* *D. bandata* *G. aprion* *T. chatareus* *G. giuris* *O. lineolata*	*C. marianae*	*M. nigrans*
Lowland backflow billabong	*S. jardinii* *A. leptaspis* *N. ater* *N. hyrtlii* *P. rendahli* *T. chatareus* *O. lineolata*	*M. cyprinoides* *N. erebi* *M. splendida inornata* *P. tenellus* *A. macleayi* *D. bandata* *L. unicolor* *G. aprion*	*N. erebi* *P. rendahli* *S. krefftii* *L. unicolor*	*N. hyrtlii* *A. agrammus*	*N. hyrtlii* *P. rendahli* *S. krefftii* *A. macleayi* *L. unicolor* *M. mogurnda* *O. lineolata*	*A. leptaspis* *M. splendida inornata* *C. stercusmuscarum* *P. tenellus* *A. agrammus* *D. bandata* *G. aprion*

Table 150 continued

	Smaller juveniles		Larger juveniles/smaller adults		Larger adults	
Habitat	Primary	Secondary	Primary	Secondary	Primary	Secondary
Corridor billabong	*N. erebi*	*A. agrammus*	*A. leptaspis*	*M. cyprinoides*	*N. erebi*	*M. cyprinoides*
	C. stercusmuscarum	*L. calcarifer*	*N. ater*	*S. jardinii*	*C. stercusmuscarum*	*N. ater*
	A. macleayi	*T. chatareus*	*M. splendida inornata*	*H. compressa*	*D. bandata*	*S. butleri*
	A. percoides	*L. alata*	*C. stercusmuscarum*		*L. calcarifer*	*T. chatareus*
	G. giuris	*H. compressa*	*A. macleayi*		*A. percoides*	*L. alata*
		O. lineolata	*D. bandata*		*G. giuris*	*H. compressa*
			L. calcarifer			
			G. aprion			
			T. chatareus			
			G. giuris			
			O. lineolata			
Floodplain billabong	*M. cyprinoides*	*A. leptaspis*	*M. cyprinoides*	*A. leptaspis*	*M. cyprinoides*	*N. erebi*
	S. krefftii	*N. ater*	*A. agrammus*	*P. rendahli*	*S. jardinii*	*P. rendahli*
	P. tenellus	*P. rendahli*	*H. compressa*		*A. leptaspis*	*S. krefftii*
	A. agrammus	*C. stercusmuscarum*			*N. ater*	*A. macleayi*
	D. bandata				*M. splendida inornata*	*L. calcarifer*
	L. calcarifer				*P. tenellus*	
	G. aprion				*A. agrammus*	
	L. alata				*G. aprion*	
	H. compressa				*L. alata*	
					H. compressa	

Smaller juveniles

The smaller juveniles of the largest numbers of species were found in lowland backflow billabongs and floodplain billabongs; for nine species these were primary habitats and for four, secondary habitats. The lowland backflow billabongs alone were a primary habitat for seven species and a secondary for eight. These two habitats therefore appear to be important nursery areas. The smaller juveniles of fewer species were found in corridor billabongs and sandy lowland creekbed pools; they were both primary habitats for five species, but the corridor billabongs were secondary habitats for six species and the sandy lowland creekbed pools for three. There were fewest species with smaller juveniles in escarpment perennial streams and escarpment mainchannel waterbodies, which indicates that the more diverse escarpment communities recruit larger juveniles/smaller adults from downstream habitats in the Wet season. Although escarpment habitats appear to be of little importance as nurseries for downstream species, they may be nurseries for some of the species of the more upstream communities.

Larger juveniles/smaller adults

The greatest number of species with larger juveniles/smaller adults were found in corridor billabongs, and slightly fewer species in sandy lowland creekbeds. Corridor billabongs were primary habitats for eleven species and secondary habitats for three; sandy lowland creekbeds were primary habitats for only three species, but secondary habitats for nine. These two habitats therefore appear to be important for some species when the juveniles are just becoming sexually mature. As the more permanent waterbodies (the floodplain and escarpment mainchannel waterbodies) connect with each other and the lowland backflow billabongs in the Wet season, corridor billabongs and sandy lowland creekbeds appear to be migration or dispersion routes for sexually maturing fish of various species.[246] Larger juveniles/smaller adults of fewer species were found in lowland billabongs and floodplain billabongs; both habitats were secondary for two species, but the floodplain billabongs were primary for four species, and the lowland backflow billabongs were primary for three. This suggests that sexually maturing fish move from floodplain and lowland backflow billabongs to corridor and sandy creekbed habitats. Larger juveniles/smaller adults of the fewest species were found in escarpment mainchannel and perennial stream habitats: the former was primary habitat to three species, secondary to three; the latter was primary to two and secondary to one.

Larger adults

The floodplain billabongs had the highest diversity of species present as larger adults: for ten they were the primary habitat, and for five the secondary. The lowland backflow billabongs were primary habitats for seven species, and secondary for seven. These habitats thus provided shelter for large adults, as did corridor billabongs and, to a lesser extent, escarpment mainchannel waterbodies. The corridor billabongs were primary habitats for six species and secondary for six; the escarpment mainchannel was primary habitat for four and secondary for five. This would be expected in these deeper and more permanent waterbodies. The lowest diversity of species present as large adults was in lowland sandy creekbeds (primary for one species and secondary for one) and escarpment perennial streams (primary for one species and secondary for three). The small size of these habitats and the seasonal nature of the lowland sandy creekbeds would account for these low numbers.

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[246] Bishop et al (1995) reported studies on fish movement dynamics within Magela Creek. Corridor billabongs were shown to be used as major movement routes between the floodplains and the lowlands towards the end of the Wet season.

‘Reservoirs’ of large adults of many species are thus found in floodplain, lowland backflow and corridor billabongs and, to a lesser extent, in escarpment mainchannel waterbodies. Smaller juveniles are recruited from these habitats. As they become sexually mature, many appear to disperse via the corridor billabongs and lowland sandy creekbeds that link between the reservoirs. Recolonisation of lowland billabongs, which shrink during the Dry season, is described in section 4.6 and volume 2. It appears that these habitats become important feeding areas for many species during the Wet season (‘Feeding habits’ section of the Discussion). The exact species- and size-composition and timing of fish migrations to and from the reservoirs is unknown and should be investigated in detail in future studies.[247]

Distribution of species relative to Ranger Uranium Project Area (RUPA)

The distribution of fish species downstream and upstream of RUPA is shown in table 151. It is important to know which species are abundant within the Magela Creek catchment downstream of RUPA, as they could be exposed to contaminants intentionally or accidentally released from the project area. It is also important to know whether the species found downstream have upstream populations, so that any effects of contaminants on downstream populations can be assessed. However, upstream populations may be based on migrations from downstream communities and so they could possibly be indirectly affected by impacts arising from contaminants. Of the 24 species found abundantly in many sites downstream of RUPA, 5 were found rarely in some upstream sites, 12 were found commonly in a few upstream sites, and 7 were found abundantly in many upstream sites. Upstream of RUPA, 13 species, including the last 7 species, were abundant in many sites, and 3 were found commonly, and 3 rarely, in a few sites.

Table 151 Distribution of fish species relative to the Ranger Uranium Project Area (RUPA) within the Magela Creek catchment

Downstream of RUPA/Upstream of RUPA				
++/–	++/+	++/++	+/++	–/++
M. cyprinoides	*N. erebi*	*M. splendida inornata*	*S. jardinii*	*H. fuliginosus*
O. gutturale	*A. leptaspis*	*C. marianae*	*S. butleri*	*P. midgleyi*
L. calcarifer	*N. ater*	*C. stercusmuscarum*	*M. mogurnda*	*M. nigrans*
L. alata	*N. hyrtlii*	*A. macleayi*		
H. compressa	*P. rendahli*	*A. percoides*		
	S. krefftii	*L. unicolor*		
	P. tenellus	*T. chatareus*		
	A. agrammus			
	D. bandata			
	G. aprion			
	G. giuris			
	O. lineolata			

++ Found abundantly in many sites; + Found commonly in a few sites; – Found rarely in some sites

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[247] This work was initiated in the studies of Bishop et al (1995).

Seasonal recruitment of juveniles

The seasonal pattern of juvenile recruitment of fish species for which adequate biological information was obtained is shown in table 152. Recruitment is defined as occurring when juveniles become abundant in the samples; larvae are generally smaller than the minimum effective mesh size of the nets used for capture and may or may not be present in unsampled habitats.

Table 152 Seasonal juvenile recruitment of various fish species for which adequate biological information was collected

	Seasons				
	Late-dry	Early-wet	Mid-wet	Late-wet–Early-dry	Mid-dry
Recruitment peak usually in only one season					
Primary		*N. erebi* *N. ater* *A. percoides* *L. unicolor* *T. chatareus*	*M. cyprinoides* *L. calcarifer* *L. alata* *S. jardinii* *A. leptaspis* *S. krefftii* *H. fuliginosus* *S. butleri* *P. midgleyi*	*H. compressa*	
Secondary	*A. percoides* *T. chatareus*				*A. percoides*
Continuous recruitment with a few peaks					
Primary		*M. splendida inornata* *A. agrammus* *M. macleayi*	*M. nigrans* *C. stercusmuscarum* *D. bandata* *M. mogurnda*	*P. tenellus* *G. aprion*	*C. marianae* *G. giuris*
Secondary	*C. marianae* *G. giuris*			*D. bandata* *M. mogurnda*	*M. splendida inornata* *M. nigrans* *C. stercus-muscarum* *A. agrammus* *G. aprion* *H. compressa*
Continuous recruitment with no apparent peaks					
		O. lineolata (no season)			

Three types of juvenile recruitment were apparent:

- *Type A* recruitment usually limited to one season
- *Type B* continuous recruitment, with a few peaks during the year
- *Type C* continuous recruitment, with no apparent peaks during the year.

Where recruitment peaked in more than one season, the largest peak was defined as primary and the next largest as secondary.

Type A recruitment was mainly apparent in medium-, large- and very large-sized species. The juveniles of most of these species were recruited to their populations during the Early-wet and Mid-wet seasons, when the whole aquatic environment was expanding or had expanded due to rising water levels. Juvenile recruits of two or three catadromous species (*M. cyprinoides*, *L. calcarifer* and possibly *L. alata*) enter the freshwaters of the study area mainly during the Mid-wet season when these waters connect with estuarine middle/lower reaches of the main rivers. *Amniataba percoides* and *T. chatareus* also had secondary peaks in the Late-dry seasons. Large numbers of juvenile recruits of the former species were also found in the Mid-dry seasons in sandy corridor billabongs.

Type B juvenile recruits were mainly of small species, which would not require as much space (particularly depth in the Dry season) in waterbodies as the larger species. However, environmental conditions in the Wet season are generally optimal for juvenile survival. Large numbers of species therefore recruited primarily in the Mid-wet season, while fewer species recruited in the Late-wet–Early-dry and Mid-dry seasons, and none in the Late-dry season. The secondary recruitment for some of these species extended over the Late-wet–Early-dry season and the Late-dry season, the largest numbers of species being recruited in the Mid-dry season. This secondary peak may arise because many of the small fish species reach their LFM in less than one year (table 153) and therefore fish present as juveniles in the Wet season may have sexually matured towards the Mid-dry season and be themselves then producing juveniles. Marchant (1982) noted a secondary resurgence of macroinvertebrate communities in corridor billabongs during the 1979 Mid-dry and Late-dry seasons. This increase in available food would coincide with the presence of juvenile fish in some corridor billabongs.

Only one species (*O. lineolata*) displayed type C recruitment.

Juvenile recruitment was generally higher for most species towards the end of 1978 than the end of 1979. This annual variation in juvenile recruitment was apparently caused by the more severe 1979 Dry season, with rainfall lower than average in the 1978–79 Wet season (so billabongs in the Dry season shrank further than in previous years), and rains in the 1979–80 Early-wet season later than average (so the creeks did not flow strongly at the same time as the previous year).

Table 153 Estimated time periods in which various fish species attain their length at first maturity

Time taken to attain LFM						
Within one Wet season	Less than one year	One year	One to two years	Two years	Three years	Four years
M. nigrans	*P. rendahli*	*M. cyprinoides*[1]	*A. leptaspis*	*S. krefftii (F)*	*S. jardinii*[2]	*L. calcarifer*[3]
M. splendida inornata	*C. marianae*	*N. erebi*	*S. krefftii (M)*	*T. chatareus*		
C. stercus-muscarum	*P. tenellus*	*N. ater*				
A. agrammus	*A. macleayi*	*A. percoides*				
D. bandata	*L. unicolor*	*H. compressa*				
	G. giuris					
	M. mogurnda					

M = male; F = female; 1 Based on Wade et al (1966); 2 Based on Lake & Midgley (1970a) for *S. leichardti;* 3 Based on Reynolds (1978)

Time taken to attain the LFM

Lowe-McConnell (1975) found that the growth rates of tropical fishes in natural waters are very difficult to determine, as the breeding seasons are generally not well defined, which makes it difficult to follow length-frequency mode progressions. This was a problem in the present study, and it was compounded by the effects of fishing-gear selectivity and the wide variety of habitats sampled (seasonal length-frequency analyses for this report were carried out on data from combined habitats). Further studies are required before our tentative growth estimates can be confirmed.

Tentative estimates of early growth rates were possible for 19 species. Generally, growth was fastest between the Early-wet and Late-wet–Early-dry seasons, and had stopped for most species towards the Late-dry season. Lowe-McConnell (1975) found that the ‘highwater’ time in tropical freshwaters is the main feeding, growing and fattening season for nearly all species.

Estimates of growth rate were undertaken primarily to obtain an indication of the time species took to attain their LFM. Catches of species that attain their LFM very young rapidly reflect environmental conditions that adversely affect spawning success. Tentative time periods in which various fish species attained their LFM in the study area are shown in table 153.

Most (17) of the fish species studied attain the LFM in one year or less. The 12 species that attain the LFM in less than one year were nearly all small-sized species (except *L. unicolor* and *P. rendahli*, which are widely distributed medium-sized species). The 5 species that attained the LFM within one Wet season were (except for *M. nigrans*) the most abundant and widely distributed species in the study area. These may be considered to be the most ‘successful’ of the small fish species.

The species that may attain the LFM after their first year are mainly medium, large and very large: the very large species *S. jardinii* attains it in four years; *L. calcarifer* in three years; *A. leptaspis* (which apparently grows very rapidly) in one to two years.

Seasonal changes in body condition

A concomitant of somatic growth in fish is change in body condition during life. Such changes can be great or small, smoothly progressive, intermittent, or cyclically related to breeding. The many studies detailing changes in condition of fish populations frequently provide insight into the lives of fishes in relation to food supply and the timing and duration of breeding activity.

Nikolski (1963) suggested that, in several species of fishes, temperature acts as a ‘signal factor’, in that a reduction of the temperature below a certain level leads to a cessation of protein growth and the start of fat accumulation. Pollard (1972) thought that external factors probably influence the timing and control of the mobilisation of nutrient reserves.

Sampling seasons during which the highest and lowest body conditions were recorded for various fish species are shown in table 154. Most species attain their best body condition from the Mid-wet to the Mid-dry seasons, with a peak in the Late-wet–Early-dry season. This trend reflects that observed for the relative numbers of fish species per season showing the greatest feeding activity (see section 4.4). However, peak body condition appears to follow slightly after peaks in feeding activity. More species attained their best body condition in the 1978 Late-dry season than in the same season in 1979; environmental conditions appear to have been much less favourable in the 1979 Dry season. Some species (eg *T. chatareus*) attained greater gonadal maturation in the 1978 than in the 1979 Late-dry seasons.

Seasonal trends in the numbers of species of fish with poorest condition were more complex. The greatest number of species in their poorest condition during the study occurred in the 1978–79 Early-wet season, caused mainly by the presence of recently spent specimens of several species (eg *N. erebi* and *A. leptaspis*). Such a peak in the number of species with low condition did not recur in the 1979–80 Early-wet, as few species appeared to have bred successfully in this season, presumably because the creeks and channels had not begun to flow by the time sampling ended, unlike the 1978–79 Early-wet season.

Table 154 Sampling seasons in which the highest and lowest body condition (K) was recorded for various fish species in the study area

	Sampling season						
Condition	1978 Late-dry	1978–79 Early-wet	Mid-wet	Late-Wet–Early-dry	Mid-dry	1979 Late-dry	1979–80 Early-wet
Highest	*S. jardinii*	*A. macleayi*	*S. krefftii*	*N. erebi*	*M. cyprinoides*	*O. lineolata*	*G. giuris*
	D. bandata		*M. splendida inomata*	*M. nigrans*	*A. leptaspis*		
	H. fuliginosus		*P. midgleyi*	*C. marianae*	*P. rendahli*		
	T. chatareus		*H. compressa*	*P. tenellus*	*N. hyrtlii*		
				L. calcarifer	*C. stercusmuscarum*		
				A. percoides	*A. agrammus*		
				L. unicolor			
				G. aprion			
				L. alata			
				M. mogurnda			
	Total number of species						
	4	**1**	**4**	**10**	**6**	**1**	**1**
Lowest	*M. cyprinoides*	*N. erebi*	*S. butleri*	*P. rendahli*	*S. krefftii*	*C. stercusmuscarum*	*S. jardinii*
	M. nigrans	*A. leptaspis*		*A. agrammus*	*P. midgleyi*	*A. percoides*	*N. hyrtlii*
	L. alata	*N. ater*		*G. giuris*	*T. chatareus*	*H. fuliginosus*	*M. splendida inomata*
	O. lineolata	*C. marianae*		*H. compressa*		*L. unicolor*	*A. macleayi*
		D. bandata					*G. aprion*
		L. calcarifer					
		M. mogurnda					
	Total number of species						
	4	**7**	**1**	**4**	**3**	**4**	**5**

Four species were in their poorest body condition in the Late-dry seasons of both 1978 and 1979. However, most species lost more condition in the 1979 Dry season than in the 1978. A secondary peak in the numbers of fish species in their lowest condition occurred during the Late-wet–Early-dry season, which was unexpected, as most other species attained their best condition in this season. The phenomenon may have been a result of the anoxic conditions recorded in the bottom waters of most lowland backflow and floodplain billabongs during this season, as most of the species (eg *P. rendahli*, *N. ater*, *G. giuris* and *N. erebi*) with low body condition at this time were benthic feeders. However *N. erebi* adapted by changing its feeding habits during this period: from being predominantly a benthic feeder, it became a midwater feeder.

Seasonal changes in the body condition of various fish species in the present study appeared to show the effects of breeding activity, supply of food and other environmental variables. Before such factors can be used to predict environmentally induced stresses on fish species in the Alligator Rivers Region, the effects on seasonal body condition of such phenomena as the sex and size of fish, the habitat in which they are captured, and the occurrence of parasites, must be elucidated.

4.2 Environmental associations

Although this study was carried out over only 16 months, much useful information indicative of the environmental associations of 32 fish species was obtained. Many of the abiotic factors, such as dissolved oxygen, water temperature, pH and substrate, interact with one another, but will generally be considered separately here. The rankings of fish species by various physico–chemical and habitat–structural variables are shown in table 155. Refer to table data in appendix 6 and 7. Further work of this type is necessary, as well as supplementary laboratory and experimental work, particularly on the effects of disturbances on particular characteristics in the environment of a species. The trends observed for each physico–chemical and habitat–structural variable are briefly discussed below in the same order as in the accounts of the individual species in chapter 3.

The physico–chemical characteristics studied at each sampling site were water temperature, dissolved oxygen concentration, water visibility, pH, conductivity, type of substrate and vegetation. Bank vegetation and water flow were also recorded.

Water temperature

The surface and bottom water temperatures (means, standard errors and ranges) for the fish species captured in the study are shown in figures 170a and b, respectively.

Water temperatures in the study area varied widely, since they are affected by a number of factors.

- the topographic difference between the escarpment and lower reaches of the catchment: waterbodies in the escarpment areas have steep valley sides and overhanging terrestrial vegetation, so they are generally cooler than the waterbodies of the lower reaches.
- the water depths and surface areas of the channels: the shallower, wider channels are more influenced by changes in air temperature than are the narrower, deeper channels more commonly found in escarpment areas.
- the velocity and turbidity of the water: slow-moving, turbid waters will absorb more heat than fast-moving, clear waters. As the escarpment waterbodies are usually narrower, faster-flowing and clearer than the waterbodies of the lower reach habitats, they are usually cooler.

Table 155 Rank numbers for *in situ* physico–chemical and habitat structural parameters for the majority of the species studied. The greater the rank number, the higher the mean value, or dominance, of a parameter.

	Physico–chemical							Substrate				Hydrophytes			
	Temp		DO		pH										
Species	S	B	S	B	S	B	Visibility	Bedrock	Mud	Sand	Clay	Floating-attached	Emergent	Submergent	Vegetation-occurrence index
‘No catch’	23	13	6	9	20	12	19	1	23	14	29	33	12	9	17
M. cyprinoides	8	9	21	2	31	22	24	28	20	9	33	25	7	33	24
N. erebi	25	15	26	13	21	11	20	11	22	10	32	28	9	29	20
S. jardinii	4	3	12	11	4	6	29	34	7	27	11	35	4	27	10
A. leptaspis	15	11	9	3	12	7	22	14	29	5	36	27	8	26	26
A. proximus	10	1	31	9	19	6	29	2	33	1	37	20	1	35	35
A. graeffei	7	13	2	4	2	31	28	3	9	39	13	8	13	18	2
A. dahli	12	12	16	19	4	27	31	4	14	32	6	34	3	36	3
Neosilurus sp. A	29	27	10	8	7	4	25	13	18	21	7	32	27	15	18
Neosilurus sp. B	9	9	11	26	5	8	30	32	5	29	8	32	2	2	6
Neosilurus sp. C	24	13	18	5	29	18	11	29	31	3	26	34	12	7	12
N. ater	4	1	3	6	5	14	26	1	12	13	33	33	10	5	14
N. hyrtlii	7	1	20	10	23	21	9	19	26	8	28	36	6	16	13
P. rendahli	10	7	5	12	17	19	4	6	35	2	30	29	12	14	31
S. krefftii	16	14	28	14	30	20	21	21	21	17	32	30	15	19	21
M. splendida inornata	20	24	13	25	15	16	12	26	15	23	17	14	20	22	19
M. nigrans	2	5	13	29	1	2	30	36	4	25	1	16	21	4	4
C. marianae	17	25	23	32	25	29	13	14	6	33	4	7	25	34	8
C. stercusmuscarum	28	28	7	27	16	28	15	17	11	24	20	12	23	25	25
P. tenellus	29	32	31	28	9	–	16	18	19	7	34	10	30	8	32

Table 155 continued

	Physico–chemical							Substrate				Hydrophytes			
	Temp		DO		pH										
Species	S	B	S	B	S	B	Visibility	Bedrock	Mud	Sand	Clay	Floating attached	Emergent	Submergent	Vegetation-occurrence index
A. agrammus	33	27	16	17	28	18	5	16	27	22	9	26	29	5	28
A. macleayi	18	20	23	20	18	24	14	15	17	18	19	15	24	13	23
D. bandata	27	29	15	16	26	26	7	7	28	12	13	18	18	20	33
L. calcarifer	14	10	1	6	1	13	17	24	30	13	27	6	32	10	30
A. percoides	12	18	22	32	22	23	27	23	10	11	12	23	11	31	9
H. fuliginosus	3	6	17	33	3	3	33	37	1	26	2	2	33	3	1
L. unicolor	13	16	25	18	13	9	18	31	13	19	16	24	17	23	11
S. butleri	6	12	20	30	8	15	32	33	3	30	10	1	35	1	7
P. midgleyi	1	4	14	31	2	5	34	35	2	28	3	3	5	6	5
G. aprion	19	19	24	23	24	14	10	25	23	14	24	6	16	21	29
T. chatareus	21	23	17	15	14	10	23	22	16	20	21	22	28	11	16
L. alata	12	27	1	1	24	17	6	27	36	6	14	4	34	12	34
G. giuris	21	26	29	33	32	30	33	20	8	31	5	5	31	28	15
H. compressa	30	31	19	–	33	–	2	9	34	4	15	9	22	32	36
M. mogurnda	11	17	4	24	6	1	1	30	20	15	18	11	20	17	22
O. lineolata	26	21	14	21	27	25	3	10	32	8	23	19	14	24	27

S = Surface

B = Bottom

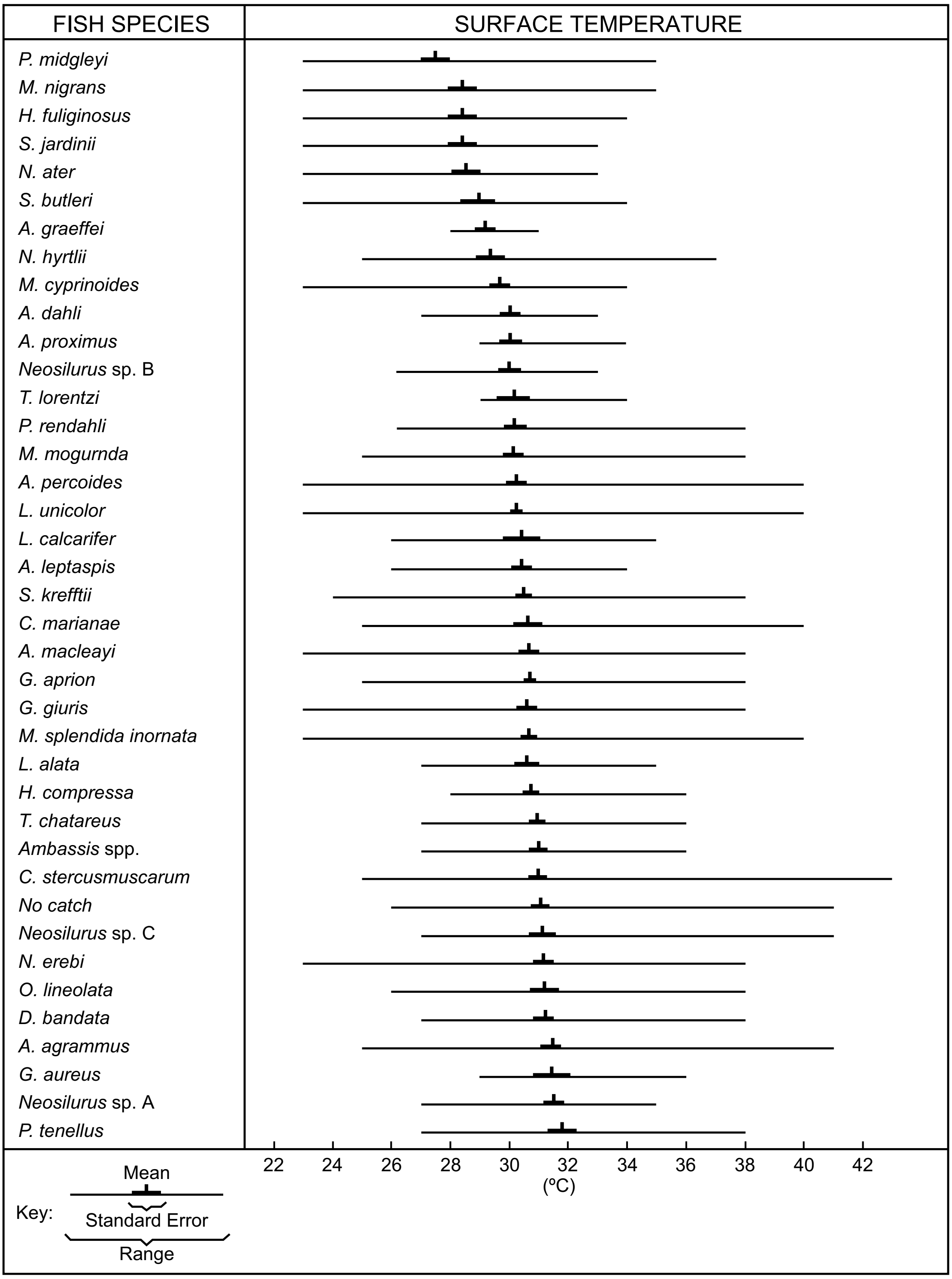

Figure 170a *In situ* surface water temperatures (means, standard error and ranges) for various fish species captured during the study period (see appendix 6)

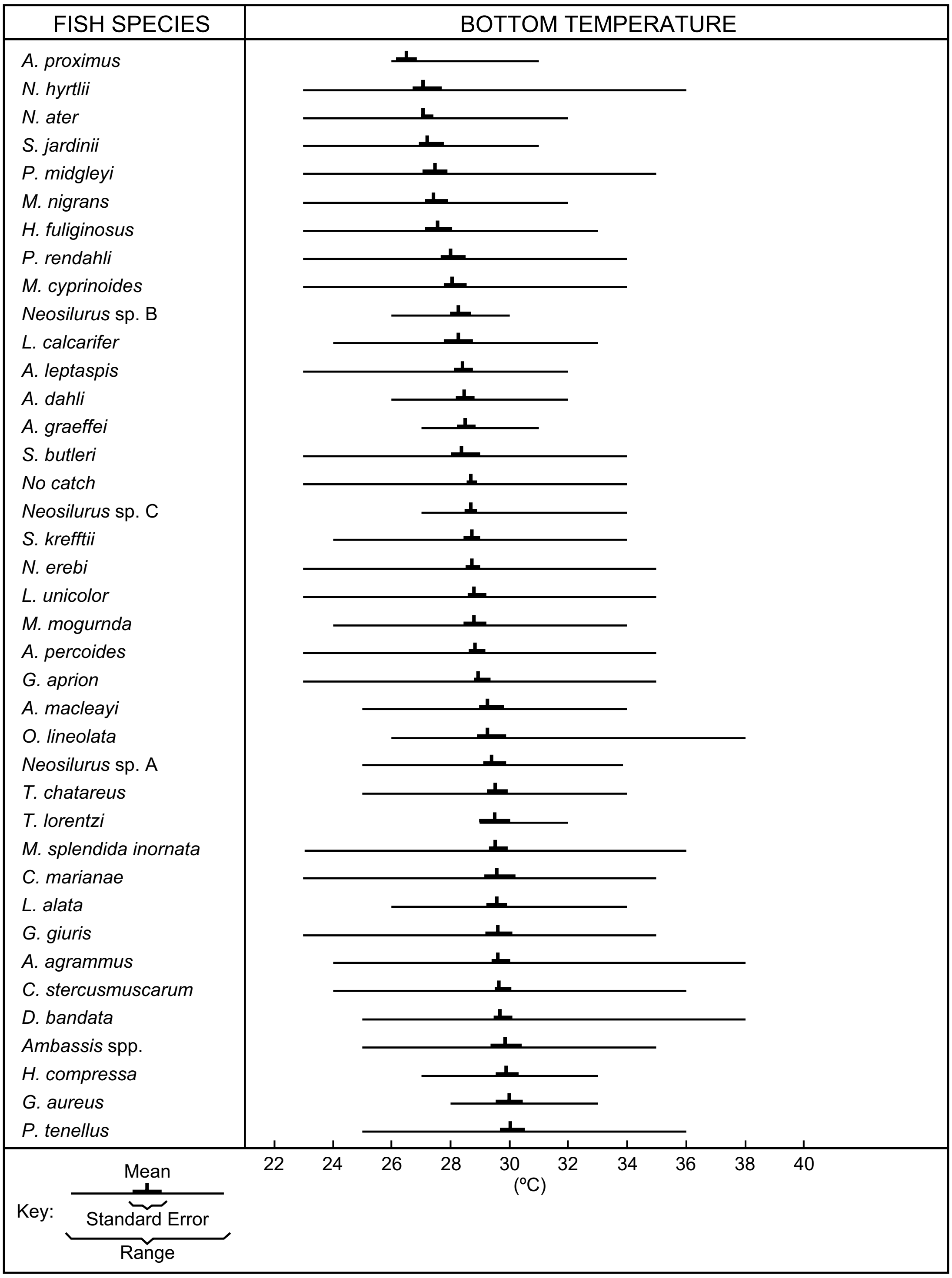

Figure 170b *In situ* bottom water temperatures (means, standard error and ranges) for various fish species captured during the study period (see appendix 6)

Water temperature limits both the broad geographical distributions of stream fishes and their local occurrences within a single watercourse. Their tolerance to different water temperatures clearly affects the overall distribution of fish species (Hynes 1970).

During the present study, water temperatures ranged from 23° to 43°C. As water temperature varies vertically (ie from top to bottom of the water column), both the surface and bottom water temperatures were recorded at each sampling site to give a more representative estimate of temperatures at that site and to quantify the difference between the two environments potentially available to fish. Many species were found typically in either surface or bottom waters; some plotosid catfishes, for example, spend most of their time feeding in benthic areas and are thus classified as 'bottom dwellers'. For these, and other 'vertically specialised' species, surface (or conversely bottom) water temperature readings may not be very relevant. With these vertical habitat differences in mind, the range of water temperatures associated with a species was usually found to be a good indicator of that species' distribution and often confirmed or added to the findings of other workers on the temperature tolerances of that species or its family or genus.

Generally, fish found primarily in the escarpment zone lived in cooler waters with lower means and narrower ranges than those found primarily in lower reaches. The species found in waters with the widest ranges of temperatures (*A. percoides*, *L. unicolor*, *C. stercusmuscarum*, *M. splendida inornata*, *C. marianae*, *N. hyrtlii*, *N. erebi* and *A. agrammus*) were the most common and/or widely distributed species. More temperature readings were taken in waters in which the more abundant species were found than in those inhabited by less abundant species. This 'sample size' effect must be kept in mind when considering the relationship between a species and its apparent 'preferred' water temperatures. Thus species like *A. dahli* and *H. compressa* were associated with narrow ranges of water temperatures, but this narrowness may be a function of the small number of temperature readings taken in conjunction with these species. Other workers have found that *H. compressa* tolerates a wider range of temperatures than is indicated in this study. The other narrow-range species were *L. calcarifer*, *A. leptaspis* and *A. graeffei*, plotosid catfishes and other bottom-dwelling species.

The plotosids and escarpment-area dwellers, such as *S. jardinii*, *P. midgleyi*, *H. fuliginosus*, *M. nigrans* and *S. butleri*, were captured in waters with low minimum and mean temperatures. These species are typically found in cooler bottom or escarpment waters. At the other extreme, *A. agrammus*, *C. stercusmuscarum*, *A. percoides*, *L. unicolor*, *M. splendida inornata* and *N. hyrtlii* were found in waters with temperatures up to and above 40°C. Previous workers have found some of these species to be tolerant of hot waters (eg *Craterocephalus* spp.) or desiccation (eg *L. unicolor*). Generally, fish found typically in the lower reaches of the catchment, and widely distributed hardy species, could withstand the greatest ranges of, and extremely high, temperatures. Since these species were usually common, 'sample size' error was reduced.

Water temperatures recorded for a particular species are a function of the distribution of the species and may reflect its tendency to be found in bottom, middle or surface levels of its 'preferred' habitats. Some good indications of the natural temperature tolerances of individual species have been obtained, but further work is necessary. The upper and lower water temperatures that are lethal to a species should be tested in the laboratory for all stages of the life cycles of the species studied. Further field studies should also be done on the effects of water temperature on the biology of a species, perhaps including experimental manipulations to find out whether, for example, populations of a particular species found in escarpment habitats have the same upper lethal temperature as populations of the same species from the lower reaches of the catchments.

Dissolved oxygen

The surface and bottom dissolved oxygen levels (means, standard errors and ranges) for the fish species captured in the study are shown in figures 171a and b, respectively.

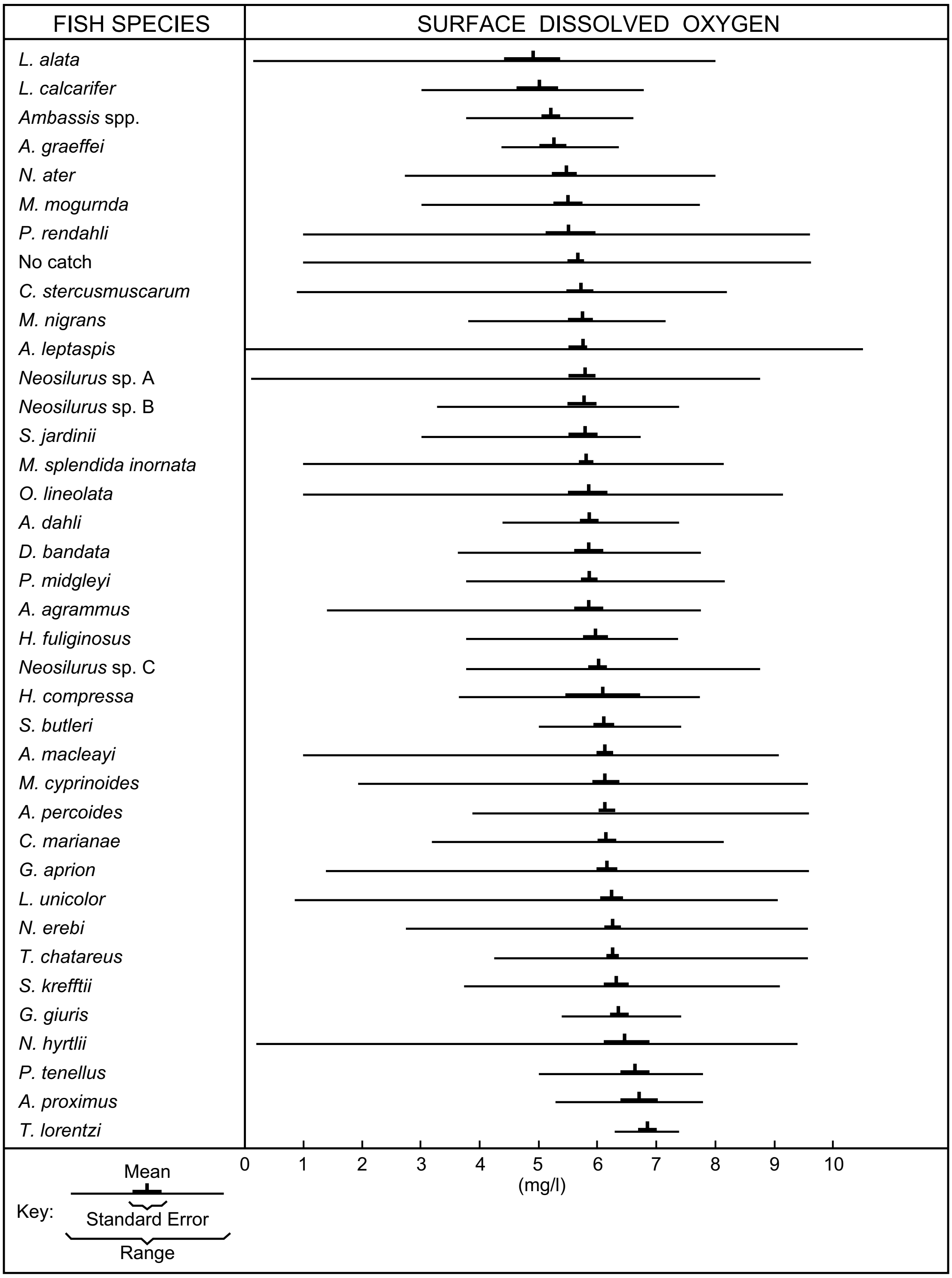

Figure 171a *In situ* surface dissolved oxygen levels (means, standard errors and ranges) for various fish species captured during the study period (see appendix 6)

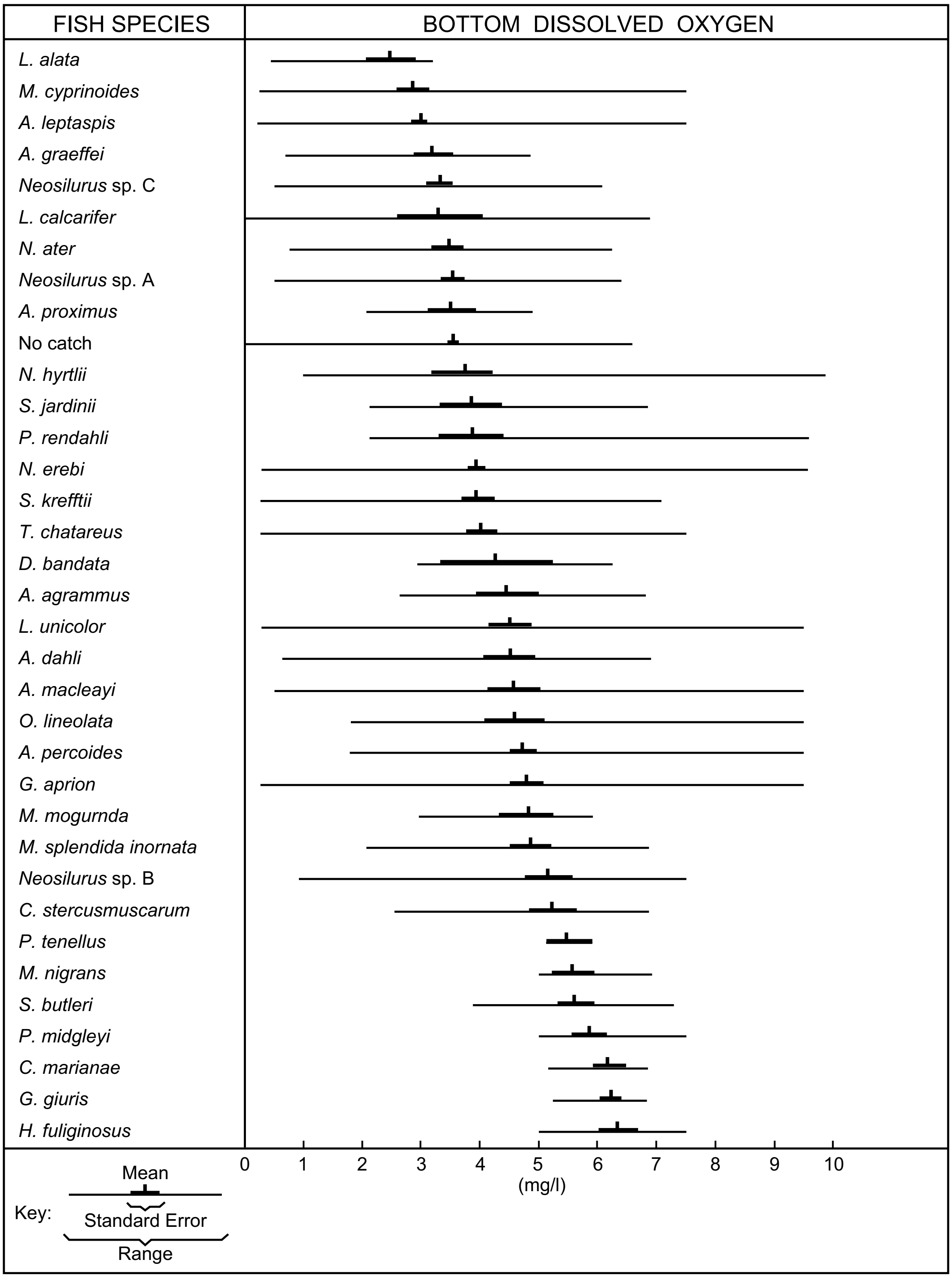

Figure 171b *In situ* bottom dissolved oxygen levels (means, standard errors and ranges) for various fish species captured during the study period (see appendix 6)

The dissolved oxygen (DO) concentration in water limits the distribution and abundance of fish species (Hynes 1970), many species being adapted to tolerate the range of DO concentration characteristic of their preferred environment. DO concentration in water varies with water temperature, depth and surface area of the channel or waterbody, pH, velocity of water flow and the vegetation content of the waters. For example, DO concentrations are likely to be higher in cool, fast-flowing, shallow streams than in warm, deep, lentic billabongs. Owing to diffusion characteristics, DO levels of surface waters are generally higher than of bottom waters, especially in still, unmixed waterbodies. Fish acclimated to running waters use more oxygen than do fish from still waters, where DO may be in short supply (Winberg 1956). DO readings were taken at both the water surface and the bottom at most sample sites.

Escarpment and lowland waters are distinguished by a difference in DO concentrations, which is a result of the differences in flow, water temperature, depth and pH. DO concentrations ranged from 0.0 to 10.0 mg/L in the waters sampled. In turbulent waters, surface and bottom DO levels are similar; in unmixed waters they are different, which would not affect species that are generally bottom-dwelling or surface-swimming fish. DO variables are best interpreted in the light of the species' vertical distribution in the waterbodies it inhabits and other aspects of its ecology.

Species of fish found in escarpment or shallow waters were associated with higher mean DO concentrations than species found in other habitats. Since surface waters are more influenced by temperature, diffusion and wind, their DO levels are generally more variable than bottom-water DO levels, which are therefore more likely to be reliable indicators of 'average' local DO characteristics at the sampling sites. High levels of DO at the bottom indicate waters that are cool, well mixed or heavily vegetated; the highest mean bottom-water DO levels were found in cool, turbulent escarpment streams. The species typically inhabiting these streams were *M. nigrans*, *H. fuliginosus*, *C. marianae*, *S. butleri* and *P. midgleyi.* Other species associated with waters with high mean bottom-water DO values were *O. lineolata*, *A. percoides*, *G. aprion*, some of which are lowland dwellers found in heavily vegetated or shallow waters. Surface DO values (means and extremes) do not show any clearcut relationships with the distribution of species.

The lowest mean DO concentrations in bottom-water were associated with *L. alata*, *M. cyprinoides*, *A. leptaspis*, *A. graeffei*, *L. calcarifer* and *N. ater*; the lowest bottom-water DO recorded were found in waters associated with *L. calcarifer*, *A. percoides*, *G. aprion*, *N. erebi*, *S. krefftii*, *L. unicolor* and *T. chatareus*. The species found in waters with the lowest mean surface-water DO were *L. calcarifer*, *A. graeffei* and *N. ater*; those waters with the lowest surface-water DO were *P. rendahli*, *A. leptaspis* and *N. hyrtlii*. Plotosid and ariid catfishes occurred in waters that were almost anoxic, and some of the more widely ranging species (*L. unicolor*, *A. percoides*, *M. cyprinoides* and *G. aprion*) tolerated low DO levels. However, many of these species were present in a fish kill in Leichhardt Billabong that was thought to be caused by low DO levels (Bishop 1980).

The most widely distributed species were associated with wide ranges of DO levels, as they were with other variables. These species were *L. unicolor*, *A. percoides*, *G. aprion*, *M. cyprinoides*, *P. rendahli* and *N. hyrtlii*. Two others — *O. lineolata* and *A. leptaspis* — associated with wide ranges of DO are less widely distributed. However, they are often associated with thick aquatic vegetation and show a tolerance of anoxic bottom-water. The species associated with the narrowest ranges of both surface and bottom DO concentrations included the more typically 'escarpment' associated species *P. midgleyi*, *H. fuliginosus*, *S. butleri*, *M. nigrans* and *G. giuris*, and the shallow-water dwellers *C. marianae* and *C. stercusmuscarum,* all of which were associated with higher levels of DO. *Lates calcarifer* and *L. alata*, which are typically found in turbid floodplain waters, were associated with a narrow range of DO, but at the lower concentrations.

DO concentration may be a useful indicator of a species' distribution, when interpreted along with other variables such as flow, water temperature (including thermocline position), groundwater inflows, time of day (lowest DO occur at dawn after aquatic plants respire through the night) and hydrophyte occurrence. The groups of species that could be most readily distinguished by DO characteristics were the escarpment dwellers (high DO), the catfishes (low or widely ranging DO) and floodplain dwellers such as *L. calcarifer* and *L. alata* (low DO). Whether all these species differ in their respiratory requirements is unknown. There is no reason to expect fishes from different environments to show differences in their basal rates of oxygen consumption, but Winberg (1956) suggested that the amount of oxygen a fish uses would vary according to the environment it was inhabiting. Further work should be done on the respiratory tolerances of the species studied.[248]

Visibility

Measurements of visibility in the water column (visibilities less than the greatest depth of the waterbody, given as means, standard errors and ranges) for various fish species captured during the study period are shown in figure 172.

Water visibility was estimated by Secchi disc measurements classified as maximum (M, Secchi depth greater than depth of waterbody) and non-maximum (non-M). In the environmental associations discussions in chapter 3, only non-M visibilities are discussed, with reference to M visibilities where relevant. The Secchi disc technique proved to be quick and convenient for the purposes of this study, giving reliable and easily standardised estimates of water turbidity at the sampling sites.

The variables that most affect water turbidity are the type of substrate and the turbulence of the water. The conductivity of the water and the temperature determine the maximum colloid load that can be suspended. There was also a seasonal effect on water turbidity in this study. The first flush of the Wet season brings down large quantities of dissolved solids and suspended silt as it flows over the dusty soil and through the muddy, dried-up watercourses. After this flush, visibility increases at all sites during the Wet season. The frequency and intensity of flooding also affects visibility, as does the position of a site within the catchment. Escarpment streams (and to a lesser extent corridor billabongs) tend to be clear, whilst the downstream reaches of a river tend to be more turbid, mainly owing to the accumulation of fine sediments. Algal blooms also influence Secchi depth measurements.

Species typically found in specialised habitats are associated with the visibilities characteristic of those habitats, eg the *Craterocephalus* spp. are often found in clear, sandy watercourses (although, because of the shallowness of these waters, Secchi depths may give misleading visibility estimates) and *L. calcarifer*, which is typically found in the deep, turbid, lower reaches of the catchment.

Many fish species are limited in their distributions by their inability to tolerate high turbidity or silt concentrations in the water (Hynes 1970). Increases in turbidity due to industrial or agricultural siltation affect a variety of species (Lachner 1956).

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[248] Investigations into the effects of changing dissolved oxygen concentrations have subsequently been undertaken by Wells et al (1997) on *M. cyprinoides*, *S. jardinii* and *L. calcarifer*, Gehrke and Fielder (1988) on *L. unicolor*, Gee and Gee (1991) on *H. compressa*, and Geevarghese and John (1984) on *G. giuris*.

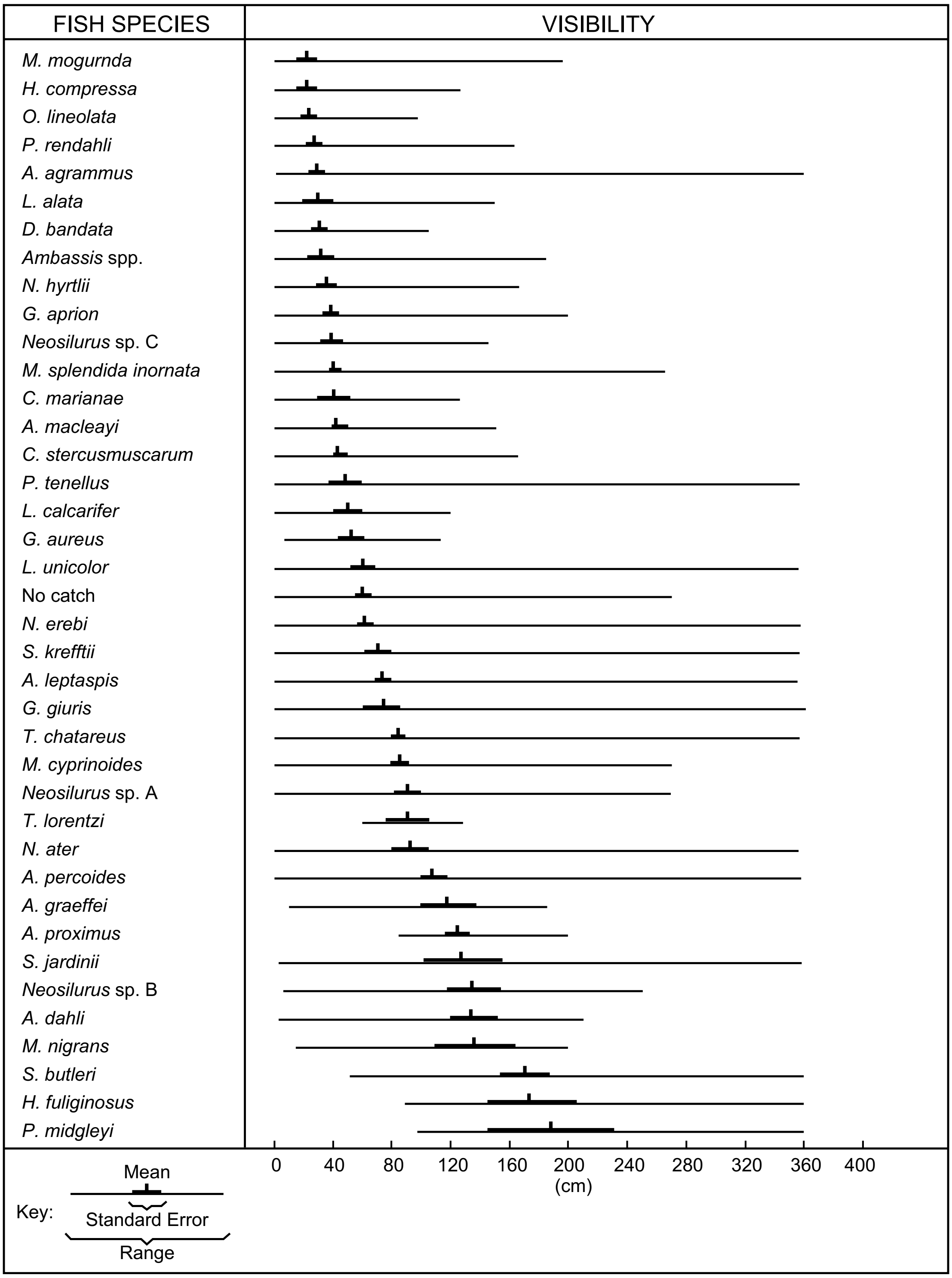

Figure 172 *In situ* visibility measurements (visibility < maximum depth of waterbody) (means, standard errors and ranges) for various fish species captured during the study period (see appendix 6)

Overall, Secchi depths ranged from 1 to 360 cm, the latter value being the greatest fishing depth of an escarpment mainchannel waterbody. Readings may vary widely for widely distributed fish; in these cases mean depths are only useful when considered together with their standard error. Visibility estimates are best interpreted in association with other variables and a knowledge of the ecology of the species.

As with other physico–chemical variables, the most common, widely distributed species had wide ranges of associated water visibilities; for example, the species associated with the greatest ranges of visibility (1 to 360 cm) included the widespread species *L. unicolor*, *A. percoides*, *A. agrammus*, *N. ater*, *S. jardinii*, *S. krefftii*, *P. tenellus*, *A. leptaspis*, *N. erebi* and *T. chatareus*.

Species living over rocky or sandy substrates are usually associated with clear waters. This is particularly true for primarily escarpment-dwelling species such as *M. nigrans*, *P. midgleyi*, *H. fuliginosus* and *S. butleri*, all of which inhabit waters with high mean Secchi depth values and wide ranges. Species that were commonly found in very turbid waters included *M. mogurnda*, *H. compressa*, *O. lineolata*, *P. rendahli*, *L. alata* and *D. bandata*. These fish were captured mainly in lower reaches of the catchment (although *M. mogurnda* was also found abundantly in escarpment waters).

Species such as *P. rendahli* and *N. hyrtlii*, both of which are bottom-dwelling plotosid catfishes, may actually contribute to the turbidity of the water by stirring up the mud over which they feed. *M. mogurnda* has the widest range here (corresponding to its wide distribution), followed closely by *G. aprion*, *M. splendida inornata*, *M. nigrans*, *S. butleri* and *L. unicolor*. The habitats of *D. bandata*, *G. giuris*, *H. compressa*, *O. lineolata* and *P. rendahli* have low, narrow ranges; those of *A. leptaspis* and *N. ater* have high, narrow ranges. Escarpment-dwelling species again have the highest means (eg *S. butleri*, *S. jardinii*, *H. fuliginosus*, *N. ater*). Low mean visibility was associated with *H. compressa*, *G. giuris*, *C. marianae*, *A. agrammus*, *D. bandata*, *O. lineolata* and *P. rendahli*. However, these low mean visibility values may also indicate shallow, clear waters (eg *O. lineolata*, *D. bandata*, *H. compressa*). Maximum visibility readings are therefore more useful in evaluating such cases than are non-Maximum readings.

Generally, water visibility proved to be a good indicator of a species' longitudinal distribution: escarpment-dwelling species were found in distinctly clearer waters than were species typical of the lower reaches. To a lesser extent, visibility is also an indicator of a species' vertical distribution within waterbodies (eg the plotosids were often found in muddied bottom waters).

Secchi-depth estimates of turbidity, although convenient in the field, may be misleading in the final analysis, especially with respect to shallow waters. Other methods of estimating turbidity may provide additional useful information. However, the trends indicated by Secchi-depth estimates of visibility were similar to those of other variables.

pH

Surface and bottom pH levels (means, standard errors and ranges) for various fish species are shown in figures 173a and b respectively.

Most species of fish have a wide tolerance to pH (and hence presumably also to water hardness and specific conductivity). However, some species prefer waters with specific pH characteristics, and pH may indirectly affect the growth rates of some fish and their invertebrate prey (Hynes 1970).

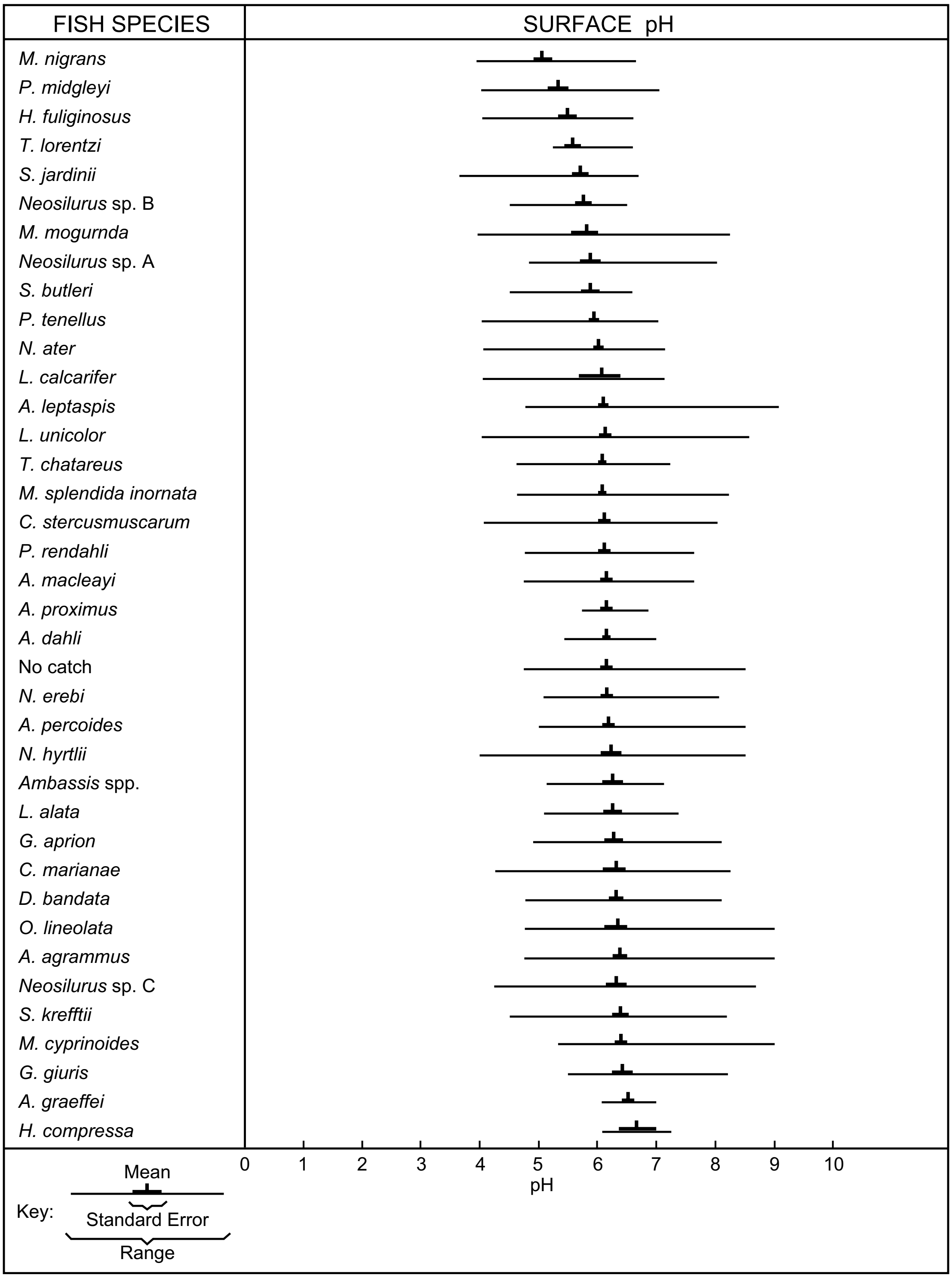

Figure 173a *In situ* surface pH levels (means, standard errors and ranges) for various fish species captured during the study period (see appendix 6)

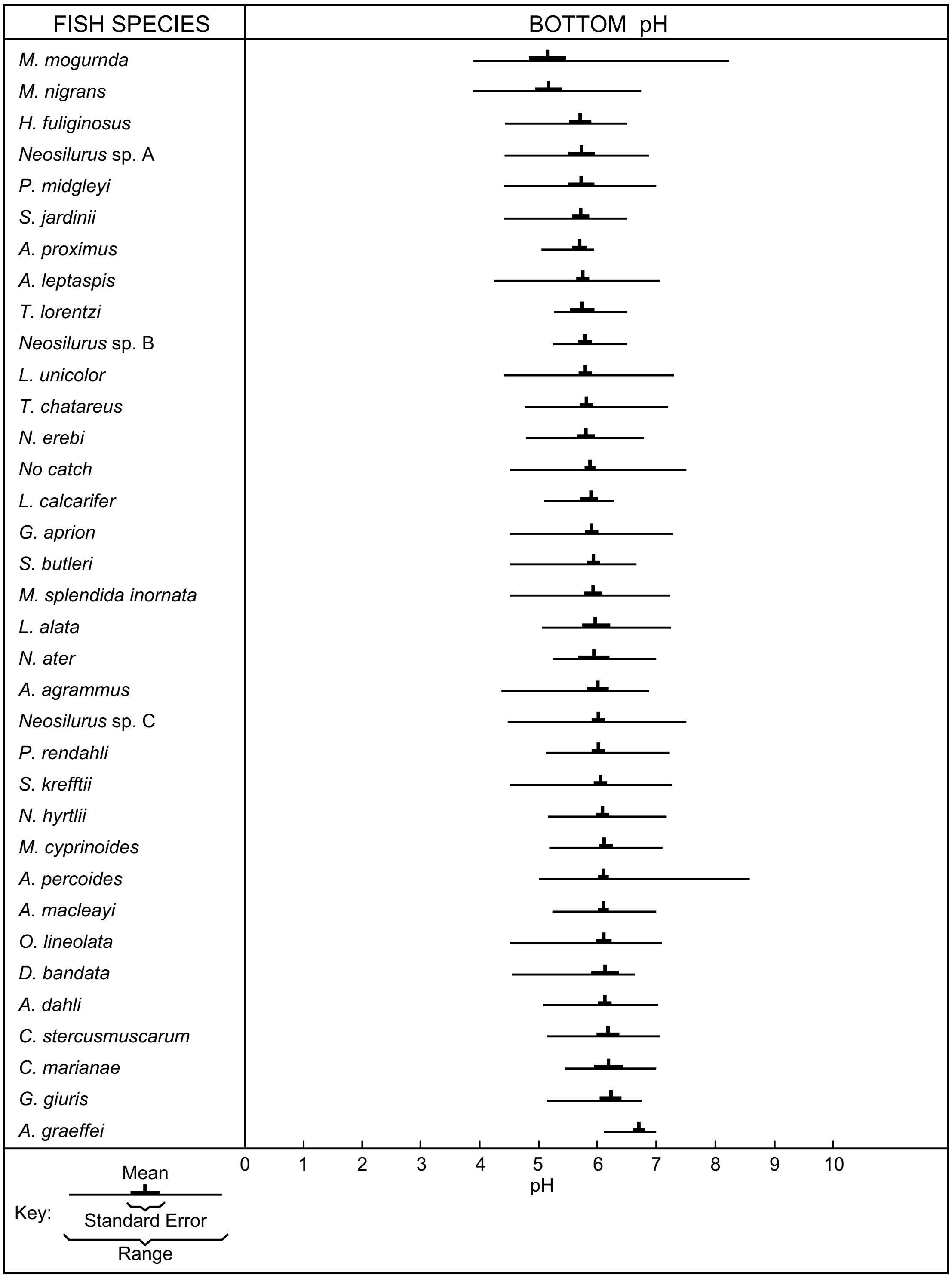

Figure 173b *In situ* bottom pH levels (means, standard errors and ranges) for various fish species captured during the study period (see appendix 6)

The waters sampled during this study were generally acidic, although the pH range was between 3.8 and 9.2. pH is affected by water temperature, type of substrate, conductivity, and the content of dissolved oxygen and carbon dioxide (the last two being a function of hydrophyte content, rate of detrital decay and water temperature). pH is a highly variable characteristic, and wide diurnal variations were measured at many sites. Despite this, the mean pH values for both surface and bottom waters were clustered around a median value, although the ranges varied widely. As with other variables, there was a difference between the values for escarpment and lowland waters, for surface and bottom waters, and for species with wide and narrow distributions. These distinctions were less obvious than for other variables.

Generally, the most acidic waters were found in the seasonal and perennial streams of the escarpment. Species such as *M. mogurnda*, *H. fuliginosus*, *P. midgleyi*, *M. nigrans* and *S. jardinii* were found in waters with mean pHs lower than those associated with other species, in both surface and bottom waters. All these species are found typically in escarpment waters. The perennial streams of the escarpment area are fed by seepage through rocks. In transit, the seepage becomes highly ionised, which appears to lead to acidic conditions. *Arius graeffei*, *G. giuris* and *H. compressa* inhabited waters with the highest mean pH values; those inhabited by *G. giuris* had a high range and mean at both the surface and bottom.

The species inhabiting waters with the widest surface pH range were *M. mogurnda*, *A. percoides*, *A. leptaspis*, *L. unicolor* and *N. hyrtlii,* followed by the two *Craterocephalus* spp., *O. lineolata* and *A. agrammus*. All except *O. lineolata* were found in habitats from the escarpment to the floodplain zones. The narrowest ranges of surface- and bottom-water pH were associated with *L. calcarifer*, *A. graeffei*, *H. compressa*, *P. tenellus*, *S. butleri* and *A. proximus*, although the samples were all small, which may have biased the range. Some catfishes (*A. leptaspis*, *A. graeffei*, *N. hyrtlii*, *N. ater*) were characteristically found in acidic waters, probably because they are usually at the bottom, where decaying matter and anoxic conditions promote a build-up of carbon dioxide.

pH is a useful environmental variable when used in association with others; on its own, the differences between ranges and mean pHs associated with individual species are not sufficiently clear to be good indicators of these species' distributions. This may be because, as previously noted, most fish species tolerate fairly wide fluctuations in pH. Bottom pH is less variable than surface pH, and is thus a more reliable estimate of local pH conditions, although it may be relevant only to bottom-dwelling species.

Conductivity

Conductivity is a measure of the water's electrolytic salt content, which gives an indication of its dissolved solids load and some measure of its salinity. Fresh, flowing waters subject to low evaporation generally have lower electrolyte concentrations than lentic, turbid waters subject to high evaporation. Cooler waters may hold less dissolved solids than warmer waters. The distinction here between escarpment habitats and the lower reaches of the catchment is apparent: escarpment streams, being cooler, faster-flowing and fresher, have lower conductivity readings than the warmer, slower-moving waters of the lowlands and floodplains.

Conductivity readings proved to be so highly variable that any mean conductivity values were relatively worthless, so the range of conductivity associated with each species is therefore discussed instead. As conductivity often varied vertically, both surface and bottom conductivities were read at each site. The values ranged from 2 to 1600 µS/cm, however, fish were recorded only within the range 2 to 620 µS/cm . The lower conductivity values indicate fresher waters, and the higher values more turbid, stagnant lentic waters. Fish are generally found to be tolerant of wide ranges of conductivities and salinities (Hynes 1970) and (except in specialised cases) conductivity is unlikely to be a limiting factor in the freshwater distribution of the species studied.

The species associated with the widest range of water conductivities were *G. aprion*, *L. unicolor*, *A. macleayi*, *P. rendahli*, *N. hyrtlii* and *A. leptaspis*, all of which were widely distributed, common, or both. The species with the narrowest ranges were *S. jardinii*, *S. butleri*, *P. midgleyi*, *S. krefftii* and *A. proximus*, the first three of which were typically found in escarpment streams or corridor billabongs. The narrow range for *A. proximus* is probably biased by the small sample size. Most species were found in waters with conductivities of less than 10 µS/cm, which indicates they can tolerate waters with fairly low concentrations of dissolved solids. The species associated with the widest ranges of conductivity were all found in waters with conductivities as low as 2 µS/cm (as in escarpment streams) and as high as 620 µS/cm, the latter reading indicating a tolerance to higher levels of dissolved solids, such as might be found in the more turbid or lower reaches of the system.

Substrate

In situ percentage dominance of boulder (including bedrock), rock, sand, clay and mud substrates in the sites in which various fish species were captured during the study period is shown in figures 174a, b, c and d respectively.

The percentage dominance system used for the seven subclasses of substrate type defined in this survey proved to be a fairly accurate index of both the distribution and the microhabitat preferences of the species studied. For example, a high percentage dominance figure for mud and clay substrates was commonly associated with species typically found in turbid billabongs and other downstream waterbodies, whilst boulder, rock, gravel and/or leaf litter substrates typically dominated the habitats of escarpment-dwelling species. *Craterocephalus marianae* (and to a lesser extent *C. stercusmuscarum*) showed a marked preference for shallow, sandy watercourses.

The type of substrate over which water flows plays a large part in determining the visibility and conductivity of the water, and the type and amount of vegetation growing in it. It may, therefore, be important to various aspects of the ecology of different fish species, from water quality influences to the provision of shelter and feeding areas.

It is apparent that the type of substrate is one of the most important variables in the environmental requirements of the fish species examined, and may reveal the most about the ecology of a species. In contrast, Cleary and Greenbank (1954) concluded that ‘although many species [of North American fish] are definitely associated with substrates, for the great majority of species, the type of substrate is of little consequence, except at times of breeding, and current velocity and depth of the water seem more important’. In this study, both dominant and subdominant types of substrate were noted at each sample site (these readings were summed up for each species, using the weighted ‘percentage dominance’ method) in order to more accurately represent the overall occurrence of each substrate type. The fact that a fish was caught over a particular substrate at a sampling site does not automatically mean that fish prefers or inhabits only waters with that substrate type. A knowledge of the biology of the species is a necessary adjunct to final interpretation.

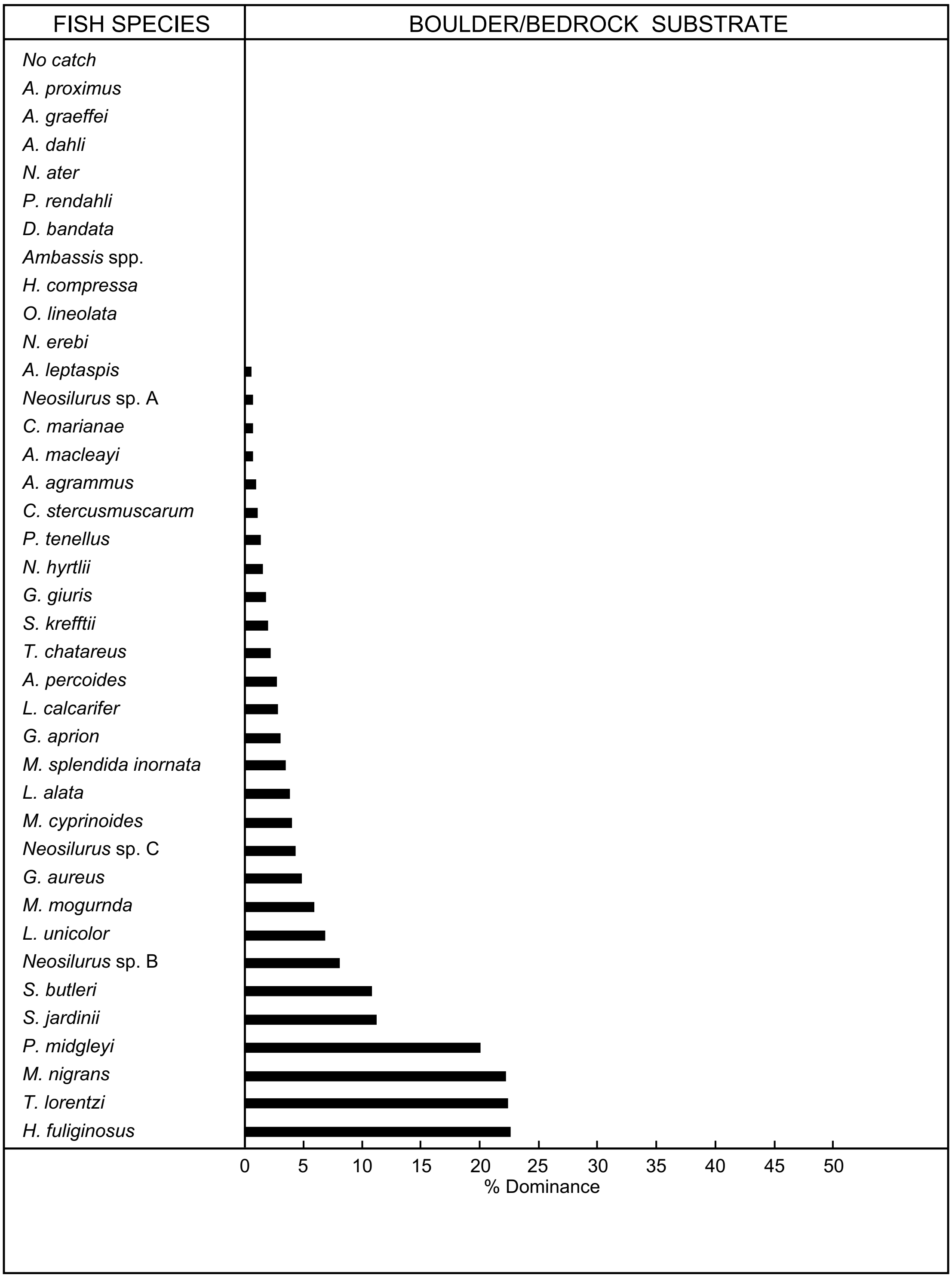

Figure 174a *In situ* percentage dominance of bedrock substratum in sites in which various fish species were captured during the study period (see appendix 7)

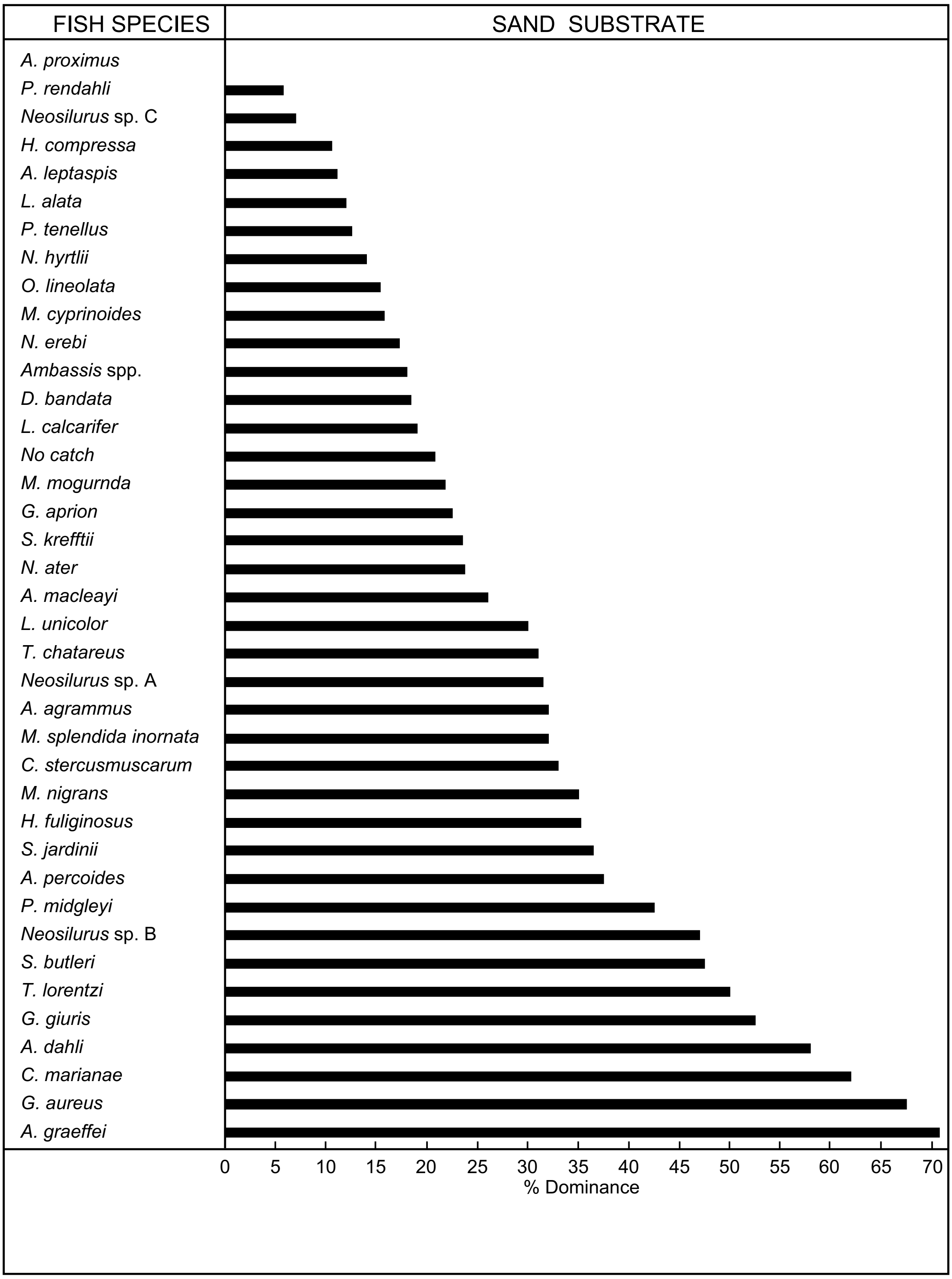

Figure 174b *In situ* percentage dominance of sand substratum in sites in which various fish species were captured during the study period (see appendix 7)

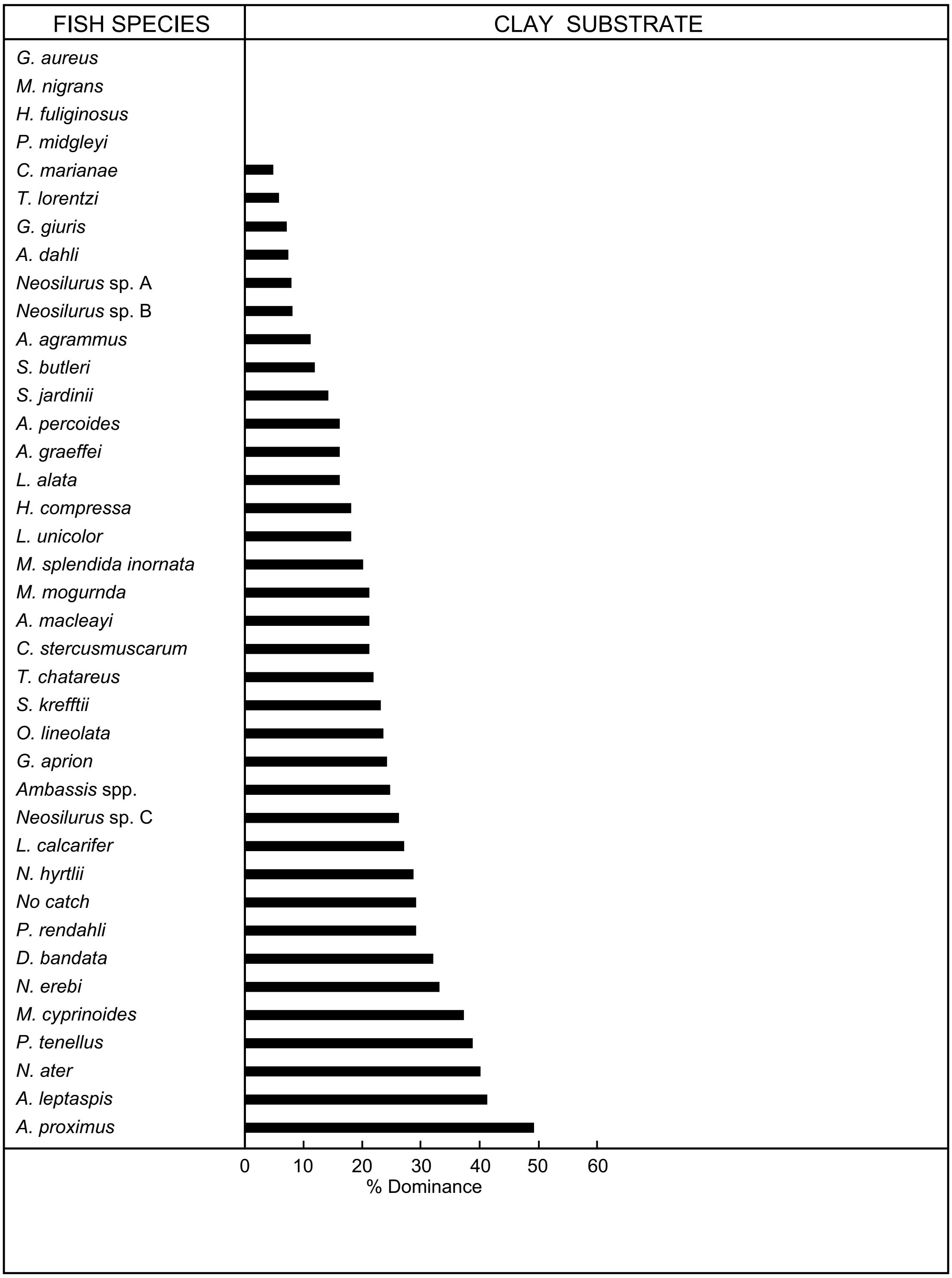

Figure 174c *In situ* percentage dominance of clay substratum in sites in which various fish species were captured during the study period (see appendix 7)

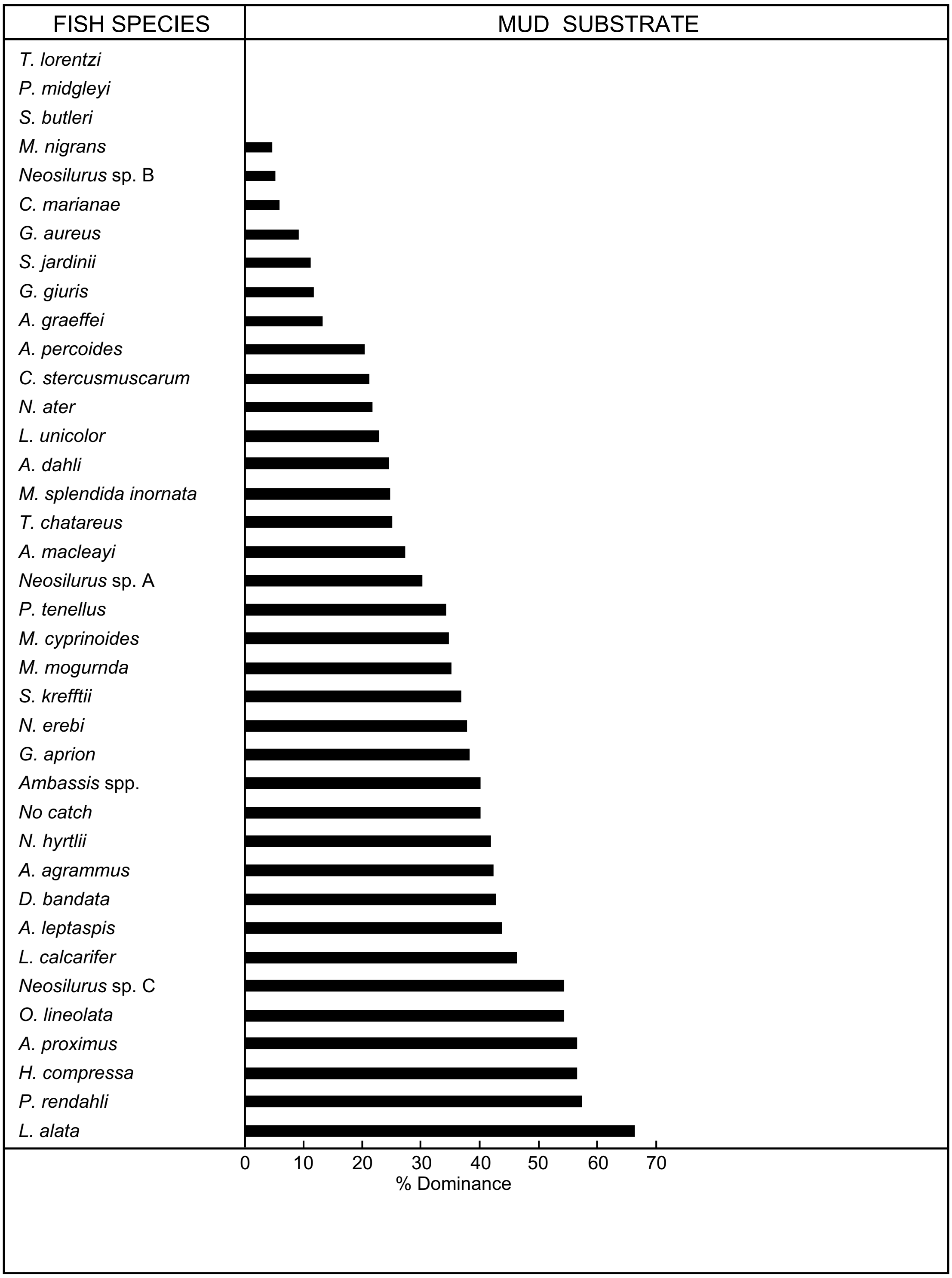

Figure 174d *In situ* percentage dominance of mud substratum in sites in which various fish species were captured during the study period (see appendix 7)

As a reference point, the overall frequency of occurrence of substrate types for all species (including 'no catch') is given in table 156. This is, in effect, the number of times a substrate type was found at all sampling sites. This frequency is a useful reference when comparing the apparent preferences species show for different substrates. The substrate type most commonly found was mud, followed by clay and sand, and less frequently, leaf litter, rocks, gravel and boulders. If a species is most commonly associated with mud, a significant proportion of the association may be due to random factors (eg the species was captured over mud while in transit to its preferred substrate); but if a species is most commonly associated with boulders, it is more obvious that an active preference may be involved. However, by analysing other variables and taking into account the biology of the species, the actual preferences for substrate type may be fairly satisfactorily defined.

Table 156 Proportional and absolute frequency of occurrence of substrate parameters over all sites sampled in study

	Substrate type						
Occurrence type	Boulders (including bedrock)	Rock	Gravel	Sand	Mud	Clay	Leaf litter
% occurrence	4.1	6.3	4.0	39.1	29.8	20.8	6.6
Standard error	1.03	1.06	0.73	2.82	2.98	2.02	0.72
Absolute occurrence	143	347	371	1581	2095	1609	550

Proportional occurrence = % occurrence of substrate type for each species / total number of species (*n* = 36)

Absolute occurrence = total number of times substrate type occurred at sampling sites; includes 'no catch'

As with the preceding environmental variables, the most widely distributed and common species were found over the entire range of substrate types defined in this study. These species were *M. splendida inornata*, *L. unicolor*, *M. mogurnda*, *C. marianae*, *C. stercusmuscarum*, *G. aprion*, *A. leptaspis*, *N. hyrtlii*, *L. unicolor*, *A. macleayi*, *N. erebi* and *S. jardinii*. More specialised or rarer species tended to be found over only a few types of substrate, eg the plotosid catfishes *P. rendahli* and *A. dahli* and the fork-tailed catfishes *A. proximus* and *A. graeffei*, were all found almost exclusively over sand, mud or clay substrates, and were rarely or never found over rock, boulder, gravel or leaf substrates. The two species of *Craterocephalus* were most commonly found over sand, but *C. stercusmuscarum*, which has a wider distribution than *C. marianae*, was found more often over other substrate types. Generally, the greater the variety of substrates a fish was associated with, the greater the variety of preferred micro-habitats or the wider its distribution.

An alternative method of interpreting substrate data is to examine each substrate type and the species of fish most commonly associated with it. However, high percentage dominance figures for the relatively rare species could be deceptive, as sample sizes were small. For the more common species, determining a species' degree of association with different types of substrate can help build a clearer picture of its environmental requirements.

The species most clearly associated with boulder/rock substrates (fig 174a) were *H. fuliginosus*, *M. nigrans*, *P. midgleyi*, *S. jardinii* and *S. butleri*, all of which are typically found in escarpment streams. These streams, which are mostly fed by water seeping through the bedrock, cut through steep, rocky valleys overhung by thick bank vegetation. Not surprisingly, the species most commonly associated with leaf litter (*M. nigrans*, *H. fuliginosus*, *G. giuris*, *C. marianae*, *C. stercusmuscarum*, *P. midgleyi* and *N. hyrtlii*) are also almost all escarpment-dwellers. The common species most often associated with gravel substrates were *A. macleayi*, *L. unicolor* and *S. krefftii*.

Species that were most commonly associated with sandy substrates (fig 174b) were *A. graeffei*, *C. marianae* and *A. dahli*, but the samples of *A. graeffei* and *A. dahli* were small. Most of the other species listed are primarily escarpment-dwellers, sandy shallows and pools being common in the lower escarpment area.

As might be expected, plotosid catfishes, other bottom-dwellers, and other species typically found in turbid waters, were all strongly associated with muddy substrate (fig 174d). These included *L. alata*, *P. rendahli*, *H. compressa*, *A. proximus*, *O. lineolata*, *L. calcarifer* and *A. leptaspis*. Some of these species were found mainly in the lower reaches (eg *O. lineolata*, *L. alata*, *L. calcarifer*, *H. compressa*), the rest being bottom-dwelling catfishes that often feed in the mud. The species most often associated with clay substrates were *A. proximus*, *A. leptaspis*, *N. ater*, *P. tenellus*, *M. cyprinoides*, *N. erebi*, *D. bandata* and *P. rendahli* (fig 174c).

As before, a clear-cut distinction is apparent, on the basis of substrate preferences, between escarpment and 'lower reach' species. Other distinctive groups, such as the bottom-dwelling catfishes or the hardyheads, can also be distinguished. To be able to predict the occurrence of fish species from substrate data, further field work on the importance of particular substrates to a species, and laboratory experiments on habitat preferences should be undertaken.

Hydrophytes

The percentage dominance of emergent, submergent and floating-attached hydrophytes in sites in which various fish species were captured during the study period is shown in figures 175a, b and c, respectively.

As with substrates, the types of hydrophytes associated with a species are often a good indication of the type of habitat preferred by that species. Since the amount of vegetation found in waters associated with a species is also important, the vegetation-occurrence index will also be discussed.

The amount of vegetation at a given place varied a great deal between Wet and Dry seasons, owing to changes in nutrient levels and evaporation rates, growth of algal blooms and the effects of flooding. The amount and type of vegetation is affected by the type of substrate, which also affects plant growth rates and settlement of seeds (Hynes 1970). As with substrate type, fish species that were collected rarely could be ranked misleadingly. The relations of fish species to vegetation are often unclear, or unknown, and further work is required, particularly on the breeding of fish.

The species found in waters with the heaviest vegetation content (according to the vegetation-occurrence index) were *H. compressa*, *D. bandata*, *A. proximus*, *P. rendahli*, *G. aprion*, *A. agrammus* and *O. lineolata*, of which *H. compressa*, *G. aprion* and *O. lineolata* have some important aspect of their biology associated with hydrophytes. Many of the fish species studied include vegetation in their diet. Thus, the type and quantity of hydrophytes associated with some species are good indicators of the type of environment or microhabitat preferred by these species, rather than of their spatial distribution as are substrate and the physico–chemical variables.

The species most commonly associated with emergent hydrophytes (fig 175a) were *S. butleri*, *L. alata*, *H. fuliginosus*, *L. calcarifer*, *G. giuris*, *P. tenellus* and *A. agrammus*, a list that includes both lowland and escarpment-dwelling fish. Unlike all other variables, emergent hydrophyte variables could not distinguish between the two zones. *S. butleri*'s strong association may be attributable to the small sample size.

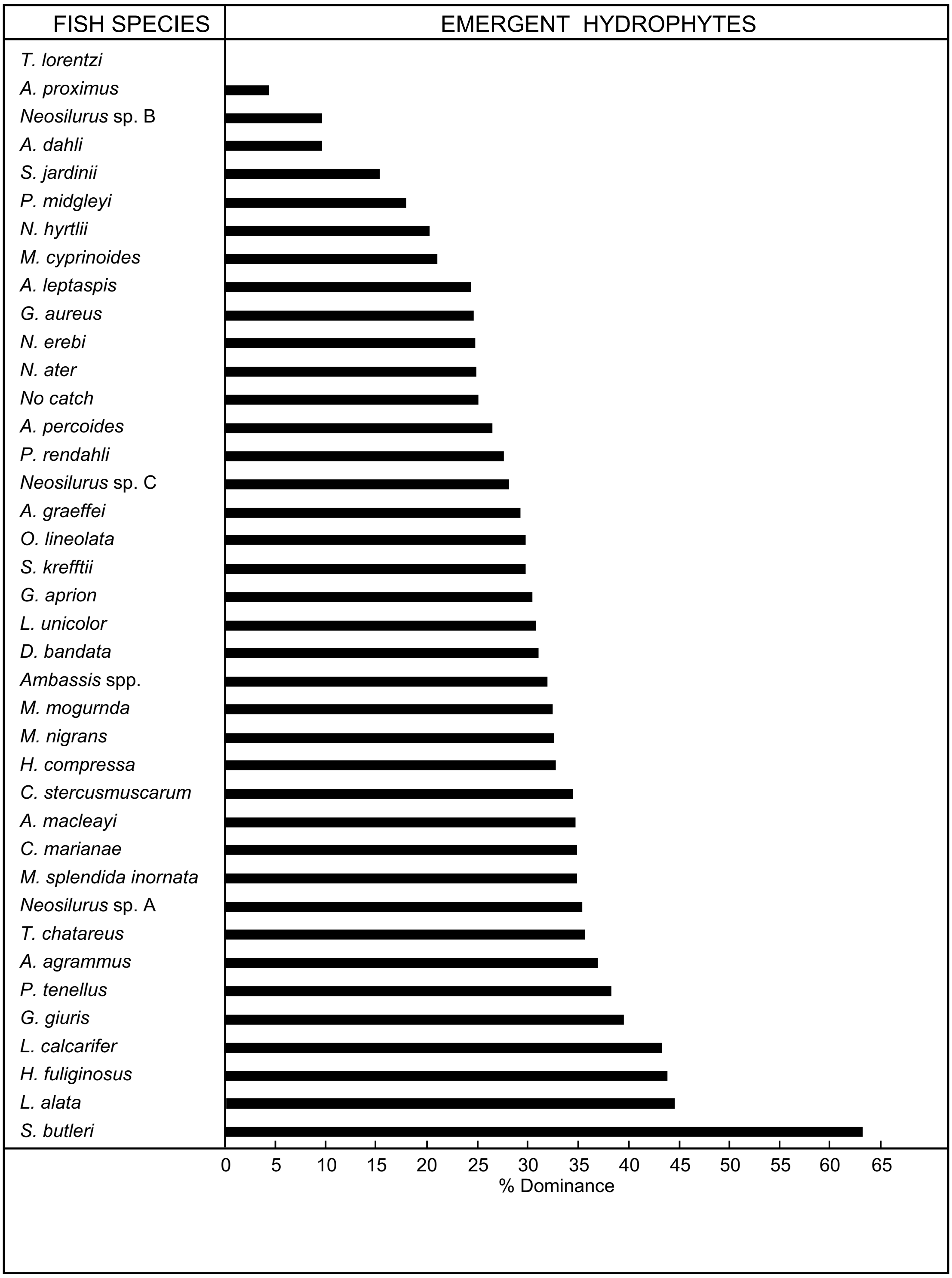

Figure 175a *In situ* percentage dominance of emergent hydrophytes in sites in which various fish species were captured during the study period (see appendix 7)

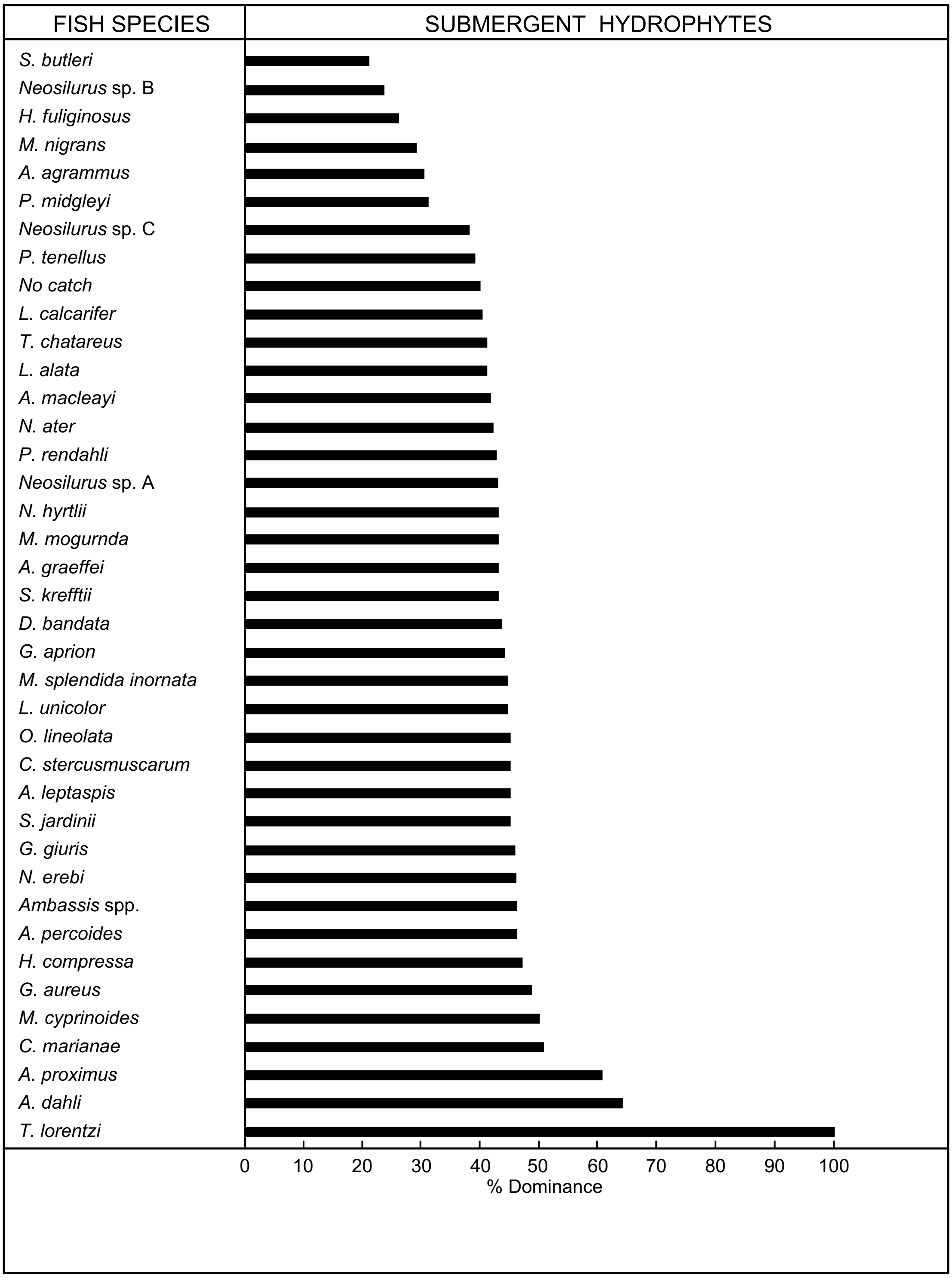

Figure 175b *In situ* percentage dominance of submergent hydrophytes in sites in which various fish species were captured during the study period (see appendix 7)

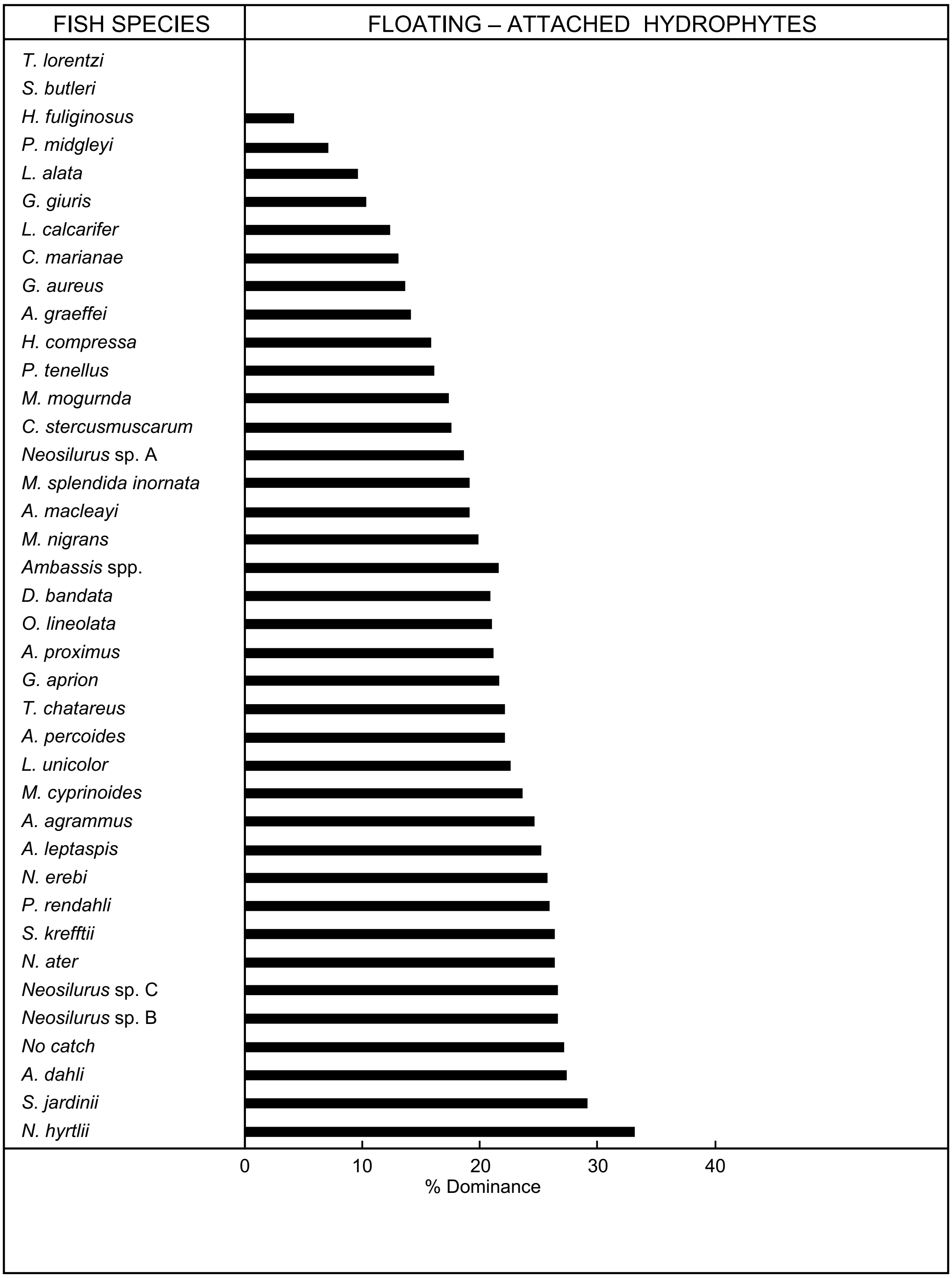

Figure 175c *In situ* percentage dominance of floating-attached hydrophytes in sites in which various fish species were captured during the study period (see appendix 7)

Submergent hydrophytes (fig 175b) were associated predominantly with *A. dahli*, *A. proximus*, *C. marianae*, *M. cyprinoides*, *H. compressa*, *A. percoides* and *N. erebi*. The association for *A. dahli* was exaggerated by its small sample size, but species such as *H. compressa* lay their eggs on submergent vegetation. Again, the preference for type of hydrophyte is apparently independent of the zone in which the species was typically found.

A most interesting phenomenon is apparent with respect to floating-attached vegetation and the plotosids. Floating-attached vegetation (fig 175c) were most dominant in waters containing *N. hyrtlii*, *S. jardinii*, *A. dahli*, *N. ater*, *S. krefftii* and *P. rendahli* (with other plotosid catfishes close behind). The connection between the presence of floating vegetation and plotosid occurrence may thus warrant investigation.

Synthesis

It is apparent that few of the environmental variables examined actually limit the distribution of a fish species at a local level. Potentially, the most limiting factors were temperature, dissolved oxygen concentration and visibility. However, a species of fish that inhabits a particular type of environment may be associated with a particular set of environmental variables. A species' distribution, therefore, may also be correlated with the range of environmental variables for waters in which it is found. Thus, sets of seasonally changing environmental variables may be used as indices describing aspects of the environment in which a fish was found.

The three main groups of species distinguished by characteristic combinations of associated factors were species that lived on the escarpment, species that lived in the lower reaches, and widely distributed species found in both of these zones. Escarpment-dwelling species were usually associated with waters with low temperatures, high DO concentrations (especially in bottom waters), acidic pH values, low conductivity, low turbidity, and substrates of rock, boulder, gravel, leaf or sand. Species in the lower reaches were typically associated with high temperatures, low DO concentrations, more neutral pH values, high conductivities, high turbidity, greater vegetation content, and predominance of mud, clay and sand substrates. Widely ranging species inhabited waters with correspondingly wide ranges of environmental variables.

These three groups are broadly defined, although often distinctive, but there were some exceptions and some uncertainties where sample sizes were small. Overall, some useful data were obtained for many species and gaps in knowledge were highlighted.

The most important aspect of the environmental associations section is that there now exists a fairly solid database, descriptive (some more than others) of the types of environments in which the different fish species are typically found. These data can be used as a basis for further work that could lead to describing the Alligator Rivers catchment, and distinguishing its habitat types, in terms of the physico–chemical and habitat–structural characteristics, and to predicting with some confidence the species composition of fish communities in these habitats.[249]

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[249] Arthington and Pusey (1994) presented information, arising from studies in a range of Queensland rivers, which indicated that the influence of habitat factors on fish communities is likely to be low in river systems with highly-variable flow regimes. Magela Creek has such a regime, but it has a highly predictable seasonal component to the variability, ie the Wet/Dry cycle. In response to Arthington and Pusey's findings, Grant and Bishop (1998) noted that such rivers have extended periods when flows are remarkably stable (eg recessions after floods, during the Dry season, etc). Grant and Bishop argued that habitat factors are likely to have a major influence during these times.

4.3 Reproduction

Among the few accounts of the reproductive biology of fishes from Australia's tropical freshwaters are those of Dunstan (1959) on *Lates calcarifer*, Beumer (1976, 1979b) on *Therapon* (= *Leiopotherapon*) *unicolor* and *Nematocentris* (= *Melanotaenia*) *splendida*, and Lake and Midgley (1970a and b) on freshwater ariids and *Scleropages leichardti*.[250] The reproduction of tropical freshwater fishes has also been studied in British Guiana (Lowe-McConnell 1963), Panama (Kramer 1978), Africa (Welcomme 1969) and New Guinea (Haines 1979; Roberts 1978).

A number of the Alligator Rivers Region species, or their close relatives, are also found in the Murray–Darling River system. Some of the studies on their reproductive biology are Merrick (1974) on *L. unicolor*; Davis (1977b) on *T. tandanus*; Llewellyn (1971) on *C. fluviatilis* (a subspecies of *C. stercusmuscarum,* Ivantsoff, pers comm), *L. unicolor* and *M. mogurnda*; Llewellyn (1973) on *L. unicolor*; Llewellyn (1979) on *C. fluviatilis*; and Auty (1978) on *H compressa*.

The objectives of our study of the Alligator Rivers Region freshwater fishes included determining, for each species, the length of the fish at first sexual maturity, whether the sex ratio was significantly different from 1:1, the seasonality of reproduction and the duration and peak of spawning activity, the site of spawning or larval development or both, the mean fecundity and egg size, and any other general aspects of their reproductive biology.

Estimating gonad maturity stages was quicker than calculating gonosomatic indices (GSIs). Maturity stages were subjectively attributed (see section 2.5) and an advance to the next stage does not necessarily correspond to an arithmetic progression in the weight of the gonads. The feasibility of accurately determining a fish's reproductive period by calculating an index of mean gonad maturity stage (GMSI) for each season was investigated and the GMSI compared with the calculated GSI values. Histological sections of gonads were examined to confirm visual staging techniques, but a comparative seasonal histological analysis was not undertaken.

The combination and interaction of the fish's physiology and behaviour and its approach to reproduction is here termed the 'reproductive strategy' (Bond 1979). Such strategies must ensure survival of at least a portion of the eggs by various means — force of numbers or concealment or parental care — and the strategies include the placement of the earliest feeding stage of the young near to ample and suitable food.

Lowe-McConnell (1975) classified fishes into 'big bang' spawners, which spawn once in a lifetime and then die; 'total' spawners, which are mostly highly fecund and often make seasonal migrations; 'partial' spawners, which either produce many broods throughout a season or have a seasonal spawning; and 'small brood' spawners, which generally spawn seasonally and often guard their eggs and young.

Roberts (1978) used the following categories to describe spawning fish:

1 Those that reproduce locally in middle and upper reaches of the river are of three types:

  - spawners of numerous small eggs (newly hatched young less than 10 mm long)

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[250] Investigations into various aspects of the reproductive biology of fish species found in the Alligator Rivers Region have subsequently been undertaken by Puckeridge and Walker (1990) on *N. erebi*, Rimmer (1985b&c) on *A. graeffei*, Orr and Milward (1984) on *N. ater* and *N. hyrtlii*, Ivantsoff et al (1988) on *M. nigrans*, *M. splendida inornata*, *C. stercusmuscarum* and *A. macleayi*, Howe (1987) on *P. tenellus*, Semple (1986) on *C. marianae*, Davis (1982 & 1985b) on *L. calcarifer*, Moore (1982) on *L. calcarifer*, Semple (1985) on *A. agrammus*, and Hogan (1994) on *H. fuliginosus*.

- oral brooders with relatively few, large eggs (newly hatched young more than 10 mm long in some species)
- ovoviviparous (young probably longer than 50 mm)

2 Those that migrate to tidal or estuarine areas to spawn (catadromous)

- generally large species with very many small eggs.

A refined classification based on Lowe-McConnell's and Roberts's categories, and using the information collected on the fishes of the Alligator Rivers Region, is outlined in this report.

Enough data were collected on at least 32 species to outline some general characteristics of their reproductive biology. The reproductive data from the present study, together with information from research on the same or closely related species in other parts of Australia, are summarised in table 157. The data on species that were collected either infrequently or in small numbers are likely to be modified with further research.

Length at first maturity

Because of the relatively small samples of some species collected, the method used for estimating the LFM, which was adopted from that described in State Pollution Control Commission (1981), often meant the line of best fit had to be chosen from a number of very close alternatives.

A summary of lengths and sizes of smallest maturing fish and other reproductive information for the common fish species is presented in table 158.

No species had a length at first maturity that was less than 25% of the largest size at which it was captured during the study. The LFM was generally between 25% and 75% of that length (table 159) . Species with the LFM greater than 75% of the largest specimen of the species captured were *Megalops cyprinoides*, male *Denariusa bandata*, female *Syncomistes butleri* and male *Oxyeleotris lineolata*. *Megalops cyprinoides* is reported to grow up to 1000 and possibly 1500 mm (Pollard 1980). The LFM in our study appeared to be high because the largest fish captured was only 410 mm. For the other species listed, the proportionately high LFM was probably due to the small numbers of mature fish captured; additional data might change the estimate.

The difference between the LFM for each sex in five species was greater than 10% of the longest specimen. In *M. nigrans* and *D. bandata* the females had a smaller LFM, while in *H. fuliginosus*, *S. butleri* and *S. krefftii* the males had a smaller LFM. Wide differences in LFM can be due to sex reversal; only *S. krefftii* was tested for this, but no evidence of it was found. For the remaining species the large differences in estimated LFM were probably due to the low numbers of maturing fish collected.

A difference in the size of the sexes is sometimes related to parental behaviour: the sex that guards the nest or exercises other parental care is usually the larger. A difference in size is also found in species that produce many eggs: the female is generally the larger (Breder & Rosen 1966). Of those species with significantly different male and female LFM, only in *M. nigrans* were the greatest lengths recorded for males and females significantly different (60 mm and 50 mm LCF respectively). This species is not known to exhibit any form of parental care.

Two species in which the longest females were substantially longer than the longest males were *A. leptaspis* and *A. agrammus*. Supporting the generalities above, *A. agrammus* is fecund. In contradiction, male *A. leptaspis* guard (mouth brood) the eggs, yet this sex is the smaller.

Table 157 Breeding sites and seasons, with other reproductive parameters, for 33 fish species in the Alligator Rivers Region

Family and species	Marine or Fresh	Breeding seasons	Breeding sites **	Fecundity	Egg diam. (mm) (embryos)	Egg type	Incubation period	Development or size of larvae at hatching	Reproductive strategy	Additional information sources *
Carcharhinidae										
C. leucas	Marine	–	F	5–13*	600–700*	ovoviviparous*	10–11 mths*	juvenile*	live bearer	1
Megalopidae										
M. cyprinoides	Marine	Early-wet	F	High	Small	pelagic*	?	leptocephalus	pelagic	2
Clupeidae										
N. erebi	Fresh	Aseasonal	C	80 000–230 000	0.4	pelagic	?	poor	pelagic	3
Osteoglossidae										
S. jardinii	Fresh	Late-dry Early-wet	AE	90	8–10	yolky	10–14 days*	advanced*	buccal incubat.*	4
Ariidae										
A. leptaspis	Fresh	Late-dry Early-wet	ABCDE	26–70	12–16	yolky	4 weeks*	advanced	buccal incubat.	4
A. proximus	?	?	?	?	?	?	?	?	?	3
A. graeffei	(?) Fresh	Wet	D	?	2–5	?	?	?	? nests*	5
Plotosidae										
A. dahli	Fresh	Wet	?	?	?	?	?	?	nests/territ.*	6
N. ater	Fresh	Early-wet	ABCDE	8000	1.4	demersal* non-adhesive	<1 week*	poor*	nests/territ.*	6
N. hyrtlii	Fresh	Early-wet	C	4000	1.3	demersal* non-adhesive	<1 week*	poor*	nests/territ.*	6
P. rendahli	Fresh	Early-wet	C	900	1.3	demersal* non-adhesive	<1 week*	poor*	nests/territ.*	7
Belonidae										
S. krefftii	Fresh	Early-wet	ABCD	?	4	adhesive threads	1–5 weeks*	?	aquat. veg.*	
Melanotaeniidae										
M. nigrans	Fresh	Extended	A	350	?	tendrils	~1 week	advanced	aquat. veg.	
M. splendida inornata	Fresh	Extended	ABCDE	170	0.6	tendrils	~1 week	advanced	aquat. veg.	
Atherinidae										
C. marianae	Fresh	Aseasonal	AB	400	0.74	adhesive threads	–	–	demersal	
C. stercusmuscarum	Fresh	Extended	ABCE	70	1.0	adhesive	–	advanced	demersal	

Table 157 continued

Family and species	Marine or Fresh	Breeding seasons	Breeding sites **	Fecundity	Egg diam. (mm) (embryos)	Egg type	Incubation period	Development or size of larvae at hatching	Reproductive strategy	Additional information sources *
Pseudomugilidae										
P. tenellus	(?) Fresh	Aseasonal	CE	40	1.0	(?) adhesive or threads	2 weeks* 21–26°C		?	8
Ambassidae										
A. agrammus	Fresh	Late-dry Early-wet	BCE	1614	0.3	(?) adhesive demersal	36 h* 28°C	(?) undeveloped	demersal	7
A. macleayi	Fresh	Extended	BC	1340	0.3	(?) adhesive demersal	36 h*	(?) undeveloped	demersal	7
D. bandata	Fresh	Aseasonal	CE	?	?	?	?	?	?	
Centropomidae										
*L. calcarifer**	Marine	Wet	F	2.2–16.8 x 10^6	6.7 x 6.8	demersal pelagic ?	short	undeveloped	pelagic	9
Terapontidae										
A. percoides	Fresh	Late-dry Early-wet	ABCDE	125 000	0.4	demersal* non-adhesive	?	?	nests/territ.*	3
H. fuliginosus	Fresh	Early-wet	AB	710 000*	3.0*	demersal* non-adhesive	short*	?	?	10
L. unicolor	Fresh	Early-wet	C	48 000	0.27	demersal* non-adhesive	50 h 23–26°C	undeveloped	?	
S. butleri	Fresh	Late-dry Early-wet	ABD	30 000	0.86	?	?	?	?	
P. midgleyi	Fresh	Early-wet	AB	?	?	?	?	?	?	
Apogonidae										
G. aprion	Fresh	Aseasonal	CE	250	1.5	demersal* non-adhesive	2 weeks*	advanced	buccal incubat.	10
Toxotidae										
T. chatareus	Fresh	Late-dry Early-wet	ABC	70 000	0.4	pelagic	?	undeveloped	pelagic	11
Mugilidae										
L. alata	Marine	Late-dry Early-wet	F*	2 x 10^6*	tiny*	pelagic	?	?	?	5, 12, 3
Gobiidae										
G. giuris	Fresh	Late-dry	CD	7000	0.3 x 0.1	non-adhesive demersal	short*	pelagic*	nests/territ.*	3, 13, 5
Eleotridae										
H. compressa	Fresh	Mid-wet	E	18 000	0.16	adhesive demersal	10 h* 30°C	pelagic	nests/territ.*	14
M. mogurnda	Fresh	Early-wet Mid-wet	ABC	430	1.0	adhesive	3–8 days	4 mm	nests/territ.*	15
O. lineolata	Fresh	Aseasonal	CE	100 000		adhesive	5–6 days*		nests/territ.*	11

* Information from additional sources: (1) Bass et al (1973) (2) Wade (1962) (3) Breder & Rosen (1966) (4) Lake & Midgley (1970b) (5) Haines (1979) (6) Davis (1977b) (7) Lake (1971) (8) Ivantsoff (1980 for *P. signifer*) (9) Reynolds (1978) (10) Lake (1978) (11) Midgley (pers comm) (12) Scott (1973) (13) Hoese & Larson (1980) (14) Auty (1978) (15) Llewellyn (1971) for *M. adspersa*

** (A) Escarpment area (B) Lowland sandy creekbed (C) Lowland backflow billabong (D) Corridor billabong (E) Floodplain billabong (F) Estuarine or coastal

Table 158 Reproductive information on males and females of species captured: longest and shortest specimens, sizes of smallest maturing fish, length at first maturity (LFM), number of specimens at LFM, highest Gonadosomatic Index (GSI), and highest gonad stage

Fish species	Sex	*n*	Shortest (mm)	Longest (mm)	Min. length at gonad stage >3	LFM (mm)	Number at LFM	Max. GSI	Highest gonad stage
Carcharhinus leucas	M	6	850	1020	–	–	–	0.5	2
	F	3	825	910	–	–	–	0.53	2
Megalops cyprinoides	M	7	186	360	353	300	2	0.66	5
	F	2	390	410	390	300	2	1.83	7
Nematalosa erebi	M	157	110	340	130	130	154	8.96	7
	F	168	106	325	140	140	150	15.32	7
Scleropages jardinii	M	3	440	660	440	?	?	1.26	4
	F	7	420	560	435	?	?	3.70	5
Arius leptaspis	M	271	165	460	187	270	235	0.74	7
	F	360	190	600	270	300	336	12.07	7
Arius proximus	M	2	245	395	–	–	0	0.05	2
	F	4	360	400	400	?	?	0.79	7
Arius graeffei	M	10	191	352	285	?	?	0.25	7
	F	17	186	395	270	?	?	2.99	7
Anodontiglanis dahli	M	15	226	400	356	370	10	0.74	7
	F	14	380	490	404	400	11	4.71	7
Neosilurus ater	M	119	110	420	260	255	107	2.21	7
	F	214	120	508	220	275	192	10.79	7
Neosilurus hyrtlii	M	36	110	240	130	135	18	1.12	4
	F	54	110	240	140	135	35	10.13	5
Porochilus rendahli	M	112	70	385	100	100	100	1.12	7
	F	209	60	288	100	110	183	11.25	7
Strongylura krefftii	M	102	195	615	267	290	67	3.19	7
	F	68	133	640	317	410	20	3.40	7
Melanotaenia nigrans	M	72	24	66	24	39	29	10.00	6
	F	81	23	50	27	27	77	7.64	7
Melanotaenia splendida inornata	M	445	20	97	28	33	395	6.00	7
	F	470	17	90	29	25	446	10.00	7
Pseudomugil tenellus	M	35	17	30	23	23	35	4.00	4
	F	69	16	31	18	23	46	11.33	5
Craterocephalus marianae	M	137	22	67	22	29	121	6.70	6
	F	186	20	70	28	32	149	6.63	6
Craterocephalus stercusmuscarum	M	274	18	60	22	27	224	7.00	6
	F	429	18	67	22	29	328	10.50	7

Table 158 continued

Fish species	Sex	*n*	Shortest (mm)	Longest (mm)	Min. length at gonad stage >3	LFM (mm)	Number at LFM	Max. GSI	Highest gonad stage
Lates calcarifer	M	3	375	1000	–	–	–	0.18	2
	F	–	–	–	–	–	–	–	–
Ambassis agrammus	M	349	20	48	27	27	324	8.72	7
	F	235	18	62	21	26	220	14.42	6
Ambassis macleayi	M	285	16	74	31	33	260	6.00	6
	F	195	20	81	27	29	188	7.27	7
Denariusa bandata	M	255	12	41	29	31	78	5.00	7
	F	205	18	38	22	25	189	9.50	6
Amniataba percoides	M	219	50	180	70	65	216	2.96	7
	F	188	40	180	50	45	186	8.33	7
Hephaestus fuliginosus	M	34	80	320	150	200	21	1.13	7
	F	16	170	340	260	250	9	1.11	7
Leiopotherapon unicolor	M	132	61	205	81	74	130	7.70	7
	F	138	64	231	94	94	126	5.35	7
Syncomistes butleri	M	19	125	320	125	125	19	5.55	7
	F	21	122	304	227	234	18	10.75	7
Pingalla midgleyi	M	34	70	120	75	75	31	5.92	7
	F	26	71	116	79			0.66	7
Glossamia aprion	M	158	33	140	61	63	109	1.23	7
	F	146	33	157	70	65	104	18.00	7
Toxotes chatareus	M	82	80	307	120	176	68	5.07	7
	F	40	82	260	156	190	29	9.26	7
Liza alata	M	5	167	405	398	?	?	0.24	5
	F	12	224	484	350	?	?	0.52	7
Glossogobius giuris	M	25	32	108	–	–	–	1.50	3
	F	22	35	110	35	?	?	6.25	5
Glossogobius aureus	M	12	48	100	82	?	?	0.38	5
	F	8	41	125	48	?	?	8.38	5
Hypseleotris compressa	M	20	35	62	38	37	17	14.35	5
	F	13	43	67	43	42	13	40.50	5
Mogurnda mogurnda	M	53	34	103	58	55	43	1.00	4
	F	55	27	88	51	50	44	4.73	7
Oxyeleotris lineolata	M	22	65	395	330	315	3	0.36	5
	F	17	80	395	285	284	11	2.58	5

? unknown; – no maturing fish captured

Table 159 The length at first maturity (LFM) in relation to the longest specimen of each species whose LFM was determined

LFM as percentage of longest specimen		
25–49%	50–74%	75–100%
N. erebi	*A. leptaspis*	*M. cyprinoides*
P. rendahli	*N. ater*	*D. bandata* (M)
M. splendida inornata	*N. hyrtlii*	*S. butleri* (F)
C. marianae	*M. nigrans*	*O. lineolata* (M)
C. stercusmuscarum	*P. tenellus*	
A. agrammus (F)	*A. agrammus* (M)	
A. macleayi	*D. bandata* (F)	
A. percoides	*H. fuliginosus*	
L. unicolor	*P. midgleyi* (M)	
S. butleri (M)	*T. chatareus*	
G. aprion	*H. compressa*	
G. giuris (F)	*M. mogurnda*	
S. krefftii (M)	*S. krefftii* (F)	

F = female fish only; M = male fish only

Sex ratio

Table 160 gives the seasons in which significant differences from a 1:1 sex ratio were found and indicates the more numerous sex.

Only five species showed no significant difference from a 1:1 sex ratio in all seasons (table 160). Of the species with significant differences, 80% had an unequal ratio in the 1978 Late-dry season (but only 30% of the species had unequal ratios in the 1979 Late-dry season) and 45% in the 1978–79 Mid-wet season. The highest percentage found in any season except the first was 45%, which suggests that inexperience in sexing the fish at the beginning may have accounted for at least some of the unequal sex ratios recorded. Without breaking down the sex ratio data by habitats, which would require larger sample sizes, it is difficult to determine what is happening throughout the entire system. Generally, the sex ratios found may reflect: (a) the true situation, (b) bias in sex determination, or (c) sampling bias, due either to localised movements of a species within the waterbody or to a behavioural characteristic of a particular sex.

Because of the abnormal 1979–80 Early-wet season, it was difficult to determine whether the sex ratios were changing during breeding cycles. For most species, they appeared not to be related; however, *M. mogurnda*, *H. compressa*, *A. agrammus* and three members of the family Terapontidae may have unequal sex ratios connected with their breeding cycles.

Small fish and fish caught outside their breeding season were often difficult to sex. All fish with gonad stages less than IV were termed immature; mature fish had a gonad stage of IV or above. All fish with a length greater than LFM were termed adults; those less than the LFM were termed juveniles.

There were thus six categories of fish:

Juveniles (length less than LFM) (i) Sexually indistinguishable
(ii) Male
(iii) Female
Adults (length greater than LFM) (i) Sexually indistinguishable
(ii) Male
(iii) Female

Table 160 Seasonal changes in sex ratio for 25 fish species over all habitats combined

	Sampling period						
Ratio type with fish species indicated	1978 Late-dry	1978–79 Early-wet	Mid-wet	1979 Late-wet–Early-dry	Mid-dry	Late-dry	1979–80 Early-wet
‘A’ 1:1 ratio all seasons							
N. erebi							
O. lineolata							
A. percoides							
S. butleri							
G. giuris							
‘B’ Higher ratio of males							
S. krefftii	M (ad)	M (ad)	M	M (ad)	M (ad)		
A. macleayi	M		M (all)		M		
A. agrammus	M	M					
H. fuliginosus	M						
L. unicolor	M						
P. midgleyi	M (all)						NS
G. aprion	M (all)	M (all)	M (all)				
H. compressa	M					NS	NS
M. mogurnda	M					M	NS
‘C’ Higher ratio of females							
N. ater	F			F (all)	F	F (ad)	
P. rendahli	F			F (all)	F	F	
N. hyrtlii	NS	NS	NS	F (all)		F (ad)	
M. nigrans		F (ad)	F (ad)	F (ad)		F (ad)	F (ad)
M. splendida inornata		F					
C. marianae	F				F (all)		
C. stercusmuscarum	F	F (all)			F		
P. tenellus			F	F (all)			NS
‘D’ Ratio varies throughout year							
T. chatareus	M	M	M (all)		F (all)		
D. bandata	M (all)		F (ad)	F (ad)	F (ad)	F (ad)	NS
A. leptaspis	F		F (all)		M (all)		

M = male fish dominant; F = female fish dominant; NS = no fish captured
ad = sample of adult (≥LFM) fish only; equal ratio for all fish
all = sample of all male and female fish; equal ratio in adult fish only

Before development, both male and female gonads are thin and strap-like, which makes sexing difficult. The sex ratios of the immature fish are therefore tentative.

Unless squash preparations of fresh material or histochemically stained sections are prepared and the gonad checked under the microscope, it is very difficult to avoid these misidentifications, although accuracy does improve both with knowledge of the fish species and with practice. Further work might clarify whether some of the unequal sex ratios observed are due to sex misidentification, and find out why there are genuinely unequal ratios in a fish population.

Breeding season

The breeding seasons of the fish must coincide with the conditions that offer the greatest amount of protection for the eggs, and food and shelter for the newly hatched young. The duration and timing of reproductive activity are thus two critical components of an organism's life-history strategy. Factors contributing to species having different breeding seasons include: variability in the physico–chemical environment; biotic factors such as predation, and inter- and intra-species competition for breeding sites and food for the young; and the social system of the species (Kramer 1978).

Some species are aseasonal spawners, breeding continuously at intervals throughout the year (eg *Glossamia aprion*, the Melanotaeniidae [Roberts 1978], and *Craterocephalus stercusmuscarum*). Most fish species, however, breed around the onset of the Wet season. Of the 29 species in the Magela Creek system for which breeding seasons were determined, 25 appeared to have peaks in reproductive development (as indicated by mean GSI for the common species, and based on research in other areas for the less abundant species) around the Early-wet season (table 161). Fish take advantage of the extensive flooding, which often causes an increase in plankton and other foods (see fig 176). Flooding also hugely increases the area and diversity of aquatic habitats available. Many species have become largely dependent on these floods for the initiation and induction of spawning. This normally occurs when water temperatures are rising and are relatively high (Lake 1967; Lowe-McConnell 1975). The young are spawned when food is plentiful and when aquatic plant communities are most dense, affording them protection from predation. The rapid growth of that year's young contributes to a rapid increase in fish biomass. Floodplain fishes are reported to have short life-cycles — many of them mature within one year, for example — as has been found for a close relative of *Melanotaenia splendida inornata* (Beumer 1979b) and *Craterocephalus stercusmuscarum* (Llewellyn 1979).

Kramer (1978) suggests that tropical freshwater fish may be an exception to the generalisation that tropical species have longer breeding seasons than temperate species (which has been documented in many groups, including mammals, amphibians and marine invertebrates). Seasonal breeding generally occurs in areas where there are major fluctuations in physico–chemical conditions, which is the case in the waterbodies of the Alligator Rivers Region. From the limited data, it appears that 16 of the species studied have a well-defined breeding season, and that the remaining species have either an extended breeding season or breed continuously throughout the year.

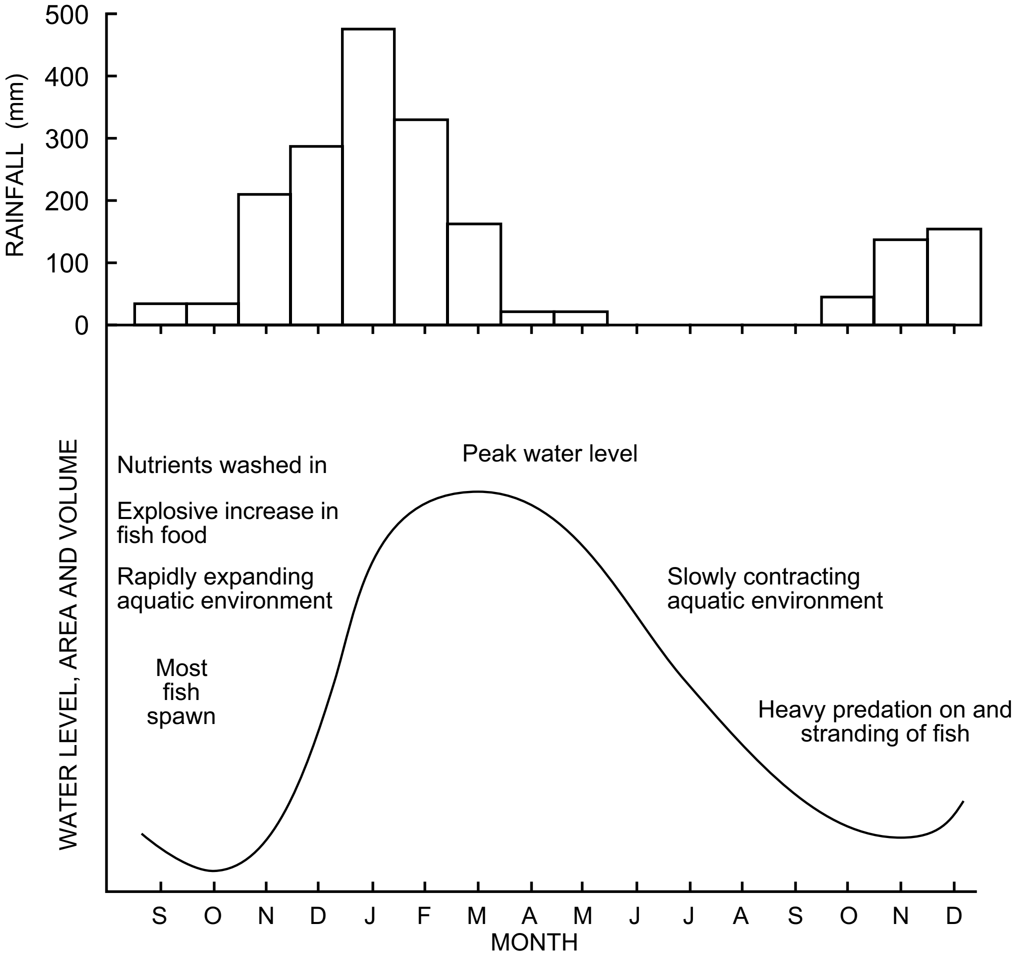
As noted, the Early-wet is the main season for reproduction of most of the species. No species appeared to breed exclusively during the Dry season, although at least three species had breeding seasons extending from the Mid-dry to the Early-wet seasons, and seven species that are aseasonal spawners had high mean GSIs at that time. Ten species appeared to have either an extended breeding season or to breed continuously throughout the year. These species all showed a peak in reproductive development during the Early-wet season.

Table 161 Breeding seasons of the more abundant species of the Magela system as indicated by the mean gonadosomatic index (GSI) for each sampling period (adult males and females combined)

	Sampling period						
Fish species and season	1978 Late-dry	1978–79 Early-wet	1978–79 Mid-wet	1979 Late-wet–Early-dry	1979 Mid-dry	1979 Late-dry	1979–80 Early-wet
A Early-wet season							
M. cyprinoides							
N. ater		>3.9				1–1.9	3–3.9
N. hyrtlii	NS	NS	NS				2–2.9
P. rendahli		2–2.9					3–3.9
L. calcarifer *							
H. fuliginosus *							
L. unicolor		>3.9					3–3.9
P. midgleyi		>3.9					NS
S. krefftii *							
B Late-dry–Early-wet season							
S. jardinii *							
A. leptaspis	1–1.9	1–1.9				2–2.9	
A. agrammus	2–2.9	>3.9				1–1.9	>3.9
A. percoides	1–1.9					1–1.9	2–2.9
S. butleri	>3.9	3–3.9				2–2.9	>3.9
T. chatareus	1–1.9	3–3.9				1–1.9	3–3.9
L. alata *							
C Late-dry season							
G. giuris	1–1.9					2–2.9	NS
D Mid-dry to Early-wet season (ie extended)							
M. nigrans	1–1.9	3–3.9			1–1.9		2–2.9
M. splendida inornata	1–1.9	2–2.9			1–1.9	1–1.9	2–2.9
A. macleayi	1–1.9	2–2.9			1–1.9	1–1.9	1–1.9
E Mid- to Late-wet season							
H. compressa			>3.9	2–2.9		NS	NS
F Early- to Mid-wet season							
M. mogurnda							NS
G Aseasonal							
N. erebi	2–2.9	2–2.9	1–1.9	1–1.9	2–2.9	2–2.9	>3.9
C. marianae	2–2.9	>3.9	1–1.9	3–3.9	2–2.9	3–3.9	>3.9
C. stercusmuscarum	2–2.9	>3.9	2–2.9	1–1.9	2–2.9	3–3.9	2–2.9
P. tenellus	1–1.9	3–3.9	2–2.9	1–1.9	1–1.9	2–2.9	NS
D. bandata	1–1.9	>3.9	2–2.9	1–1.9	1–1.9	2–2.9	NS
G. aprion	3–3.9		1–1.9		2–2.9		
O. lineolata **	1–1.9	1–1.9		1–1.9	1–1.9	1–1.9	NS

* less common species; data from other studies used, as no GSI figures were obtained in the present study

** mean female GSI only; NS no fish sampled



Actual month depends on rainfall and time taken for water to travel down to lower reaches

	Fish movements	
Upstream: (corridor and floodplain) Downstream: (escarpment) Lateral: (floodplains)	Disperse into lowlands and across floodplains	Movement back into dry season refuge areas via creekbed channels
	Fish biomass	
Production of young	Very rapid growth	High mortality
	Fishing/predation	
Destructive for migratory species	Difficult as fish dispersed; much cover	Intensive – fish confined and concentrated in refuge areas

Figure 176 Season cycle of events for fish in the lower reaches of Magela Creek

The precise regulatory role of environmental factors on the reproductive cycles in fish is not known; it has been studied in only about 50 of the 20 000 or so species of fish in the world. It has been suggested that an endogenous reproductive rhythm is triggered approximately annually by environmental factors so that reproduction can occur at the best time of the year (Bangalore et al 1978).

Site of spawning

Table 162 shows the spawning sites for 29 species. Although general breeding sites may be indicated by the presence of running-ripe, mature and spent fish, it is not known in which microhabitats within those sites they actually spawn.

Since no fish in breeding condition were found throughout its entire range, species were selecting certain areas in which to spawn in preference to other areas. Some sites, such as Radon Springs (RS), were monitored mainly by underwater observation and therefore do not show up in the general biological data as potential spawning sites.

The escarpment area and sandy creekbed habitats were the most usual spawning sites for at least 14 species. *Melanotaenia nigrans*, which spawned in the small escarpment perennial streams, was the only species that appeared to spawn exclusively within the escarpment area, while *H. fuliginosus*, *C. marianae* and *P. midgleyi* apparently spawned only in the escarpment streams and the lowland sandy creekbed habitats. *Syncomistes butleri* bred mainly in the escarpment and lowland sandy creek areas, but may also spawn further downstream in the corridor billabongs.

Other species that appeared to breed in the escarpment area and sandy creekbed habitats were *M. mogurnda* and *T. chatareus*, which also bred in lowland backflow billabongs. Species such as *C. stercusmuscarum*, *M. splendida inornata*, *A. percoides*, *N. ater* and *S. krefftii* also bred in backflow billabongs. *Arius leptaspis* and *S. jardinii* appeared to spawn in the escarpment area, although *A. leptaspis* possibly breeds mainly in the lower reaches and *S. jardinii* also spawns in some of the floodplain billabongs.

Only two species — *A. agrammus* and *A. macleayi* — apparently spawned in the lowland sandy creekbed habitats, but were not recorded as also spawning in the escarpment area, although the adults of these species were found there.

The most important spawning habitat was the lowland backflow billabongs, where 19 species showed evidence of spawning. Four species apparently breed at no other location and therefore may be totally dependent on these billabongs; these are *N. erebi*, *L. unicolor*, *N. hyrtlii* and *P. rendahli*.

Although our data indicate that *L. alata* may possibly spawn in the lowland backflow billabongs, there was also an indication that at least part of the population had made a spawning migration downstream. Such migrations have been recorded for this species in Papua New Guinea (Haines 1979).

Species that appear to breed only in the lowland backflow billabongs and floodplain billabongs are *O. lineolata*, *D. bandata*, *G. aprion* and *P. tenellus*. *Glossogobius giuris* possibly breeds only in lowland backflow billabongs and corridor billabongs. No species was apparently breeding exclusively in the corridor and floodplain billabongs.

Three species — *M. cyprinoides*, *L. calcarifer* and *L. alata* — appear to migrate downstream to the estuarine or coastal areas to spawn. Seven species apparently breed in at least four of the five habitat areas in the Alligator Rivers Region, excluding estuarine or marine areas: *A. leptaspis*, *M. splendida inornata*, *A. percoides*, *N. ater*, *S. krefftii*, *C. stercusmuscarum* and *A. agrammus*.

Table 162 Sites where running-ripe (Stage VI), mature (Stage V) or spent (Stage VII) fish were captured during each season; the species that are reported to migrate to the estuarine or coastal areas to spawn are also indicated. See appendix 1 for site codes.

	Escarpment																		
	Seasonal stream	Perennial stream		Mainchannel waterbody			Lowland sandy creekbed			Lowland backflow billabong						Corridor	Flood-plain	Lower riverine floodplain	Estuarine or coastal
Fish species	SY* NS*	RS	BS*	BD	ST*	CP*	MU	NC*	MD GD	FS	DR*	CA CL DA GL	NR*	BX*	GA GN IM	MI BO MX	ID LT JJ JA NN	WL CH	RH CC MMa MMb
M. nigrans	V/VII	VI																	
H. fuliginosus				V/VII	V/VII	VI			VI										
C. marianae				VI	VI	VI	VI		VI										
P. midgleyi			V/VII	V/VII					VI										
S. butleri				VI	V/VII	VI			VI							VI			
M. mogurnda	VII			VII			VII					VII							
T. chatareus				VI	VI	VI						VI	VI						
S. jardinii																	VII		
N. erebi										VI		VI	V/VII	VI	VI				
L. unicolor										VI		VI							
N. hyrtlii												V/VII			V/VII				
P. rendahli												V/VII		V/VII	V/VII				
O. lineolata												V/VII		V/VII	V/VII			V/VII	
A. macleayi								VI							VI				
A. leptaspis					V/VII						VI	V/VII			V/VII	V/VII	VI		
M. splendida inornata				V/VII	V/VII			V/VII	VI			V/VII			V/VII	V/VII	V/VII		
A. percoides				VI	VI				VI			VI			VI	VI	VI		
N. ater				V/VII	VI				V/VII			V/VII	VI		V/VII	VI	VI	VI	
S. krefftii					VI				VI			VI	VI		VI	V/VII			
C. stercusmuscarum				VI			VI	VI	VI			VI					VI		

Table 162 continued

	Escarpment																		
	Seasonal stream	Perennial stream		Mainchannel waterbody			Lowland sandy creekbed			Lowland backflow billabong						Corridor	Flood-plain	Lower riverine floodplain	Estuarine or coastal
Fish species	SY* NS*	RS	BS*	BD	ST*	CP*	MU	NC*	MD GD	FS	DR*	CA CL DA GL	NR*	BX*	GA GN IM	MI BO MX	ID LT JJ JA NN	WL CH	RH CC MMa MMb
A. agrammus									VI			VI	VI	VI	VI		VI		
G. giuris											V/VII					V/VII			
D. bandata										V/VII		V/VII					V/VII		
G. aprion												V/VII			V/VII		V/VII		
H. compressa																	V/VII	V/VII	
P. tenellus													V/VII				V/VII		
M. cyprinoides																			VI
L. calcarifer																			VI
L. alata																			VI
Sub total	**2**	**1**	**1**	**10**	**9**	**4**	**3**	**3**	**10**	**2**	**2**	**16**	**6**	**4**	**12**	**7**	**11**	**3**	**3**
Total per habitat	**2**	**2**		**12**			**12**			**19**						**7**	**11**	**3**	**3**

* = Nourlangie catchment

Breeding strategy

The breeding strategy is determined by such factors as variability in the physico–chemical environment, predation, and inter- and intra-species competition for breeding sites and food for the young. The type and numbers of eggs laid, stage of development at hatching and measures to protect the newly hatched young have been selectively evolved to achieve maximum survival for the species.

Each of the more common species has been put into one of the following broad, sometimes overlapping, categories of breeding strategies:

- bear live young
- incubate in mouth
- build nest and/or guard territory
- attach eggs to aquatic vegetation
- scatter eggs at depth
- spawn pelagic eggs

Table 157 summaries the reproductive variables for all the common species.

A high proportion of the species studied appear to exhibit some form of parental care (ovoviviparity, buccal incubation, guarding of nests). This strategy may have evolved in response to the variable conditions imposed by the extreme Wet and Dry seasons, and to the strong competition for food and other 'niche variables' in this tropical freshwater region with its high species richness and biomass.

Live-bearing species

The most specialised strategy found in the evolution of fishes is the production of live young that do not pass through a larval stage (ie they are viviparous or ovoviviparous). The female is fertilised internally by the male, which has specially developed organs ('claspers') on the pelvic or anal fins, and often an elongated urinogenital papilla.

At least four families represented in the Region have members that bear live young: Carcharhinidae (*Carcharhinus leucas,* Boeseman 1964), the Pristidae (*Pristis microdon,* also from New Guinea) (Roberts 1978; Haines 1979), the Dasyatidae (Breder & Rosen 1966) and the Hemiramphidae (*Zenarchopterus,* also from New Guinea) (Haines 1979).

Buccal-incubating species

The eggs, generally few in number, are incubated in the mouth by the male or female parent (rarely both). Typically large and yolky, they have a long incubation period and the hatched larvae are usually relatively large and well developed. Mouth-brooding has the advantage over egg-laying in tropical environments in that the mouth-breeding parent can avoid areas of low dissolved oxygen or other detrimental water conditions, and protect the young from predators.

Three species caught in the Region are mouth-brooders: *S. jardinii* (female broods), *A. leptaspis* (male) and *G. aprion* (male).

Scleropages jardinii and *A. leptaspis* were two of the largest fish caught in the Region, yet were amongst the least fecund species observed (mean number of eggs laid were 90 and 42 respectively). However, these eggs were the largest recorded (8.4 and 13.8 mm), and had very large yolks. The incubation periods are longer than one week, and the newly hatched young are well-developed alevins (the yolk-attached larvae transform directly into juveniles [Hubbs 1943]).

Glossamia aprion has a higher fecundity (220 eggs), with a smaller mean egg diameter of 1.5 mm. Lake (1978) recorded eggs with diameters of 3 mm and a two-week incubation period — depending on temperature — for this, or a closely related, species in Queensland. The newly hatched young are about 6 mm long and are quite well developed.

These three mouth-brooding species did not all breed during the same season: *A. leptaspis* and *S. jardinii* have well-defined breeding periods around the Early-wet season, while *G. aprion* appears to breed almost continuously throughout the year.

Nest-building and/or guarding species

Most fish that use this breeding strategy are multiple spawners, producing batches of eggs at intervals throughout the breeding season. Some, however, are aseasonal breeders. Producing several batches of eggs ensures that at least some survive when water levels fluctuate. It is usually the male that selects either a site for nest building, or a territory, generally in shallower water. The site is usually in a cave or hollow log, or amongst gravel or litter, which he protects against intruders or predators. These species often make rapid fin movements to aerate the eggs and supply them with additional oxygen, bring fresh water around the nest and remove metabolic waste from it. Nest builders often have complex courtship behaviour, which helps synchronise spawning — this is important, as the broods are small — and they do not make extensive migrations (Lowe-McConnell 1975). The eggs vary in size and shape between species and are often adhesive. The incubation period is generally less than a week, and the larvae are poorly developed, although usually better developed than those of pelagic spawners. The male, after hatching the eggs, often spawns again and then protects the next batch of eggs. They generally do not guard the larvae.

Other workers studying the same species or closely related species in other areas found that a high proportion of the species found in the Region exhibit some sort of nest-building or territorial-guarding behaviour. These include the family Plotosidae (Davis 1977a; Breder & Rosen 1966), probably some members of the Terapontidae (Breder & Rosen 1966), the family Gobiidae (Breder & Rosen 1966), and the family Eleotrididae (Breder & Rosen 1966; Llewellyn 1971; Pollard 1974; Auty 1978; Lake 1978).

Almost all members of these families in the Region have a large number of small (usually less than 1 mm diameter) demersal eggs, which may or may not be adhesive. The incubation periods are all less than one week and the larvae at hatching are not well developed. In all cases it is believed that nests are constructed or a territory is selected and guarded during spawning and incubation.

This type of breeding strategy, while affording greater protection from predators, and in some cases from low dissolved-oxygen concentrations, is at risk from changes in water level. The short incubation time and the numerous eggs laid in a number of separate spawnings may overcome this disadvantage.

Species that attach eggs to aquatic vegetation

This group lays fewer and larger eggs than the nest builders. The eggs hatch into well-developed larvae after an incubation period greater than a week.

The disadvantage of producing a smaller number of offspring from each spawning may be partly offset by the advanced stage of development of the newly hatched young. They are good swimmers, efficient feeders and fast growers. Also, the non-pelagic larvae, unlike planktonic larvae, do not have to expend energy on returning upstream.

The eggs are attached by adhesive threads or tendrils to aquatic plants and other objects in the water, which hide them from predators. However, the eggs are subject to desiccation if the water level drops or to dispersal if there is a flood.

The melanotaeniids increase the chances of some eggs surviving by spawning repeatedly throughout the year. The reproductive strategy of *S. krefftii* is not known, but other members of the genus attach their large eggs to aquatic vegetation, and they have a long incubation.[251]

Species that scatter demersal eggs over the substrate
Two strategies are used by fish in this category.

1 A small number of relatively large eggs, which usually adhere to substrates, are scattered over the bottom, sinking between rocks and amongst the vegetation. The large, well-developed larvae probably have an increased chance of survival, which may offset the species' low fecundity.

2 A large number of smaller eggs are scattered as in (1), but the incubation period is short and the hatched larvae are poorly developed. The short incubation period decreases the risk of desiccation when water levels drop. The poor development of the newly hatched fry is counterbalanced by the large number of eggs.

Scattering the eggs reduces the chance of the whole brood being destroyed simultaneously. However, the eggs may be susceptible to detrimental changes in the physico–chemical environment, such as a decrease in dissolved oxygen.

The atherinids exhibit strategy type (1). Members of this family are generally aseasonal spawners, probably breeding throughout the year.

Leiopotherapon unicolor, an example of a species exhibiting strategy (2), also scatters its eggs demersally. However, unlike atherinids it has a well-defined breeding season, high fecundity and a small egg diameter. The incubation period is short (about two days; Llewellyn 1973; Lake 1978; Merrick 1980) and the larvae at hatching are small (about 2.2 mm) with poorly developed eyes and fins (Llewellyn 1973).

Species that deposit eggs on surface waters (pelagic)
This strategy is usually adopted by 'total spawners' (Lowe-McConnell 1975): all the eggs ripen at one time each year. These are seasonal spawners and may make extensive breeding migrations. Generally, their fecundity is very high and the pelagic eggs are small. At the end of a short incubation period, poorly developed, planktonic larvae emerge.

Megalops cyprinoides and *L. calcarifer* migrate to the estuarine or coastal areas to breed (Roberts 1978; Haines 1979). *Megalops cyprinoides* spawns in estuarine or shallow inshore waters and the eggs hatch into leptocephalus-type larvae, approximately 12 mm long and with poor fin development. The larvae undergo metamorphosis and the young fish do not attain full adult appearance until they are about 300 mm long (Wade 1962).

Lates calcarifer has a complex life history, which involves a protandrous sex change and a seasonal catadromous breeding migration. The species is reported to spawn up to 16.8 x 10^6 eggs, with diameters of 0.7 by 0.8 mm (Reynolds 1978). Conflicting reports suggest that eggs are pelagic (Moore 1979) or demersal (Reynolds 1978). The newly hatched larvae are 4 mm long (Reynolds 1978).

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[251] Smith (1998) indicated that *S. krefftii* have been observed spawning within macrophyte beds along the shore of Lake Moondarra in north-western Queensland.

Toxotes chatareus and *N. erebi* also have high fecundities and very small eggs. These two species breed within the Magela Creek system, although both have also been recorded as breeding in estuarine waters (Roberts 1978; Haines 1979). *T. chatareus* breeds during the Early-wet season. Its pelagic larvae have been collected from flooded lowland backflow billabongs. *Nematalosa erebi* has a very high fecundity and very small eggs, but may breed aseasonally, although a peak in reproductive development was observed during the Early-wet season.

Dispersal of the species is also facilitated by its having pelagic eggs. These, however, are very susceptible to damage by high stream velocities as they float on the surface, but the enormous numbers of eggs generally produced may counteract this loss.

Future studies

The Early-wet season appears to be the most important period for reproduction: the reproductive activity of 25 species peaks at this time. A second Wet season sampling is needed to confirm and expand the reproductive data collected in the present study.

In ecological studies, it is important to understand the problems that arise in relation to reproduction. The methods a species uses, and their success or failure in a given setting, can be the key to understanding an ecological complex. Conversely, the effects of the reproductive pattern on the ecological complex in which a species is involved may have a profound influence on the continued existence of other forms (Breder & Rosen 1966).

Apart from extending and confirming the existing data, the reproductive strategies of species should be further studied to assess any impact of mining activity on the communities. Information on habitat requirements for spawning, the type of egg spawned and the duration of the incubation period is essential to determine the effects of mining activity on this biologically critical parameter.

Fluctuations in water level, the abundance and distribution of aquatic plants and the type of substrate found in the waterbody may affect breeding success. All of these variables should be monitored closely and any changes in their natural ranges should be kept to an absolute minimum. Because food availability is a critical factor in initiation of spawning and spawning success, the invertebrate fauna, aquatic plants and smaller fish species that constitute food for organisms at higher trophic levels must be maintained at their natural levels.

Increased silt loads in the water from areas of disturbed land may affect fish reproduction indirectly by interfering with aquatic plants, nesting sites and food availability, or directly by interfering with visual cues that may be essential in courtship behaviour and spawning.

Chemical pollutants can enter the Alligator Rivers Region waterbodies by controlled or uncontrolled discharges of water containing mining treatment wastes, organic pollutants from sewage treatment works, pesticides from the township, or fertilisers from the revegetating areas of the mine site or town gardens. These pollutants may affect reproduction in many different ways. Teratological development of embryos may result in deformed or malfunctioning larvae that do not survive hatching. There may be behavioural changes in the adults during the mating season. The production of eggs and sperm, the secretion of egg membranes, egg shells and production of egg nutrients may all be affected by changes in hormone function and enzyme activity. Changes in the ecosystem may influence reproductive success when vitellogenesis is directly influenced by the availability of food (Davis 1972).

Chronic exposure to toxic chemicals throughout the various stages of a fish's life history has been regarded as the best means of estimating long-term, safe concentrations of toxicants for fish. The early stages of embryonic development are far more sensitive than later stages to pollution by irradiation (Davis 1972).

The effects of pollutants on behavioural aspects of reproduction have hardly been touched on by any of the investigators in this field, and the physiological effect of pollution on reproduction and on the development of embryos and larvae, including metamorphosis, is little understood (Davis 1972).

More work on the effects of pollutants and the synergistic and antagonistic effects of various pollutants, both singly and combined, on the reproduction and life history of species in the Region is urgently required to enable safe concentration limits to be determined.[252]

4.4 Feeding habits

The main components of the diet of the fish collected during the study are summarised in the pie diagrams in each species section in chapter 3 of this report.

Similarity of feeding habits [253]

Polythetic agglomerative (MULCLAS in figure 177) analysis (CSIRO Taxon Library) was undertaken on the relative abundances (quantitative estimated volume data) of items in the overall diets of fish species. Discussion in the following section progresses from top to bottom on the dendrogram in figure 177.

Syncomistes butleri, P. midgleyi and *L. alata* were grouped separately from most of the other species, as they ate primarily algae and detritus. The two upstream escarpment zone terapontids and the mullet, which was mainly found in corridor and floodplain billabongs, were classified in earlier sections as herbivores/detritivores. *Hephaestus fuliginosus,* which is usually found associated with these terapontids, was grouped separately because of the abundance of aquatic and terrestrial insects in its stomachs. A large gap separated these species from the following, more carnivorous, species.

The plotosid catfishes were generally combined together in one large group. However, the 'colour-type' *Neosilurus* sp. A was grouped separately because an abundance of unidentified organic material and conchostracan microcrustaceans was found in the stomachs. Possibly the organic material was unidentified due to our inexperience in the early stages of the study, and the size of the conchostracan component may have been due to seasonality in the availability of food in the study period when the 'colour-type' classification used. The plotosid catfishes ate mainly dipteran insect larvae (mostly chironomids) and cladoceran microcrustaceans (all the plotosids were classified as meiophagic benthic carnivores).

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[252] Biological testing of mine waste waters using reproductive parameters has subsequently been developed (see Holdway 1991).

[253] Nine feeding guilds are identified within the species-account section and this analysis: herbivores/detritivores (3 species), microphagic omnivores (2 species), meiophagic omnivores (4 species), macrophagic omnivores (4 species), microphagic carnivores (6 species), meiophagic carnivores (6 species), meiophagic insectivore (1 species), macrophagic insectivore (1 species), and macrophagic piscivore/carnivores (6 species). There is clearly substantial discrimination in respect to the trophic level of foods utilised (ie herbivore/detritivores, omnivores, carnivores, piscivores, etc) and the size of the food (ie microphagic, meiophagic and macrophagic, etc), which relates to the body size of the particular fish species. In contrast to these results, a study (Pusey et al 1995b) into the feeding ecology of freshwater fishes from two rivers in the Australian wet tropics revealed only five trophic guilds discriminated primarily on the basis of body size of the constituent fish species.

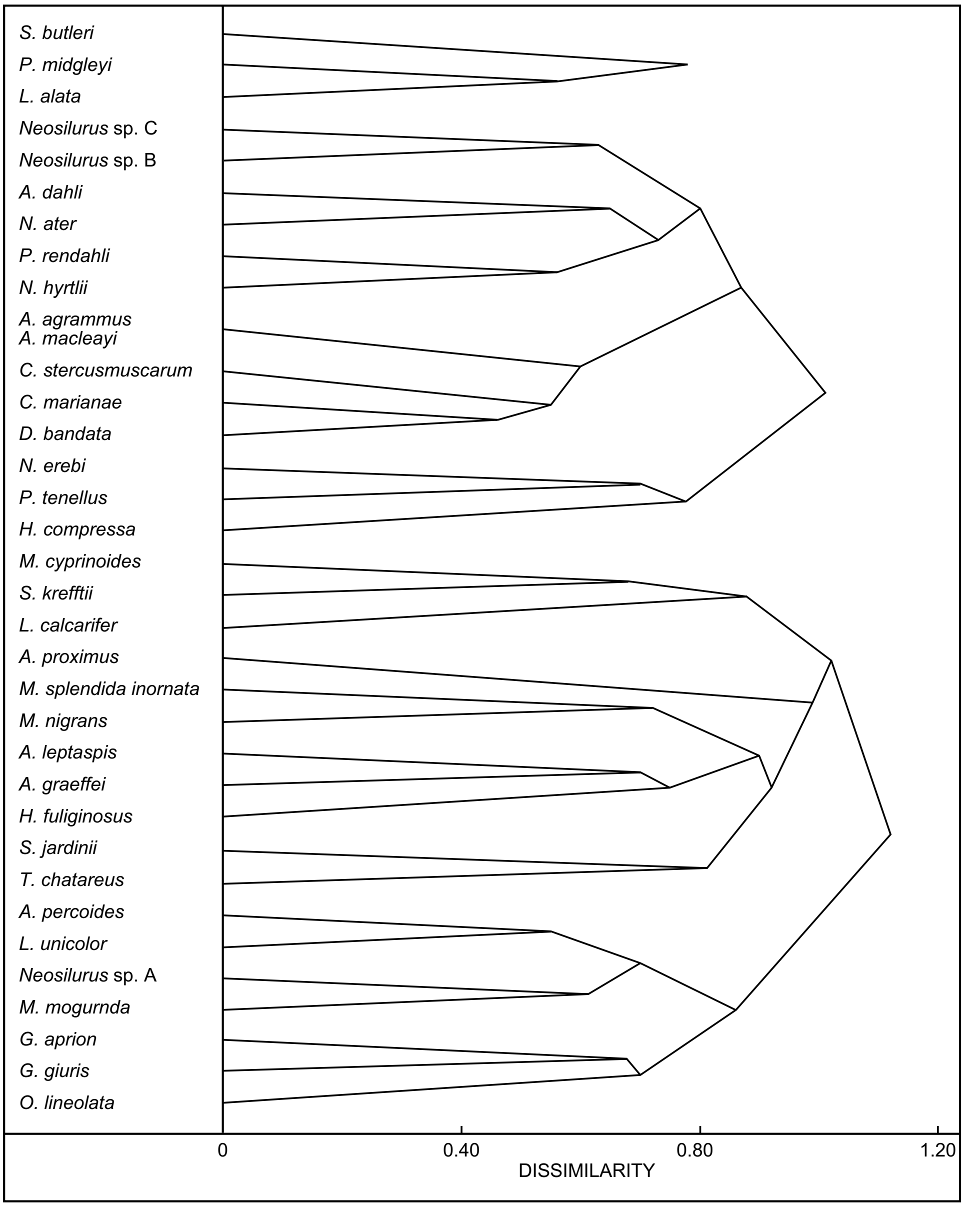

Figure 177 MULCLAS analysis of the relative abundance of stomach contents items in the overall diets of fish species captured in this study period

The small ambassids (*A. agrammus, A. macleayi* and *D. bandata*) and atherinids (*C. stercusmuscarum* and *C. marianae*) were grouped together, as their diets were based on aquatic dipteran insect larvae and microcrustaceans. The diets of the two *Ambassis* species were very similar (mainly cladocerans), but *D. bandata* was grouped more closely with the atherinids, because of the strong chironomid component in its diet. Both *Ambassis* and *Craterocephalus* species were classified as microphagic carnivores feeding in littoral benthic or midwater habitats or both; *D. bandata* was considered to be a meiophagic carnivore that feeds in similar zones.

Nematalosa erebi and *P. tenellus* were grouped together because of the common presence of algae, detritus and, to a lesser extent, cladocerans and unidentified matter in their diets. The occurrence of the unidentified component caused *H. compressa* to be incorrectly grouped with these species. *Nematalosa erebi* and *P. tenellus* were classified as microphagic omnivores (*N. erebi* more specifically as a detritophage/planktivore feeding in mid- and benthic waters, and *P. tenellus* feeding in littoral benthic waters). *Hypseleotris compressa* was classified as a microphagic carnivore that is occasionally omnivorous. A large gap separated these species from the next group, which consisted of carnivores that were generally more predatory.

Macrophagic piscivores/carnivores (*M. cyprinoides, S. krefftii* and *L. calcarifer*) were placed together in the first group of a larger set of groups. (*Carcharhinus leucas*, which was excluded from the analysis because the few specimens captured were not from the regular sampling sites, would have been placed in this group, as it was entirely piscivorous.)

The next six species to some extent displayed omnivorous feeding habits. (The grouping position of *A. proximus* [a macrophagic omnivore] was possibly not very meaningful, as only a few specimens were examined.) The melanotaeniids (meiophagic omnivores) were grouped together, as they usually fed on aquatic insects, terrestrial insects and filamentous algae. *Melanotaenia nigrans* fed over many substrate types and from the water's surface, and *M. splendida inornata* fed opportunistically throughout most waterbody zones. The other two ariid catfishes (*A. leptaspis* and *A. graeffei*) were classified as macrophagic omnivores that feed in benthic and midwater zones, so they are grouped together. *Hephaestus fuliginosus* (a predominantly escarpment-zone terapontid) was grouped near them, as it also was considered to be a macrophagic omnivore.

Scleropages jardinii and *T. chatareus* were grouped together, as they commonly fed on insects, both terrestrial and aquatic, but *T. chatareus* ate mainly terrestrial insects, and *S. jardinii* also ate some teleosts. *Scleropages jardinii* was classified as a macrophagic carnivore/insectivore, and *T. chatareus* as a meiophagic insectivore.

The remaining terapontids (*A. percoides* and *L. unicolor*) were placed together in the next group. These species were meiophagic omnivores and fed extensively in benthic and midwater zones. They were both opportunistic feeders, eating aquatic insects, crustaceans, algae, hydrophytes and terrestrial plant material.

The remaining species (except for the plotosid 'colour type' *Neosilurus* sp. A) had varied carnivorous diets. *Mogurnda mogurnda* and *G. giuris* were classified as meiophagic carnivores that feed in benthic and midwater zones, primarily on aquatic insects and crustaceans. *G. giuris* was an opportunistic feeder. *Oxyeleotris lineolata* and *Glossamia aprion* were classified as macrophagic carnivores, feeding on crustaceans, teleosts and aquatic insects, also in the benthic and midwater zones.

Sharing of food resources

Fishes in Amazonian tributary streams apparently do not generally have distinct specialisations in the foods they eat; the stomach contents of the various fish families present are rather uniform because most species have a more or less varied diet (Knoppel 1970). Lowe-McConnell (1975) explained that this apparent contradiction (in view of the adaptive radiations of characoids in the Amazon basin) seems to arise from only omnivorous (eurytrophic) fishes being able to penetrate to the headwater streams. The same effect is seen in the present study, where about 50% (table 163) of species in escarpment perennial streams and terminal mainchannel waterbodies were omnivores, while only 20 to 30% in lowland, corridor and floodplain habitats were.[254] Omnivorous species include the melanotaeniids, *L. unicolor* and *H. fuliginosus***.** Two terapontid herbivores/detritivores (*S. butleri* and *P. midgleyi*) are also found in the escarpment zone in the study area (table 163); their specialised ability to feed upon periphyton on submerged bedrock, particularly in terminal mainchannel waterbodies, as well as their ability to reach and occupy these upstream habitats in the Wet season, appear to be the main reasons for their successful colonisation of such habitats.

Lowe-McConnell (1975) stated that omnivorous fish species that penetrate to the headwaters are usually the most widely distributed, and suggested that their particular feeding specialisations may be more useful in downstream areas throughout the year, or possibly in some seasons, or that they may have been more significant in the past when the fish species were evolving. *Leiopotherapon unicolor* and *M. splendida inornata* were the only upper escarpment zone species also found abundantly in lowland, corridor and floodplain habitats in the present study.

Specialisations may be more advantageous in the middle and lower reaches of rivers, where so many species coexist (Lowe-McConnell 1975). In the present study many closely related species found in lowland, corridor and floodplain habitats had very similar diets in sites where these species were captured together, eg the main forage fish species, including the ambassids, melanotaeniids, plotosids and atherinids, and some terapontids (*L. unicolor* and *A. percoides*). The diets of the main predatory species (*L. calcarifer*, *A. leptaspis*, *S. krefftii* and *M. cyprinoides*) also overlapped: their stomach contents were rather uniform, as Knoppel (1970) found in Amazon tributary fishes; however, there were differences between families (eg plotosids fed mainly on benthic dipteran larvae, while ambassids fed mainly on microcrustaceans), so specialisation may occur more at the family rather than the species level.

There are great seasonal variations in pressure on food resources in rivers. In Costa Rica, fish diets overlapped least in the Dry season, when food is most scarce and competition probably strongest (in accordance with Gause's competitive exclusion principle) (Zaret & Rand 1971). In Zaire, however, Matthes (1964) found that fishes ate similar food in the Dry season when mainly bottom detritus was available. In the Rupununi savanna district of British Guiana, Lowe-McConnell (1963) found a similar uniformity in the Dry season. She suggested that

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[254] In the study of Pusey et al (1995b) which focused on the feeding ecology of freshwater fishes from two rivers in the Australian wet tropics, dietary overlap was highest at sites characterised by high water velocities, coarse substrates and dense riparian canopy. This equates to escarpment habitats in the Alligator Rivers Region (ARR). A high level of dietary overlap is expected in escarpment areas given the dominance of omnivory. The omnivorous feeding habitats are likely to be beneficial in habitats where food availability is low. Pusey et al (1995b) found dietary overlap to be least in areas characterised by low water velocities and sandy substrates, an equivalent of corridor habitats in the ARR. Pusey et al suggested that the low dietary overlap was driven by low food availability in such habitats. In contrast, food availability is likely to be high in ARR corridor habitats as they act as a staging area for migrating taxa in the wet season and function as a depositional area for taxa washed down from the lowland sandy creek habitat. Pusey et al did emphasise that dietary overlap varied within and between the two rivers they studied.

trophic specialisations here would come into play in the Wet season, which is the main feeding period.

The pressure on resources is apparently greatest when water levels fall after the Wet season and the number of species rises as they leave the contracting Wet season environments. This is the period when unique feeding habits would be most beneficial; *T. chatareus,* for example, would have an obvious specialist advantage.

Detailed analyses of the seasonal variation in food overlap between species were not undertaken in the present study; however, such analyses in future studies could ascertain the degree of stress caused by the lack of food resources and its repercussions on body condition.

Trophic relationships

The energy pool available in the biomass of primary producers (microorganisms, periphyton, hydrophytes and phytoplankton) is ultimately the only food available for fish production unless it is supplemented by a supply of allochthonous material. In freshwaters, Lowe-McConnell (1975) argued that two alternative chains run: either from bottom detritus through microorganisms to detritus-feeding invertebrates (and/or fish) to invertebrate-eating fish to several levels of piscivores; or (in the pelagic zone) from phytoplankton to zooplankton to zooplankton-feeders and then to one or more levels of piscivores. She noted that in river systems the detrital chain appears to be more important. Bottom detritus tends to be allochthonous in origin in the upper reaches and derived from hydrophytes in the lower reaches.

The Purari River System of Papua New Guinea has low primary productivity, virtually no plankton, few filamentous algae and rooted hydrophytes, opaque water (due to the heavy silt load), rapid flow, and frequent fluctuations in water level (Haines 1979). The notable feature of the Purari fish fauna is the paucity of herbivores and lack of planktonic feeders, which is attributable to the lack of hydrophytes and plankton. The sources of nutrition in this system were thought to be allochthonous materials from terrestrial plant communities becoming bottom detritus. Some fish ate the terrestrial material directly (or, at the next trophic level, in the form of insects), others were detritophages, but most ate detritophagic prawns, which predominated in this system.

The nutrient cycle and trophic relationships between fishes in our study area appeared to be different from those of the Purari River; however, the source of nutrition in the upper Magela and Nourlangie systems is likely to be the same as in the Purari system — from allochthonous terrestrial plant material via detritus. The main difference is that in lowland and floodplain billabongs nutrients appear to be recycled from bottom detritus. This detritus mainly comes from (a) the decomposition of hydrophytes, and (b) phytoplankton (Dry season benthic waters of these habitats have been classified as mesotrophic [Hart & McGregor 1978] and eutrophic [Walker & Tyler 1979]). Zooplankton populations develop, perhaps in part because more nutrients become available when large amounts of organic material decompose and become more concentrated by evaporation after the seasonal flow has ended. More niches may therefore be available for microphage- or plankton-feeding fishes and herbivorous fishes than in the Purari River System. We found seven species of microphagic fishes (atherinids, *H. compressa*, *N. erebi*) in the study area, no strictly herbivorous species (except the upstream terapontids in the escarpment zone), but many omnivorous species (eg *L. unicolor, A. percoides, M. splendida inornata*). No strictly detritophagic fish species were found, although *L. alata* had a detrital component in its stomach contents. The main trophic group appeared to be the carnivores (15 species), which generally fed on aquatic insects and crustaceans. It is notable that the Purari fauna had few species similar in size to most of the microphagic feeders in our study area.

Table 163 Percentage frequencies of the total number of fish species occupying various trophic niches in a longitudinal array of habitats in the Magela Creek catchment

	Escarpment			Lowlands				Overall
Trophic niche	Terminal main-channel	Perennial stream	Mainchannel	Sandy creek	Backflow billabong	Corridor billabong	Floodplain billabong	
Piscivores/ carnivores	–	–	7.1 (1)	18.1 (2)	10.5 (2)	13.6 (3)	15.8 (3)	10.7 (3)
Carnivores	–	22.2(2)	50.0 (7)	54.5 (6)	57.8 (12)	54.5 (12)	57.9 (11)	53.5 (15)
Omnivores	50.0 (2)	55.6 (5)	35.7 (5)	27.2 (3)	31.5 (6)	22.7 (5)	21.1 (4)	25.0 (7)
Herbivore/ detritivores	50.0 (2)	22.2 (2)	7.1 (1)	–	–	9.1 (2)	5.3 (1)	10.7 (3)
Total number of abundant species	4	9	14	11	19	22	19	28

(Number of fish species shown in parentheses)

The features typical of freshwater fish faunas of the other three tropical continents (Asia, Africa and South America) were summarised (Lowe-McConnell 1975) as (1) the importance of allochthonous plant material as direct food for fish species, (2) the important role of insects as fish food, (3) the important role of mud and detritus as direct food for some species, and (4) the presence of large numbers of individuals and kinds of piscivorous fishes. The Alligator Rivers Region fish fauna did not appear to closely follow the above pattern. Allochthonous plant material was only directly important to a few species in the escarpment zones of the catchment; however, some omnivores ate this material in the lower reaches during the Dry season. Terrestrial insects and aquatic insect larvae were important fish foods, but crustaceans were of comparable importance in the aquatic component of the diets. Mud and detritus as food was fairly important to only a few species. There are relatively few primarily piscivorous fish species in the freshwaters of the Region, and their populations appeared small.

The percentage frequency of the total number of abundant fish species from various trophic niches in a longitudinal array of habitats in the Magela Creek catchment is shown in table 163. The greatest numbers of species overall were classified as carnivores, followed by omnivores, piscivores/carnivores and then herbivores/detritivores. Carnivorous species were found most often in floodplain and lowland billabongs, followed closely by corridor billabongs and sandy creekbed habitats and then escarpment mainchannel waterbodies. Many more niches are available in the lower reaches of tropical rivers, which have more bottom mud, phytoplankton and hydrophytes, providing more food sources for the generally more diverse communities (Lowe-McConnell 1975).

Compared with other habitats, there were few carnivores in escarpment perennial streams in the Alligator Rivers Region (probably because there are no, or very few, zooplankton to support microphagic carnivores [pers obs]). No carnivores (except for occasional *Crocodylus johnstoni*) were found in escarpment terminal mainchannel waterbodies. The highest frequency of omnivorous fish species was found in escarpment perennial streams and terminal mainchannel waterbodies (see earlier sections for explanation), decreasing to the lowest frequency in corridor and floodplain billabongs. All omnivorous fish had very high mean fullness indices. Piscivore/carnivore species were most common in lowland sandy creekbeds (these species preyed upon forage fish, which used these habitats as migration routes in the Wet season), followed by floodplain and corridor billabongs, then lowland billabongs and escarpment mainchannel waterbodies; none were found abundantly in escarpment perennial streams (except in the Nourlangie catchment, where *M. cyprinoides* was observed) and terminal mainchannel waterbodies. All piscivorous/carnivorous fish had very low mean fullness indices. The highest frequency of herbivore/detritivore species was found in escarpment terminal mainchannel waterbodies and perennial streams (the specialised terapontids), followed by corridor billabongs (where *S. butleri* and *L. alata* were captured), escarpment mainchannel waterbodies and floodplain billabongs. All herbivore/detritivore fish species had very high mean fullness indices.

The percentage frequencies of the major feeding categories of the total numbers of abundant fish species from various trophic niches in the Purari River catchment in Papua New Guinea and in the three tropical South American waterbodies mentioned are shown in tables 164 and 165, respectively. Herbivore/detritivore fish species occurred most often in the Purari River catchment tributary springs and least often in the most downstream freshwater delta habitats (as in our study area); omnivores were rare in the catchment and, unlike our study, none were collected in spring-fed streams entering the river; carnivores were common in the river and the freshwater delta, and also in tributary springs (unlike in our study); piscivores/carnivores appeared to be more diverse than in the Alligator Rivers Region.

Table 164 Percentage frequency of the total number of fish species occupying various trophic niches in the Purari River catchment, Papua New Guinea (after Haines 1979) (number of fish species shown in parentheses)

Trophic niche[1]	Springs off river		River above delta		Freshwater delta	
Piscivores/carnivores	11.1	(1)	15.8	(6)	19.2	(5)
Carnivores	44.4	(4)	42.1	(16)	57.6	(15)
Omnivores	–		7.9	(3)	3.8	(1)
Herbivore/detritivores	44.4	(4)	34.2	(13)	19.2	(5)
Total number of abundant species	9		38		26	

1 Trophic niches redesignated by present authors

Table 165 Percentage frequency of the total numbers of fish species occupying various trophic niches in the present study area and in three tropical South American waterbodies (number of fish species shown in parenthesis)

Trophic niche	Overall habitats in present study		Tributary forest streams [1]		Lowland lake [2]		Oxbow lagoon [3]	
Piscivores/carnivores	11.1	(3)	5.0	(2)	12.5	(5)	19.6	(11)
Carnivores	55.5	(15)	30.7	(12)	45.0	(18)	21.0	(12)
Omnivores	25.9	(7)	26.6	(10)	25.0	(10)	21.0	(12)
Herbivore/detritivores	7.4	(2)	38.4	(15)	17.5	(7)	37.5	(21)
Total number of abundant species	27		39		40		56	

Trophic niches designated (or redesignated) by present authors:

1 Amazon tributaries near Manaus (specimens collected by Fittakau) (Knoppel 1970)

2 Lake Redondo in the Amazon River catchment (Marlier 1967)

3 Oxbow lagoons of the seasonally flooding Middle Parana–Paraguai River system (Ringuelet et al 1967)

The trophic niches of the fish species in forested Amazonian tributary streams (Knoppel 1970) were similar in the fish communities of the escarpment mainchannel waterbodies we studied, the main differences being the relative numbers of omnivores and herbivores/detritivores. The fish communities examined by Marlier (1967) in Lake Redondo, Amazon River system, were also similar to those in the escarpment waterbodies. The high diversity of herbivores/detritivores and piscivores/carnivores in an oxbow billabong of the middle Parana–Paraguai River system (Ringuelet et al 1967) resulted in the trophic structure of these fish communities being vastly different from any communities examined in the present study.

Food chains

A tentative food chain (based on the examination of stomach contents) for the freshwater fishes of the Alligator Rivers Region is shown in figure 178. The return pathways of energy and nutrients have not been shown on this figure. The main pathways by which the energy is fixed from allochthonous material into the detrital chain, recycled (especially in the lower reaches of the catchment) by the primary producers, and eventually transferred to the fish and via some fish species to humans, is thus tentatively shown for the aquatic ecosystems in the Region.

Food chains are very complex, although some may be based on relatively few sources. In the rocky shore habitat of Lake Malawi (Africa), numerous species depend on only aufwuchs (organisms that are closely associated with or attached to a submerged surface but do not penetrate into it); however, in sandy inshore habitats of the same lake numerous species depend on plankton, terrestrial insects, aufwuchs on *Vallisneria*, *Vallisneria* itself, and bottom detritus and algae (Fryer 1959). Lowe-McConnell (1975) noted that, as in any food chain, there are rarely more than four or five links, as longer chains are expensive bioenergetically (80 to 90% of potential energy is lost at each successive stage).

The Alligator Rivers fish fauna appears to utilise a broad range of food resources; however, most do so indirectly (particularly via aquatic invertebrates). Only three species solely utilised the first trophic level (the escarpment terapontids and *L. alata*); however, many partially used it (the most important being *N. erebi* and the melanotaeniids). *Toxotes chatareus* mainly (and *H. fuliginosus* and *S. jardinii* partially) utilised allochthonous material in the form of terrestrial insects and (in the case of *H. fuliginosus*) plant material.

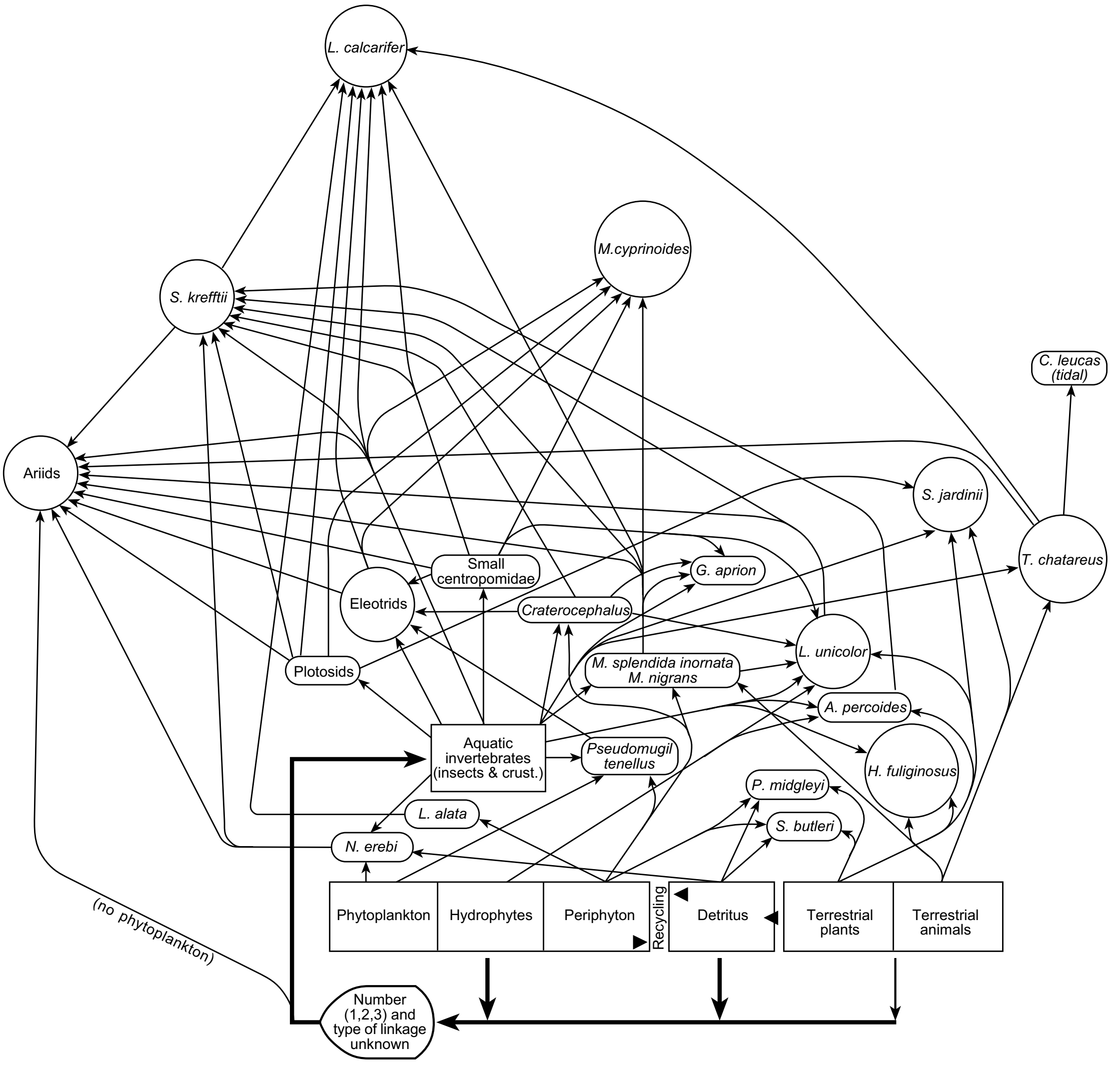

Figure 178 Pathways of energy and nutrient transfer between various trophic levels. Circles indicate that the species is eaten by humans in the tropics.

The main transfer of energy from the primary producers (the first trophic level, including microorganisms on the detritus) to the fish fauna thus appears to be via invertebrates — mainly aquatic insects and crustaceans in the benthic/substrate zone, and mainly microcrustaceans (zooplankton) in the pelagic open-water zone. The number of links in the chain between the primary producers and the invertebrates (primary and possibly secondary consumers) in tropical Australian freshwater ecosystems is unknown. A major source of food for macroinvertebrates may be, as Marchant (1980) suggested, organic detritus (macrophytes themselves do not seem to be a source) within the littoral zone of lowland billabongs in the Magela Creek system (the guts of ephemeroptera and trichoptera larvae were often full of detritus); much of this detritus appeared to be decomposing leaves of *Pandanus aquaticus*, *Barringtonia acutangula* and *Melaleuca*.

The aquatic invertebrates (secondary and possibly tertiary consumers) are eaten by a variety of smaller fish species: ambassids and atherinids ate mainly zooplankton, and plotosids and eleotrids ate mainly aquatic insects and larger crustaceans. The trophic relationships are very complex at these levels, as the opportunistic feeding habits of most species result in frequent overlaps in the food items; many of the fish species partially utilise lower trophic levels (eg the atherinids, melanotaeniids and the more downstream terapontids); some of the fish species also prey upon other smaller fish species (so are partly piscivorous; eg some eleotrids, *G. aprion*, *L. unicolor*); and the larger, predominantly piscivorous fish species may also prey upon larger invertebrates (notably *Macrobrachium*). In New Guinea, such freshwater prawns appear to fill the detritophagic niche that is occupied by fishes in other continents with true or primary division freshwater fish faunas (Haines 1979).

The smaller fish species are eaten by three primarily piscivorous fish species (and also fish-feeding waterbirds and reptiles): *L. calcarifer*, *M. cyprinoides* and *S. krefftii*. The first species is that most frequently eaten by humans in the Region. Fish species that utilise the lowest trophic levels appear to be of minor importance (with invertebrates possibly being of more secondary importance) to these primarily piscivorous species. The macrophagic omnivorous ariid catfishes (*A. leptaspis* and *A. graeffei*) ate large volumes of smaller fishes in the Wet and Late-wet seasons. By following various pathways of energy and nutrient transfers, the primarily piscivorous fish species can be classified as feeding from the third to the seventh trophic levels, though possibly most commonly at the fourth to fifth levels.

In the Purari system, ariid catfishes dominate in both biomass and number of species (Haines 1979). They occupied virtually all trophic niches available; Haines (1979) concluded that the lack of a ‘true’ (ie primary division) freshwater fish fauna allowed the adaptive radiation of this predominantly marine family to take place in estuaries and rivers. In the Alligator Rivers Region, the ariid catfishes also dominate the biomass in the lower reaches of the catchments and occupy all available trophic levels (fig 178). The same may apply to *L. unicolor* in the upper reaches of the catchments in the Region.

Plasticity of fish diets

Most fishes, according to Lowe-McConnell (1975), display great dietary plasticity: they eat different foods as they grow and change their biotope. Different foods become seasonally available or they actively select preferred foods; this is particularly true of riverine fishes in the more seasonal rivers. The diet of *Lates niloticus* in Lake Chad changed with size of fish, biotope, season and year (Hopson 1972); this species could not be assigned to a particular narrow trophic niche because of the great variation in its feeding habits.

The following sections summarise the main changes in the feeding habits of the Alligator Rivers fish fauna with seasons and habitats. The data collected in the present study will be analysed at a later time to describe changes in feeding habits in relation to size of fish, time of day and year.

Seasonal changes

Marchant (1980) recorded the greatest number of macroinvertebrate taxa, and the highest density of individuals, in the littoral zone of lowland billabongs and corridor billabongs of the Magela Creek system in the Late-wet–Early-dry seasons; both the number and density fell for the rest of the Dry season but rose rapidly in the Early-wet season.

Terrestrial insects appeared more frequently in the diets of most carnivorous and omnivorous fish species during the 1978–79 Early-wet season. These insects would have been washed into creekbeds and hence into billabongs as the Wet season flows covered previously dry land. *Arius leptaspis*, *M. splendida inornata*, *M. nigrans*, *H. fuliginosus* and *T. chatareus* ate large quantities of these insects in this season. *Toxotes chatareus* may have eaten washed-in insects, but, as a result of inundation by flood waters, this species could also move close to terrestrial vegetation and eat insects that were not in contact with the water. Anuran larvae were abundant in littoral waters during the Early-wet season and were eaten frequently by *O. lineolata* and occasionally by *L. calcarifer*.

The Early-wet to Mid-wet seasons saw a resurgence of microcrustaceans, including copepods and cladocerans (pers obs), and conchostracans and ostracods (recorded by Marchant 1980). The microcrustacean component of the diets of the plotosids and the ambassids, *N. erebi*, *A. percoides*, *L. unicolor*, *P. tenellus*, *M. mogurnda*, *H. compressa*, *G. giuris* and *G. aprion* increased markedly during the Early-wet season as the microcrustaceans became available in the billabongs. Also, ostracods were abundant in the diets of *C. marianae*, *C. stercusmuscarum* and *D. bandata* during the Wet season.

Aquatic insect larvae also showed peak abundances in the billabongs during the Wet season; the most notable was the emphemeropteran *Cloen* sp. A ('Baetidae' in stomach contents tables) recorded by Marchant (1980). *Cloen* sp. A became abundant in the billabongs in the Early-wet season, which was reflected by its abundance in the stomachs of the plotosids and of *G. aprion* and *L. unicolor*. Chironomid larvae were most abundant in the billabongs towards the end of the Wet season, and many fish species (notably the plotosids) ate them.

Macrobrachium spp. disappear during the Wet season; Marchant (1980) suggested they migrate (probably downstream). Likewise, *Macrobrachium* virtually disappeared in the Wet season from the diets of fish species (*G. aprion* and *O. lineolata*) that frequently ate them in the Dry season.

Hydrophytes grew extensively in the billabongs during the Wet season but virtually disappeared from most of them by the end of the Dry season. The amounts of hydrophytes in the stomachs of *A. leptaspis*, *L. unicolor* and *A. percoides* peaked in the Late-wet–Early-dry season.

More fish appeared in the stomachs of *L. calcarifer*, *M. cyprinoides*, *A. leptaspis*, *G aprion*, *L. unicolor* and *O. lineolata* during the Wet season, and particularly towards the Late-wet–Early-dry season. The numbers of fish species captured in the billabongs also peaked in the Late-wet–Early-dry season. Although *S. krefftii* also ate many fish in the Wet season, its fish-feeding peaked towards the Early-wet (and even the Late-dry) seasons.

More algae were eaten during the Mid-wet and Late-wet–Early-dry seasons by a number of fish species. *Liza alata*, *S. butleri* and *P. midgleyi* grazed more commonly on filamentous green algae, while *N. erebi*, *P. tenellus* and to a lesser extent *C. stercusmuscarum* more commonly ate phytoplankton.

Habitat differences

Marchant (1980) did not find marked differences in the macroinvertebrate taxa of lowland billabongs and corridor and floodplain billabongs in the Magela Creek system. However, as seasonal fluctuations in the numbers and density of taxa in corridor billabongs were not as marked as in other billabongs, he considered the corridor billabongs to be reservoirs for some species that are not found in the Dry season in other, shallower, billabongs. Marchant (pers comm) found marked differences between the macroinvertebrate communities of lowland sandy creekbed pools and escarpment mainchannel waterbodies, and also of those in the other billabongs he studied in greater detail.

Chironomid larvae (together with oligochaetes) were the dominant taxon Marchant (1980) found in the billabongs. Not surprisingly, they were also the dominant taxon in the stomachs of the smaller carnivorous and omnivorous fish species in these billabongs. Dipteran larvae were the main fauna captured on the muddy substrates in the deeper areas of billabongs examined by Marchant. Plotosid catfishes, which are thought to feed predominantly in these areas, had larger dipteran larvae components in their diets than other species (except perhaps *D. bandata*).

Primarily piscivorous fish species apparently ate fish mostly in the floodplain and corridor billabongs; however *M. cyprinoides* and *S. krefftii* frequently ate fish in lowland sandy creekbed channels. *Arius leptaspis*, *L. unicolor* and *G. aprion* appeared to eat fish mostly in lowland billabongs.

Species collected over sandy substrates (eg *C. marianae*, *C. stercusmuscarum*, *L. unicolor*, *A. percoides* and *N. erebi*) appeared to eat more microcrustaceans in the corridor and lowland zones than in the escarpment zone. Species such as ambassids, plotosids, *M. splendida inornata*, *G. aprion* and *L. unicolor* captured over muddy substrates in lowland, corridor and floodplain billabongs ate more microcrustaceans than those captured over sandy substrates. Similarly, some gobiid and eleotrid species (eg *G. giuris*, *M. mogurnda* and *O. lineolata*) ate more crustaceans in downstream habitats than in upstream areas. These differences presumably reflect the relative abundances of crustaceans in the upper reaches (usually sandy) and downstream reaches (usually muddy) of the creek system. The quantities of nutrients and detritus available in the waterbodies (affecting microcrustacean abundance) may be the cause of these apparently longitudinal effects.

More terrestrial insects were eaten by fishes (eg *T. chatareus*, *M. splendida inornata*, *L. unicolor* and *S. jardinii*) in escarpment habitats than by the same species in more downstream habitats. This may be because there is more overhanging terrestrial vegetation around most escarpment habitats than around downstream habitats (also aquatic insects appear to be less abundant [pers obs] in escarpment habitats).

Hydrophytes grew extensively in lowland backflow billabongs and floodplain billabongs during the Wet season. Some fish species (eg *A. leptaspis*, *A. percoides* and *L. unicolor*) ate more hydrophytes in those billabongs than they did in sites with sparse hydrophyte cover.

Phytoplankton was more common in the stomachs of small fish species (eg *C. stercusmuscarum*, *P. tenellus* and *M. splendida inornata*) found in lowland billabongs, corridor billabongs and floodplain billabongs than in other habitats. *Nematalosa erebi* fed more extensively on phytoplankton in the downstream muddy substrate habitats; over sandy substrates in escarpment mainchannel waterbodies this species fed extensively on diatomaceous periphyton. Filamentous green algae were found more frequently in the diets of *M. splendida inornata* captured in clearwater streams such as escarpment mainchannel waterbodies and lowland sandy creekbeds.

Main feeding seasons and habitats

The following resume is based on Lowe-McConnell's (1975) summary of the annual sequence of events in seasonal tropical rivers. The production and biomass of most fish foods (except zooplankton) increase rapidly when water levels rise with the onset of Wet season flow. When terrestrial Dry season lands are covered by Wet season floods, the water is greatly enriched in nutrient salts from the breakdown of organic matter; this leads to explosive growth of bacteria, algae and zooplankton (in most tropical seasonal rivers zooplankton develops best in still-water pools while the waters are subsiding after the Wet season), which in turn support a rich macroinvertebrate fauna. The high-water time is the main feeding, growing and fattening season for most tropical fish species. Small fish are susceptible to predation by piscivores when the flood waters subside and billabongs contract as the Dry season progresses. Fish populations are thus geared to this expansion and contraction of their environment and resources. Fishes in tropical seasonal rivers have been known to make long migrations between feeding and spawning areas. As the nutrients are depleted and the water level falls, the fish move to the main river channels. The first to move are the predators, which lurk around the mouths of the channels down which abundant young fish pass on their way back to the main stream.

Macroinvertebrate communities in the littoral zone of lowland billabongs in the Magela Creek catchment were found to have a similar pattern of resurgence in numbers and density of taxa during the Wet season (Marchant 1980). The resurgence peaked in the Early-wet season in lowland billabongs (to two-fold that recorded in corridor billabongs). The highest densities and numbers of taxa were recorded in the Late-wet–Early-dry season due to the concentrating effects of falling waters. The density of taxa decreased slightly in the Early- to Mid-wet season when the floodwaters peak. There was a secondary resurgence between the Mid-dry and Late-dry seasons in the corridor billabongs.

Zooplankton were abundant during the 1978–79 Early-wet season in the first floodwaters from lowland sandy creekbeds and lowland backflow billabongs (pers obs), which is in contrast to Lowe-McConnell's (1975) observation; however, zooplankton were also abundant towards the end of the Wet season.

The season of the greatest feeding activity (based on fullness indices) of fish species in the study area (table 166) was, as other research workers in tropical seasonal rivers have found, the Wet season.

The mean number of species most actively feeding per season per habitat increased dramatically into the Early-wet season from a low in the Late-dry season. By the Mid-wet season feeding activity had peaked (nearly five-fold that in the Late-dry season), and then began to decrease slightly by the Late-wet–Early-dry season. During the Mid-dry season feeding activity returned to a slightly higher level than in the previous Late-dry season.

The mean number of species feeding most actively per habitat per season was far greater in habitats downstream than upstream of the Ranger Uranium Project Area (RUPA).

Upstream of RUPA the highest feeding activity occurred in escarpment mainchannel waterbodies, followed by lowland billabongs and then lowland sandy creekbeds. In all of these habitats, the greatest feeding activity was in the Mid-wet season; however, some fish in escarpment mainchannel waterbodies feed extensively throughout the year.

Downstream of RUPA the highest feeding activity was recorded in lowland billabongs and then floodplain billabongs. Possibly floodplain habitats are more important feeding areas than lowland billabongs because of their higher volume of water during the Wet season; however, large numbers of fish from down- and upstream areas (many species from Magela Creek migrate upstream in response to flow)[255] enter the lowland billabongs during the Early-wet season, where they remain in large densities throughout the Wet.

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[255] This has been confirmed in subsequent studies (Bishop et al 1995) on fish movement dynamics in the Region.

Table 166 Habitats and seasons of greatest feeding activity of fish species in the study area (RUPA: Ranger Uranium Project Area)

	Sampling seasons					
Habitat	Late-dry	1978–79 Early-wet	Mid-wet	Late-wet–Early-dry	Mid-dry	Mean number of species per habitat
Escarpment mainchannel waterbody	*C. marianae* *C. stercusmuscarum*	*M. mogurnda* *M. nigrans*	*M. mogurnda* *M. nigrans* *C. marianae* *C. stercusmuscarum* *H. fuliginosus* *M. splendida inornata*	*M. splendida inornata* *A. percoides* *H. fuliginosus*	*M. splendida inornata* *A. percoides*	3.0
Lowland sandy creekbed (upstream of RUPA)	*C. marianae*	*M. mogurnda*	*M. mogurnda* *C. marianae* *M. splendida inornata*	*M. splendida inornata* *A. percoides*	*A. percoides*	1.6
Lowland backflow billabong (upstream of RUPA)	*A. agrammus*	*M. mogurnda* *G. aprion*	*M. mogurnda* *L. unicolor* *D. bandata* *G. aprion* *M. splendida inornata*	*M. splendida inornata* *L. unicolor*		2.0
Lowland sandy creekbed (downstream of RUPA)	*C. marianae*		*C. marianae* *S. krefftii* *M. splendida inornata* *M. cyprinoides*	*A. leptaspis* *S. krefftii* *M. splendida inornata* *A. percoides*	*M. splendida inornata*	2.0
Lowland backflow billabong (downstream of RUPA)	*A. macleayi* *A. agrammus*	*T. chatareus* *G. aprion* *O. lineolata* *A. agrammus* *N. hyrtlii* *P. rendahli* *L. unicolor* *S. krefftii*	*T. chatareus* *N. hyrtlii* *O. lineolata* *S. krefftii* *C. stercusmuscarum* *G. aprion* *D. bandata* *M. splendida inornata*	*T. chatareus* *N. hyrtlii* *O. lineolata* *S. krefftii* *M. splendida inornata* *L. unicolor* *M. cyprinoides* *A. leptaspis*	*O. lineolata* *M. splendida inornata* *A. percoides*	9.2

Table 166 continued

	Sampling seasons					
Habitat-type	Late-dry	1978–79 Early-wet	Mid-wet	Late-wet–Early-dry	Mid-dry	Mean number of species per habitat
Lowland backflow billabong (downstream of RUPA) *(cont'd)*			*M. cyprinoides* *L. unicolor* *A. leptaspis* *A. percoides* *P. rendahli*	*P. rendahli*		
Corridor billabong	*A. macleayi* *G. giuris* *N. ater*	*T. chatareus* *L. alata* *G. giuris* *A. macleayi* *S. butleri*	*T. chatareus* *M. splendida inornata* *S. krefftii* *S. butleri*	*T. chatareus* *P. tenellus* *N. ater* *S. krefftii* *M. splendida inornata*	*P. tenellus* *S. krefftii* *N. ater* *M. splendida inornata* *G. giuris*	4.2
Floodplain billabong		*L. alata* *G. aprion* *H. compressa* *O. lineolata* *A. agrammus* *P. rendahli*	*L. alata* *N. hyrtlii* *H. compressa* *S. krefftii* *O. lineolata* *M. splendida inornata* *C. stercusmuscarum* *G. aprion* *D. bandata* *T. chatareus* *M. cyprinoides* *A. leptaspis* *L. unicolor* *P. rendahli* *A. percoides*	*L. alata* *N. hyrtlii* *P. tenellus* *S. krefftii* *N. ater* *O. lineolata* *M. splendida inornata* *M. cyprinoides* *A. leptaspis* *P. rendahli*	*P. tenellus* *N. ater* *O. lineolata* *M. splendida inornata*	7.0
Mean number of species per season	1.25	2.86	5.88	4.5	1.75	

The lowest mean numbers of species feeding with greatest activity per habitat occurred in lowland sandy creekbeds. This habitat had the highest proportion of piscivores/carnivores with high fullness indices (mainly in the Mid-wet and Late-wet–Early-dry seasons) of any habitat in the catchment. The lowland sandy creekbeds may be used mainly as a migration channel for fish in the Wet season.[256]

Corridor billabongs were apparently much less important feeding areas than floodplain and lowland billabongs, but more important than sandy creekbed pools or any other habitat upstream of the Ranger Uranium Project Area. The number of species with highest mean fullness indices per season in this habitat varied only slightly throughout the year; the greatest activity occurred in the Late-wet–Early-dry and Mid-dry seasons. These observations correlate with those of Marchant (1980), who found the numbers and types of macroinvertebrate taxa (ie fish food) to vary less markedly in this habitat than in lowland billabongs; he also reported a small resurgence of macro-invertebrates in this habitat from the Mid-dry to Late-dry seasons. Corridor billabongs may be used by fish mainly as a migration channel in the Wet season,[256] and as a refuge in the Dry season.

4.5 Parasites and predators

Parasites and predators of the freshwater fishes of the Alligator Rivers Region exploit the highest trophic niches available in the aquatic systems.

Parasites

The parasites (identified by Dr L Cannon, Queensland Museum) found infecting freshwater fish species of the region, or known from other studies to infect them, are listed in table 167. The taxonomy of these parasites is not clear primarily because many of them have complex life cycles. Summaries (Cannon, pers comm) of the life cycles of some groups are given below:

Nematodes (roundworms)

Thynnascaris and **Contracaecum** Larvae are passed from copepods to small zooplankton-feeding fishes and then to more predatory fish. *Thynnascaris* matures in the predatory fish, while *Contracaecum* matures in fish-eating birds (Cannon 1977).

Philometra Adult females form cysts in fish; they extend the posterior of their body into the water and disgorge young, which may be eaten by zooplankton and thence by fish.

Eustrongylides The larvae of this genus are usually found in a variety of fishes. The adult host is a piscivorous bird. The first intermediate host is thought to be an arthropod, and probably a crustacean. One of the effects of this nematode on its fish hosts is that the females do not lay eggs when the cyst is in the ovary or vent (Pollard 1973b).

Physalopteroids The larvae may end up in water monitors, file snakes or frogs. Related subfamilies occur in amphibians and reptiles.

Trematodes (flukes)

Clinostomum The large and well-developed fluke lies in thin-walled cysts in fishes; when warmed, as in the mouth or throat of a water bird eating the fish, the cercaria quickly leaves the fish and attaches itself to the bird’s throat.

Cestodes (tapeworms)

The effects of cestodes on host fish may include a loss of body condition, an inhibition of gonad maturation and an inhibition, during the reproductive season, of movements to spawning areas.

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[256] This has been confirmed in subsequent studies (Bishop et al 1995) on fish movement dynamics in the Region.

Table 167 Parasites found or known to infect some freshwater fish species of the Region

Fish host	Parasite	Affected tissue
Nematalosa erebi	Trematode metacercariae	Intestine
Arius spp.	Ascaridoid nematodes	
	Contracaecum sp. (?)	Stomach
	Thynnascaris sp. (4th stage)	Stomach
	Spiruroid nematode (immature)	
	Philometra sp. (?)	Stomach wall
	Trematode metacercariae	
	Clinostomum sp. (?)	Adipose
	Ptychobothriid cestode (adult)	
	Senga sp. (?)	Body cavity
Plotosidae	Spiruroid nematode (immature)	
	Philometra sp. (?)	Gonad
	Physalopterids	Gonad and intestines
	Caryophyllidean cestode (monozoic)	
	Notolytocestus sp.	Stomach
Strongylura krefftii	Spiruroid nematodes (immature)	
	Philometra sp. (?)	Body wall and cavity
	Encysted nematodes	
	Eustrongylides sp.	Body wall
Melanotaenia splendida inornata and *M. nigrans*	Hirudinae (leech)	Body wall
	Spiruroid nematode (immature)	
	Philometra sp. (?)	
Craterocephalus stercusmuscarum	Porohalacarid arachnid	
	Astacopsiphagus parasiticus (?)	Stomach
Ambassis agrammus	Spiruroid nematode (immature)	Stomach
Lates calcarifer	*Philometra* on *Lates* in India (Rasheed 1965)	Body wall
	Trematode *Transversotreme laruei* (Velasquez 1961) may develop to progenetic metaceraria	
	Trypanorhynch cestodes (Coulter 1959)	
Amniataba percoides	Cestode pleuroceroid (immature)	
	Senga sp. (?)	Body cavity
	Brachiuran crustacean	
	Argulus sp.	Stomach
Leiopotherapon unicolor	Spiruroid nematode (immature)	
	Physalopterids	Body cavity
	Philometra sp. (?)	Body cavity
	Camallanid nematode (Merrick 1974)	
	Procamallanus sp.	Intestine and stomach
	Cestode cysticercoid (immature)	Gonad
	Cestode pleuroceroid (immature)	
	Senga sp. (?)	Body cavity
	Crytogonomia trematodes (Watson 1980)	Stomach
Oxyeleotris lineolata	Encysted nematodes	
	Eustrongylides sp.	Body wall

Notolytocestus Transmitted to a fish when it eats aquatic oligochaetes infected with the immature cestodes.

Senga (Ptychobothriidae) Previously only recorded from no closer to Australia than Sri Lanka. When the host is alive, this cestode lives healthily in the host's intestine; when the host dies it may crawl anywhere within or outside the host.

Hirudinae (leeches)
Previously recorded to be parasitic on fishes.

Porohalicaridae
Only one porohalicarid species has been previously recorded from Australia. It was found in the gillchamber of a freshwater crayfish in Queensland (Williams 1968).

Brachiura (fish lice)
Argulus Blood-sucking on fish and amphibians; usually outside or in gill chamber. There are only a few records of such brachiurans occurring on Australian freshwater fish (eg on *Mogurnda australis* and *Mugil* sp. from the Murray River [Riek 1946]). It may have been introduced through infested exotic aquarium fishes (Williams 1968). This genus was found in the present study in the stomach of *A. percoides*, a species that was observed cleaning other fish species by pecking over their bodies and particularly around their gill chambers.

The seasonal incidence of macroscopic parasite infestations in various fish species from the study area is shown in table 168.

Table 168 Seasonal percentage frequency of the incidence of macroscopic parasite infestations in various fish species examined during the study period

	Sampling period							Across all seasons	
Fish species	Late-dry 1978	Early-wet 1978–79	Mid-wet	Late-wet Early-dry 1979	Mid-dry	Late-dry	Early-wet 1979–80	N	Mean
C. leucas	20.0							13	7.6
M. cyprinoides				5.5				151	0.6
N. erebi	1.2							1493	0.2
A. leptaspis	54.9	6.7	9.2	5.3	6.5	16.0	50.0	633	18.3
A. dahli	18.1							22	14.8
N. ater	40.0	2.5	8.0	9.0	12.5	69.2	12.5	317	18.3
P. rendahli	1.4	20.5		7.6	5.6	24.1	10.0	426	7.3
S. krefftii	12.7	11.8	71.2	94.1	84.6	88.0	25.0	215	61.8
M. nigrans	9.5	10.8	41.9	7.4	7.1	11.9	15.0	206	15.0
M. splendida inornata	17.4	3.4	24.4	24.3	25.2	21.7	9.7	1109	20.1
C. stercusmuscarum	0.7	1.2	4.0			1.6		766	1.7
P. tenellus		12.9				3.0		189	2.7
A. agrammus	2.7	3.8	12.0	15.4	6.9	6.1	10.0	736	6.9
A. macleayi	2.2				4.4	4.5		519	2.3
D. bandata	0.9	6.2	2.4		1.7	3.3		477	2.0
L. calcarifer	22.2	88.8	20.0					35	54.3
A. percoides	32.0	10.5	1.1	5.4	5.3	20.4	28.6	484	13.4
L. unicolor	40.0	5.2	33.9	6.1	33.9	40.9	100.0	371	26.1
G. aprion	5.8	4.2	3.4		5.8	1.6		557	3.6
T. chatareus	7.1							236	0.4
G. giuris		7.1						117	1.7
M. mogurnda	22.4	33.3	17.0		14.2	77.7		163	23.3
O. lineolata	20.0		33.3	10.0	17.2	16.7	50.0	133	16.5

The mean overall incidence of such infestations was highest in *S. krefftii*, *L. calcarifer*, *L. unicolor*, *M. mogurnda*, *M. splendida inornata*, *A. leptaspis*, *N. ater* and *O. lineolata*. The incidence of infestation of *A. leptaspis*, *N. ater*, *P. rendahli*, *A. percoides*, *M. mogurnda* and *O. lineolata* (all primarily benthic species) appears to be lower in the Wet season, increasing towards the end of the Dry season. *Leiopotherapon unicolor* had a secondary peak of infestation in the Mid-wet season. *Melanotaenia nigrans*, *M. splendida inornata*, *S. krefftii* and *Ambassis* spp. (mid-water and surface-dwelling species) had an increasing incidence of parasite infestation during the Wet season and a decreasing incidence towards the end of the Dry season.

The incidence of macroscopic parasite infestations in fish species from various habitats in the study area are shown in table 169. The highest incidence in most fish species was in samples taken from lowland backflow billabongs and floodplain billabongs (this may be related to the occurrence of zooplankton populations, which may be the initial hosts for many parasites); however, *A. leptaspis*, *M. nigrans*, *L. unicolor* and *O. lineolata* were exceptions to this generalisation. The lowest incidence of infestations was generally in samples from lowland sandy creekbeds and corridor billabongs.

The incidence of parasitic infestations appears therefore to vary between species, seasons and habitats, and possibly with many other factors. Severe infestations can affect body condition, migration and the reproductive success of some species, just as adverse environmental conditions can.

Table 169 Percentage frequency of the incidence of macroscopic parasite infestations in fish species from various habitats examined in the study area

	Escarpment habitat		Lowlands habitat				
Fish species	Main channel	Perennial stream	Sandy creekbed	Backflow billabong	Corridor	Floodplain	N
M. cyprinoides						3.4	151
N. erebi				0.3			1493
A. leptaspis	20.0		12.5	9.1	19.1	13.3	633
N. ater	42.8			100.0	72.5	17.6	317
P. rendahli				14.8		4.1	426
S. krefftii	50.0		55.5	59.0	50.0	55.5	215
M. nigrans	83.3	25.5	18.5				206
M. splendida inornata	14.1		10.5	32.6	11.6	14.6	1109
C. stercusmuscarum	4.9		0.7	1.7	1.8	1.6	766
P. tenellus				3.7		1.0	189
A. agrammus			3.7	8.7	6.7	8.0	736
A. macleayi	3.1		16.6	3.3		2.2	519
D. bandata				3.0	1.1	3.5	477
L. calcarifer					88.8	20.0	35
A. percoides	12.5		8.3	15.7	36.6	41.4	484
L. unicolor	20.0	50.0	10.0	31.9		16.7	371
G. aprion				1.7	1.7	6.3	557
T. chatareus			3.3		20.0		236
G. giuris	12.5				2.3		117
M. mogurnda			6.7	38.9	14.2		163
O. lineolata			40.0	20.0	14.2	6.7	133

Predators

Predators of freshwater fishes in the Alligator Rivers Region include six species of reptiles (9 species if some estuarine species are included), at least 31 species of birds, and humans. The known feeding habits of these species are summarised below.

Birds

A list of piscivorous birds found on the Arnhem Land plains (after M. Ridpath, derived from published literature) is given in table 170. Little or nothing is known about which fish species they eat, and in which habitats and seasons.

Table 170 Fish-eating birds found on the Arnhem Land plains (after M Ridpath[3*])

Species	Common name
Tachybaptus novaehollandiae	Little grebe
Pelecanus conspicillatus	Australian pelican
Phalacrocorax sulcirostris	Little black cormorant
Phalacrocorax varius	Pied cormorant
Phalacrocorax melanoleucos	Little pied cormorant
Anhinga melanogaster	Darter
Ardea sumatrana	Great-billed heron
Ardea pacifica	White-necked heron
Egretta novaehollandiae	White-faced heron
Ardea picata	Pied heron
Butorides striatus	Mangrove heron
Ardea alba [1*]	Large egret
Egretta garzetta	Little egret
Egretta intermedia [2*]	Intermediate egret
Nycticorax caledonicus	Nankeen night heron
Ixobrychus flavicolis	Black bittern
Ephippiorhynchus asiaticus	Black-necked stork
Threskiornis molucca	Australian white ibis
Platalea regia	Royal spoonbill
Platalea flavipes	Yellow-billed spoonbill
Haliastur indus	Brahminy kite
Haliaeetus leucogaster	White-bellied sea eagle
Pandion haliaetus	Osprey
Larus novaehollandiae	Silver gull
Chlidonias hybridus	Whiskered tern
Sterna nilotica	Gull-billed tern
Sterna caspia	Caspian tern
Alcedo azurea	Azure kingfisher
Alcedo pusilla	Little kingfisher
Todiramphus sanctus	Sacred kingfisher
Todiramphus chloris	Mangrove kingfisher

1* The stomach of one specimen contained 1 ‘mullet’ (105 mm) and 4 other ‘fish’ (24–37 mm) (M Ridpath pers comm)

2* The stomach of one specimen contained 11 ‘perch’ (47 mm in length) (M Ridpath pers comm);

3* Nomenclature from Christidis and Boles (1994)

Large numbers of *Pelecanus conspicillatus* (Australian pelican) were observed feeding on plotosid catfishes in the Magela Creek catchment towards the end of the 1978 Dry season. Many of the birds suffered torn bills from the pectoral and dorsal spines of these fish. Over 40 *Haliastur sphenurus* (whistling kites) and *Haliaeetus leucogaster* (white-bellied sea eagles) were observed feeding on fish carcasses (mainly *L. alata*) on the banks of Leichhardt Billabong after a fishkill in the 1978–79 Early-wet season.

Reptiles

***Acrochordus javanicus* (file snake)** This species was occasionally observed attacking fish captured in gillnets. The published literature records that this species eats fish, but does not record which species it most commonly eats. Aboriginal people living in the study area frequently eat this species of snake.

***Acrochordus granulatus* (little file snake)** This is a coastal and estuarine species that is common around the coast of Kakadu. It relies heavily on fish in its diet.

***Cerberus rynchops* (Bockadam)** A water snake which is found in coastal and wetland areas usually associated with mangroves. This is a fish eating species.

***Fordonia leucobalia* (white-bellied mangrove snake)** Like the bockadam, this species is common amongst the mangroves of Kakadu. Eats largely crustaceans and also fish.

***Enhydris polylepis* (Macleay's water snake)** A freshwater species which in certain situations can be abundant. This snake feeds on frogs, tadpoles and fish.

***Chelodina rugosa* (northern snake-necked tortoise)** This species was readily lured to dead fish left in the water. Aboriginal people of the area also frequently eat this species.

***Varanus mertensi* (water monitor)** This species was frequently observed in escarpment perennial streams with mainly small fish. It was observed feeding on *Melanotaenia* spp. and *Craterocephalus* spp. at the upstream end of an escarpment mainchannel waterbody (Jim Jim Creek catchment) during the 1980 Mid-dry season (pers comm, Ian Morris, Australian National Parks and Wildlife Service).

***Crocodylus johnstoni* (Johnston's freshwater crocodile)** The feeding habits of this species in the upper escarpment reaches of the Mary River, Northern Territory, is being studied by G Webb (pers comm). His study, based on regurgitated stomach contents, has showed that fish predominate in the diet during the Wet season and particularly towards its end when the flow decreases and the fish populations concentrate as they move to Dry season refuge areas. Generally, this species ate small schooling species such as the melanotaeniids, ambassids and the smaller plotosids, as well as some terapontids and, on one occasion, an individual was seen capturing a specimen of *S. butleri.*

***Crocodylus porosus* (saltwater or estuarine crocodile)** The feeding habits of this species in freshwater environments are not known. Taylor (1979), who examined the stomach contents of sub-adult (less than 180 cm TL) specimens from coastal areas of Arnhem Land and Melville Island, found that they had eaten mainly crabs, *Macrobrachium* and terrestrial insects. The virtual absence of fish (*Pseudogobius* sp. was the only species eaten regularly in small quantities) is astonishing; however, larger specimens ate more vertebrates than did the smaller specimens. C. Limpus (pers comm) observed that larger specimens of this species in freshwater rivers of north-eastern Queensland eat fish of all sizes.[257]

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[257] Griffin (1994) undertook radio tracking studies on *L. calcarifer* in the Mary River in 1991/92. The loss of one tagged individual was explained by predation from *C. porosus*.

In the St Lucia estuary in South Africa, *Crocodylus niloticus* is oriented at certain times of the year to intercept migrating populations of sea mullet (*Mugil cephalus*) as they enter narrows in the estuary (Whitfield and Blaber 1979).

Humans [258]

The fish species eaten by Aboriginal and non-Aboriginal people in the Alligator Rivers Region and adjacent catchments are listed in table 171.

Thirteen fish species are eaten: twelve by Aboriginal people and eight by non-Aboriginal people. *Lates calcarifer* is the most important fish species eaten by humans in the region. Amateur anglers target this species in all rivers of the region except for the West Alligator, with most effort being concentrated in the South and East Alligator Rivers.[259] Amateur anglers regularly fish for *Lates calcarifer* downstream of the Ranger uranium project area in the Magela Creek system and downstream from corridor billabongs in the Nourlangie Creek system.

Table 171 Fish species eaten by Aboriginal and non-Aboriginal people in the Alligator Rivers Region and adjacent catchments

	Aboriginal people			Non-Aboriginal people	
Fish species	Magela Creek near Jabiru *A	Other areas in Region*B	Featured in regional art	Amateur	Commercial
Nematalosa erebi	+	–	–	–	–
Scleropages jardinii	–	+	–	–	–
Arius leptaspis	+	+	+	+	–
Plotosidae spp.	+	+	+	–	–
Lates calcarifer	–	+ *1	+	+	+
Leiopotherapon unicolor	+	+ *2 *3	–	–	–
Hephaestus fuliginosus	–	+	–	+	–
Toxotes chatareus	–	+	–	–	–
Liza alata	–	–	–	+	–
Oxyeleotris lineolata	–	+ *4	–	+	–
Strongylura krefftii	–	+	+	+	–
Polynemus sheridani (estuarine)	–	+ *5	–	–	+
Eleutheronema tetradactylum (estuarine)	–	+ *5	–	–	+

+ eaten; – not eaten

*A Local Aboriginal family (Peter), traditional owners

*B Senior Murrumbur elder (pers comm), traditional owner and cultural advisor to Parks Australia

*1 Local Aboriginal people at Cannon Hill removed and ate most of this species from Precarious Billabong as it was drying out in the 1979 Dry season.

*2 Harris (1975) describes local Aborigines capturing this species from escarpment streams in Arnhem Land. Dams are made out of woven *Pandanus* and sheets of *Melaleuca* bark. The fish are coralled behind the dams and then funnelled into narrow channels from which they are captured.

*3, *4 Anbarra people capture these species (in Gidjngali language: An-gayapadja [or Gurrayurraba] and Bilerra [or Wadakurdorrk], respectively) from the freshwater swamp, Djibadjirra, between the Liverpool and Blyth Rivers in Arnhem Land.

*5 Piers Barrow (pers com), project officer, Natural Resource Management, Kakadu National Park

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[258] Other piscivorous mammals include the bottle-nosed and Irrawaddy dolphins which are found around the coast and in the estuaries of the Alligator River Region. Information from Greg Miles, Public Relations Officer, Kakadu National Park.

[259] Surveys of the *L. calcarifer* and *S. jardinii* populations of Yellow Waters Billabong on the South Alligator River (Griffin 1993, 1995, 1997 & 1998) indicate high population densities for these species.

The other species shown in table 170 to be eaten by non-Aboriginal people are rarely targeted by amateur anglers. They are caught occasionally and some of those caught are eaten. Other species such as *Scleropages jardinii* and the catfish are rarely, if ever, eaten by non-Aboriginal people. If caught, they are generally released.

Commercial fishing is prohibited throughout Kakadu National Park. Large areas are also closed to recreational fishing, including the whole catchment of the West Alligator River and all the country to the south and east of the Kakadu Highway. This area includes all of the sandstone country, containing the permanent pools that are the dry season refugia for many fish species. The area also contains the majority of the habitat of species such as *Hephaestus fuliginosus* — an excellent sport and food fish keenly sought by some amateur fishers in the top end of the Northern Territory. Consequently the pressure on this species from recreational angling is currently negligible due to the fishing closures.

4.6 Movements

Many tropical freshwater fishes migrate upriver as the water level rises, and then move out onto the flooded plain when conditions permit (Lowe-McConnell 1975). Their reactions to water flow are thus complex and, as yet, have been little investigated. Migration, particularly in freshwater fishes, is often regarded as an adaptive phenomenon for increasing growth, survival and abundance, all of which may increase production. Like many other seemingly obvious generalisations in ecology, there is by no means a mass of well-documented and conclusive evidence in its support.

Fortuitously, during the 1978 Late-dry season, an unusual event enabled us to note which small fish species are the first to move upstream out of lowland billabongs when flow begins. Groundwater was pumped (at 0.1 m^3 s^{-1}) and allowed to flow (via site IF) into a close-by lowland backflow billabong (II) adjacent to Magela Creek and downstream of the Ranger Uranium Project Area. Six fish species — *M. splendida inornata*, *Craterocephalus stercusmuscarum*, *A. agrammus*, *D. bandata*, *Glossamia aprion* and *M. mogurnda* — were found in site II before flow started (table 171); as flow entered the billabong, large numbers of *A. agrammus*, *M. splendida inornata* and somewhat fewer *D. bandata* moved upstream through the newly created riffle area towards the groundwater pump. What was the stimulus? Whitehead (1979) described changes in hydrological conditions of the Nzoia River, Kenya, during floods; he found that no single factor could be isolated as the stimulus for fish migration, since all these changes are almost simultaneous. Van Someren (1963), however, suggested that the initial movement of fish is stimulated by a complex set of factors, including water height and velocity, but that the fish themselves must be in a physiologically receptive state before the changing external conditions will affect them.

The most dramatic effect of fish movements in the present study was the recolonisation of lowland sandy creekbeds and lowland backflow billabongs after the Dry season when the Wet season flow began. The biomass of catches increased rapidly in lowland backflow billabongs when these became connected to the inundated lowland sandy creekbeds (these habitats are important migration routes), and thence to corridor and floodplain billabongs. During the 1978–79 Early-wet season in Gulungul Billabong (table 172), typical Late-dry season fish species (eg *P. rendahli*, *A. agrammus*, *G. aprion*, *M. mogurnda* and *O. lineolata*) were replaced (or they spread out as the volume of water in the lagoon increased) by larger-bodied fish species (eg *N. erebi*, *A. leptaspis* and *T. chatareus*, some of which were in breeding condition) and smaller fish species (eg *C. stercusmuscarum*, *P. tenellus*, *A. macleayi* and *L. unicolor*). Presumably, most of these fish moved upstream from corridor and floodplain billabongs when these were connected to the main creek channel; however, this speculation requires verification. Upstream movement of fish species is also detectable in escarpment perennial streams during the Wet season.

Table 172 Abundance and total weight of fish caught in samples from habitats where water had just started to flow

	Site code and date						
	II	IF	GL				MJ
	18 Sept 1978		5 Dec 1978		18 Dec 1978		13 Dec 1979
Fish species	Abund. (*n*)	Abund. (*n*)	Abund. (*n*)	Wt (g)	Abund. (*n*)	Wt (g)	Abund. (*n*)
N. erebi	0	0	0	0	1	270.0	0
A. leptaspis	0	0	0	0	16	12465.0	0
P. rendahli	0	0	15	220.6	0	0	0
M. nigrans	0	0	0	0	0	0	1
M. splendida inornata	43	71	0	0	0	0	145
C. marianae	0	0	0	0	0	0	2
C. stercus-muscarum	2	5	0	0	15	11.9	0
P. tenellus	0	3	0	0	2	0.5	0
A. agrammus	43	371	79	90.1	0	0	0
A. macleayi	0	0	0	0	17	22.2	1
D. bandata	58	12	0	0	0	0	0
A. percoides	0	0	0	0	0	0	62
L. unicolor	0	0	0	0	3	1.4	3
G. aprion	1	0	2	47.2	0	0	0
T. chatareus	0	0	0	0	9	1710.0	0
M. mogurnda	11	0	2	4.5	0	0	0
O. lineolata	0	0	1	13.1	0	0	0
Total	**158**	**462**	**102**	**375.5**	**63**	**14481.0**	**212**
No of species	**6**	**5**	**5**		**7**		**6**

Some fish appear to move downstream from Dry season refuge areas in escarpment habitats (once again, this requires verification). During the 1979–80 Early-wet season, several species (mainly *M. splendida inornata* and *A. percoides*, and some *L. unicolor*, *C. marianae* and *M. nigrans*) were present in the first-flowing water that reached as far downstream as MJ (table 171, also see map in appendix 8) near the Ranger Uranium Project Area. Also, throughout the Wet season typical escarpment-dwelling fish species (eg *H. fuliginosus*, *P. midgleyi*, *S. butleri* and *M. nigrans*) were found in lowland sandy creekbed habitats.

Recolonisation of temporary streams by fish and invertebrates in Illinois, USA, was studied by Larimore et al (1959). Larimore found that most of the fish species withstood the extreme drought conditions in at least a few parts of the stream. Re-establishment of the populations began as stream flow resumed. Fish moved upstream, with the result that within two weeks, 21 of the 29 regularly occurring species moved into most of the stream course — a rate similar to that observed in the present study.

As a result of the great diversity of freshwater fishes in tropical regions (Fryer & Illes 1972), there are special forms of feeding migrations, the most common of which is associated with the seasonal inundation of river floodplains (Welcomme 1974, 1975): the adults, and the young which have hatched out in areas along flooded rivers, migrate laterally into rich feeding habitats (Roberts 1972; Petr 1974, 1975). This strategy, which is followed by many tropical freshwater fishes, is to rapidly exploit a temporarily rich food source brought about by flooding and washing in of terrestrial resources and the upsurge of nutrients. The young of some tropical fishes remain to feed at or near where they were spawned for some time before migrating to their main feeding area.

The spawning migrations of most tropical freshwater fishes are within rivers and their floodplains or from lakes into rivers. These migrations seem to be aimed at enabling the adults and young to exploit the rich resources that result from flooding (Northcote 1978). This type of migratory activity was also apparent in our study area: many large-bodied fish species in breeding condition appeared in lowland billabongs during the Wet season after these were connected to corridor billabongs via inundated lowland sandy creekbeds. The occurrence of high proportions of sexually maturing (or just matured) fish in the sandy creekbed habitats and corridor billabongs (section 4.3) supports these observations. Many small juveniles (eg those of *T. chatareus*) were observed to be washed downstream in creekbed channels during the Wet season, which would explain why many juveniles of species normally found in the lowlands in the Dry season (eg *T. chatareus*, *L. unicolor*, *A. percoides*) were found in floodplain habitats in the Wet season.

The migrations of many tropical fishes back to lakes or to mainstream rivers to avoid being trapped in lateral marshes and side channels (Santos 1973; Lowe-McConnell 1975) minimises mortalities from predation and from desiccation of aquatic habitats during the Dry season. The migratory activity of fish in the present study appeared to be at a high level in lowland sandy creekbed channels during the Late-wet–Early-dry season when water levels were receding.[260]

Migrations of fish from marine feeding areas to freshwater spawning habitats do not seem to be nearly as common in tropical waters as in temperate and arctic regions (Northcote 1978). In the present study no anadromous species were captured, but three apparently catadromous species (*L. calcarifer*,[261] *M. cyprinoides* and probably *L. alata*) were found. They appeared to

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[260] Dramatic upstream movements of a considerable range of fish species were subsequently documented during studies on fish movement dynamics reported by Bishop et al (1995). The movements were considered to be a part of refuge-seeking migrations. Bishop (1987) utilised these migrations in Magela Creek to demonstrate avoidance responses of the fish to releases of waste waters from the Ranger Uranium Mine.

[261] There has subsequently been a number of investigations into the movements of *L. calcarifer*. From radiotracking work in the Mary River, Griffin (1994) concluded that *L. calcarifer* was a roving predator rather than a 'lie in wait' predator. In freshwater reaches the overall mean distance travelled per day was 3.9 km (SE=1.3). Greater speeds (up to 42 km/day or 1.8 km/hr) were observed over time periods of a few hours. Griffin (1987) undertook tagging work in the Daly River between 1980 and 1984. Downstream movement was apparent in the Dry season months of July and August. Russell and Garrett (1988) undertook tagging work on juvenile barramundi in tidal creeks of two NE Queensland coastal bays. Within their first year most juveniles were recaptured at the original tagging location in the creeks. After this they moved out to the main estuary and dispersed into adjacent streams and coastal habitats. Distances of 7.6 to 23 km were involved. Moore and Reynolds (1982) studied the migration patterns of barramundi in PNG. Adult *L. calcarifer* released in inland waters migrated to coastal spawning grounds and then returned to the inland areas. Distances up to 622 km were involved. Juveniles left coastal nursery swamps when about 6 months old and became distributed throughout coastal and estuarine regions. A general easterly movement from the Gulf of Papua was apparent. During their second and third year they moved into inland waters.

migrate in the Late-wet–Early-dry season in western drainage channels of the Magela Creek floodplain. A study of upstream fish movements through a central Queensland coastal fishway (within the tidal influence of the Fitzroy River) (Kowarsky & Ross 1981) suggests that more species in the Alligator Rivers Region may be diadromous. The following species used the fishway: mullet (several species including *M. cephalus*), *N. erebi*, *H. compressa*,[262] *Arius* sp., *Melanotaenia* sp., *M. cyprinoides*, *Neosilurus* sp., *A. agrammus*, *S. krefftii*, *A. percoides*, *C. stercusmuscarum* and *G. aprion*.[263] The diversity of fish species was greatest in the summer, as was the peak use by mullet and *N. erebi*, which were generally the most abundant species using the fishladder. *Nematalosa erebi* is frequently observed in freshwater streams after rises in flow, aggregating in large shoals at the base of obstructions such as weirs and rapids (Grant 1978). This behaviour was observed in the present study in Magela Creek just downstream of culverts beneath the Oenpelli Road during the 1978–79 Early-wet season.

The diversity of fish communities decreased with increasing elevation of regular sites (Bishop et al 1990, section 4.2, pp 75–8). The most obvious cause of this reduction in diversity was species dropping out during upstream movements because they could not surmount obstacles in escarpment cascades during the Wet season. The successful species were *M. mogurnda*, *L. unicolor*, *H. fuliginosus* and *M. nigrans*, all of which are frequently found in the upper reaches of escarpment perennial streams. *Syncomistes butleri* and *P. midgleyi* must have comparable migratory abilities, as they are commonly found in escarpment terminal mainchannel waterbodies. Plotosid catfishes are often found upstream in large migrating schools during the Late-wet–Early-dry season in some escarpment habitats.

Migration may be one of the most important survival strategies for fishes in the study area. It is probably an adaptation of major significance in the production of freshwater fish, especially in environments subject to sharp fluctuations or to marked spatial patchiness in habitat fertility. Studies are needed to determine more precisely the degree to which phases of migration regulate the species and size composition of fish communities and the extent to which they would affect the value of ecological monitoring surveys of freshwater fishes in the Region. Only when fishes are in Dry season refuges in pools cut off from rivers and creeks is the composition of the communities relatively stable, at least until predation becomes significant.

Tagging studies of selected fish species (eg *L. unicolor*, *M. splendida inornata* and *N. ater*) from Magela Creek and other sites on its tributaries adjacent to the Ranger Uranium Project Area are required to define the degree of independence of upstream sites from populations downstream of the project area.

4.7 Mortality

The mortality of freshwater fish appears to be greatest at the end of the tropical Wet season when water levels are receding; many fishes are then stranded in drying pools and predation is at a maximum (Lowe-McConnell 1975). Mortality, caused primarily by deoxygenation, desiccation and reduced cover, is also very high in Dry-season billabongs.

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262 Massive upstream migrations of *H. compressa* have subsequently been reported (Bishop 1993) at the estuary-freshwater interface of the Bellinger River, coastal NSW.

263 Further studies (Stuart 1997) on a modified version of the same fishway additionally recorded the following species: *A. graeffei*, *M. cyprinoides*, *L. calcarifer*, *C. stercusmuscarum*, *P. rendahli*, *N. hyrtlii*, *L. unicolor* and *O. lineolata*. The bulk of the biomass (70%) was made up of *A. graeffei* of which 81% were immature.

The length-frequency distributions of various fish species in the present study (see biological sections) suggested that for only a few species was adult mortality a seasonal phenomenon. Adults of *A. percoides*, *D. bandata*, *M. nigrans* and *M. splendida inornata* decreased in abundance in samples between the 1979 Late-dry and the 1978–79 Mid-wet seasons; adults of *C. stercusmuscarum* disappeared after the Late-wet–Early-dry season. However, as these effects may result from adult migration to unsampled habitats, further studies are required.

Fish kills at the beginning of the Wet season are common in the tropical coastlands of the Northern Territory. Bishop (1980) related fish kills in Magela Creek at the beginning of the 1978–79 tropical Wet season to physical and chemical changes (mainly low dissolved-oxygen levels); this is just one possible mechanism for natural fish mortality in tropical freshwaters of northern Australia.[264] Bishop (1980) stressed that differentiation between human-induced and natural mortalities is very difficult owing to our scant knowledge of the factors and mechanisms that affect fish survival in such waters.[265]

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[264] Discussing fish kills in the Alligator Rivers Region, Bishop and Forbes (1991) argued that a complex of factors is surely responsible for kills. Which factor is dominant probably depends on annual climatic phenomena such as the severity of the Dry season and the amount of rainfall and hence how rapidly the first flows cover the floodplains in the Early-wet season. It is easy to understand why most fish kills occur in the Early-wet season, as this is when fish are most stressed from deteriorating environmental conditions over the Dry season, and when they are most exposed to terrestrial toxicants that reach waterbodies in concentrated form with first flows. The ability of a species to avoid toxic waters in the first flow period is likely to be the most positive strategy to ensure survival and thus breeding opportunity later in the season.

[265] An example of the complexities involved arises from Bishop's (1994) investigation of a large fishkill in the Middle Fly River of Papua New Guinea in October 1994. Hypoxia was considered to be the primary fishkill mechanism. The major predisposing factors for the kill appeared to be a rapid drop of water levels and a large volume of deoxygenated water present on the floodplain. Conditions leading to the development of the large volume of deoxygenated water were considered to be quite complex. It was considered possible that the deoxygenation could have been induced by the large-scale release of sediments from the Ok Tedi mine further upstream. The sediments could have altered the structure of the river's levees thus altering their hydrology, particularly the rate at which they drain. Greatly enhanced densities of aquatic plants on the floodplains could also have resulted from the sediment inputs. This too would affect the levee formation as well as creating a large additional biomass which would decay and subsequently adversely affect the dissolved oxygen climate of floodplain waters.

5 Conclusions/Synthesis

As identified in Section 1.2, the essential objective of the study was to identify the locations and timing of activities critical in the life cycles of the fish species considered. By cross-relating such knowledge to information on the locations and timing of potential mining-induced physical and chemical (abiotic) impacts, the life-cycle components of those species most at risk can be identified, an important task in impact risk assessment. Clearly, knowledge of the species which might potentially be exposed to abiotic impacts is fundamentally important in the process of understanding and ameliorating resultant biological impacts.[266] Such knowledge is also vitally important when designing and interpreting monitoring investigations which aim to assess the effectiveness of management actions.[267] Such investigations are a fundamental component of any adaptive stream management strategy.[268]

Primary biological/ecological information was obtained and analysed for each of the 37 freshwater fish taxa found in the Alligator Rivers Region in relation to the following generic species-account structure: size composition, environmental associations, reproduction and feeding habits. Each of these components revealed complementary information on the location and timing of activities critical in the life cycles of the fish taxa considered.

5.1 Size composition

Location

Smaller juveniles of the largest number fish species were found in lowland backflow billabongs and floodplain billabongs. These two habitats appear to be particularly important as nursery areas. ‘Reservoirs’ of large adults of many species were found in floodplain, corridor, escarpment mainchannel and (larger/deeper) lowland backflow billabongs.

Timing

Three types of juvenile recruitment were apparent: Type A: recruitment usually limited to a single season; Type B: continuous recruitment with a few peaks occurring during the year; Type C: continuous recruitment with no apparent peaks (applicable to only one species). Type A recruitment was mainly apparent in the larger fish species. Juveniles of most of these species recruited to their adult populations during the Early-wet and Mid-wet seasons. Type B recruitment was mainly apparent in the smaller fish species. For most of these species the primary recruitment occurred in the Mid-wet season. The secondary recruitment occurred in the Mid-dry season for most, but across all such species it extended from the Late-wet–Early-dry season to the Late-dry season.

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[266] Smith and Pollard (1996) indicated that there are two conceptually distinct elements in fisheries management – the management of the resource itself, and the management of the users (ie the impactors). They further state that resource management activities include research on and regulation of the resource, and fundamentally require a knowledge of the biology and ecology of the fish species involved.

[267] Apart from ensuring the sensitivity of monitoring, through the identification of the potentially most-vulnerable fauna and their lifecycle components, Underwood (1997) indicated that biological information has key importance in developing well-focused hypotheses and selecting the most appropriate statistical procedures (to analyse monitoring data), given that there will be shortcomings if their specific requirements and assumptions are not met.

[268] Sensu Walters (1986)

An examination of variations in body condition indicated that most species obtained their best condition from the Mid-wet to the Mid-dry season, with a peak in the Late-wet–Early-dry season. Seasonal trends in the number of species with poorest body condition were complex, being complicated by the presence of recently-spent individuals in the Early-wet season.

5.2 Environmental associations

Useful information indicative of the environmental associations of 32 fish species was obtained. Three main groups of species were distinguished by characteristic combinations of associated environmental factors: species that typically inhabited the escarpment area (although making incursions to the lowlands in the Wet season), species that typically inhabited the lower reaches of the catchment, and those widely distributed species found in both of these areas. Escarpment associated species were usually associated with low temperature, high DO concentration, low conductivity, low turbidity and coarse substrate. These species therefore displayed a generally ‘clean water’ association. Accordingly, when they make incursions to the lowlands in the Wet season, or are trapped therein throughout the Dry season, they are potentially the most vulnerable component of the fish fauna to mining induced abiotic impacts. They are therefore likely to be the most useful candidates for monitoring and biological testing.[269]

5.3 Reproduction

Six breeding strategies were exhibited by the fishes studied:

- live-bearing: only the river whaler shark
- buccal incubating: the saratoga, ariid catfishes and mouth almighty
- nest building/guarding (demersal and/or adhesive eggs): the plotosid catfishes, some terapontids, gobiids and eleotrids
- aquatic vegetation attachment (adhesive eggs): melanotaeniids, ambassids, blue-eyes, longtom
- scattering over the substrate (demersal eggs): atherinids and a terapontid
- deposited in the water column (pelagic eggs): tarpon and barramundi in the estuarine or coastal waters, bony bream and archer fish in freshwaters

Species which lay demersal eggs are most prone to impacts associated with siltation, and/or the release of toxic materials from sediments when anoxic conditions develop at depth within waterbodies. Accordingly, such species are therefore likely to be the most useful candidates for monitoring and biological testing.

Location

The most important spawning habitat was the lowland backflow billabongs where 19 species showed evidence of spawning. Four species apparently breed at no other location and are therefore totally dependent on these billabongs. The escarpment area and lowland sandy creekbed habitats were the usual spawning sites for at least 14 species.

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[269] This view was also expressed by Bishop (1987) who examined an extended time series of fish-community data from the Alligator Rivers Region. Bishop also examined the movements of fish within Magela Creek in relation to the effects of the release of mine waste waters. Escarpment-associated species were found to avoid a plume of waste water in the creek, while other species were attracted to the plume.

Timing

Most fish species (25) bred around the onset of the Wet season. This is the time when initial flooding hugely increases the area and diversity of aquatic habitats available as well as initiating major increases in plankton and other foods. No species appeared to breed exclusively during the Dry season, although at least three species had breeding seasons extending from the Mid-dry to the Early-wet seasons. Ten species appeared to have an extended breeding season or to breed continuously throughout the year. These species all showed a peak in reproductive development during the Early-wet season.

5.4 Feeding habits

Nine feeding guilds were identified:

- herbivores/detritivores: two terapontids and Ord River mullet
- microphagic omnivores: bony bream and the blue-eye
- meiophagic omnivores: melanotaeniids and two terapontids
- macrophagic omnivores: ariid catfishes and one terapontid
- microphagic carnivores: ambassids, atherinids and one eleotrid
- meiophagic benthic carnivores: plotosid catfishes, gobiids and one eleotrid
- meiophagic insectivore: archerfish
- macrophagic carnivore/insectivore: saratoga
- macrophagic carnivore/piscivore (peak carnivores): river whaler shark, tarpon, longtom, barramundi and sleepy cod

If biomagnification effects are the focus of future investigations then the peak carnivores are the most suitable candidates for monitoring. Similarly, if exposure to disturbed contaminated sediments is a key factor, then the herbivore/detritivores, omnivores and/or benthic carnivores are the most suitable candidates.

Location

Downstream of the Ranger Uranium Mine (RUM) the highest feeding activity was recorded in lowland backflow billabongs followed by floodplain billabongs. Upstream of RUM the highest feeding activity was recorded in escarpment mainchannel waterbodies followed by lowland billabongs.

Timing

The season of greatest feeding activity was, as other researchers in tropical seasonal rivers have found, the Wet season. Feeding activity increased most dramatically between the Late-dry season and the Early-wet season. By the Mid-wet season feeding activity had peaked, and then decreased slightly by the Late-wet–Early-dry season.

5.5 Importance of lowland backflow billabongs

A finding from the study that stands out is the crucial importance of lowland backflow billabongs to the ecology of the majority of the freshwater fish fauna. They function as key breeding sites during the Wet season,[270] particularly the Early-wet season, for a large range of fish species. Accordingly, they function as important nursery areas through this season. Feeding activity of juveniles and adults is also focused on these billabongs and this continues into the Late-wet–Early-dry season.[271]

5.6 Wider application of the study findings

The detailed information presented in this report constitutes a major contribution to the autecological knowledge of the freshwater fish fauna of the Alligator Rivers Region. Because many of the species have a wide distribution, the information will be valuable to researchers across Australia,[272] especially those working in the Timor Sea, Gulf of Carpentaria and north-east coast drainage divisions (map 3; sensu Lake 1978). It will also be of considerable value in Papua New Guinea and Irian Jaya, as a high proportion of the tropical fish fauna of Australia are also found in these countries. Insights gained into the processes 'driving' the ecology of this tropical riverine fish fauna also have world-wide application.

Importantly, the information arising from the present study will have considerable application when assessing the nature and magnitude of impacts arising from a range of freshwater-associated developments, and particularly those in the mining arena. The risk of errors in such assessments is minimised if i) the necessary background biological/ecological information is available, and ii) if serious efforts are made to source and effectively utilise best-available information.[273]

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[270] The importance of the Wet season flooding cycle can not be over emphasised as highlighted by Bishop et al (1986, 1990) and Bishop and Forbes (1991). Herbert et al (1995) stated that the Wet season flooding cycle was of vital importance to the freshwater fish fauna at Cape York Peninsula – floods rejuvenate habitats, allow colonisation, breeding and migrations of many species.

[271] The high value of lowland backflow billabong habitats to the Alligator Rivers Region's freshwater fish fauna was also emphasised by Bishop and Forbes (1991). In studying the fish movement dynamics within Magela Creek during the Wet season, Bishop et al (1995) concluded that lowland billabongs play a significant role in providing recruits to upstream dry-season refuges – a key ecological process in this seasonally flowing stream. Unfortunately, in 1996, a large lowland billabong system well connected to the Magela Creek mainchannel (the Djalkmara/Indium complex, see DA and IM in Appendix 8) was isolated from the creek system by a bund wall in order that the Ranger Uranium Mine could exploit their Ore Body No 3. The crucial importance of billabong/lagoon systems to the freshwater fish fauna of Cape York Peninsula was emphasised by Herbert et al (1995).

[272] The value of the autecological information is evidenced by its citation (as a draft manuscript) on 57 occasions within Merrick and Schmida's book *Australian freshwater fishes: biology and management*, published in 1984. The Alligator Rivers Region (ARR) studies represent the single largest contribution to autecological information on Australian freshwater fishes ever made. From diffuse sources, there have been gradual, piecemeal additions to knowledge relevant to ARR fish since the time the work was undertaken. The ARR studies were undertaken at a time when there was a research 'culture' favouring investigations aiming to understand key aspects of the biology and ecology of aquatic biota. This culture went 'out of fashion' in the early 1980s, and as a result, more recent contributions to the knowledge of the basic biology/ecology of aquatic biota are quite rare. The current research culture favours investigations into biological patterns and processes using sophisticated experimental designs and associated statistical analyses. Ironically, to be sensitive and well-focused, such investigations require a spectrum of basic biological and ecological information in order to select target biota, develop meaningful hypotheses and designs, select appropriate statistical procedures, and finally, make ecological interpretations of the findings. Given the rarity of such detailed biological and ecological information, the present research culture appears to have 'put the cart before the horse'. Fortunately, this is now not the case for present-culture investigations into the freshwater fish fauna of the Alligator Rivers Region.

[273] A prime example of a situation where such errors can have drastic consequences arises from the Ok Tedi Mining operation in the Fly River catchment of Papua New Guinea, where hundreds of kilometres of the river system has been destroyed by the release of tailings and waste rock. In a review of available biological and ecological information on fauna from the river system, Smith (1998) stated that 'overall the current state of knowledge of the population, community and ecosystem biology of the Fly River system is poor, and this will severely limit the potential for making predictions of the responses of the species assemblages to the Fly River stressors'.