The trophic ecology of the freshwater fishes of an Australian rainforest river

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Abstract

In tropical rivers, seasonal cycles of flooding and drying have a major influence on the dynamics of biotic communities. Several global paradigms have been developed which attempt to account for the relationships between river flow, primary productivity, instream habitats, invertebrate and fish communities, fish feeding and food web structure. However, information from Australia is limited, particularly for rivers in the Wet Tropics region of north Queensland, which feature unique hydrogeomorphological characteristics and diverse freshwater fish assemblages. This thesis tests the applicability of global paradigms of riverine ecology to the Mulgrave River, a typical Wet Tropics system.

Four lowland, main-channel sites were sampled on five occasions under a range of flow conditions, from dry season base flows to a one-in-ten year wet season flood. At each site, water quality and habitat data was collected, invertebrate communities in littoral and benthic habitats were sampled and fish were surveyed using a combination of boat electrofishing, gill netting and bait traps. This data was analysed using both univariate and multivariate statistical methods, before being collated into seasonal food web diagrams of the feeding links between fish and their food sources. Stable isotopes analysis was used to identify the most important pathways of energy transfer through these webs and a conceptual model of the factors affecting fish resource use and community structure was constructed.

A total of 1530 fish were caught, representing 36 species. Longitudinal variation in fish community structure was identified, with species such as *Melanotaenia splendida splendida* and *Tandanus tandanus* abundant in upstream areas and *Ambassis agrammus*, *Redigobius bikolanus* and *Lates calcarifer* more common downstream. Some species, such as *Nematalosa erebi*, preferred open waters, while others were associated with particular microhabitat features (e.g., *Notesthes robusta* was generally found near root masses of riparian trees). During the dry season, the community was dominated by *Gerres filamentosus*, *Neosilurus ater* and the introduced *Tilapia mariae*, while during the wet season the community was dominated by *Glossamia aprion* and *Nematalosa erebi*.

The fish fauna was classified into eight habitat guilds and seven feeding guilds. Most species preferred specific habitat features, such as root masses and instream vegetation, during the dry season, and then shifted to larger, deeper habitats with mud substrates and woody debris during the wet season. At this time, instream vegetation was removed from the main channel by high flow velocities and the scour of bed sediments, which reduced habitat heterogeneity. A range of foods were consumed by fish species, from detritus, algae and fruit, to aquatic invertebrates, molluscs and fish. While the availability of these foods tracked temporal changes in habitat, seasonal shifts in dietary composition were limited to two species and ontogenetic shifts were observed in just three species. Nonetheless, food consumption by the fish community as a whole reflected seasonal fluctuations in productivity and food supply: during the wet season, aerial and surface invertebrates, algae and some detritus appeared to be consumed more frequently, while macrophytes, microcrustaceans and molluscs appeared more important in the mean diet during the dry season.

I hypothesise that fish were limited in their prey selection by their phylogeny and that they tracked changes in food availability by moving between habitat types, which resulted in the observed changes in fish assemblage structure. However, while the identity of fish species comprising the assemblage present in lowland reaches changed seasonally, food web structure did not change substantially, with many weak links and a few strong links at all times. Stable isotope analysis indicated that energy was transferred through these webs via algal and detrital pathways, with a greater diversity of productivity sources contributing to animal production during the wet season than during the dry season.

In general, the dynamics of fish communities in the Mulgrave River are regulated by the unique hydrogeomorphological features of the catchment, which are typical of the Wet Tropics region. Specifically, upland streams in these systems are steep and main channels in lowland reaches are deeply incised relative to the surrounding floodplain. As a result, floodplain habitats in Wet Tropics catchments are poorly connected to the main channel, limiting their influence on primary productivity and their utility to freshwater fish species. While wet season flows are predictable, they act as disturbances in main-channel habitats, rather than the gentle flood ‘pulses’ documented in other tropical areas.

The results of this study emphasise the importance of flow seasonality in governing the spatial and temporal dynamics of productivity, instream habitat, invertebrate and fish populations, fish feeding and, therefore, the structure and function of aquatic food webs. Elements of several global models appear to apply under differing flow conditions, but no single model accounts for all of the dynamics observed in the lowland fish communities of the Mulgrave River. Given the inherent similarities of Wet Tropics catchments, the results of this study are widely applicable to other rivers across the region and provide support for the long-standing doctrine of the importance of maintaining natural flow regimes if freshwater fish diversity is to be conserved.

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Chapter 1: Freshwater fish communities in tropical rivers

1.1 Introduction

Tropical rivers are important centres of freshwater fish diversity: of the 21 000 fish species known to science, over 40 percent live in fresh waters and most are restricted to low-latitudes (Lowe-McConnell, 1975; Dudgeon 2000; Lundberg 2001). Fish assemblages in these systems are structured by a series of nested hierarchical filters acting first at regional and subsequently at local scales (Arrington and Winemiller, 2003; Matthews, 1998). Within individual catchments, lateral and longitudinal gradients in species richness and community composition are also usually evident (Angermeier and Karr, 1983; Frissell *et al.*, 1986; Schlosser, 1982; Inoue and Nunokawa, 2002). Seasonal cycles of flooding and drying regulate this spatial variability and have a major influence on patterns of primary productivity, that in turn influences the upper trophic levels of aquatic food webs (Junk *et al.*, 1989; Thorp and Delong, 1994; Johnson *et al.*, 1995; Power *et al.*, 1995). Freshwater fishes, for example, show marked seasonality in food uptake: periods of fasting coincide with low or falling water levels, whereas high feeding rates are associated with the increased abundance and diversity of prey items during the wet season (Lowe-McConnell, 1963; Goulding, 1980a, 1981; Welcomme, 1986).

The dependence of fish species on seasonal patterns of hydrology, not only for feeding but also for migration and reproduction (Welcomme, 1986; Winemiller, 1992c), means that the maintenance of natural flow regimes is pivotal for the conservation of tropical riverine ecosystems (Power *et al.*, 1996; Naiman *et al.*, 2002). This fact is of particular relevance to fisheries managers, given the increasing pressure on natural flow regimes from land clearing, agriculture, river regulation and water extraction (QDPI, 1993), along with the potential impacts of future, human-induced climate change (Elliot *et al.*, 1999; Walsh *et al.*, 2000). Several models have been developed that relate riverine processes to fish communities and our understanding of the factors affecting these relationships have been greatly enhanced by the regional testing of such paradigms. However, knowledge of temporal dynamics is limited in Australian systems, particularly in tropical areas. This thesis describes the influence of seasonal flooding on fish communities in general, and fish feeding in particular, in the main channel of the Mulgrave River, north Queensland.

1.2 Resource use by freshwater fish communities

The dynamics of fish communities have often been examined within a framework of ecological guilds. Root (1967, p. 335) first defined the term ‘guild’ as a ‘group of species that exploit the same class of environmental resources in a similar way’. As Root (1967) suggests, guild membership is independent of phylogenetic relationships (Root, 1967), but because species tend to share similar life history traits and adaptations through common evolutionary history, guild associates are often closely taxonomically related (Blondel, 2003). The guild concept stemmed from the earlier work of authors such as Elton (1927), MacArthur (1958) and Hutchinson (1957), who suggested that species coexistence is facilitated by morphological differentiation of traits of importance for resource acquisition, and encouraged the perspective that organisms occupy particular resource 'niches' according to their requirements (Matthews, 1998). Root (1967) simply extended this notion to group species whose niches overlapped.

Two of the most important resources for most animals, including freshwater fishes, are habitat and food (Ross, 1986). Freshwater fish species are often grouped into habitat or diet guilds on the basis of their relative abundance or dietary composition, respectively (Angermeier and Karr, 1983; Moyle and Senanayake, 1984; Sutton and Hopkins, 1996; Martin-Smith, 1998). For example, in a 1995 study of two Australian rivers, Pusey *et al.* (1995a, 1995b) identified five dietary guilds, with fish size and mouth gape important in determining guild membership. The number and type of diet guilds identified vary considerably among authors, depending on factors such as species morphology, prey density and the degree of taxonomic resolution (Angermeier and Karr, 1983; Moyle and Senanayake, 1984; Pusey *et al.*, 1995b). Despite this variability, some guild types are relatively common: as Matthews (1998) notes, the system devised by Karr *et al.* (1986) comprising five simple guilds (piscivore, insectivore, herbivore, omnivore and planktivore) has been widely adopted in North America.

The rationale behind the guild concept is that the ecological relationships among guild associates are moulded by competition for the available, often limited, resources (Blondel, 2003). The term ‘resource partitioning’, meaning how species differ in resource use, was introduced in the 1960s (Toft, 1985) to describe the limits that interspecific competition places on the number of species that may stably coexist (MacArthur, 1965; Schoener, 1974). One way in which researchers estimate the degree of resource partitioning is by calculating niche breadth or niche overlap between species pairs using various indices (e.g., Levins, 1968; Pianka, 1974). The extensive resource partitioning literature was reviewed by Schoener (1974) and Ross (1986), with a focus on metazoans and fishes, respectively. Both reviews concluded that three major resource axes could account for sufficient ecological separation to permit species coexistence: these were food, space and time. In addition, Ross (1986) concluded that diet separation is more important than habitat separation in fish assemblages, which is not the case for terrestrial assemblages (Schoener, 1974).

1.3 The influence of flow seasonality on fish feeding

The degree of separation between fish species along a resource axis, such as food or habitat, often varies according to the abundance of that resource (Matthews, 1998; Figure 1.1). Temporal variability in the environment (e.g., flow seasonality) can result in variation in resource abundance, the intensity of competition and the importance of competition in determining community organisation (Wiens, 1977). At low levels of resource abundance, if food is scarce, for example, resource overlap should be high, as fishes compete for whatever limited food is available (to the left of Figure 1.1). At the other extreme when, for example, food is super-abundant, all species are likely to exploit this abundant resource and have a high degree of dietary overlap, although the abundance of food will reduce the degree of interspecific competition. Between these two extremes, at times of intermediate food abundance, species may diverge on this resource spectrum, with each specialising on that part for which it is best adapted (Matthews, 1998).

From the 1960s, authors have described, and in some cases accounted for, the temporal dynamics of various ecological processes underway in tropical fish communities. These dynamics included migrations, respiratory adaptations to low dissolved oxygen and reproductive strategies, along with resource partitioning and seasonal dietary shifts related to river flows (Lowe-McConnell, 1963; Bonetto *et al.*, 1969; Welcomme, 1969). For example, Lowe-McConnell (1963) described fish dynamics in the Rupununi savanna district of Guyana in South America. Although her study did not focus on a particular site, she discussed numerous ecological factors associated with wet/dry seasonality, including the observation that feeding habits among species varied with food availability. During the wet season food was abundant and diverse; at this time there was extensive specialisation on the diverse food resources and differentiation in feeding habitats was probably at its greatest (Lowe-McConnell, 1963). In contrast, during the dry season food was scarce, but interspecific competition was reduced by a reduction in feeding rates, with fish living off their fat stores (Lowe-McConnell, 1963).

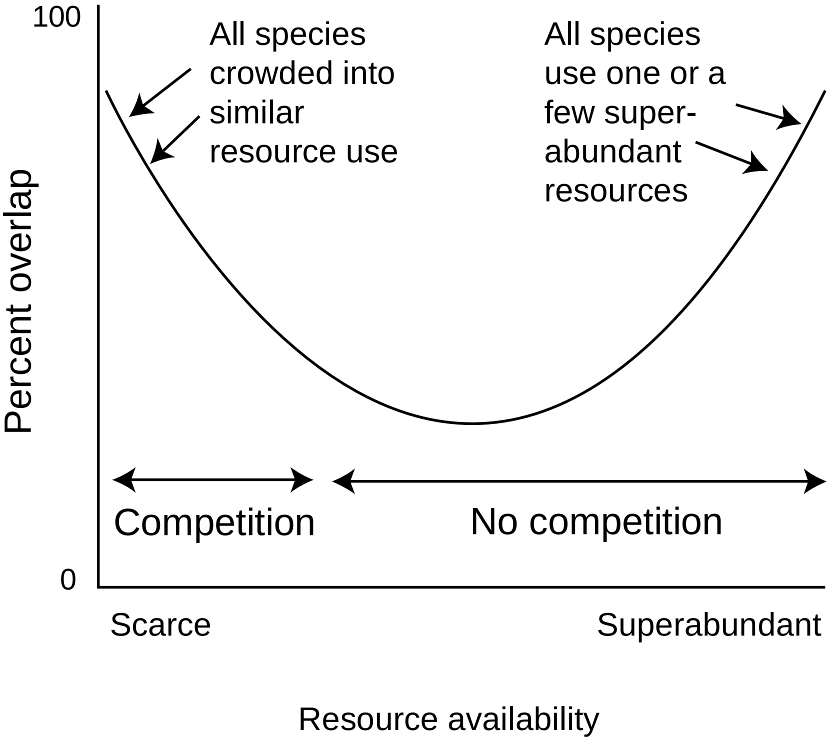

Figure 1.1 Hypothetical overlap on resource use axes as a function of resource availability in a local habitat (source: Matthews, 1998, p.459).

Since these early studies, the relationship between seasonal flow dynamics and changes in fish diets has been repeatedly demonstrated, such that seasonal variation in diet is now considered more the norm than the exception for fish species (Angermeier, 1982; Werner and Gilliam, 1984; Little *et al.*, 1998). For example, Zaret and Rand (1971) collected dry and wet season samples of fishes from a Panamanian lowland stream. By quantifying gut contents and calculating dietary overlap, they demonstrated that the degree of resource partitioning was high in the dry season sample, with those species sharing similar habitats having the most distinct food preferences. During the wet season some species retained their specialised feeding habits of the dry season, whereas others showed less restriction in diet diversity or exhibited a complete dietary shift. This movement, from distinct food niches during the dry season to widely overlapping ones in the wet season, was most probably due to contemporaneous changes in resource abundance and the degree of interspecific competition (Zaret and Rand, 1971). Zaret and Rand (1971) suggested that their results, together with those of Lowe-McConnell (1963), represent a continuum of food availability.

In contrast, Goulding (1980) reported that dietary overlap of fish in the Amazonian flooded forest was high during the dry season, but decreased in the wet season, as fish specialised on foods that were previously unavailable (e.g., fruits). He also discussed the degree of omnivory in tropical fish communities, hypothesising that most taxa appear to be omnivorous on a seasonal basis, but tend to feed on only one general prey category in a particular habitat. Together, the results of Goulding (1980), Zaret and Rand (1971) and Lowe-McConnell (1963) emphasise the importance of accounting for seasonal changes in resource abundance in the environment when considering fish feeding dynamics at the community level, and suggest that the specific mechanisms regulating resource use by freshwater fishes in tropical systems can vary substantially with the type of river, the species present, the position in the catchment and the specific characteristics of the flow regime. Additionally, the relative size of fish and their prey is known to influence feeding relationships, as fish may shift their diets during ontogeny as the size, and therefore diversity, of prey items that they are able to consume increases with their mouth gape (Schmitt and Holbrook, 1984; Ryer, 1988; Winemiller, 1989; Brose, 2006).

1.4 Models of riverine productivity

There are three models that attempt to predict, and account for, the relationship between flow and ecological communities. Each model considers the energy sources driving biotic production, and the effect that changes in these sources may have on aquatic food webs. The river continuum concept (RCC) is a simple linear model based on the hypothesis that a continuous gradient of physical conditions exist in the river from upstream to downstream Vannote *et al.* (1980). It predicts that downstream communities will be fashioned to capitalise on the inefficiencies of upstream nutrient processing, or nutrient ‘leakage’ (Vannote *et al.*, 1980). In headwater streams, terrestrial inputs of coarse particulate organic matter (CPOM) are shredded or collected by macroinvertebrates, whereas in lowland reaches fine particulate organic matter (FPOM), derived from upstream processing, may become more important, as the proportional input of CPOM from the riparian zone declines as the main channel increases in width (Johnson *et al.*, 1995). Despite these supporting principles, the RCC has been criticised for a number of reasons (Barmuta and Lake, 1982). Firstly, this linear model was developed on small temperate streams and extrapolated to large rivers without elaboration, and secondly, its use is limited to habitats that are permanent and lotic (Junk *et al.*, 1989), although Ward and Stanford (1983) went some way to addressing this deficiency. In other words, the RCC does not take into account that, in large rivers, the inundation of floodplain areas may be a major determinant of biotic dynamics through its influence on the energy sources used for primary production.

The latter argument provides the basis for the flood-pulse concept (FPC) of Junk *et al.* (1989). This model predicts that lateral exchange of nutrients between the floodplain and the river channel is likely to have a more direct impact on the biota than the longitudinal nutrient transport discussed in the RCC (Junk *et al.*, 1989). Specifically, as water levels rise during the wet season a 'moving littoral' extends throughout the 'aquatic/terrestrial transition zone'. Nutrients accumulated on the floodplain are released into the aquatic system upon inundation, where they support an increase in production (Gehrke, 1991). As Junk *et al.* (1989) explained, the predictable and prolonged flood pulse typical of large rivers favours the development of anatomical, morphological, physiological, and/or ethological adaptations, of terrestrial and aquatic organisms, that allow them to exploit the seasonally available resources of the floodplain. For example, many fish species living in the main channel depend on the floodplain for spawning, shelter and food supply (Winemiller, 1990).

The RCC and the FPC accentuate the importance of nutrients derived from headwater streams and seasonally inundated floodplains, respectively, and downplay the importance of local instream primary production and riparian inputs (Thorp and Delong, 1994). A third concept, the riverine productivity model (RPM), hypothesises that 'autochthonous production and direct organic inputs from the riparian zone together represent the "principal" source of carbon driving the food webs of large rivers primarily characterised by a constricted channel' (Thorp and Delong, 1994, p.306). Unlike the RCC, that contended that the majority of macroinvertebrates in large rivers were collectors exploiting FPOM originating upstream, and the FPC, that redefined the primary source of FPOM, but still predicted that collectors were the primary functional feeding group, the RPM suggests that carbon sources other than FPOM have important influences on food web composition (Thorp and Delong, 1994).

1.5 Aquatic food webs in tropical rivers

Food webs in tropical river landscapes are complex, a reflection of their environmental setting, featuring many weak trophic links between relatively rare species (Winemiller, 1990; Power and Dietrich, 2002). In most systems, a few strong feeding links are responsible for the majority of energy transfer from basal sources, through intermediate consumers, to top predators (Winemiller, 2005). Allocthonous production by macrophytes and algae, supplemented by inputs of nutrients from upstream, riparian and floodplain sources, is thought to drive the majority of production at upper trophic levels (Vannote *et al.*, 1980; Junk *et al.*, 1989; Thorp and Delong, 1994; Dettmers *et al.*, 2001; Finlay *et al.*, 2002; Thorp and Delong, 2002; Baxter *et al.*, 2005). However, despite comprising the dominant consumer group in these webs, freshwater fish rarely eat macrophytes and algae directly (Forsberg *et al.*, 1993; Lewis Jr *et al.*, 2001). Instead, analysis of carbon and nitrogen stable isotopes ratios suggests that they consume this material via indirect detrital pathways, particularly through the food chain that links piscivorous fish with detritivorous fish and detritus (Winemiller, 2005).

As seasonal flooding in tropical rivers can affect sources of primary productivity and populations of consumers, it can also affect the transfer of energy through aquatic food webs. Consequently, a food web gathered in a single season may not accurately reflect the food web during any other season, or the whole year (Thompson and Townsend, 1999). For example, Winemiller (1990; 1996) described shifts in primary productivity driving the food web of Caño Maraca, a lowland stream in the Venezuelan llanos. He showed that high densities of aquatic and emergent macrophytes were present on the floodplain during the wet season, that supported periphyton growth and herbivorous consumers. As the system dried, these macrophytes decomposed and the resulting detrital material became the principal source of basal production. At this time, resource competition became more intense; benthic algivores shifted to detritivory and invertebrate feeders and omnivores showed increased food and habitat segregation (Winemiller, 1990; Winemiller, 1996).

1.6 Australia’s Wet Tropics rivers

The majority of Australia’s tropical river systems are characterised by large catchments with seasonally inundated floodplains. Seven river typologies are represented in the region, that extends from the Fitzroy River near Broome in Western Australia to the other Fitzroy River, near Rockhampton in Queensland (Figure 1.2; Erskine *et al.*, 2005). Discharge from these rivers represents ~70% of the continent’s freshwater run-off and is highly seasonal in almost all catchments (Douglas *et al.*, 2005; Hamilton and Gehrke, 2005; Webster *et al.*, 2005). Extended periods of low flows during the dry season not only separate main-channel habitats from off-channel floodplain lagoons, but can also reduce contiguous main-channel habitats to a string of shallow, isolated pools (Beumer, 1980; Bishop *et al.*, 2001). In drier areas, these habitat changes can dramatically influence fish community composition by increasing density-dependent interactions and causing extreme water quality conditions (Bishop *et al.*, 2001; Medeiros, 2004).

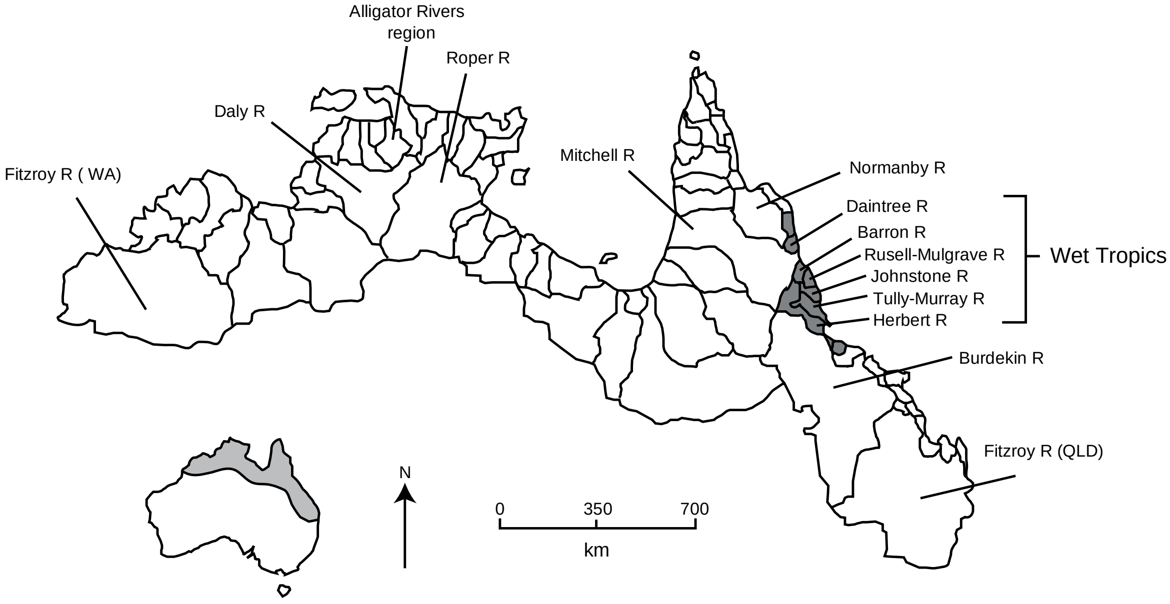

Figure 1.2 A map of the drainage basins of tropical Australia, indicating the relatively small size of the Wet Tropics bioregion, which is shaded in dark grey (after Erskine *et al*., 2005).

Rivers in the Wet Tropics bioregion are the exception to this general trend. Here, 'dry' season baseflows are maintained at relatively high levels by orographic rainfall, on basaltic peaks in catchment headwaters (see Chapter 2 for a full description). Freshwater fish diversity is high in the region: 107 species (including four exotic species), representing 37 families, are known to occur in the area (Pusey *et al.*, 2006). These species include approximately 40% of the continent's freshwater fish species and 66% of the genera (Pusey and Kennard, 1996). Species assemblages are quite consistent across Wet Tropics catchments, with each river featuring upstream reductions in species richness caused by the presence of natural barriers to upstream fish movements (Pusey *et al.*, 1995a; Pusey and Kennard, 1996; Russell *et al.*, 1996; Russell *et al.*, 2003; Pusey *et al.*, 2006). The Mulgrave River catchment has a particularly diverse fish fauna: Pusey *et al*. (1995a) caught 36 species from 12 sites located on the main channel and its primary tributaries and subsequent sampling has increased this number to over 70 species, including estuarine vagrants (Pusey, *pers. comm*., 2003; Halliday *et al*., 2001). This figure is nearly twice as high as the most speciose catchment in NSW (Gehrke and Harris, 2000). Pusey *et al*. (1995a) attributed the high fish diversity of the Mulgrave River to the high level of flow constancy that allows year-round access to the variety of habitats found in the river, with the exception of particularly steep upland regions.

1.7 Freshwater fish feeding in tropical Australia

While spatial patterns of Australia's tropical freshwater fish communities are well established, little is known about their temporal dynamics and information on the seasonal aspects of their feeding ecology is limited to a small number of studies (see Kennard *et al*. (2001) and Pusey *et al*. (2004) for reviews). The most comprehensive of these was the work of Bishop *et al*. (2001) on the autecology of species from 19 families in the Alligator Rivers region, Northern Territory. The authors presented seasonal distribution, growth rate, reproductive characteristics and feeding habits for each species. Nine feeding guilds were identified: 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). Omnivory was common across the fauna, probably due to the seasonal variation in food resource supply, and a feeding peak was recorded in the wet season (Bishop *et al.*, 2001).

Kennard (1995) analysed seasonal resource use by freshwater fishes in floodplain lagoons of the Normanby River, Cape York Peninsula. He found that dietary partitioning was high, but habitat partitioning was low. In addition, temporal variation in prey choice by fish was restricted to changes in the relative abundances of a small group of prey categories in the diet, rather than major shifts in prey choice (Kennard, 1995). These changes, however, did not correspond with seasonal variations in food abundances, suggesting that fish were foraging independently of measured fluctuations in the resource base. Pusey *et al.* (2000a) also studied monsoonal tropical rivers on Cape York Peninsula, classifying 23 species into seven trophic guilds. As in the Alligator Rivers region (Bishop *et al.*, 2001), there was a prevalence of omnivory and piscivory, while detritivory and planktivory were less common. Pusey *et al.* (2000a) ascribed much of the trophic structure they observed to the effects of phylogenetic determinants of body size, morphology and foraging mode.

Only two studies of fish feeding have been conducted within the Wet Tropics region. Hortle and Pearson (1990) documented the fauna of the Annan River in far north Queensland, with reference to the impact of tin mining. Gut contents analysis of 14 freshwater species identified six carnivores, four omnivores, three algivores/detritivores and one piscivore. No analysis of dietary overlap or resource partitioning was undertaken. Pusey *et al.* (1995b) quantitatively classified 24 species from the Mulgrave and South Johnstone rivers into five feeding guilds. These guilds were related to the body size of the species present, with three size classes of fish (small, <5 g; medium, 10-20 g; large, 100-

500 g) consuming a variety of aquatic and terrestrial invertebrates and fish, supplemented by different types of vegetable material. The fourth group consumed detritus and some bivalve molluscs; and the fifth group, composed of only two species, specialised on gastropod molluscs. At lowland sites, characterised by deep pools with low water velocities and sandy substrates, the authors found that gut fullness, diet diversity and niche breadth were low and that resource partitioning was high (Pusey *et al.*, 1995b). To date there has been no analysis of temporal dynamics of fish communities in Wet Tropics rivers.

1.8 Aims and structure of thesis

An appreciation of feeding ecology is pivotal to our understanding of fish distribution in space and time (Livingston, 1997). In this thesis I examine the response of fish communities and their feeding dynamics to wet season floods in an Australian Wet Tropics river. Whilst it is possible that elements of the trophic ecology of Wet Tropics freshwater fish communities may be similar to those reported in other tropical areas, I hypothesise that the applicability of global paradigms of riverine productivity to Wet Tropics rivers may be limited, owing to their unique channel geomorphology, hydrology, floodplain size, fish fauna and land use practices. I will argue that while frequent flooding influences food and habitat availability in the main-channel of Wet Tropics rivers, the low interannular flow variability and constant baseflow conditions of the dry season, together with phylogenetic limitations on feeding, are likely to limit the temporal variability of fish diets and, therefore, aquatic food web structure. The Mulgrave River represents an ideal system to test these hypotheses as it features the most diverse fish fauna of any Wet Tropics river and has particularly low interannular flow variability.

This thesis is structured as follows: Chapter 2 describes the Wet Tropics region in general and the Mulgrave River in particular. Aspects of geomorphology, geology, climate, hydrology, vegetation, land-use and management arrangements are covered. Chapter 3 addresses the influence of seasonal flows on instream habitats at four lowland main-channel study sites. Specifically, I examine the relative importance of three habitat axes, hydrogeomorphology, vegetation and water quality, in determining fish-habitat characteristics under a range of flow conditions, from dry season base flow, to a one-in-ten-year high flow event. Using this information I construct a conceptual model of temporal main-channel habitat dynamics which is applicable to the lowland reaches of most Wet Tropics rivers, within the context of processes acting at the catchment scale.

Chapter 4 describes the relationship between flow-mediated habitat structure and both riverine productivity and the abundance and diversity of invertebrate populations (one of the main sources of food for freshwater fish). Spatial and temporal variation in invertebrate samples collected from benthic and littoral habitats are analysed and these data are discussed in the context of the habitat dynamics modelled in chapter 3. In chapter 5, I extend this discussion to the freshwater fish fauna, by analysing the response of individual species to spatial and temporal heterogeneity in habitat structure. I then utilise multivariate techniques to assess the effect of these changes on the structure of the fish community. Chapter 6 contains information on the feeding ecology of the species caught, in relation to the changing availability of food resources during the study. I group fish species caught during wet and dry seasons into trophic guilds using classification analysis. This approach allows for the consideration of seasonal shifts in trophic guild structure. In addition, I investigate ontogenetic diet shifts in the fauna. Lastly, I consider the impact of seasonal changes in habitat and food preferences by individual fish species on the consumption of food at the community level.

Chapter 7 combines the population and gut contents data presented in previous chapters with analysis of nitrogen and carbon stable isotope ratios for basal, intermediate and upper trophic levels. The aim of this chapter is to consider not only changes in the structure of the fish component of the aquatic food web, but also the transfer of energy through the web at different times of the year. These results are compared to other studies of stable isotope ratios in the Wet Tropics and used to assess the applicability of five food web principles derived by Douglas *et al*. (2005) for systems in the wet-dry tropics of northern Australia. In chapter 8, I summarise the findings of the study and discuss their relevance in the context of global paradigms of biotic dynamics in tropical river systems. I present a simplified model of processes influencing freshwater fish communities and their trophic ecology in Wet Tropics rivers, before concluding the thesis with a discussion of the resilience of Wet Tropics freshwater fishes to future anthropogenic pressures, including global climate change.

Chapter 2: Study area

2.1 Location

The Wet Tropics bioregion extends through four degrees of latitude in a narrow strip (~100 km wide) of the northeast coast (Figure 1.2). The Mulgrave River catchment lies at the centre of this region (17° 07’ S, 145° 51’ E) and covers approximately 810 km2 (Figure 2.1 Russell *et al.*, 1996). Like most catchments of the Wet Tropics, it comprises high mountain ranges in the upper reaches and fertile alluvial floodplains in the lowlands. While most of the upper catchment has been protected within the borders of the Wet Tropics World Heritage area, substantial degradation of the lower catchment has occurred during the last 200 years (Russell *et al.*, 1996; Veitch and Sawynok, 2005). The aim of this chapter is to summarise the main characteristics of the catchment, including geology, geomorphology, climate, hydrology, vegetation and land-use.

2.2 Geology and geomorphology

The Wet Tropics is characterised by an eventful geologic history, involving alluvial and volcanic activity. Willott and Stephenson (1989) provide a comprehensive overview of the geology of the Mulgrave River catchment, from the sedimentation of the Hodgkinson Basin, between 420-360 million years ago (MYA), to the volcanic activity of 320-230 MYA, when heating 30-50km below the surface led to extensive igneous granite intrusions, and the last 100 million years of erosion. The latter period exposed the high granitic ranges of Mt Bellenden Ker and Mt Bartle Frere and incised the Mulgrave River corridor (Willmott and Stephenson, 1989). During the last few million years, additional volcanism, coupled with erosive action, created many of the present day geological features, such as small volcanos that remain as hills (e.g., Green Hill, to the south of Cairns) and crater lakes (e.g., Lake Eacham and Lake Barrine). Quaternary alluvial fans form many of the raised river terraces in the Mulgrave River catchment, into which the present day river channels have incised (Willmott and Stephenson, 1989; Thomas *et al.*, 2001). As a result of this geological history, soils in the catchment are primarily derived from granitic, metamorphic, and basaltic rocks, and Quaternary alluvium (Spain, 1991; Connell Wagner, 1992).

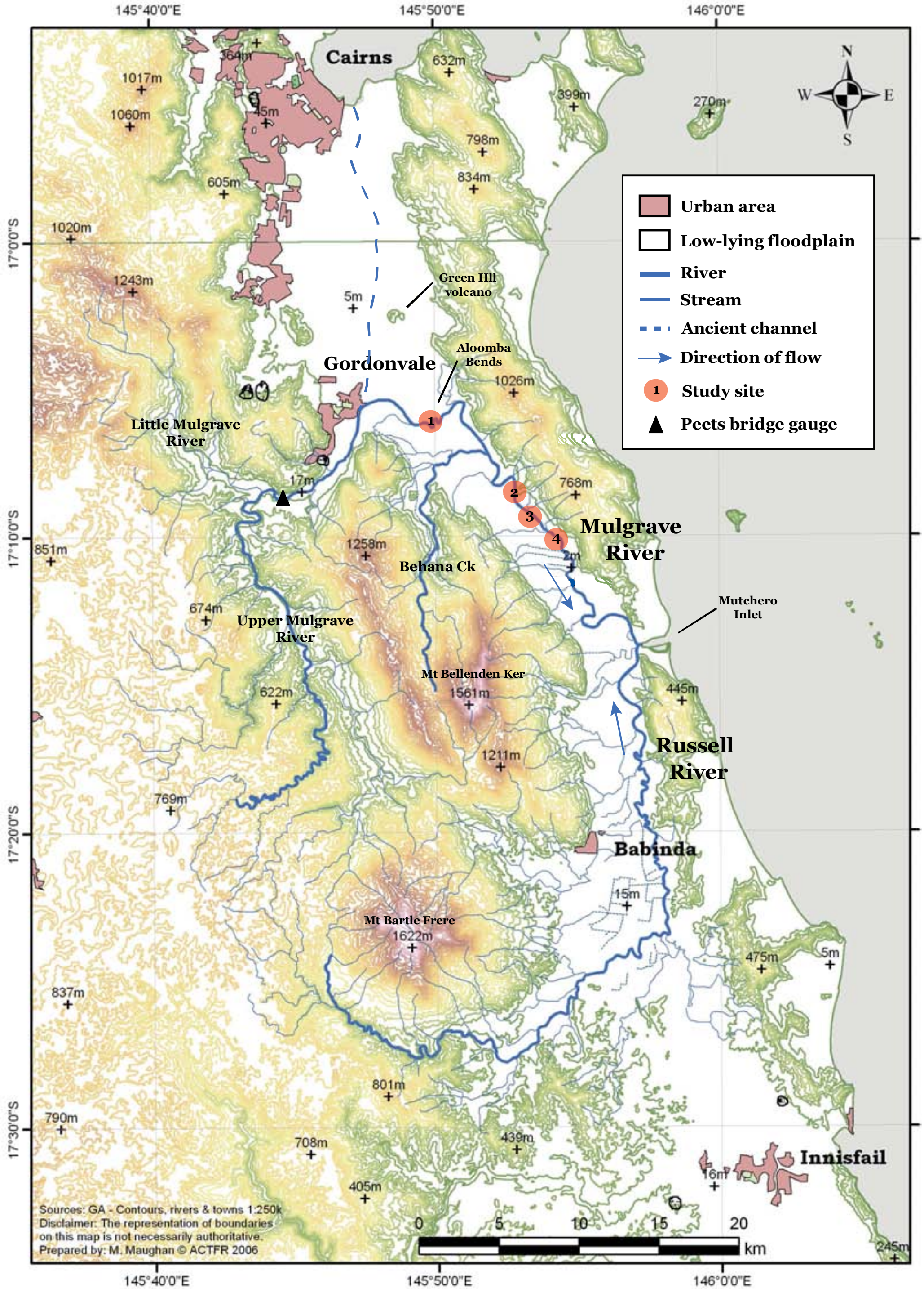

Figure 2.1 A map of the Mulgrave and Russell River catchments. Topography of the area is shown, along with major tributaries, urban areas and the locations of study sites 1-4 on the lowland reach of the Mulgrave River.

There has been some discussion regarding the role of Late Quaternary alluvial fans in determining the course of the Mulgrave River (Nott *et al.*, 2001; Thomas *et al.*, 2001). Much of this has focused on the Mulgrave Fan, the largest in the catchment, that extends about 10km from the present day base of the Mulgrave River Corridor onto the floodplain (Nott *et al.*, 2001; Thomas *et al.*, 2001; Nott, 2003). As Willott and Stephenson (1989, p.17) explain, it was originally thought that the Mulgrave River flowed north to enter the sea at Trinity Inlet, adjacent to Cairns (Figure 2.1), before it was, 'diverted south to meet the Russell River by damming of the valley floor by the Green Hill volcano'. However, recent dating of sediments north of Gordonvale (Nott *et al.* 2001; Thomas *et al.*, 2001), combined with pollen records (Thomas *et al.* 2001), suggest that the formation of the alluvial fan itself choked the valley floor and forced the river into its current course. While the river originally crossed the Mulgrave Fan in a series of anabranched streams, frequently switching between a northerly to a southerly course, when the sea level fell during the last glacial maximum (~20-14 ka, Chappell *et al.*, 1983), the river was at that time flowing to the south and this lower channel was trapped in this position (Willmott and Stephenson, 1989).

At present the Mulgrave River drains the eastern edge of the Atherton tablelands and the western side of the Bellenden-Ker range. It then flows north down the Goldsborough valley, turns slowly east across the lower slopes, crosses the narrow coastal plain, turns sharply south at the base of the Malbon Thompson range, and discharges into the sea with the Russell River at Mutcheroo Inlet (Figure 2.1). There appears to have been limited lateral migration of the main channel since European settlement. Leonard (2003) analysed planform changes at a number of sites on the main channel, finding that, while a large volume of material had been eroded in some places (e.g. >20 000 m^3 during the formation of Aloomba Bends), most of the river had undergone only slight shifts in main-channel position. Leonard (2003) concluded that, given the granitic structure of bed load sediments, main-channel accretion in the lower reaches may be the result of natural sediment delivery from the upper catchment slopes. Unfortunately, the study did not consider substantial decreases in the channel sinuosity and riparian vegetation cover of main channel tributaries, conspicuous from the aerial photos presented in her thesis, the implications of which are considered in the discussion of land use below.

2.3 Climate and hydrology

The maritime tropical climate of Wet Tropics bioregion is characterised by seasonal rainfall during the warmer summer months (Figure 2.2; Linacre and Hobbs, 1977; Lee and Neal, 1984). The average annual rainfall of the Mulgrave River catchment is 3233 mm (Leonard, 2003). Most of this rainfall is orographic and falls on the south-eastern slopes of the Bellenden Ker range in the lower portion of the catchment (Crowley *et al.*, 1990). Cloud capture by rainforests (condensation on foliage, that percolates down to the soil) on the high peaks of the catchment contribute up to 40-50% more water during the dry season (McJannet and Reddell, 2002), possibly helping to maintain the perennial dry season baseflows. Consequently, discharge exhibits relatively low inter-annual variability; the coefficient of variation of mean annual discharge is among the lowest in Australia at 28% (Pusey *et al.*, 2000b). The variability that does exist can be linked to El Nino – Southern Oscillation phenomena (Kapizke *et al.*, 1998) and tropical cyclones (Cameron McNamara, 1985). While flooding of lowland areas occurs during most wet seasons, larger floods resulting in large-scale over bank flooding occur every 3-5 years (Cameron McNamara, 1985; Table 2.1).

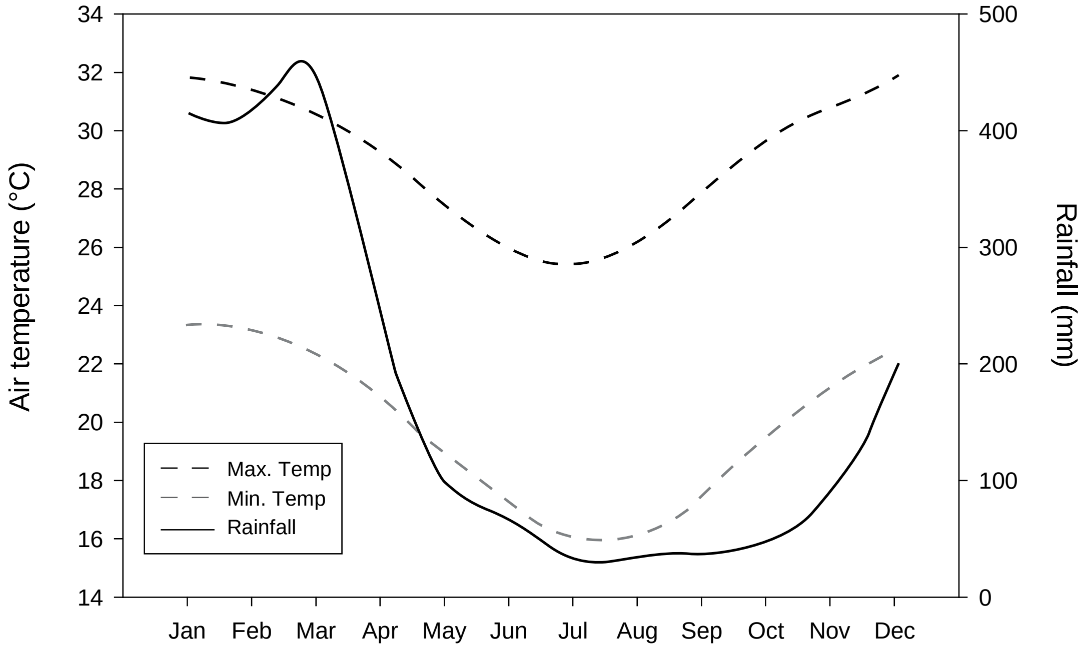

Figure 2.2 Mean monthly maximum and minimum air temperatures and mean monthly rainfall at Cairns Post Office (1882-1957; -16.9333 S; 145.7833 E; Elevation = 2.0 m; data source: Australian Bureau of Meteorology).

Table 2.1 Return periods for floods on the Mulgrave River near Gordonvale, based on a Log Pearson III distribution (source: Cameron McNamara, 1985).

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2.4 Land use and vegetation

The Mulgrave River catchment is the traditional land of several Aboriginal language groups, including the Yidinydji, from the northern section of the catchment, and the Malanbara, from the lower Mulgrave River. European ‘settlement’ began in 1873 and the first sugar growing areas were developed in 1882 (Mulgrave Central Mill, 1947). Since then, anthropogenic disturbance of the riverine landscape has continued. Russell *et al.* (1996) documented the land use of the Russell-Mulgrave catchment, reporting that 66% (mostly uplands and mangroves) was included in the Wet Tropics World Heritage Area. Other forested areas outside this zone, 9.2% of the catchment area, were included in the forestry system. The majority of lowland floodplain (16.9% of the total catchment) was under sugar cane, 4% of the catchment was dedicated to grazing, and the remaining 3.9% was split between urban areas and other uses (Russell *et al.*, 1996). Unfortunately, between 1952 and 1992 a total of 45.6% of wetlands within the catchment were destroyed, including a 2300 ha *Melaleuca* wetland. As stated by Russell *et al.* (1996, p. 13), “agricultural expansion is responsible both directly and indirectly [through altered hydrology] for most of these losses”. Now, three deepwater off-stream wetlands, immediately adjacent to the present course of the river upstream of Deeral Landing, are the only remaining major wetland habitats in the Mulgrave catchment (Veitch and Sawynok, 2005). Fortunately, most of the remaining wetlands in the area, such as large portions of Wyvuri Swamp near Bramston Beach, have finally been preserved within National Parks, some of which were established as recently as 1996 (WTMA, 2004, p.82).

Most other vegetation types within the lower catchment have suffered a similar fate to the wetland habitats. In 2001, the remnant vegetation communities were mapped by the Queensland Environmental Protection Agency as part of the Regional Ecosystem Mapping project. This process revealed the extent of floodplain clearing and identified the importance of remnant riparian vegetation communities. The entire riparian buffer of the lowland section of the river, that comprises primarily mesophyll vine forest with dominant palms (Type 3a, Tracey and Webb, 1975), is classified as either ‘endangered’ or ‘of concern’ (Sattler and Williams, 2001). To help restore these communities, the Mulgrave Landcare Catchment Group has planted thousands of seedlings along sections of stream bank, with the aim of increasing the lateral connectivity of riparian vegetation (Bruce Corcoran *pers. comm.*, 2005).

Chapter 3: Spatial and temporal variation in fish habitats

3.1 Introduction

The characteristics of instream habitats, including their water quality conditions, have a strong influence on freshwater fish communities (Harris, 1994). In general, fish occupy habitats that suit their physiological requirements, while at the same time taking into account ecological factors such as the relative predation risk, food availability, and reproductive potential of an area (Rice, 2005). Consequently, as the availability of suitable habitat varies, so too does the abundance of individual species and, therefore, the structure of freshwater fish assemblages (Davies, 1989; Thevenet and Statzner, 1999; Inoue and Nunokawa, 2002). An understanding of these fish-habitat dynamics, under a variety of flow conditions, is essential for the successful management of fish communities (Naiman and Latterell, 2005; Rice, 2005). This is particularly true for degraded catchments, where the diversity and availability of fish habitats may be limited by anthropogenic disturbance (Russell *et al.*, 1996).

Spatial variation in fish habitat occurs laterally, longitudinally and vertically in the riverine landscape at a variety of scales (Frissel *et al.*, 1986). As Matthews (1998) described, fish assemblages tend to reflect the hierarchical organisation of river systems and instream habitats. For example, the fish assemblage at an individual site is influenced firstly by variation at the regional scale, which determines the species pool available for colonisation, before the relative abundance of component species is determined by variation in habitat variables at finer scales (Moir *et al.*, 1998; Gehrke and Harris, 2000; Pusey *et al.*, 2000b, 2006). In most rivers, the greater size and variety of habitats in lowland rivers, when compared to upland streams, is matched by an increase in fish diversity, as more species find habitat patches that meet their requirements (Sheldon, 1968; Pusey *et al.*, 1995a; Inoue and Nunokawa, 2002). In this chapter I consider fish habitat at several spatial scales, but focus primarily on dynamics occurring at the scale of mesohabitats – the pools, runs and riffles within which fish reside, and between which they move.

There are three main groups of characteristics that describe fish habitat: hydrogeomorphology, vegetation, and water quality. Each of these groups comprises a subset of variables that influence fish in different ways. Hydrogeomorphology includes: depth, that provides refuge from predators and extreme thermal conditions (Wooley and Crateau, 1983; Schlosser, 1987; Van Den Ayvle and Evans, 1990; Harvey and Stewart, 1991); substrate, that influences the abundance of invertebrates (an important food source for many fishes), and the selection of spawning sites (Flecker and Allan, 1984; Downes *et al.*, 1998; Moir *et al.*, 1998; Downes *et al.*, 2000; Kennard *et al.*, 2001); flow velocity, that regulates energetic costs, food supply, and the downstream transport of propagules (Vannote *et al.*, 1980; Muth and Sschmulbach, 1984; Bisson *et al.*, 1988; Schlosser, 1998; Bond and Downes, 2003); and channel gradient, that controls the degree of longitudinal connectivity (Pusey *et al.*, 1995a; Church, 2002).

Vegetation, be it instream, littoral, or riparian, plays a key role in fish-habitat associations. Instream macrophytes and filamentous algae, along with submerged and emergent littoral plants, provide protection from predation, particularly for larval and juvenile fishes (Pusey *et al.*, 1993; Pusey *et al.*, 1998; Pusey and Arthington, 2003). The fine-scale structure and dynamics of these vegetation types can also regulate the supply of food, directly for herbivores, and indirectly for invertivores and piscivores. For example, Power *et al.* (1990a) found that larval chironomids in the upper Eel River, California, were 15-16 times more likely to be consumed by fish when exposed in thin algal turfs on the river bed, than when concealed in detached algal mats floating on the surface. In an earlier experiment, Power *et al.* (1983) demonstrated that fishes can have reciprocal effects on vegetation in the habitats they occupy. They added piscivorous bass (*Micropterus salmoides* and *M. punctulatus*) to pools in small Oklahoma streams, which then displaced and consumed the resident alga-grazing minnows (*Campostpma anomalum*), resulting in a significant increase in the standing crop of filamentous algae.

Links between the riparian zone and fishes are so strong that some authors consider the riparian zone to be ‘fish habitat’ (Naiman and Latterell, 2005). Pusey and Arthington (2003) provide a comprehensive review of the important functions of the riparian zone for freshwater fishes. For instance, overhanging vegetation provides cover for fishes and moderates water temperatures by shading the stream channel (Meyers *et al.*, 1992; Rutherford *et al.*, 2004), while the input of terrestrial organic matter (e.g. leaves, fruit and invertebrates) is an important driver of aquatic productivity, especially in headwater streams (Vannote *et al.*, 1980). Other inputs from the riparian zone, such as the recruitment of woody debris to the stream channel, can greatly enhance fish habitat (Keller and Swanson, 1979; Lisle, 1979; Angermeier and Karr, 1984; Abbe and Montgomery, 1996; Webb and Erskine, 2005). In the Ovens and Murray Rivers, radio-tracking studies have documented fine-scale associations between woody debris and Murray cod (*Maccullochella peelii peelii*), trout cod (*Maccullochella macquariensis*), and golden perch (*Maquaria ambigua*) (Kohen, *et al.*, 1996, 1997; Crook and Robertson, 1999).

Hydrogeomorphology and vegetation often interact to determine habitat characteristics at fine scales (Tabacchi *et al.*, 2000). For example, stream depth, flow velocity and substrate type are all important in regulating the growth of aquatic macrophytes. In shallow areas with stable substrates, macrophyte beds can become well established and have a strong influence on local processes of scour and deposition (Bunn *et al.*, 1998). The latter effects are even more pronounced in the case of large woody debris which, once in the stream channel, reduces stream velocity, decreases pool spacing, increases pool depth and the amount of overhead cover (Lisle, 1986; Kohen *et al.*, 1994; Beechie and Sibley, 1997; Inoue and Nakano, 1999; Rayner, 2001).

The third axis of fish habitat is water quality. In the context of this chapter, the term 'water quality' refers specifically to the chemical and physical properties of water: temperature, pH, dissolved oxygen concentration, conductivity, and turbidity. These properties often interact to influence biotic communities, particularly in disturbed systems. For example, water temperature affects the abundance and species composition of invertebrate and fish communities both directly and indirectly (through its effects on diffusion, oxygen solubility and metabolic rates of organisms - (Rutherford *et al.*, 2004)). Water temperatures may be highly variable between habitats only a few metres apart – slow-flowing backwaters are often much warmer than waters in the main stream channel (Hauer and Hill, 1996), whereas streams with dense overhanging vegetation may be cooler than those with degraded riparian areas (Quinn *et al.*, 1997).

The relative importance of these three groups of variables, in determining the range of fish habitats present at a given site, may change considerably both spatially and temporally. As shown in Figure 3.1, under stable dry season baseflow conditions, vegetation and water quality may be the most important determinants of fish habitat. However, elevated wet season flows may cause channel scour, the destruction of macrophyte beds and more homogeneous water quality conditions, resulting in an increase in the importance of hydrogeomorphologic variables for fish-habitat associations. These temporal dynamics, ranging in scale from days to decades, can often override the influence of spatial variability in fish habitats (Townsend, 1989; Bunn and Arthington, 2002).

In tropical rivers, one of the most important temporal phenomena affecting fish is seasonality of the flow regime (Winemiller, 1990). The duration and magnitude of elevated flows determine the availability of various habitat types, by regulating lateral and longitudinal connectivity, influencing local hydrology and geomorphology, removing instream vegetation, and affecting water quality (Junk *et al.*, 1989). Many fish and other aquatic organisms exhibit a range of life history adaptations to exploit these temporal dynamics (Junk *et al.*, 1989; Bunn and Arthington, 2002). For example, black catfish (*Neosilurus ater*) migrate upstream during the wet season, from lowland areas to small streams with sand substrates, in order to spawn – a tactic that may provide larvae with the opportunity to exploit certain habitat types only available at that time of year (Pusey *et al.*, 2004).

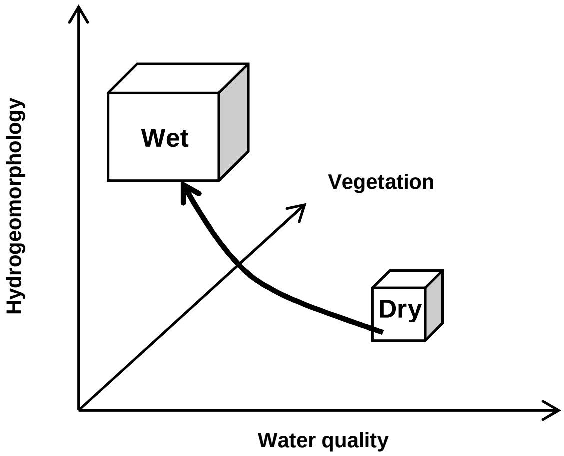


Figure 3.1 The relative importance of the three main habitat variables, in determining the range of fish habitats present at a site (represented as boxes), may change both spatially and temporally (here between dry and wet seasons).

Many of the processes described above are applicable to rivers in the Wet Tropics bioregion. These rivers rise in upland rainforests, before flowing down steep escarpments and meandering across the coastal floodplain. The freshwater fish inhabiting these systems rely heavily upon lowland riverine habitats, particularly within the main channel, for the following reasons:

1. Instream barriers limit upstream movement. Only species with specific adaptations for overcoming obstacles such as long sections of rapids, cascades or waterfalls, are capable of colonising upland streams (Pusey and Kennard, 1996);
2. Lowland channels are deeply incised. Wet Tropics rivers are restricted to the main channel for almost all of the year. When floodplain inundation does occur, under high wet season flows, it is brief (usually less than two weeks – Nott, 2001; Nott, 2003);
3. Larger rivers provide a greater range and extent of habitats than smaller streams (Galat and Zweimuller, 2001); and

4. Extensive human disturbance of lowland floodplains. Clearing for agriculture and urban development has changed hydrological regimes and dramatically reduced the diversity and availability of off-channel fish habitats (Russell *et al.*, 1996).

It is important that we increase our knowledge of fish-habitat associations in Wet Tropics rivers, not only to understand the distributions and ecologies of fish species, but also to help set conservation priorities and management goals. In this chapter, I investigate spatial and temporal variation of lowland main-channel fish habitats along the three axes discussed above. Specifically, I quantify temporal shifts in hydrogeomorphology, vegetation and water quality under a range of flow conditions, from stable dry-season base flows, to the elevated flow conditions of a one-in-ten-year flood event. I ask: what variables are most responsible for spatial variability in fish habitats; are some habitat variables more responsive to seasonal flows than others; do some habitat variables recover more quickly following high wet season flows; and are some habitat types only available at certain times of the year? My overall goal in this chapter is to develop a conceptual model of seasonal habitat dynamics in the main-channel of a Wet Tropics lowland river, which can later be related to the diversity and composition of invertebrate and fish communities.

3.2 Methods

3.2.1 Study sites

Sampling was conducted at four sites on the lowland floodplain reach of the Mulgrave River (Figure 2.1). Each site was approximately 200 m in length and 50 to 80 m wide. Under dry-season, baseflow conditions, Site 1, the most upstream site, was characterised by a large, mobile point bar on the left bank (Figure 3.2a). An abundance of deep undercut banks and overhanging vegetation dominated the right bank, while both large and small woody debris were common throughout the site. The limited amount of instream and littoral vegetation present during the dry season (Figure 3.2b, d) was reduced by wet season flow events (Figure 3.2c). Site 2 was characterised by a substantial large woody debris snag (Figure 3.3a, b), with a mid-channel sand bar covered by emergent and submerged vegetation during the dry season (Figure 3.3c). A narrow and broken band of riparian vegetation overhung portions of each bank, with instream macrophytes and emergent vegetation colonising the channel where canopy gaps occurred. Several root masses were present on the left bank (Figure 3.3d).

Site 3 was similar to site 2 (Figure 3.4a, b). An exposed sand bar covered by emergent vegetation was present on the left bank, with exposed root masses on the left bank at the base of large overhanging Ficus spp. trees (Figure 3.4c), separated by emergent reeds (Figure 3.4d). Site 4, the most downstream site, was similar to site 1. The main feature of this site was a large, shallow, submerged sand bar running along the left bank (Figure 3.5a). The water's edge on the right bank followed the river channel, with a small, shallow backwater bordered by primary riparian forest with emergent palms (Figure 3.5b, c). Large woody debris from this forested area accumulated in the main channel, as a result of bank erosion and mass movement under elevated flows. A pocket of small woody debris also occurred on the left bank (Figure 3.5d).

3.2.2 Hydrology

Sampling was conducted under a range of flow conditions, from dry season base flow, to a wet season high flow event with a return period of approximately ten years (Figure 3.6; Table 2.1) For the two years prior to the commencement of sampling (in October 2003), wet season discharge had been substantially below the long-term average. Following this extended dry period, discharge associated with the 2004 wet season was well above the long-term average, with a peak instantaneous discharge of 2445 m^3/s indicating at least a one-in-ten-year event (Table 2.1; Cameron MacNamara, 1985). Two sampling dates were conducted in response to these high flows, one in April 2004 and one in June 2004. A second dry season sample was conducted in October 2004 and the final wet season sample in April 2005. Mean daily discharge during the 2005 wet season appeared relatively consistent with the long term average.

3.2.3 Habitat sampling

At each site, on each sampling occasion, hydrogeomorphological, vegetation, and water quality variables were estimated using a methodology similar to that of Pusey *et al.* (2004) and Kennard (2005). These variables encompassed the full range of lowland, main channel habitat features available to fishes. Geomorphology and vegetation data were collected at each shot of fishing effort (i.e. at each gill net, bait trap and electrofishing shot). As a result of slight differences in fish sampling effort between sites (see chapter 4), the number of replicate habitat measures taken at each site also varied, with a minimum of 13 and a maximum of 20 replicates (Table 3.1).

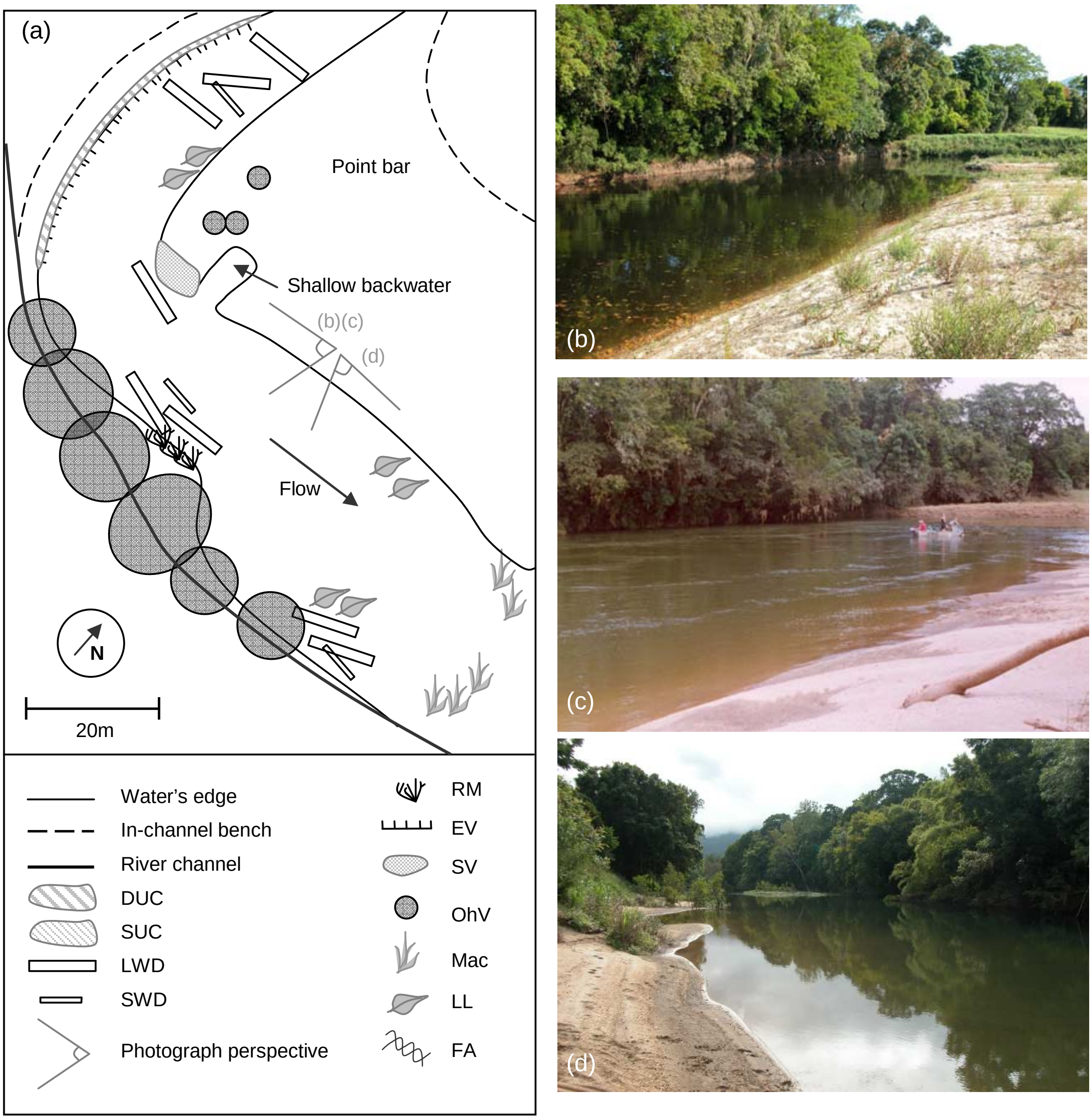


Figure 3.2 Geomorphology and vegetation features of site 1 under base flow, dry season conditions (a), with photos facing upstream under dry (b) and wet season (c) conditions, and downstream during the dry season (d). See Table 3.2 for explanation of habitat codes.

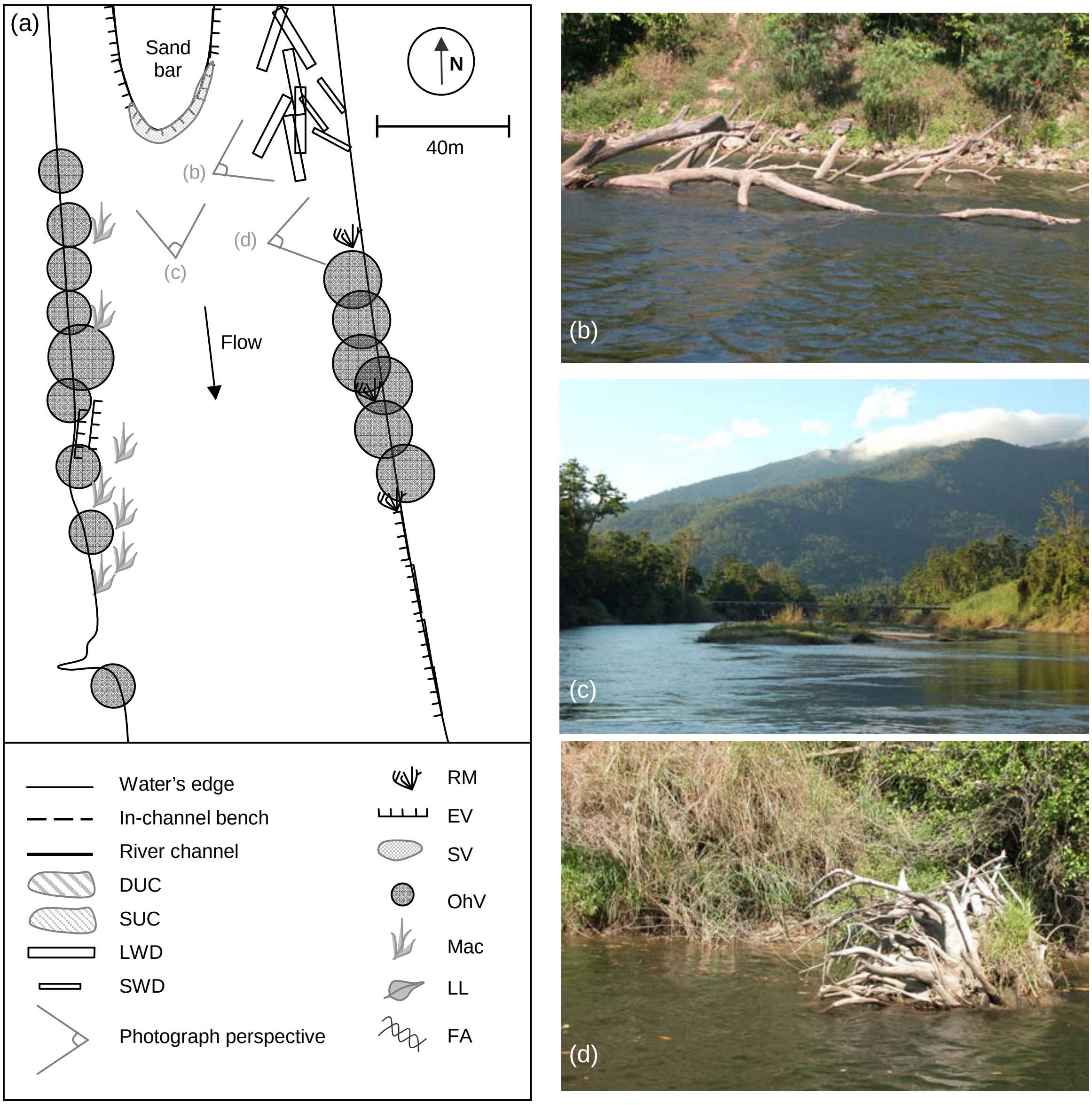


Figure 3.3 Geomorphology and vegetation features of site 2 under base flow, dry season conditions (a), with a photo of the large woody debris snag at the upstream end of the site (b), the view looking upstream (c). Several root masses are present on the left bank (d). See Table 3.2 for explanation of habitat codes.

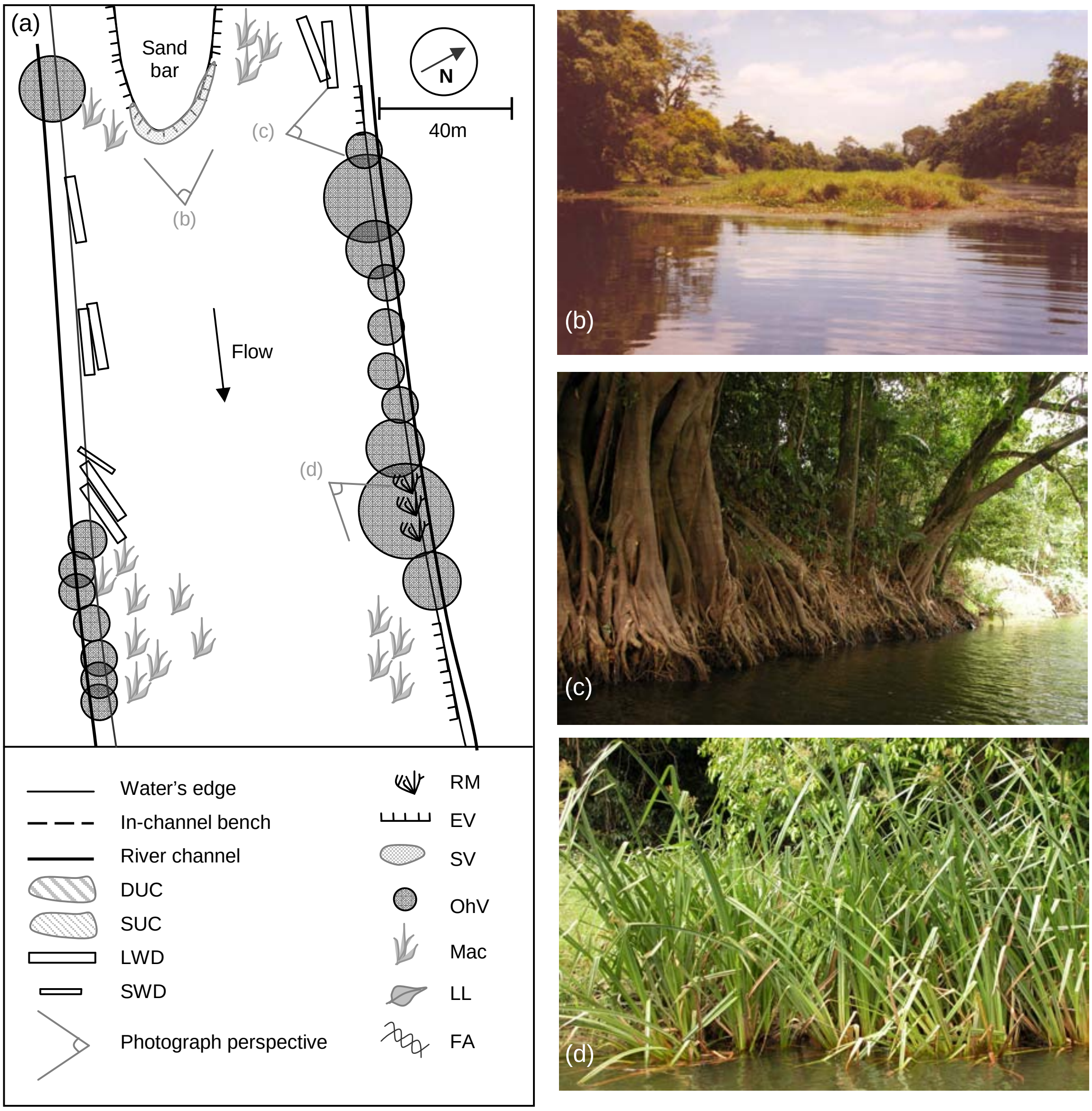


Figure 3.4 Geomorphology and vegetation features of site 3 under base flow, dry season conditions (a). As with site 2, the upstream end of this site is characterised by an exposed sand bar covered by emergent vegetation and grasses (b). Exposed root masses dominate the bank under two large *Ficus* trees (c), while emergent reeds colonise portions of the left bank without overhanging vegetation (d). See Table 3.2 for explanation of habitat codes.

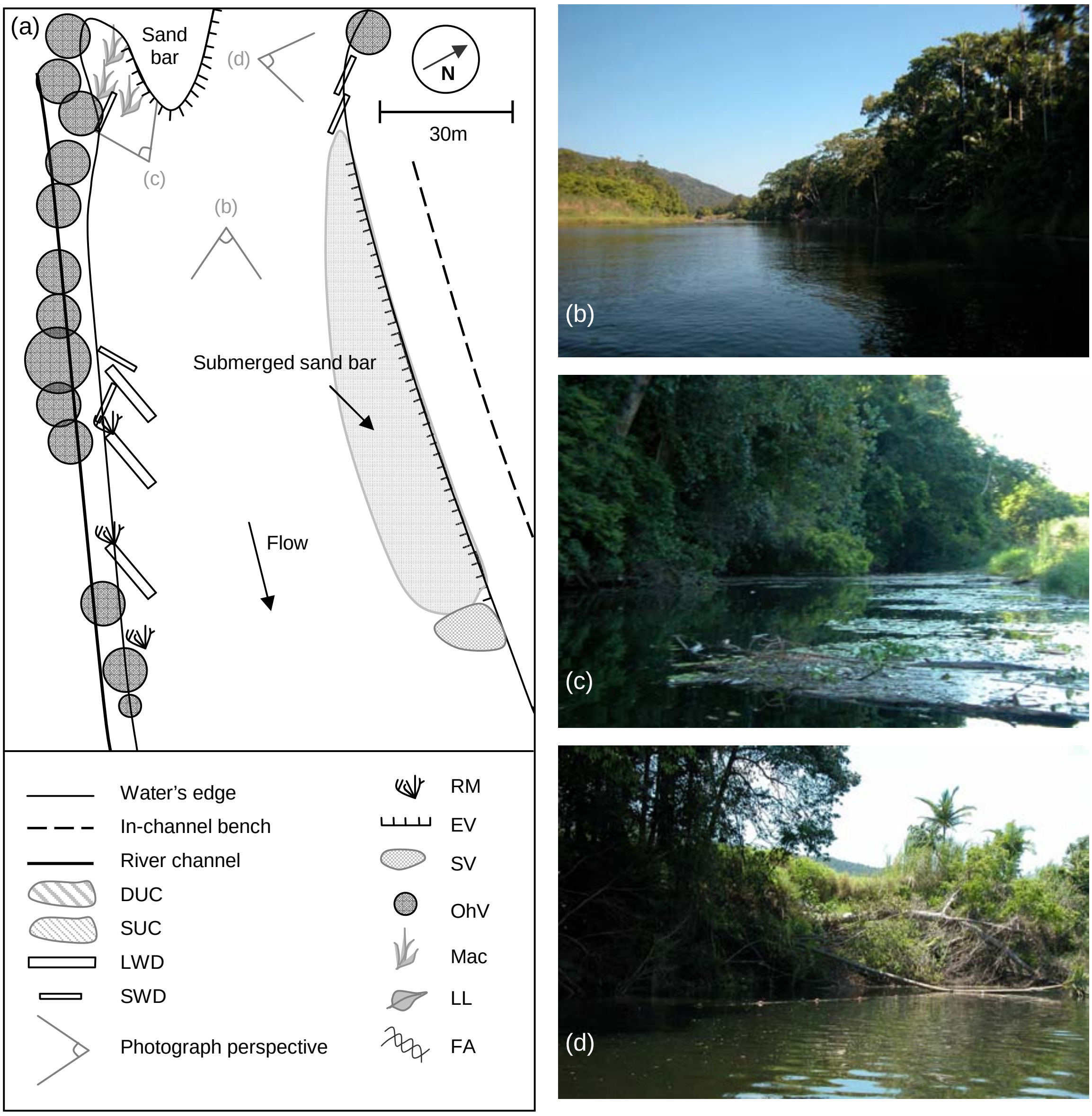


Figure 3.5 Geomorphology and vegetation features of site 4 under base flow, dry season conditions (a). The main feature of this site is a large, shallow submerged sand bar running along the left bank. The right bank is bordered by primary riparian forest with emergent palms (b, c). A pocket of small woody debris also exists on the left bank (d). See Table 3.2 for explanation of habitat codes.

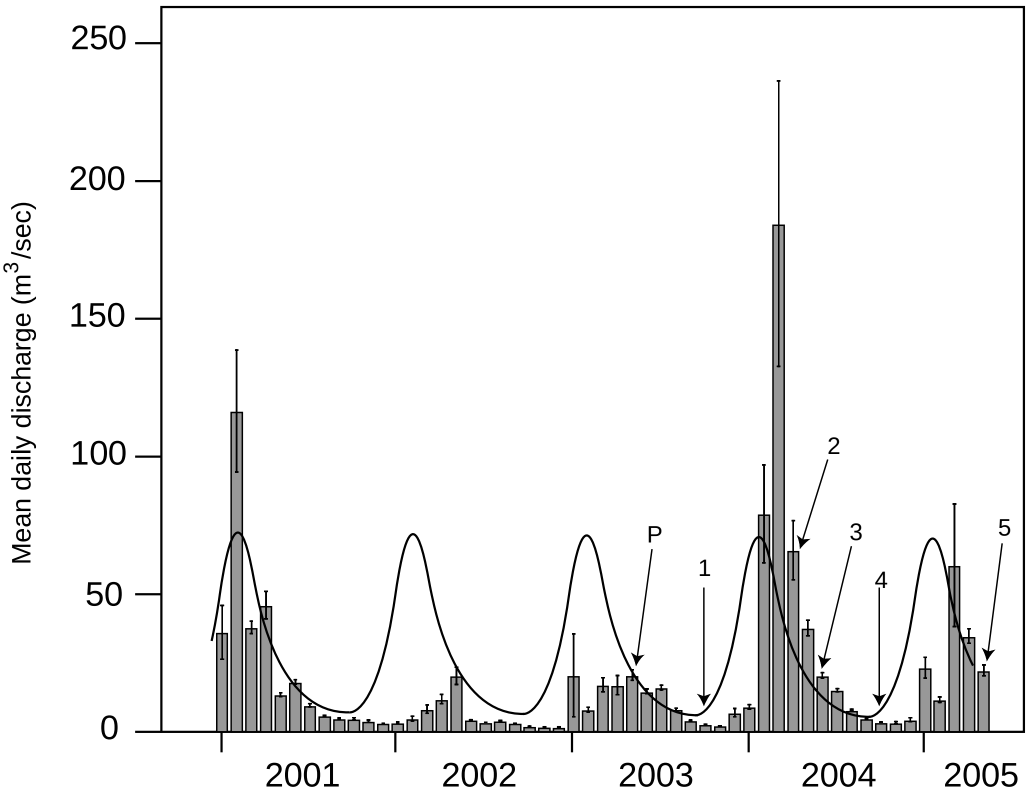


Figure 3.6 Mean daily discharge (m^3/sec ± SE) for the Mulgrave River at Peet's Bridge (gauging station 111007A – ca. 10 km upstream from the study sites). Data are presented for each month between January 2001 and May 2005 (bars), along with the long-term average calculated for 1973-2005 (line). The timing of the pilot study (P) and sampling dates (1-5) is also indicated. (data source; Queensland Department of Natural Resources Mines and Energy).

Table 3.1 The number of hydrogeomorphology and vegetation replicates collected at each site during each sampling date.

Site no	Oct 03	Apr 04	Jun 04	Oct 04	May 05	Total
1	15	19	19	18	19	90
2	15	19	18	19	19	90
3	13	20	19	19	20	91
4	16	20	19	19	16	90
Total	59	78	75	75	74	361

Three subsets of hydrogeomorphological variables were measured or estimated at each shot of electrofishing effort: hydraulic characteristics, substrate composition, and the degree of undercut banks (Table 3.2). Hydraulic variables were: wetted width, that was measured once per site using a tape measure and then estimated for each subsequent replicate; depth, that was measured using a graduated pole; and flow velocity, that was measured using a Pigmy-Ott meter or, when this was unavailable, estimated using the floating orange method (Bilby, 1977; Nilsson, 1987). All other hydrogeomorphology and vegetation variables were estimated in one of two ways: substrate composition, which varies across the river bed, was estimated as the percentage of total surface area sampled during each shot of fishing effort (which varied between 10 and 750 m^2), while microhabitat structures confined to the river margins (e.g. undercut banks) were measured as the linear portion/percentage of total bank length sampled during each shot of fishing effort (Figure 3.7). Instream and littoral vegetation variables, estimated as percent surface area, were macrophyte beds, filamentous algae, leaf litter, emergent vegetation (semi-aquatic plants) and submerged vegetation (drowned terrestrial vegetation). Structural vegetation elements associated with, or derived from, the riparian zone – including large and small woody debris, overhanging vegetation and exposed root mass – were estimated as percent bank length.

Ambient water quality conditions were measured using commercial multi-probe devices (Hydrolab DS4 and DS3 – Hach® Environmental, Loveland, CO, USA; or YSI 556 MPS – YSI Environmental, Yellow Springs, OH, USA). Variables recorded were: temperature (ºC), pH, dissolved oxygen (mg/L and % saturation) and conductivity (μS/cm). Water quality measurements in the pilot study indicated no areal or vertical variation within sites (see Appendix 1), so three replicates were collected at each site during each sampling date, at a depth of 0.5 m. Turbidity was measured using a Secchi disk (m; Preisendorfer, 1986), or as total suspended solids (mg/L, using the YSI instrument only). However, limited availability of this equipment for the all sampling dates meant that turbidity values were not included in statistical analyses. Turbidity was generally low (Secchi distance >2.5 m) and unlikely to affect sampling efficiency.

Table 3.2 Geomorphology and vegetation variables recorded, with abbreviation codes used in figures.

Habitat axis	Variable group	Variable	Code	Details
Hydrogeo-morphology	Hydraulic characteristics	Wetted width (m)	Width	Horizontal distance perpendicular to stream flow between water edges.
		Depth (m)	Depth	Vertical distance from existing water surface to channel bottom
		Velocity (m/s)	Vel	Speed at which surface water moves downstream. See text for categories.
	Substrate composition (% surface area)	Mud	M	<0.06 mm
		Sand	S	0.06 mm-2.0 mm
		Fine gravel	FG	2.0 mm-16.0mm
		Coarse gravel	CG	16.0 mm-63.0 mm
		Cobble	C	63.0 mm - 128.0 mm
		Rock	R	>128.0 mm
		Bedrock	BR	Continuous exposed bedrock
	Undercut banks (% bank length)	Deep	DUC	Undercutting only below surface of the water
		Shallow	SUC	Undercutting extends above surface of the water as overhanging bank
Vegetation	Instream (%surface area)	Macrophytes	Mac	Aquatic plants
		Filamentous algae	FA	Mostly benthic green algae turfs
		Leaf litter	LL	Dead leaves from terrestrial and aquatic plants
	Littoral (%surface area)	Emergent vegetation	EV	Semi-aquatic plants with large emergent component (i.e., reeds)
		Submerged vegetation	SV	Drowned terrestrial vegetation
	Structural/riparian (% bank length)	Large woody debris	LWD	Woody debris >10 cm minimum stem diameter
		Small wood debris	SWD	Woody debris <10 cm maximum stem diameter
		Overhanging vegetation	OhV	Riparian trees and shrubs extending over the water
		Root mass	RM	Exposed roots of riparian trees and shrubs

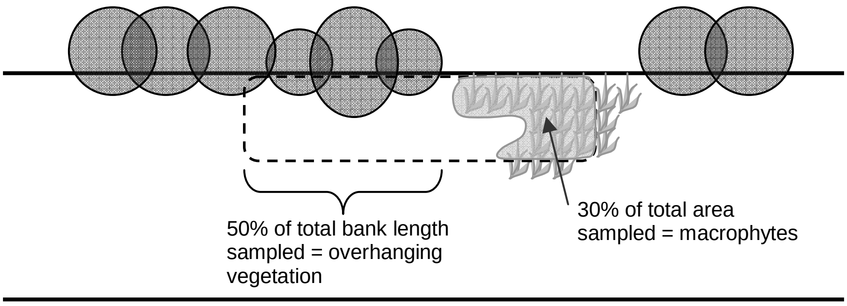


Figure 3.7 Schematic diagram of a river channel showing the total area sampled during a typical shot of fish sampling effort (e.g. a single electrofishing shot; ⊏). Two different measures were used. 'Percent bank length' refers to the percentage of the total bank length sampled, that is occupied/covered by the habitat variable. This method was used for structural habitat variables, such as overhanging vegetation (●). 'Percent surface area' refers to the percentage of total area sampled, covered by the habitat variable. This method was used for the remaining vegetation and substrate variables, such as instream macrophytes (▨).

3.2.4 Data analysis

Three dimensional semi-strong hybrid multidimensional scaling (SSH MDS) was used for analysis of hydrogeomorphology, vegetation and water quality data using PATN Version 3.03 (Belbin, 1991). The Gower-Metric association measure was used (cut-off value = 0.9, 10 random starts, random seed number = 1235, 100 iterations). This Euclidean measure, with built-in range standardisation, is favoured for physical habitat data (Gower and Legendre, 1986). In order to identify the variables that were most important in determining spatial and temporal variation in fish habitats, Principal Component Correlation (PCC) was applied to all variables, and tested using the Monte-Carlo Attributes in Ordination (MCAO) permutation test (seed value = 1235, 1000 iterations). PCC vectors were plotted on ordination figures if the percentage of MCAO permutation r-squared values that exceeded the real r-squared (the r-squared value from the real groups) was less than or equal to 5%, and coded as follows: *** = 0%, ** = 1%, * = 2-5%.

Following ordination, habitat axes were investigated individually, using Multivariate Analysis of Variance (MANOVA) of hydrogeomorphology (width, depth, and velocity) and water quality variables (conductivity, temperature, dissolved oxygen, and pH). Tukey's HSD post hoc test was used to identify homogeneous subsets. Repeated measures testing was not applied because habitat was assessed at random sampling points within each site during each sampling date, rather than tracking dynamics at a specific point within each site through time (M. Steele, School of Mathematical and Physical Sciences, James Cook University, *pers. comm*. 2006). Other vegetation and substrate variables (i.e. percent cover and percent bank length) did not conform to the assumptions of normality for ANOVA testing because values were usually either 0% or 100% within microhabitats. Dissolved oxygen data from site 4 during the October 2003 sampling date was unreliable due to a faulty meter, so these values were replaced with the mean dissolved oxygen concentration and saturation of all water quality samples collected during that round of sampling (7.65 mg/L, 99.7% saturation).

3.3 Results

3.3.1 Relative importance of habitat axes in determining spatial and temporal habitat variability

The relative importance of hydrogeomorphological, vegetation, and water quality variables in determining the composition of main-channel fish habitats varied both spatially and temporally. While hydrogeomorphology variables were most important in determining spatial variability between sites, a combination of vegetation and water quality variables accounted for much of the temporal variability in fish habitats between sampling dates. In general, the distribution of sites in ordination space reflected their major habitat features (section 3.2.1), with a range of habitat types available – from shallow, fast-flowing areas with aquatic macrophytes and sand substrate, to deep, slow-flowing pools with mud substrate, overhanging vegetation and woody debris. In particular, there was a significant difference between sites 1 and 4 and sites 2 and 3 in ordination bi-plots (Figure 3.8a and b; ANOSIM, Real F = 1.187, Best F = 1.114, % randomized F > real F = 0). Sites 1 and 4 were positioned to the lower right hand side of the bi-plots and were correlated with shallow depths and sandy substrates. In contrast, sites 2 and 3 were positioned to the upper left hand side of the bi-plots and were correlated with wider, deeper channels and mud substrate.

PCC vectors representing deep and shallow undercut banks were significantly correlated with the distribution of study sites, particularly site 1 (Figure 3.8c). Instream and littoral vegetation was most common at sites 2, 3, and 4 (Figure 3.8d). While relatively little instream vegetation was found at site 1, terrestrial leaf litter was common in depositional areas. Structural vegetation elements, such as woody debris and root masses exhibited more complex relationships between sites and seasons, which are discussed later. Lastly, higher temperature, conductivity, and pH values were associated with sites 1 and 4, especially during the dry season (Figures 3.8d). Although sites differed in their habitat characteristics, each site responded in a similar manner to high flow events, with each site following a similar trajectory through ordination space (Figure 3.9). All sites increased in width, depth and, consequently, the amount of vegetation overhanging the channel during the wet season. Increased scour activity at this time led to greater amounts of exposed root mass and the recruitment of small woody debris to the channel.

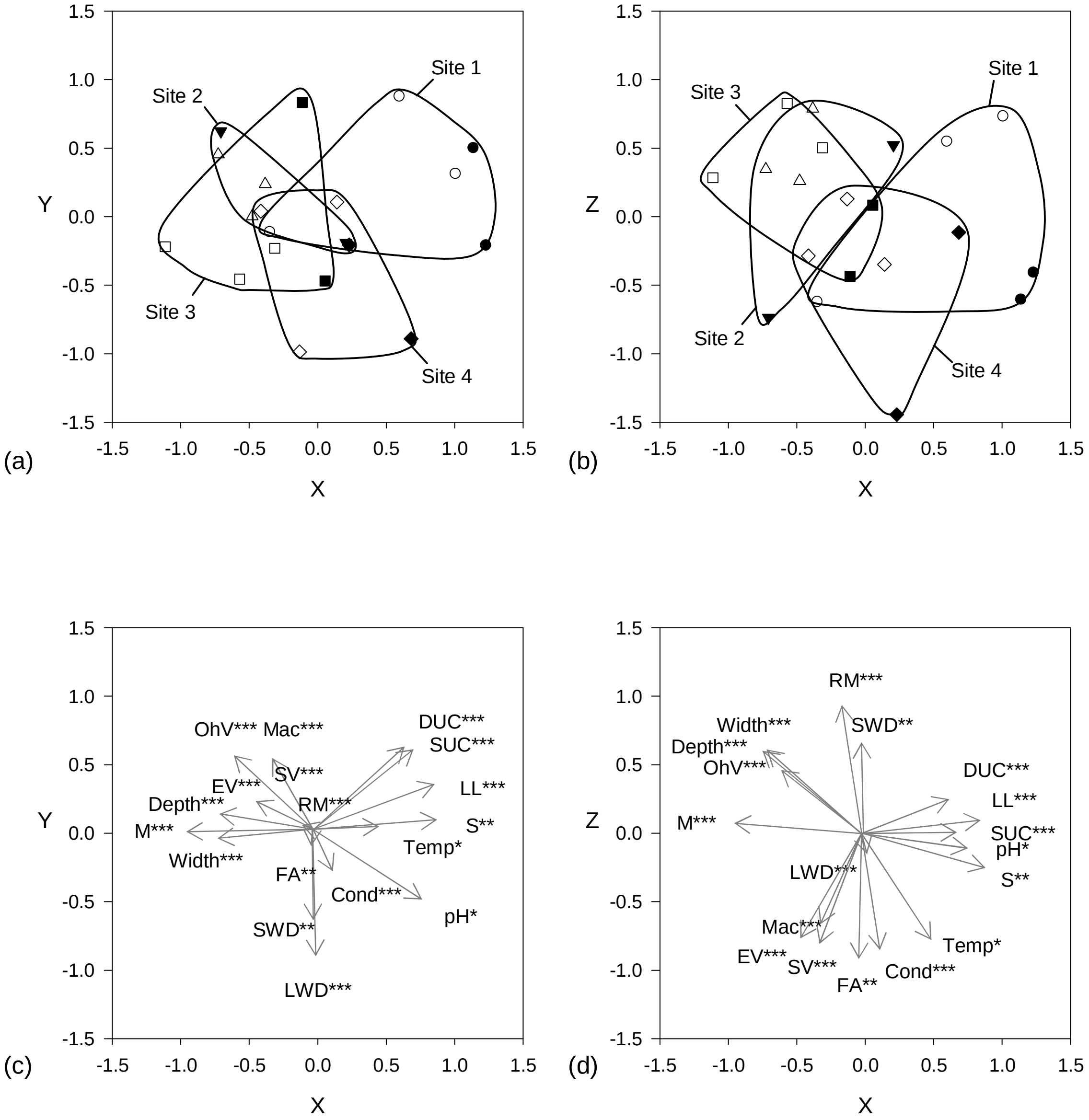


Figure 3.8 The distribution of study sites in three-dimensional ordination space, as defined by SSH MDS of habitat variables (Gower-Metric, stress = 0.1447), during wet (open) and dry (shaded) season sampling dates (a, b) (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). PCC vector lines (including temperature (Temp), conductivity (Cond) and pH) are shown with MCAO r-squared values (c, d); *** = 0%, ** = 1%, * = 2-5%. Hydrogeomorphology and vegetation vector codes are provided in Table 3.2. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space.

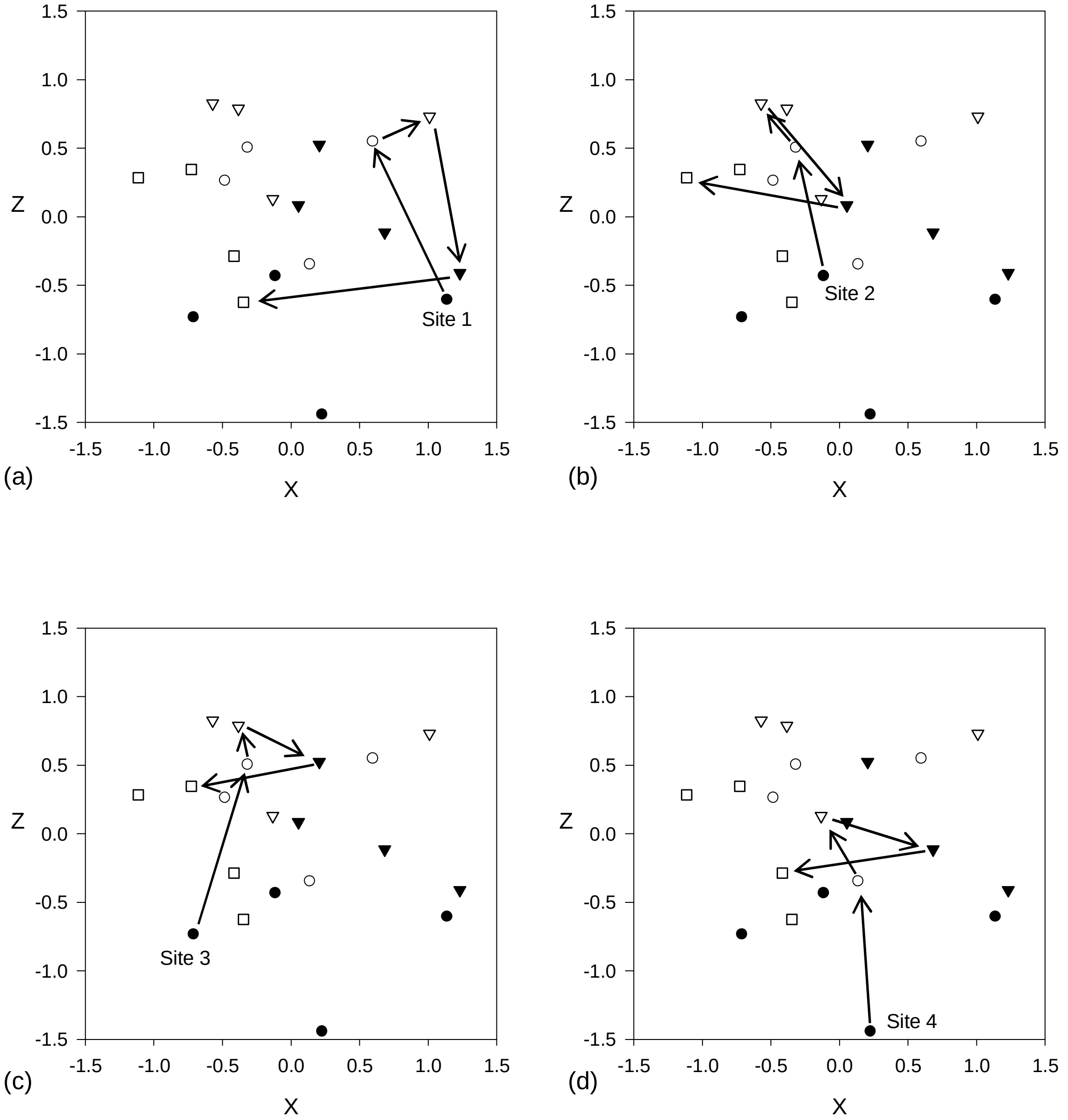


Figure 3.9 The temporal shifts in habitat characteristics of each study site relative to axes X and Z of the three dimensional SSH MDS ordination presented in Figure 3.8 (Gower-Metric, stress = 0.1447), during wet (open) and dry (shaded) season sampling dates conducted in October 2003 (●), April 2004 (○), June 2004 (▽), October 2004 (▼) and May 2005 (□). The PCC vectors relating to these ordination axes are presented in Figure 3.8d.

3.3.2 Analysis of individual habitat axes

3.3.2.1 Hydrogeomorphology

Hydrogeomorphological variables varied substantially between sites and, to a lesser extent, sampling dates. A two-factor MANOVA of mean depth, wetted width and velocity showed significant differences between sites and between sampling dates, along with a significant interaction (Table 3.3). Mean water depths at sites 1 and 4 were significantly less than those at sites 2 and 3 throughout the study, while depth was significantly higher during the wet season sampling dates (October 2003 and October 2004) than during the dry season (June 2004, April 2004, and May 2005) (Table 3.4 and Figure 3.10). Both mean wetted width and velocity showed significant interactions between sites and dates (Table 3.4). However, all sites were wider and exhibited higher flow velocities under wet season conditions than during the dry season (Figures 3.11 and 3.12). Site 1 had the highest flow velocities of all the sites (Figure 3.12), particularly during the wet season sample, which probably contributed to the relative abundance of undercut banks (Figure 3.13). Flow velocity also influenced the substrate composition at each site. Sites 2 and 3 were wider, deeper and had lower mean velocities than sites 1 and 4. Sites 1 and 4 had predominantly sand substrates, whereas sites 2 and 3 were characterised by mud substrate (Figure 3.14). Although mean substrate composition did not vary substantially between dates, it is important to note that substrate was patchy at the microhabitat scale, usually either 100% sand or 100% mud, depending on microhabitat-scale processes of scour and deposition.

Table 3.3 Within-treatment multivariate test results (MANOVA, Pillai's Trace) for hydrogeomorphology variables (width, depth and velocity). * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Treatment	d.f.	*F*
Site	9, 1023	43.31***
Date	12, 1023	17.66***
Site X Date	36, 1023	2.904***

Table 3.4 Results of between-subjects ANOVA testing on individual hydrogeomorphology variables. * $p<0.05$, ** $Pp<0.01$, *** $p<0.001$.

		***F*-value and significance level**		
Treatment	**d.f.**	**Depth (m)**	**Width (m)**	**Velocity (m/s)**
Site	3, 341	10.34***	368.28***	21.18***
Date	4, 341	4.11**	56.46***	9.45***
Site X Date	12, 341	0.36	6.47***	2.92***

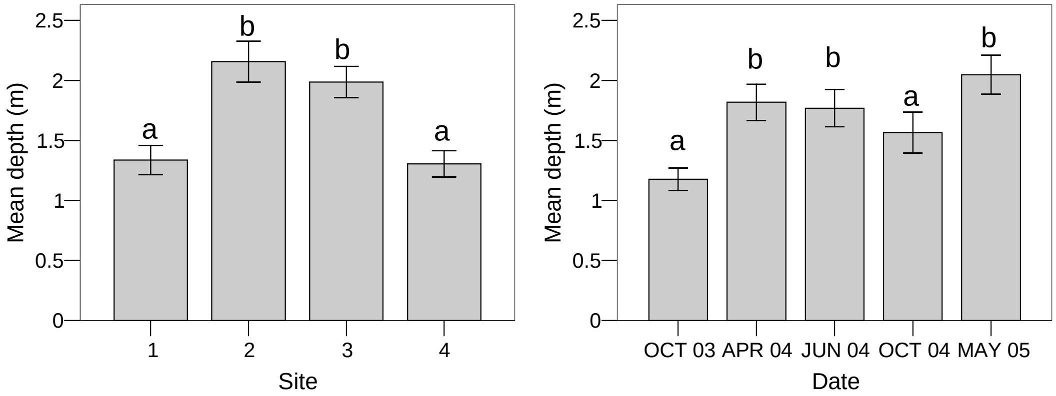


Figure 3.10 Mean depth (±SE) of sites 1 to 4 (pooled across sampling dates) and sampling dates (pooled across sites), with homogeneous subsets determined by Tukey's HSD *post hoc* testing.

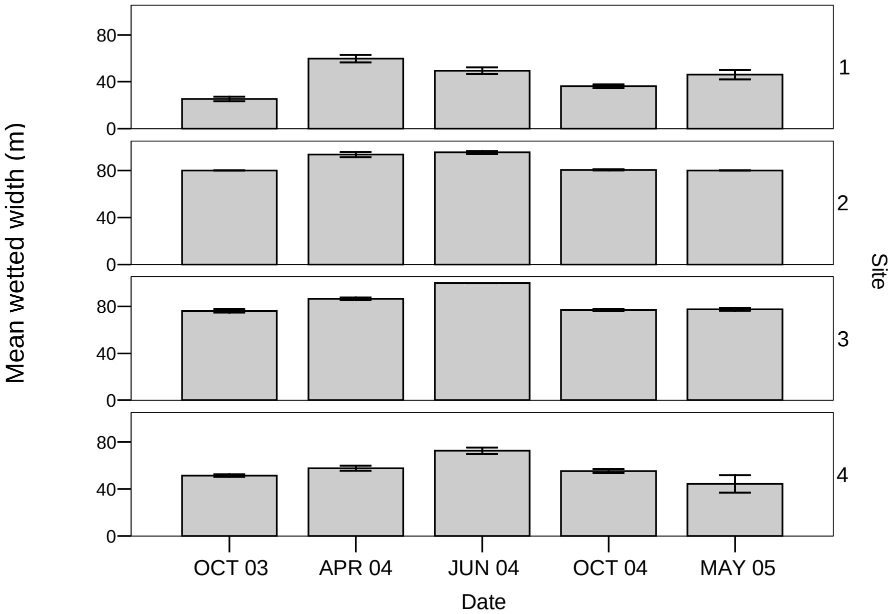


Figure 3.11 Mean wetted width (±SE) of sites 1 to 4 during each sampling date.

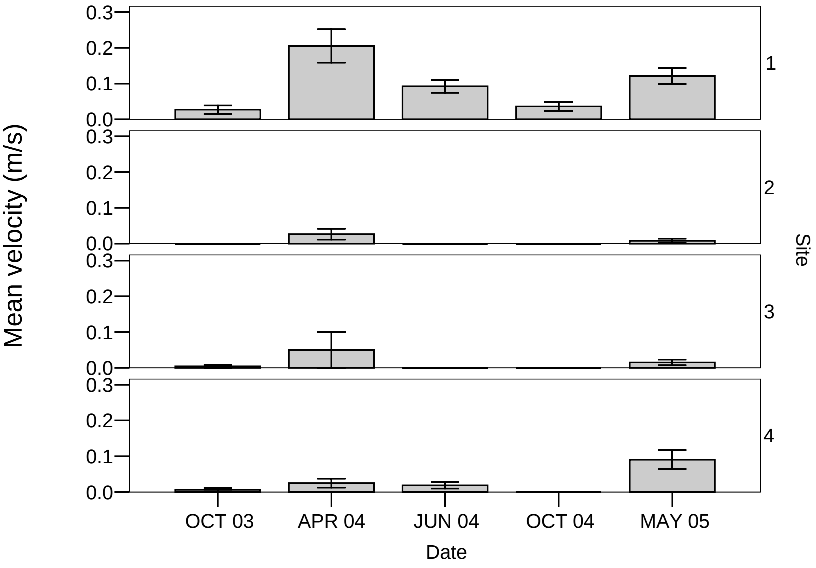


Figure 3.12 Mean flow velocity (±SE) of sites 1 to 4 during each sampling date.

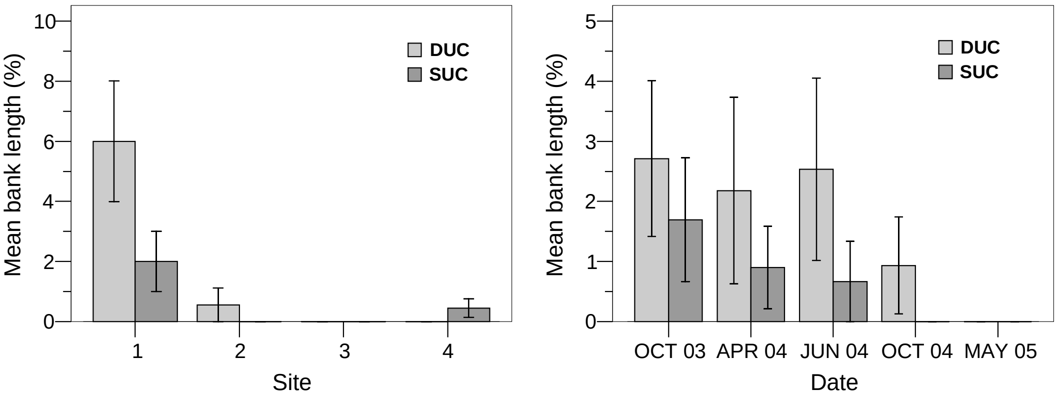


Figure 3.13 Mean percent bank length (±SE) occupied by deep (DUC) and shallow (SUC) undercut banks at sites 1 to 4 (pooled across sampling dates) and for each sampling date (pooled across sites).

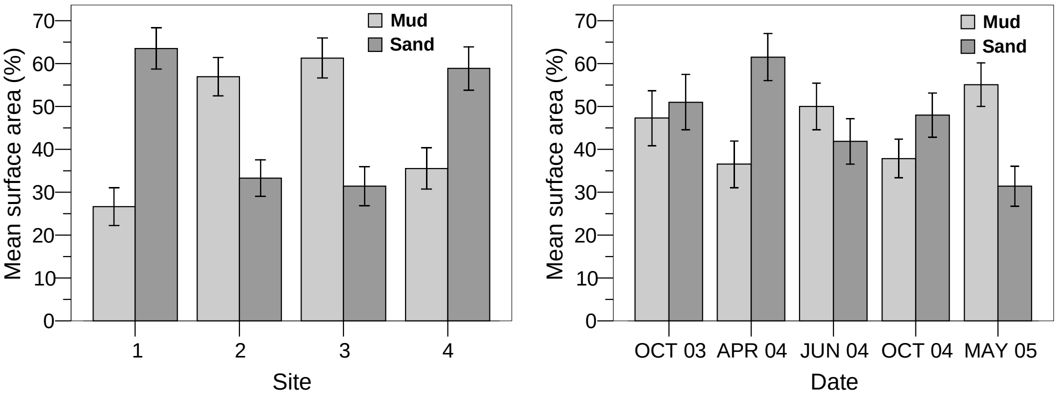


Figure 3.14 Mean percent surface area (±SE) covered by mud and sand substrate at sites 1 to 4 (pooled across sampling dates) and for each sampling date (pooled across sites).

3.3.2.2 Vegetation

Vegetation variables were more strongly related to seasonal flows than to hydrogeomorphological variables and, as a result, accounted for much of the temporal variation in fish habitats across the sites (Figure 3.8). The response of vegetation to elevated wet season flows was consistent across sites, with the location of sites in ordination space determined by their 'starting' conditions. In ordination bi-plots, wet season samples were located to the upper left of the total range of conditions for each site, wheras dry season samples were positioned to the lower right (Figure 3.8b).

During the first dry season sample (October 2003), all categories of instream and littoral vegetation were abundant. However, following the elevated flows of the 2004 wet season, macrophytes, submerged vegetation, emergent vegetation, and filamentous algae were removed from the study area by reworking of the river bed (Figure 3.15b). In contrast, structural vegetation variables, namely overhanging vegetation and exposed root masses, increased during the wet season (Figure 3.15d), due to increased channel width (i.e. the water's edge moved under riparian trees) and bank scour. As a result of these seasonal dynamics, habitats during the October 2004 sampling period were generally more similar to the preceding wet season (June 2004) than the previous dry season (Figure 3.9).

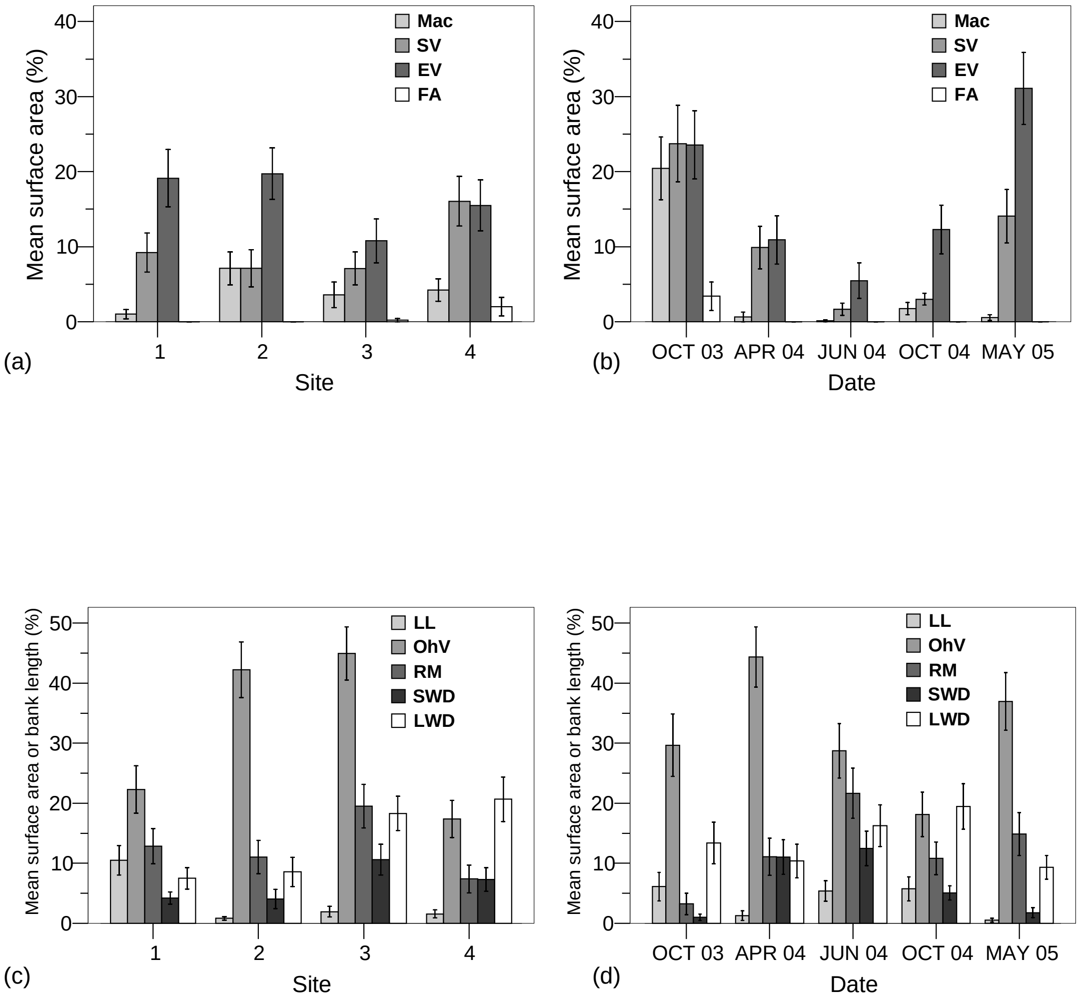


Figure 3.15 Mean percent surface area or bank length (LWD, SWD, and OhV) (±SE) covered by vegetation variables at sites 1 to 4 (pooled across sampling dates, a and b) and for each sampling date (pooled across sites, c and d). See Table 3.2 for variable codes.

3.3.2.3 Water quality

Spatial variability in water quality was limited. There was no evidence of stratification, even under low-flow dry season conditions (Appendix 1). Two-factor MANOVA of water quality parameters identified significant differences between both sites and sampling dates (Table 3.5). The only significant interaction term was in the case of conductivity (Table 3.6). This was due to the greater tidal influence at site 4, the most downstream site, during the October 2003 dry season sampling date (Figure 3.16). At this time conductivities of up to 340 µS/cm were recorded at site 4, and over 13000 µS/cm at high tide approximately 3 km further downstream.

Mean temperature, dissolved oxygen concentration (% saturation) and pH differed significantly between sampling dates (Table 3.6). Mean temperature was highest during dry season sampling dates (~28 °C in October 2003 and 2004) and lowest during wet season samples (21-23 °C in June 2004 and May 2005; Figure 3.17b). Variation in mean dissolved oxygen concentration (spot measures) showed no distinct seasonal pattern (Figure 3.17d). As with temperature, pH was significantly higher during the dry season than during the wet season (Figure 3.17f). There were also significant differences in mean pH between sites (*p*=0.044; Table 3.6), although post hoc testing (Tukey’s HSD) did not identify any homogeneous subsets (Figure 3.17e).

Table 3.5 Within-treatment multivariate test results (MANOVA, Pillai’s Trace) for water quality variables (conductivity, dissolved oxygen concentration, temperatures and pH). * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Treatment	d.f.	*F*-value and significance level
Site	12, 57	3.89***
Date	16, 80	9.10***
Site X Date	48, 80	1.32

Table 3.6 Results of between-subjects ANOVA testing on individual water quality variables. * *p*<0.05, ** *p*<0.01, *** *p*<0.001.

		***F*-value and significance level**			
Treatment	**d.f.**	**Conductivity (μs/cm)**	**Dissolved Oxygen (% sat.)**	**Temperature (℃)**	**pH**
Site	3, 20	115.62***	0.61	0.03	3.23*
Date	4, 20	129.51***	7.30*	86.86***	19.95***
Site X Date	12, 20	115.44***	1.47	0.48	0.51

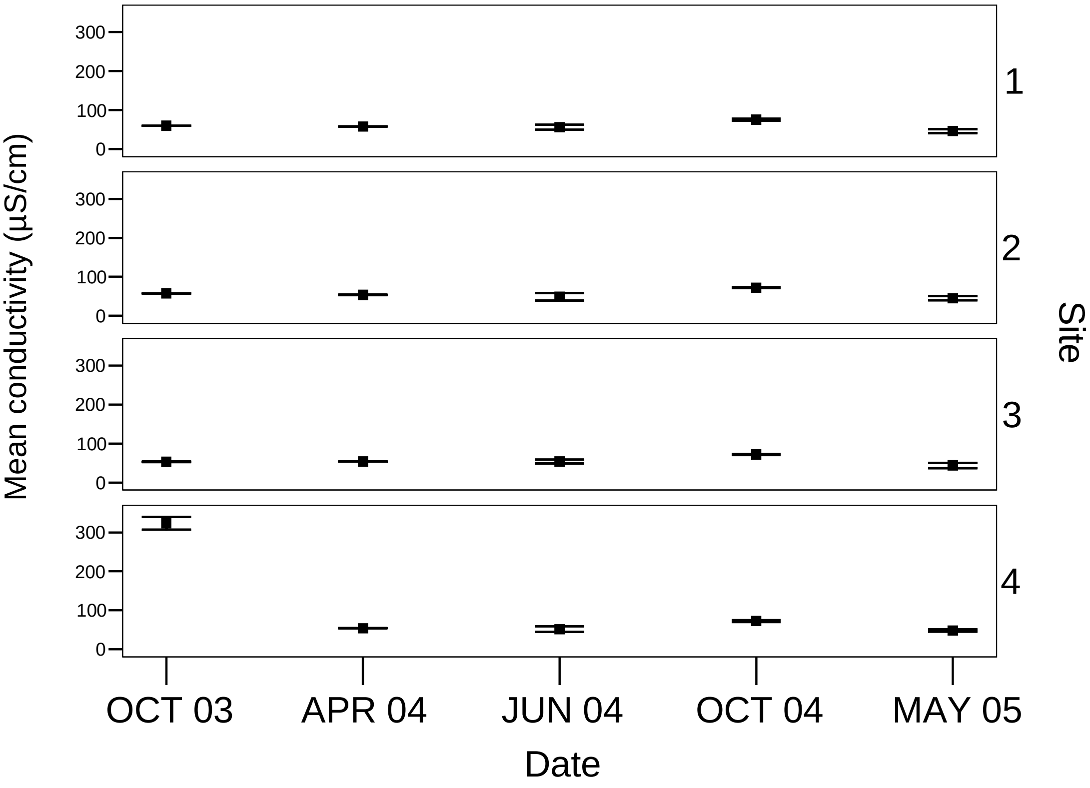


Figure 3.16 Mean conductivity (µS/cm ±SE) of sites 1 to 4 during each sampling date. The higher conductivity at site 4, and to a lesser extent during the dry season samples (October 2003 and October 2004), was due to the greater tidal penetration in the lower reaches of the Mulgrave River at this time.

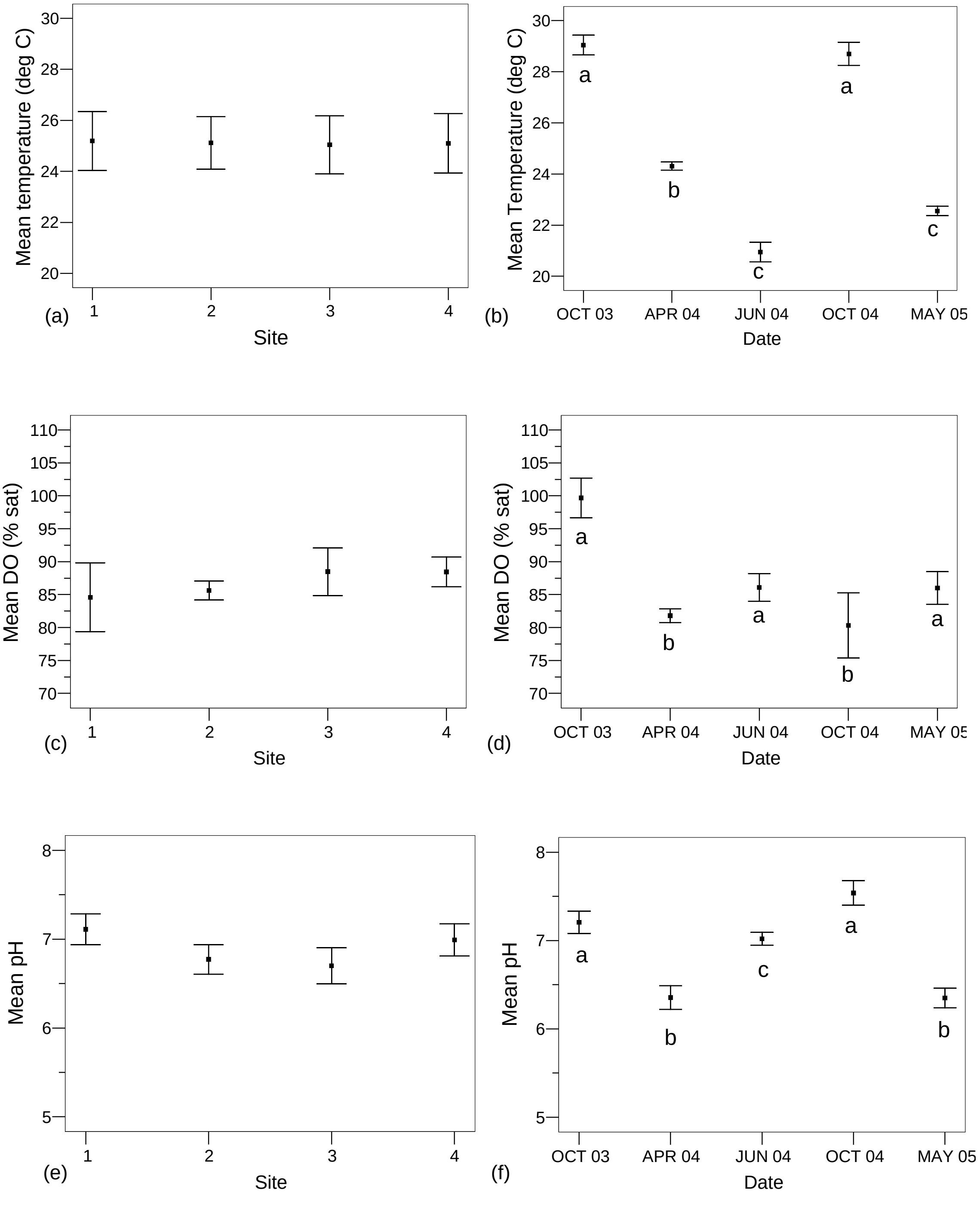


Figure 3.17 Mean temperature (a, b), dissolved oxygen (DO, percent saturation, c, d), and pH (e, f) of sites 1 to 4 (pooled across sampling dates ±SE) and sampling dates (pooled across sites), with homogeneous subsets determined by Tukey's HSD *post hoc* testing.

3.4 Discussion

The flow regime is a major determinant of aquatic habitat structure, which in turn is a major determinant of fish and invertebrate community composition (Gorman and Karr, 1978; Angermeier and Karr, 1983; Benke, 2001; Bunn and Arthington, 2002). In large, undisturbed tropical rivers, highly predictable seasonal flow regimes increase the extent and diversity of aquatic habitats by increasing the degree of connectivity between main-channel and floodplain areas (Junk *et al.*, 1989). In Wet Tropics rivers, however, the incision of the main-channel relative to the surrounding floodplain increases the probability that high flow events will be erosive rather than expansive. Unlike expansive floods, that typically inundate floodplains for several months, erosive floods are characterised by a short pulse of fast-moving, turbulent water, with the power to entrain substrates. Matthews (1998, p.329) listed the following short-term effects of erosive floods on instream fish habitats:

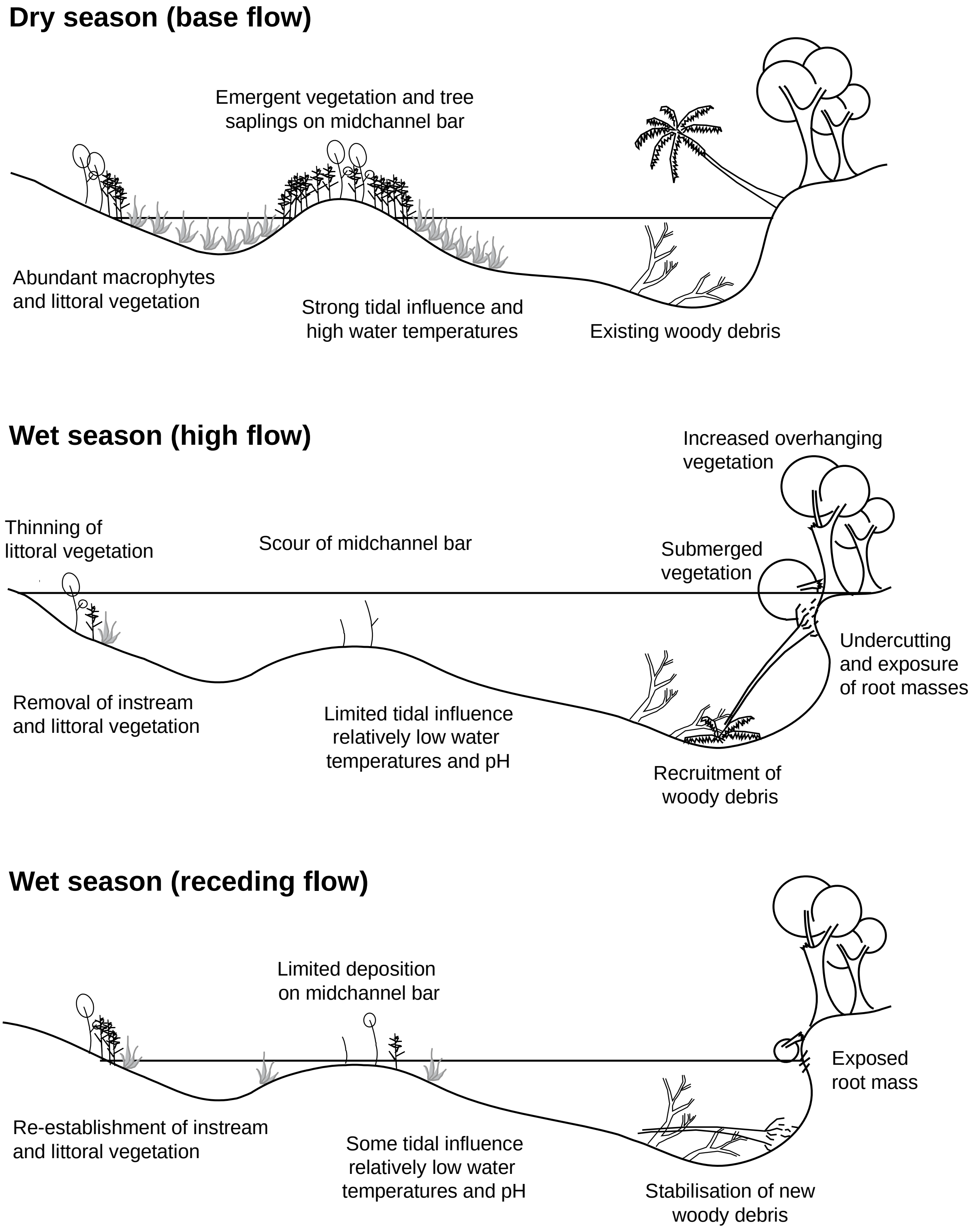
- scouring of the channel bed and removal of silt and organic debris;
- removal of algae and macrophytes;
- maintenance of channel morphology by removal of littoral vegetation that stabilises midchannel bars;
- erosion of banks, with potential in-filling of existing pools (and exposure of root masses);
- removal of gravel where fish spawn and destruction of fish nests; and
- removal or deposition of large woody debris.

In the present study, main-channel habitats varied spatially, across the lowland reach of the Mulgrave River, as a function of their hydrogeomorphological characteristics: width, depth, velocity and substrate. While this spatial variability was important in providing a variety of habitats across the lowland reach of the river, all sites reacted similarly to the large increase in discharge during March 2004. This highly erosive event not only triggered all of the immediate responses listed by Matthews (1998), but also initiated a series of habitat changes, the effects of which lasted for more than 12 months. While hydrogeomorphology and water quality variables responded immediately to high flow conditions but quickly returned to their pre-flood levels, instream and littoral vegetation was almost completely removed from the study area. Only emergent vegetation, consisting mostly of damaged Para grass (*Urochloa mutica* (Forssk.) T.Q. Nguyen), which is a highly flood tolerant and invasive weed (Bunn *et al.*, 1998), had recovered to pre-flood levels by May 2005.

A conceptual model of main-channel habitat dynamics in a Wet Tropics river is presented in Figure 3.19. During the dry season, aquatic macrophytes, combined with emergent vegetation and tree saplings, colonise and stabilise mid-channel bars. At this time, dense littoral vegetation covers river margins and filamentous algae blooms in warm, shallow backwaters, adding to the diel fluctuation of dissolved oxygen. With low flow velocities throughout the lowland main channel, higher water temperatures (up to 32 °C) reflect the lengthy water residence times at this time of year and are unusually high, given the ambient air temperatures at this time of year (Figure 2.3). Low discharge also increases the tidal influence further inland. In the Mulgrave River under baseflow conditions, freshwater is pushed ~20 km upstream by the incoming tide, resulting in increasing conductivity and dissolved oxygen concentrations in downstream areas.

With the onset of the wet season, increased flow velocities mobilise bed sediments, causing substantial scour of midchannel bars and river banks. These geomorphological changes are accompanied by a reduction in the abundance of instream and littoral vegetation. Meanwhile, woody debris is recruited to the channel where bank scour occurs and higher water levels result in an increased influence of overhanging riparian vegetation, submerged littoral vegetation, and exposed root masses. During the wet season, precipitation in upland rainforests is quickly transported to the lowland main-channel; shorter water residence times limit instream temperatures and reduce the pH of river water, because rainwater is naturally more acidic (due to CO_2, NO, and SO_2; Hart *et al.* 1987). In addition, the force of high discharges also limits upstream tidal penetration and conductivity is low (<30 µS/cm).

Following the flood peak, habitat variables in the main-channel enter a transition mid-way between the conditions of the wet season and those of the dry season. As flood waters recede, so too does wetted width, water depth and flow velocity across the lowland reach of the river. Limited deposition of sand and organic matter occurs across the channel, but particularly on and around mid-channel bars. As substrates stabilise, aquatic plants begin to slowly expand from small patches (<1 m^2) remaining after the flood. In deeper areas of the channel, newly recruited woody debris adds to existing snags and continues to influence local scour and deposition. Lastly, the tidal influence becomes more important in determining water quality conditions in the main channel, although water temperatures remain relatively low (~21-23 °C) until later in the dry season.



Dry season (base flow)

Wet season (high flow)

Wet season (receding flow)

Figure 3.19 A conceptual model of seasonal fish habitat dynamics in the main channel of a typical Wet Tropics river.

This model represents the first assessment of temporal habitat variability in a lowland Wet Tropics river. However, it must be viewed within the context of processes operating at larger scales (Frissell *et al.*, 1986; Bis *et al.*, 2000; Hamilton and Gehrke, 2005). As discussed in chapter 1, most research in the Wet Tropics to date has been conducted as snapshots at larger spatial scales (Hortle and Pearson, 1990; Pusey *et al.*, 1995a; Pusey and Kennard, 1996; Russell *et al.*, 1996; Pusey *et al.*, 1998; Russell *et al.*, 2003). For example, Pusey *et al.* (1995a) and Russell *et al.* (1996) surveyed sites across the Mulgrave River catchment, with a greater emphasis on smaller tributaries than the main-channel. Their results, combined with more recent modeling work (e.g. Pusey *et al.* 2000b), emphasise the importance of catchment level factors, such as the presence of instream barriers in determining the presence/absence of species abundance at individual sites. Nonetheless, as Pusey *et al.* (1996) stated, most Wet Tropics rivers share a similar array of habitats (with the exception of floodplain lagoons) and, therefore, the model presented in this chapter may apply to other catchments in the region that feature deeply incised main channels.

3.5 Conclusion

The results of this chapter clearly show that all three ‘axes’ of fish habitat – hydrogeomorphology, vegetation and water quality – are highly responsive to seasonal flows. However, while hydrogeomorphology and water quality respond to a reduction in discharge at the end of the wet season by returning to pre-flood conditions, instream vegetation can take more than 12 months to recolonise the channel following a high-flow disturbance event. In general, the influences of instream vegetation on fish habitat are greater during the dry season, whereas structural elements such as exposed root masses, small woody debris and submerged and overhanging vegetation are more influential during the wet season.

Chapter 4: Spatial and temporal variability in invertebrate community structure

4.1 Introduction

The diversity of habitats found in tropical rivers provides a wide range of potential food resources for freshwater fish, including algae, vegetation, detritus, invertebrates and other fish (Welcomme, 1979). Kennard *et al.* (2001) reviewed the published dietary data for 127 of Australia's freshwater fish species (including 13 introduced species), finding that aquatic insects were the most important dietary component, contributing almost 35% of the total mean diet. Other important food categories were microcrustaceans (14.4%), algae (8.5%), terrestrial items (8%) macrocrustaceans (6.4%) and fish (4.2%). Kennard *et al.* (2001, p.31) also reported substantial regional variation in fish diets, suggesting that this pattern may be the result of a complex interaction between regional variation in food availability and phylogenetic constraints on the foraging of individual species. This suggestion is consistent with the international literature, which has repeatedly identified the importance of food availability in determining the feeding rates of fish (Lowe-McConnell, 1963; Goulding, 1980a; Xie *et al.*, 2000), the degree of dietary overlap between individual species (Ross, 1986; Matthews, 1998), and, therefore, the structure and function of fish assemblages (Zaret and Rand, 1987; Winemiller, 1989, 1992b).

Despite the fact that resource-mediated shifts in fish diets are considered more the norm than the exception (Werner and Gilliam, 1984; Little *et al.*, 1998), the majority of researchers examining the trophic dynamics of freshwater fishes have not collected contemporaneous food-availability data (e.g., Blaber *et al.*, 1994; King, 2005). Instead, they have chosen to rely upon the gut fullness of individual fish – a highly variable parameter (Piet and Guruge, 1997) – as a surrogate for overall food availability, and upon dietary composition as an indicator of the abundance of prey items in the environment. A notable exception to this trend was Pusey and Bradshaw's (1996) dietary assessment of six fish species from seasonally inundated wetlands in Western Australia. They sampled invertebrate communities and found that abundances tended be high throughout the year, with zoobenthos densities commonly above 5000 individuals.m^{-2}. Approximately 70% of this benthic fauna was chironomid larvae, that were heavily consumed by species with relatively small mouths. In contrast, species with larger mouths consumed a greater proportion of terrestrial invertebrates, particularly ants (Pusey and Bradshaw, 1996).

A range of factors regulate aquatic invertebrate communities found in littoral, benthic and adjacent riparian habitats (Malmqvist, 2002). As Minshall (1984, p.367) summarised, both the abundance and diversity of invertebrates generally increase with the size, stability and heterogeneity of the substratum. However, these variables often interact with other factors, such as flow velocity (Hart and Finelli, 1999), the presence of vegetation (Newman, 1991), light intensity (Holt and Waters, 1967) and water quality (Rabeni and Minshall, 1977) to determine the suitability of an area as habitat for individual invertebrate species (Minshall, 1984, p.379). In the main channels of lowland rivers, sediments are generally fine (i.e., sand or silt), unstable and homogeneous (Leopold *et al.*, 1964; Dietrich and Dunne, 1978). Under these conditions, aquatic invertebrates may occur at lower densities and/or diversities than in upstream or floodplain areas (Adis and Junk, 2002; Sommer *et al.*, 2004) and are likely to be concentrated in patches with the most stable substrates (Effenberger *et al.*, 2006). For example, Benke *et al.* (1984) estimated that the standing stock biomass of invertebrates on woody debris in the lower Satilla River, USA, was 20-50 times higher than in sandy habitats and 5-10 times higher than in muddy habitats. This result may be linked to the presence of biofilms on the more stable wood substrates (Hax and Golladay, 1993).

Knowledge of aquatic invertebrate ecology is relatively well advanced in small streams across the Wet Topics region, owing to a series of experiments examining fine-scale processes (Pearson and Connolly, 2000; Connolly *et al.*, 2004; Cheshire *et al.* 2005; McKie and Pearson, 2006) and region-wide assessments (Christidis, 2003; Pearson, 2004; McKie *et al.*, 2005) but limited in the lowlands (Connolly *et al.*, 2006). Connolly (unpublished data) surveyed four lowland streams in the Russell-Mulgrave catchment, finding that species richness declined downstream as a function of sediment size, with fine sediment specialists (e.g. larvae of caenid mayflies and leptocerid caddisflies) favouring the most downstream sites (Connolly *et al.*, 2006). To date, the only data that have been published for the main channels of lowland rivers in the Wet Tropics is a study of pollution in Babinda Ck in the Russell River catchment (Pearson and Penridge 1987) and a report on a broad survey of Wet Tropics rivers (Pearson and Penridge 1992). These authors identified the relative abundance of *Caridina* spp. (shrimp), Baetidae, Cryptocerata (Hempitera), Chironomidae and Trichoptera in these areas. However, at present there are no standardised estimates of invertebrate density per unit area in main-channel habitats.

I suggest that invertebrates will occur at lower densities in downstream sections of Wet Tropics rivers than in upstream areas, because these habitats are dominated by unstable sand substrates. In addition, the evidence presented in the previous chapter suggests that seasonal flows in these systems act as erosive disturbances, rather than gentle flood pulses. Given the poor connectivity between main-channel and floodplain areas, along with the degraded nature of the floodplain itself and the 'flashy' nature of wet season flows, there is little opportunity for the build up of 'huge stocks of water hyacinths, grasses, or other macrophytes' during the wet season, as predicted by the FPC (Winemiller, 2005, p.289). Instead, the reverse is true: instream and littoral vegetation accumulates in the main channel under base-flow conditions, before being removed by wet season floods (chapter 3).

As a result of these habitat dynamics, it is altogether possible that invertebrate abundances and densities may decline in main-channels during the wet season. If so, the concepts embodied in the riverine productivity model (Thorp and Delong, 1994) are likely be more applicable to Wet Tropics rivers than those of the flood-pulse concept (FPC; Junk *et al.*, 1989). That is, a combination of local autochthonous production, together with inputs from the riparian zone, probably represents the principal source of carbon driving aquatic food webs in these systems, especially during the dry season (Thorp and Delong, 1994). Additionally, invertebrates in littoral areas, particularly with grazing feeding modes, may constitute a much larger portion of the total invertebrate biomass than would be predicted by either the riverine continuum concept (Vannote *et al.*, 1981) or the flood-pulse concept (Junk *et al.*, 1989).

The aim of this chapter is to document the dynamics of invertebrate communities in the main channel of the Mulgrave River, under a range of flow conditions. As invertebrates form a major dietary component of Australian freshwater fishes (Kennard *et al.*, 2001), this description will provide a context for the discussion of fish feeding dynamics and food web structure in later chapters. In particular, I aim to test global paradigms of riverine function by asking: does invertebrate abundance in benthic and littoral habitats vary seasonally; if so, are these changes due to habitat disturbance by high flows; and how do these dynamics relate to instream productivity? An objective of this study is to incorporate invertebrate dynamics into the conceptual model of flow-mediated habitat dynamics developed in chapter 3.

4.2 Methods

4.2.1 Productivity

Phytoplankton biomass, measured as the concentration of chlorophyll *a* and phaeophytin, was used as a surrogate for riverine productivity (Webster *et al.*, 2005). One-litre water samples were collected at each site during each sampling date and stored on ice. They were analysed by the Australian Centre for Tropical Freshwater Research, James Cook University, within 24 hours of collection using standard spectrographic methods (APHA, 1998). Replicate samples within sites were not collected due to the cost of analysing samples. As a result, the hypothesis that chlorophyll *a* and phaeophytin concentrations varied between sites (pooled across sampling dates) and sampling dates (pooled across sites) was tested using separate one-factor ANOVAs for each variable, rather than a single two-factor MANOVA. The dataset was log transformed prior to analysis, in order to meet assumptions of normality and homogeneity of variance. Tukey's HSD *post-hoc* testing was then used to identify homogeneous subsets.

4.2.2 Invertebrate sampling and sorting

Invertebrate communities were sampled in littoral and benthic habitats. Littoral habitats were sampled using a triangular dip-net (25 x 25 x 25 cm x 63 µm mesh) and standardised by conducting five one-metre sweeps through littoral vegetation without making contact with the substrate. Benthic habitats were sampled using a van Veen grab (0.04 m^2). A total of 6-10 dip-net samples, and 9-13 benthic grab samples were collected at each site during each sampling date, according to fish sampling effort (Table 4.1). Samples were washed into a 20-L bucket before triple elutriation and preservation with 70% ethanol. In the laboratory, invertebrates greater than 500 µm in length (the minimum size of identifiable invertebrates in fish gut contents) were sorted into categories and counted. Nine invertebrate categories were used, based on those of Pusey *et al.* (1995b; 2004): aerial and surface invertebrates, aquatic insects, macrocrustaceans, microcrustaceans, molluscs other macroinvertebrates, other microinvertebrates, terrestrial invertebrates and unidentified (Table 4.2). The unidentified category, composed of mainly arthropod fragments, represented <1% of each sample. This category was excluded from ordination analyses, and calculation of diversity and evenness indices.

4.2.3 Statistical methods

Littoral dip-net (catch per unit effort, CPUE) and benthic grab (density) samples were analysed separately. Richness and evenness of broad invertebrate categories were calculated for each replicate sample. Non-parametric Kruskal-Wallis tests were used to test for differences between sites and sampling dates, as data were unevenly replicated (Table 4.1) and did not conform to ANOVA assumptions of normality or homogeneity of variance, even after transformation. MANOVA was used to test for differences in richness and evenness (Pielou, 1969, p. 223). Three-dimensional semi-strong hybrid multidimensional scaling (SSH MDS) was used for multivariate analysis of invertebrate samples (PATN Version 3.03 – Belbin, 1991). In order to identify the variables that were most important in determining spatial and temporal variation in community composition, Principal Component Correlation (PCC) was applied to invertebrate abundance data and habitat variables (including water quality and productivity measures) and tested using the Monte-Carlo Attributes in Ordination (MCAO) permutation test (seed value = 1235, 1000 iterations). PCC vectors were plotted on ordination figures if the percentage of MCAO permutation r-squared values that exceeded the real r-squared (the r-squared value from the real groups) was less than or equal to 5%, and coded as follows: *** = 0%, ** = 1%, * = 2-5%. While these percentages approximate p-values of <0.001, <0.01 and <0.05, respectively (Lee Belbin, *pers. comm.* 2005), because actual 'p-values' are not produced by MCAO testing, in this chapter I describe PCC vectors with 'significant' results as 'strongly' correlated with the distribution of sites in ordination space.

Table 4.1 The number of littoral dip-net (D) and benthic grab (G) replicates collected at each site during each sampling date.

Site no	Method	Oct 03	Apr 04	Jun 04	Oct 04	May 05
1	D	9	10	10	10	7
	G	11	13	13	13	9
2	D	6	10	9	10	10
	G	9	12	12	13	13
3	D	10	10	10	10	10
	G	13	13	13	13	13
4	D	7	10	10	10	6
	G	10	13	13	12	10

Table 4.2 Composition of broad invertebrate categories (after Pusey *et al.*, 1995b; 2004).

Broad category	Code	Fine category
Aerial and surface inverts	Air	Diptera – adults and emergers
		Water surface inverts – Gerridae etc.
		Collembola
Aquatic insects	Aqua	Chironomidae – larvae and pupae
		Ephemeroptera – larvae
		Trichoptera – larvae, including cases
		Simuliidae – larvae
		Odonata – nymphs
		Coleoptera – larvae
		Corixidae and Notonectidae – incl. *Plea*
		Other Hemiptera
		Other Diptera larvae (than Chironomidae)
		Coleoptera adults (aquatic spp.)
Macrocrustaceans	MacC	*Macrobrachium* spp.
		Atyidae
Microcrustaceans	MicC	Planktonic crustaceans – e.g., Cladocera and Copepoda
		Ostracoda
Molluscs	Moll	Mostly Gastropoda but including some Bivalvia
Other macroinvertebrates	OMac	Worms – mostly Nematoda and Planaria
Other microinvertebrates	OMic	Testate amoeba
		Hydra
Terrestrial invertebrates	Terra	Orthoptera (cricket hoppers)
		Hymenoptera
		Arachnida
		Small terrestrial inverts (<=5mm)
		Large terrestrial inverts (>5mm)
		Lepidoptera larvae (butterflies, moths)
Unidentified	Unid	Unidentified

4.3 Results

4.3.1 Productivity

Chlorophyll *a* and phaeophytin concentrations ranged from 0.2-16.6 and 0.2-8.2 µg/L, respectively. Mean concentrations of both variables were significantly higher during the dry season than during the wet season (Figure 4.1; Table 4.3). However, spatial variation was limited, with no significant difference in mean concentrations of either chlorophyll *a* or phaeophytin between sites, pooled across all dates (Table 4.3).

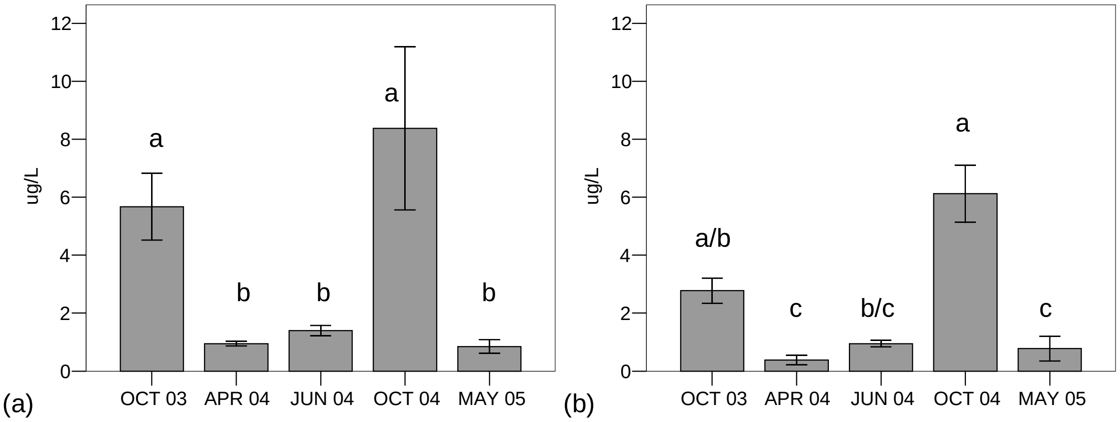


Figure 4.1 Mean concentration (µg/L ± SE) of (a) chlorophyll *a* and (b) phaeophytin, pooled across sites for each sampling date, with homogenous subsets determined by Tukey's HSD *post hoc* test.

Table 4.3 Results of one-way ANOVA tests performed on log-transformed mean chlorophyll *a* and phaeophytin concentrations between sites and sampling dates. Significant differences (*p*<0.05) are highlighted in bold.

Variable	Treatment	d.f.	*F*	*p*
Chlorophyll *a*	Site	3, 16	0.45	0.72
	Date	4, 15	15.76	**<0.001**
Phaeophytin	Site	3, 16	0.26	0.86
	Date	4, 15	14.39	**<0.001**

4.3.2 Littoral invertebrate communities

Invertebrate communities in littoral habitats were dominated by aquatic insects, microcrustaceans and macrocrustaceans (Table 4.4; Figure 4.2). Together these categories accounted for more than 85% of the total invertebrate abundance in an average sample (Table 4.4). The most common types of invertebrates within these broad categories were Ephemeroptera nymphs, Chironomidae larvae, Trichoptera larvae, Coleoptera larvae (mostly Elmidae), Corixidae and Notonectidae adults, other Hemiptera adults, Odonata nymphs, Atyidae shrimps, and Ostracoda. Spatial variation in the abundance of invertebrate categories was limited (Figure 4.2a): only four of the nine invertebrate categories differed significantly between sites, pooled across sampling dates (Table 4.4), and there was little differentiation of sites in ordination space (Figure 4.3). In contrast, seven of the nine categories differed significantly between sampling dates, pooled across sites (Table 4.4): the abundance of invertebrates was consistently higher in dry season samples (October 2003 and 2004) than in wet season samples (April, June 2004 and May 2005). The mean CPUE of aquatic insects, in particular, was significantly higher during the dry season than during the wet season (Figure 4.2b, Table 4.4). The maximum number of individuals recorded in a single sample was 462, at site 2 in October 2003.

Table 4.4 Descriptive statistics for broad invertebrate categories in littoral dip-net samples, across all sites and sampling dates, along with Kruskal-Wallis test results between sites (pooled across sampling dates) and sampling dates (pooled across sites). Significant differences are highlighted in boldface.

					Site (d.f.=3)		Date (d.f.=4)	
Method	**Variable**	**Max.**	**Mean**	**Std. Deviation**	**Chi-Squared**	**Asymp. Sig.**	**Chi-Squared**	**Asymp. Sig.**
Dip-net	Air	30	1.92	4.52	3.28	0.35	32.51	**0.00**
(N=184)	Aqua	344	17.14	37.66	10.13	**0.02**	20.93	**0.00**
	MacC	41	4.33	8.08	27.58	**0.00**	30.92	**0.00**
	MicC	286	6.33	28.81	2.61	0.45	67.26	**0.00**
	Moll	47	1.30	5.31	8.32	**0.04**	41.68	**0.00**
	OMac	2	0.11	0.37	11.22	**0.01**	6.66	0.15
	OMic	9	0.10	0.78	0.93	0.82	29.29	**0.00**
	Terra	9	0.72	1.55	0.21	0.98	11.88	**0.02**
	Unid	3	0.19	0.52	6.07	0.11	5.95	0.20

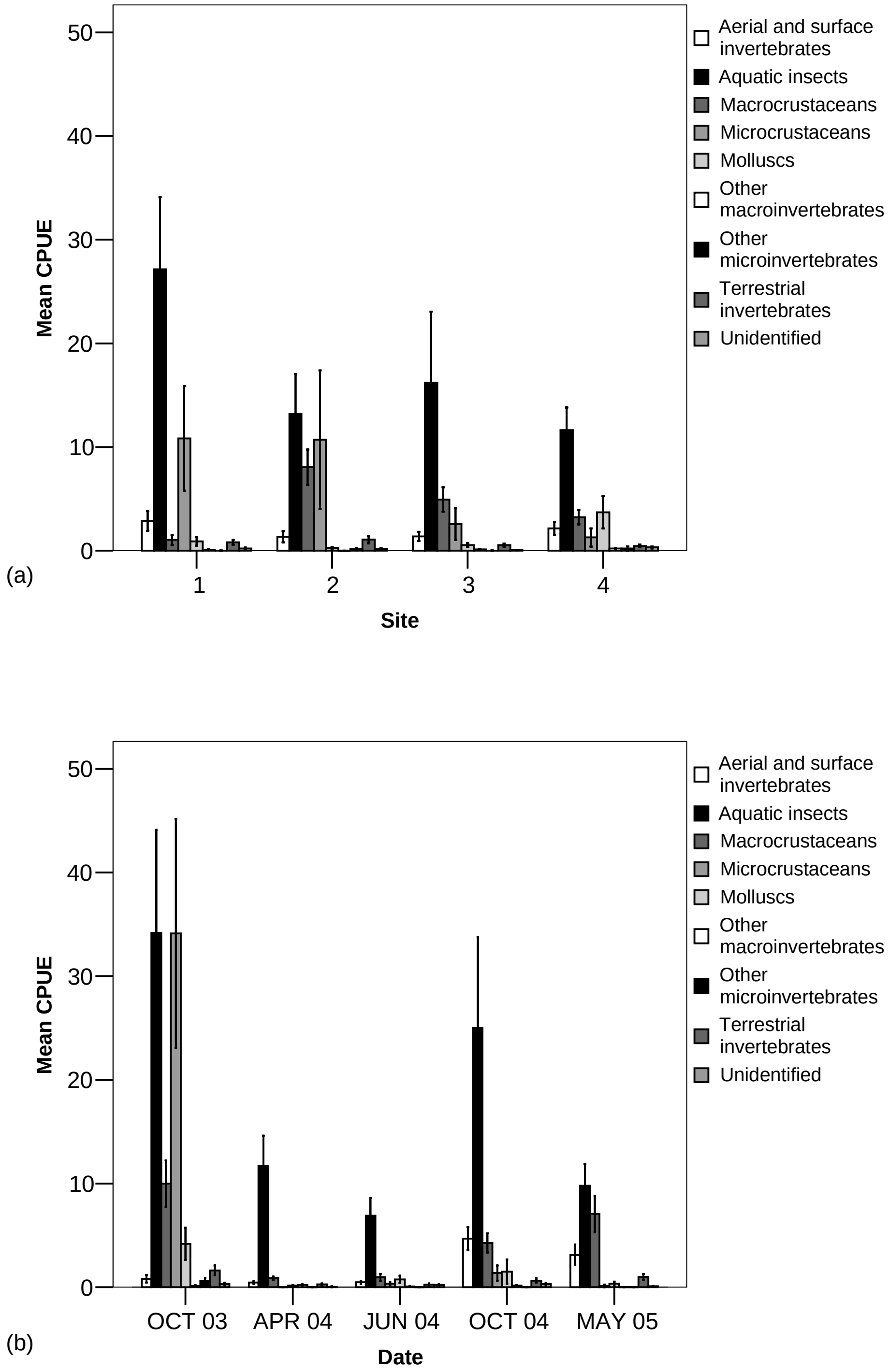


Figure 4.2 Mean catch per unit effort (± SE) of the nine invertebrate categories in littoral dip-net samples for sites, pooled across sampling dates (a), and sampling dates, pooled across sites (b).

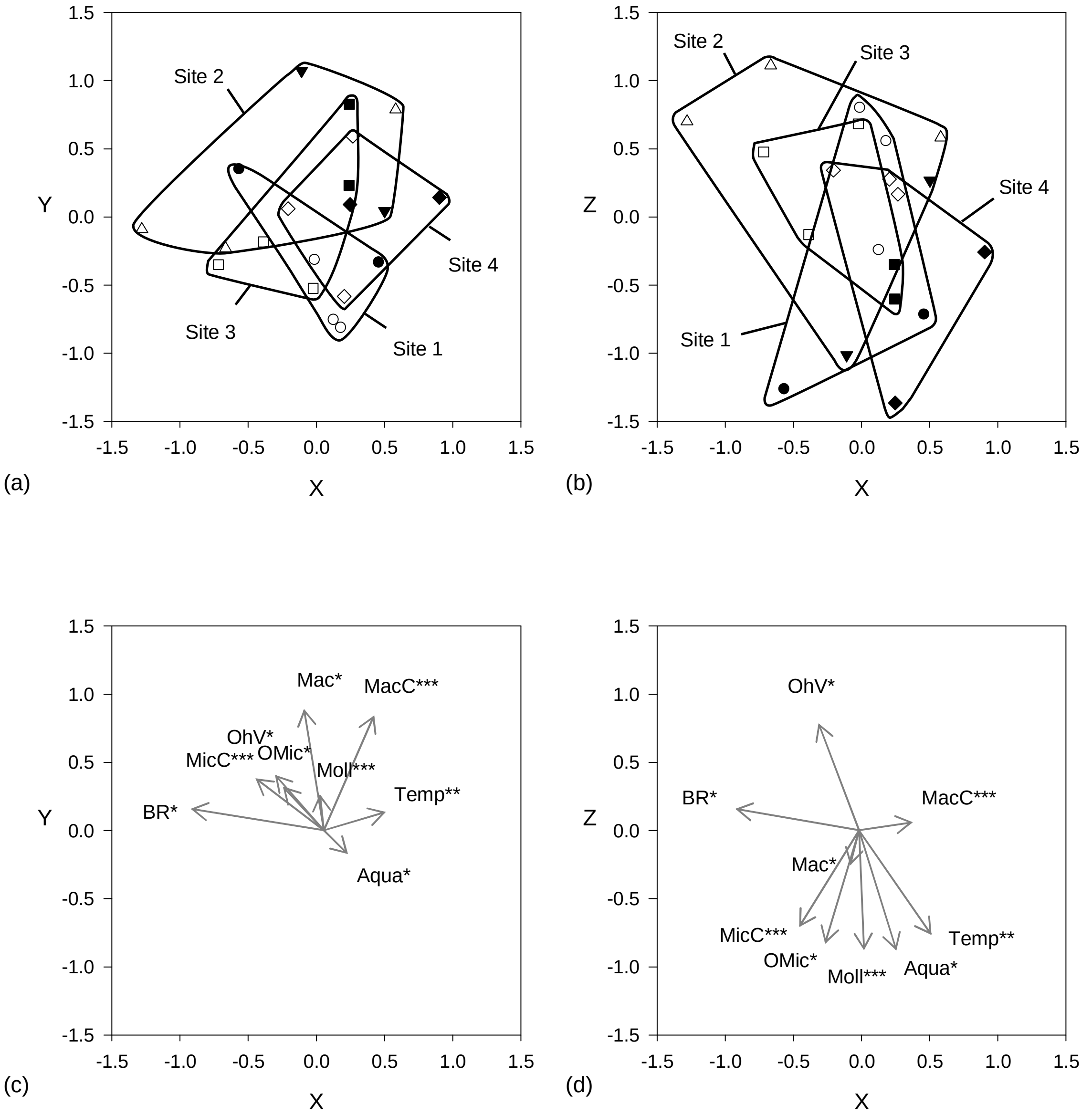


Figure 4.3 The distribution of study sites in three-dimensional ordination space (a, b), as defined by SSH MDS of littoral invertebrate communities (range standardised, Bray Curtis, stress = 0.1112), during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). PCC vector lines are shown with MCAO r-squared values (c, d): *** = 0%, ** = 1%, * = 2-5%. See Tables 3.2 and 4.2 for vector codes. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space.

The seasonal patterns of invertebrate abundance described above were reflected in the distribution of sites in ordination space. While sites overlapped considerably in their community composition, dry and wet season samples were very clearly delineated within the range of each site (Figure 4.3b). Dry-season samples were positioned to the bottom-right of Figure 4.3b, whereas wet-season samples were positioned to the upper-left. The PCC vectors with strong MCAO test results were the dominant invertebrate categories (aquatic insects, microcrustaceans, macrocrustaceans), along with other microinvertebrates and molluscs. Strongly correlated habitat variables were the percent surface area covered by bed-rock and macrophytes, the percent bank length covered by overhanging vegetation, and water temperature (Figure 4.3).

4.3.3 Benthic invertebrate communities

Benthic invertebrate communities were dominated by five broad categories: aquatic insects, microcrustaceans, molluscs, other macroinvertebrates and aerial and surface invertebrates (Table 4.5; Figure 4.4). Together these groups accounted for more than 85% of the total invertebrate density in an average sample (Table 4.5). The most common types of invertebrates within these broad categories were Chironomidae larvae, Trichoptera larvae, Coleoptera larvae (mostly Elmidae), Ephemeroptera nymphs, Corixidae and Notonectidae adults, and Ostracoda. Each of these categories differed significantly between sites (Table 4.5) and this spatial variation was reflected by the distribution of sites in ordination space (Figure 4.5). Sites 1 and 4, characterised by shallow, sandy habitats with relatively high flow velocities, had higher abundances of aquatic insects and other microinvertebrates and were positioned to the lower-left of Figure 4.4b, while sites 2 and 3, that overlapped almost entirely in ordination space, were positioned slightly to the upper-right. The latter sites were deeper and muddier, with a greater abundance of terrestrial invertebrates, probably related to the relatively high amount of overhanging vegetation.

Benthic invertebrate community structure also varied temporally, with six of the invertebrate categories differing significantly between sampling dates (Table 4.5). In general, densities were higher during the dry season than during the wet season, particularly for aquatic insects, microcrustaceans and molluscs (Figure 4.4b). The highest density – 13350 individuals.m^{-2}, comprising mainly shrimps, nematodes and chironomid larvae – was recorded at site 1 during the October 2004 sampling date. This strong seasonal variation in individual invertebrate categories was reflected in overall community structure. As shown in Figure 4.5b, dry season samples were associated with the increased importance of molluscs, aerial and surface invertebrates, microcrustaceans and aquatic insects – in line with the results of univariate testing (Table 4.5). In contrast, no invertebrate groups were strongly correlated with wet season samples. Habitat and water quality variables, shown to account for spatial and temporal variation between sites and sampling dates in chapter 3, that were also strongly correlated with benthic invertebrate community structure were: overhanging vegetation, submerged vegetation, width and velocity, all associated with wet season samples; and temperature, pH, conductivity, leaf litter, deep undercut banks, and chlorophyll *a* and phaeophytin concentrations, associated with dry season samples (Figure 4.5d).

Table 4.5 Descriptive statistics for broad invertebrate categories in benthic grab samples, across all sites and sampling dates, along with Kruskal-Wallis test results between sites and sampling dates. Significant differences are highlighted in boldface.

					Site (d.f.=3)		Date (d.f.=4)	
Method	**Variable**	**Max.**	**Mean**	**Std. Deviation**	**Chi-Squared**	**Asymp. Sig.**	**Chi-Squared**	**Asymp. Sig.**
Benthic grab	Air	4175	67.43	322.53	13.05	**0.00**	58.11	**0.00**
(N=241)	Aqua	5450	533.92	775.70	59.58	**0.00**	20.09	**0.00**
	MacC	50	1.45	7.07	2.73	0.44	1.22	0.87
	MicC	5650	163.17	690.96	22.49	**0.00**	54.12	**0.00**
	Moll	6500	112.14	472.46	31.99	**0.00**	13.29	**0.01**
	OMac	5550	81.22	381.44	40.87	**0.00**	10.28	**0.04**
	OMic	1500	7.99	98.48	5.38	0.15	4.48	0.35
	Terra	350	38.38	59.51	48.19	**0.00**	9.64	0.05
	Unid	150	8.20	22.07	4.84	0.18	15.40	**0.00**

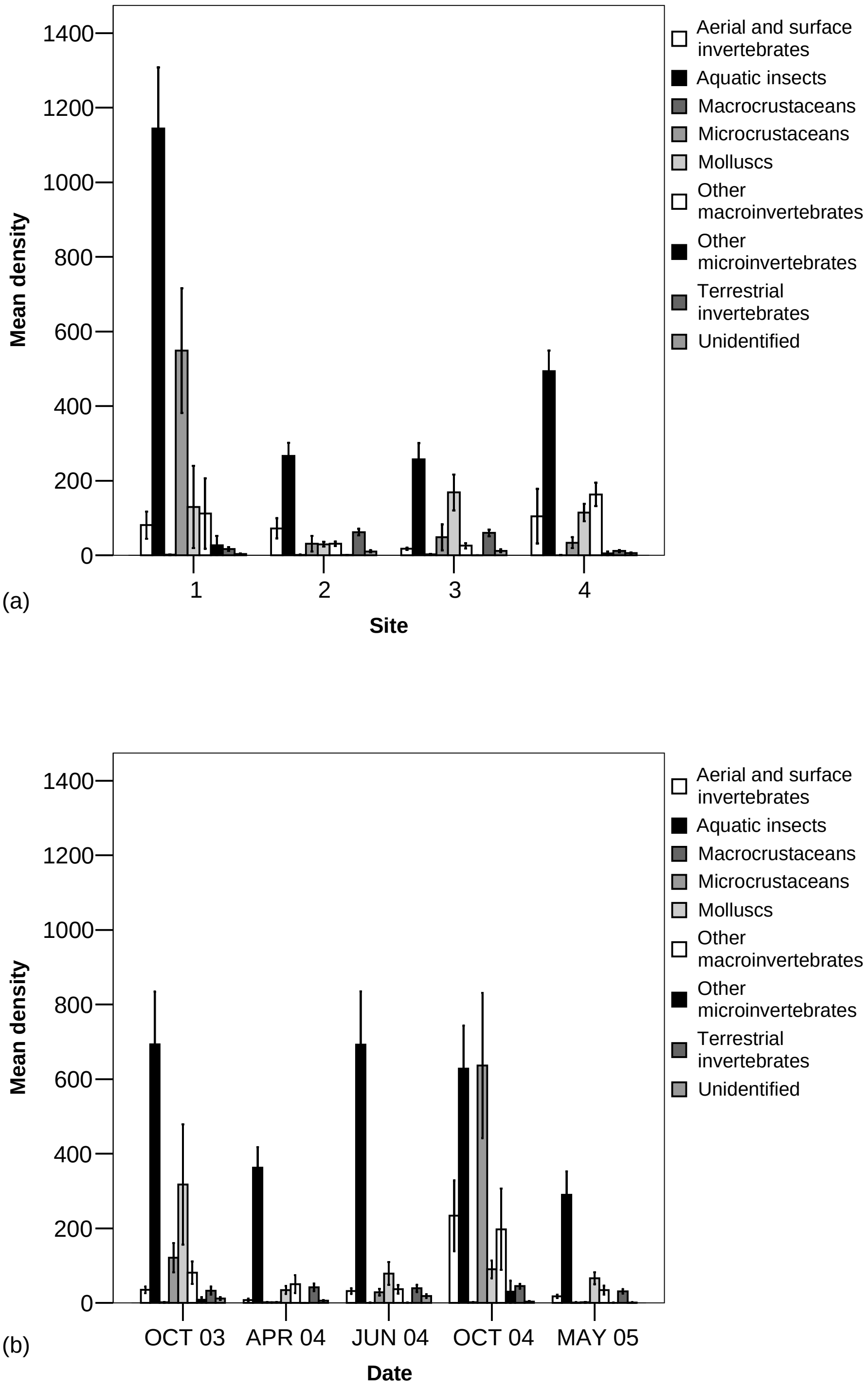


Figure 4.4 Mean densities (number of individuals per m^2 ± SE) of the nine broad invertebrate categories in benthic grab samples for sites, pooled across sampling dates (a), and sampling dates, pooled across sites (b).

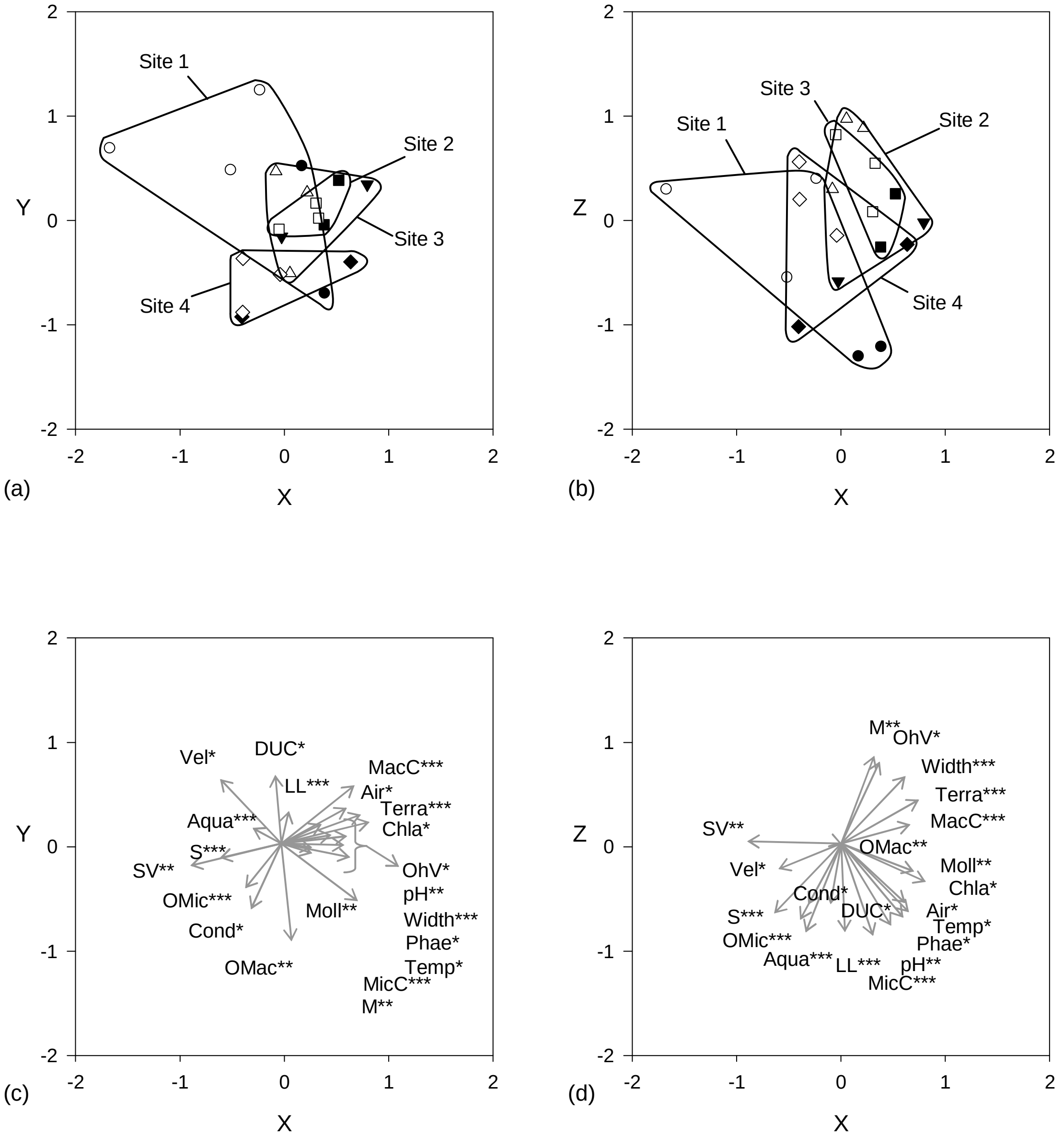


Figure 4.5 The distribution of study sites in three-dimensional ordination space (a, b), as defined by SSH MDS of benthic invertebrate communities (range standardised, Bray Curtis, stress = 0.1068), during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). PCC vector lines are shown with MCAO r-squared values (c, d): *** = 0%, ** = 1%, * = 2-5%. See Tables 3.2 and 4.2 for vector codes, some vectors have not been drawn in order to aid clarity. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space.

4.3.4 Richness and evenness of invertebrate samples

While there was evidence of both spatial and temporal variation in the richness and evenness of invertebrate communities, MANOVA testing revealed complex interactions between sites and sampling dates (Tables 4.6 and 4.7). Mean richness, which generally ranged between two and four broad invertebrate categories per sample, was significantly higher at site 2 than the other sites, for both littoral dip-net and benthic grab samples (Table 4.7 and Figure 4.7a). While richness of benthic grab samples did not vary temporally, richness of littoral dip-net samples was significantly lower during the April 2004 post high-flow sampling date than at any other time, and significantly higher during the May 2005 wet season sampling date than at any other time (Figure 4.7b). Evenness of both littoral dip-net and benthic grab samples showed limited spatial and/or temporal variation (Figure 4.7c, d), with a weakly significant difference identified in the case of benthic grab samples at site 1, relative to the other sites.

Table 4.6 Within-treatment test results (MANOVA, Pillai's Trace) for richness and evenness of broad invertebrate categories in littoral dip-net and benthic grab samples. * p<0.05, ** p<0.01, *** p<0.001.

Method	Treatment	d.f.	*F*-value and significance level
Dip-net	Site	6, 270	2.253*
	Date	8, 270	3.197**
	Site X Date	24, 270	2.786***
Benthic-grab	Site	6, 392	15.153***
	Date	8, 392	1.120
	Site X Date	24, 392	3.41***

Table 4.7 Results of individual between-subjects ANOVA testing for mean richness and evenness of broad invertebrate categories in littoral dip-net and benthic grab samples. * p<0.05, ** p<0.01, *** p<0.001.

			F-value and significance level	
Method	**Treatment**	**d.f.**	**Richness**	**Evenness**
Dip-net	Site	3, 135	4.626**	0.107
	Date	4, 135	4.673**	1.833
	Site X Date	12, 135	5.085***	1.479
Benthic-grab	Site	3, 20	3.450***	30.782*
	Date	4, 20	0.851	1.295
	Site X Date	12, 20	3.566***	3.167***

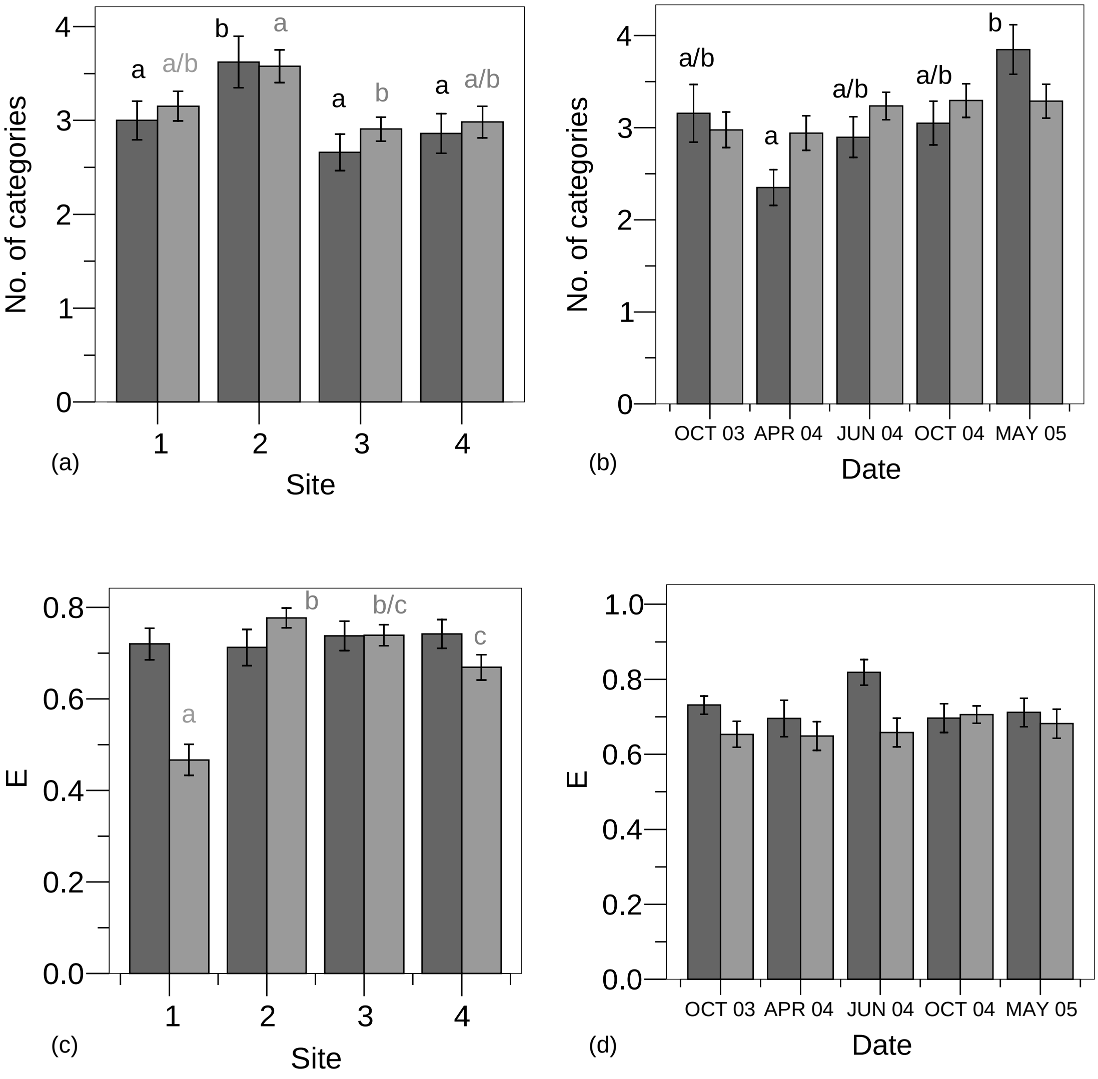


Figure 4.7 Mean (± SE) richness (a, b) and evenness (c, d) of invertebrate categories in littoral dip-net (■) and benthic grab (▨) samples for sites, pooled across sampling dates, and sampling dates, pooled across sites. Significant Tukey's *post hoc* test results are presented where applicable.

4.4 Discussion

The abundance and richness of invertebrates varied spatially within the main channel of the Mulgrave River as a function of habitat composition. Aquatic insects (Trichoptera, Emphemeroptera, Coleoptera etc.), microcrustaceans (Ostracoda) and other microinvertebrates (Testacea) were most abundant at sites 1 and 4, that featured sandy substrates and relatively high flow velocities (Chapter 3). In contrast, mud substrates and greater amounts of overhanging and littoral vegetation at sites 2 and 3 were correlated with increased abundances of terrestrial invertebrates (Formicidae) and macrocrustaceans (atyid shrimps). These relationships are consistent with results from the literature, which emphasise the importance of substrate size, stability and heterogeneity (Benke *et al.*, 1984; Minshall, 1984; Hart and Finelli, 1999). However, as each site contained a range of microhabitat types, sites also overlapped substantially in their invertebrate community composition. Rabeni and Gibbs (1977) identified similar patterns in their study of a deep section of the Peneobscot River, Maine, USA. They distinguished four benthic invertebrate community types, with typical and distinguishable assemblages, spread across 33 sites. While taxa were generally concentrated within a single community type, according to their individual flow velocity and substrate preferences, they were not excluded from others, with substantial overlap in community composition occurring across the river reach (Rabeni and Minshall, 1977).

In the present study, habitat variables at all sites were strongly influenced by flooding, which scoured bed sediments and removed instream vegetation (Chapter 3), leading to declines in invertebrate abundance and richness during the wet season. Similar negative effects have been documented in other systems. For example, Rosser and Pearson (1995) assessed the response of rock-dwelling fauna to physical disturbance in two Australian tropical rainforest streams. They found that both the density and richness of macroinvertebrates were lowest following wet season floods (March), with a peak in the dry season (July). Responses to disturbance were highly taxon-specific and generally varied with season. However, the most common response was a decline in density as disturbance intensity increased (Rosser and Pearson, 1995). In the main-channel of the Mulgrave River, I found that habitat conditions were most stable during extended base-flow periods (i.e., the dry season). At this time, a range of invertebrate groups were significantly more abundant.

High productivity, as indicated by the extent of macrophyte beds and the concentrations of chlorophyll *a* and phaeophytin in the water column, was associated with stable dry season conditions, rather than the wet season inundation of floodplain areas. Bishop *et al.* (2001) and Webster *et al.*

(2005) reported similar results for rivers in the Northern Territory, suggesting that this inverse relationship between productivity and flow was probably due to a combination of: increased flow velocities, cloud cover and turbidity; lower temperatures; and shorter water residence times. In their study of trophic dynamics in the Mulgrave River, Pusey *et al.* (1995b) found that the number of fishes with empty or near-empty guts was higher in habitats dominated by low water velocities and sandy substrates than in other areas (i.e., upland tributaries). Given that their study was conducted during the dry season (B. Pusey *pers. comm.* 2006), such a result suggests that the abundance of invertebrate prey available for fish to consume could be low, even under the most productive conditions. If this is the case, it is possible that food abundance plays an important role in regulating freshwater fish populations in these systems, particularly during the wet season, when food availability is at its lowest. These issues are discussed further in chapter 6.

The riverine productivity model is the most appropriate ecosystem model in rivers with hydrologically disconnected main channels and floodplains (Thorp and Delong, 1994; Thorp *et al.*, 1998). Thorp *et al.* (1998) proposed that, in such systems, ‘phytoplankton and detritus of autochthonous origin represents a more usable energy source for benthic (bivalve molluscs, hydropsychid caddisflies) and planktonic (microcrustaceans) suspension feeders than the more refractory allochthonous materials derived from upstream processing of terrestrial organic matter’. While the Ohio River, USA, was the focus of their study, similar processes are probably important in the lowland section of the Mulgrave River. Power and Dietrich (2002) modeled food webs in headwater and mainstream sections of river networks, finding that algal production in the main channel supports both edible grazers (soft bodied invertebrates) and inedible grazers (armored and sessile invertebrates) in these systems. The former group is then consumed by two trophic levels of predators (invertebrates and fish). Based on the evidence presented in this chapter, it appears that a similar algae-driven trophic pathway dominates energy flow within the main channel of the Mulgrave River (see chapter 7).

The patterns described above fit the conceptual model of habitat dynamics generated in Chapter 3. During the dry season, autochthonous production is high and a range of habitat types are available for invertebrates. These include stable sediments, extensive macrophyte beds, relatively contiguous littoral vegetation, and large woody debris. Wet season flooding reduces the abundance of invertebrates, particularly in benthic habitats. Those in littoral habitats are also negatively affected if vegetation is removed. As floodwaters penetrate the riparian zone, more terrestrial invertebrates are contributed to aquatic habitats (drowned, stranded on floating terrestrial plant matter etc.). When flood waters recede the abundance of invertebrates increases, presumably due to increased habitat stability and the return to more productive conditions.

4.5 Conclusion

This chapter documented the spatial variability and temporal dynamics of invertebrate populations in benthic and littoral-main channel habitats of the Mulgrave River. Abundance and density of invertebrates reflected instream productivity and microhabitat characteristics, particularly substrate size and stability. While some groups favoured particular habitat types, there was a high degree of overlap in community composition across sites. Invertebrates were significantly more abundant under stable dry season base-flow conditions, when habitat stability and instream productivity were at a maximum, but responded negatively to sediment mobilisation and other habitat changes caused by wet season flooding.

Chapter 5: Spatial and temporal variation in fish community structure

5.1 Introduction

The structure and function of freshwater fish communities are influenced by a range of factors operating at various spatial and temporal scales (Jackson *et al.*, 2001). Several conceptual models have been developed to account for this variation by: (a) predicting flow-mediated shifts in riverine productivity and habitat structure along lateral and/or longitudinal gradients (Vannote *et al.*, 1980; Schlosser, 1982; Junk *et al.*, 1989; Thorp and Delong, 1994); or (b) constructing a hierarchical framework of factors, often viewed as a series of filters, in order to determine the presence or absence of fish species at large scales such as regions, and their relative abundance at finer scales such as river reaches (Frissell *et al.*, 1986, Johnson *et al.*, 1995; Lorenz *et al.*, 1997; Poff, 1997). While these approaches are relevant to the systems in which they were developed, in the tropical lowland rivers of north-eastern Australia, elements of several models may apply simultaneously, or individually, under different flow conditions. The aims of this chapter are to describe the spatial patterns of freshwater fish assemblages in a Wet Tropics river, to relate these patterns to species' habitat use, and to investigate the response of these assemblages to wet season floods of different magnitudes.

The freshwater fish fauna of the Wet Tropics region is distinct from surrounding areas (Unmack, 2001; Pusey *et al.*, 2004, 2006). Total freshwater fish diversity of the region is currently estimated at 107 species contained within 37 families, including at least nine endemic species and four exotic species, with almost half (52/107) within six families (Pusey *et al.*, 2006). This fauna represents approximately 40% of the continent's total diversity, with new endemic species, such as the Bloomfield River cod *Guyu wujalwujalensis* and *Stiphodon* sp., being discovered only relatively recently (Pusey and Kennard, 2001; Pusey *et al.*, 2004; Paul Thuesen *pers. comm.*). Pusey and Kennard (1996) analysed geographical variability of fish assemblage structure across the Wet Tropics, identifying a strong latitudinal gradient within the region. Rivers in the extreme north (streams near Cape Tribulation) and south (streams near Cardwell) contained the most distinctive faunas, with the remaining seven drainages forming a homogeneous group with little inter-basin separation (Pusey and Kennard, 1996).

The species richness of individual Wet Tropics river basins is linked to catchment size and flow variability, with greatest richness occurring in large rivers with predictable flow regimes (Pusey *et al.*, 1995a; Pusey and Kennard, 1996). Rivers of the Wet Tropics are short and steep, with significant discontinuities in profile in their middle sections, culminating in relatively short, low gradient, meandering lowland reaches (~20 km in length; Pusey *et al.* 1995a). As a result of these longitudinal habitat gradients and instream barriers to fish movement, fish assemblage structure varies substantially within individual Wet Tropics catchments (Pusey *et al.*, 1995a; Russell *et al.*, 2003). This trend is common in river systems worldwide, in both temperate and tropical areas, with fish species being added, and in some cases replaced, as one moves from headwaters to lowlands (Sheldon, 1968; Horowitz, 1978; Matthews, 1998). For example, Pusey *et al.* (1995a) found that in the Mulgrave River a gradual downstream change in fish assemblage structure was correlated with changes in substrate and type of instream cover. However, in the nearby South Johnstone River, species richness was depressed in the upper regions by two high-gradient sections (Pusey *et al.*, 1995a).

Given the importance of position in the catchment as a determinant of freshwater fish assemblage structure (Pusey *et al.*, 1995a; Pusey *et al.*, 2000b, 2004), it is not surprising that lowland habitats are centres of freshwater fish diversity within Wet Tropics catchments (Russell *et al.*, 1996; Pusey *et al.*, 2004; Veitch and Sawynok, 2005). However, as Amoros and Bornette (2002) explained, the maintenance of biodiversity in these habitats relies on the maintenance of natural patterns of connectivity and habitat heterogeneity. If rivers become deeply incised relative to their surrounding floodplain, as is the case for most Wet Tropics rivers (Willmott and Stephenson, 1989; Nott *et al.*, 2001; Nott, 2003), connectivity to off-stream habitats is reduced and the importance of habitats within the main channel increases (Power *et al.*, 1995; Galat and Zweimuller, 2001; Amoros and Bronette, 2002). Unfortunately, both floodplain and main-channel habitats have been heavily degraded throughout the region (Veitch and Sawynok, 2005; see chapter 2). In these systems, models such as the Flood-Pulse Concept (Junk *et al.*, 1989), that emphasises lateral transfer of nutrients, the River Continuum Concept (Vannote *et al.*, 1980), that emphasises longitudinal gradients, and the Riverine Productivity Model (Thorp and Delong, 1994), that emphasises the importance of instream primary production, are all likely to apply to some degree at different times of the year, within the context of the hierarchical factors described above.

The flow regimes of Wet Tropics rivers exhibit low interannular variability, with predictable wet season floods punctuating otherwise stable dry season baseflow conditions. Unlike other tropical areas, the incised nature of the main channel, combined with the degraded state of floodplain habitats, ensures that only large scale flow events result in floodplain inundation: when flooding does occur it is usually brief, lasting for days or weeks, rather than months. Compared to systems like the Amazon

River, wet season flow events may act as predictable disturbances rather than gradual inundation opportunities (Poff, 1992), reducing the abundance of instream habitat vegetation and invertebrates (as documented in chapters 3 and 4) and limiting opportunities for freshwater fish to access floodplain habitats. It is possible that reproductive, dietary and habitat preference strategies aimed at exploiting this seasonal shift in resource availability, which are widespread in other tropical areas (Welcomme, 1979; Gerking, 1994), may not be as common in the case of Wet Tropics freshwater fish species, especially within the main channel.

To date, no other published studies have collected empirical data on the temporal dynamics of fish assemblage structure in Wet Tropics rivers. However, fish assemblage structure in streams of the region may remain relatively stable over a range of flow conditions (Pusey unpublished data). The goals of this chapter are to: investigate spatial and temporal patterns in lowland main channel fish assemblages under a range of flow conditions; determine which species dominate assemblages and whether the longitudinal changes in community structure observed in the upper catchment continue into the lowland reach; examine how assemblage structure responds to elevated flow conditions of different magnitudes; and identify which habitat and water quality variables are most important for fish species. My overall aim is to asses whether or not the dramatic changes to instream habitats during the wet season, detailed in chapter 3, are a major driver of fish species abundance and diversity, and community structure.

5.2 Methods

5.2.1 Fish surveys

A combination of boat electrofishing, gill nets and bait traps were used to sample fish communities at four sites on the lower Mulgrave River under a range of flow conditions. Over 5 hours of electrofishing ‘power-on’ time, 245 gill net hours and 728 bait trap hours were undertaken over the five sampling dates across all sites. Electrofishing was conducted using a 2.5 KvA Smith-Root GPP boat-mounted unit (500-1000 volts, 60 pulses per second, 60-100 duty cycle range and 3-4 amps). Based on the results of the pilot study (Appendix 1), six shots, each five minutes in duration, were undertaken at each site during each round of sampling (Figure 5.1).

While electrofishing is an effective method for the sampling of cryptic species in complex habitats, and is more rapid, less selective, and less invasive than netting, it is relatively inefficient in depths greater than 3m and open water habitats (Faragher and Rodgers, 1997). In order to sample fish in these habitats, three multi-panel gill nets were used. Each net consisted of three 10 m panels with mesh sizes of 45, 90, and 120 mm. In most studies, gill nets are set perpendicular to the bank and therefore the direction of flow (Craig and Fletcher, 1982; Chiasson *et al.*, 1997; Finstad *et al.*, 2000). However, when this method was used in the lowland Mulgrave River, even under low discharge dry-season conditions, nets were drowned out and pushed flat, quickly becoming clogged with mobile debris and floating aquatic plants (e.g., water hyacinth) and snagged on submerged logs. Subsequently, therefore, nets were set parallel to the bank, with the added benefit of increasing the capture of species moving into and out of littoral habitat features, such as woody debris snags. To address diurnal patterns of fish movement and activity, gill net sampling is often conducted at dusk. However, catch rates during the pilot study did not differ substantially between afternoon and evening net sets and, given the difficulties and dangers (i.e., much more frequent encounters with saltwater crocodiles) associated with night sampling, nets were soaked for four hours (from 1200 to 1600 hrs).

Small ‘bait’ traps (40 cm x 20 cm x 20 cm, 3 mm mesh) were used to sample cryptic fish species in shallow littoral habitats. Up to 10 traps were set at each site for the same period as gill nets. Traps were set unbaited to allow accurate dietary analysis. Catch rates of unbaited traps do not differ significantly from those of baited traps, as fish often use the unbaited traps as cover from overhead predation (J. Knight, New South Wales Department of Primary Industries, unpublished data, 2002). At each site and on each sampling occasion, a sample of fish caught by each method was euthanased in Benzocaine (Ethyl p-aminobenzoate, 100 mg/L), or an icy slurry, and preserved in 10% Formalin (37% aqueous solution of formaldehyde, diluted in water) for later gut contents analysis. Formalin was also injected into the body cavity and gut of larger fishes. Standard length and mass of fish were recorded in the laboratory for biomass analyses.

5.2.2 Statistical methods

The total abundance (number of individuals) and biomass (grams) of each species caught at each site during each sampling date were standardised by sampling effort (i.e., number of seconds of boat electrofishing ‘power-on’ time, gill net hours and bait trap hours expended). Catch per unit effort (CPUE) and biomass per unit effort (BPUE) for each method were then analysed separately. The mass of fish measured in the field (standard length only for all species) was estimated using length-weight relationships generated during this study (Appendix 2), or from Pusey *et al.* (2004). Non-parametric Kruskal-Wallis tests were used to test for differences in fish CPUE and BPUE between sites and dates, as data did not conform to ANOVA assumptions of normality or homogeneity of variance, even after transformation. ANOVA testing was, however, used to test for differences in richness and evenness (Pielou, 1969, p.223). Some fish samples from the electrofishing survey of site 2 in October 2003 were lost in transit from the field to the laboratory. As a result, this sample was removed from all analyses of electrofishing CPUE and BPUE. No fish were caught using gill nets at site 4 in May 2005 and this result was removed from ordinations of community structure, to better elucidate relationships between the other samples, but not from tests of variation of CPUE and BPUE.

Three-dimensional semi-strong hybrid multidimensional scaling (SSH MDS) was used for multivariate analysis of fish communities (PATN Version 3.03; Belbin, 1991). In order to identify the variables that were most important in determining spatial and temporal variation in community composition, Principal Component Correlation (PCC) was applied to fish abundance data and habitat variables (including water quality and productivity measures) and tested using the Monte-Carlo Attributes in Ordination (MCAO) permutation test (seed value = 1235, 1000 iterations). As in previous chapters, PCC vectors were plotted on ordination figures if the percentage of MCAO permutation r-squared values that exceeded the real r-squared (the r-squared value from the real groups) was less than or equal to 5%, and coded as follows: *** = 0%, ** = 1%, * = 2-5%. While these percentages approximate p-values of <0.001, <0.01 and <0.05, respectively (Lee Belbin, *pers. comm.* 2005), because actual ‘p-values’ are not produced by MCAO testing, in this chapter I describe PCC vectors with ‘significant’ results as ‘strongly’ correlated with the distribution of sites in ordination space.

In order to assess the importance of fluvial main-channel habitats to freshwater fishes in the Mulgrave River, each species caught during the study was assigned to one of three broad habitat groups according to the method described in Galat and Zweimüller (2001) after Kinsolving and Bain (1993), from which the following descriptions are taken. *Fluvial specialists* are those species that are almost always found only in streams and rivers or are described as using flowing water habitats throughout life. These species may be occasionally found in a lake, but most information on them pertains to lotic systems. *Fluvial dependent* species are found in a variety of habitats including estuaries, but require flowing water at some stage in their life cycle. Lastly, *microhabitat generalists* are commonly found in lakes, floodplain water bodies, streams and rivers, but are capable of completing their life cycle in lentic systems.

Following this broad classification, seasonal habitat preferences of fish species were investigated. This was achieved by dividing the habitat use of each species over a range of habitat variables, during wet and dry seasons, by habitat availability in the study area at those times. Habitat 'use' was defined as the mean value of each habitat variable (Table 3.2 plus water quality variables) recorded at the locations where individuals of each species were captured using electrofishing. Habitat 'availability' was defined as the mean value of each habitat variable across all electrofishing shots (calculated separately for wet and dry seasons). Flexible UPGMA analysis was then performed (using PATN) on the resulting matrix of species habitat preference values, in order to classify seasonal species samples into habitat guilds (see Figure 5.15).

5.3 Results

5.3.1 Gear selectivity

A total of 1530 fish specimens, representing 36 species (including two exotic spcies), 33 genera and 26 families, were caught during the study (Table 5.1). Thiry-three of these species were caught using electrofishing, particularly surface swimming and cryptic littoral species (e.g., *Melanotaenia splendida splendida* and *Bunaka gyrinoides*). However, this method was inefficient in open water, where fish could more easily escape the charged field, and in deep (>3 m), fast flowing water (>1 m/s), where stunned fish were quickly swept out of reach of the dip-netter by the current. Open-water species (e.g., *Nematalosa erebi*) and those that preferred deeper, benthic habitats (e.g., *Neosilurus ater*) were collected using multi-panel gill nets. *Tilapia mariae,* an exotic species that is notoriously difficult to stun using electrofishing (Colton Perna, Australian Centre for Freshwater Research, *pers. comm.*, 2005) and is therefore almost certainly underrepresented in figures of electrofishing catch per unit effort, was also captured using gill nets. Bait traps accounted for *Ophisternon gutturale* and *Xiphophorus maculatus* (the second exotic species), that were the only species not caught using the other methods.

Table 5.1 Full taxonomic details of the 36 species caught during the study. Species codes used in ordination figures are give, along with the total number of individuals of each species caught (N), their mean standard length (SL), the SL range and habitat classes. * indicates introduced species.

Code	Species	Authority	Family	Common name	N	Mean SL	SL range	Habitat class
Acaaus	*Acanthopagrus australis*	(Günther, 1859)	Sparidae	Yellowfin bream	4	195	152-242	Fluvial dependent
Acaber	*Acanthopagrus berda*	(Forsskål, 1775)	Sparidae	Pikey bream	3	239	222-250	Fluvial dependent
Ambagr	*Ambassis agrammus*	Günther,1867	Chandidae	Glass perch	234	38	18-54	Microhabitat generalist
Angobs	*Anguilla obscura*	Günther,1872	Anguillidae	One-gilled swamp eel	1	435	435-435	Fluvial dependent
Angrei	*Anguilla reinhardtii*	Steindachner, 1867	Anguillidae	Long-finned eel	9	280	170-405	Fluvial dependent
Arrscl	*Arrahamphus sclerolepis*	Günther, 1866	Hemiramphidae	Snub-nosed gar	16	239	208-308	Fluvial dependent
Awaacr	*Awaous acritosus*	Watson, 1994	Gobiidae	Roman-nosed goby	16	89	54-130	Fluvial specialist
Bungyr	*Bunaka gyrinoides*	(Bleeker, 1853)	Eleotridae	Greenback guavina	22	265	130-345	Fluvial dependent
Carign	*Caranx ignobilis*	(Forsskål, 1775)	Carangidae	Giant trevally	2	106	99-112	Fluvial dependent
Craste	*Craterocephalus stercusmuscarum*	(Günther, 1867)	Atherinidae	Fly-specked hardyhead	13	45	23-62	Microhabitat generalist
Elefus	*Eleotris fusca*	(Bloch and Schneider, 1801)	Eleotridae	Brown gudgeon	10	70	58-89	Fluvial specialist
Gerfil	*Gerres filamentosus*	Cuvier, 1829	Gerreidae	Threadfin silver biddy	53	75	34-131	Fluvial specialist
Giumar	*Giurus margaritacea*	(Valenciennes, 1837)	Eleotridae	Snakehead gudgeon	9	192	54-235	Microhabitat generalist
Gloapr	*Glossamia aprion*	(Richardson, 1842)	Apogonidae	Mouth almighty	109	53	11-125	Microhabitat generalist
Glosp1	*Glossogobius* species 1	(after Allen *et al.* 2002)	Gobiidae	Mountain goby	17	49	22-76	Fluvial specialist
Hepful	*Hephaestus fuliginosus*	(Macleay, 1883)	Terapontidae	Sooty grunter	6	193	101-236	Fluvial specialist
Heptul	*Hephaestus tulliensis*	DeVis, 1884	Terapontidae	Tully grunter	14	199	112-285	Fluvial specialist
Hypcom	*Hypseleotris compressa*	(Krefft, 1864)	Eleotridae	Empire gudgeon	73	35	11-58	Microhabitat generalist
Kuhrup	*Kuhlia rupestris*	(Lacépède, 1802)	Kuhliidae	Jungle perch	2	173	160-185	Fluvial specialist
Latcal	*Lates calcarifer*	(Bloch, 1790)	Centropomidae	Barramundi	21	516	345-750	Fluvial dependent
Leiequ	*Leiognathus equulus*	(Forsskål, 1775)	Leiognathidae	Ponyfish	12	73	61-88	Fluvial dependent
Lutarg	*Lutjanus argentimaculatus*	(Forsskål)	Lutjanidae	Mangrove jack	14	251	144-380	Fluvial dependent
Melspl	*Melanotaenia splendida splendida*	(Peters, 1866)	Melanotaeniidae	Eastern rainbowfish	360	51	14-125	Microhabitat generalist
Mesarg	*Mesophristes argenteus*	(Cuvier,1829)	Terapontidae	Sand bream	2	218	200-235	Fluvial dependent
Micbra	*Microphis brachyurus brachyurus*	(Bleeker, 1853)	Syngnathidae	Short-tailed river pipefish	3	195	193-198	Fluvial specialist
Mugcep	*Mugil cephalus*	Linnaeus, 1758	Mugilidae	Mullet	7	418	330-450	Microhabitat generalist
Nemere	*Nematalosa erebi*	(Günther, 1868)	Clupeidae	Bony bream	196	268	88-390	Microhabitat generalist
Neoater	*Neosilurus ater*	(Perugia, 1894)	Plotosidae	Black catfish	118	360	133-490	Microhabitat generalist
Notrob	*Notesthes robusta*	(Günther,1860)	Scorpaenidae	Bullrout	7	177	123-205	Fluvial dependent
Ophgut	*Ophisternon gutturale*	(Richardson, 1845)	Synbranchidae	One-gilled swamp eel	1	126	126-126	Fluvial dependent
Psesig	*Pseudomugil signifer*	Kner, 1865	Pseudomugilidae	Pacific blue eye	33	23	16-35	Fluvial specialist
Redbik	*Redigobius bikolanus*	(Herre, 1927)	Gobiidae	Speckled goby	90	18	10-34	Fluvial dependent
Tantan	*Tandanus tandanus*	Mitchell, 1838	Plotosidae	Freshwater catfish	4	343	262-392	Fluvial specialist
Tilmar	*Tilapia mariae**	Boulenger, 1899	Cichlidae	Tilapia	47	120	14-290	Microhabitat generalist
Toxcha	*Toxotes chatareus*	(Hamilton,1822)	Toxotidae	Seven-spot archerfish	1	21	21-21	Fluvial dependent
Xipmac	*Xiphophorus maculatus**	(Günther, 1866)	Poeciliidae	Swordtail	1	27	27-27	Microhabitat generalist

5.3.2 Analysis of electrofishing catch

Melanotaenia splendida splendida and *Ambassis agrammus* dominated the electrofishing catch and were three to five times more abundant than the next most abundant species, *Gerres filamentosus* and *Glossamia aprion* (Figure 5.1). Other relatively abundant species were *Pseudomugil signifer, Hypseleotris compressa, Bunaka gyrinoides, Neosilurus ater, Redigobius bikolanus* and *Awaous acritosus*. *Hephaestus tulliensis* was relatively more abundant than the closely related *H. fuliginosus*. The biomass of the electrofishing catch was dominated by larger bodied species such as *Lates calcarifer, B. gyrinoides, N. ater*, and *Lutjanus argentimaculatus* (Figure 5.2), with smaller bodied species such as *M. s. splendida* and *A. agrammus* making limited contributions, despite their numerical abundance. There was no significant difference in species richness or evenness of the electrofishing catch between sites or sampling dates (Table 5.2).

Kruskal-Wallis testing identified significant differences in mean electrofishing CPUE and BPUE between sites for several species (Table 5.3). However, these differences were limited. Of the ten most numerically abundant species, the only significant differences in CPUE were for *A. acritosus* between sites and *G. aprion* between sampling dates (Figure 5.3). The former species was more abundant at sites 1 and 4, whereas the latter was more abundant during the wet season than during the dry season. Of the 10 species providing the greatest contribution to overall fish biomass, two showed significant differences in BPUE between sites: *Tandanus tandanus* Mitchell, 1838[1] and *Lates calcarifer* were more abundant at upstream and downstream sites, respectively (Figure 5.4a). *Giurus margaritacea* was the only one of these 10 species to exhibit a significant difference in BPUE between sampling dates, being consistently more abundant during the wet season (Figure 5.4b).

Sites were delineated in ordination space according to the CPUE of their component species (Figure 5.5). *Glossamia aprion*, *M. s. splendida*, and *Leiognathus equulus* were correlated with sites 1 and 2, whereas *N. ater, A. agrammus, L. calcarifer* and *Pseudomugil signifer* were correlated with sites 3 and 4. There was also evidence of seasonal shifts in fish community composition within each site, with dry season samples positioned to the lower left of Figure 5.5b and wet season samples positioned to the upper right. Abundance of *Glossogobius* sp. 1 was strongly correlated with dry

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[1] Although I have referred to this species as *Tandanus tandanus* throughout this thesis, recent molecular research suggests that the Wet Tropics population is, in fact, genetically distinct (i.e., *Tandanus* sp.) (Dean Gerry, James Cook University, *pers. comm.* 2005).

season samples. These trends were not clear in the case of BPUE data, with sites overlapping substantially in ordination space and no obvious difference between wet and dry season samples (Figure 5.6).

5.3.3 Analysis of gill net catch

Ten species were collected using gill-netting. *Nematalosa erebi* and *Neosilurus ater* dominated the catch (Figure 5.7), although *Tilapia mariae*, *Arrhamphus sclerolepis*, *Gerres filamentosus* and *Lates calcarifer* were also abundant. *Nematalosa erebi* and *Neosilurus ater* also dominated gill net BPUE, with *T. mariae* and *L. calcarifer* making small contributions to the total biomass (Figure 5.8). As was the case with electrofishing data, the CPUE and BPUE of species caught using gill-nets did not differ significantly between sites or sampling dates in the majority of cases (Table 5.4). *L. calcarifer* and *Nematalosa erebi* were significantly more abundant (CPUE and BPUE) at sites 2 and 3, whereas *Neosilurus ater* was significantly more abundant during the dry season (Figure 5.9), but contributed a greater biomass during the wet season (Figure 5.10).

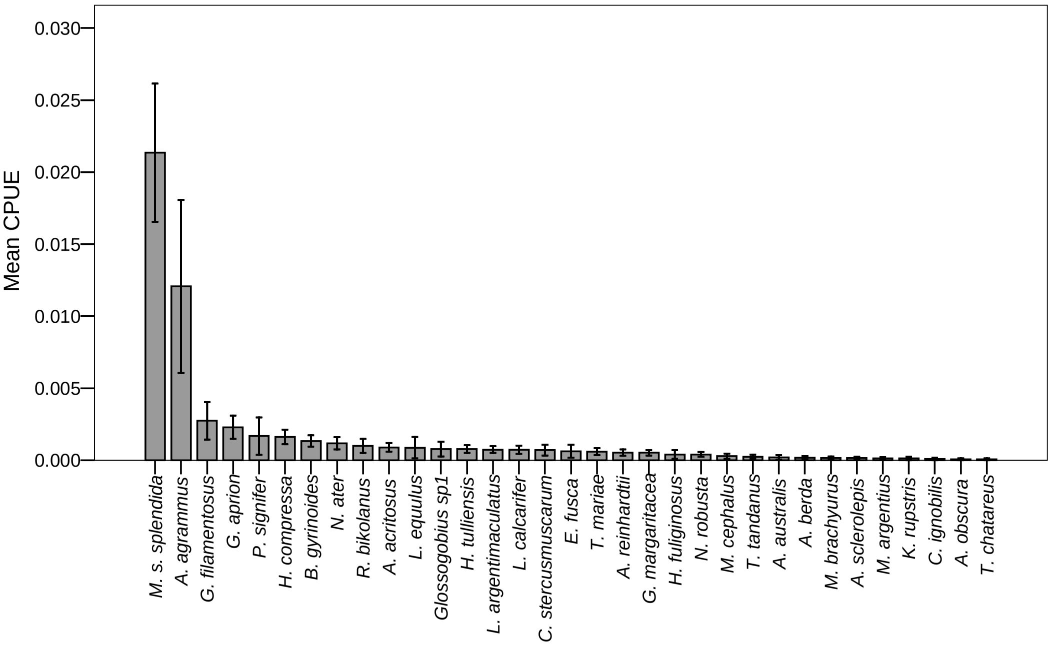


Figure 5.1 Mean catch per unit effort (number of individuals per second ±SE) of all species caught using electrofishing, averaged across sites and sampling dates, in order of descending abundance.

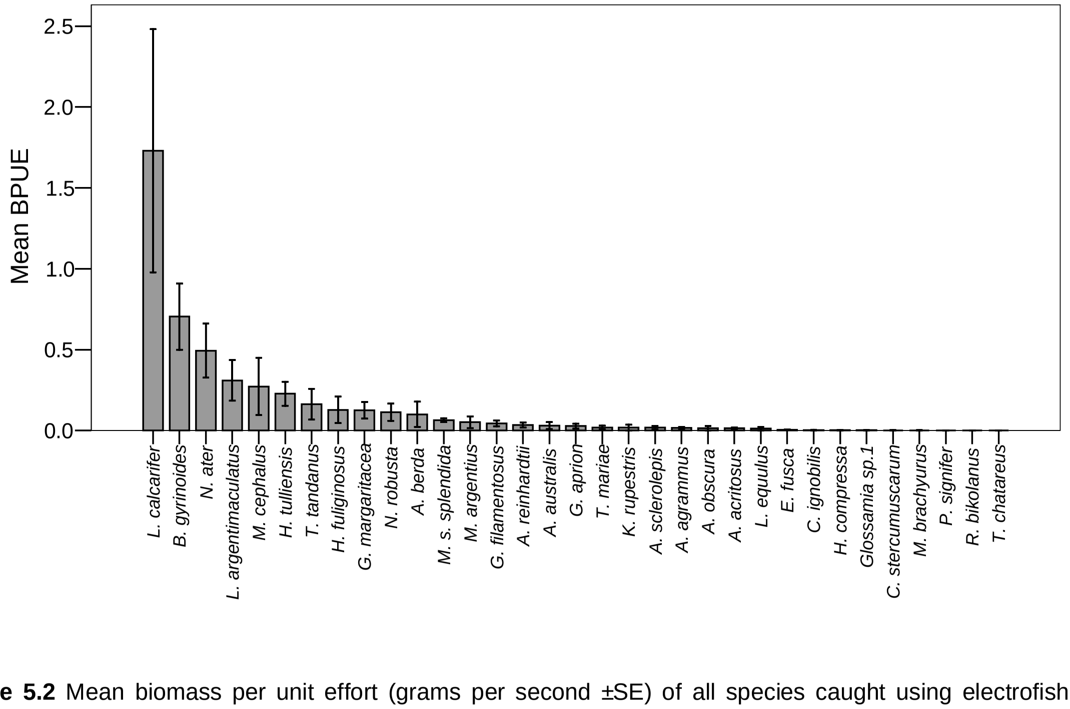


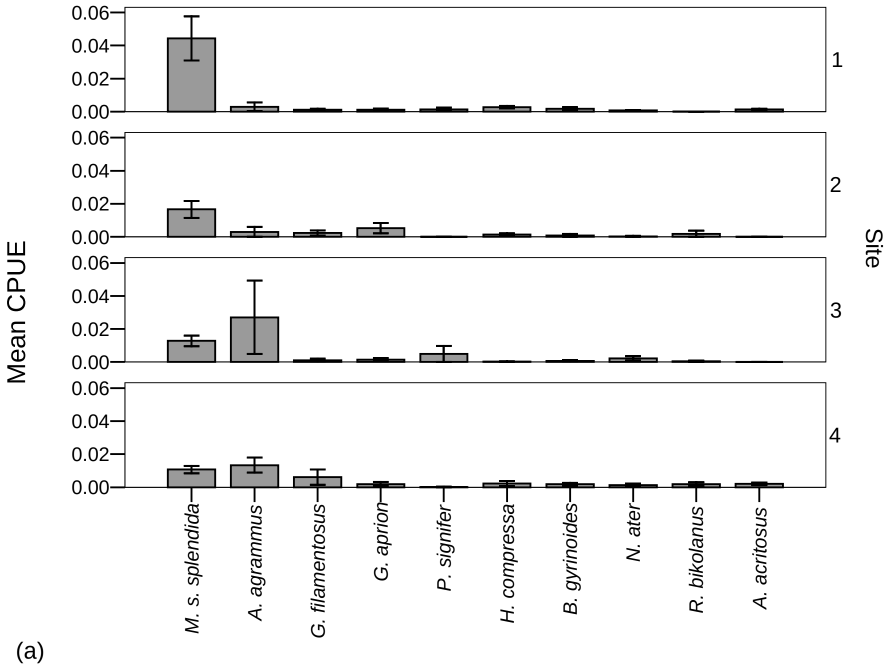
Figure 5.2 Mean biomass per unit effort (grams per second ±SE) of all species caught using electrofishing, averaged across sites and sampling dates, in order of descending biomass.

Table 5.2 Results of one-way ANOVA testing of mean electrofishing CPUE richness and evenness variables. The October 2003 sample from site 2 was removed from this analysis (see text). All *p* values were >0.1.

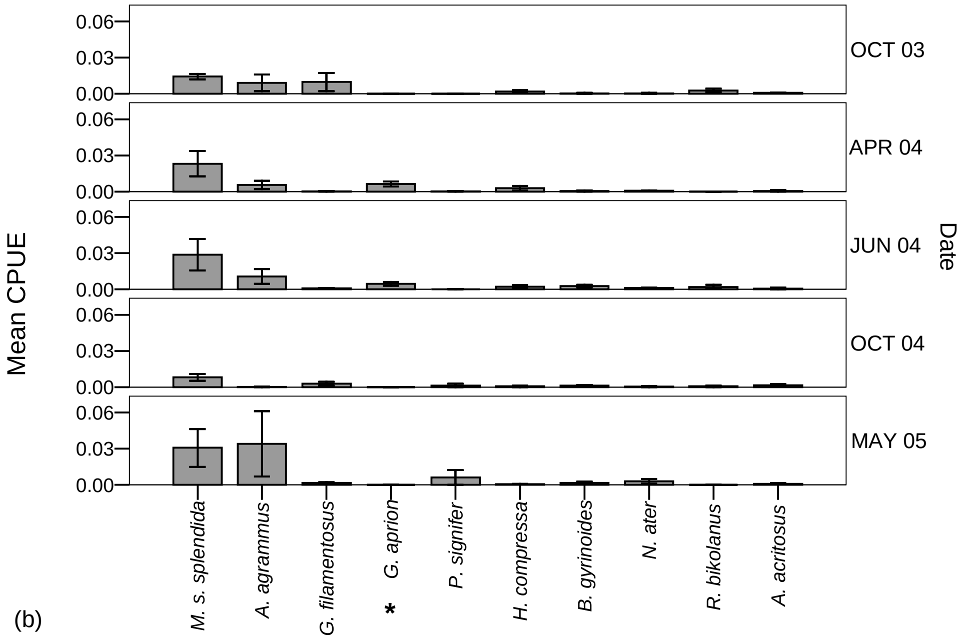
		***F*-value**	
Factor	**d.f.**	**Richness**	**Evenness**
Site	3, 15	1.81	1.24
Date	4, 15	1.04	1.70

Table 5.3 Kruskal-Wallis test results for mean electrofishing CPUE and BPUE between sites and dates. Significant differences ($p<0.05$) are highlighted in bold. The October 2003 sample from site 2 was not included in this analysis (see text).

		CPUE				**BPUE**			
		Site (d.f.=3)		**Date (d.f.=4)**		**Site (d.f.=3)**		**Date (d.f.=4)**	
Code	**Species**	X^2	***p***	X^2	***p***	X^2	***p***	X^2	***p***
Acaaus	*Acanthopagrus australis*	1.91	0.59	7.92	0.09	1.91	0.59	7.92	0.09
Acaber	*Acanthopagrus berda*	1.91	0.59	3.67	0.45	1.91	0.59	3.67	0.45
Ambagr	*Ambassis agrammus*	4.87	0.18	4.37	0.36	6.33	0.10	3.52	0.47
Angobs	*Anguilla obscura*	2.80	0.42	3.75	0.44	2.80	0.42	3.75	0.44
Angrei	*Anguilla reinhardtii*	5.01	0.17	2.51	0.64	3.67	0.30	2.40	0.66
Arrscl	*Arrahamphus sclerolepis*	3.72	0.29	5.87	0.21	4.05	0.26	5.87	0.21
Awaacr	*Awaous acritosus*	10.82	**0.01**	0.75	0.95	10.85	**0.01**	1.85	0.76
Bungyr	*Bunaka gyrinoides*	1.76	0.62	4.14	0.39	0.70	0.87	3.79	0.43
Carign	*Caranx ignobilis*	2.80	0.42	3.75	0.44	2.80	0.42	3.75	0.44
Craste	*Craterocephalus stercusmuscarum*	13.21	**0.00**	1.38	0.85	13.21	**0.00**	1.29	0.86
Elefus	*Eleotris fusca*	10.04	**0.02**	3.69	0.45	10.04	**0.02**	3.69	0.45
Gerfil	*Gerres filamentosus*	2.92	0.40	6.57	0.16	2.80	0.42	5.43	0.25
Giumar	*Giurus margaritacea*	1.58	0.66	13.26	**0.01**	1.97	0.58	11.21	**0.02**
Gloapr	*Glossamia aprion*	1.15	0.77	16.45	**0.00**	0.94	0.82	16.53	**0.00**
Glosp1	*Glossogobius* species 1	2.81	0.42	9.00	0.06	2.76	0.43	9.00	0.06
Hepful	*Hephaestus fuliginosus*	4.05	0.26	5.48	0.24	4.05	0.26	5.48	0.24
Heptul	*Hephaestus tulliensis*	12.22	**0.01**	2.01	0.73	7.05	0.07	2.65	0.62
Hypcom	*Hypseleotris compressa*	4.04	0.26	1.98	0.74	5.32	0.15	1.19	0.88
Kuhrup	*Kuhlia rupestris*	2.80	0.42	3.75	0.44	2.80	0.42	3.75	0.44
Latcal	*Lates calcarifer*	9.19	**0.03**	1.99	0.74	8.48	**0.04**	1.34	0.85
Leiequ	*Leiognathus equulus*	7.92	0.05	2.92	0.57	7.92	0.05	2.92	0.57
Lutarg	*Lutjanus argentimaculatus*	3.90	0.27	0.63	0.96	3.65	0.30	0.63	0.96
Melspl	*Melanotaenia splendida splendida*	4.99	0.17	4.47	0.35	4.18	0.24	2.42	0.66
Mesarg	*Mesophristes argenteus*	2.47	0.48	7.92	0.09	2.47	0.48	7.92	0.09
Micbra	*Microphis brachyurus*	2.36	0.50	2.92	0.57	2.36	0.50	2.92	0.57
Mugcep	*Mugil cephalus*	1.28	0.73	5.15	0.27	1.28	0.73	5.15	0.27
Neoate	*Neosilurus ater*	2.31	0.51	2.20	0.70	1.51	0.68	2.51	0.64
Notrob	*Notesthes robusta*	2.36	0.50	2.84	0.58	2.28	0.52	2.68	0.61
Psesig	*Pseudomugil signifer*	2.06	0.56	0.96	0.92	2.06	0.56	0.96	0.92
Redbik	*Redigobius bikolanus*	4.21	0.24	6.01	0.20	4.63	0.20	5.49	0.24
Tantan	*Tandanus tandanus*	9.37	**0.02**	2.71	0.61	9.37	**0.02**	2.71	0.61
Tilmar	*Tilapia mariae*	4.18	0.24	2.67	0.61	4.73	0.19	2.61	0.63
Toxcha	*Toxotes chatareus*	2.80	0.42	5.33	0.25	2.80	0.42	5.33	0.25



(a)



(b)

Figure 5.3 Mean catch per unit effort (number of individuals per second ±SE) of the eight most numerically abundant species caught using electrofishing, for sites averaged across sampling dates (a) and sampling dates averaged across sites (b). ***** denotes significant difference (Kruskal-Wallis $p<0.05$). See Table 5.3 for full test results. The October 2003 sample from site 2 was removed from this analysis (see text).

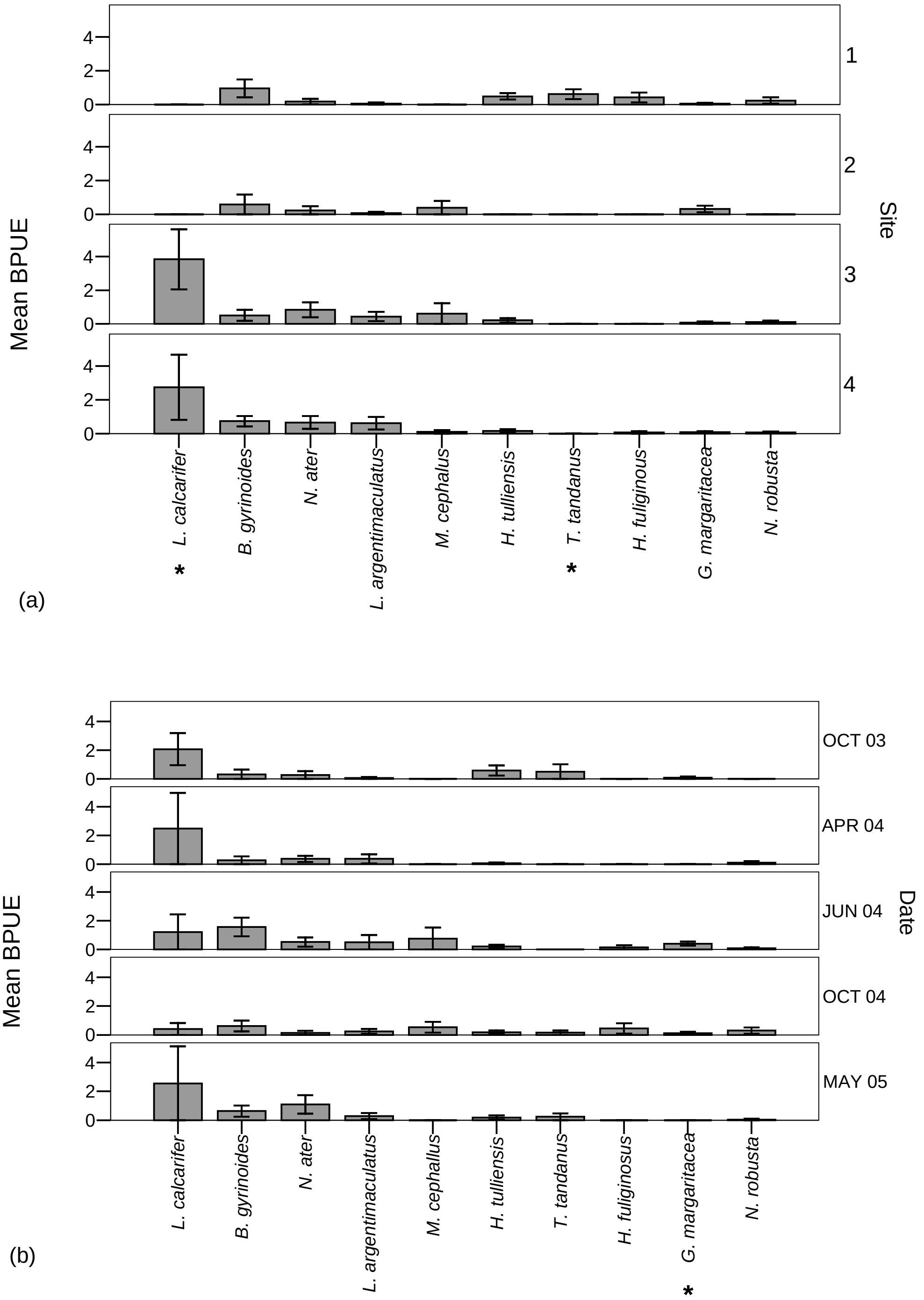


Figure 5.4 Mean biomass per unit effort (grams per second of electrofishing ±SE), of the ten species with greatest biomass, for sites averaged across sampling dates (a) and sampling dates averaged across sites (b). * denotes significant difference (Kruskal-Wallis *p*<0.05). See Table 5.3 for full test results. The October 2003 sample from site 2 was removed from this analysis (see text).

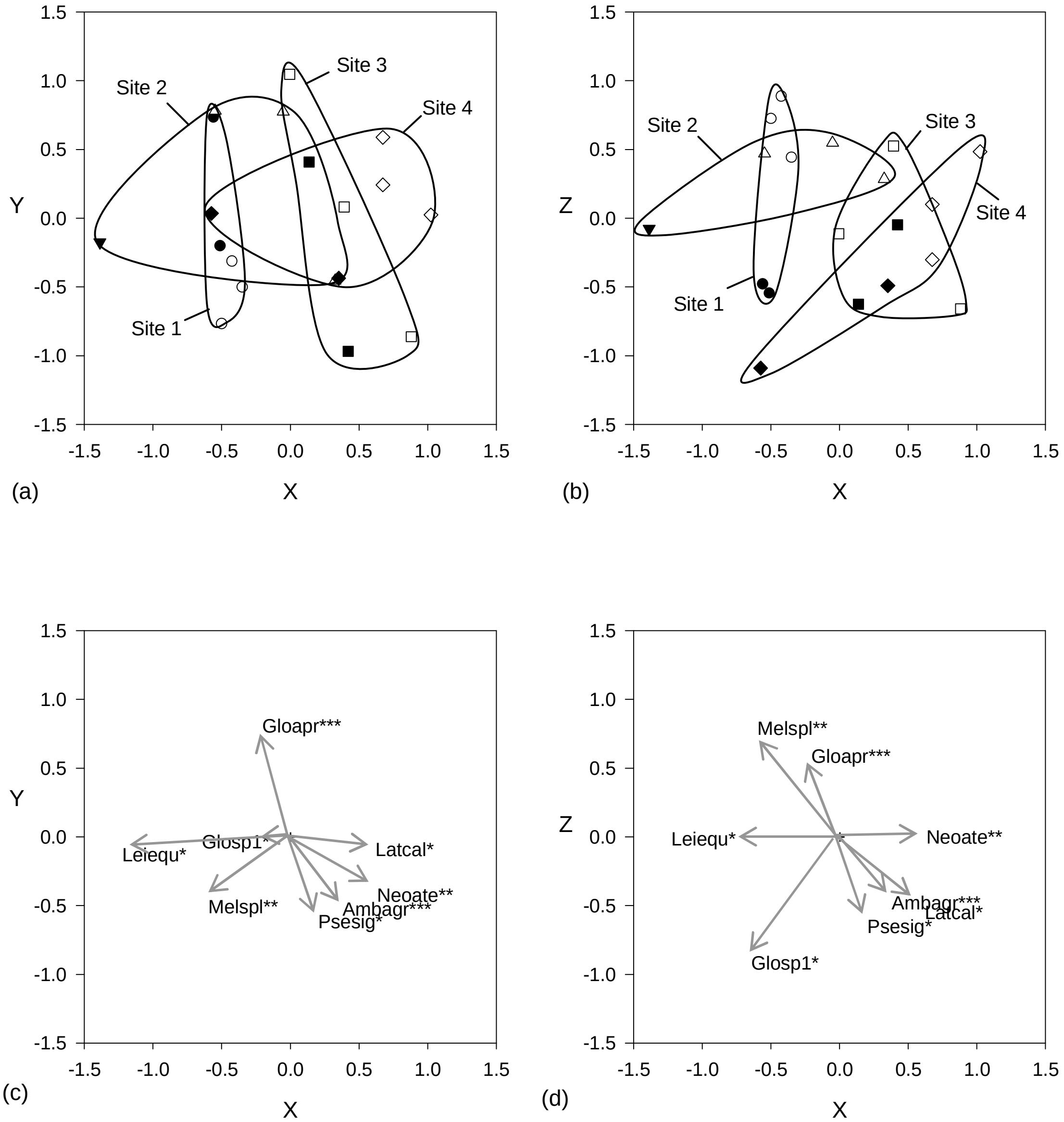


Figure 5.5 The distribution of study sites in three-dimensional ordination space (a, b), as defined by SSH MDS of electrofishing CPUE (log$_{10}$(x+1) transformed, Bray-Curtis metric, stress = 0.1882) during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). PCC vector lines are shown with MCAO r-squared values (c, d): *** = 0%, ** = 1%, * = 2-5%. See Table 5.1 for species vector codes. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space.

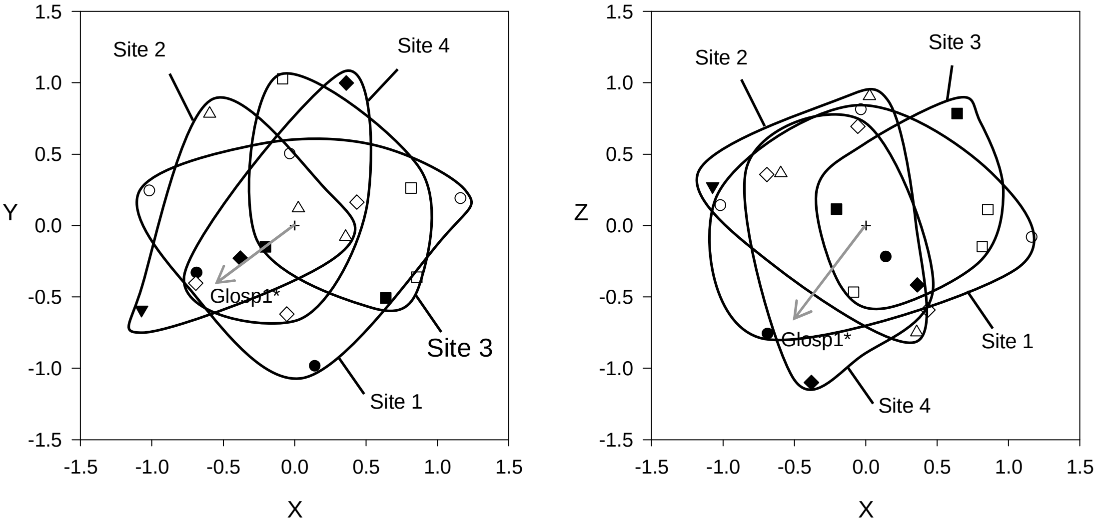


Figure 5.6 The distribution of study sites in three-dimensional ordination space (a, b), as defined by SSH MDS of electrofishing BPUE ($\log_{10}(x+1)$ transformed, Bray-Curtis metric, stress = 0.2044) during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). *Glossogobius* sp. 1 was the only species strongly correlated with the distribution of study sites in ordination space.

Table 5.4 Kruskal-Wallis test results for mean gill net CPUE (number of individuals per gill net hour) and mean BPUE (grams per gill net hour) between sites and sampling dates. Significant differences (*p*<0.05) are highlighted in boldface.

		CPUE				**BPUE**			
		Site (d.f.=3)		**Date (d.f.=4)**		**Site (d.f.=3)**		**Date (d.f.=4)**	
Code	**Species**	**X^2**	***p***	**X^2**	***p***	**X^2**	***p***	**X^2**	***p***
Arrscl	*Arrhamphus sclerolepis*	6.79	0.08	3.85	0.43	6.79	0.08	4.16	0.39
Gerfil	*Gerres filamentosus*	7.77	0.05	4.10	0.39	7.77	0.05	4.10	0.39
Gloapr	*Glossamia aprion*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Heptul	*Hephaestus tulliensis*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Latcal	*Lates calcarifer*	14.03	**0.00**	1.24	0.87	14.03	**0.00**	1.24	0.87
Melspl	*Melanotaenia splendida splendida*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Mugcep	*Mugil cephalus*	2.12	0.55	3.17	0.53	2.12	0.55	3.17	0.53
Nemere	*Nematalosa erebi*	12.56	**0.01**	4.08	0.40	13.47	**0.00**	3.41	0.49
Neoate	*Neosilurus ater*	2.18	0.54	14.09	**0.01**	1.77	0.62	12.75	**0.01**
Tilmar	*Tilapia mariae*	1.02	0.80	8.10	0.09	1.36	0.71	4.40	0.36

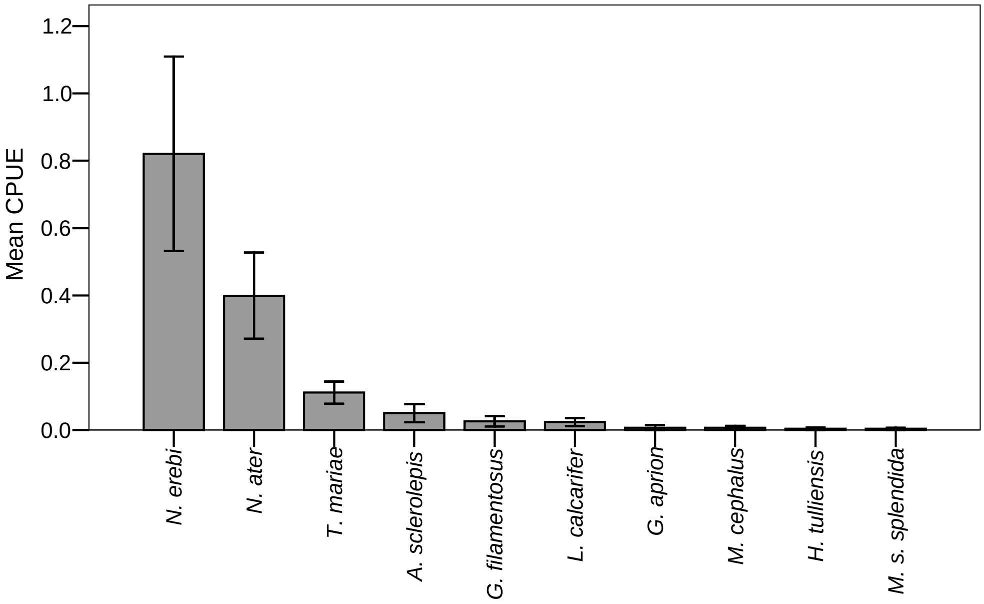


Figure 5.7 Mean catch per unit effort (number of individuals per gill net hour ±SE) of all species caught using gill netting, averaged across sites and sampling dates, in order of descending abundance.

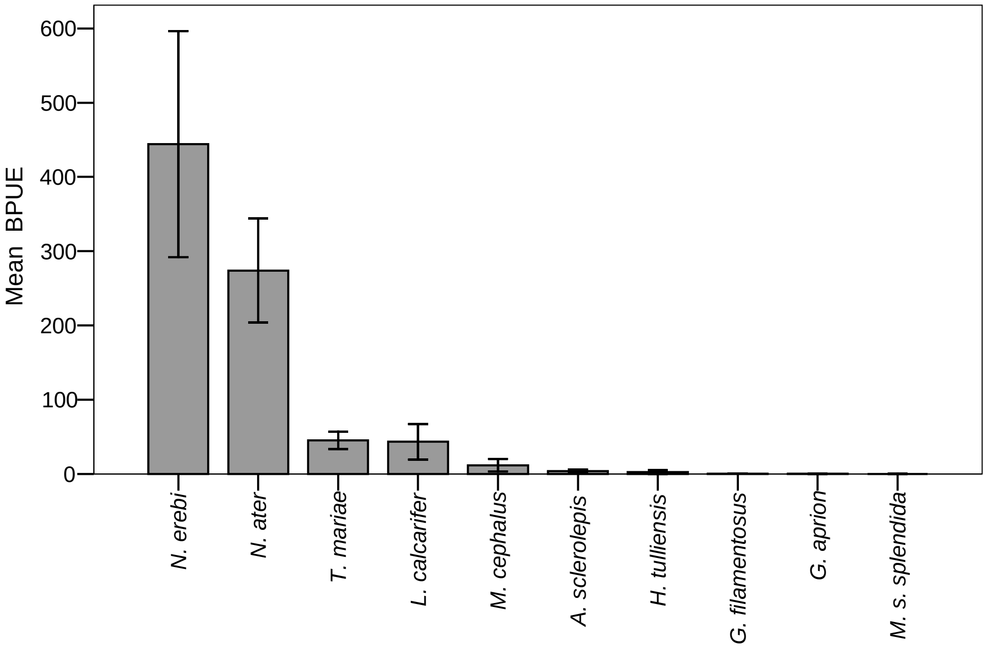


Figure 5.8 Mean biomass per unit effort (grams per gill net hour ±SE) of all species caught using gill netting, averaged across sites and sampling dates, in order of descending biomass.

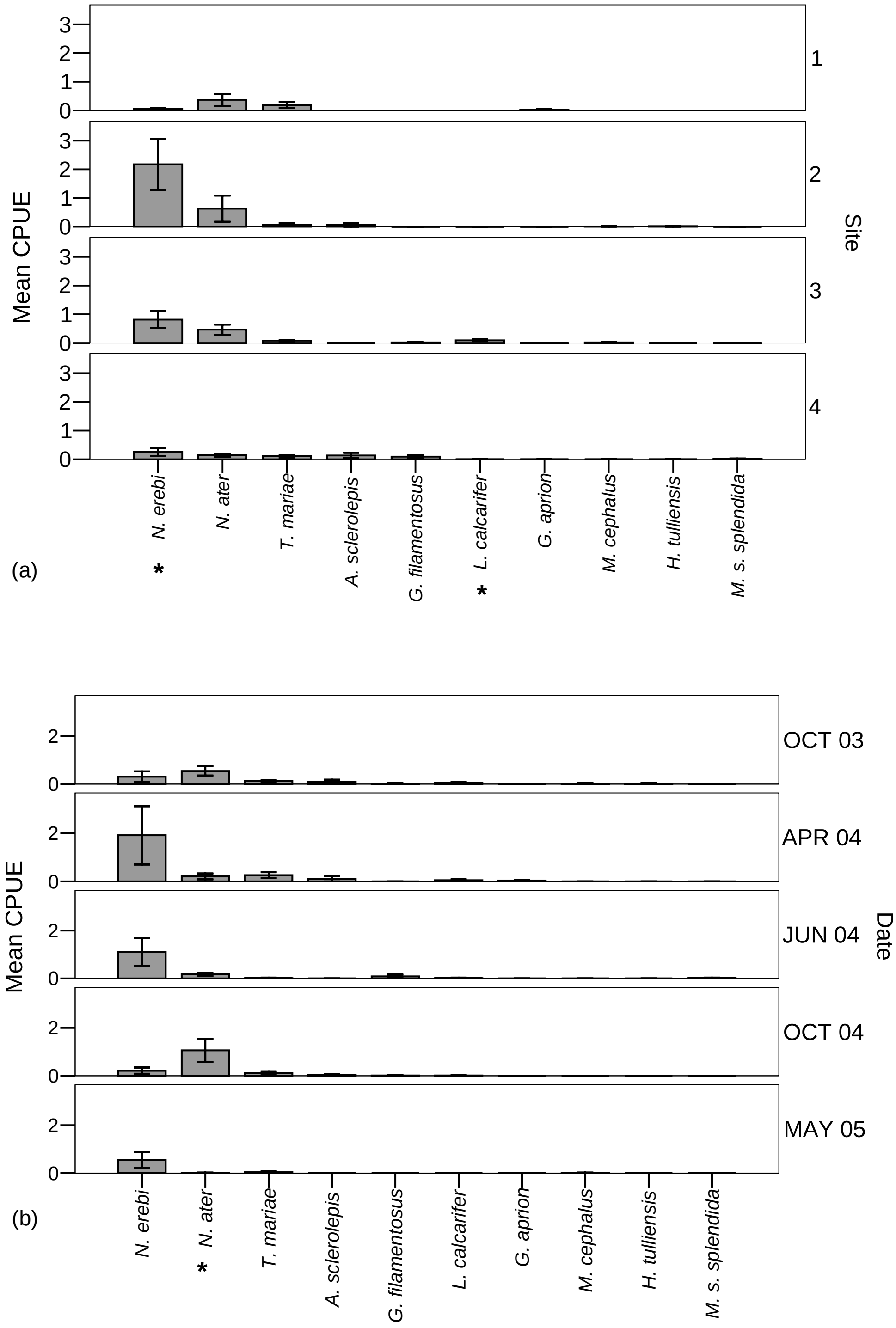


Figure 5.9 Mean catch per unit effort (number of individuals per gill net hour ±SE) of all species caught gill netting, for sites averaged across sampling dates (a) and sampling dates averaged across sites (b). ***** denotes significant difference (Kruskal-Wallis $p<0.05$). See Table 5.4 for full test results.

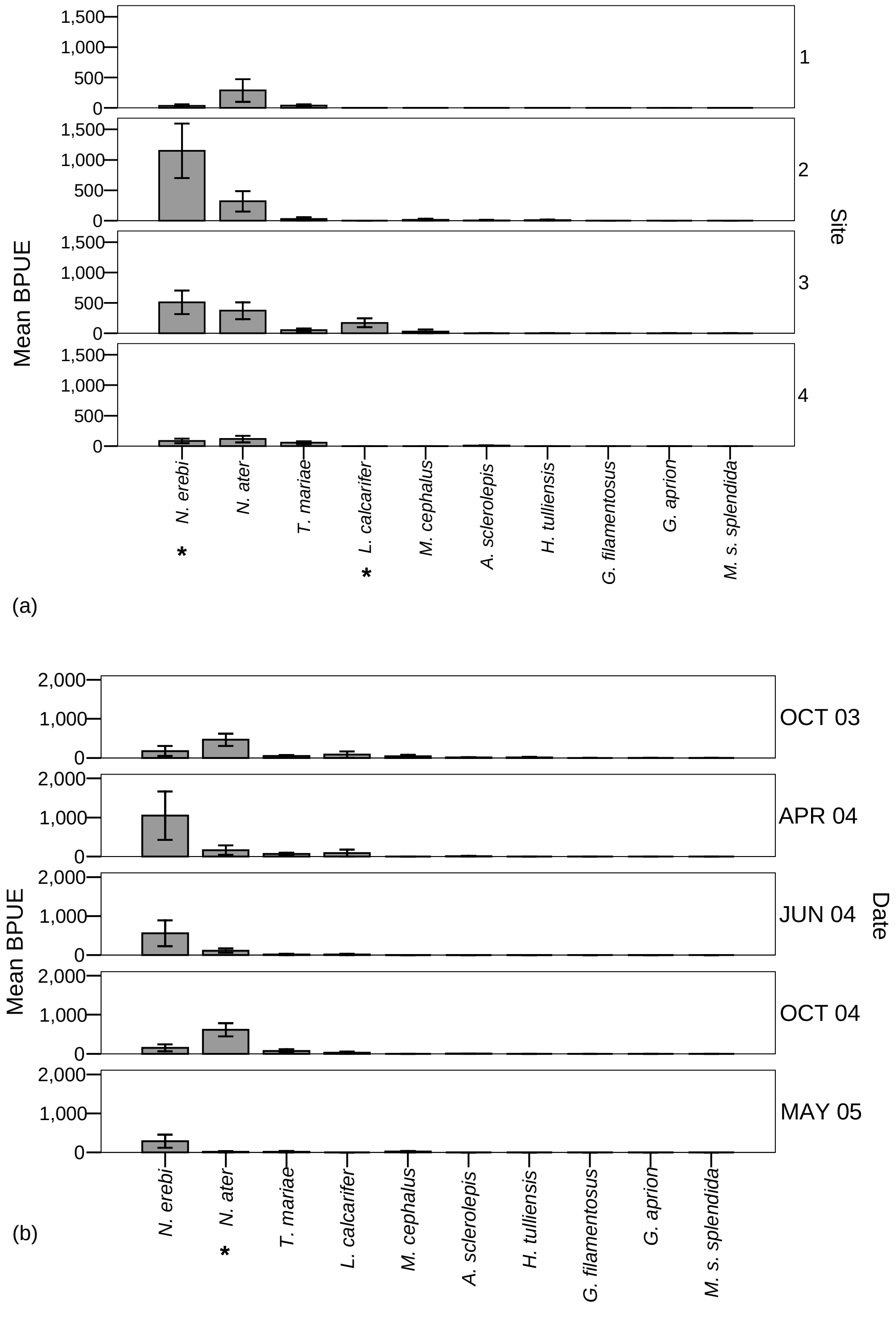


Figure 5.10 Mean biomass per unit effort (grams per gill net hour ±SE), of all species caught gill netting, for sites averaged across sampling dates (a) and sampling dates averaged across sites (b). * denotes significant difference (Kruskal-Wallis p<0.05). See Table 5.4 for full test results.

SSH MDS ordinations of CPUE for species caught using gill-netting revealed considerable overlap between sites over the course of the study (Figure 5.11). *Nematalosa erebi* was strongly correlated with wet season samples at sites 2 and 3, *Neosilurus ater* was strongly correlated with dry season samples at sites 1 and 4, and *Tilapia mariae* was relatively ubiquitous across sites and sampling dates. Trends were clearer, however, when BPUE was analysed: the degree of overlap between sites was greatly reduced, with strong seasonal differences within the total range of each site (Figure 5.12). *Lates calcarifer* was correlated with dry season samples from site 3, *N. erebi* was strongly correlated with wet season samples from sites 2 and 3, and *Arrhamphus sclerolepis* was correlated with a single dry season sample from site 2. As was the case in Figure 5.11, *T. mariae* was ubiquitous.

5.3.4 Analysis of bait trap catch

Glossamia aprion, *Redigobius bikolanus* and *Hypseleotris compressa* comprised the majority of the bait trap catch. Seven other species, including *Ophisternon gutturale* and *Xiphophorus maculatus*, were infrequently encountered (Figure 5.13). *Glossamia aprion* dominated the total biomass collected using bait-traps, with smaller contributions from *H. compressa*, *Gerres filamentosus*, *Melanotaenia splendida splendida* and *R. bikolanus* (Figure 5.14). There were no significant differences in CPUE or BPUE between sites or sampling dates for any of the species captured using bait-traps (Table 5.5). The latter result may be due to the selectivity of bait traps and their apparent inability to capture large numbers of small, mid-water species. Backpack electrofishing from a small punt may be an appropriate method for future sampling of these shallow littoral habitats, given the inherent dangers associated with seine netting in the presence of crocodiles (P. Godfrey, *pers. comm.* 2006).

5.3.5 Classification of habitat use by individual species

The 36 species caught during the study were relatively evenly distributed between the three broad habitat use groups of Galat and Zweimüller (2001) (Table 5.1). A total of 10 species (28% of total) were fluvial specialists, known to favour faster-flowing shallow water habitats (e.g. *Awaous acritosus*, *Glossogobius* sp.1, *Pseudomugil signifer*, *Tandanus tandanus*; Pusey *et al.* 2004). Fifteen (42%) fluvial-dependent species together constituted the largest group, with a diverse taxonomic range of families represented, including some species with estuarine populations (e.g., *Mesophristes argenteus*, *Acanthopagrus australis* and *Acanthopagrus berda*). Lastly, there were 11 generalist species (30%) that occurred in a variety of microhabitats. These species were relatively ubiquitous across sites and sampling dates, with the exception of *Giurus margaritacea* and *Xiphophorus maculatus*.

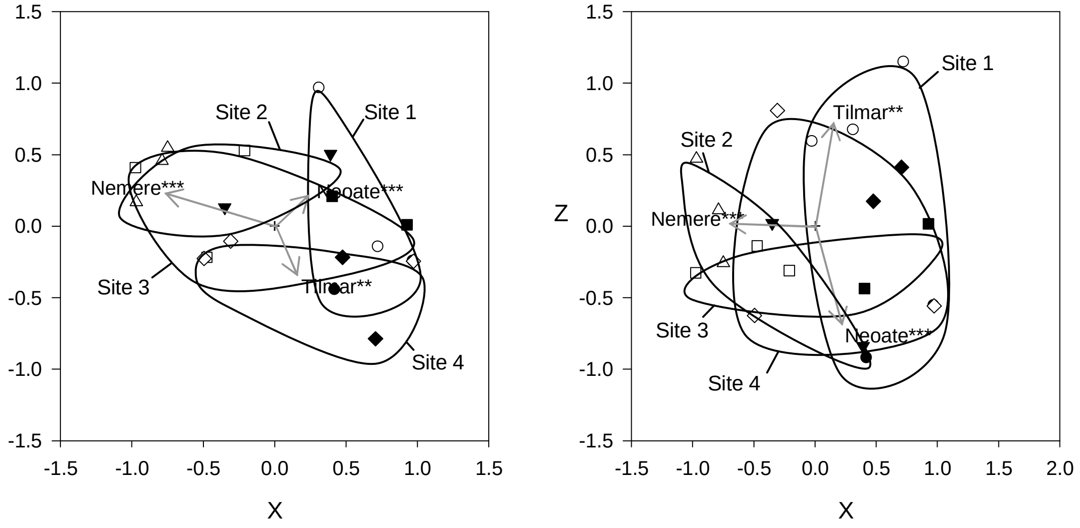


Figure 5.11 The distribution of study sites in three-dimensional ordination space (a, b), as defined by SSH MDS of gill netting CPUE ($\log_{10}(x+1)$ transformed, Bray-Curtis metric, stress = 0.1357) during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). PCC vector lines are shown with MCAO r-squared values (c, d): *** = 0%, ** = 1%, * = 2-5%. See Table 5.1 for species vector codes. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space. The May 2004 sample from site 4 was excluded from this analysis due to zero catch.

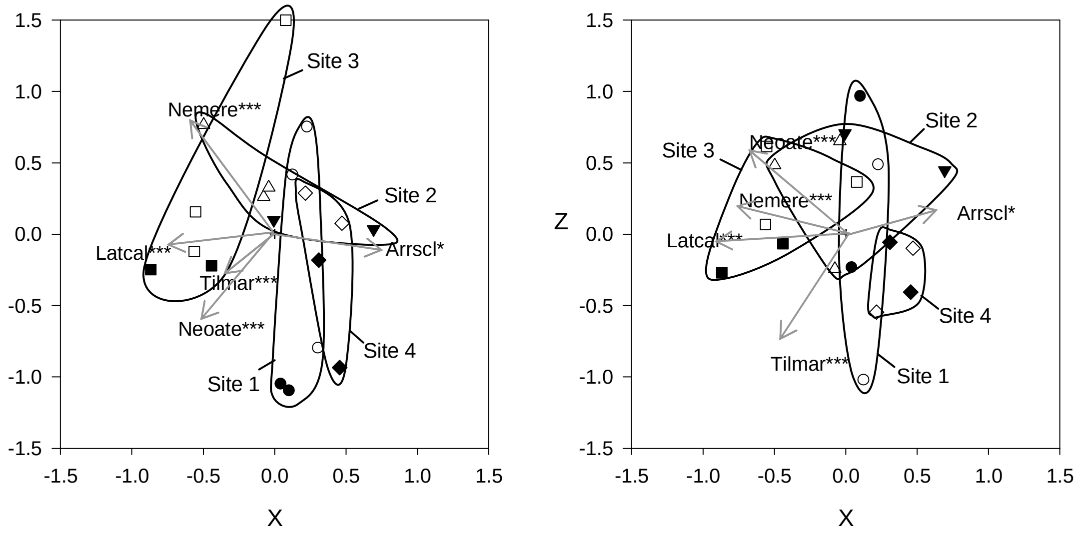


Figure 5.12 The distribution of study sites in three-dimensional ordination space (a, b), as defined by SSH MDS of gill netting BPUE ($\log_{10}(x+1)$ transformed, Bray-Curtis metric, cut-off=1, 50 iterations, 50 random starts, stress = 0.0985; Lee Belbin, *pers. comm.,* stress = 0.0985) during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). Other details as in Figure 5.11.

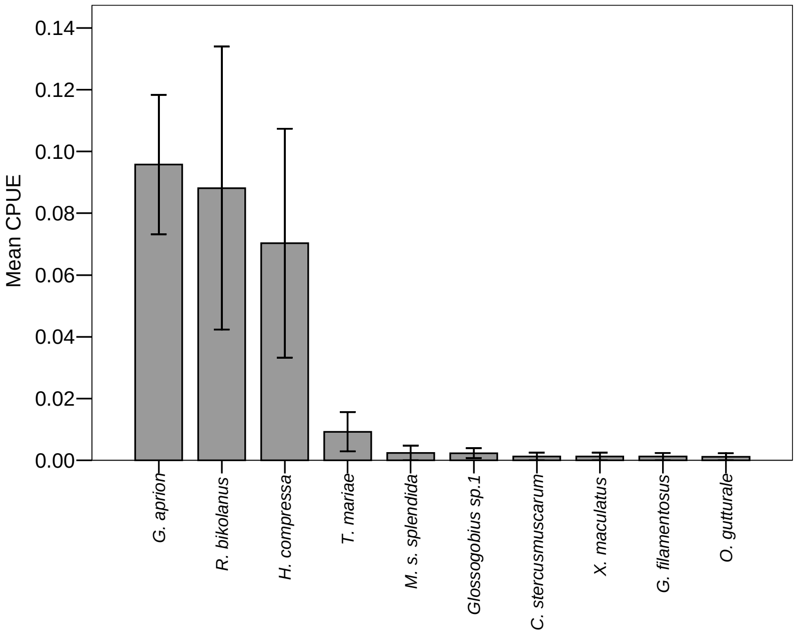


Figure 5.13 Mean catch per unit effort (number of individuals per bait trap hour ±SE) of all species caught bait trapping, averaged across sites and sampling dates, in order of descending abundance.

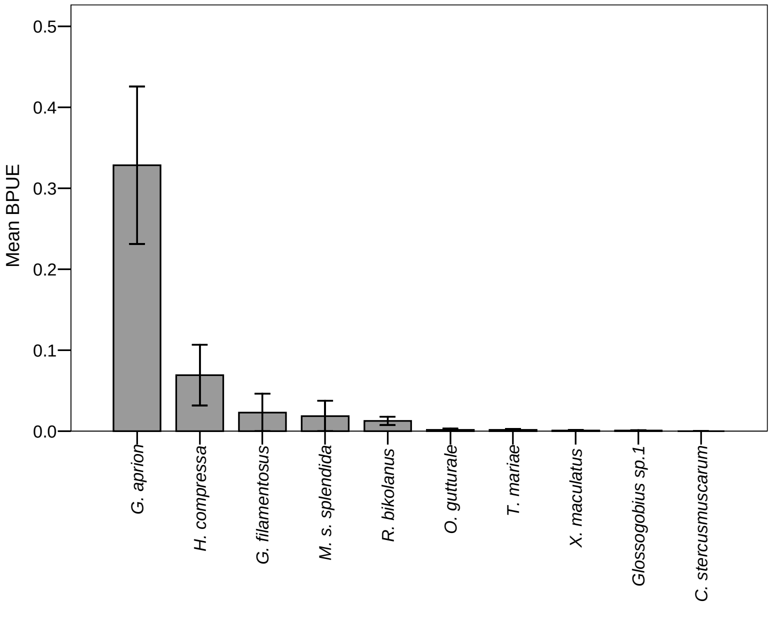


Figure 5.14 Mean biomass per unit effort (grams per bait trap hour ±SE) of all species caught bait trapping, averaged across sites and sampling dates, in order of descending biomass.

Table 5.5 Kruskal-Wallis test results for bait trap CPUE (mean number of individuals per bait trap hour) and mean BPUE (grams per bait trap hour) between sites and sampling dates.

		CPUE				**BPUE**			
		Site (d.f.=3)		**Date (d.f.=4)**		**Site (d.f.=3)**		**Date (d.f.=4)**	
Code	**Species**	X^2	p	X^2	p	X^2	p	X^2	p
Craste	*Craterocephalus stercusmuscarum*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Gerfil	*Gerres filamentosus*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Gloapr	*Glossamia aprion*	5.71	0.13	6.21	0.18	4.13	0.25	8.79	0.07
Glosp1	*Glossogobius* species 1	2.12	0.55	8.42	0.08	2.12	0.55	8.42	0.08
Hypcom	*Hypseleotris compressa*	5.55	0.14	3.54	0.47	5.32	0.15	3.72	0.45
Melspl	*Melanotaenia splendida splendida*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Ophgut	*Ophisternon gutturale*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41
Redbik	*Redigobius bikolanus*	4.92	0.18	6.87	0.14	4.15	0.25	7.11	0.13
Tilmar	*Tilapia mariae*	2.12	0.55	8.42	0.08	2.12	0.55	8.42	0.08
Xipmac	*Xiphophorus maculatus*	3.00	0.39	4.00	0.41	3.00	0.39	4.00	0.41

5.3.6 Seasonal shifts in habitat use by fish species

Habitat use by freshwater fish in the main channel of the Mulgrave River varied seasonally. A total of eight habitat guilds were identified for species caught using electrofishing, on the basis of the mean habitat use by each species relative to habitat availability during wet and dry seasons (Figure 5.15). Members of guild 1 covered a diverse taxonomic spectrum with a variety of habitat preferences (from gobies to a larger lutjanid species), but a general trend towards wide, deep sections of the river, with mud substrates and large woody debris elements. Most of the members of this first guild were from wet season samples. Guild 2 was composed of root mass specialists, *Anguilla reinhardtii*, *Hephaestus fuliginosus* and *Notesthes robusta*, from dry season samples. Overhanging vegetation appeared to be important to *Pseudomugil signifer*, the sole member of guild 3, although only three individuals of this species were caught using electrofishing.

The two members of guild 4, *Hephaestus tulliensis* and *Tandanus tandanus*, were associated with deep undercut banks, whereas the two goby species in guild 5, *Awaous acritosus* and *Glossogobius* sp. 1, preferred high velocity areas with fine gravel substrates and an abundance of leaf litter. All of these habitat types were most abundant at site 1, the most upstream site (Chapter 3). All members of guild 7 were from dry season samples and favoured emergent vegetation, filamentous algae, submerged vegetation and aquatic macrophytes (e.g., *Gerres filamentosus* and *Hypseleotris compressa*). Lastly, guild 8, like guild 3, was composed of a single species, *Lates calcarifer* from dry season samples, that used both large woody debris and macrophyte beds.

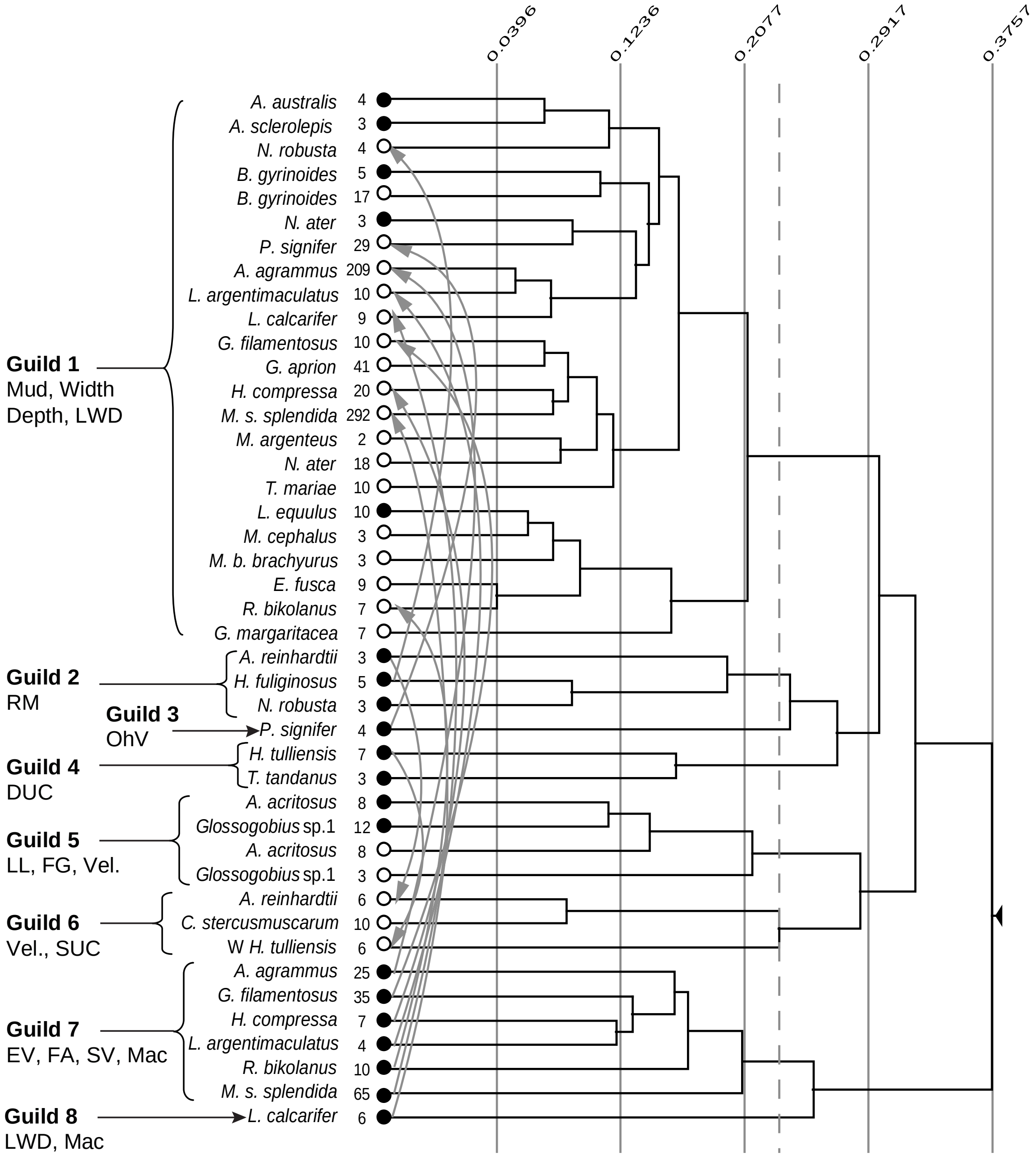


Figure 5.15 Habitat guild structure of the freshwater fish community (caught using electrofishing) of the lowland Mulgrave River, during dry (closed circles) and wet (open circles) season samples, showing guilds 1 to 8 as defined by flexible UPGMA classification (grey dashed line). Grey arrows represent seasonal habitat shifts resulting in movement between guilds. Note that some species were only caught in one season.

As shown by the grey arrows in Figure 5.15, there was a high degree of seasonal variability in habitat guild membership. Most species that were caught using electrofishing in both seasons moved between guilds, particularly from guilds 7 and 8 during the dry season (instream vegetation) to guild 1 during the wet season (wide, deep habitats with mud substrate and large woody debris). Exceptions to this trend were *Neosilurus ater* and *Bunaka gyrinoides*, which favoured the latter habitats in both seasons, and *Glossogobius* sp. 1 and *Awaous acritosus*, which both remained in guild 5 at all times (velocity, fine gravel and leaf litter). In general, fish species collected during the dry season belonged to guilds with more specific habitat preferences (i.e., guilds 2-8, but not guild 6) than those species collected during the wet season, most of which belonged to guild 1.

5.4 Discussion

5.4.1 Spatial variability in fish community structure

Fish community structure varied spatially in the main channel of the Mulgrave River, reflecting both the longitudinal and hierarchical organisation of fish habitats within the catchment. For example, *Melanotaenia splendida splendida*, *Tandanus tandanus* and *Hephaestus fuliginosus* were common at upstream sites (1 and 2), whereas *Ambassis agrammus*, *Redigobius bikolanus*, *Lates calcarifer* and *Lutjanus argentimaculatus* dominated numerical abundance and biomass at downstream sites (3 and 4), where main-channel habitats were generally larger and the influence of tides was greater. Some species, including *Giurus margaritacea*, and *Nematalosa erebi*, preferred deeper, relatively open waters in wide sections of the main channel (mostly at sites 2 and 3), while others, such as *Glossogobius* sp. 1 and *Awaous acritosus*, were usually found in shallower habitats with fine gravel and sand substrates. Overall, nearly 75% of the native species caught during the present study were fluvial specialists or fluvial dependents (Table 5.1). This percentage is higher than reported for rivers in North America (45-67%) and Europe (41-54%; Galat and Zwiemuller, 2001), emphasising the importance of fluvial habitats in the Mulgrave River, especially as floodplain habitats are degraded and poorly connected to the main channel.

Similar spatial variability in fish assemblages has been well documented in a range of temperate (Kohen *et al.*, 1994; Gehrke *et al.*, 1999; King, 2004), sub-tropical (Pusey *et al.*, 1993; Arthington *et al.*, 2005) and tropical river systems (Gorman and Karr, 1978; Martin-Smith, 1998; Pusey *et al.*, 1998; Bishop *et al.*, 2001). In general, these studies show that species richness tends to increase downstream, as the greater diversity and extent of aquatic habitats allows for colonisation by additional species, particularly larger species (Sheldon, 1968; Schlosser, 1982; Angermeier and Schlosser, 1989; Harvey and Stewart, 1991; Arunachalam, 2000). When Pusey *et al.* (1995a) surveyed the Mulgrave River, they identified a shift in fish community composition with gradual downstream change in substrate size and the type of instream cover. While their research focussed on upland streams and lowland tributaries, rather than main-channel habitats, the data presented in this chapter suggest that the longitudinal patterns identified by Pusey *et al.* (1995a) are also present within the short lowland reach of the system.

Habitat use by most fish species was consistent with their published habitat preferences (Pusey *et al*., 2004). While some habitat generalists, such as *Tilapia mariae* and, to a lesser extent, *Hypseleotris compressa*, were relatively ubiquitous across sites, the abundance of many species was strongly correlated with the presence of the specific micro-habitat features that they favoured. *Bunaka gyrinoides* and *Notesthes robusta*, for example, were usually associated with root masses in littoral areas. Inoue and Nunokawa (2002) demonstrated that the abundances of two fish species (*Oncorhynchus masou* and *Leuciscus ezoe*), in a third-order Japanese stream, were related to the abundance of their preferred habitat at this microhabitat scale, rather than at the mesohabitat scale. In the present study, however, a range of microhabitats were sampled during each electrofishing shot. As a result, it is possible that the fine-scale microhabitat preferences of individual fish species were overlooked and that, had fish habitats been described using a higher level of resolution, differences in habitat use between fish species might have been more pronounced.

5.4.2 Temporal variation in fish community structure

Temporal change in fish community structure was pronounced in the main channel of the Mulgrave River and was related to flow-mediated changes to instream habitats. *Gerres filamentosus*, *Neosilurus ater* and *Tilapia mariae* were most abundant during the dry season, when fish habitats appeared to be stable and structurally complex (see Chapter 3). In contrast, when the diversity of fish habitats declined during the wet season, other species, such as *Glossamia aprion* and *Nematalosa erebi*, were more common. Despite these changes, however, the species richness and evenness of the fish community did not differ significantly between sampling dates, suggesting that individual species that moved out of the study area were quickly replaced by others. As shown by Winemiller (1989) in South American river systems, these movements were probably related to seasonal reproductive activity. For example, *N. ater* is known to undertake upstream spawning migrations during high flow events, whereas *Hypseleotris compressa* and *N. erebi* may move downstream at the same time of year (Pusey *et al.*, 2004; Paul Godfrey *pers. comm.* 2006).

The temporal dynamics of fish-habitat relationships have not been previously assessed in Wet Tropics rivers, but are well documented in other regions of Australia (e.g., Kohen *et al.*, 1994; Pollino *et al.*, 2004). For example, Arthington *et al.* (2005) described seasonal change in the fish assemblages of Cooper Ck, an arid-zone floodplain river. They found that marked changes in fish community structure between the early (April) and late (September) dry season were related to habitat loss. As water levels receded and pools dried up, within-waterhole features, such as boulders, root masses and large woody debris, were exposed and the number of sheltered places where fish could rest and forage was reduced (Arthington *et al.*, 2005). Unlike systems in these drier areas, rivers in the Wet Tropics rarely, if ever, experience periods of no flow. As a result, mesohabitats in lowland main channels remain connected throughout the dry season and the extreme total habitat shortages described by Arthington *et al.* (2005) are not usually encountered.

Seasonal habitat use by fish species in the present study appeared to follow variations in habitat availability. Kennard (1995) reported similar results in floodplain lagoons of the Normanby River, where most species utilised the most common microhabitat type within each lagoon. He too found that temporal patterns in habitat use were dependent on seasonal patterns of habitat availability, rather than the outcome of competition for space. In the present study, habitats in the main channel of the Mulgrave River appeared to be more diverse and distinct during the dry season than during the wet season. When high flow events removed instream and littoral vegetation, the heterogeneity of habitats within sites was greatly reduced. Habitat guild membership reflected these dynamics, with most species belonging to guild 1 (wide, deep habitats with mud substrate and large woody debris) during the wet season, possibly because the habitats that they had preferred during the dry season were unavailable.

5.5 Conclusion

The data presented in this chapter demonstrate a strong relationship between flow seasonality, habitat structure and fish community composition in the Mulgrave River. Spatial variability in species assemblage structure occurred between sites, along a longitudinal gradient of habitat conditions, and within sites, as a function of micro-habitat features. Instream habitat conditions were stable during the dry season, but regular wet season flooding disturbed habitats. Nonetheless, a range of fish species utilised the main channel at all times of the year. These results combine with the relative unsuitability and inaccessibility of the floodplain to emphasise the importance of main-channel areas. As indicated by Galat and Zweimüller (2001), the diversity of habitats inherent in main-channel complexes is essential to meet the requirements of native fluvial fishes. These habitats should be protected and/or restored in Wet Tropics catchments.

Chapter 6: Spatial and temporal variation in fish feeding

6.1 Introduction

Freshwater fish possess a range of morphological adaptations for efficiently locating, capturing and consuming prey items that best meet their nutritional requirements (Pyke, 1984; Gerking, 1994). At tropical latitudes, high species diversity is associated with extensive morphological diversification (Winemiller, 1992a), that may result in unusual feeding modes, such as fin-nipping in piranhas (Winemiller and Kelso-Winemiller, 1993) or lepidophagy (scale eating) in characids (Sazima, 1983). Most species, however, conform to several key feeding modes, or trophic guilds: herbivores with rasping dentition and long, coiled alimentary canals (e.g., *Tilapia mariae*); detritivores, some with muscular crops located in the anterior region of the gut (e.g., *Nematalosa erebi*); benthic, aquatic, planktonic or surface invertivores with a variety of jaw and gut morphologies (e.g., *Neosilurus ater* cf. *Melanotaenia splendida splendida*); and deep-bodied piscivores with large fins, jaws and stomachs (e.g., *Lates calcarifer*) (Karr *et al.*, 1986; Kennard *et al.*, 2001; Pusey *et al.*, 2004). Additionally, omnivorous species may consume prey from multiple trophic levels and share morphological and dietary characteristics with members of other feeding groups (Karr *et al.*, 1986; Fagan, 1997).

The type and number of feeding guilds present in a fish community vary with the species present, the density of prey items and the degree of taxonomic resolution employed by the authors (Angermeier and Karr, 1983; Moyle and Senanayake, 1984). For example, Angermeier and Karr (1983) assigned fish to 7 feeding guilds (algivores, aquatic insectivores, general insectivores, piscivores, scale-eaters, terrestrial herbivores, omnivores), while Goldstein and Simon (1999), in a bid to create a working tool for determining biotic integrity in North American streams, proposed a trophic classification framework consisting of five guilds with nine sub-guilds and 26 modes of feeding. Despite this variability, the general theory behind the guild concept is that the ecological relationships among guild associates are determined by a combination of interspecific competition for resources, phylogenetic/morphological constraints on resource use and optimal foraging dynamics (Blondel, 2003; Piet, 1998; Pyke, 1984). As discussed in chapter 1, the degree of overlap in resource use by fishes has been shown to vary as different food items become more or less abundant (Angermeier, 1982; Little *et al.*, 1998; Matthews, 1998).

In tropical rivers, fluctuations in food availability are regulated largely by seasonal, flow-mediated changes in primary productivity (Junk *et al.*, 1989; Thorp and Delong, 1994). However, the specific responses of fishes to these fluctuations may vary considerably according to the fine-scale dynamics of predator-prey interactions and local habitat structure (Angermeier and Karr, 1983; Power, 1983). Lowe-McConnell (1963) and Goulding (1980) documented the seasonal diet shifts of stream fish in South American savannas and flooded forests, respectively. They found that food was most abundant and diverse during the wet season, at which time extensive adaptive radiation to use previously unavailable food resources, such as fruit, came into play and differentiation in feeding habits was at its greatest (Lowe-McConnell, 1963; Goulding, 1980a). In contrast, Zaret and Rand (1971) found that fish in a Panamanian lowland stream shifted from distinct food niches during the dry season, to widely overlapping ones in the wet season. While these results appear conflicting, they probably represent a continuum of resource availability, with the extreme food shortages reported by Lowe-McConnell (1963) not encountered by Zaret and Rand (1971) during the course of their study. In general, there is a consistent trend of species' movements between guilds on a seasonal basis; as Werner and Gillam (1984) stated, seasonal variation in diet is now considered more the norm than the exception.

In Australia, 13 studies have examined trophic ecology of freshwater fish at the community level (Hortle and Pearson, 1990; Arthington, 1992; Kennard, 1995; Pusey *et al.*, 1995b; Pusey and Bradshaw, 1996; Pusey *et al.*, 2000a; Bishop *et al.*, 2001; Kennard *et al.*, 2001; Bunn *et al.*, 2003; Gill and Morgan, 2003; Meredith *et al.*, 2003; Pusey, 2003; Balcombe *et al.*, 2005; King, 2005). As described in section 1.7, only two studies have provided a detailed analysis of fish feeding in the Wet Tropics region: those of Hortle and Pearson (1990) and Pusey *et al*. (1995). The latter study identified the importance of fish body size in determining fish species membership to trophic guilds. This result is not unusual: size has repeatedly been identified as an important determinant of predator-prey interactions and therefore the dietary composition of freshwater fish (Winemiller, 1989; Winemiller, 1990; Winemiller *et al.*, 1997; Oyarzun *et al.*, 2001; Gill and Morgan, 2003; King, 2005).

As fish grow, their increasing gape size allows a larger range of prey sizes to be handled and consumed, leading to ontogenetic diet shifts. In addition, because larger fish prefer deeper habitats (Gorman and Karr, 1978; Angermeier and Karr, 1983; Angermeier and Schlosser, 1989), that provide overhead cover from terrestrial predators, the types (and sizes) of prey encountered by individual fish may also change over time (Bustard and Narver, 1975; Sechnick *et al.*, 1986; Boulton and Lake, 1992; King, 2004). For example, adult piranha (*Pygocentrus notatus*) are piscivorous, but exhibit strong diet shifts from microcrustacea as larvae (<20 mm), to aquatic insects as juveniles (20-40 mm), and to fish as sub-adults and adults (>40 mm; Winemiller, 1989). In this way, different size classes of a single species may belong to different trophic guilds (Munoz and Odjeda, 1998; King, 2005). Pusey *et al*. (2004) documented a similar shift in *Lates calcarifer*.

To date, the influence of temporal flow, habitat and food variability on the trophic dynamics of Wet Tropics freshwater fish remains unstudied. In addition, neither Hortle and Pearson (1990) nor Pusey *et al.* (1995b) directly quantified resource availability, relying instead on gut fullness as a surrogate measure of food availability. As a result, the authors had difficulty accounting for some of the more complex feeding patterns they observed. Pusey *et al.* (1995b) concluded their study by asking: was the degree of dietary partitioning they observed due to differences in microhabitat usage; does the overall pattern of resource partitioning change seasonally; and if dietary overlap is high, but food does not appear to be limited, what other factors act to restrict fish abundance? In chapters 3 and 4 I described a decline in productivity, habitat diversity, and invertebrate abundance at lowland sites during the wet season, when elevated flows acted as a disturbance pressure. Given the sensitivity of freshwater fish to changes in the type and abundance of their prey (Gerking, 1994), it is possible that these factors interact to cause flow effects at higher trophic levels, such as seasonal shifts in dietary composition and the intensity of competition for food resources (Mattila, 1992; Livingston, 1997; Livingston *et al.*, 1997).

My aim in this chapter is to address the questions posed by Pusey *et al.* (1995b) by describing the trophic ecology of the lowland main-channel freshwater fish community in the Mulgrave River, with particular reference to temporal dynamics. I also address to following questions. What are the most important dietary items for each fish species and for the entire community? What is the relative importance of items derived from benthic, littoral and riparian habitats? Does the relative importance of these food items change seasonally? Are trophic guilds present and, if so, is guild structure temporally stable, or are feeding dynamics linked to the fluctuations in food abundance described in chapter 4? My overall goal is to continue the development of a conceptual model of riverine function from previous chapters and to provide a background for a discussion of seasonal food web dynamics in chapter 7.

6.2 Methods

6.2.1 Specimen collection, morphological measurements and gut contents analysis

Fish were collected using the stratified sampling protocol detailed in chapter 5. Fish were euthanised using either benzocaine or an icy slurry, before preservation in formalin solution (10%). The body cavity of larger specimens (>300 mm) was also injected with formalin solution to improve the preservation of gut contents. Specimens were later transferred to 70% ethanol, prior to examination of gut contents. Morphological measurements (i.e., standard length (SL) and vertical and horizontal mouth gape), gut fullness estimation and gut contents analyses were conducted using the methods described in Pusey *et al.* (1995b). These methods are based on the standardised volumetric approach described by Hyslop (1980), in which items within each dietary category are grouped together and 'squashed' to a uniform depth of 1 mm. The area covered is then taken to represent the volumetric contribution by that food category. This method is most appropriate when considering the effect of food availability on predators (Fedriani and Travaini, 2000).

Dietary items were divided into 38 prey categories. These 'fine' categories were later collapsed down to 14 'broad' categories that matched those used for analysis of invertebrate communities in chapter 4. These were: aerial and surface invertebrates, aquatic insects, macrocrustaceans, microcrustaceans, molluscs, other macroinvertebrates, other microinvertebrates and terrestrial invertebrates, with additional categories for algae, fruit, terrestrial vegetation, macrophytes, fish, detritus and unidentified (Table 6.1). The entire gut was analysed for all species, with the exception of *Neosilurus ater* and *Tandanus tandanus*, in which the contents of the anterior third only were examined due to the decomposed nature of gut contents in the posterior two-thirds; *Tilapia mariae*, in which only the stomach was examined due to the extreme length of the entire gut (up to 2 m); and *Nematalosa erebi*, in which the content of the muscular crop only was examined as contents posterior to this is point in the alimentary canal were unidentifiable.

6.2.2 Data analysis

Mean gut fullness was calculated for each site and date (N=1360), before the dataset was restricted to those individuals with a gut fullness of at least 0.2 (N=981). As described by Pusey *et al.* (1995b), the exclusion of near-empty stomachs prevents overestimation of the importance of rare taxa in the diet. For example, if a single, small prey item had been consumed by a fish before it was examined, that item may have been opportunistically engulfed and may not represent the actual importance of the corresponding dietary category in the diet of the individual as whole. Unidentified items were then excluded, before raw volumetric data from gut contents analysis were converted into the proportional contribution of each diet category to the total diet of each individual fish. The mean of these values (i.e., the mean proportional contribution of each category) was then calculated for fish collected during wet season (April 2004, June 2004 and May 2005) and dry season (October 2003 and 2004) sampling dates for each species. Non-parametric Kruskal-Wallis tests were used to test for differences in these values between sites and dates, as data did not conform to ANOVA assumptions of normality or homogeneity of variance, even after transformation.

Classification analysis (flexible UPGMA in PATN v3.03 based on Bray-Curtis association matrix, beta = -0.1) was then used to examine whether feeding guilds were well defined. The analysis was limited to 22 of the 36 species caught during the study, that had at least three individuals in at least one season (i.e., wet and/or dry) with a gut fullness of at least 0.2 (N=944). Following trophic guild classification, and the associated examination of seasonal shifts in dietary composition, seasonal gut contents samples of nine species for which there was sufficient data were further divided into juvenile, sub-adult and adult size classes (Table 6.2). This dataset was then reanalysed using SSH MDS in order to examine the extent of age/size related variation in diet (PATN v3.03; Bray Curtis association measure, cut-off value = 0.9, 10 random starts, random seed number = 1235, 100 iterations). Principal Component Correlation (PCC) was applied to diet composition data to identify the variables that were most important in determining diet shifts.

The mean diet of all fish present was calculated for each site during each sampling date. This data set was ordinated in PATN using the procedure described above, in order to assess changes in the food consumption of the entire fish community between sites and sampling dates. Sites and sampling dates were then assigned to *a priori* groups for Analysis of Similarity (ANOSIM) testing between sites and of wet versus dry season samples.

Table 6.1 Composition of broad diet categories used in gut contents analysis (after Pusey *et al.*, 1995b; 2004).

Broad category	Code	Fine category
Aerial and surface inverts	Air	Diptera – adults and emergers Water surface invertebrates – Gerridae etc. Collembola
Aquatic insects	Aqua	Chironomidae – larvae and pupae Other Diptera larvae Ephemeroptera – nymphs Trichoptera – larvae, including cases Simuliidae – larvae Odonata – nymphs Coleoptera – larvae Corixidae and Notonectidae – incl. *Plea* Other Hemiptera Coleoptera adults (aquatic spp.)
Macrocrustaceans	MacC	*Macrobrachium* spp. Atyidae
Microcrustaceans	MicC	Planktonic crustaceans – e.g., Cladocera Ostracoda
Molluscs	Moll	Mostly Gastropoda but including some Bivalvia
Other macroinvertebrates	OMac	Mostly Nematoda and Planaria
Other microinvertebrates	OMic	Testate amoeba Hydra
Terrestrial invertebrates	Terra	Orthoptera Hymenoptera Arachnida Small terrestrial invertebrates (<=5 mm) Large terrestrial invertebrates (>5 mm) Lepidoptera larvae
Algae	Algae	Algae
Fruit	Fruit	Fruits of riparian trees
Terrestrial vegetation	Tveg	Material derived from terrestrial plants such as leaves, soft stems and roots (>1 mm in size).
Macrophytes	Mac	Leaves and stems of aquatic plants
Detritus	Det	Detritus (including terrestrial vegetation ≤1mm in size)
Unidentified	Unid	Unidentified

Table 6.2 The number of individuals with gut fullness values of at least 0.2 in juvenile (J), sub-adult (SA) and adult (A) size classes for nine fish species caught during wet and dry season sampling dates.

			N	
Species	**Class**	**SL mm**	**Dry**	**Wet**
Redigobius bikolanus	J	<20	12	5
	A	20	3	20
Pseudomugil signifer	J	<20	0	12
	SA	20-30	4	12
	A	>30	0	5
Hypseleotris compressa	SA	≤30	15	5
	A	>30	17	10
Ambassis agrammus	J	≤30	1	13
	SA	31-40	0	61
	A	>40	3	55
Glossamia aprion	SA	≤40	11	3
	A	>40	1	37
Melanotaenia splendida splendida	J	≤40	10	60
	SA	41-50	10	69
	A	>50	38	126
Gerres filamentosus	SA	≤80	20	10
	A	>80	14	4
Nematalosa erebi	SA	≤200	0	9
	A	>200	10	47
Neosilurus ater	SA	≤350	4	13
	A	>350	18	10

6.3 Results

6.3.1 Gut fullness

The gut contents of 1360 fish from 36 species were analysed. Gut fullness was highly variable, with values ranging from 0 to 1 in all seasons. A total of 379 fish, or 27.9 % of those analysed, had gut fullness values <0.2. Mean gut fullness differed significantly between sites ($X^2 = 53.13$, d.f. = 3, $p < 0.001$) and sampling dates ($X^2 = 130.64$, d.f. = 4, $p < 0.001$). However, as shown in Figure 6.1, this spatial and temporal variation in gut fullness was complex. In general, mean gut fullness ranged between 0.2 and 0.7 (Figure 6.1).

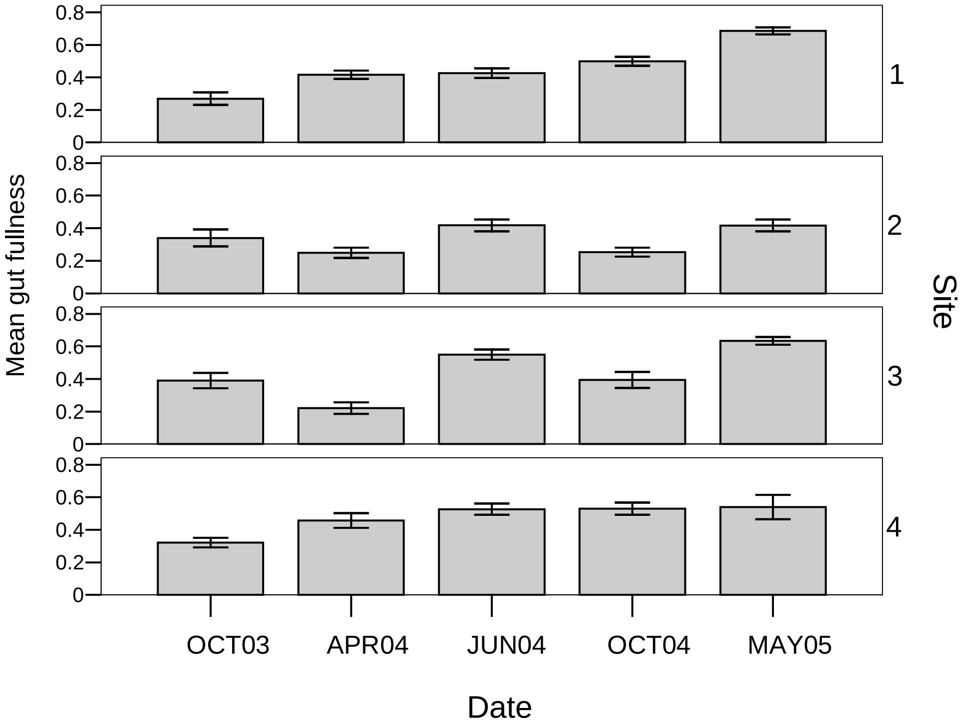


Figure 6.1 Mean gut fullness (±SE) at each site across all species during each sampling date.

6.3.2 Temporal variation in species composition of feeding guilds

Seven feeding guilds were identified (Figure 6.2 and Appendix 3). The first guild consisted of four species that fed on molluscs to differing extents, along with the detritus that was presumably consumed as the molluscs were captured. The first two species, *Acanthopagrus australis* and *Bunaka gyrinoides* specialised on bivalve molluscs (96% of total diet) and gastropod snails 5-40 mm long (68-85%), respectively. The third species, *Gerres filamentosus*, was one of two species caught during the study that exhibited a seasonal dietary shift, moving from a dry season diet of aquatic insects (48%), mostly benthic trichopteran larvae, supplemented by small snails (37%), to a wet season diet composed almost entirely of aquatic insects (89%). *Neosilurus ater*, the last species in this group, ate a combination of aquatic insects (21-29%), molluscs (24-42%) and detritus (23-42%) during both wet and dry seasons.

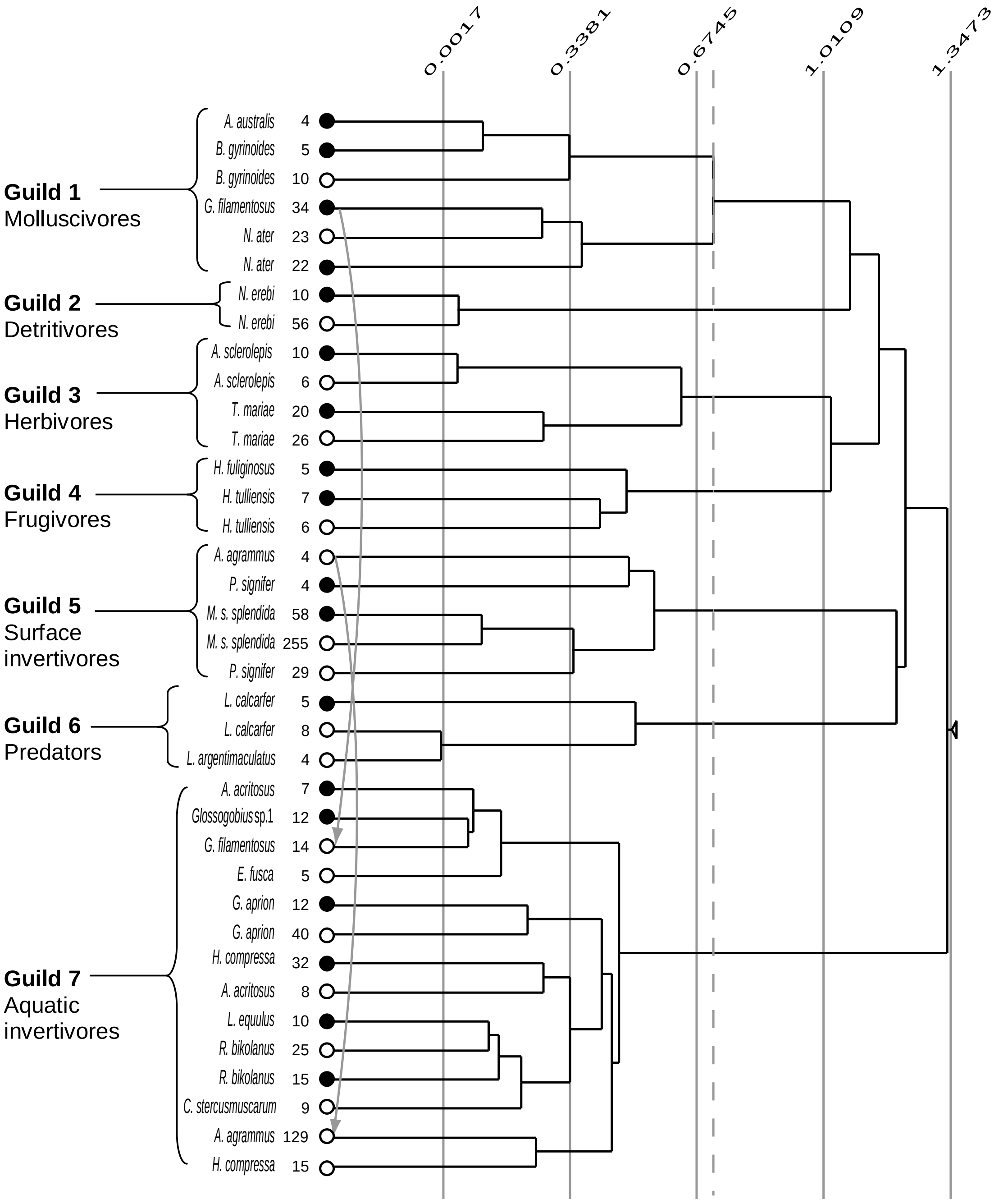


Figure 6.2 The trophic structure of the freshwater fish community of the lowland Mulgrave River. Seven feeding guilds were defined by flexible UPGMA classification on the basis of broad diet categories (grey dashed line) of species collected during dry (closed circles) and wet (open circles). Species names are followed by sample size (i.e., the no. individuals with gut fullness of at least 0.2). Grey arrows represent seasonal feeding shifts resulting in movement between guilds. Note that some species were only caught in one season (e.g., *C. stercusmuscarum*).

The second feeding guild was represented by a single species, *Nematalosa erebi*. While this species fed almost exclusively on detritus (95-98%), resources from six other categories made minor contributions: aquatic insects, microcrustaceans, molluscs, other microinvertebrates, algae and macrophytes (all ≤5%). Sub-samples of the detrital component, from ~20 individuals, were mounted on slides and examined under a high-power microscope. While some diatoms and desmids were present, the majority of the material was organic detritus. Two herbivores, *Arrhamphus sclerolepis* and *Tilapia mariae*, comprised the third guild. The former species specialised on macrophytes such as *Vallisineria* sp. (95-100%), while the latter species ate a combination of macrophytes (31-54%), filamentous algae (17-25%) and detritus (21-26%), with minor portions of five other categories. The terapontid grunters in the fourth feeding guild, *Hephaestus fuliginosus* and *H. tulliensis*, consumed fruit (45-69%) supplemented by small percentages of aquatic insects, terrestrial invertebrates and macrocrustaceans. These species were frequently observed schooling under fruiting riparian trees (e.g., *Ficus* spp.) and rising to take fruits at the surface.

The fifth feeding guild consisted of three small-bodied species, *Ambassis agrammus*, *Pseudomugil signifer* and *Melanotaenia splendida splendida*, which swam at or near the surface. These species specialised on a combination of aerial and surface insects (28-92%), particularly emerging chironomid nymphs, and terrestrial invertebrates (up to 43%), principally green ants (*Oecophylla smaragdina*), that had presumably fallen on to the water surface from overhanging vegetation. Like *Gerres filamentosus*, *A. agrammus* exhibited a seasonal diet shift, in this case from surface invertebrates during the dry season, to aquatic insects during the wet season. *Lates calcarifer* and *Lutjanus argentimaculatus* belonged to the sixth feeding guild. Both of these species preyed on macrocrustaceans (53-92%), such as penaeid shrimps and *Macrobrachium* sp., and fish (up to 47%). However, gut fullness was highly variable in this group (often either 0 or 1), with individuals apparently eating large prey items infrequently.

The final, and largest, feeding guild contained 10 species. This group consumed varying proportions of aquatic insects (44-94%). The diet of *Awaous acritosus* was dominated by aquatic insects during the dry season (89%), but was more varied during the wet season, with microcrustaceans, other microinvertebrates and algae each contributing >10% of the diet during this period. *Glossogobius* sp.1 and *Eleotris fusca* both specialised on aquatic insects, while *Glossamia aprion* fed on aquatic insects combined with crustaceans and some fish during both wet and dry seasons. *Hypseleotris compressa* ate mostly aquatic insects, with some microcrustaceans during the dry season (32%) and some aerial and surface invertebrates during the wet season (25%). Lastly, *Leiognathus equulus*, *Redigobius bikolanus* and *Craterocephalus stercusmuscarum* also ate a combination of aquatic insects (59-63%), microcrustaceans (especially ostracods, 13-24%) and aerial and surface invertebrates (6-24%). The seasonal trophic plasticity of *A. acritosus* and *H. compressa* did not result in movement of these species between feeding guilds.

6.3.3 Diet composition of species with low catch rates

The dietary compositions of species with low catch rates are presented in Table 6.3, together with the number of individuals of each species caught during the study with gut fullness values of at least 0.2. Although sample sizes were very small, these species fit into the seven feeding guilds described above. *Acanthopagrus berda* and *Anguilla reinhardtii* consumed molluscs and detritus and would probably group with members of guild 1. *Xiphophorus maculatus*, *Mugil cephalus* and *Tandanus tandanus* ate detritus, much like species from guild 2. *Giurus margaritacea* and *Toxotes chatareus* consumed terrestrial and aerial invertebrates, whereas *Notesthes robusta and Caranx ignobilis* preyed upon fish and macrocrustaceans. These diets are similar to those of guilds 5 (surface invertivores) and 6 (predators), respectively. Lastly, five species, *Anguilla obscura*, *Kuhlia rupestris*, *Mesophristes argenteus*, *Microphis brachyurus brachyurus* and *Ophisternon gutturale*, consumed large portions of aquatic invertebrates, with some crustaceans, reflecting the diet of guild 7.

6.3.4 Ontogenetic diet shits

Feeding guild structure did not change when wet and dry season samples of 9 species were further divided into size classes (Figure 6.3; see section 6.3.2.3 for a full description of the methodology used). Of these nine species, only three exhibited ontogenetic shifts that resulted in changes in guild membership. In addition, all of these shifts were restricted to the dry season; during the wet season the different size classes of every species (for which sufficient samples were available) remained within a single feeding guild. *Neosilurus ater*, *Melanotaenia splendida splendida* and *Gerres filamentosus* all shifted from a diet of aquatic insects to other groups as they grew: *Neosilurus ater* juveniles (≤350mm SL) ate increasing amounts of detritus as adults (>350mm SL); *M. s. splendida* juveniles (≤40mm SL) consumed more aerial and surface invertebrates as sub-adults (41-50mm SL) and adults (>50mmSL); and sub-adult *G. filamentosis* (≤80mm SL) shifted into the molluscivore guild as adults (>80mm SL).

Table 6.3 The proportional contributions of each dietary category to the total diet of species with low catch rates. Species are ordered according the guild, from Figure 6.2, to which they might be ascribed from this data. Values ≥0.2 are highlighted in boldface.

Possible guild	Species	N	Air	Aqua	MacC	MicC	Moll	OMic	Terra	Algae	Fish	Det
Guild 1	*A. berda*	3					**0.97**				0.03	
Molluscivores	*A. reinhardtii*	2					**0.50**					**0.50**
Guild 2	*X. maculatus*	1						0.08		0.17		**0.75**
Detritivores	*M. cephalus*	4					<0.01	**0.37**		**0.37**		**0.25**
	T. tandanus	4		**0.22**	0.03	**0.27**	0.19		<0.01	<0.01		**0.29**
Guild 5	*G. margaritacea*	2		0.13	0.50				**0.38**			
Surface invertivores	*T. chatareus*	1	**0.71**						**0.29**			
Guild 6	*N. robusta*	4			**0.50**						**0.50**	
Predators	*C. ignobilis*	2									**1.00**	
Guild 7	*A. obscura*	1		**1.00**								
Aquatic invertivores	*K. rupestris*	1		**0.90**					0.10			
	M. argenteus	1		**0.87**							0.13	
	M. b. brachyurus	3		**0.70**	0.30							
	O. gutturale	1		0.13		**0.87**						

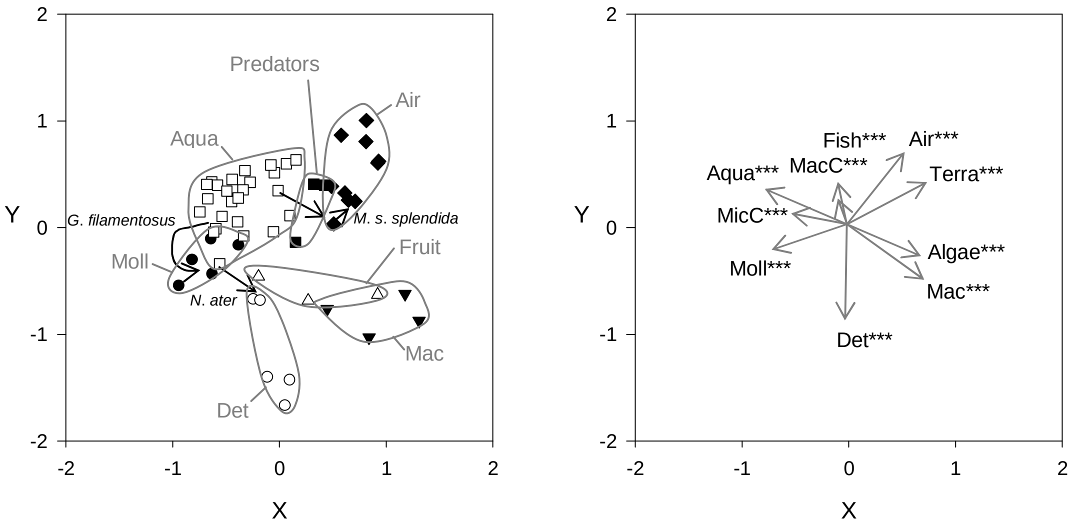


Figure 6.3 The distribution of fish species from wet and dry seasons (not delineated in plot), some divided into size classes, in ordination space as defined by SSH MDS axes X and Y of an ordination (3D, untransformed, Bray-Curtis metric, stress = 0.1538) of mean dietary composition (mean proportional contribution of each diet category), with guilds shown as defined by flexible UPGMA classification (a), and associated PCC diet category vectors with MCAO testing results (b). *** = 0%, ** = 1%, * = 2-5%. See Figure 6.2 for guild descriptions and Table 6.1 for prey category codes. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space. Ontogenetic diet shifts in ordination space, resulting in movement between feeding guilds, are shown for three species; *N. ater*, *M. s. splendida* and *G. filamentosus*. Each species switched from a diet of aquatic insects to other prey items with increasing size/age.

6.3.5 Spatial and temporal variability in mean diet composition

The richness of dietary categories and evenness of fish diets (pooled across all species) differed significantly between sites and dates (Table 6.4). Dietary richness ranged from 1 to 6 categories, with a mean of 1.79 (individual fish with gut fullness of at least 0.2 pooled across sites and sampling dates). Evenness of fish diets ranged from 0 to 1, with a mean of 0.38. Values of both dietary indices were lower at sites 2 and 4 than at sites 1 and 3, and lower during wet season high-flow event of April 2004 than at other times (Figure 6.4).

Although feeding guilds were well defined, with limited seasonal and ontogenetic diet shifts between guilds (Figures 6.2 and 6.3), the mean diet composition (i.e., the mean diet of all individuals, irrespective of species, collected at each site during each sampling date) differed significantly between wet and dry seasons (as revealed by ANOSIM testing of *a priori* season groups: 1% of randomised ANOSIM F values > real F value), but not sites (17% of randomised ANOSIM F values > real F value; Figure 6.5). During the wet season, aerial and surface invertebrates, algae and some detritus appeared to be consumed more frequently, whereas macrophytes, microcrustaceans and molluscs appeared more important in the mean diet during the dry season.

Table 6.4 Kruskal-Wallis test results for diet indices between sites (pooled across sampling dates) and sampling dates (pooled across sites).

	Site (d.f.=3)		**Date (d.f.=4)**	
Index	**X^2**	***p***	**X^2**	***p***
Richness	11.64	0.009	35.02	<0.001
Evenness	10.40	0.015	28.58	<0.001

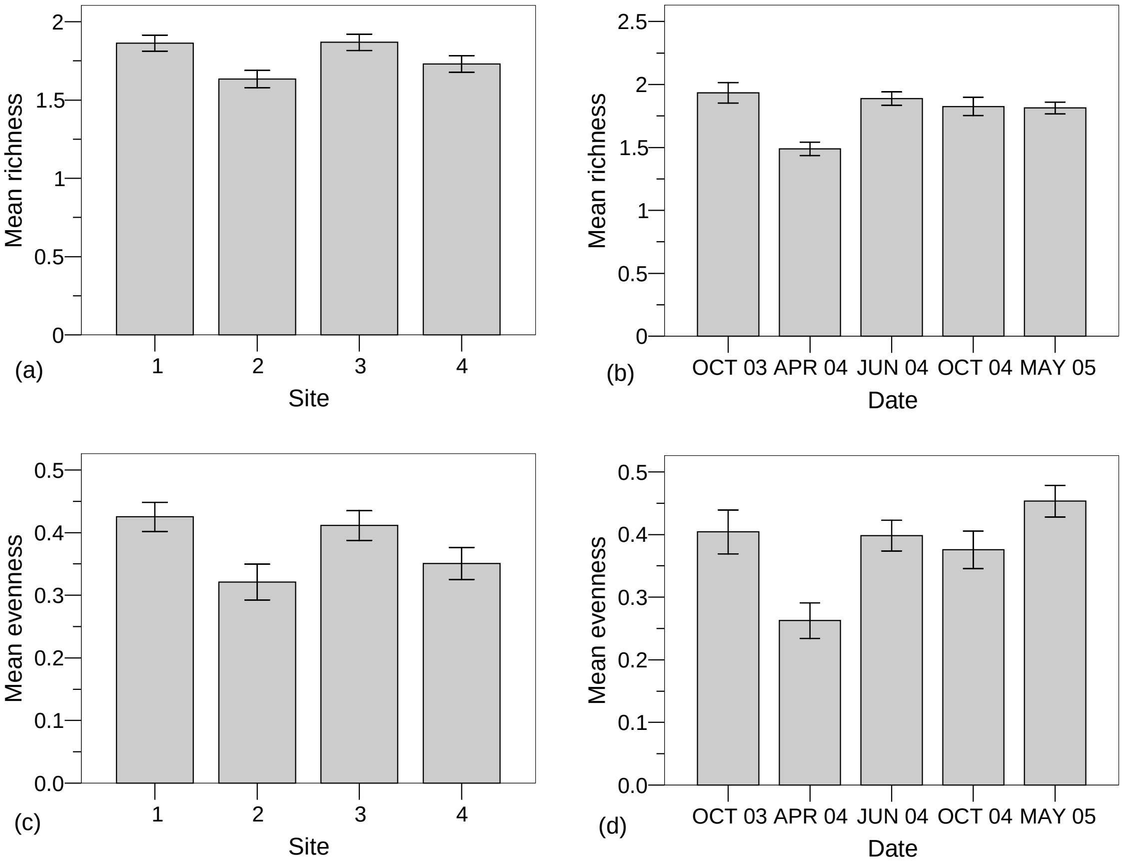


Figure 6.4 Mean dietary richness (a, b) and evenness (c, d) of all fish with gut fullness values ≥0.2 at sites (pooled across sampling dates) and sampling dates (pooled across sites). Kruskal-Wallis test results are presented in Table 6.3 above.

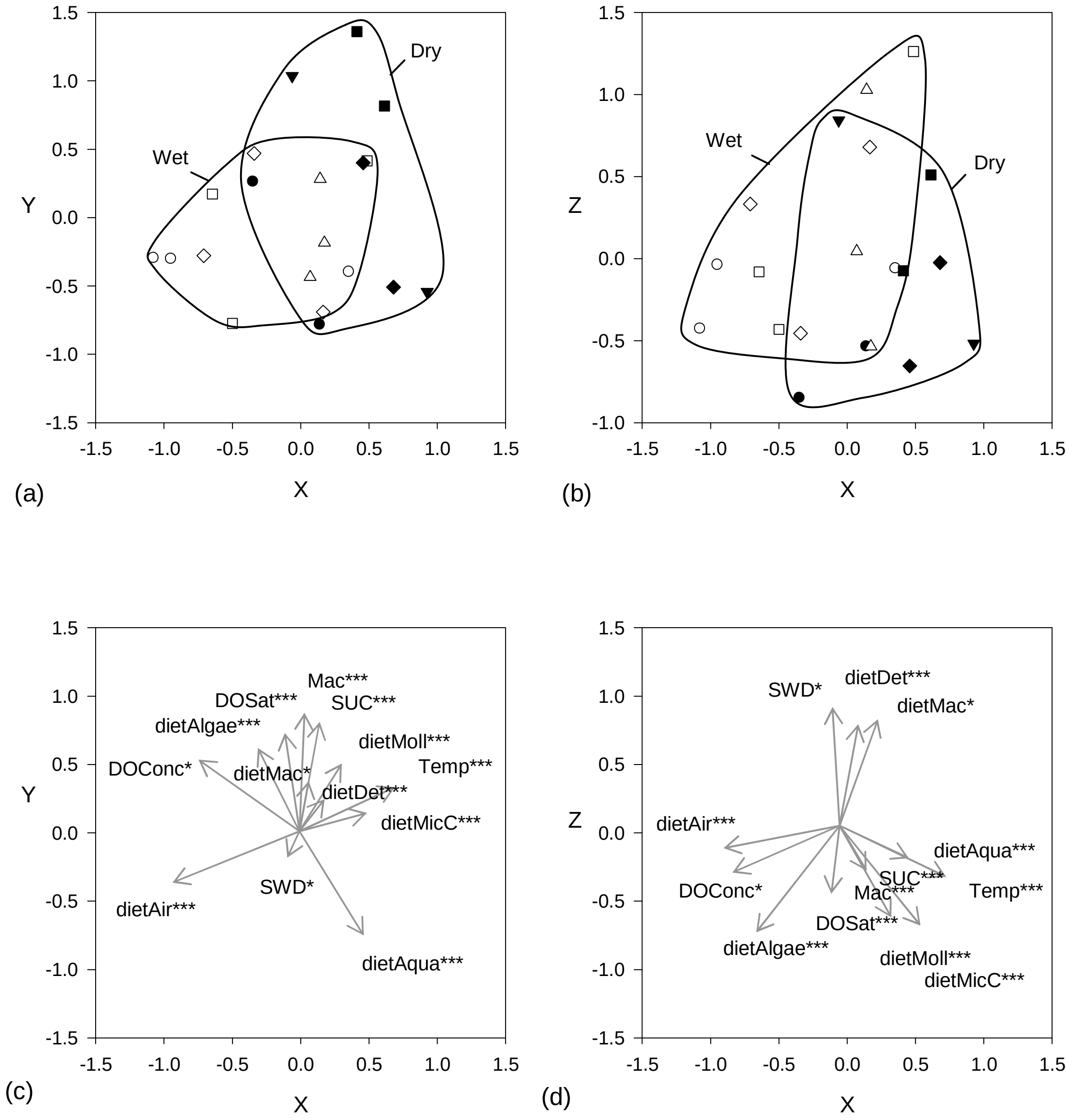


Figure 6.5 The distribution of study sites in ordination space (a, b) as defined by SSH MDS axes X, Y and Z of an ordination (3D, untransformed, Bray-Curtis metric, stress=0.1389) of mean dietary composition of all fish present, during wet (open) and dry (shaded) season sampling dates (Site 1 = ○●, Site 2 = △▼, Site 3 = □■, Site 4 = ◇◆). PCC diet, habitat and food availability vectors are shown with MCAO r-squared values (c, d): *** = 0%, ** = 1%, * = 2-5%. See Tables 6.1, 3.1 and 4.2, for respective vector codes. Note: vector length is indicative of the orientation in three dimensions, not the relative importance in determining the distribution of sites in ordination space.

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6.4 Discussion

6.4.1 Trophic guild structure

The dietary composition of freshwater fish species in the main channel of the Mulgrave River was consistent with previous research (Kennard *et al.*, 2001; Pusey *et al.*, 2004). Seven distinct feeding guilds were identified: molluscivore, detritivore, herbivore, frugivore, aerial and surface invertivore, predator and aquatic insectivore. These names reflect the dominant items in gut contents only, as each members of each guild consumed a variety of food types. For example, aquatic insects, particularly chironomid larvae, ephemeropteran nymphs and trichopteran larvae, were present in the diet of most species. These results broadly matched those of Australian studies (Hortle and Pearson, 1990; Bishop *et al.*, 2001; Kennard *et al.*, 2005), including previous results from the Mulgrave River. Pusey *et al.* (1995b) defined five feeding guilds, ranging from detritivore to piscivore. The two additional guilds recognised in the present study were: herbivore, that comprised two lowland species (*Arrhamphus sclerolepis* and the introduced species, *Tilapia mariae*) not encountered by Pusey *et al.* (1995b) in the smaller streams of their study; and frugivore, that was composed of two closely related terapontid grunters (*Hephaestus fuliginosus* and *H. tulliensis*) that Pusey *et al.* (1995b) grouped with other invertivores (a finding supported by Bishop *et al.*, 2001). The terapontid specimens collected in the present study were typically larger than those collected by Pusey *et al.* (1995b) and frugivory is typically only seen in these larger specimens, with mouth gapes sufficient to consume terrestrial fruits that range from 5 to 20mm in diameter (Pusey *pers. comm.* 2006).

Additional feeding guilds, along with greater taxonomic diversity within guilds, are to be expected in lowland habitats, due to the greater abundance and richness of fish species, particularly large-bodied piscivores, and their potential food items (Horowitz, 1978). Bishop *et al.* (2001) assigned 33 species from the Alligator Rivers region of the Northern Territory into nine feeding guilds, finding substantial discrimination with respect to the trophic level of foods utilised by guilds (i.e., herbivore/detritivores, omnivores, carnivores and piscivores) and the size of the food items (i.e., microphagic, meiophagic and macrophagic), that varied with the body sizes of the guild members. In addition, Bishop *et al.* (1995) reported that omnivory was more abundant in upland reaches than in lowland floodplain reaches. Citing the work of Lowe-McConnell (1975) in the Amazon, they suggested that the varied diet of omnivorous species, such as *Hephaestus fuliginosus* and *Melanotaenia splendida inornata* (Castelnau, 1875), may have allowed for colonisation of upstream areas, where food abundance was low. As in the present study, dietary specialisations were common in lowland habitats, possibly because so many species coexisted (Bishop *et al.*, 2001). Nonetheless, some foods appeared to be under-utilised by the fish assemblage. For example, filamentous algae accounted for up to 54% of the diet of *Tilapia mariae*, but made only minor contributions to the diets other species. Furthermore, this suggests that *Tilapia mariae* may now occupy what was a vacant feeding niche, prior to the introduction of this species into the Mulgrave River approximately 10 years ago (Alan Webb, James Cook University, *pers. comm.* 2006).

6.4.2 Temporal variation in trophic guild structure

Seasonal shifts of fish species between trophic guilds were limited to two of the 22 species analysed. *Gerres filamentosus* and *Ambassis agrammus* shifted from dry season diets of molluscs and surface invertebrates, respectively, to wet season diets dominated by aquatic insects. This result contrasts with global studies of tropical streams and rivers, which typically suggest that seasonal diet shifts, driven by changes in food abundance, are more the norm than the exception for freshwater fishes (Lowe-McConnell, 1963; Goulding, 1980b; Werner and Gilliam, 1984; Zaret and Rand, 1987; Matthews, 1998). Given the significant reductions in productivity, the density of invertebrate prey and the abundance of aquatic vegetation due to high wet-season flows (see chapters 4 and 5), it is surprising that seasonal diet shifts were not more widespread. Kennard (1995) reported comparable results in floodplain lagoons of the Normanby River, Cape York Peninsula. In that system, partitioning was high for foods, but limited for habitats. Temporal variation in prey choice by fish was restricted to changes in the relative abundances of a small group of prey categories in diets, rather than major changes in prey choice (Kennard, 1995). As in the Mulgrave River, Kennard (1995) also found that changes in fish diets did not correspond with seasonal variations in food abundances, suggesting that fish were foraging independently of measured fluctuations in the resource base and/or that invertebrate abundances may not have reached levels at which they became truly limiting to the resident fish population. It is possible that trophic plasticity is not well developed in the Wet Tropics, because predictable flows enable fish to consume the prey items that they prefer at all times of the year, unlike fish in more systems with more variable intraannual flow (Arthington, 1992).

6.4.3 Body size, predator-prey interactions and ontogenetic diet shifts

Size has been repeatedly identified as an important determinant of predator-prey interactions, particularly for fish species (Winemiller, 1989; Munoz and Odjeda, 1998; Oyarzun *et al.*, 2001; Gill and Morgan, 2003; Adite *et al.*, 2005; King, 2005). Data collected during the present study were published in a database documenting the body sizes of consumers and their resources from a variety of metabolic categories, ecosystems and latitudes (Brose, 2005). Analysis of this large dataset (over 16 000 trophic links) indicated that consumer-resource body-mass ratios were higher for ectotherm vertebrate predators in freshwater habitats than in terrestrial or marine habitats (Brose, 2006). While the mechanism driving this relationship remains unclear, I suggested fish are typically forced to consume their prey whole and, as a result, are limited in their prey selection by mouth gape (Brose, 2006).

Ontogenetic diet shifts were limited in the present study. Three species – *Neosilurus ater*, *Melanotaenia splendida splendida* and *Gerres filamentosus* – shifted from diets of aquatic insects, as juveniles and sub-adults, to other dietary items, such as molluscs and terrestrial insects, as adults. However, sample sizes were very small for some species. This may have led to: the identification of dietary shifts where they may not actually be present (i.e., *N. ater* and *G. filamentous*), because dietary breadth and sample size are strongly positively correlated; and the underestimation of dietary shifts in the community as a whole, as not all species were analysed. For example, *Anguilla reinhardtii*, *Tandanus tandanus* and *Hephaestus fuliginosus*, which were caught in low numbers during the present study, were shown by Pusey *et al.* (1995) to shift from consuming small insect larvae as 0+ fish, to large aquatic insects, fish and macrophytes as 1+ fish. Additionally, Kennard (1995) reported ontogenetic shifts between feeding guilds for *M. s. splendida* and *Glossamia. aprion*, while Pusey *et al.* (2004, p.321) documented a shift by *Lates calcarifer*, from a diet of microcrustaceans as post larvae (<80 mm TL), to macrocrustaceans and fish as juveniles (80-400 mm) and adults (>400 mm). In all cases, these differences were related to the increased size of prey items consumed by the larger fish (Kennard, 1995; Pusey *et al.*, 1995b; Pusey *et al.*, 2004). The subject of ontogenetic diet shits warrants further investigation in the Wet Tropics fish fauna.

6.4.4 The influence of taxonomic resolution of fish diets on guild classification

The level of taxonomic resolution used to define fish diets, and calculate dietary indices, is thought to affect the assignment of species into feeding groups. Kennard (1995), for example, hypothesised that, had a higher level of resolution been employed in his study, different conclusions concerning food resource use and partitioning may have been reached. I tested this hypothesis by reclassifying species into trophic guilds on the basis of more than 30 fine dietary categories, rather than the 14 broad categories used to generate Figure 6.2 (see Table 6.1 for category details). While substantial changes to guild structure could be expected at this higher resolution, guild membership remained exactly the same (Appendix 4). Differences were only seen in the order of guilds, relative to one another; the position of species, relative to one another, within their original guilds; and the 'confidence' with which groups were defined. It appears, therefore, that broad invertebrate categories (aquatic insects, molluscs etc.) are sufficient to delineate between species at the trophic guild scale.

6.4.5 Community level changes in food consumption

In the lowland main channel of the Mulgrave River, wet season flooding resulted in major disturbance of instream habitats and an almost complete loss of instream vegetation. However, individual fish species did not appear to shift their diets in response to these changes, and food resources were highly partitioned at all times. As discussed above, such a result could imply that fish foraged independently of fluctuations in the food resources (Kennard, 1995), although the dietary composition of individual species is likely to be influenced by a combination of their feeding mode, body form and body size, together with food availability (Pusey *et al.*, 2000a). In contrast, the seasonal movement of fish, at scales ranging from microhabitat to river reach, was pronounced and habitat guild membership was highly variable. While it is possible that partitioning of habitats at fine scales was underestimated (see Chapter 5), I suggest that it was these movements of fishes resulted in changes in the abundance of the seven feeding guilds and, therefore, a significant difference between the mean wet and dry season diets of the entire fish community.

6.5 Conclusion

The results presented in this chapter show that although diets of fishes in the Mulgrave River are broad, dietary composition is relatively stable across a range of flow conditions and body sizes. Based on the results of chapters 3, 4 and 5, I expected fish diets to be highly variable between seasons, with fish switching between trophic guilds in much the same way as they did with respect to habitat guilds. However, despite the fluctuations in food abundance (chapters 3 and 4), seasonal feeding shifts between guilds were limited. Food consumption did, however, change at the community level, apparently as a result of changes in the abundance of fish from various feeding guilds within the study reach.

Chapter 7: Food web structure

7.1 Introduction

Food webs provide tractable depictions of biodiversity, species interactions, and ecosystem structure and function (Dunne *et al.*, 2002). In their simplest form, food webs represent chains of feeding interactions between predators and their prey (Cohen *et al.*, 1990; Williams and Martinez, 2000). However, in floodplain rivers, trophic networks reflect the complexity of their physical setting, with an abundance of weak feeding links dominated by several strong links (Power and Dietrich, 1995; Winemiller, 2005). For example, Winemiller (1992b) examined food webs in the four representative habitat types of the Brazos River catchment, Texas: the river channel, an old shallow oxbow lake, an old deep oxbow lake, and a young, medium depth oxbow lake. In each of these habitats a small number of species comprised the bulk of the standing biomass and production. These ‘primary’ species included copepods, shrimp, shad, catfish and gar. ‘Secondary’ and ‘tertiary’ species were also identified, but they tended to have lower standing biomasses, were strongly influenced by the abundance of primary species and had little impact on energy transfer through the food web (Winemiller, 1992b).

In tropical rivers, food webs are thought to be driven by instream productivity, predominantly macrophytes and algae (Thorp and Delong, 1994, 2002), supplemented by inputs of nutrients from upstream, riparian and floodplain sources (Vannote *et al.*, 1980; Junk *et al.*, 1989; Dettmers *et al.*, 2001; Finlay *et al.*, 2002; Baxter *et al.*, 2005). Figure 7.1 shows a hypothetical, simplified food web for a lowland river (after: Winemiller, 2005; Power and Dietrich, 2002; Lowe-McConnell, 1987), in which these basal sources are consumed directly by both invertebrates and fishes. Secondary consumer invertebrates (e.g., Odonata larvae) prey upon smaller invertebrates (e.g., Chironomidae larvae) and, in turn, are eaten by insectivorous fishes. Individual fish from a range of trophic groups then contribute to the diet of piscivorous species, before they, in turn, are consumed by higher-order predators (e.g., birds, crocodiles etc.) and humans.

Seasonal flows in tropical rivers regulate the relative importance of various productivity sources in driving food webs (Winemiller, 2005). These changes may then have bottom-up effects on higher trophic levels, such as dietary shifts in consumers, and thereby play a major role in determining overall food web structure and energy transfer (Power, 1992). For example, Winemiller (1990; 1992b) documented temporal dynamics of food webs in streams and swamps in Venezuela and Costa

Rica. During the wet season, an abundance of algae, coupled with an abundance of juvenile fishes in the greatly expanded aquatic environment, was reported. However, in the transition between wet and dry seasons, macroinvertebrates and detritus gained increasing importance in the diets of local fish populations, which comprised mainly sub-adult and adult fishes. Detritus remained important into the dry season, but there were also increased inputs of terrestrial primary production (Winemiller, 1990; Winemiller, 1992b).

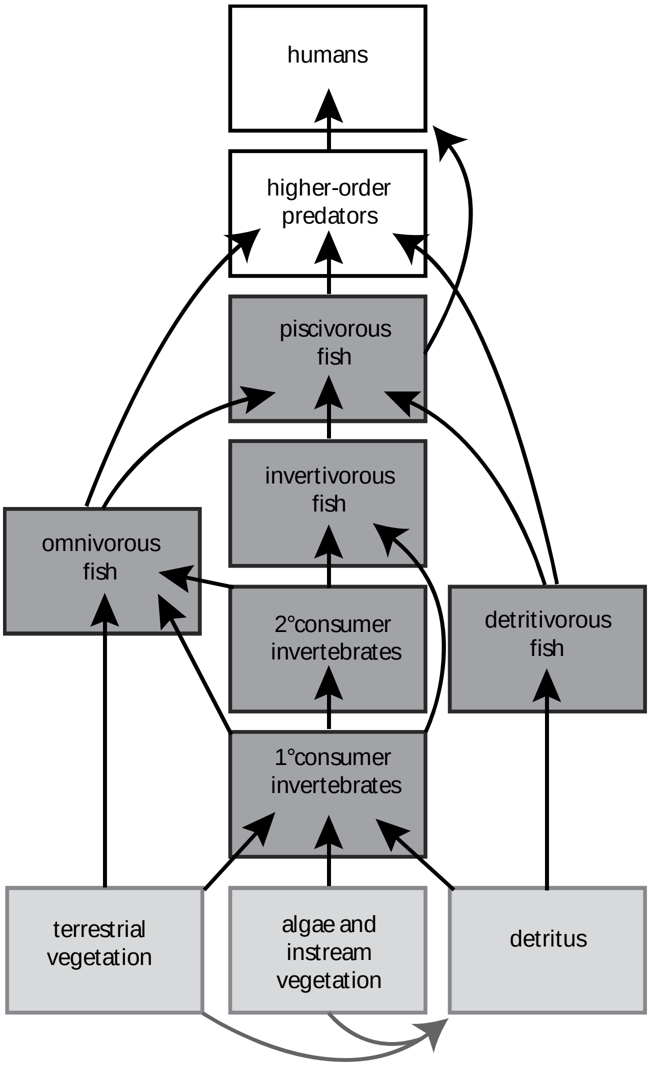

Figure 7.1 Simplified food web for a lowland river (after: Winemiller, 2005; Power and Dietrich, 2002; Lowe-McConnell, 1987). Boxes represent aggregate material pools and vectors represent the main consumer-resource interactions. Food web elements that are quantified in this chapter using traditional methods and stable isotopes data are shaded dark grey, while elements that are assessed using stable isotopes data only are shaded light grey.

Confirming the fine-scale transfer of energy from multiple basal productivity sources to upper trophic levels can be difficult when using traditional methods, such as the quantification of gut contents (Cohen *et al.* 1993, Martinez *et al.* 1999; Goldwasser and Roughgarden 1997). In these cases, stable isotope analysis may provide a useful alternative approach (Zanden and Rasmussen, 1999; Thompson *et al.*, 2005) or accompaniment to traditional methods (Jones and Waldron, 2003), as it goes some way to accounting for temporal variability in food consumption by predators (Peterson and Fry, 1987; Thompson and Townsend, 1999). For example, macrophytes generally produce well over half of the primary production on South American floodplains, yet have been shown to contribute only a small fraction of the total carbon directly assimilated by fishes (Forsberg *et al.*, 1993; Lewis Jr *et al.*, 2001). Instead, fish appear to consume this material indirectly through detrital pathways (Winemiller, 2005). Bunn *et al.* (1997) reported similar results in a tropical Australian stream, finding that C_4 carbon from native macrophytes (e.g., *Vallisneria*) and introduced grasses (incl. para grass, *Urochloa mutica*, and sugar cane, *Saccharum officinarum*) made only a limited contribution to the aquatic food web.

The work of Bunn *et al.* (1993; 1997; 2003; Boon and Bunn, 1994) represents a large portion of the body of Australian research that focuses specifically on aquatic food web processes, with studies on stream invertebrates (e.g. Cheshire *et al.*, 2005) and riverine fish (Arthington, 1992; Arthington *et al.*, 1994; Kennard, 1995; Pusey *et al.*, 1995b; Pusey and Bradshaw, 1996; Arthington and Marshall, 1999; Pusey *et al.*, 2000a; Kennard *et al.*, 2001; Balcombe *et al.*, 2005) constituting the remainder. Based on this and other (Bishop *et al.*, 2001; Townsend and Padovan, 2005; Webster *et al.*, 2005) research, Douglas *et al.* (2005) derived five general principles that characterise food webs in the wet-dry rivers of northern Australia. These were: (1) seasonal hydrology is a strong driver of ecosystem processes and food web structure; (2) hydrological connectivity is largely intact and underpins important terrestrial-aquatic food web subsidies; (3) river and wetland food webs are strongly dependent on algal production; (4) a few common macroconsumer species have a strong influence on benthic food webs; and (5) omnivory is widespread and food chains are short. Douglas *et al.* (2005) intended these principles to form the basis of future hypothesis generation and testing in the region.

In this thesis I have documented the impact of seasonal flooding on instream habitats, primary productivity and consumer populations in the main-channel of the Mulgrave River. The aim of this chapter is to asses the influence of these temporal dynamics on the transfer of energy from food resources to the fish feeding guilds identified in chapter 6. This is to be achieved by combining biomass and feeding data into seasonal food web diagrams and by investigating seasonal shifts in stable isotope signatures of fish and their food sources. What sources of primary productivity are most important in the food web? Does seasonal hydrology affect the relative importance of these sources, and therefore food web structure, in main-channel habitats? Do a small number of fish species dominate standing biomass, while many rarer fish species exhibit weaker trophic links with different food types? I also examine the applicability of the principles derived by Douglas *et al.* (2005) to the Mulgrave River and other systems in the Wet Tropics region.

7.2 Methods

Seasonal food web diagrams, depicting the feeding links between fish and their food resources, were constructed. The resulting ‘webs’ provide estimates of the relative strength of trophic links (i.e., energy transfer) between fish and their food sources, within the context of the entire food web (Figure 7.1). Three trophic levels were considered – basal productivity sources (e.g., detritus, algae, macrophytes etc.), primary consumers (i.e., invertebrates) and secondary consumers (i.e., fish), as follows:

1. *Basal sources*. Relative biomasses of basal sources in the environment were estimated using habitat surveys (chapter 3) and other field observations collected over the course of the study. Directly quantifying the total abundances of materials such as detritus within the main-channel was beyond the scope of this study.
2. *Invertebrate categories*. Eight invertebrate prey categories were used (chapter 4). For each category, the littoral dip-net abundance and benthic grab density of each category were summed, before the mean was calculated for samples collected during wet and dry seasons. These means were then multiplied by an estimated mean dry mass for each category (Table 7.1), in order to compensate for differences in biomass of taxa between invertebrate categories. Range standardisation was then performed on the combined wet and dry season dataset, to enable accurate scaling of the circles in Figure 7.2, relative to the largest value. (standardised value = value – minimum value / maximum value – minimum value).
3. *Fish trophic guilds*. Total guild biomasses were calculated by summing the seasonal biomass of the same individual fish used for analysis of feeding relationships (chapter 6). For example, the dry season biomass of molluscivores was calculated by summing the masses of *Acanthopagrus australis*, *Bunaka gyrinoides*, *Gerres filamentosus* and *Neosilurus ater* individuals with gut fullness values of at least 0.2 collected during dry season samples, (N = 65; Figure 6.2). These values were then range standardised across seasons (as above).

Table 7.1 Estimated mean dry-masses of individual animals from each invertebrate category. Estimations were made using data from the present study, combined with length-weight relationships reported by Barmgartner and Rothhaupt (2003) and Ganihar (1997).

Invertebrate category	Estimated mean dry mass (g)
Aerial and surface invertebrates	0.02
Aquatic insects	0.05
Macrocrustaceans	0.28
Microcrustaceans	0.001
Molluscs	0.02
Other macroinvertebrates	0.05
Other microinvertebrates	0.001
Terrestrial invertebrates	0.05

Trophic links between fish and their food sources were quantified using volumetric gut contents data (chapter 6). The total biomass of each prey category consumed by each trophic guild was calculated by summing the diets of the individual fish within that guild, which had gut fullness values of at least 0.2 (as above). Once these figures had been calculated for each of the seven fish feeding guilds, the link biomass values (i.e., all links) were range standardised across seasons to give an indication of relative link strength. When these calculations were complete, food web diagrams were drawn manually, using Adobe Illustrator.

The approach described above is limited to the main relationships of the fish and their food. It does not include higher order consumers such as birds, or basal species and microbial loops. The functional categories used in the webs lump species, so it is inappropriate to calculate food web statistics, many of which are sensitive to the way in which the webs themselves are constructed (Sugihara *et al.*, 1997; Solow and Beet, 1998). Further, the biomasses of organisms and the strength of links between them are estimates; and excluded from the webs are rare species and those with low gut fullness, despite the fact that they obviously add to total biomass and contribute to food web dynamics.

To complement the analysis of food webs based on seasonal biomasses, stable isotope analysis was performed on samples collected during dry (October 2004) and wet (May 2005) seasons. Additional benthic grab and littoral dip-net samples were collected using the methods described in chapter 4 and frozen. These were later sorted into broad categories in the laboratory and processed as individual samples. Additional samples were collected from potential primary productivity sources, such as macrophytes, periphyton, sugar cane and detritus. Flesh samples were taken from the shoulder area of up to seven fish from each species, frozen and transported to the laboratory, where they were dried for 24 to 48 hours at 60 °C. The samples were ground, then oxidized at high temperature and the resultant CO_2 and N_2 were analysed with a continuous-flow isotope-ratio mass spectrometer at Griffith University. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per mil (‰) difference between the sample and conventional standards (PDB carbonate and N_2 in air; see Bunn *et al.*, 1997). Additional source data from Bunn *et al.* (1997) was added to the plots. The values used, their sources and the number of replicates are detailed in Appendix 5.

7.3 Results

7.3.1 Seasonal food webs based on field survey and gut contents data

Three trophic guilds dominated the fish community biomass during the dry season (Figure 7.2): predators, molluscivores and frugivores. Aquatic insectivores had the smallest biomass of any feeding guild, despite the fact that they were the most numerically abundant group and aquatic insects, their favoured prey, had the greatest standing biomass of any invertebrate category at this time. The strongest feeding link was between each fish feeding guild and its main food type (e.g., herbivorous fish consuming macrophytes). However, the dominance of the link between molluscivorous fish and molluscs was most probably a function of the volumetric method used to quantify gut contents (Hyslop, 1980), in which the volume of molluscs was measured including the shell. Conversely, the link between detritivorous fish and detritus appears to have been underestimated. While *Nematalosa erebi*, the sole member of this feeding guild, dominated biomass in the gill net catch (chapter 5), only dietary items anterior to the muscular crop (i.e., a short section of the alimentary canal) could be identified and quantified during gut contents analysis (chapter 6).

The overall structure of the wet season food web was similar to the dry season web. The predator, molluscivore and frugivore fish feeding guilds continued to dominate the fish community biomass, although detritivores became relatively more important. Food availability was reduced during the wet season: while the biomass of aquatic insects was still greater than any other invertebrate category, all invertebrates were less abundant than during the dry season. Despite this, there were more strong links between fish and their food sources (e.g., between predatory fish and smaller fish and macrocrustaceans). In addition, there was an increase in the strength of the link between herbivores (predominantly the introduced *Tilapia mariae*) and macrophytes). In both seasons, more than 50 trophic links were recorded. The number of links per fish trophic guild ranged from 3 to 11, but the mean number of links per guild did not differ significantly between seasons (two-tailed t-test, d.f.=12, *p*=0.783). Most links were weak (<0.05 of the strongest link; Figure 7.3), with no significant difference in mean relative link strength between wet and dry seasons (two-tailed t-test on $\log_{10}$ transformed relative link strength, d.f.=105, *p*=0.231). Omnivory appeared to be common, with all fish trophic guilds consuming a wide diversity of prey items and exhibiting links with two lower trophic levels (i.e., invertebrates and basal food sources) over the course of the study. During the dry season, the majority of link biomass was associated with molluscs (probably overestimated), macrocrustaceans and macrophytes, whereas during the wet season the majority of link biomass was associated with fish, macrophytes, detritus and macrocrustaceans (Figure 7.4).

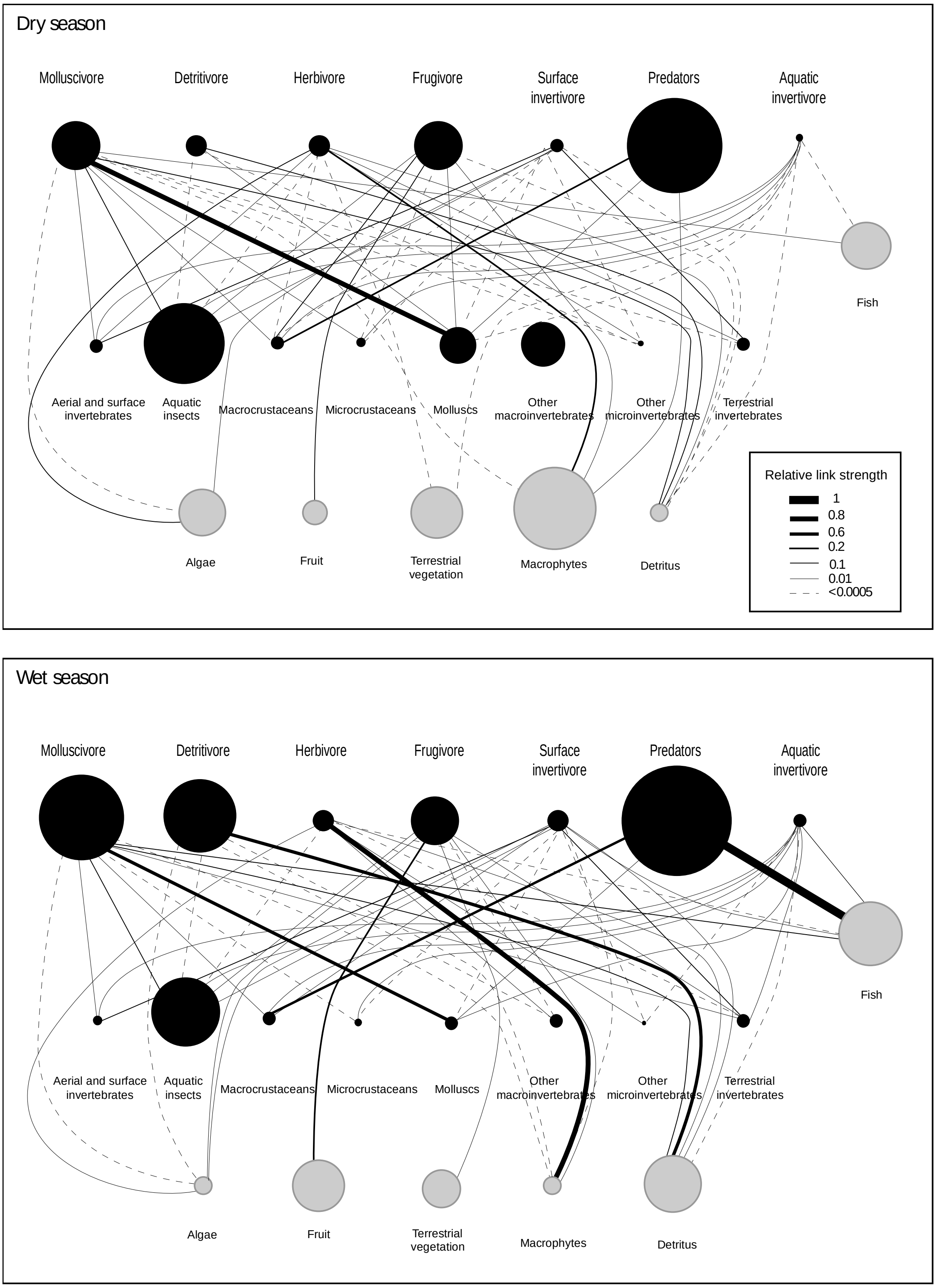

Figure 7.2 Seasonal trophic links between fish feeding guilds, invertebrate prey categories and basal trophic levels in the main-channel food web of the Mulgrave River. The size of circles is indicative of relative biomass within each trophic level, while grey circles are estimates from habitat sampling and field observations. Very weak links (<0.0005% of strongest link) are shown as dashed lines.

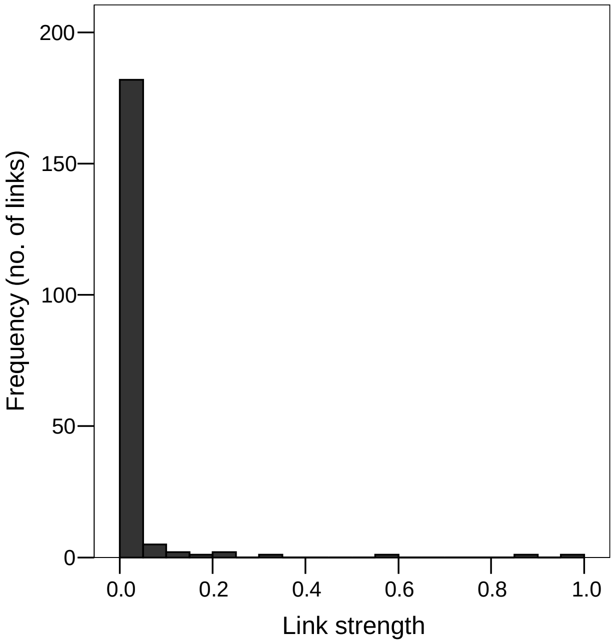

Figure 7.3 Frequency histogram of relative feeding link strength (range standardised across both seasons) between fish guilds and their food sources.

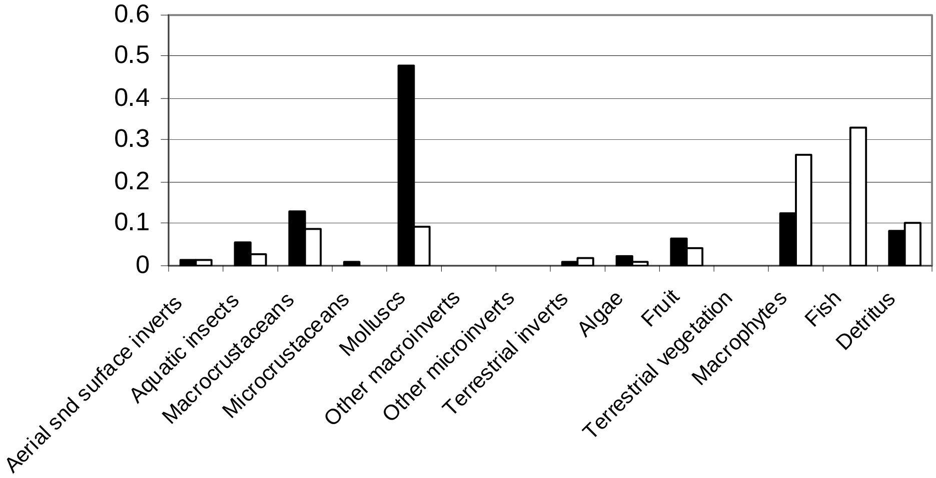

Figure 7.4 Proportion of total feeding link biomass (energy transfer) associated with each measured food source during dry (shaded bars) and wet (open bars) seasons.

7.3.2 Stable isotope analysis

7.3.2.1 Basal sources

Sources of primary production exhibited distinct δ ^{13}C values in both seasons (Figure 7.5). The most ^{13}C-depleted sources were filamentous algae (*Spirogyra*) and macrophytes (*Vallisneria*), with values of <-32 ‰. Para grass (both live and dead samples) and sugar cane were the most ^{13}C-enriched sources (-12 to -13 ‰), while riparian vegetation was intermediate (-28 ‰). The benthic organic matter (FPOM and CPOM) measured by Bunn *et al.* (1997) was derived from a combination of aquatic C_4 carbon, namely *Vallisneria* and *Spirogyra*, and a more ^{13}C-depleted source (Bunn *et al.*, 1997). Terrestrially derived leaf litter had the most depleted δ ^{15}N signal recorded during the study (1 ‰). During the wet season, Bunn *et al.* (1997) reported minor changes in the δ ^{13}C and δ ^{15}N signals of some primary sources, although the pattern of enrichment across sources remained consistent. My samples of fruit and detrital material (decomposing instream leaf litter) were slightly less ^{15}N-enriched, but more ^{13}C-enriched, than the riparian vegetation signal reported by Bunn *et al.* (1997). Littoral vegetation (*Persecaria*, Knot Weed, and *Sphagneticola trilobata*, Singapore Daisy) and aquatic macrophytes (*Vallisneria* and *Cabomba*) were more ^{15}N-enriched than riparian vegetation and more ^{13}C-enriched than either the *Vallisneria* or *Spirogyra* samples of Bunn *et al.* (1997). My sample of epiphytic Phaeophyta was the most ^{13}C-depleted primary source during the wet season. Para grass (both live and dead samples) and sugar cane signals remained constant during the wet season, although my samples were more ^{15}N-enriched than those of Bunn *et al.* (1997).

7.3.2.2 Primary consumers

During the dry season, primary consumers had similar isotopic signatures: δ ^{13}C values ranged between -21 and -27 ‰, while δ ^{15}N values ranged between 8 and 11 ‰. Exceptions to this trend were trichopteran larvae and small terrestrial invertebrates, which were more ^{15}N-enriched and more ^{13}C-enriched, respectively (see Appendix 5). During the wet season, a wider range of ^{13}C and ^{15}N signals was recorded for primary consumers. At this time, Orthoptera, Coleoptera larvae and adults, small terrestrial invertebrates, Trichoptera and Arachnida had the most ^{15}N-depleted signals, but spanned a range of δ ^{13}C values, from -32 ‰ to -22 ‰. Ephemeroptera, Odonata, Atyidae and Hemiptera were more ^{15}N-enriched, occupying a trophic level between invertebrate primary consumers and fish species. Mollusca and Crustacea (*Macrobrachium* sp.) were the most ^{15}N-enriched invertebrates. Most invertebrates appeared to derive their carbon from a combination of aquatic (algae and FPOM) and terrestrial carbon (riparian vegetation or detritus) during both seasons. It is not possible to be more precise about the sources used by each invertebrate group, except to say that ephemeropteran nymphs appeared to consume more macrophytes and algae than other groups, such as Mollusca and *Macrobrachium*, which probably ate particulate organic matter and detritus.

7.3.2.3 Higher-order consumers

During the dry season, fish species were tightly clustered in a pyramid between 10 to 14 ‰ δ^{15}N and -20 to -28 δ^{13}C (Figure 7.5). The position of each species generally corresponded to the dietary data from gut contents analysis (chapter 6). For example, predatory species such as *Lutjanus argentimaculatus* and *Lates calcarifer,* had the most ^{15}N-enriched signals, whereas frugivores and invertivores, such as *Hephaestus fuliginosus* and *Redigobius bikolanus*, were relatively ^{15}N-depleted. *R. bikolanus*, *Nematalosa erebi*, *Hypseleotris compressa*, *Acanthopagrus australis*, *Lates calcarifer* and *Lutjanus argentimaculatus* appeared to consume food sources with algae and macrophyte isotope signatures; and *Tandanus tandanus*, *Hephaestus tulliensis*, *Hephaestus fuliginosus, Bunaka gyrinoides*, *Mugil cephalus* and *Neosilurus ater*, which had relatively ^{13}C-enriched signals, appeared to consume foods with based on detrital production (including terrestrial leaf litter) .

Wet season isotope signatures of fishes were not as tightly clustered as those of the dry season, but spanned similar ranges of δ^{13}C and δ^{15}N values. Individual species, particularly *Melanotaenia splendida splendida, R. bikolanus*, *N. erebi*, *T. mariae* and *P. signifer,* exhibited more variable stable isotope signatures at this time. The ordering of trophic positions of the dry season was maintained into the wet season, with *L. argentimaculatus* and *L. calcarifer* still at the top of the aquatic food chain. Delineating between different trophic pathways was much more difficult for wet season samples, as species appeared to consume a range of foods based on different primary sources. Seasonal changes in the mean isotopic signatures of fish species did not exhibit a uniform trend, with some species becoming both more and less enriched in ^{13}C and ^{15}N (Figure 7.6). This is not surprising, given the vagaries of ingestion, assimilation and incorporation of prey signals into muscle tissue (Perga and Gerdeaux, 2005). It should be noted that the statements above are highly speculative and the future application of a mixing model, such as Isosource (Phillips and Gregg, 2003; 2005), would be of great value.

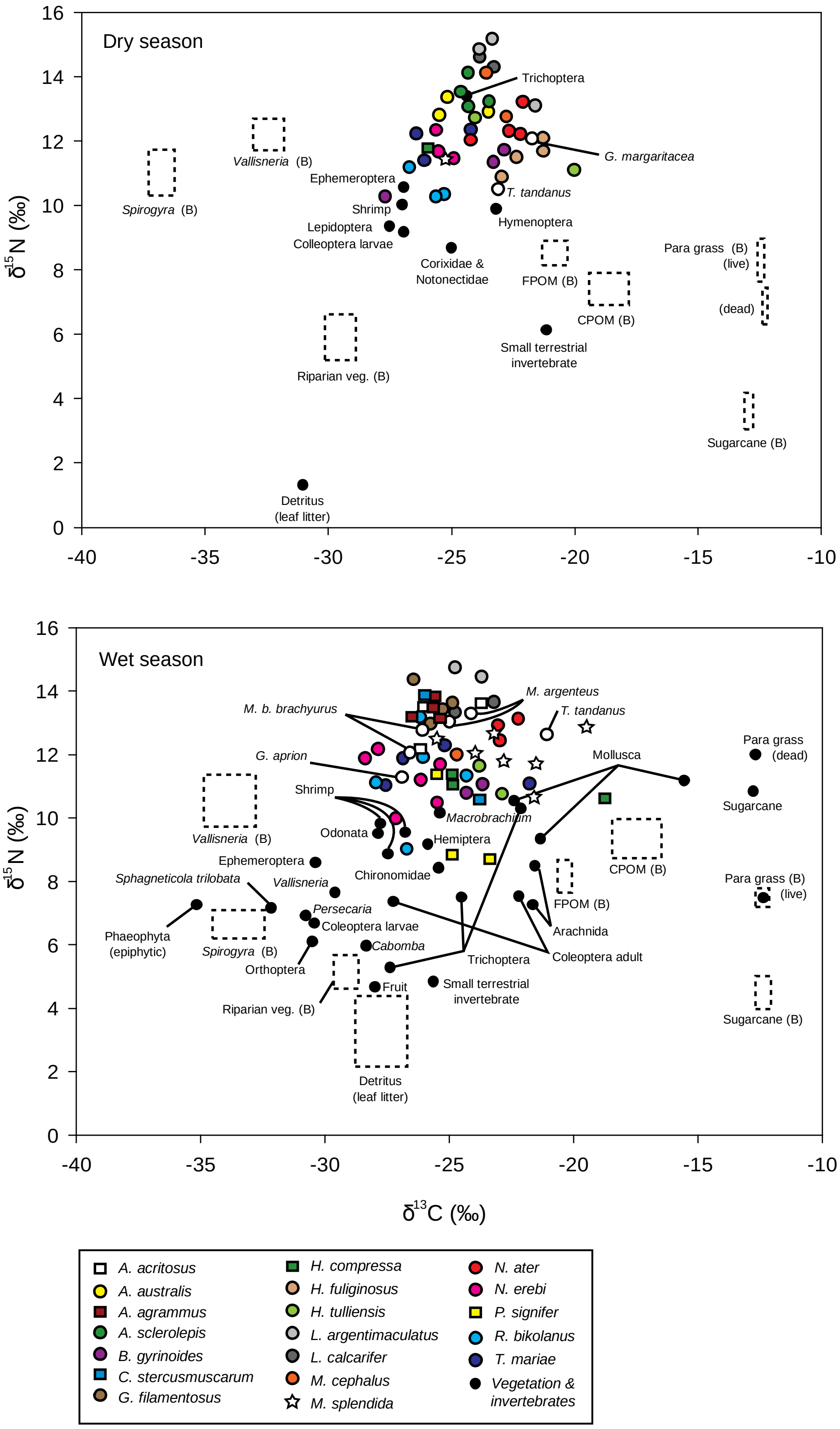

Figure 7.5 Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) during dry and wet season samples. Primary sources are plotted as boxes ± SE about the mean, with samples from Bunn *et al.* (1997) suffixed with (B).

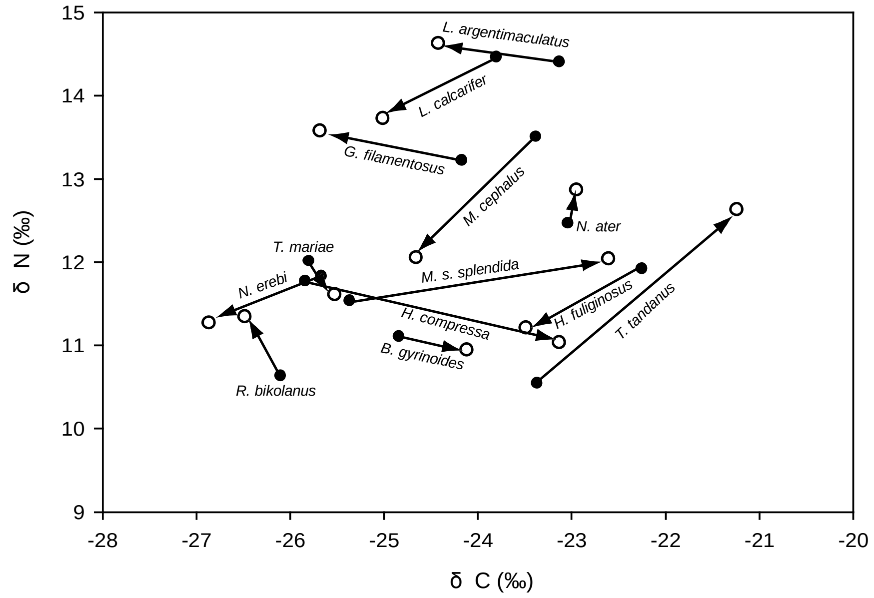

Figure 7.6 Changes in mean stable isotope signatures of fish species caught during dry (shaded) and wet (open) seasons.

7.4 Discussion

7.4.1 Food web structure

Fishes are conspicuous, important components of tropical river food webs (Winemiller and Jepsen, 1998). In the main channel of the Mulgrave River, trophic interactions between fish and their food sources were complex, with an abundance of weak links dominated by several strong links. All fish feeding guilds consumed a range of food types during both wet and dry seasons. Guilds consisting of relatively large-bodied species such as predators, molluscivores, frugivores and detritivores had the greatest biomasses throughout the year. In contrast, aquatic and surface insectivore guilds had relatively low biomasses despite their numerical abundance (chapter 5), because they comprised small-bodied species such as *Melanotaenia splendida splendida* and *Ambassis agrammus*. These patterns are consistent with the international literature on floodplain river food webs (Winemiller 2005). In tropical systems, standing biomass is often dominated by a relatively small number of species, often detritivorous fishes, and the magnitude of trophic links is strongly negatively skewed (Winemiller, 1990; Winemiller, 1996; Arrington and Winemiller, 2003). The richer assemblage of small species, many of them uncommon, greatly increases overall food web complexity, but has relatively little influence on energy flow (Winemiller, 2005).

Most energy passes through a comparatively small subset of the total pathways present in aquatic food webs and the trophic pathway from detritus to detritivorous fishes and then piscivorous fishes is considered particularly important (Winemiller, 2005, p.292). As described above, the food web diagrams presented in this chapter probably underestimated the importance of detritus and overestimated the importance of molluscs. For example, *Nematalosa erebi*, which is known to rely on detritus as a major food source (see Pusey *et al*., 2004, p.99), was very abundant in deep, open-water habitats in the main-channel of the Mulgrave River. However, because only a small portion of the total alimentary canal was considered in gut contents analysis, the volume of detritus consumed by this species 'appeared' to be low, when in fact, the total amount of detritus consumed and the rate of consumption were likely to be much high. In addition, detritus contributed 42% of the mean diet of *Neosiluris ater* in the present study, but this species, which was also abundant, was classified as a molluscivore. Lastly, links between detritus and invertebrates likely to consume detritus (i.e., molluscs) were not quantified. In general, omnivory was common in the fish community, with all fish guilds feeding on both basal sources and primary consumers at some point during the study. Detritus, for example, was identified in the gut contents of 5 of the 7 feeding guilds in both seasons.

7.4.2 Temporal change in food web structure

Flooding of the main channel resulted in dramatic changes to habitat structure and food availability in the Mulgrave River. In the previous chapters I documented the decline in habitat diversity and the associated declines in invertebrate abundances. As sediments were reworked in the wet season, almost all instream vegetation, including macrophytes and filamentous algae, was removed from the channel (chapter 3). Fish responded to these changes by moving into and out of the study area (i.e., the lowland reach of the river; chapter 5). However, the diets of individual species remained relatively constant and, although there were changes in the abundances of these species, those species that left the study area appeared to be quickly replaced by species with similar dietary requirements (chapter 6). The consequence of these changes is that the expected seasonal contrasts in food web structure, predicted by models of riverine productivity (Junk *et al.*, 1989; Thorp and Delong, 1994) and studies in other systems (Winemiller, 1992b, 2005), did not occur.

Seasonal change in the structure of the food web was limited: there were no significant differences in either the number of links per fish feeding guild or the relative link strength between wet and dry seasons. In his study of South American rivers, Winemiller (1990) found that, despite the shifting availabilities and qualities of aquatic food and habitat resources, along with seasonal and ontogenetic diet shifts exhibited by most of the fish species, there was a general lack of significant seasonal variation in food web statistics. Such results are unexpected in tropical rivers, given the potential for seasonal shifts in fish feeding to affect food web properties (Winemiller, 1990). However, in the Mulgrave River, seasonal and ontogenetic feeding shifts were limited to a small number of the total fish species present. Under these conditions, with fish continuing to consume their preferred prey at all times of the year, food web structure is likely to be sensitive to changes in the abundance of the taxa present, although, changes in the abundances of the largest-bodied species would be required in order to influence overall patterns of energy transfer.

7.4.3 Sources of production driving the food web

Stable isotope data confirmed the results of gut contents analysis, with the trophic position of species generally reflecting their known dietary composition (chapter 6; Pusey *et al.*, 2004). In accordance with gut contents analysis, a range of basal food sources and invertebrates appeared to be important in maintaining production in the fish community. During the wet season, isotope signals of both fish species (e.g., *Redigobius bikolanus*) and invertebrate groups (e.g. Trichoptera) were more variable than during the dry season. In addition, seasonal shifts in the mean isotopic signatures of individual fish species were limited and showed no clear trend. These results are consistent with the work of Thorp *et al.* (1998) in the constricted main channel of the Ohio River, U.S.A. They found that between-month differences in mean isotopic signatures of fish were small, but that within month, within species variability was large. Additionally, consumers were even more isotopically similar between months at their main-channel site than at their floodplain site, indicating temporal stability in food sources utilised by fish species (Thorp *et al.*, 1998).

The majority of stable isotope research supports the paradigm that most aquatic food webs in lowland rivers are based on autocthonous primary production by planktonic, epiphytic and benthic algae, rather than macrophytes, leaf litter or other terrestrial inputs (Douglas *et al.*, 2005; Winemiller, 2003; Hamilton *et al.*, 1992; Fosberg *et al.*, 1993; Lewis *et al.*, 2001). For example, Bunn *et al.* (1999) showed that species such as *Melanotaenia splendida splendida*, *Nematalosa* spp., *Glossamia aprion* and *Lates calcarifer* were dependent on algal carbon sources in the lower Ord and Fly Rivers. These results are consistent with the data presented in this chapter. However, I found that species such as *Tandanus tandanus*, *Hephaestus tulliensis*, *Mugil cephalus* and *Neosilurus ater* were dependent on detrital and terrestrial sources. The latter result concurs with the gut-contents analysis presented in chapter 6 and suggests that a wider range of sources support the food web in the Mulgrave River, compared with other tropical systems.

7.4.4 Applicability of food web principles derived by Douglas **et al.** *(2005)*

When Douglas *et al.* (2005) derived five general food web principles for rivers in the wet-dry tropics of northern Australia, they were intended as hypotheses for future research. Here I address these principles individually, briefly discussing the applicability of each to the Wet Tropics bioregion.

7.4.4.1 Seasonal hydrology is a strong driver of ecosystem processes and food web structure

Seasonality of flow in the Mulgrave River is strong, with distinct wet and dry seasons characterizing the annual flow regime. However, because baseflows are maintained throughout the dry season, fish habitats in the main channel are never separated into isolated pools, even under the driest conditions. As discussed in chapter 5, the implication is that the availability of resources may not reach the critical lows documented in drier systems (e.g., Arthington *et al.*, 2005; Balcombe *et al.*, 2005) and, therefore, that food web structure may not exhibit the dramatic temporal changes of rivers in Australia's wet-dry tropics (Finlayson *et al.*, 1988; Marchant, 1982; Bishop *et al.* 2001). The results of the present study support this hypothesis, as seasonal change in structure of feeding links between fish and their food sources was limited, despite substantial flow-mediated changes in habitat and food availability.

7.4.4.2 Hydrological connectivity underpins important terrestrial-aquatic food web subsidies

Longitudinal hydrological connectivity in Wet Tropics rivers is strong, owing to the stable baseflows throughout the dry season. However, lateral connectivity is limited by the deep incision of the main channel, combined with the short duration of wet season floods and the degraded state of the floodplain itself. Unlike rivers in the wet-dry tropics, floodplains in Wet Tropics catchments are not inundated for several months each year (Finlayson *et al.*, 1988). As a result, large-scale terrestrial inputs from these floodplain areas, predicted by the flood-pulse concept (Junk *et al.*, 1989), are likely to be limited. However, in littoral areas of the main channel, particularly where dense emergent vegetation or overhanging riparian vegetation is present, terrestrial subsidies may be locally important, as shown by the abundance of terrestrial invertebrates, especially ants, in the diets of surface invertivores such as *Melanotaenia splendida splendida.* Prior to the clearing of floodplain areas for agriculture, floodplain water bodies were more abundant and extensive (Russell *et al.*, 1996; Veitch and Sawynok, 2005). Under such conditions, it is possible that terrestrial productivity associated with seasonal flood-pulses was relatively more important (Junk *et al.*, 1989).

7.4.4.3 River food webs are strongly dependent on algal production

As discussed above, most tropical riverine food webs are dependent on algal production. In the Mulgrave River, filamentous algae were infrequently observed during habitat assessments and during sorting of invertebrate samples in the laboratory. However, this material was present in the gut contents of individuals from a variety of species, including *Awaous acritosus*, *Tilapia mariae* and *Melanotaenia splendida splendida*. Stable isotope data on the subject was equivocal: algae did appear to be important, but this primary production was supplemented by inputs from terrestrial C_3 vegetation (i.e., leaf litter, fruits and terrestrial invertebrates). During the wet season, main-channel substrates were highly mobile (chapter 3), presumably limiting the growth of benthic algae. In addition, macrophytes occurred in very low abundances at this time and little surface area was available for the colonisation by epiphytic algae. Together, these factors may go some way to explaining the apparently limited importance of algae as a food source outside stable dry-season baseflows conditions - but note the importance of algae in the diet of *Tilapia mariae*, as discussed in chapter 6.

7.4.4.4 A few common macroconsumer species have a strong influence on benthic food webs

In the main-channel food web, most of the energy passed from food resources to fish via a small number of links, and a few fish feeding guilds dominated the assemblage in terms of biomass. It is generally accepted that, in tropical systems, a few common macroconsumers are likely to exert a disproportionately large influence on benthic communities (Winemiller, 2005). Strong top-down trophic effects have been documented by Power *et al.* (1990a; 1990b) in the Eel River, California. Douglas *et al.* (2005) cited two small projects in Walker Creek, a small, upland, perennial stream in the Northern Territory, as evidence that similar trophic controls also operate in Australia’s wet-dry river systems: Kent (2001) and Wirf (2003) found that catfish (*N. ater* and *N. hyrtlyii*) and shrimp (*Macrobrachium bellatum*) significantly reduced benthic algal biomass and invertebrate abundance, while other fish species had little effect. In the present study, however, main-channel algae and benthic invertebrate populations appeared to be more sensitive to habitat modification, particularly substrate mobilisation by high-flow events, than to fish density (which did not change substantially between seasons).

7.4.4.5 Omnivory is widespread and food chains are short

Omnivory was widespread in the Mulgrave River fish community. All feeding guilds consumed foods from basal and intermediate trophic levels over the course of the study. While this is consistent with the first part of the fifth principle of Douglas *et al.* (2005), the length of food chains were difficult to assess because upper trophic levels were poorly resolved (i.e., birds, crocodiles and other higher-order consumers were not included) and because links between invertebrates and their food sources were not quantified. Omnivory in fish species is considered an adaptation to variability in food resource supply, with fish consuming a range of food sources that become more or less available under a range of flow conditions (Goulding, 1980b; Lowe-McConnell, 1987). In the Mulgrave River food resource availability was variable, but temporal and ontogenetic diet shifts in fish species were limited. Fish appeared to continue to consume their preferred prey items at all times and in many cases probably consumed basal food sources, such as algae and detritus, as they fed on items from higher trophic levels, such as benthic and littoral invertebrates.

7.5 Conclusion

In this chapter I have shown that temporal changes in the structure of aquatic habitats, and therefore in the invertebrate populations utilising those habitats, has surprisingly limited influence on the trophic links between fish and their food sources. Most fish appear to consume a range of prey items from both intermediate and basal trophic levels and, as a result, food web structure is complex at all times, with a small number of strong links dominating energy transfer through the food web. A range of food sources, not just algal production, appear to be important in supporting communities in the main-channel. While food webs in Wet Tropics rivers share some characteristics with other tropical systems (e.g., Winemiller, 2005; Douglas *et al.*, 2005), constant dry-season baseflows, deeply incised main-channels and relatively degraded floodplain areas, which are irregularly inundated, suggest that lowland main-channel food webs in the region may be unique.

Chapter 8: General discussion

8.1 Summary of major findings

In this thesis I have documented the main elements of riverine ecology that influence the freshwater fish communities in the Mulgrave River, a perennial system in Australian tropical. I have described spatial and temporal variability in primary productivity, instream habitat structure, invertebrate and fish populations, fish feeding and food web structure at four main-channel sites under a range of flow conditions. Chapter 3 assessed instream habitats using three groups of variables: hydrogeomorphology, vegetation and water quality. There was significant variation in these variables, with a range of habitats present across the lowland reach of the river. Using a conceptual model, I described the correlation between stable baseflow conditions and the abundance of aquatic macrophytes and emergent littoral vegetation. When discharge increased during the wet season, the erosive action of flood waters caused a major reworking of bed sediments and the removal of this vegetation. At this time, large woody debris was recruited to the river, root masses were exposed and overhanging riparian vegetation was more abundant.

Chapter 4 analysed the effect of this habitat variability on invertebrate populations. I found that the abundance and density of invertebrates from eight broad categories reflected both productivity, which was significantly higher during the dry season than during the wet season, and fine-scale habitat characteristics, particularly substrate size and stability. Aquatic insects, microcrustaceans and other microinvertebrates were most abundant in shallow, sandy sites with relatively high flow velocities, whereas areas with mud substrates and an abundance of overhanging vegetation were associated with increased abundances of terrestrial invertebrates (particularly ants) and macrocrustaceans. In general, densities of aquatic invertebrates were highest during the dry season, when habitat heterogeneity was high and substrates were stable. During the wet season, invertebrate populations declined markedly as a result of substrate mobilisation and the loss of instream vegetation caused by flood waters.

The structure of fish assemblages also varied as a function of both large-scale (i.e., longitudinal) and fine-scale (i.e., microhabitat patches) habitat changes (chapter 5). Species such as *Melanotaenia splendida splendida* and *Tandanus tandanus* were abundant in shallower upstream areas, whereas *Ambassis agrammus*, *Redigobius bikolanus* and *Lates calcarifer* were more common downstream. Some species, such as *Nematalosa erebi*, preferred open waters, while others were associated with particular microhabitat features (e.g., *Notesthes robusta* was generally found near root masses of riparian trees). As instream habitats changed seasonally, so too did the species composition of the fish assemblage: the community was dominated by *Gerres filamentosus*, *Neosilurus ater* and the introduced *Tilapia mariae* in the dry season, and *Glossamia aprion* and *Nematalosa erebi* in the wet season. Seven habitat guilds were identified and seasonal shifts in habitat use by individual species were common. I suggested that the observed shifts in community structure were most likely related to physical movements of common species, as there was little change in species richness or evenness between wet and dry seasons and a range of uncommon species were present at all times.

Unlike habitat use, food consumption by fish species was stable, both spatially and temporally. In chapter 6 I identified seven trophic guilds: molluscivores, detritivores, herbivores, frugivores, surface invertivores, predators (shrimp and fish eaters) and aquatic invertivores. Although these guilds were well defined and seasonal and ontogenetic shifts were limited, food consumption by the entire fish community was significantly different between dry and wet seasons. During the dry season, molluscs, microcrustaceans and aquatic invertebrates were readily consumed, while aerial and surface invertebrates were favoured in the wet season. These patterns appeared to reflect the seasonal changes in food availability, but were also probably related to the seasonal movements of fish in relation to changing habitat conditions and possibly reproductive activity.

In chapter 7 I combined invertebrate and fish population data with my analyses of gut contents to form seasonal food web diagrams. These figures emphasised the complex structure of this part of the riverine food web, with an abundance of weak trophic links dominated by several very strong links. While this structure was consistent with results from rivers elsewhere in the tropics, there was no substantial seasonal change in food web structure between seasons. Investigation of stable isotope signatures of fish and their food sources suggested that a broad range of energy sources contributed to the aquatic food web in the Mulgrave River, with energy being transferred via algal and detrital pathways during the dry season. In the wet season, however, isotope signatures were more variable (both within and between fish species and invertebrate groups), despite dietary richness and evenness being reduced at this time of year. Many of the features of the Mulgrave River food web were consistent with the five general principles derived by Douglas *et al.* (2005) for rivers in drier areas. However, lateral connectivity was limited and a range of food sources, rather than just algae, were important.

8.2 Conceptual model of findings

These findings are outlined in Figure 8.1. The relative importance of various processes in regulating the ecology of freshwater fish communities is indicated by the size of the arrows. As with most tropical river systems, rainfall, and therefore flow, exerts an over-riding influence on the dynamics of the lower Mulgrave River. The main effect of flow is on the physical structure of instream habitats, namely hydrogeomorphology (width, depth, velocity and substrate) and vegetation. Flow also played a substantial role in controlling physico-chemical parameters, such as temperature and conductivity. During the wet season (i.e., summer), water temperatures in the main channel are low relative to the ambient air temperature, because high flow velocities quickly transport cool water from high-elevation streams in the upper catchment to lowland areas. Tidal penetration into freshwater areas and conductivity are also lower at this time. Despite this seasonal variation, however, the values of water quality parameters recorded during the present study appeared to be well within the physiological limits of all of the fish species that were collected (Pusey *et al.*, 2004).

As described above, invertebrate and fish communities were highly sensitive to flow-mediated changes in habitat structure, as well as the antecedent effects of flow itself (Bond and Downes, 2003). While most invertebrates appeared to be almost completely removed from the main channel by habitat disturbance (i.e., washed into the estuary), freshwater fish, including *Tandanus tandanus*, *Lates calcarifer* and *Nematalosa erebi*, probably responded to high flows by undertaking migrations into and out of the study area (Bishop *et al.*, 2001; Pusey *et al.*, 2004). Despite temporal changes in the abundance of food (including invertebrates), however, the dietary preferences of individual fish species were stable between seasons. In his review of resource partitioning studies, Ross (1986) concluded that diet separation is more important than habitat separation in fish assemblages. Of 37 studies that concurrently examined habitat, food and temporal axes, 57% showed the greatest separation by food, 32% showed primary separation by habitat and 11% showed temporal separation to be most important (Ross, 1986). In the present study, results were equivocal: both habitat and food preferences appeared to influence fish community structure.

I propose two alternative hypotheses that could account for the observed patterns. The first is that fish respond to flow-mediated habitat changes by moving through the catchment in order to find habitat patches that best suit their individual requirements. This hypothesis assumes that food is not limiting and that fish are able to consume their preferred diet at all times. The second hypothesis is that prey selection by fish is limited by external factors (e.g., phylogenetic and morphological constraints) and that fish do, in fact, track fluctuations in the availability of food items. If this is the case, individual fish would be required to traverse habitats in order to locate their preferred prey items. Based on the data presented in this thesis, the second hypothesis appears to be more applicable. For example, seasonal movements of fish species between habitat guilds (Figure 5.15) were far more pronounced (10 species) than seasonal shifts in dietary composition (2 species), even when highly resolved dietary categories were used for the classification of feeding groups (Figure 6.2 and Appendix 4).

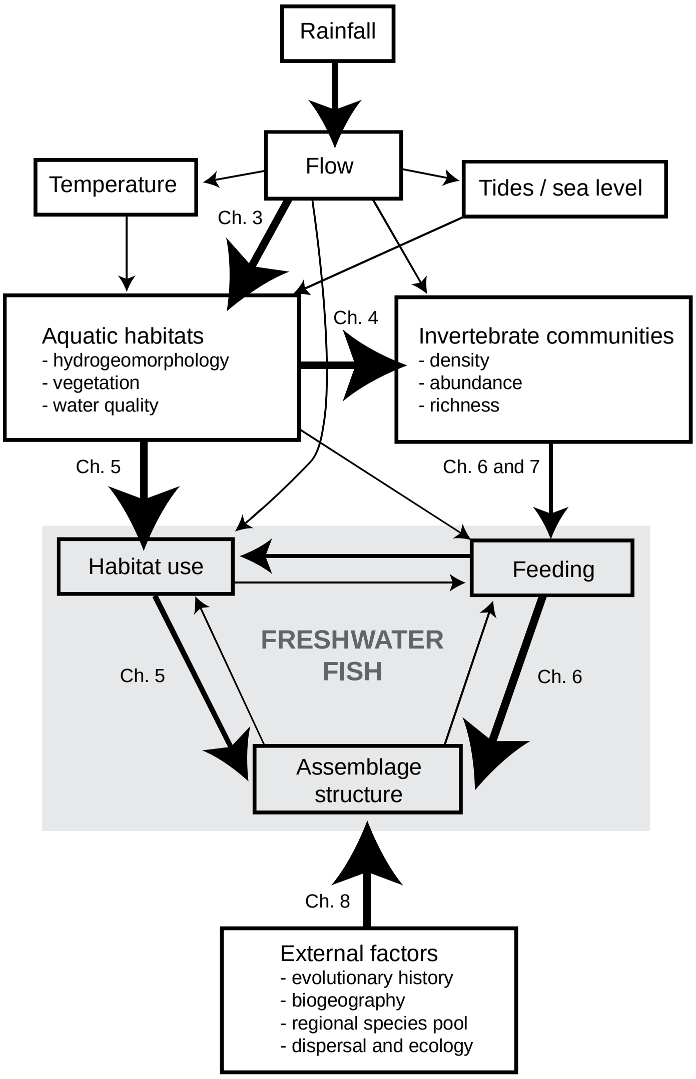

Figure 8.1 A conceptual model of the main influences on freshwater fish communities in the main channel of the lower Mulgrave River, with large arrows indicating the most important processes and the relevant thesis chapters.

I suggest that these dynamics are regulated by a combination of the biogeographic history of the Wet Tropics fish fauna and the hydrogeomorphological characteristics of Wet Tropics river catchments themselves. A total of 107 species, belonging to 37 families, have been found in the region (Pusey *et al.*, In press). These families can be divided into two groups: those distinguished by low within-family generic and specific diversity (i.e., one species per family); and those characterised by higher specific or generic diversity, due to the occurrence of Wet Tropics endemics (Pusey *et al.*, 2006). While the exact mechanisms responsible for this pattern of diversity are yet to be determined, it may be a result of those families with extant species in the present day fauna individually colonising rivers from marine waters over geological time, rather than diverging from ancient lineages already inhabiting the continent (i.e., Gondwanan origin) or speciating *in situ* from a single dominant family (cf., Cichlidae in Africa; see Unmack (2001) for further discussion). Alternatively, selective species assembly from larger-scale species pools may be responsible (e.g., ariid catfishes are conspicuously absent from freshwater habitats of the Wet Tropics), or the pattern could be random.

Whatever the cause, the implication of this pattern of diversity is that morphological factors determined by phylogeny, such as body morphology, gut morphology, mouth size relative to body size and the ability to assimilate different food types, may limit prey selection by fish, potentially reducing the degree of competition for food (Pusey and Bradshaw, 1996; Pusey *et al.*, 2000). In their review of dietary studies of Australian freshwater fish, Kennard *et al.* (2001) identified a strong relationship between the magnitude of within-family trophic diversity and within family generic diversity. They suggested that low trophic diversity in families such as Melanotaeniidae is probably due to low rates of divergence at the generic level, that may constrain trophic style by morphology, and small body size, that may limit the diversity of food types that can be consumed. Additionally, Kennard *et al.* (2001) identified a large amount of regional variation in fish dietary composition that was linked to family designation. For example, species from northern families were widely arrayed in ordination space, compared to those that were more common in southern Australia. Northern families were characterised by a diversity of feeding styles, including piscivory (e.g. Megalopidae, Belonidae and Centropomidae), algivory (e.g., Hemiramphidae) and terrestrial invertivory (e.g., Kuhliidae and Toxotidae; Kennard *et al.*, 2001).

Rivers in the Wet Tropics region feature short, deeply incised lowland reaches with narrow floodplains that are laterally confined by mountain ranges. Elevations in these catchments reach over 1500 m above sea level and most tributary streams are steep, even those which discharge directly into the main channel near the river mouth (see Figure 2.1). Consequently, a larger portion of the total stream length occurs at higher altitudes than in other systems: most of the tropical rivers in drier areas of northern Australia, for example, have long lowland reaches and expansive floodplains (Figure 8.2). As is typical of low-latitude systems, annual discharge of Wet Tropics rivers features the typical wet and dry seasonality. However, the steep catchment geomorphology results in high specific stream power and wet season floods that, although predictable, act as short, intense disturbances, rather than the gradual 'pulses' found in larger systems (Junk *et al.*, 1989). While successions of instream vegetation are reset by these events and habitat heterogeneity is reduced, the total volume of aquatic habitats increases during the wet season (Chapter 3). Additionally, continuous dry season baseflows prevent the isolation of mesohabitat units in the main-channel. At no time does the availability of fish habitats appear to approach the major shortages identified by other authors in drier systems (e.g., Arthington *et al.*, 2005). Consequently, competition for habitat should be reduced.

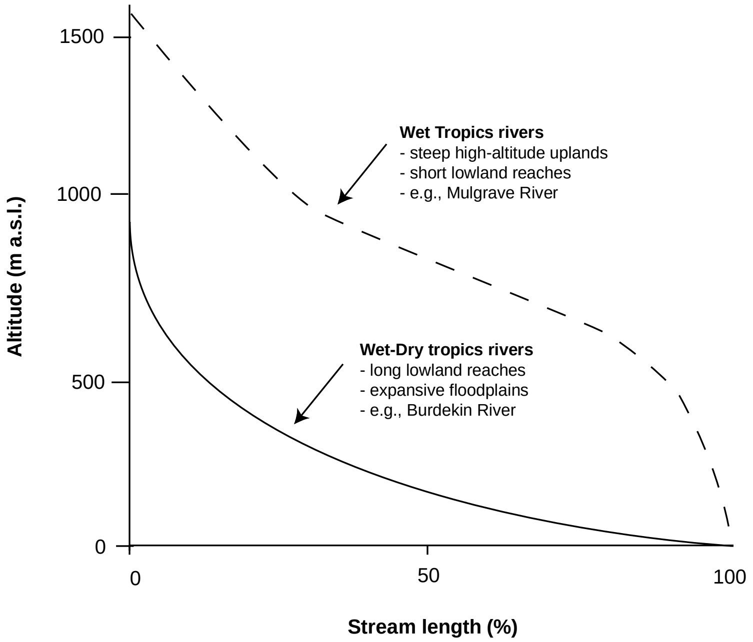

Figure 8.2 Estimated altitudinal distribution of stream length characteristic of wet-dry and Wet Tropics river catchments in northern Australia.

8.3 Resilience of the Mulgrave River to future change

Anthropogenic changes to riverine habitats are a well documented cause of declining fish populations (Galat and Zweimuller, 2001). In Australia, the degradation of freshwater ecosystems by humans (Connell, 1974; Kingsford, 2000; Bunn and Arthington, 2002; Erskine and Webb, 2002) has substantially reduced the distributions and population sizes of many freshwater fish species (Mallen-

Cooper, 1993; Gehrke *et al.*, 1999; Pollino *et al.*, 2004). In the Wet Tropics region, fish habitats have been substantially degraded by human activity (Russell *et al.*, 1996; Veitch and Sawynok, 2005). While the high annual rainfall of the region presently supplies volumes of water sufficient to maintain the majority of ecological processes in main channel environments, future climate change threatens to decouple existing fish-habitat relationships. If current predictions are correct, climate changes over the next century are likely exacerbate existing pressures on aquatic ecosystems and fish (Arnell, 1999; IPCC, 2001; Schindler, 2001; Poff *et al.*, 2002; Dudgeon *et al.*, 2006), by increasing instream temperatures, altering patterns of rainfall and therefore flow, and reducing the extent of lowland freshwater habitats, through a rise in mean sea level (Elliot *et al.*, 1999; Walsh *et al.*, 2000; CSIRO, 2001). Such changes will likely lead to substantial range shifts and increased probabilities of extinction for many species, particularly those with restricted habitat, dietary and/or reproductive requirements (Kennedy, 1990; Regier and Meisner, 1990; Sinokrot *et al.*, 1995; Mullholland *et al.*, 1997; Oberdorff *et al.*, 1999; Poff *et al.*, 2002; Chu *et al.*, 2005; Xenopoulos *et al.*, 2005).

There are ten known endemic species in the Wet Tropics region: *Glossogobius* sp.1 and sp. 4, *Hephaestus tulliensis, Cairnsichthys rhombosomoides, Stiphodon allenii, Tandanus* sp., *Guyu wujalwujalensis*, *Melanotaenia eachamensis*, *Melanotaenia utcheensis* and *Schismatagobius* sp. Of these, the first six are found within the Mulgrave River catchment and all are potentially at risk from future climate change as a result of their specific habitat, food and reproductive requirements that restrict their distributional range (Pusey *et al*., 2004). However, as interannular flow variability is low and stable dry season baseflows are relatively constant in the Mulgrave River, owing to flow supplementation from upland cloud capture and groundwater recharge from basalt aquifers (R. Pearson *pers. comm.*), the habitats upon which these species rely (riffles, runs etc.) may be somewhat buffered from climate change. Such conclusions are, of course, highly speculative and the potential threat posed by climate change requires further examination in future studies.

8.4 Conclusion

This thesis clearly reinforces the important role that natural seasonal flow regimes play in regulating the dynamics of instream habitats, primary productivity, invertebrate and fish populations and biotic interactions between fish species. I conclude that these biotic processes observed were largely controlled by the hydrogeomorphological characteristics of the catchment and, in this sense, the majority of processes documented in this thesis are consistent with accounts of main-channel habitats in rivers elsewhere, particularly in the tropics (Thorp and Delong, 1994; Winemiller and Jepsen, 1998; Dettmers *et al.*, 2001; Galat and Zweimuller, 2001; Winemiller, 2005). However, the unique phylogenetic history of the Wet Tropics fish fauna also played a role in regulating these biotic dynamics, by placing phylogenetic limits on prey selection by fish. The results of this study are widely applicable across rivers within the Wet Tropics, that share similar fish faunas and physical characteristics (Pusey and Kennard, 1996; Russell *et al.*, 1996; Russell *et al.*, 2003; Erskine *et al.*, 2005; Pusey *et al.*, 2006). It is essential that natural flow regimes and habitats in Wet Tropics rivers are protected and/or restored, in order to maintain the diversity of freshwater fish assemblages and protect these systems against future climate change.

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Appendix 1: Pilot study

Additional data relating to spatial patterns of water quality parameters and electrofishing efficicency are presented in this appendix. Even under the dry season conditions of October 2003, longitudinal zonation in the freshwater lowland reach of the Mulgrave River (>16 km from the river mouth) was limited (Figure A1.1). Conductivity, pH and dissolved oxygen concentrations increased in tidal areas downstream from this point. A depth profile collected under similar baseflow conditions shows the limited degree of vertical stratification (Figure A1.2). Lastly, species cumulation curves compiled from pilot study data show that a minimum of 10 minutes of boat electrofishing was required. When this data was collected, the project methodology (including electrofishing settings) was still being developed. Six shots, each five minutes in duration, were employed in the study proper.

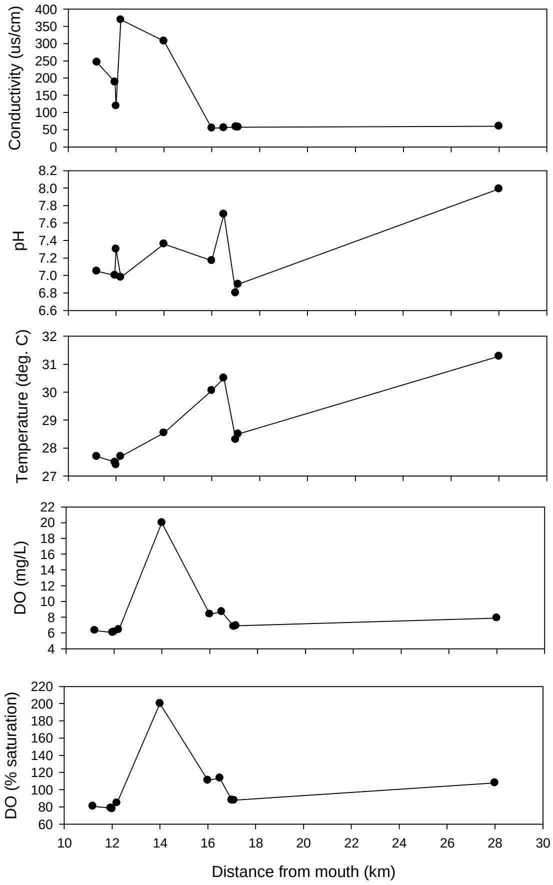

Figure A1.1 Longitudinal profile of water quality parameters collected 27 October 2003 at a depth of 0.5 m below the surface using a Hydrolab DS4 and DS3 – Hach® Environmental, Loveland, CO, USA.

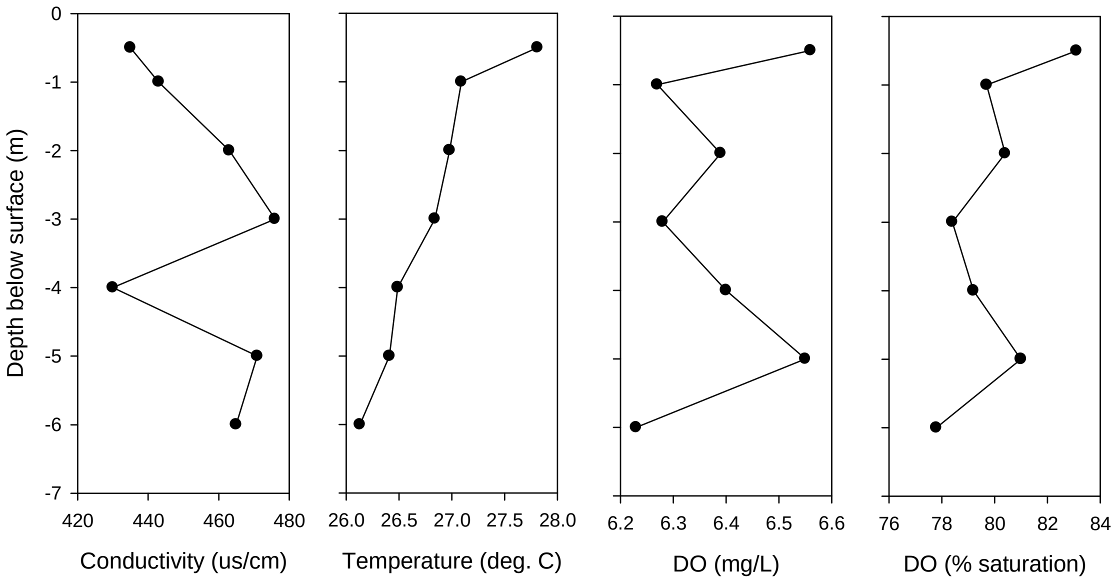

Figure A1.2 Vertical profile of water quality parameters collected at 1500 hrs on 20 October 2005 during a flood tide, approximately 16 km upstream from the river mouth.

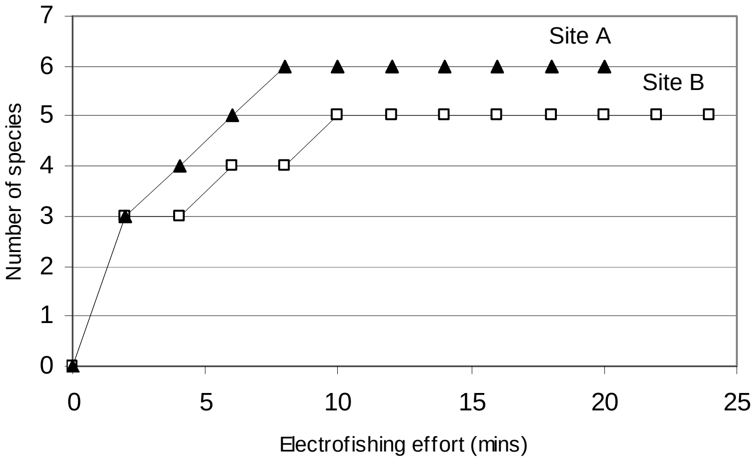

Figure A1.3 Species accumulation curves for two sites located approximately 16-18 km upstream from the river mouth.

Appendix 2: Length-weight relationships

Table A2.1 Length-weight relationships for some of the species caught during the study. These relationships were used to estimate biomass per unit effort and seasonal standing biomasses for food web analyses.

		Standard length						
Species	**N**	Mean	SE	Min	Max	***a***	***b***	r^2
Ambassis agrammus	193	38.08	0.479	18	54	2.34E-05	2.980	0.742
Awaous acritosus	16	88.69	5.562	54	130	2.55E-06	3.438	0.982
Bunaka gyrinoides	14	263.14	13.543	130	330	3.11E-05	2.972	0.940
Craterocephalus stercusmuscarum	13	45.46	2.683	23	62	3.07E-06	3.370	0.977
Eleotris fusca	10	69.60	2.982	58	89	1.57E-06	3.568	0.908
Gerres filamentosus	53	75.23	2.313	34	131	2.07E-05	3.090	0.970
Giurus margaritacea	8	187.00	19.892	54	235	1.11E-05	3.167	0.996
Glossamia aprion	109	52.59	2.243	11	125	4.53E-05	2.880	0.984
Glossogobius sp. 1	17	48.76	3.827	22	76	2.76E-05	2.855	0.997
Hephaestus tulliensis	11	200.00	16.287	112	285	8.09E-05	2.850	0.962
Hypseleotris compressa	72	34.64	1.236	11	58	1.68E-05	3.031	0.892
Leiognathus equulus	12	72.75	2.199	61	88	4.17E-05	2.966	0.932
Melanotaenia splendida	351	50.99	0.781	14	125	1.57E-05	3.042	0.971
Nematalosa erebi	25	209.44	18.179	88	352	8.48E-06	3.197	0.993
Neosilurus ater	32	378.69	15.058	133	490	1.17E-05	3.011	0.945
Redigobius bikolanus	87	17.62	0.567	10	34	5.49E-05	2.702	0.795
Tilapia mariae	33	83.39	12.157	14	232	1.94E-05	3.205	0.994

Table A2.2 Additional length-weight relationships from the scientific literature and other sources. TL = total length, FL = fork length.

Species	**Reference**	***a***	***b***
Hephaestus fuliginosus	Pusey *et al*. (2004)	1.90E-05	3.129
Kuhlia rupestris	Lewis and Hogan (1987)	3.63E-05	2.9628
Lates calcarifer	John Russell (unpublished data) TL	2.295E-05	2.89
Notesthes robusta	Pusey *et al*. (2004)	6.70E-06	3.378
Pseudomugil signifer	Pusey *et al*. (2004)	1.40E-05	3.104
Arrhamphus family average	Fishbase.org FL	4.00E-03	3.0381
Acanthopagrus genus average	Fishbase.org FL	0.017	3.0334
Lutjanus argentimaculatus	John Russell (unpublished data) FL	0.00004	2.8609
Mugil cephalus	Fishbase.org FL cm NZ	2.60E-02	2.754

Appendix 3: Diet composition data

Table A3.1 The proportional contribution of each dietary category to the total diet of each species, used as the basis for the classification of trophic guilds presented in Figure 6.2. Values ≥0.2 are highlighted in bold.

Season	Species	Air	Aqua	MacC	MicC	Moll	OMac	OMic	Terra	Algae	Fruit	Tveg	Mac	Fish	Det
Dry	***Acanthopagrus australis***		0.04			**1**									
Dry	***Bunaka gyrinoides***		0.1			**0.9**							0.05		
Wet	***Bunaka gyrinoides***			0.2		**0.7**			0.02					0.1	
Dry	***Gerres filamentosus***	<0.01	**0.5**		0.09	**0.4**			<0.01						0.05
Wet	***Neosilurus ater***	0.06	**0.3**		<0.01	**0.4**			<0.01	<0.01			<0.01	<0.01	**0.2**
Dry	***Neosilurus ater***	<0.01	**0.2**	0.03	0.07	**0.2**		<0.01		<0.01				0.01	**0.4**
Dry	***Nematalosa erebi***		<0.01			0.05		<0.01							**1**
Wet	***Nematalosa erebi***		<0.01		<0.01			<0.01		<0.01			<0.01		**1**
Dry	***Arrhamphus sclerolepis***	0.02	<0.01						<0.01	0.02		<0.01	**1**		
Wet	***Arrhamphus sclerolepis***		<0.01										**1**		
Dry	***Tilapia mariae***	0.02	0.1		0.02			0.04	0.01	**0.3**			**0.3**		**0.3**
Wet	***Tilapia mariae***		<0.01					0.07	<0.01	0.17			**0.5**	<0.01	**0.2**
Dry	***Hephaestus fuliginosus***		**0.3**		0.06						**0.7**				
Dry	***Hephaestus tulliensis***		<0.01	0.14	<0.01	0.1				0.02	**0.6**		0.05		0.12
Wet	***Hephaestus tulliensis***		<0.01				0.01		0.08	0.17	**0.5**	0.08	0.15		0.04
Dry	***Ambassis agrammus***	**0.5**		0.25						**0.3**					
Dry	***Pseudomugil signifer***	**0.9**							0.08						
Dry	***Melanotaenia s. splendida***	**0.3**	0.17	0.02	0.04	<0.01		0.02	**0.3**	0.15					0.01
Wet	***Melanotaenia s. splendida***	**0.4**	0.15	0.02	<0.01	<0.01		<0.01	**0.3**	0.11			<0.01	<0.01	<0.01
Wet	***Pseudomugil signifer***	**0.5**	<0.01	0.03					**0.4**	<0.01					
Dry	***Lates calcarifer***			**0.9**		0.05							0.03		
Wet	***Lates calcarifer***			**0.5**										**0.5**	
Wet	***Lutjanus argentimaculatus***			**0.5**										**0.5**	
Dry	***Awaous acritosus***	0.02	**0.9**		0.09										<0.01
Dry	***Glossogobius* sp. 1**	0.05	**0.9**		<0.01										
Wet	***Gerres filamentosus***	0.03	**0.9**		<0.01	0.08									
Wet	***Eleotris fusca***	0.15	**0.8**		0.05										
Dry	***Glossamia aprion***	0.09	**0.5**	0.16	0.15									0.06	
Wet	***Glossamia aprion***	<0.01	**0.6**	**0.2**					<0.01					0.19	
Dry	***Hypseleotris compressa***	0.08	**0.4**		**0.3**				0.09	0.05					0.02
Wet	***Awaous acritosus***	0.08	**0.5**		0.13			0.11		0.17					0.04
Dry	***Leiognathus equulus***		**0.7**		**0.2**										0.06
Wet	***Redigobius bikolanus***	0.06	**0.7**		**0.2**	<0.01			0.06						
Dry	***Redigobius bikolanus***	0.09	**0.6**		**0.2**	0.08									
Wet	***Craterocephalus stercusmuscarum***	**0.2**	**0.6**		0.13										
Wet	***Ambassis agrammus***	**0.4**	**0.5**	0.03	0.04				0.04						
Wet	***Hypseleotris compressa***	**0.3**	**0.5**		0.04	0.09		<0.01		0.01					0.11

Appendix 4: Trophic guilds based on fine dietary categories

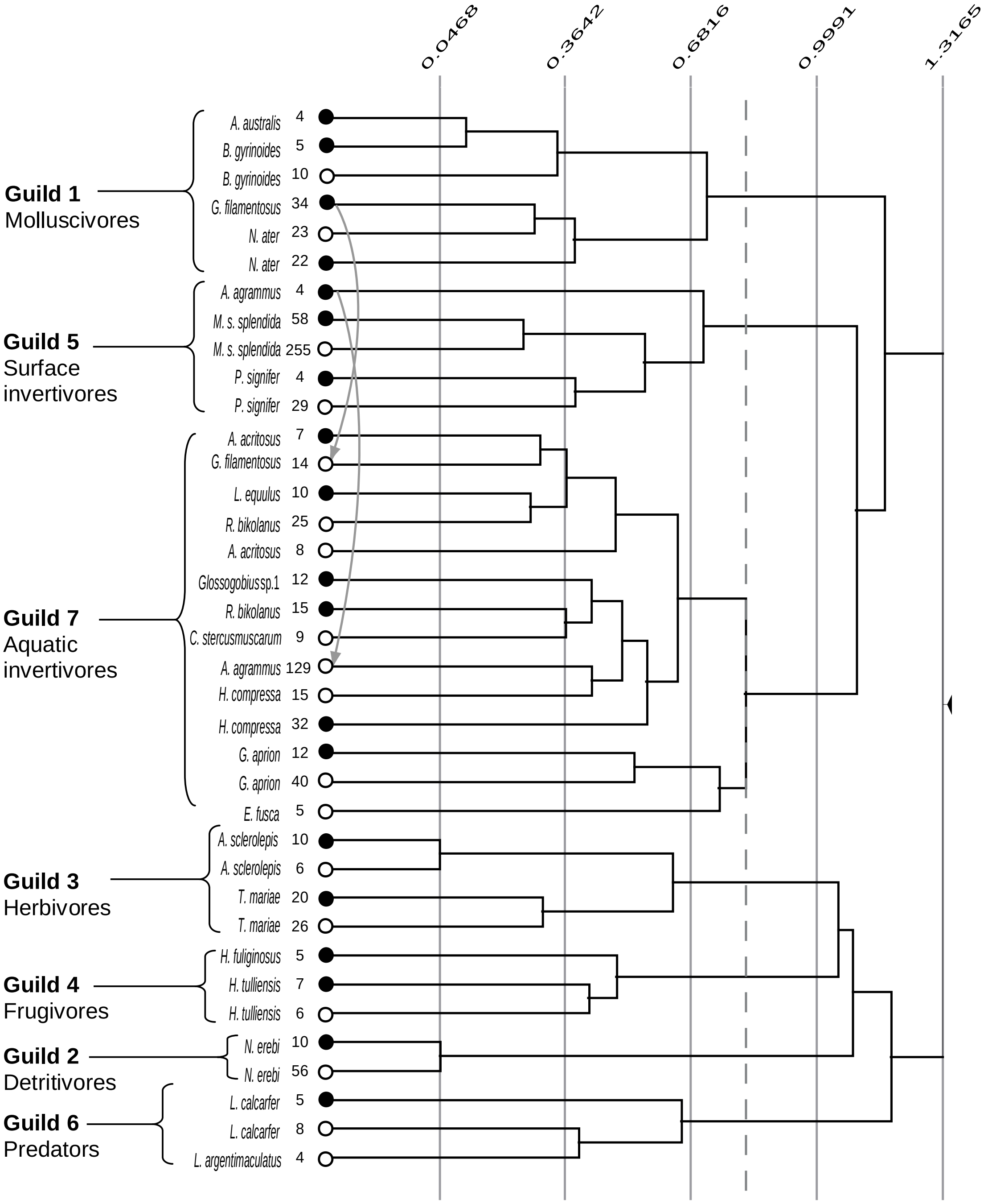

Figure A4.1 The trophic structure of the freshwater fish community of the lowland Mulgrave River. Seven feeding guilds were defined by flexible UPGMA classification on the basis of fine diet categories (grey dashed line) of species collected during dry (closed circles) and wet (open circles). Species names are followed by sample size (i.e., the no. individuals with gut fullness of at least 0.2). Grey arrows represent seasonal feeding shifts resulting in movement between guilds. Note that some species were only caught in one season (e.g., *C. stercusmuscarum*).

Appendix 5: Stable isotope signature data

Table A5.1 Stable isotope signatures of basal sources, invertebrates and fish collected during dry and wet season samples, with additional data from Bunn *et al*. (1997).

	Dry season							Wet season						
	δ^{13}C			δ^{15}N			*n*	δ^{13}C			δ^{15}N			*n*
Basal sources														
Periphyton (brown algae)								-35.30			7.35			1
Singaore daisy								-32.30			7.21			1
Persecaria								-30.75			7.00			1
Macrophyte A								-29.73			7.78			1
Macrophyte B								-28.37			6.13			1
Sugar cane								-12.76			10.91			1
Para grass (live)								-12.58			12.00			1
Para grass (dead)								-12.53			7.52			1
Fruit								-28.07			4.84			1
Invertebrates														
Arachnida								-21.51	±	0.03	7.97	±	0.58	2
Chironomidae	-25.99			10.73			1	-25.42			8.51			1
Coleoptera adults								-24.58	±	2.60	7.55	±	0.08	2
Coleoptera larvae	-26.78			9.21			1	-30.46			6.81			1
Corixidae and Notonectidae	-24.88			8.63			1							
Ephemeroptera nymphs	-26.84			10.57			1	-30.46			8.70			1
Hemiptera								-25.86			9.36			1
Hymenoptera	-23.14			9.92			1							
Lepidoptera	-27.47			9.40			1							
Macrobrachium								-25.36			10.22			1
Molluscs								-19.68	±	2.05	10.30	±	0.53	3
Bivalve molluscs								-36.36			10.40			1
Gastropod molluscs								-15.10			10.44			1
Ostracods								-27.87			9.60			1
Odonata	-30.90			1.35			1	-27.76	±	1.06	3.45	±	1.10	3
Orthoptera								-30.53			6.21			1
Shrimp	-26.85			9.98			1	-27.04	±	0.31	9.91	±	0.50	4
Small terrestrial invertebrates	-20.98			6.16			1	-31.24	±	2.90	5.41	±	2.80	3
Trichoptera larvae	-24.93			13.04			1	-24.39	±	2.91	7.78	±	2.54	2
Fish species														
A. australis	-24.49	±	0.49	13.06	±	0.11	4							
A. agrammus								-25.56	±	0.26	13.43	±	0.14	4
A. sclerolepis	-24.16	±	0.23	13.49	±	0.23	4							
A. acritosus								-24.98	±	0.80	13.08	±	0.46	3
B. gyrinoides	-24.58	±	1.65	11.10	±	0.46	3	-23.87	±	0.35	10.94	±	0.10	2
C. stercusmuscarum								-25.04	±	0.43	11.83	±	0.93	3
G. filamentosus	-23.98			13.24			1	-25.49	±	0.33	13.56	±	0.29	4
G. margaritacea	-21.56			12.12			1							
G. aprion								-26.87			11.35			1
H. fuliginosus	-22.01	±	0.42	11.55	±	0.25	4							
H. tulliensis	-22.03	±	2.01	11.92	±	0.79	2	-23.26	±	0.41	11.23	±	0.45	2
H. compressa	-25.57			11.78			1	-22.84	±	2.04	11.04	±	0.24	3
L. calcariger	-23.61	±	0.28	14.48	±	0.17	2	-24.79	±	0.92	13.72	±	0.29	3
L. argentimaculatus	-22.94	±	0.68	14.40	±	0.63	3	-24.13	±	0.52	14.58	±	0.14	2
M. s. splendida	-25.11			11.54			1	-22.36	±	0.72	12.03	±	0.27	7
M. argenteus								-24.35	±	0.48	13.21	±	0.08	2
M. b. brachyurus								-25.88	±	0.21	12.43	±	0.37	2
M. cephalus	-23.12	±	0.32	13.49	±	0.67	2	-24.39			12.04			1
N. erebi	-25.39	±	0.23	11.86	±	0.26	3	-26.60	±	0.51	11.28	±	0.35	6
N. ater	-22.77	±	0.50	12.49	±	0.25	4	-22.67	±	0.26	12.86	±	0.19	3
P. signifer								-24.49	±	0.62	9.68	±	0.91	3
R. bikolanus	-25.86	±	0.44	10.64	±	0.28	3	-26.24	±	0.47	11.35	±	0.68	5
T. tandanus	-23.09			10.58			1	-21.00			12.63			1
T. mariae	-25.59	±	0.68	12.02	±	0.30	3	-25.29	±	1.30	11.60	±	0.31	4
Bunn *et al*. (1997)	**August**							**November**						
Sugar cane	-12.89	±	0.11	3.60	±	0.56	10	-12.26	±	0.04	4.68	±	0.51	5
Para grass (live)	-12.40	±	0.11	8.28	±	0.62	10	-12.33	±	0.08	7.61	±	0.30	5
Para grass (dead)	-12.18	±	0.11	6.85	±	0.55	10							
Terrestrial vegetation	-29.39	±	0.62	5.90	±	0.69	8	-29.18	±	0.53	5.32	±	0.53	9
CPOM	-18.41	±	0.81	7.32	±	0.49	5	-17.38	±	1.02	9.43	±	0.63	5
FPOM	-20.65	±	0.44	8.49	±	0.38	5	-20.31	±	0.30	8.33	±	0.44	5
Vallisneria	-32.24	±	0.68	12.15	±	0.56	6	-33.78	±	1.05	10.70	±	0.82	5
Spirogyra	-36.56	±	0.54	10.97	±	0.70	4	-33.52	±	1.07	6.75	±	0.42	6