

Food web dynamics in an Australian Wet Tropics river

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Abstract. In Australia's Wet Tropics rivers, perennial base flows punctuated by wet season floods drive instream responses across a range of spatial and temporal scales. We combined gut-content and stable-isotope analyses to produce preliminary webs depicting trophic links between fish, their main prey items and basal productivity sources. We then used these webs to test the applicability of general food web principles developed in other tropical systems. Although a range of sources appeared to underpin fish productivity, a large portion of total energy transfer occurred through a subset of trophic links. Variability in food web structure was negatively correlated with spatial scale, being seasonally stable at river reaches and variable at smaller scales. Wet Tropics rivers are similar to those in other tropical areas, but exhibit some unique characteristics. Their high degree of channel incision improves longitudinal connectivity, thereby allowing fish to move between mesohabitats and target their preferred prey items, rather than shifting their diet as resources fluctuate. However, this also inhibits lateral connectivity and limits terrestrial energy inputs from beyond the littoral zone.

Additional keywords: connectance, disturbance, flood, movement, pulse, scaling, seasonality.

Introduction

Food webs provide tractable depictions of biodiversity, species interactions and ecosystem function (Dunne *et al.* 2002). In large rivers, food webs reflect their environmental setting – they are complex, yet exhibit high degrees of organisation (Power and Dietrich 2002). Natural patterns of wetting and drying affect connectivity and alter the relative importance of various autochthonous and allochthonous productivity sources (Junk *et al.* 1989; Thorp and Delong 2002; Zeug and Winemiller 2008). However, standing biomass is usually dominated by a core set of species connected by several short food chains, with an abundance of weaker food chains linking rarer species (Winemiller 2005). Fishes are conspicuous, important components of these webs because they are both abundant and highly mobile (Winemiller and Jepsen 1998). For example, they have an ability to increase food web stability by spatially coupling smaller, otherwise disparate groups of prey (McCann *et al.* 2005).

We previously documented the influence of wet season floods on instream habitat structure, prey availability, fish assemblages and fish feeding in the lower Mulgrave River, north-eastern Australia (Pusey *et al.* 1995a, 1995b; Rayner *et al.* 2008, 2009). Unlike larger tropical rivers, this system is small and laterally confined. Floods rarely escape the deeply-incised main channel and tend to act as disturbances rather than gentle

flood pulses. Prey availability is reduced during the wet season, but fish exhibit specialised dietary preferences and move between habitats within the main channel to access their preferred food items (Rayner *et al.* 2009). These dynamics differ markedly from those documented in larger tropical river–floodplain systems, where seasonal shifts in fish diets are typical (Goulding 1980).

Douglas *et al.* (2005) developed five general food web principles for the rivers of Australia's tropical north. 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. We aimed to test the applicability of these principles to the Mulgrave River in light of the spatial confinement, consumer mobility and dietary specialisation observed in this system (Rayner *et al.* 2008, 2009).

Methods

Rayner *et al.* (2008, 2009) presented full details of the study area and methodology used for this study. Briefly, surveys of fish and

invertebrate communities were conducted at four sites on the lowland main channel under wet and dry season flow conditions. Boat electrofishing effectively sampled most species, with mobile and cryptic fish sampled using multi-panel gill-nets and small traps, respectively. Specimens were preserved in formalin for later gut-contents analysis. Benthic and littoral invertebrate samples were collected to provide information on ambient food availability.

Food web diagrams, depicting the feeding links between fish and their food, were constructed using these data. The resulting webs provide estimates of the relative strength of trophic links (i.e. energy transfer) within the context of the entire food web. Three trophic levels were considered – basal 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 (Rayner *et al.* 2008) and other field observations collected during the study. However, 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 (Rayner *et al.* 2009). 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 1), to compensate for differences in biomass of taxa between invertebrate categories, and range-standardised across seasons.
- (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 (Rayner *et al.* 2009). 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 (members of the molluscivore guild) with gut fullness proportions of at least 0.2 collected during dry season samples ($n = 65$; Rayner *et al.* 2009). These values were then range-standardised across seasons.

Table 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 Baumgärtner and Rothhaupt (2003) and Ganihar (1997)

Invertebrate category	Estimated mean dry mass (g)
Aerial and surface invertebrates	0.020
Aquatic insects	0.050
Macrocrustaceans	0.280
Microcrustaceans	0.001
Molluscs	0.020
Other macroinvertebrates	0.050
Other microinvertebrates	0.001
Terrestrial invertebrates	0.050

Trophic links between fish and their food sources were quantified using volumetric gut contents data (Rayner *et al.* 2009). 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 that had gut fullness values of at least 0.2. 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. Independent two-tailed *t*-tests were used to examine differences in the number of links per trophic guild and mean link strength between seasons, after assumptions of the test had been satisfied. Using these data, food web diagrams were drawn manually. This approach is limited to the main relationships of the fish and their food. It does not include higher-order consumers such as crocodiles or birds, or basal species and microbial loops. As functional categories used in web construction led to lumping of trophic species (Pimm *et al.* 1991), the calculation of food web statistics is not appropriate. Many food web statistics are sensitive to the way in which the webs themselves are constructed (Sugihara *et al.* 1997; Solow and Beet 1998).

Stable isotope analyses were performed on samples collected during dry and wet seasons (October 2004 and May 2005, respectively). Benthic grab and littoral dip-net samples were collected using the methods described in Rayner *et al.* (2009) and frozen. These were later sorted into broad categories in the laboratory and processed as individual samples. Additional samples were also collected (October 2004, May 2005 and October 2007) from potential basal sources, such as macrophytes (leaves of live plants), periphyton (scraped from rocks and logs), sugarcane (leaves of live and dead plants) and detritus (decomposing leaf litter from river bed). Samples of benthic detritus were collected with a 250- μ m dip net and sieved into fine (250 μ m–1 mm) and coarse (>1 mm) fractions of particulate organic matter (FPOM and CPOM). Zooplankton samples (predominately copepods) were collected at night by towing an 80- μ m plankton net from behind a small boat across the water surface at sites 3 and 4.

Half of each zooplankton sample was treated with HCl for two hours to remove their inorganic carbonate structures, whereas the second half remained untreated to compare the influence of inorganic carbon on the carbon isotopic signature. Tissue 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 24–48 h at 60°C. Tissue was chosen as the most appropriate material to analyse seasonal changes in isotopic signatures (Jardine *et al.* 2005). All basal source, invertebrate and fish tissue samples were then ground and oxidised at high temperature. The resultant CO₂ and N₂ were analysed with a continuous-flow isotope-ratio mass spectrometer at Griffith University, Brisbane, Australia. Ratios of ¹³C/¹²C and ¹⁵N/¹⁴N were expressed as the relative per mil (‰) difference between the sample and conventional standards (PDB carbonate and N₂ in air: see Bunn *et al.* 1997). Analysis using a mixing model (IsoSource v1.3.1) was undertaken, with the aim of determining the relative importance of algal v. detrital sources for fish consumers. However, the results obtained were not particularly informative and we concluded that their inclusion here would not provide insights beyond the existing analyses.

Results

Seasonal food webs based on field survey and gut contents data

Three trophic guilds dominated the fish community biomass during the dry season: predators, molluscivores and frugivores (Fig. 1). Aquatic insectivores had the smallest biomass of any feeding guild, despite being the most numerically abundant group and despite their favoured prey having the greatest standing biomass of any invertebrate category at this time. The strongest feeding links were between each fish-feeding guild and its main food type (e.g. herbivorous fish consuming macrophytes). The overall structure of the wet-season food web was similar to the dry-season web (Fig. 1). The feeding guilds comprising predatory, molluscivorous and frugivorous fish continued to dominate the fish community biomass although detritivores became more important. Food availability was reduced during the wet season (Rayner *et al.* 2009). 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 ($t_{12} = -0.282$, $P = 0.783$). Most links were weak (<5% of the strongest link; Fig. 2), with no significant difference in mean relative link strength between wet and dry seasons (\log_{10} transformed, $t_{105} = 1.206$, $P = 0.231$). Omnivory was 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, macrocrustaceans and macrophytes, whereas during the wet season the majority of link biomass was associated with fish, macrophytes, detritus and macrocrustaceans (Fig. 3).

Stable isotope analysis

Basal sources

Sources of primary production exhibited distinct $\delta^{13}\text{C}$ values in both seasons (Fig. 4). The most ^{13}C -depleted sources were epiphytes, with delta values of less than 32‰, whereas *Brachiaria mutica* (both live and dead samples) and sugarcane were the most ^{13}C -enriched sources (−12 to −13‰). $\delta^{13}\text{C}$ values for FPOM and CPOM samples were tightly clustered around −29‰, more enriched than terrestrially derived leaf litter at −32‰, but close to riparian fruits and littoral vegetation (e.g. *Persicaria* and *Sphagneticola trilobata*) collected during the wet season. Our single filamentous algae sample was relatively ^{13}C -enriched.

Primary consumers

During the dry season, primary consumers had variable isotopic signatures, with $\delta^{13}\text{C}$ values ranging between −21 and −30‰, and $\delta^{15}\text{N}$ values ranging between 4 and 11‰. Exceptions to this trend were trichopteran larvae and molluscs, which were more ^{15}N -enriched and more ^{13}C -enriched, respectively. Wet season

samples of Orthoptera, Coleoptera larvae, small terrestrial invertebrates, Trichoptera and Arachnida were ^{15}N -depleted, but spanned a range of $\delta^{13}\text{C}$ 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 also relatively ^{15}N -enriched. Most invertebrates appeared to derive their carbon from a combination of aquatic (algae, CPOM and FPOM) and terrestrial (riparian vegetation or detritus) sources during both seasons.

Higher-order consumers

During the dry season, fish species were tightly clustered in a pyramid between 10 to 14‰ $\delta^{15}\text{N}$ and −20 to −28‰ $\delta^{13}\text{C}$ (Fig. 4). The position of each species generally corresponded to the dietary data from gut contents analysis (Rayner *et al.* 2009). For example, piscivorous 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. Both algal and detrital trophic pathways were apparent; *Redigobius 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 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Individual species, particularly *Melanotaenia splendida splendida*, *Redigobius bikolanus*, *Nematalosa erebi*, *Tilapia mariae* and *Pseudomugil 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 *Lutjanus argentimaculatus* and *Lates calcarifer* still at the top of the aquatic food chain. However, delineating between algal and detrital 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 (Fig. 5).

Discussion

Food web structure

In the main channel of the Mulgrave River, trophic interactions between fish and their food sources were complex, with an abundance of weak links and a few strong links. Feeding activity of each guild focused consistently on several key food items, although omnivory was observed in most guilds during the study. These patterns are consistent with other studies on tropical river food webs, where the magnitude of trophic links is strongly negatively skewed (Winemiller 2005). Guilds consisting of large-bodied species, namely piscivores, molluscivores, frugivores and detritivores, had the greatest biomasses throughout the year. In contrast, aquatic and surface insectivore guilds had

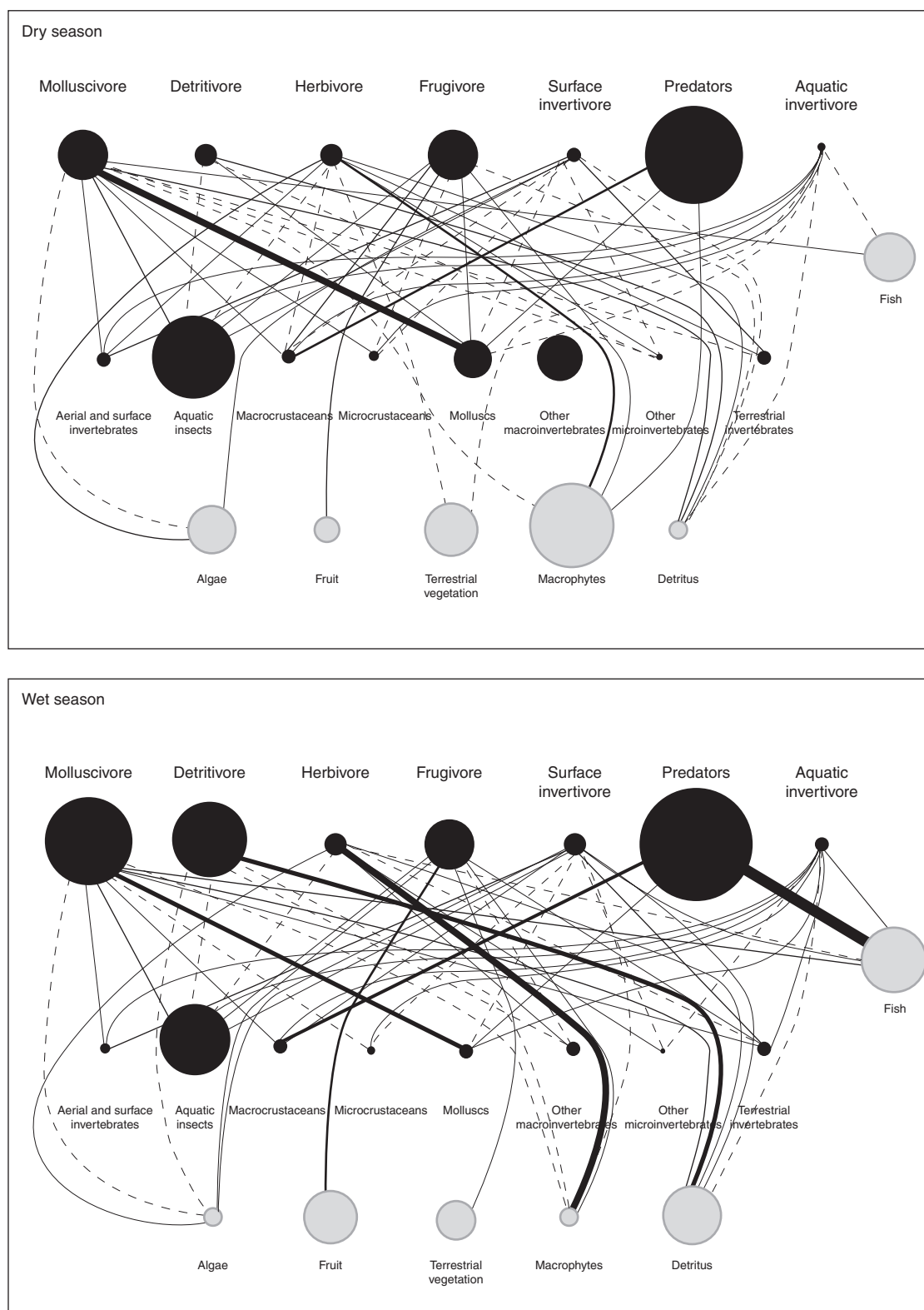


Fig. 1. Seasonal trophic links between fish feeding guilds, invertebrate prey categories and basal trophic levels in the main-channel food web of the Mulgrave River. The size of circles is indicative of relative biomass within each trophic level, whereas grey circles are estimates from habitat sampling and field observations. Very weak links (<0.0005% of strongest link) are shown as dashed lines.

relatively low biomasses, despite their numerical abundance, because they comprised small-bodied species such as *Melano-taenia splendida splendida* and *Ambassis agrammus* (Rayner *et al.* 2008, 2009). The richer assemblage of these small species greatly increased overall food web complexity, but had relatively little influence on total energy transfer (Winemiller 2005).

Trophic pathways linking detritus, detritivorous fishes, and then piscivorous fishes are known to be central to tropical river food webs (Winemiller 2005). This is also likely to be true in the Mulgrave River, where detritus was identified in the gut contents of five of the seven feeding guilds in both seasons (Rayner *et al.* 2009). However, the food web diagrams presented here possibly underestimated the importance of detritus and over-estimated the importance of molluscs. *Nematalosa erebi* is known to rely on detritus as a major food source (see Pusey

et al. 2004: p. 99) and was very abundant in deep, open-water habitats, but 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. In addition, detritus contributed 42% of the mean diet of *Neosilurus ater* (Rayner *et al.* 2009). More rigorous sampling of basal sources, particularly those known to exhibit marked spatial and temporal variation (e.g. periphyton and filamentous algae (Trudeau and Rasmussen 2003)), should be a focus of future studies.

Temporal change in food web structure

Flooding of the main channel reduced habitat diversity and the abundance of invertebrates (Rayner *et al.* 2008, 2009). When sediments were disturbed in the wet season, almost all instream vegetation, including macrophytes and filamentous algae, was removed from the channel (Rayner *et al.* 2008). Fish species responded to these changes by moving between study sites. However, their diets remained relatively constant (Rayner *et al.* 2009). 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 2005), did not occur at large spatial scales; 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 at the river-reach scale. However, fish movements between sites altered food web structure at micro- and mesohabitat scales, with food consumption by fish reflecting food availability.

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 (Pusey *et al.* 1995a, 2004; Rayner *et al.* 2009) and a range of sources maintaining production in the fish community. Algal and detrital energy-transfer pathways were identified during the dry season, but results from wet-season samples were more equivocal. At this time, isotope signals of both fish (e.g. *Redigobius bikolanus*) and invertebrates (e.g. Trichoptera) were more variable. Additionally, seasonal shifts in the mean isotopic signatures of individual fish species were limited and showed no clear trend. These

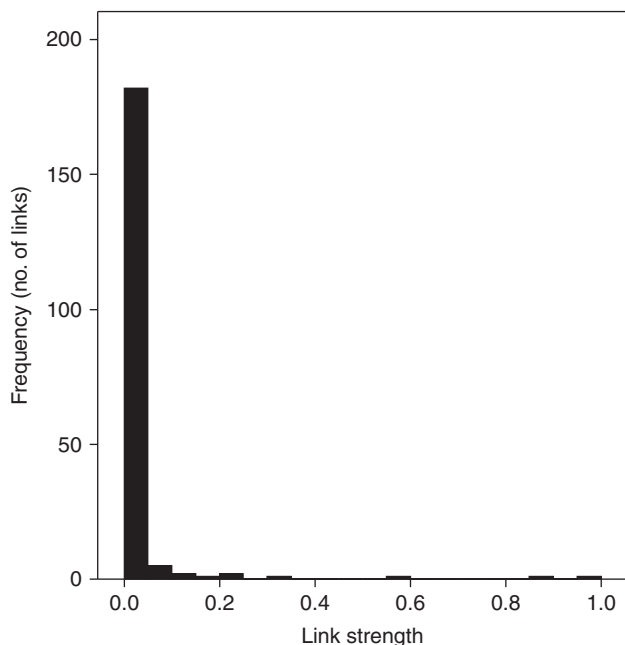


Fig. 2. Frequency histogram of relative feeding link strength (range standardised across both seasons) between fish guilds and their food sources.

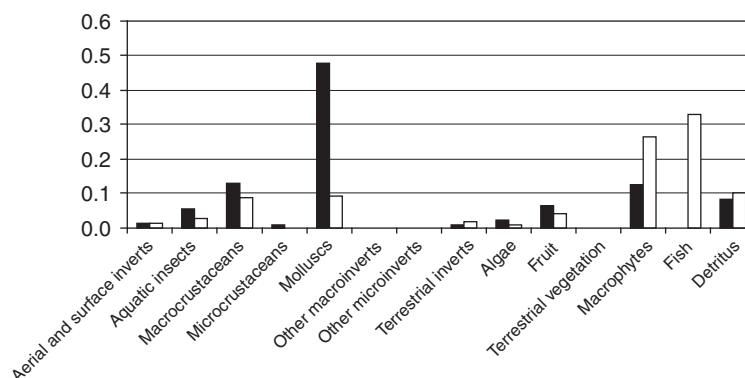


Fig. 3. Proportion of total feeding link biomass (energy transfer) associated with each measured food source during dry (shaded bars) and wet (open bars) seasons.

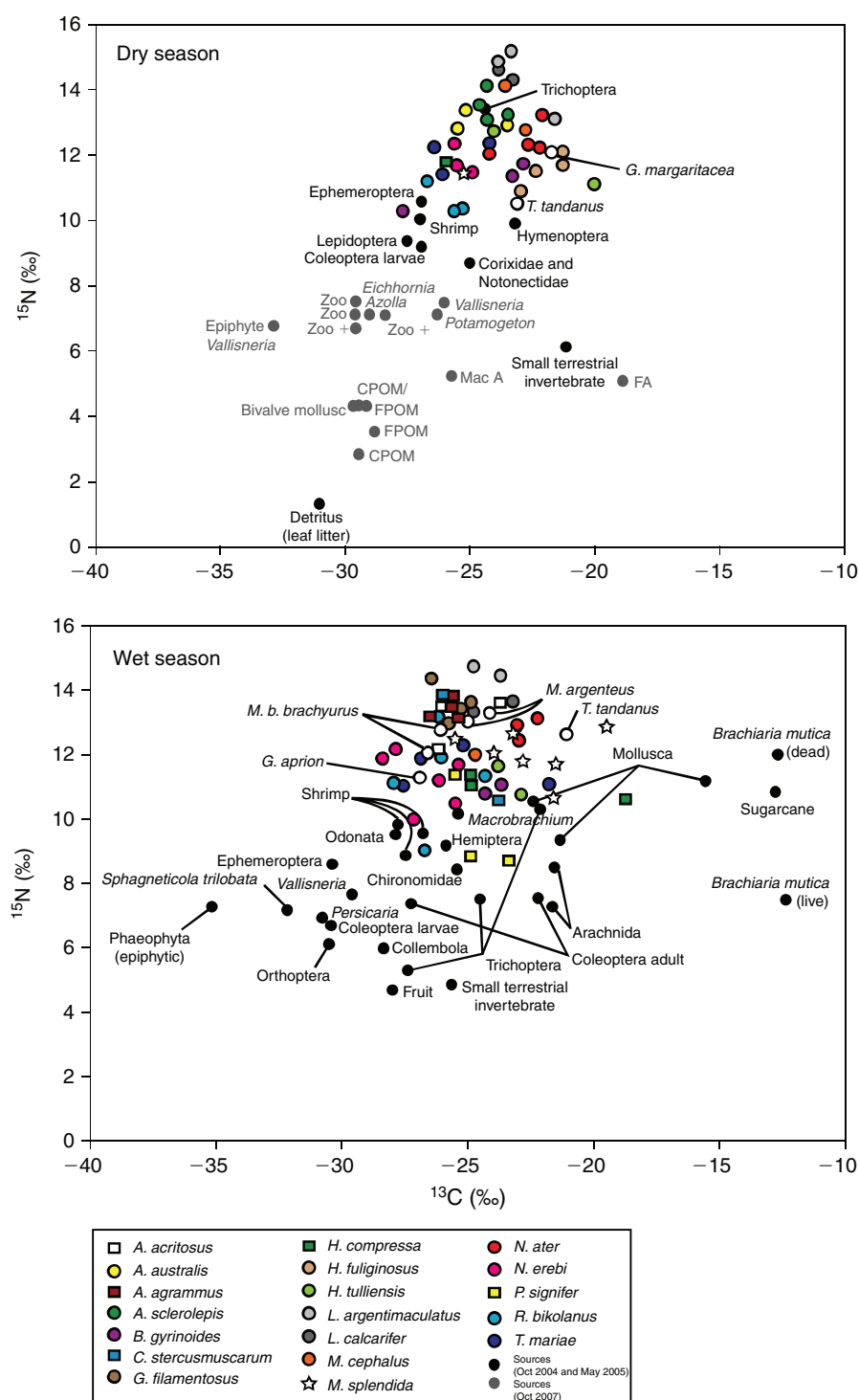


Fig. 4. Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) during dry and wet season samples. Samples from October 2007 shown in grey. FA, filamentous algae; Zoo, zooplankton; Zoo +, zooplankton processed using HCl.

results are consistent with the work of Thorp *et al.* (1998) in the constricted main channel of the Ohio River, USA, who found that consumers were more isotopically similar between months at their main-channel site than at their floodplain site, indicating temporal stability in fish diets.

The majority of stable isotope research supports the paradigm that most aquatic food webs in lowland rivers are based on autochthonous primary production by planktonic, epiphytic and benthic algae, rather than macrophytes or terrestrial inputs (Hamilton *et al.* 1992; Forsberg *et al.* 1993). 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. However, more recent data suggest that terrestrial sources might have been underestimated in earlier studies (Zeug and Winemiller 2008). We found that species such as *Tandanus tandanus*, *Hephaestus tulliensis*, *Mugil cephalus* and *Neosilurus ater* were dependent on detrital and terrestrial sources, indicating that a wide range of sources might support the Mulgrave River food web.

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

(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 characterising the annual flow regime. However, because base flows 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 by Rayner *et al.* (2009), the implication is that the availability of resources might 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 (Marchant 1982; Finlayson and McMahon 1988; 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.

(2) Hydrological connectivity underpins important terrestrial-aquatic food web subsidies

Longitudinal hydrological connectivity in Wet Tropics rivers is strong, owing to the stable base flows 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 and McMahon 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). It is possible that inputs from terrestrial basal sources have been reduced since European settlement.

(3) River food webs are strongly dependent on algal production

As discussed above, most tropical riverine food webs appear 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

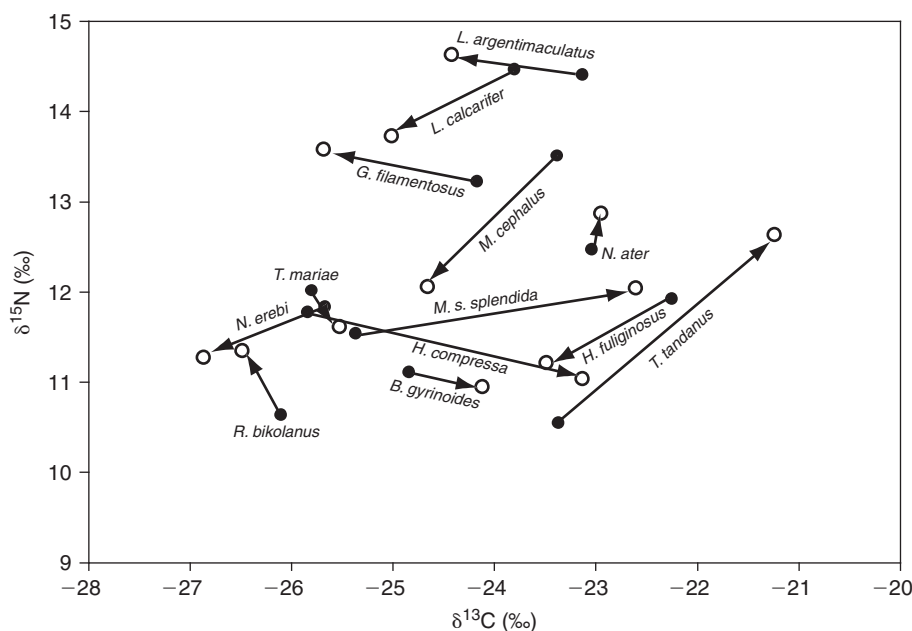


Fig. 5. Changes in mean stable isotope signatures of fish species caught during dry (shaded) and wet (open) seasons.

Awaous acritus, *Tilapia mariae* and *Melanotaenia splendida splendida*. Stable isotope data on the subject were equivocal; algae did appear to be important, but this primary production was supplemented by inputs from terrestrial C₃ vegetation (i.e. leaf litter, fruits and terrestrial invertebrates). During the wet season, main-channel substrates were highly mobile (Rayner *et al.* 2008), 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 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, although a low standing biomass of algae could also indicate high levels of consumption by herbivores, and algae may make a large contribution to CPOM and FPOM in the system.

(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 a few common macroconsumers exert a disproportionately large influence on benthic communities in tropical systems (Winemiller 2005). Strong top-down trophic effects have been documented by Power (1990a, 1990b) in the Eel River, California. Douglas *et al.* (2005) cited two small studies 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 (*Neosilurus ater* and *Neosilurus hyrtlii*) and shrimp (*Macrobrachium bellatum*) significantly reduced benthic algal biomass and invertebrate abundance, whereas 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: Rayner *et al.* 2009).

(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 during the study. Although 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 which become more or less available under a range of flow conditions (Goulding 1980; 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 sources, such as algae and

detritus, as they fed on items from higher trophic levels, such as benthic and littoral invertebrates (Rayner *et al.* 2009).

Conclusion

Together with our previous research, this study demonstrates 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 in the Mulgrave River. 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, were important in supporting communities in the main channel. However, seasonal shifts in food web structure occur predominantly at spatial scales finer than river reach. This is likely a result of spatial confinement of the food web and the linking of webs within the lowland reach by an abundant and mobile population of secondary consumers.

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