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Carbon from periphyton supports fish biomass in waterholes of a wet-dry tropical river

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Abstract

Identification of the dominant sources of carbon supporting consumer biomass in aquatic food webs is often difficult but essential to understanding the limits to aquatic secondary production. Stable isotope analysis (SIA) is a powerful tool to estimate the contribution of different sources to consumers, but most food web studies using this approach limit analyses to a few key consumer taxa rather than measuring biomass-weighted contribution of sources to the entire community. Here we combine SIA with standardized measurements of abundance and biomass of fishes and invertebrates in seven waterholes of a wet-dry tropical river sampled early and late in the dry season. We show that periphyton (as opposed to phytoplankton and terrestrial C3 plant detritus) was responsible for the majority of standing fish biomass (range 42 to 97%), while benthic invertebrates were reliant on a mixture of the three sources (range 26 to 100%). Furthermore, larger, older fishes at high trophic levels (catfish *Neoarius* spp., sleepy cod *Oxeleotris lineaolatus*, and barramundi *Lates calcarifer*) were supported almost exclusively by periphyton. Phytoplankton and detritus supported a considerable biomass of benthic and pelagic invertebrates, but only in taxa that occupied low trophic levels (e.g. snails). These measurements provide further evidence that although periphyton is relatively inconspicuous relative to other sources it contributes disproportionately to metazoan biomass in wet-dry tropical rivers.

Key words: benthic algae, tropics, detritus, phytoplankton, stable isotopes

Introduction

Understanding what sources of carbon underpin the growth of consumers is a fundamental question in food web ecology (Brett *et al*., 2009; Cole *et al*., 2011). In streams and rivers, two dominant forms of carbon contribute to consumer biomass – terrestrial material entering as detritus and periphyton (Allan and Castillo, 2007). In lowland reaches where turbulence is reduced and resultant water residence time increases in larger pools, the number of available sources expands, including production from within the water column in the form of phytoplankton. Models developed to describe the dominant biophysical processes occurring in rivers ascribe varying importance to these three sources (Vannote *et al*., 1980; Junk *et al*., 1989; Thorp and Delong, 1994) which can vary as a function of position in catchment, flow status and the consumer of interest (Finlay, 2001; Bunn *et al*., 2003; Rasmussen, 2010).

Most aquatic food web studies now use stable isotope analysis (SIA) of sources and consumers to estimate the relative importance of different carbon pathways. However, most of these studies have not quantified the relative abundance or biomass of the taxa on which SIA was conducted. As such, only qualitative determinations of the importance of different food sources to the food web can be ascertained. While the estimated importance of different carbon sources derived from a few key species is in itself useful, coupling SIA with measurements of standing biomass of all available taxa will result in stronger estimates of the importance of sources to overall production (Lewis *et al*., 2001; McNeely *et al*., 2007). For example, one particular species may account for a large proportion of the weight of total fish catch and thus it would be important to determine the percent of its biomass derived from different sources of carbon, and the percent of the total fish biomass this

represents in the system. Also, by standardizing sampling effort in space and time, biomass comparisons within and among locations in the river network can be made with greater confidence.

In the wet-dry tropics and other areas that experience prolonged periods of low or no flow, river channels contract back to a series of disconnected waterholes. These waterholes are important refugia for aquatic animals, and understanding sources of food responsible for sustaining consumers is critical in their effective management (Bunn *et al*., 2006). From a research perspective, one advantage of this disconnection and contraction is that food webs become more spatially defined (Post *et al*., 2007) with no movement of consumers or carbon sources among locations as would commonly occur in most riverine settings (Cunjak *et al*., 2005).

We used SIA of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$), coupled with quantitative catch statistics for fishes and invertebrates, to calculate sources supporting consumer biomass and their resultant trophic level in seven waterholes in the main channels of the Flinders and Cloncurry Rivers, Queensland, Australia. Previous work in this system suggested that benthic invertebrates consume a mixture of sources (Leigh *et al*., 2010), but little is known about carbon sources for higher consumers in these rivers. Given that fish make up the largest carbon pool in other dryland river waterholes (Burford *et al*., 2008), dietary information for fishes is needed to gain a system-level understanding of sources of production sustaining consumers. Although terrestrial and pelagic carbon sources are important in some floodplain river systems (Hoberg *et al*., 2002; Oliviera *et al*., 2006; Hoeinghaus *et al*., 2007; Roach *et al*., 2009; Zeug and Winemiller, 2008), we hypothesized that periphyton would dominate the diet of benthic invertebrates and fishes based on work conducted in adjacent dryland river systems (Bunn *et al*., 2003). Furthermore,

because short food chains have been observed in other tropical systems (Layman *et al*., 2005), we predicted that most fish biomass would be distributed among the lower trophic levels close to primary sources of production. These analyses are useful in understanding key attributes of food web structure in wet-dry tropical rivers that are known to have high biodiversity and are important in providing high quality fish protein to the developing world (Dudgeon, 2000).

Methods

Study Area

The Flinders River (S 17.8º E 140.8 º) is the largest of five catchments (109,000 km^2) in the Southern Gulf region, north-west Queensland. It rises near Reedy Springs in the Great Dividing Range and flows in a westerly direction towards Julia Creek before flowing north into the Gulf of Carpentaria, near the township of Karumba. The majority of the catchment consists of flat and undulating plains that are dominated by two land types, Mitchell grass and Bluegrass browntop plains. The vast plains and savannahs of the catchment support a large cattle grazing industry.

The climate of the catchment transitions from semi-arid in the south, to tropical monsoonal in the north. The southern zone of the catchment has an average annual rainfall of 600 mm, increasing to 900 mm along the Gulf of Carpentaria coastline (Bureau of Meteorology, www.bom.gov.au). Approximately 80% of the annual rainfall occurs during the hot monsoonal season (December-April), with the remainder of the year (May-November) being considerably cooler and dryer than the wet season. The catchment contains deep braided channels that overflow their banks during the wet season and are reduced to a series of turbid main-channel waterholes during the dry season. The Flinders and Cloncurry Rivers (a major tributary of the

Flinders) have a flow regime classified as "predictable summer highly intermittent" (Kennard *et al*., 2010), indicating an annual wet season flood followed by a dry season transition into a string of ephemeral and perennial waterholes, a characteristic of many northern dryland rivers throughout Australia (Leigh and Sheldon, 2008). Both rivers have steep banks composed of heavy grey and brown clays and have medium to thick riparian tree cover.

Seven waterholes (four from the Cloncurry, two from the Flinders and one off-channel waterhole) were sampled twice during the 2009 dry season. Five of these sites (Stanley Waterhole, Seaward Lagoon, Williams Lagoon, Ten Mile Lagoon, and the off-channel waterhole) were located close together (Table 1), and four of the five were intensely studied (invertebrate biomass estimated and fish biomass estimated by two methods – boat electrofishing and fyke nets). The other two distant sites (Walker's Bend and Rocky Waterhole) provided supplementary data (electrofishing only and non-quantitative sampling of invertebrates) to determine if trends persisted more broadly in the catchment. The seven sites were selected based on their perennial nature, accessibility, human disturbance and longitudinal position in the catchment and therefore are representative but not random samples of waterholes in the system. Each site was relatively shallow (typical channel depths 2 to 3 m) and some included slow flowing riffles during the early dry season.

Water Quality and chlorophyll

At each site, water quality was assessed using a 'Quanta' Hydrolab multi-parameter probe, where discrete samples were taken for turbidity and pH. Unfiltered water was collected in 250 ml bottles for analysis of total nitrogen (TN) and phosphorus (TP). Additionally, known volumes of surface water were filtered on

0.45µm glass-fibre filters to measure phytoplankton chlorophyll *a*. To measure periphyton chlorophyll *a*, known areas of submerged surfaces were sampled with toothbrushes (rocks and/or woody debris) or a small corer (mud). Samples from rocks and wood were rinsed in a small plastic zip lock bag then filtered on a glass-fibre filter, while mud samples were placed directly in zip lock bags. Triplicate samples of each type were collected, placed in the dark and frozen immediately for subsequent analysis for chlorophyll *a* in the laboratory.

Food web sampling

At each site, primary carbon sources were generally collected at three locations along the length of each waterhole over a 24 hr period from a boat or land to capture spatial and temporal variability of sources available to higher trophic levels. Triplicate samples of each source were collected for SIA, including pasture grasses, riparian tree leaves (*Melaleuca* spp. and *Eucalyptus* spp.), occasional submerged and emergent macrophytes, suspended particulate organic matter (seston) and periphyton attached to rocks, macrophytes and woody debris. Epiphytes on emergent grasses and macrophytes were removed via agitation in buckets of water, and then filtered onto pre-combusted glass-fibre filters. Epilithic and epixylic samples were collected via toothbrush scrapes and filtered. All higher plant samples were rinsed of epiphytes in the field and stored in plastic ziplock bags. Seston was collected by filtering surface water on pre-combusted glass-fibre filters.

Zooplankton were collected at dusk by towing a 150 and 250 µm plankton net for approximately 100 m. Samples were stored frozen in 50 ml tubes and were identified in three samples, with copepods (50-70%) dominant in abundance over cladocerans (20-30%) and rotifers (10-30%) (S. Faggotter, unpublished data).

Benthic invertebrates were sampled using 1-2 m sweeps with a dip net over littoral detritus, grasses and *Melaleuca* spp. root systems. All benthic invertebrates collected were placed in sorting trays and hand picked with tweezers and plastic pipettes, then stored frozen in 10 ml tubes to preserve skeletal integrity for future laboratory ID, weighing and isotope analysis. Gastropods, molluscs and riparian spiders were occasionally collected by dip net, however, most were collected by hand. Adult decapods were predominately collected by baited traps, fyke nets and electro-fishing. All benthic invertebrates were sorted to order in the field, and only those captured in standardized dip net sweeps were used to estimate biomass.

Fish were collected by two complementary methods, passive sampling using fyke nets and active sampling using boat electro-fishing. Boat electrofishing was used at six sites, while fyke nets were used at five of the sites. Length measurements (mm) were taken for all fish captured by both methods and all individuals were also weighed (0.1 g) when collected by fyke net. Catch per unit effort was recorded for each waterhole. The fyke net sampling consisted of setting three nets (1.5 m diameter, 13 mm stretched mesh, 8 m wings) by boat just before dusk followed by retrieval at dawn, while the boat electrofishing was conducted during the day with a Model 2.5KvA (Smith-Root, Inc. Vancouver, WA, USA). A back pack electro-fisher (LR-24, Smith-Root, Inc.) was used in riffles at one of the sites (SDD); these data were not used for fish biomass estimates.

For SIA of fishes, three individuals of each species, encompassing the range of different body sizes, were sampled from each site. A non-lethal fin clip was taken if the fish was >20 cm in length, while smaller fish were killed by severing the spinal cord under anaesthetic. Isotope ratios in fin tissue are a reliable surrogate for those in

muscle tissue of Australian freshwater fishes (Jardine *et al*., 2011). All food web samples collected were labelled and immediately frozen.

Laboratory Processing

Upon return to the lab, animal and plant samples were processed and analysed for stable isotopes. All periphyton and benthic invertebrate collections were rinsed with distilled water and inspected under a dissecting microscope to clean and remove any organic debris that was mixed in the sample. Benthic invertebrate samples were sorted and classified to family. Muscle tissue samples were excised with a scalpel from each small fish. All samples were dried in an oven at 60ºC for at least 24 h before being ground and homogenized with a ball-mill grinder or mortar and pestle. Samples were weighed to approximately 0.8 mg and 3 mg for animals and plants, respectively, and then combusted in an EA 3000 elemental analyser (Eurovector, Milan, Italy). Sample gases were delivered to an Isoprime mass spectrometer (GV Instruments, Manchester, UK) for isotope analysis of C and N. Working standards were liquids calibrated against IAEA CH6, CH7, N1 and N2, and had elemental composition that matched the samples (44% C and 11% N for animal tissues, 41% C and 2% N for plant tissues). Samples of fish (muscle from spangled perch, *Leiopotherapon unicolour*) and plant (water lily *Nymphaea* sp.) tissues analysed repeatedly to measure precision over time yielded $\delta^{13}C$ = -21.9 ± 0.2‰ S.D. and $\delta^{15}N$ = 5.5 ± 0.4‰ S.D. (n = 29) for the fish sample and $\delta^{13}C$ = -26.1 ± 0.1‰ S.D. and $\delta^{15}N$ = 1.2 ± 0.4‰ S.D. (n = 4) for the plant sample. The average difference between duplicate samples within runs was 0.3‰ for C and 0.4‰ for N (n = 97).

Analysis of nutrients in water samples and chlorophyll *a* from the water column and benthos followed standard procedures. All nutrient samples were

analysed using standard colorimetic methods by Queensland Health Scientific Services (Brisbane, QLD) with detection limits of 0.04 mg L^{-1} and 0.01 mgL^{-1} for TN and TP, respectively. Chlorophyll *a* analyses were also conducted using standard colorimetric methods; chlorophyll *a* was extracted in 100% acetone and measured spectrophotometrically (American Public Health Association, 1985).

Biomass and isotope mixing model calculations

The standing biomass of invertebrates and fishes were assessed at five of the seven sites (Table 1). The wet weight of invertebrates collected in a sweep of a defined area was determined by gently tamping excess moisture from each individual on a cotton cloth before weighing. Snails (Viviparidae) were weighed with shells included but total weight was divided by four to account for inorganic material in the shells (Beeby *et al*., 2002; Kuris *et al*., 2008). We did not adjust crab (Sundathelphusidae) weights for inorganic carbon in the carapace because it represents less than 15% of the wet weight (Cameron and Wood 1985). We estimated weight for each individual fish that was collected by electrofishing using available L-W regressions from our fyke net data and the literature where appropriate (Pusey *et al*., 2004). Contributions of species to total biomass are reported in two ways: 1) average % contribution (by summing the mean contributions to biomass across the five sites and dividing by five); and 2) % of total (by summing the total mass of the species from all sites and dividing by the total mass of all species at all sites). Disparities between these two figures occur when a species dominates the biomass at one or few sites where the total biomass (all species) is low relative to other sites.

We used simple isotope mixing models to determine the contribution of sources to consumer diet (Jardine *et al*., 2006). Leaves from the dominant riparian

trees at each site, *Eucalytpus* and *Melaleuca* (i.e. C3 plants), were considered indicative of the detrital carbon available to food webs. Macrophytes and charophytes were rare, occurring at only two of the sites and were thus excluded. Seston is a mixture of phytoplankton and detritus and thus was not used as the pelagic end-member. Instead, zooplankton were used because values are more likely to represent long term variability in phytoplankton carbon (Cabana and Rasmussen, 1996) and samples are far easier to obtain than pure phytoplankton. Zooplankton were ^{13}C-depleted and ^{15}N-enriched relative to seston and all other sources, further illustrating that they were likely representative of a pure phytoplankton signal. For the benthic end-member we used periphyton scraped from submerged surfaces. While the dominant substrate in these waterholes is mud, we avoided sampling periphyton from this surface for isotope work because of the difficulty in obtaining reasonably pure samples. However, we did analyse mid-channel sediment samples for $\delta^{13}C$ and found values (-23.2 ± 1.0‰ S.D., n = 36) that were similar to those for epiphytes and epilithon reported here, so we are confident that the values are representative of periphyton growing in these waterholes (Bunn *et al*., 2003).

Although native and naturalized C4 grasses vastly outnumber C3 grasses in the study region (Hattersley, 1983), they were excluded from our analyses because of their rarity immediately adjacent to the waterholes and their unlikely contribution to the food web (Hamilton *et al*., 1992; Forsberg *et al*., 1993; Clapcott and Bunn, 2003). To confirm that this was a valid assumption, we ran a very coarse analysis using the Bayesian mixing model SIAR (Parnell *et al*., 2010) that can accommodate excess sources while still allowing estimates of uncertainty to be included for sources, consumers, and diet-tissue fractionation. We ran the model for fishes with four sources (periphyton, phytoplankton – estimated from zooplankton, leaf litter, and C4

plants) with no fractionation for $\delta^{13}C$ and 2.5 ± 1.3‰ fractionation per trophic level for $\delta^{15}N$ (Vanderklift and Ponsard, 2003). For this exercise, we loosely classified fish as herbivores (1 trophic level above producers), omnivores (1.5 trophic levels above producers), or carnivores (2.5 trophic levels above producers) (Pusey *et al*., 2004) and adjusted fractionation accordingly. In these analyses, the contribution of C4 grasses to consumers was always less then 10% (minimum = 1.5 ± 1.3% S.D. for carnivores, maximum = 9.5 ± 6.9% S.D. for large herbivores), supporting our assertion that they could be reliably excluded from further analyses.

By excluding C4 grasses, we were able to collapse our subsequent mixing model analyses to a single isotope, thus reserving $\delta^{15}N$ to do more detailed trophic level calculations. We used $\delta^{13}C$ data to calculate the proportion of the diet of an individual taxa composed of periphyton ($PER_{consumer}$) versus that of zooplankton/leaf litter. We combined the latter two sources because their $\delta^{13}C$ was similar (Figure 1, Phillips *et al*., 2005) and our interest was in the importance of periphyton as a food source (Bunn *et al*., 2003). Because C/N was high in invertebrates, indicative of high lipid content, all invertebrate $\delta^{13}C$ values were lipid corrected using an equation from Logan *et al*. (2008), while fishes were left uncorrected because lipid levels were almost uniformly low (C/N < 4). When non-lethal fin tissue was used in place of muscle, we subtracted 0.9‰ from the $\delta^{13}C$ value for fin because fin is enriched in ^{13}C by this amount relative to muscle (Jardine *et al*., 2011). To calculate $PER_{consumer}$, we assumed no trophic fractionation of $\delta^{13}C$ and used simple mixing models of the form:

$$PER_{consumer} = (\delta^{13}C_{consumer} - \delta^{13}C_{detritus\&zooplankton})/(\delta^{13}C_{periphyton} - \delta^{13}C_{detritus\&zooplankton})$$

where $\delta^{13}C_{detritus\&zooplankton}$ was the mean value of these two sources at a given site and $\delta^{13}C_{periphyton}$ was the site-specific value for periphyton. Values for $PER_{consumer}$ can

sometimes exceed 1 because of small uncertainties in source and fractionation values; in these instances we constrained the value at 1, assuming 100% contribution of periphyton to biomass of the consumer.

Within a site, we calculated the biomass accounted for by periphyton for all taxa using the equation (Table 2):

$$Biomass_{periphyton} = PER_{consumer} * Biomass_{consumer}$$

To calculate the overall contribution of periphyton to the consumer biomass at a given site, we used the equation:

$$\%\ periphyton_{site} = \sum Biomass_{periphyton} / \sum Biomass_{consumer} * 100$$

To generate error estimates to accompany $\%\ periphyton_{site}$ for fishes, we multiplied standard deviations around mean $PER_{consumer}$ for each taxon at each waterhole by $Biomass_{consumer}$ and summed these for the site. Because we ran pooled samples of benthic invertebrates and did not have variance among individuals, we did not attempt to estimate error.

To calculate a continuous trophic level (TL) for consumers, we used $\delta^{15}N$ after standardizing to a habitat-specific baseline (Vander Zanden and Rasmussen 1999). The $\delta^{15}N$ of primary consumers varied along a pelagic to littoral gradient, similar to patterns observed in temperate lakes (Vander Zanden and Rasmussen, 1999). To account for this variation in our trophic level calculations, we estimated baseline $\delta^{15}N$ for each individual fish using its $\delta^{13}C$ according to the polynomial function relating $\delta^{15}N$ to $\delta^{13}C$ in primary consumers based on data derived from this study: $\delta^{15}N = 0.035*(\delta^{13}C)^2 + 1.520*(\delta^{13}C) + 22.448$, $r^2 = 0.23$, $n = 119$). Primary consumers included larvae of mayflies (Baetidae, Caenidae, Leptophlebiidae), caddisflies (Leptoceridae, Glossosomatidae), true flies (Culicidae, Ceratopogonidae,

Chironomidae), molluscs (snails, mussels, clams), zooplankton, and true bugs (Corixidae). TL for individual consumers was then calculated using the equation:

$$TL_{consumer} = (\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/\Delta 15N + 2$$

where $\Delta 15N$ is the change in $\delta^{15}N$ per trophic level (2.54‰, Vanderklift and Ponsard 2003).

Results

Fish and invertebrate catch

A total of 2849 fish, representing 24 species, were captured by electrofishing (n = 769) and fyke netting (n = 2080) during the two sampling events. An additional 266 large crustaceans (3 taxa: prawns, crabs, crayfish) were captured in the fyke nets and are included in all "fish" calculations related to fyke nets because they often dominated the catch in this gear type. Crustaceans were not retained during electrofishing and are not included in biomass calculations associated with that gear type.

Fyke net catch per unit effort decreased between the early and late dry season sample period while electrofishing CPUE increased (Table 3). In the early dry season, the dominant taxa captured (in terms of biomass) in the fyke nets at the 5 sites were freshwater prawns (*Macrobrachium* spp., average % of biomass = 27%, % of total = 39%) followed by fork-tailed catfish (*Neoarius* spp., 14% and 15%), sleepy cod (*Oxyeleotris lineolatus*, 14% and 13%), giant glassfish (*Parambassis gulliveri*, 12% and 9%) and bony bream (*Nematalosa erebi*, 11% and 6%). In the late dry season, sleepy cod (average % of biomass = 37%, % of total = 29%) and fork-tailed catfish (30% and 43%) had the highest average biomass, followed by bony bream (11% and 9%). The dominant species in terms of biomass in the early dry season

electrofishing survey were sleepy cod (average % of biomass across 7 sites = 32%, % of total biomass = 42%), barramundi (*Lates calcarifer*, 25% and 31%), and spangled perch (16% and 2%). In the late dry season survey, sleepy cod (average % of biomass = 22%, % of total = 20%), barramundi (18% and 23%) and spangled perch (10% and 0%) remained a considerable proportion of the biomass, while gulf grunter (*Scortum ogilbyi*, 12% and 14%), bony bream (11% and 3%) and fork-tailed catfish (*Neoarius leptaspis*, 6% and 10%; *N. paucus,* 13% and 26%) also contributed large amounts.

For invertebrates captured in dip nets, biomass was dominated by crabs (average % of biomass = 14%, % of total = 47%), diving beetles (Dytiscidae, 5% and 19%), snails (17% and 10%), shrimps (Atyidae, 18% and 6%) and water scorpions (Nepidae, 18% and 6%) in the early dry season. In the late dry season, biomass shifted to snails (17% and 37%), dragonflies (Coenagrionidae, 33% and 26%), and shrimps (Atyidae 22% and 21%). All other taxa accounted for less than 7% of biomass calculated by both methods.

Sources of carbon for consumers

The $\delta^{13}C$ of zooplankton (-30.7 ± 2.3‰ S.D.) and detritus (-30.3 ± 1.6‰ S.D.) were similar to each other but very distinct from that of periphyton (-18.6 ± 4.3‰ S.D.) (Figure 1). This allowed for good resolution in mixing model analysis of consumers.

All three sources (periphyton, detritus, plankton) contributed to the biomass carbon of invertebrates (Table 3). The most commonly collected taxa (mayflies - baetids and caenids, atyid shrimps, leptocerid caddisflies, chironomids) derived approximately one-third of their carbon from periphyton with the remainder coming from a mixture of detritus and plankton. In terms of contribution to total biomass,

$PER_{consumer}$ ranged from only 0.26 at Stanley Waterhole – a site that was dominated by vivparid snails (84 and 53% of biomass in the early and late dry season sample) - to 1.00 at the off-channel lagoon in the early dry season where two large sundathelphusid crabs accounted for most (73%) of the biomass in the sample. We were unable to estimate $PER_{consumer}$ at the off-channel site in the late dry season because our sources did not differ greatly enough to provide the resolution needed for accurate source proportion estimates. However, data from the other four sites suggested that invertebrates consumed equal or less periphyton late in the dry season compared to the early dry season (Table 3).

Fishes and large crustaceans (prawns, crabs and crayfish) were heavily reliant on periphyton. Of the 2,849 fish captured by the two methods, 408 were sampled for SIA, with a target of n = 3 per species per site and time. Of these, 281 had $PER_{consumer} > 0.50$. The contribution of periphyton was even more apparent in larger fish (>20 cm standard length); 86 of 103 fish had $PER_{consumer} > 0.50$ (Figure 2).

Biomass weighted source proportions indicated clear reliance on periphyton in the fish community (Table 3). Periphyton contributions ranged from a low of 42% to a high of 97% and only two of the sampling events yielded estimates of % periphyton less than 50%. There was no obvious change from the early to the late dry season, with three sites showing a decrease in % periphyton, and three sites showing an increase (Table 3).

Trophic level of consumers

Trophic levels of invertebrate secondary consumers ranged from 1.6 (Libellulidae) to 4.5 (Protoneuridae). Values lower than 2, particularly in known predators such as Libellulidae, likely reflect errors in baseline calculations and/or

differences in trophic fractionation among taxa. Periphyton-dependent taxa that were rare but made up a large proportion of the biomass in the early dry season (crabs and dytisicids) had relatively low TL (< 3.5). Those taxa that were not feeding on the periphyton pathway achieved high relative biomass (e.g. snails and Coenagrionidae), but they were feeding at low trophic levels (< 2.5).

Average trophic level of fishes across sites ranged from 2.8 (bony bream in the late dry season) to 4.3 (barramundi, fork-tailed catfish, and glassfish, Table 4). In general, TL was consistent with expectations based on prior gut content studies (Pusey *et al*., 2004), with top predators barramundi and fork-tailed catfish having highest TL and herbivorous fish (bony bream) having low TL (Table 4).

Of the fishes and large invertebrates captured in fyke nets, those occupying the highest trophic level and accounting for the most biomass had a diet derived primarily from the pathway originating with periphyton, particularly late in the dry season (Figure 3). Because barramundi were poorly captured in fyke nets (only four individuals during the entire study) despite being known to be present, we were unable to estimate the contribution of this species to total biomass relative to its trophic level and source of carbon (Figure 3). However, in the electrofishing survey, barramundi made up 25% of the fish biomass in the early dry season, and had average $PER_{consumer}$ = 0.75 and TL = 4.1. Likewise, in the late dry season electrofishing survey, barramundi made up 18% of the fish biomass, had average $PER_{consumer}$ = 0.99, and TL = 4.3. Thus barramundi are similar in terms of diet and biomass to fork-tailed catfish (Figure 3). Surprisingly, a large proportion of the fish biomass was at high TL (> 3.0).

Discussion

There is increasing evidence that, when it is available, periphyton is the primary source of carbon for secondary production in small lentic food webs ranging from the arctic to the tropics (Hecky and Hesslein, 1995; Bunn *et al*., 2003; Sierszen *et al*., 2003). When the benthos is not light-limited by canopy cover, dissolved humic substances, inorganic turbidity, or phytoplankton blooms, benthic primary production contributes strongly to food webs and can lead to high fish yields (Vadeboncoeur *et al*., 2003; Karlsson *et al*., 2009). Our analyses show that, similar to many isotopic tracer experiments, phytoplankton and detritus can support moderate invertebrate biomass at low trophic levels (Pace *et al*., 2004, 2007; Solomon *et al*., 2008), but large-bodied fishes at higher trophic levels are supported almost exclusively by carbon pathways originating with periphyton. These results mirror earlier observations in running waters that show terrestrial detritus can be important for invertebrates in river headwaters, but the production of fish biomass, which is far higher in lower reaches, is dependent on periphyton (Finlay, 2001).

Both light and nutrients can limit benthic algal productivity, and thus fish production, in these systems (Bunn *et al*., 2003). Cultural eutrophication can stimulate phytoplankton production at the expense of periphyton growth (Vadeboncoeur *et al*., 2001) with possible negative repercussions for food webs (Muller-Navarra *et al*., 2004). However, phytoplankton biomass in these waterholes is high but not excessive, with water column chlorophyll concentrations in the range 2.0 to 78.1 mg m^{-3}. As such, despite moderate turbidity (min = 1, max = 357 nTU), there was light available to the bottom at the majority of locations at all times (S.J. Faggotter, unpublished data), suggesting that most of the benthic substrate was available for periphyton production. In systems with high inorganic turbidity such as dryland river waterholes, food webs can be based instead on a narrow fringe of

periphyton that tracks dropping water levels as the dry season progresses (Bunn *et al*., 2003, 2006). While this narrow band of periphyton contributes to fish production, it likely cannot sustain a large biomass of fish for the entire dry season (Burford *et al*., 2008). Therefore, a large surface area available for benthic production under high light conditions, as was observed in the current study, is conducive to more viable fish populations in shallow lentic habitats (Karlsson *et al*., 2009).

Quantitative assessments of consumer biomass alongside isotope data provide far better resolution in understanding the origin of the carbon that dominates in food webs (Hall *et al*., 2001; Jennings *et al*., 2002; McNeely *et al*., 2007), as opposed to studies that focus on one or few particular taxa that may provide a biased view of the contribution of sources to biomass (e.g. Jardine *et al*., 2008; Leberfinger *et al*., 2011). In this study, it is clear that the consumer biomass caught in fyke nets was dominated by catfish (*Neoarius* spp.), sleepy cod (*Oxyeleotris lineolatus*) and barramundi (*Lates calcarifer*), with a substantial contribution of prawns (*Macrobrachium* spp.) early in the dry season. We did not estimate turnover of different biomass compartments, and small fishes and invertebrates likely had higher production to biomass ratios than larger fishes (Banse and Mosher, 1980; Jennings *et al*., 2001). A full assessment of these pathways would require a carbon budget for the system; this exercise in other tropical systems has revealed periphyton to be the main contributor to fish production (Lewis *et al*., 2001).

The lack of a strong periphyton signal in the invertebrate community despite it being present in fish is difficult to resolve. Only a few invertebrate taxa in our sample were heavily reliant on periphyton – Dytiscidae and Hydrophilidae beetles, backswimmers and crabs – all of which could be feeding on microinvertebrates that directly exploit periphyton but were not sampled in the current study. In small water

supply ditches for cattle that lack fish, crabs achieve high biomass (T.D. Jardine, pers. obs.), suggesting that they may be a preferred prey for fish when available and their consumption, coupled with a time lag in isotopic turnover of higher order predators (Hesslein et al. 1993), could explain the shift towards the periphyton signal by the high-biomass predatory fishes (sleepy cod and catfish) late in the dry season. Insects feeding on periphyton may turn over rapidly, either emerging from the system or being targeted by fish. Jones and Waldron (2003) found that when fish density was high, macroinvertebrate use of periphyton decreased in favour of phytoplankton. Such would be the case in this system, where fish are increasingly concentrated into a smaller volume of water as the dry season progresses, intensifying predation and causing invertebrates to seek refuge and consume less periphyton. A related explanation is that our sampling protocol favoured the collection of invertebrates that were more reliant on detritus because we sampled in leaf packs and root masses rather than exposed mud. To test this, we analysed samples that were collected from bare mud in and adjacent to exclosure cages (in Stanley waterhole as part of a separate study) that acted as refuges from predation. In all cases, invertebrates had a greater contribution from periphyton ($PER_{consumer}$) when they were collected from the cage area compared to the leaf packs (chironomids 0.64 versus 0.26; odonates 0.60 versus 0.32; snails 0.36 versus 0.13, trichopterans 0.84 versus 0.43), and the cage samples also included corixids that had $PER_{consumer} = 0.93$ and were not present in the leaf pack samples. These data suggest that we may have overestimated the importance of plankton and detritus in the diets of invertebrates from elsewhere in the river system.

A final possibility is that the periphyton isotope signal present in fishes was derived from the surrounding floodplain (Junk *et al*., 1989; Burford *et al*., 2008; Jardine *et al*., in review). In the adjacent Cooper Creek that has a similar

geomorphology to the Flinders but flows south to Lake Eyre rather than north to the Gulf of Carpentaria, Burford *et al*. (2008) estimated that 50% of the fish biomass in dry season waterholes came from the floodplain. In that study, there was a high correlation between dry season $\delta^{13}C$ and wet season $\delta^{13}C$ in all producer and consumer taxa, and periphyton and fishes were enriched in ^{13}C relative to other sources, similar to the current study. Periphyton on the Flinders floodplain, from sites located ~50-200 km downstream from where the current study was conducted, had $\delta^{13}C = -18.7 \pm 0.3‰$ S.D. (n = 8, T.D. Jardine, unpublished data), similar to our dry season periphyton. Thus the enriched ^{13}C signal in fishes may well come from floodplain production. While the Flinders typically does not flood for an extended period of time in a typical wet season, our sampling occurred in a year following a one in thirty year flood (Bureau of Meteorology, www.bom.gov.au/water). Fish may do the majority of their growing during the wet season when temperatures are high and food availability is at its peak (Bunn *et al*., 2006; Balcombe *et al*., 2007) and then retreat to the main river channel, reducing their activity during the dry season until the arrival of the next wet season. Floods in this system occur almost every year in association with monsoonal activity (Moliere *et al*., 2009), unlike the intermittent flood regime in other dryland rivers in Australia and elsewhere (Puckridge *et al*., 1998). In order to properly resolve whether fish are feeding and growing mostly in the wet season or the dry season, a rigorous determination of growth increments over an annual cycle is needed.

Unlike some temperate rivers and lakes (Finlay, 2001; Pace *et al*., 2004; Reid *et al*., 2008; Zeug and Winemiller, 2008), terrestrial C3 detritus did not contribute substantially to fish biomass in these tropical waterholes. Similarly, C4 plants contributed little to these food webs, not surprising given that none of these fishes is

known to feed directly on C4 plants (Pusey *et al*., 2004) and aquatic invertebrates have difficulty assimilating C4 plant material (Clapcott and Bunn, 2003), thus limiting its entry into aquatic food webs (Forsberg *et al*., 1993; Bunn *et al*., 1997). An alternative path for terrestrial carbon sources to enter fish tissue is via the consumption of terrestrial invertebrates that themselves feed on a mix of C3 and C4 grasses, such as grasshoppers (Fry *et al*., 1978). Terrestrial invertebrates, however, are rarely found in the stomach contents of the fish species in the current study (archerfish *Toxotes chatareus* are an exception), with a maximum contribution of 12% of total volume (Pusey *et al*., 2004, 2010; Davis *et al*., 2010), and our initial mixing model that included both C3 and C4 plants and accounted for mixtures of the two did not suggest they were important contributors to these food webs.

The planktonic pathway can support fisheries production in other large rivers (e.g. Orinoco, Hamilton et al. 1992; Amazon, Forsberg et al. 1993; Mississippi, Delong and Thorp 2006) but appeared less important in our study system. Plankton production may be an important food source for smaller fish and for larval development of species which recruit during low flows as reported in large intermittent rivers of southern Australia (Humphries *et al*., 1999), but the small body size and low number of fish that were feeding primarily on the planktonic or detrital carbon pathways contributed little to overall fish biomass. These include bony bream (6-9% of biomass, 25-29% derived from periphyton) that are known to feed opportunistically on periphyton when it is available but also switch to detritus under certain conditions (Sternberg *et al*., 2008). The limited phytoplankton contribution to fish biomass may be due to grazing-resistant phytoplankton communities, in particular cyanobacteria - which can dominate phytoplankton assemblages in tropical regions (Fabbro and Duivenvoorden, 1996; Soares *et al*., 2009). Cyanobacteria are poorly

consumed by zooplankton due to morphological and chemical adaptations which inhibit grazing (Reynolds, 1994), and their low production of essential fatty acids (Muller-Navarra *et al*., 2004) could limit the entry of this food source into higher trophic levels. However, microscopic examination of plankton samples revealed a mixed community of green algae, diatoms, euglenoids, and cyanobacteria (M.A. Burford, unpublished data). The lack of a plankton isotopic signal in the fish community may therefore in part be explained by an absence of strong grazing impacts by zooplankton, as reported for tropical and subtropical lentic waterbodies, where macrozooplankton body size tends to be smaller than in temperate systems (Timms and Morton, 1988; Havens *et al*., 1996; Hunt and Matveev, 2005), possibly mediated by the relatively high inorganic turbidity in these systems that limits feeding efficiency (Nurminen *et al*., 2010).

The findings of our study have implications for understanding top-down and bottom-up control in intermittent rivers and small lakes. Rather than the classic phytoplankton-zooplankton-fish food chain of temperate lakes (Carpenter *et al*., 1985), these systems instead have dual food chains and possibly subsidies from elsewhere (i.e. the floodplain), with larger predators connected almost exclusively to the benthic food web and very little phytoplankton and detrital carbon moving beyond trophic level 2 (primary consumers). As such, any factors that limit periphyton production will limit fish production (Karlsson *et al*., 2009) and top down control by fish is most likely to be expressed in the benthos rather than the water column.

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Table 1. Site characteristics of waterholes sampled for food webs in the Flinders River, Queensland, Australia.

Site	Latitude	Longitude	Time	Fyke nets	Electro fishing	Turbidity (NTU)	TP (mg/L)	TN (mg/L)	Phytoplankton chl *a* (mg/m^3)	Periphyton chl *a* (wood and rocks) (mg/m^2)	Periphyton chl *a* (mud) (mg/m^2)
Stanley	S 19.55	E 141.01	Early Dry	Y	Y	18	0.061	0.48	7.2 ± 0.7	9.9 ± 5.5	4.7 ± 2.9
			Late Dry	Y	Y	28	0.150	1.20	31.8 ± 2.1	20.1 ± 10.8	66.3 ± 41.7
Seaward	S 19.37	E 140.79	Early Dry	Y	Y	4	0.030	0.35	6.2 ± 0.8	3.3 ± 0.4	6.2 ± 6.3
			Late Dry	Y	Y	28	0.040	0.56	8.7 ± 1.3	7.4 ± 1.3	23.5 ± 30.1
Ten Mile	S 19.33	E 140.86	Early Dry	Y	N	21	0.047	0.46	11.1 ± 1.2	N/A	51.4 ± 43.4
			Late Dry	Y	Y	40	0.320	2.80	19.1 ± 3.8	19.0 ± 10.1	71.2 ± 75.3
Williams	S 18.99	E 140.60	Early Dry	Y	Y	22	0.065	0.44	12.8 ± 1.4	12.7 ± 2.0	11.1 ± 0.9
			Late Dry	Y	Y	12	0.069	1.00	26.5 ± 1.8	28.8 ± 3.0	35.0 ± 41.3
Off-channel	S 18.97	E 140.57	Early Dry	Y	N	168	0.140	0.64	5.1 ± 2.2	N/A	13.9 ± 2.9
			Late Dry	Y	N	357	0.440	3.00	78.1 ± 27.3	4.2 ± 0.3	15.5 ± 6.4
Walker's Bend	S 18.16	E 140.86	Early Dry	N	Y	7	0.043	0.34	5.9	10.7 ± 0.6	N/A
			Late Dry	N	Y	11	0.062	1.20	34.1 ± 2.0	24.9 ± 10.2	N/A
Rocky	S 20.24	E 141.85	Early Dry	N	Y	N/A	0.028	0.32	2.7 ± 1.4	6.9 ± 2.8	N/A
			Late Dry	N	Y	18	0.065	0.90	21.4 ± 4.7	14.0 ± 2.8	N/A

Table 2. Example of the calculations used to derive biomass-weighted contributions of food sources to consumers in waterholes of the Flinders River, Queensland, Australia. The proportion of consumer biomass derived from periphyton ($PER_{consumer}$) is calculated from a simple mixing model using $\delta^{13}C$ data of the consumer and two sources, periphyton and "other" (phytoplankton and detritus).

Site	Time	Taxa	# of individuals	$Biomass_{consumer}$ (g)	% of site biomass	$PER_{consumer}$	$Biomass_{periphyton}$ (g)
Stanley Waterhole	Early	Archerfish	5	32.6	1	1.16 ± 0.11	32.6 ± 3.6
		Black catfish	8	121.7	3	0.96 ± 0.04	116.8 ± 4.7
		Bony bream	10	201.3	4	0.48 ± 0.16	96.6 ± 15.5
		Fork-tailed catfish	8	148.8	3	1.02 ± 0.03	148.8 ± 4.5
		Giant ambassis	191	649.7	14	0.79 ± 0.20	513.3 ± 102.7
		Gulf grunter	2	20.0	0	1.19 ± 0.06	20.0 ± 1.2
		Hyrtl's tandan	10	85.2	2	1.10 ± 0.01	85.2 ± 0.9
		Rainbowfish	6	14.6	0	0.91 ± 0.08	13.3 ± 1.1
		Spangled perch	1	3.1	0	0.73 ± 0.06	2.3 ± 0.1
		Freshwater prawn	30	3213.3	71	0.79 ± 0.24	2538.5 ± 609.2
		Redclaw crayfish	2	64.2	1	0.93 ± 0.14	59.7 ± 8.4
		Sum		4554.5			3627.1 ± 751.7
		% $periphyton_{site}$		79.6 ± 16.5			

Table 3 Catch per unit effort and biomass-weighted source proportions (% periphyton$_{site}$ ± S.D.) for consumers in waterholes of the Flinders River, Queensland, Australia.

		Benthic invertebrates		Fishes and large crustaceans			
Site	Time	Biomass in 1 m sweep	% periphyton$_{site}$	Fyke net CPUE (g hr^{-1})	% periphyton$_{site}$	E-fishing CPUE (g hr^{-1})	% periphyton$_{site}$
Stanley	Early Dry	2126	26	130	80 ± 17	2340	85 ± 11
	Late Dry	3005	27	67	75 ± 12	12708	73 ± 7
Seaward	Early Dry	91	64	189	91 ± 16	1080	97 ± 9
	Late Dry	854	53	83	67 ± 4	3744	60 ± 8
Williams	Early Dry	917	43	399	65 ± 12	2844	69 ± 18
	Late Dry	501	34	119	63 ± 6	18396	61 ± 7
Ten Mile	Early Dry	915	57	22	53 ± 7	N/A[1]	71 ± 18
	Late Dry	306	30	155	88 ± 1	6660	73 ± 5
Off-channel	Early Dry	2648	100	80	66 ± 2	N/A[4]	N/A[4]
	Late Dry	N/A[2]	N/A[3]	15	N/A[3]	N/A[4]	N/A[4]
Walker's Bend	Early Dry	N/A	N/A	N/A	N/A	1476	55 ± 7
	Late Dry	N/A	N/A	N/A	N/A	5796	75 ± 14
Rocky	Early Dry	N/A	N/A	N/A	N/A	1656	42 ± 8
	Late Dry	N/A	N/A	N/A	N/A	6768	96 ± 22

[1]banks too steep to launch electrofishing boat; [2]too much organic detritus to effectively sort invertebrates and calculate biomass; [3]sources not sufficiently distinct to calculate % periphyton$_{site}$; [4]site was too shallow to electrofish with the boat

Table 4. Trophic level (± S.D.) of fishes in waterholes of the Flinders River, Queensland, Australia, derived from $\delta^{15}N$ data.

	Ten Mile Lagoon		Walker's Bend		Williams Lagoon		Off-channel		Rocky Waterhole		Stanley Waterhole		Seaward Lagoon			
Species	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early Mean	Late Mean
Glassfish (*Ambassis* sp.)										3.4 ± 0.4		3.8 ± 0.1			4.3 ± 0.2	3.7 ± 0.3
Archerfish (*Toxotes chatareus*)	4.2 ± 0.2		3.8 ± 0.1		3.8 ± 0.2	3.8 ± 0.2	4.3 ± 0.2		3.5 ± 0.2	4.2	4.2 ± 0.1	3.7	4.2 ± 0.1	4.1 ± 0.1	4.0 ± 0.3	4.0 ± 0.2
Barramundi (*Lates calcarifer*)	4.3 ± 0.4	4.6 ± 0.2	3.6 ± 0.1	4.1 ± 0.1	4.2 ± 0.4	4.2			4.2 ± 0.1	4.4 ± 0.2	4.2 ± 0.1	3.9 ± 0.1			4.1 ± 0.3	4.3 ± 0.3
Barred grunter (*Amniataba percoides*)					4.0	3.5			2.4 ± 0.2						2.8 ± 0.6	3.5
black catfish (*Neosilurus ater*)	3.8		3.6		3.9 ± 0.3						4.5 ± 0.1				4.2 ± 0.3	
bony bream (*Nematalosa erebi*)	3.6 ± 0.2	2.8 ± 0.0	2.8 ± 0.1	2.0 ± 0.1	2.9 ± 0.2	2.6 ± 0.5	3.3 ± 0.2	2.0 ± 1.2	1.9 ± 0.4	2.5 ± 0.0	3.4 ± 0.3	2.8 ± 0.2	3.8 ± 0.2	3.6 ± 0.2	3.2 ± 0.5	2.8 ± 0.6
eel-tailed catfish (*Neosilurus* spp.)									3.3 ± 0.4						3.3 ± 0.4	
fork-tailed catfish (*Neoarius* spp.)	4.1 ± 0.2	4.6 ± 0.1	3.9 ± 0.2	4.2 ± 0.4	4.0 ± 0.4	4.0 ± 0.0			3.8 ± 0.3	4.4 ± 0.2	4.3 ± 0.2	4.3	3.7 ± 0.2	4.5 ± 0.1	4.0 ± 0.3	4.3 ± 0.2

freshwater anchovy (*Thryssa scratchleyi*)						4.1 ± 0.1						4.0 ± 0.0				4.1 ± 0.1
freshwater sole (*Brachirus selheimi*)										3.6						3.6
giant ambassis (*Parambassis gulliveri*)	4.1 ± 0.2		3.3 ± 0.2		3.8 ± 0.2	3.5 ± 0.1	4.0 ± 0.1	3.3 ± 0.5	3.4 ± 0.2		4.3 ± 0.2	4.5	3.8 ± 0.3		3.8 ± 0.3	3.5 ± 0.5
giant gudgeon (*Oxyeleotris selheimi*)						3.7			4.2 ± 0.1						4.2 ± 0.1	3.7
Goby (*Glossogobius* spp.)			3.3 ± 0.1		4.2						4.3 ± 0.1		2.9 ± 1.4	3.8	3.5 ± 0.9	3.8
gulf grunter (*Scortum ogilbyi*)	3.8 ± 0.4	3.7 ± 0.3	3.2 ± 0.2	3.3 ± 0.5	3.1 ± 0.6	3.6 ± 0.2	3.8 ± 0.1	2.7	3.4 ± 0.2	3.3	3.2 ± 0.3	3.7 ± 0.4	4.0 ± 0.3	4.1 ± 0.2	3.5 ± 0.4	3.6 ± 0.4
hyrtl's tandan (*Neosilurus hyrtlii*)			2.9 ± 0.2		3.0 ± 0.6		4.0 ± 0.2	2.7 ± 0.7			3.7 ± 0.4		3.9 ± 0.1	4.2	3.5 ± 0.4	3.5 ± 0.8
Longtom (*Strongylura krefftii*)		4.0	3.8 ± 0.0		3.8										3.8 ± 0.0	4.0
Prawns (*Macrobrachium* spp.)	4.3 ± 0.0	3.9 ± 0.0		2.9 ± 0.2	4.1 ± 0.2	3.8 ± 0.1	3.9 ± 0.2		3.4 ± 0.2	3.2 ± 0.3	4.2 ± 0.1	3.6 ± 0.2	3.9 ± 0.2	3.8 ± 0.2	3.9 ± 0.3	3.6 ± 0.4

mouth almighty (*Glossamia aprion*)		3.1 ± 0.0		3.5		2.8 ± 0.0				3.4					3.1 ± 0.2
Rainbowfish (*Melanotaenia splendida*)	4.1 ± 0.1		3.4		3.6 ± 0.3		4.2 ± 0.1		3.4 ± 0.2		4.2 ± 0.2	3.7	4.0 ± 0.0	4.4 ± 0.1	3.9 ± 0.3	4.2 ± 0.2
Sawfish (*Pristis microdon*)				3.6												3.6
sleepy cod (*Oxyeleotris lineolatus*)	4.2 ± 0.1	4.3 ± 0.1	3.5 ± 0.2	3.5 ± 0.4	3.8 ± 0.1	4.2 ± 0.1	3.3 ± 1.3	3.1 ± 0.5	4.1 ± 0.2	3.7 ± 0.2	4.2 ± 0.5	4.1 ± 0.3	3.4	4.0 ± 0.3	3.9 ± 0.5	3.9 ± 0.4
spangled perch (*Leiopotherapon unicolor*)	3.4	4.1			3.7 ± 0.5	3.5 ± 0.3		2.5	2.7 ± 0.6	3.2	4.9 ± 0.2		3.9 ± 0.2	4.4 ± 0.2	4.0 ± 0.7	3.9 ± 0.5
toothless catfish (*Anodontiglanis dahli*)	3.9 ± 0.0		3.3 ± 0.3	3.3 ± 0.2	3.6 ± 0.2	3.7 ± 0.2	4.0 ± 0.1					3.8 ± 0.3	4.3 ± 0.1		3.8 ± 0.3	3.5 ± 0.3

Figure legends

Figure 1. Stable carbon isotope ratios ($\delta^{13}C$) of sources available to consumers in waterholes of the Flinders River, Queensland, Australia. Isotope ratios of phytoplankton were estimated by analysing zooplankton that are more easily isolated.

Figure 2. Fish $\delta^{13}C$ versus body size compared to $\delta^{13}C$ of available sources in waterholes of the Flinders River, Queensland, Australia.

Figure 3. Trophic level and $PER_{consumer}$ for invertebrates captured in sweep nets (open symbols) and fishes and large invertebrates captured in fyke nets (closed symbols) in the Flinders River, Queensland at the beginning of the dry season (A) and the end of the dry season (B). The size of the symbol is proportional to the biomass that the species represented in the catch, with separate calculations for the two collection methods.

Figure 1.

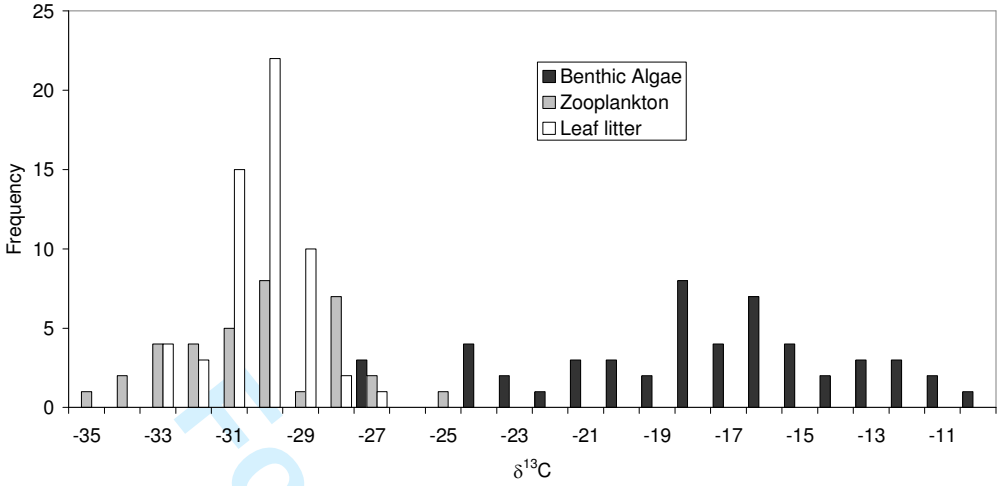

Figure 2.

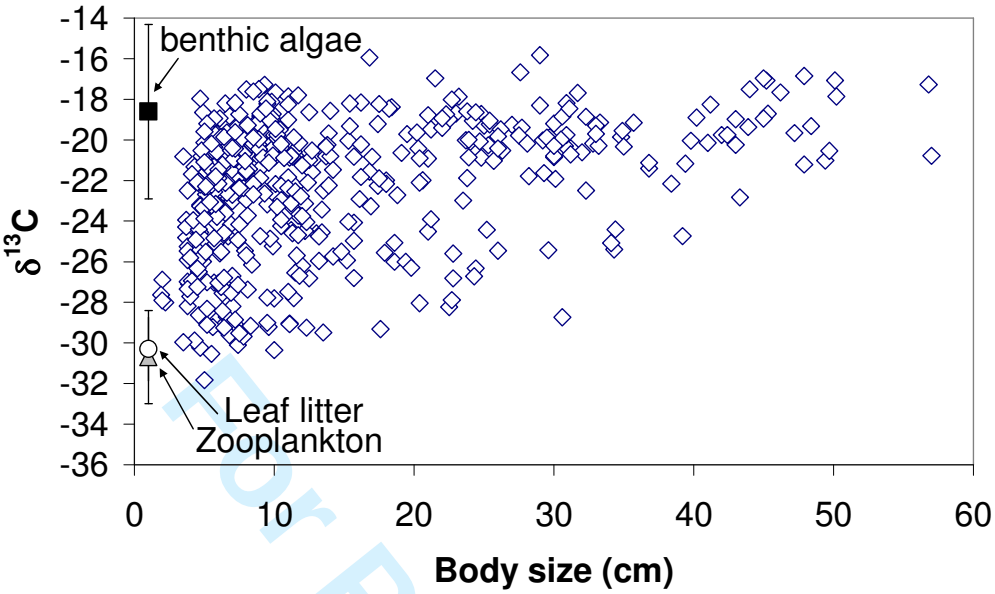

Figure 3.