Consumer–resource coupling in wet–dry tropical rivers

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Summary

1. Despite implications for top-down and bottom-up control and the stability of food webs, understanding the links between consumers and their diets remains difficult, particularly in remote tropical locations where food resources are usually abundant and variable and seasonal hydrology produces alternating patterns of connectivity and isolation.

2. We used a large scale survey of freshwater biota from 67 sites in three catchments (Daly River, Northern Territory; Fitzroy River, Western Australia; and the Mitchell River, Queensland) in Australia's wet–dry tropics and analysed stable isotopes of carbon ($\delta^{13}C$) to search for broad patterns in resource use by consumers in conjunction with known and measured indices of connectivity, the duration of floodplain inundation, and dietary choices (i.e. stomach contents of fish).

3. Regression analysis of biofilm $\delta^{13}C$ against consumer $\delta^{13}C$, as an indicator of reliance on local food sources (periphyton and detritus), varied depending on taxa and catchment.

4. The carbon isotope ratios of benthic invertebrates were tightly coupled to those of biofilm in all three catchments, suggesting assimilation of local resources by these largely nonmobile taxa.

5. Stable C isotope ratios of fish, however, were less well-linked to those of biofilm and varied by catchment according to hydrological connectivity; the perennially flowing Daly River with a long duration of floodplain inundation showed the least degree of coupling, the seasonally flowing Fitzroy River with an extremely short flood period showed the strongest coupling, and the Mitchell River was intermediate in connectivity, flood duration and consumer–resource coupling.

6. These findings highlight the high mobility of the fish community in these rivers, and how hydrological connectivity between habitats drives patterns of consumer–resource coupling.

Key-words: biofilm, energy sources, floodplain, food webs, gut contents, hydrology, stable isotope analysis

Introduction

Large, mobile consumers play important roles in aquatic food webs, conferring stability (McCann, Rasmussen & Umbanhowar 2005; Rooney *et al.* 2006) and exerting top-down control on their dietary resources (Power 1990; Taylor, Flecker & Hall 2006). However, few empirical data exist that examine the broad-scale conditions that enhance or hinder coupling between consumers and their resources. Seasonally available resource pulses in many environments are exploited by primary and secondary consumers but these pulses are often difficult to track because they can be transported away from their origin and transferred to higher trophic levels, often with time delays (Ostfeld & Keesing 2000). This is particularly true in rivers of the wet–dry tropics where annual

floods stimulate high rates of aquatic productivity in the wet season that may sustain consumers through the less-productive dry season (Junk, Bayley & Sparks 1989; Jardine *et al.* in press), and thereby weaken linkages between fish and their local food sources. Seasonal migrations of fishes in these wet–dry systems are known to influence food webs (Winemiller & Jepsen 1998), but we know little about when and where fish do most of their foraging and growth. Furthermore, the supplementation of riverine consumer diets with prey derived from other biomes (e.g. terrestrial, marine, floodplains) can sustain a higher biomass of predators than would be possible if feeding was concentrated on a single local resource (Moore *et al.* 2004). These fluxes therefore have tangible consequences for food web structure and function.

Many recent investigations in tropical and dryland systems have found that periphyton, despite forming an inconspicuous component of the total carbon biomass, is largely

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responsible for metazoan (i.e. fish) biomass (Lewis *et al.* 2001; Thorp & Delong 2002; Bunn, Davies & Winning 2003; Douglas, Bunn & Davies 2005), with detritus from terrestrial and aquatic vascular plants (C3 and especially C4) playing only a minor role (Forsberg *et al.* 1993; Bunn, Davies & Kellaway 1997; Lewis *et al.* 2001; Lau, Leung & Dudgeon 2009). Biofilms dominated by periphyton form the diet of many river fishes (Rasmussen 2010), producing strong coupling between consumers and their local resources (Taylor, Flecker & Hall 2006). However, two factors can lead to a de-coupling of these local resources (biofilm) from consumers: (i) consumer foraging in adjacent habitats (e.g. floodplains or other areas of the river network) and (ii) direct consumption of food sources that enter the local aquatic environment (e.g. riparian insects or migratory prey). In tropical rivers of northern Australia, lateral (river to floodplain and riparian zones) and longitudinal (upstream to downstream) hydrological connectivity remains intact, and strong seasonal hydrology likely results in considerable fluxes of organic matter across ecosystem boundaries (Douglas, Bunn & Davies 2005; Hamilton & Gehrke 2005; Warfe *et al.* 2011). Only by analysing relationships between consumers and their resources across a gradient of hydrological connectivity can the importance of these subsidies be determined (Polis, Anderson & Holt 1997).

In rivers, the analysis of stable carbon isotopes ($^{13}C/^{12}C$, or $\delta^{13}C$) is useful in determining broad-scale linkages between consumers and food resources. The gradient approach, wherein the $\delta^{13}C$ of a consumer collected from multiple locations is regressed against corresponding $\delta^{13}C$ of the benthos (Rasmussen, Trudeau & Morinville 2009; Rasmussen 2010), can reveal the importance of local sources to consumer growth. This is possible because terrestrial plants have little limitation on CO_2 supply and thus have consistent $\delta^{13}C$ fractionation relative to atmospheric CO_2, resulting in relatively constant $\delta^{13}C$ values ($-28 \pm 0.9‰$ SD for C3 plants, Finlay 2001; -13.5 ± 1.5 for C4 plants, O'Leary 1981). This contrasts to periphyton with $\delta^{13}C$ that can vary as a function of flow and productivity and commonly ranges from -40 to $-20‰$ (Finlay 2004). As such, the slope of a plot with periphyton $\delta^{13}C$ as the independent variable and consumer $\delta^{13}C$ as the dependent variable is a direct estimate of the proportion of locally produced periphyton in the diet of the consumer (Rasmussen 2010). Similarly, replacing periphyton $\delta^{13}C$ with biofilm $\delta^{13}C$ (representing a mixture of periphyton and detritus) in this regression yields an estimate of local feeding because movement by consumers throughout the river network results in a homogenising of $\delta^{13}C$ in the consumer to more closely match the average $\delta^{13}C$ of resources throughout its home range (Rasmussen, Trudeau & Morinville 2009). The gradient approach can therefore identify when consumers are strongly coupled to local sources and, when combined with complementary information about potential movement and preferred dietary items, can provide an integrative understanding of broad-scale fluxes of organic matter within rivers.

To assess patterns in the reliance of consumers on local vs. external carbon sources in wet–dry tropical rivers, we sampled food webs from 67 locations within three catchments in northern Australia and used a gradient approach relating the $\delta^{13}C$ of biofilm (dominated by periphyton) to $\delta^{13}C$ of consumers. To assess the importance of decoupling of consumers from local resources (biofilm) because of foraging in other locations, we analysed flood durations for the three catchments and combined those observations with known trends in flow regime (Kennard *et al.* 2010) to assess the potential for movement by fish as a function of hydrological connectivity. Finally, we examined the contributions of riparian insects and migrant prawns to diet from stomach content data from prior studies (Pusey, Kennard & Arthington 2004) in an attempt to isolate the effects of potential consumer movement from the effects of consumer foraging on prey from outside the local area. Consumption of these two external prey groups could dampen the consumer–biofilm $\delta^{13}C$ relationship and be misinterpreted as evidence of consumer movement.

We predicted that regression analysis of biofilm $\delta^{13}C$ and consumer $\delta^{13}C$ would be positive and strong in all cases, particularly in those locations where hydrological connectivity was low, because of limits on two mechanisms that rely on the movement of organic material: (i) the reduced ability of consumers to move throughout the river network in locations where hydrological connectivity may be reduced, for example, on floodplains that are annually inundated for a short duration and river channel habitats that become isolated during the dry season; (ii) reduced hydrological connectivity that limits the interaction between rivers and riparian zone vegetation (edge effects) leading to fewer riparian insects available for consumption by fishes. Both mechanisms would cause consumers to rely more extensively on local in-stream sources of carbon, strengthening important local interactions (Taylor, Flecker & Hall 2006).

Materials and methods

SITE SELECTION AND FLOODPLAIN MAPPING

Sampling was conducted at 67 sites across three large catchments in northern Australia's wet–dry tropics: the Daly River (Northern Territory), the Fitzroy River (Western Australia) and the Mitchell River (Queensland; Table S1). The climate across the study region is monsoonal with high rainfall, peak discharge and flooding occurring principally in the summer months (November to April; Warfe *et al.* 2011). All three catchments were sampled in the early dry season 2008: May and June for the Mitchell, June for the Daly and July for the Fitzroy. The number of sites sampled in each catchment (27 in the Daly, 21 in the Mitchell, and 19 in the Fitzroy) largely reflected accessibility and the remote nature of sites, northern Australia being a region of relatively low human population (1 person per 2.5 km^2, Warfe *et al.* 2011). The three catchments differ in their degree of hydrological connectivity (Kennard *et al.* 2010). The Daly River, because of groundwater inputs from various aquifers (Tindall, Oolloo, and Jindukin), has a relatively high summer baseflow and thus many of the sampled sites remain connected to one another by

perennial flow throughout the year (class 3, Kennard *et al.* 2010). The Fitzroy River, by contrast, lacks significant groundwater inputs and is far more intermittent during the dry season. Most sites in the Fitzroy were located in streams or reaches classified as predictable summer highly intermittent (class 10, Kennard *et al.* 2010). The Mitchell River is intermediate in flow characteristics, with sites located in a mix of permanent and intermittent reaches both in its headwaters and in main channel reaches; some classed as 'stable summer baseflow' (class 3) and others as 'predictable summer highly intermittent' (class 10, Kennard *et al.* 2010). While each catchment could be broadly categorised in each flow class, there was still some variation in flow regime among sites within each catchment. Sites characterised as flow classes 3 and 10, and also 12 ('extreme harsh summer intermittent', which are those with very short periods of flow; Kennard *et al.* 2010), were sampled in each catchment.

To determine whether floodplain inundation patterns were consistent with in-channel observations of connectivity (Kennard *et al.* 2010), we determined the length and extent of floodplain inundation in each catchment in the wet season prior to sampling, i.e. the 2007–2008 summer. River gauge data are commonly used to understand the seasonal hydrological cycle and flood inundation patterns. However, because of factors such as the occurrence of significant flows in ungauged distributary channels during floods (e.g. in the Mitchell), and large areas of slowly draining floodplain (e.g. in the Daly), main channel river gauge data may misrepresent floodplain inundation, extent and duration. To determine whether floodplain inundation patterns reflected the river flow regime classifications, a series of largely cloud-free MODIS satellite imagery was 'captured' for each catchment floodplain inundation phase (mostly on the receding limb of the hydrograph because of the limitations of wet season cloud cover). The Daly imagery also included some Landsat-derived data that were re-sampled to the resolution of the MODIS imagery after flood classification.

MODIS wet season flood image captures were made for the Mitchell in 2003, 2004, 2008 and 2009, in the Daly for 2004, 2005, 2008 and 2009, and in the Fitzroy for 2001, 2002, 2007 and 2009. Image classification methods (D.P. Ward, unpublished data) were applied to delineate flood extent for each image capture. Occlusion of flood water by dense, standing woody vegetation was accounted for during the image classification process and labelled as 'unknown flood inundation'. For both the Mitchell and the Daly, areas of dense, standing woody vegetation were identified using Landsat-based foliage projective cover (Armston, Danaher & Collett 2004) for the Mitchell, and ALOS PALSAR data for the Daly. The Mitchell floodplain is largely an open savannah landscape with very little area of foliage projective cover > > 30%; this cover occurs as narrow fringing vegetation along the margins of the main channels. Consequently, the flooded area will be slightly underestimated. The Daly floodplain comprises large areas of open grassland/sedges with dense, standing woody vegetation on the margins of the main channels. These areas of dense vegetation on the channel margins are more extensive than on the Mitchell system and consequently the flood area will be underestimated for the Daly, particularly during the early stages of the flood. The Fitzroy is a very open savannah landscape and therefore no correction for the influence of vegetation was necessary. For each catchment floodplain, inundation frequency was calculated by overlaying the flood image captures and calculating the frequency of occurrence of flooding for each flooded pixel across all years.

To estimate the duration of inundation, we determined the maximum extent of inundation for flood events occurring in the 2007–2008 wet seasons. Using images captured before and after the flood peak, we expressed the areal extent of the remaining floodwaters as a per cent of the maximum flood achieved and plotted this against time. Flood images were captured for the Daly on the 2 February, 23 March, 8 April, 20 May and 20 June (2008), with the largest areal extent occurring on the 23 March. For the Mitchell, images were captured on the 8, 11, 18 and 22 of March and 19 April (2008), with the largest areal extent of flooding occurring on the 11 March. Because of consistent cloud cover over the Fitzroy during the whole of the 2008 wet season, no flood imagery could be captured for that year. For comparative purposes, we analysed a Fitzroy flood series for 2007 when images were available. Monthly mean discharges for the Fitzroy were similar in magnitude for 2007 and 2008, except that the 2007 flood peaked in April and the 2008 flood peaked in March. For the Fitzroy flood series from 2007, images were captured on the 1, 4, 7, 11 and 14 April.

STOMACH CONTENT DATA

To determine fish stomach contents, we relied heavily on prior published work, most notably Pusey, Kennard & Arthington (2004) who compiled diet data for most of the taxa studied here. Supplementary unpublished data were obtained from recent studies on terapontid grunters (Davis *et al.* 2010). We focused on two dietary categories for stomach contents: (i) mean contribution of terrestrial prey items and (ii) mean contribution of prawns Palaemonidae. We restricted our summation of data to those species for which we had isotope data and only those from the study catchments.

STABLE ISOTOPE DATA

For the isotopic data, sites were selected to cover the spatial extent of each catchment as much as possible and included tributaries (< 11 000 km² catchment area and < 50 m active channel width), off-channel waterholes or billabongs, and larger, flowing main river channels (> > 11 000 km² catchment area and > > 50 m active channel width). More tributaries than main channel or floodplain waterhole sites were sampled as they were more common across the landscape. An attempt was made to sample all available sources and consumers at each location. However, the large scale of the survey, the distance between sites and remoteness of terrain meant that only a limited time was able to be spent at each location, so collections are considered representative but not exhaustive. Consumers included fish, benthic insects, prawns, shrimps, crayfish and molluscs. Backpack and boat-mounted electrofishing units were used to capture fish, and a combination of dip netting and baited traps was used to collect invertebrates. Zooplankton were collected by conducting 200 m subsurface tows with a 150 μm net; of the 67 sites, only 20 (12 off-channel waterholes and 8 main channel sites) yielded zooplankton samples. Primary sources included plant material from within and outside the waterbody. Decaying leaf material (cleaned of epiphytic biofilm), grasses and emergent and floating macrophytes represented terrestrial production because they obtain CO_2 from the air, while aquatic sources included submerged macrophytes, charophytes, filamentous algae and biofilm. Biofilm was scrubbed from submerged surfaces (mainly slippery rocks) and contains *c.* 30% detritus (Rasmussen 2010); we used two methods to reduce the proportion of detritus in the sample and obtain as pure a periphyton sample as possible. The first was to rinse the material into a 1 L measuring cylinder and allow it to stand undisturbed for at least 20 min. This allowed detritus and sediments to settle out, and the top fraction, usually greenish in colour, was extracted and filtered. The second method was a density fractionation in colloidal silica, spinning the sample to separate the bulk slurry into light (algae) and heavy (detritus) frac-

tions (Hamilton, Sippel & Bunn 2005). For our analyses, we used biofilm as our representative of local sources available to consumers because filamentous algae at these sites tended to occur in dense mats in backwaters and these and other less-palatable sources (macrophytes and charophytes) are less likely to enter food webs. The $\delta^{13}C$ of aquatic sources were highly and positively correlated (e.g. filamentous algae vs. biofilm, $r = 0.72$) so the relationships with consumers were similar regardless of which algal source was used. Furthermore, zooplankton (as a proxy for phytoplankton) were not considered in these regressions because most sites (47 of 67) were wadeable streams or fast-flowing rivers. Thus, they did not support appreciable quantities of phytoplankton, further evidenced by water column chl *a* concentrations < 4 mg L^{-1} (Webster *et al.* 2005; Townsend, Webster & Schult 2011, T.D. Jardine, unpublished data).

Samples were dried at 60 °C for 2 days, ground to a fine powder and weighed to approximately 0·8 and 3 mg for animals and plants, respectively. Samples were then combusted in an EA 3000 elemental analyser (Eurovector, Milan, Italy) and sample gases 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 that of 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 unicolor*) and plant (water lily, *Nymphaea* sp.) tissues analysed repeatedly to measure precision over time yielded $\delta^{13}C = -21.9 \pm 0.2$‰ SD and $\delta^{15}N = 5.5 \pm 0.4$‰ SD ($n = 29$) for the fish sample, and $\delta^{13}C = -26.1 \pm 0.1$‰ SD and $\delta^{15}N = 1.2 \pm 0.4$‰ SD ($n = 4$) for the plant sample. The average difference between duplicate samples within runs was 0·3‰ for C and 0·4‰ for N ($n = 97$).

In all cases, data were grouped as mean values for individual sites for a given taxon. In the Mitchell River, this mean value was obtained by analysing up to three replicates of a taxon within a site, while in the Daly and Fitzroy Rivers, mean values were obtained by pooling multiple individuals prior to laboratory analysis. For simplification, we grouped taxa that were closely related (within the same Order) and had high $\delta^{13}C$ correlations. This included baetid and caenid mayflies ($r = 0.97$, grouped as Ephemeroptera for further analyses), dragonflies and damselflies ($r = 0.90$, grouped as Odonata), and cased and filtering caddisflies ($r = 0.87$, grouped as Trichoptera).

We used the regression slopes of consumer $\delta^{13}C$ vs. biofilm $\delta^{13}C$ as an indicator of reliance on local resources (Rasmussen 2010). Given the known temporal variation in $\delta^{13}C$ of periphyton in streams and rivers (McCutchan & Lewis 2002; Hadwen, Spears & Kennard 2010), biofilm $\delta^{13}C$ measured at a single time may not be representative of the mean value experienced by the fish. However, the gradient approach expresses this seasonal variability as error in the biofilm vs. consumer $\delta^{13}C$ relationship, resulting in r values that are often low despite high slopes. Using NCSS software (Kaysville, UT, USA), 95% confidence intervals around ordinary least squares (OLS) regression slopes were used to determine whether they were different from zero and/or one. This created four different scenarios for each taxon (Fig. 1). If the slope was significantly different from zero but not different from one, a strong reliance on local sources was implied (Rasmussen 2010). If the slope differed from both zero and one, biofilm was considered important but other sources also contributed (i.e. a mixture between 0% and 100%). If the slope differed from one but not zero, the animal was clearly not feeding on local biofilm-derived sources, instead it was feeding in other areas of the river network or on other available resources (e.g. terrestrial insects, migratory prawns). If the slope was not different from one or zero, the diet was entirely unresolved, similar to mixing models with no
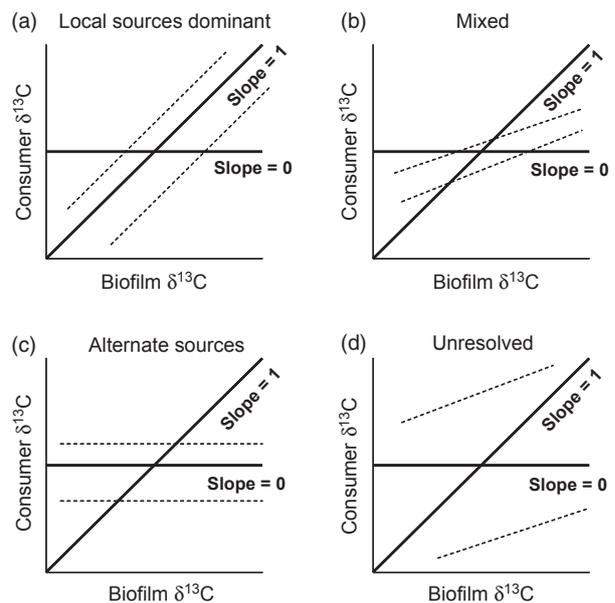

Fig. 1. Consumer-resource coupling scenarios for rivers (a - strong consumer connection to local sources; b - mix of local and alternative sources in consumer diet; c - alternative sources dominate consumer diet; d - unresolved diet) created by testing regression slopes of consumer $\delta^{13}C$ versus biofilm $\delta^{13}C$ against zero and one. Dashed lines show 95% confidence intervals in each scenario.

solution (Phillips & Gregg 2003). For these analyses, because *x* and *y* are both measured with error and OLS regression underestimates slopes, we also calculated slopes using reduced major axis regression (Slope$_{RMA}$) according to the formula Slope$_{RMA} = s_y/s_x$ where s_y and s_x are standard deviations of *y* and *x*, respectively. Patterns across catchments were similar whether RMA or OLS slopes were calculated; for example, the four most common species (spangled perch, rainbowfish, bony bream and hyrtl's tandan) had slopes that ranked Daly < Mitchell < Fitzroy for both OLS and RMA slopes, average OLS slopes for the four species were 0·16 for the Daly River, 0·41 for the Mitchell River and 0·97 for the Fitzroy River, and average RMA slopes were 0·51 for the Daly River, 0·63 for the Mitchell River and 1·48 for the Fitzroy River. We chose to report here OLS slopes because they provided more feasible values of slopes between 0 and 1 (RMA slopes were often > >1) and our method of using statistical significance as a criterion for assigning each taxa to a scenario (Fig. 1) accounted for those species that had low r (and thus underestimated slopes) by classing them as unresolved.

Results

FLOODPLAIN MAPPING

Sixteen flood images were captured for the Daly River (Fig. 2a) with the largest areal extent of flooding occurring between February and March. On the Daly floodplain, floods recede to large wetlands by approximately June and then to perennial waterholes by August. For the Mitchell River, 12 flood images were captured (Fig. 2b) and showed the majority of the flooding receding by the end of March with areas of surface flood water remaining only on the lower coastal floodplain by April for all years. The characteristics of the flood recession for the Mitchell reflected the distribu-
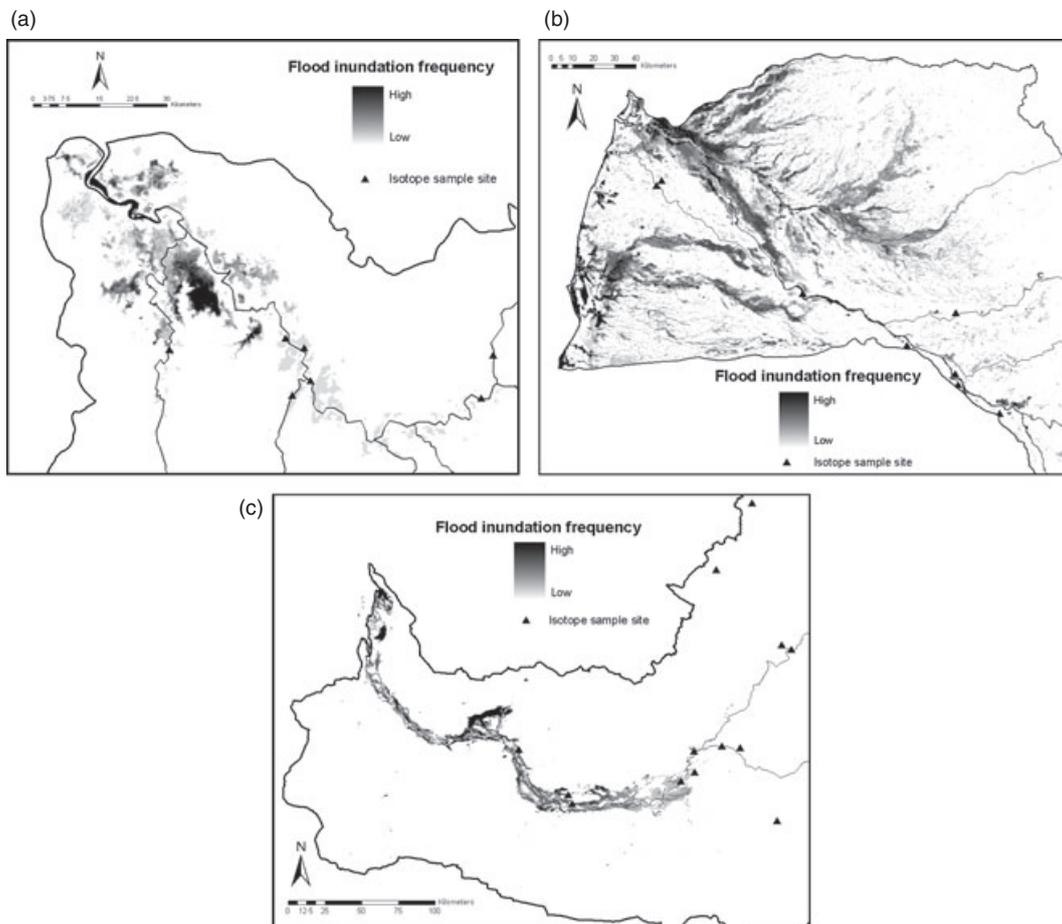
Fig. 2. Flood inundation frequency maps of the Daly River (a), Mitchell River (b) and Fitzroy River (c) of northern Australia, representing a gradient of floodplain inundation duration from long (Daly) to short (Fitzroy). Sampling sites for stable isotopes within the floodplain region are indicated for each catchment.

tary nature of the mega-fan floodplain with flood water receding from the apex of the mega-fan. For the Fitzroy, 13 flood images were captured (Fig. 2c). Floods on the Fitzroy are of very short duration with all captured flood image series lasting < 3 weeks. All flood image captures for the Fitzroy were captured on the receding limb of the hydrograph at the end of the wet season so it is likely that the Fitzroy may experience a number of short duration flood events over a single wet season. The underestimation of flood extent by standing woody vegetation canopies, assessed using Landsat and ALOS PALSAR data, is limited largely to fringing vegetation on the main channels for the Mitchell, Fitzroy and Daly and is most significant on the Daly.

Consistent with expected patterns of connectivity based on in-channel gauges (Kennard *et al.* 2010), the three catchments differed in their duration of floodplain inundation. While the area of floodplain that was inundated in the 2008 event was smaller in the Daly, the duration of inundation in the Daly was longer than the Mitchell, lasting *c.* 4 months compared to only 2 months for the Mitchell (Fig. 3). The Fitzroy River had the shortest floodplain inundation duration, lasting only 3 weeks (Fig. 3), reflecting the Fitzroy's highly intermittent flow classification.
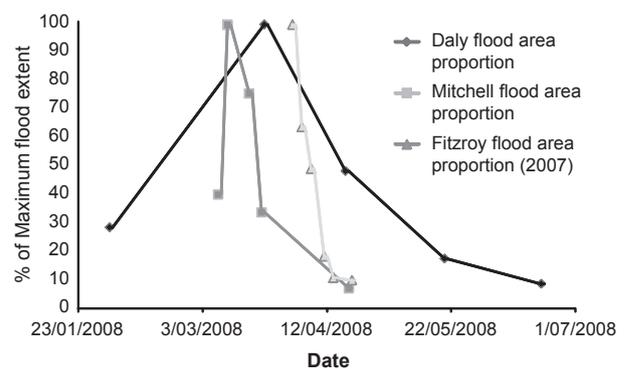

Fig. 3. Per cent of maximum flood extent vs. time for the Daly, Mitchell (2008 wet season) and Fitzroy (2007 wet season) Rivers in northern Australia.

STOMACH CONTENT DATA

Terrestrial insects made only minor contributions to the diet of fishes sampled in this study (Table 1), contributing 12·3% of the diet of rainbowfish (*Melanotaenia splendida*) and 41·3% of archerfish (*Toxotes chatareus*). Terrestrial insects were present in the diet of many other species but rarely

Table 1. Contribution of two external sources of organic matter, terrestrial insects and migratory prawns (Palaemonidae) to the diet of common fish species occurring in northern Australian rivers is analysed in this study

Species	River	Sampling time	% terrestrial insects	% Palaemonidae	Reference
Spangled perch (*Leiopotherapon unicolor*)	Daly River	Early dry	2·6	44·4	Davis *et al.* 2010
		Late dry	7·7	46·6	
Butler's grunter (*Syncomistes butleri*)	Daly River	Early dry	0·0	0	
		Late dry	0·0	0	
Sooty grunter (*Hephaestus fuliginosus*)	Daly River	Early dry	0·5	45·2	
		Late dry	1·1	57·6	
Barred grunter (*Amniataba percoides*)	Daly River	Early dry	0·1	9·0	
		Late dry	0·0	2·8	
Bony bream (*Nematalosa erebi*)	Northern Australia[a]	Dry[b]	1·0	0	Pusey, Kennard &
Rainbowfish (*Melanotaenia splendida*)	Northern Australia	Dry	12·3	1·0	Arthington (2004)
Hyrtl's catfish (*Neosilurus hyrtlii*)	Northern Australia	Dry	1·0	13·7	
Goby (*Glossogobius aureus*)	Northern Australia	Dry	0	6·0	
Mouth almighty (*Glossamia aprion*)	Northern Australia	Dry	1·2	18·8	
Sleepy cod (*Oxyeleotris lineolatus*)[c]	Northern Australia	Dry	1·6	12·4	
Long tom (*Strongylura krefftii*)	Northern Australia	Dry	1·0	3·0	
Archerfish (*Toxotes chatareus*)	Northern Australia	Dry	41·3	1·3	
Trout gudgeon (*Mogurnda mogurnda*)	Northern Australia	Dry	2·4	2·9	
Barramundi (*Lates calcarifer*) (adult)	Northern Australia	Year-round[d]	< 1	32·5[e]	

Data were sourced from Davis *et al.* (2010) for four species occurring in the Daly River and Pusey, Kennard & Arthington (2004) for the remainder. [a]The latter source summarised dietary information from a range of rivers across northern Australia. Dietary information for species in the Daly River are presented for both the early and late dry season, elsewhere information is derived from samples collected mainly during the [b]dry season or [c]over both wet and dry seasons. [d]Information provided for *Oxyeleotris lineolatus* was based on samples also containing *O. selheimi*. [e]The contribution of paleomonid prawns to the diet of *Lates calcarifer* also contains some contribution by penaid prawns.

exceeded 3% of the total. Palaemonid prawns occurred in the diet of all but two species for which data were available and were important (> >10%) in six of the 13 species and exceeded 30% contribution in three. Prawns featured prominently in the diet of species with large mouth gapes (e.g. mouth almighty, *Glossamia aprion*) or large body size (e.g. spangled perch, *Leiopotherapon unicolor*; sooty grunter, *Hephaestus fuliginosus*; hyrtl's tandan, *Neosilurus hyrtlii*; sleepy cod, *Oxyeleotris lineolatus* and barramundi, *Lates calcarifer*).

STABLE ISOTOPE DATA

Based on the gradient approach using $\delta^{13}C$, benthic invertebrates (insects, snails) had strong links to local biofilm (Fig. 4). Across all catchments, the three most common taxa were reliant on the biofilm organic matter as they had slopes that did not differ significantly from one (Ephemeroptera slope = 1·10, r = 0·73; Trichoptera slope = 0·87, r = 0·66; Odonata slope = 0·97, r = 0·75; Table 2). For these three taxa, slopes were higher in waterholes (Ephemeroptera = 1·50, Trichoptera = 1·49, Odonata = 1·34) and main channels (Ephemeroptera = 1·42, Trichoptera = 1·02, Odonata = 1·13) than in tributaries (Ephemeroptera = 0·76, Trichoptera = 0·48, Odonata = 0·66), but there was overlap in confidence intervals among the three habitat types. The lowest value across catchments and habitat types, 0·49 for water scorpions (Nepidae), suggested a mixture of local biofilm and other source pathways; this slope was significantly different from 0 and 1. Within catchments, trends were similar. In the Daly River, four taxa (Ephemeroptera,

Odonata, Pyralidae and Viviparidae) were heavily reliant on the biofilm pathway with slopes that were significantly different from zero but not one, two taxa (Trichoptera and Coleoptera) had a mixture of biofilm and other source pathways and three taxa (Tipulidae, Nepidae and Simuliidae) had unresolved sources, likely due to small sample sizes. In the Mitchell River, the three common taxa (Ephemeroptera, Trichoptera and Odonata) all were strongly reliant on the biofilm pathway with regression slopes significantly different from zero but not one (Table 2). In the Fitzroy River, the three common taxa as well as Coleoptera were tightly linked to biofilm with slopes significantly different than zero but not one, while three taxa (Tipulidae, Nepidae and Viviparidae) had unresolved source pathways even though regression slopes were > >0·50 (Table 2).

For crustaceans, patterns in consumer–resource coupling differed among catchments. In the Daly and Mitchell Rivers, palaemonid prawns were not deriving their carbon biomass from a local biofilm pathway, with slopes that were not significantly different from zero but significantly different from one (Table 2). In the Fitzroy River, however, prawns were strongly aligned with biofilm, with a slope significantly different from zero but not one (Table 2).

Unlike benthic insects and snails, but similar to the crustaceans, the connection of fish to local biofilm varied considerably across the three catchments. In the Daly River, slopes of fish-biofilm $\delta^{13}C$ regressions were generally low (average slope = 0·13, r = 0·18; Fig. 5). Of the 18 species for which we had sufficient data, only two (bony bream and hardyhead) had slopes that were significantly different than zero, with only hardyhead reliant solely on a biofilm carbon pathway
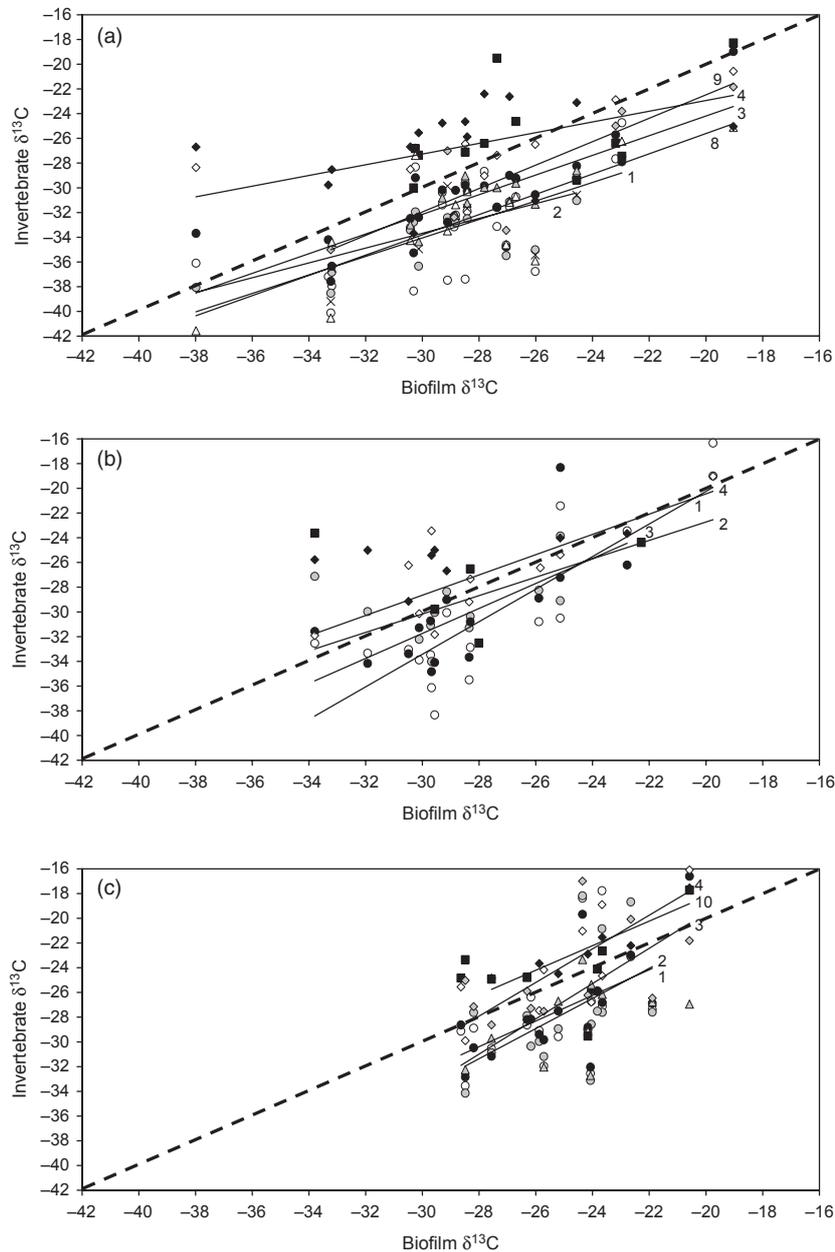
Fig. 4. Site-specific $\delta^{13}C$ of invertebrates vs. $\delta^{13}C$ of biofilm from three rivers in the wet–dry tropics of northern Australia – the Daly River (a), Mitchell River (b) and Fitzroy River (c). Open circles, mayfly larvae; solid circles, odonate larvae; shaded circles, caddisfly larvae; open diamonds, beetles; solid diamonds, prawns; shaded diamonds, snails; open triangles, aquatic moth larvae; shaded triangles, cranefly larvae; solid squares, water scorpions; X, blackfly larvae. Best-fit lines are shown for regression slopes significantly different from zero, with numbers that correspond to taxa in Table 2.

(slope significantly different from zero but not significantly different from one, Table 3). By contrast, slopes of fish-biofilm regressions in the Fitzroy River were high (average = 1·06, r = 0·72; Fig. 5), with all eight species having slopes not significantly different from one, and five of these (spangled perch, rainbowfish, giant cod, mouth almighty and glassfish) reliant on the biofilm pathway, with slopes also significantly different from zero (Table 3). In the Mitchell River, slopes were moderate (average = 0·42, r = 0·65; Fig. 5), two of seven species (rainbowfish and barred grunter) were reliant on the biofilm energy pathway with slopes significantly different from zero but not one and three of the seven species (spangled perch, hyrtl's tandan and sooty grunter) with slopes different from one but not zero and therefore not likely to have diets originating from biofilm (Table 3).

Discussion

Stable carbon isotope analyses, conducted on samples collected from a broad range of sites across tropical northern Australia, revealed varying degree of reliance on local resources by the fish community. Benthic invertebrates were strongly coupled to local resources (particularly in main river channels and waterholes), but in many cases, fishes had $\delta^{13}C$ values that were poorly correlated with that of local biofilm, suggesting the assimilation of organic matter from other source pathways. This was contrary to expectations based on earlier isotopic work in tropical systems where a local periphyton signal in fishes is common (Lewis *et al.* 2001; Lau, Leung & Dudgeon 2009). It may explain, however, how high levels of biodiversity and fish biomass can be supported in

Table 2. Slopes and correlation coefficients for $\delta^{13}C$ in biofilm vs. $\delta^{13}C$ in invertebrates from three tropical rivers of northern Australia, sampled early in the dry season

Taxa	Daly River Slope	r	n	Mitchell River Slope	r	n	Fitzroy River Slope	r	n	All rivers Slope	r	n
Insects												
1 – Ephemeroptera (mayfly larvae)	0·75[a]	0·64	23	1·32[a]	0·81	15	1·04[a]	0·49	18	1·10[a]	0·73	56
2 – Trichoptera (caddisfly larvae)	0·60[b]	0·67	18	0·74[a]	0·68	13	1·22[a]	0·50	17	0·87[a]	0·66	50
3 – Odonata (dragonfly, damselfly larvae)	0·80[a]	0·81	24	1·01[a]	0·68	14	1·43[a]	0·66	19	0·97[a]	0·75	57
4 – Coleoptera (beetles)	0·43[b]	0·80	8	0·82[a]	0·79	10	1·36[a]	0·78	9	0·72[b]	0·75	27
5 – Nepidae (water scorpions)	0·49[d]	0·48	12	−0·02[d]	0·02	5	0·52[d]	0·45	8	0·44[b]	0·42	24
6 – Tipulidae (cranefly larvae)	0·35[d]	0·31	13				0·73[d]	0·49	12	0·65[a]	0·60	25
7 – Simuliidae (blackfly larvae)	0·69[d]	0·67	7							0·86[a]	0·81	11
8 – Pyralidae (aquatic moth larvae)	0·82[a]	0·78	14							0·84[a]	0·73	16
Molluscs												
9 – Viviparidae (snails)	0·95[a]	0·87	7				0·85[d]	0·49	12	1·00[a]	0·68	19
Crustaceans												
10 – Palaemonidae (prawns)	0·21[c]	0·29	19	0·25[c]	0·52	8	1·00[a]	0·91	7	0·39[b]	0·53	34
11 – Atyidae (shrimps)										0·49[b]	0·65	11

Superscripts correspond to scenarios in Fig. 1 (a, local biofilm dominant; b, mixed; c, alternate sources; d, unresolved) and denote whether slopes were significantly different ($P < 0.05$) from 0 and 1.

these systems when rates of local aquatic primary production are low (rates of gross primary productivity < 5 mg O_2 m^{-2} day^{-1}; Bunn *et al.* 2005; Webster *et al.* 2005). In these northern Australian systems, large mobile consumers appear to couple two or more sources of energy that turn over at different rates and are available at different times of the year (Jardine *et al.* in press), a feature that may be generally applicable to aquatic food webs (Rooney *et al.* 2006).

Our indices of floodplain inundation duration confirmed previous flow classifications based on analysis of in-channel gauges (Kennard *et al.* 2010) and are consistent with a greater role for floodplain production and contribution to food webs in those systems with longer duration floods, in line with the observations from floodplain fisheries around the tropics (Bayley 1991; Lae 1995; De Graaf 2003; Welcomme & Halls 2003). In systems such as the Daly River, with a lateral drawdown of water from the peripheral floodplain into a large central basin that remains connected to a series of tributaries for almost 6 months, consumers are more likely to exploit resources in the centralised waterbody and export it to tributaries and the main channel for the remainder of the year (Winemiller & Kelso-Winemiller 1994; Jardine *et al.* in press). In systems such as the Fitzroy, where a pulse of water quickly moves down the river, briefly connecting adjacent habitats but failing to sustain large ephemeral wetlands, consumers are more likely to be restricted in their movement to and from refugia and more reliant on local sources of production. The Mitchell, meanwhile, has an intermediate flood duration, the main channel breaking out into two main distributaries at the apex of the floodplain fan at peak discharge but maintaining a series of wetlands that stay connected to the main channel for more than 1 month. A more quantitative definition of aquatic connectivity in these landscapes would be useful in creating metrics to predict organic matter production and flux, the importance of seasonally inundated areas, and the likelihood of consumer–resource

coupling at any point in the catchment (Junk, Bayley & Sparks 1989).

The few data on movement rates of fishes in these wet–dry tropical systems in Australia (Bishop, Pidgeon & Walden 1995) suggest that annual migrations, coincident with the onset of flooding, from refugial headwater streams to downstream reaches and billabongs and seasonally inundated floodplains are conceivable (Warfe *et al.* 2011). Spangled perch, rainbowfish, ambassids, barred grunter and sooty grunter have movement rates that range from 5 to 9 km day^{-1} (Bishop, Pidgeon & Walden 1995). These rates would allow a fish to effectively transit the entire length of the main channel in a matter of a few months, particularly if their downstream movements were timed to coincide with peak flooding (Barthem & Goulding 1997). Many of the juveniles in the terapontid and plotosid families inhabit tributary systems and move back into large channels as they age, while others maintain positions in main channel riffles. Less is known about lateral and longitudinal wet season movements, but recent surveys with directional fyke nets suggest that these movements can be considerable (D.M. Warfe, unpublished data). In other floodplain systems such as the Amazon and Orinoco Rivers in South America, prochilodontids make extensive seasonal migrations for feeding and spawning (Winemiller & Jepsen 1998), supplementing the diet of predators and themselves exhibiting top-down control on benthic resources (Taylor, Flecker & Hall 2006). The best analogue to this family in northern Australian rivers is the bony bream (*Nematalosa* spp.), a species that feeds year round on algae and detritus (Sternberg *et al.* 2008) and does the majority of its growing in the dry season but then makes forays on to seasonally inundated floodplain where it feeds and reproduces (Jardine *et al.* in press). Despite this migratory behaviour, bony bream in the current study still had a $\delta^{13}C$ consumer–biofilm slope that was significantly different from zero when all sites were combined, suggesting local foraging. Regres-
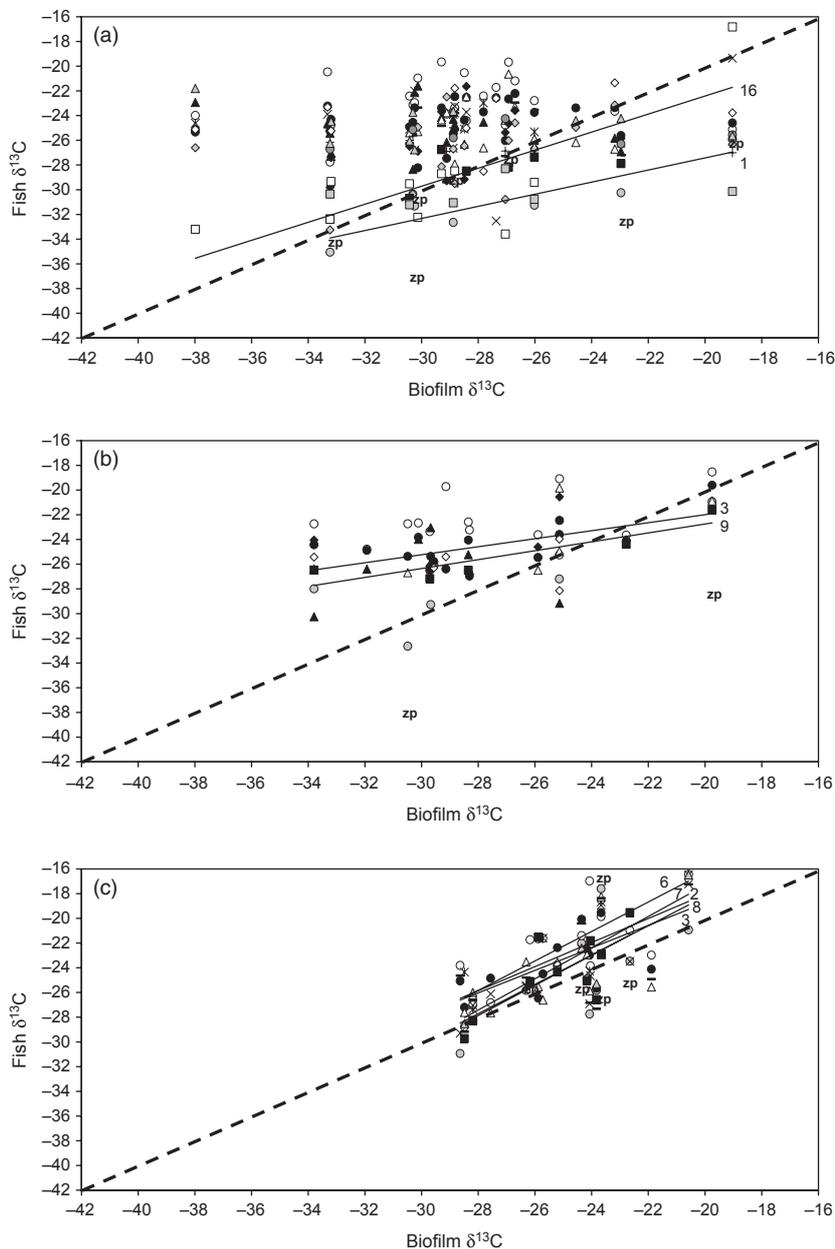
Fig. 5. Site-specific $\delta^{13}C$ of fishes vs. $\delta^{13}C$ of biofilm from 67 sites across three rivers in the wet–dry tropics of northern Australia – the Daly River (a), Mitchell River (b) and Fitzroy River (c). Open circles, spangled perch; solid circles, rainbowfish; shaded circles, bony bream; open diamonds, gudgeons; shaded diamonds, barred grunter; solid diamonds, sooty grunter; open triangles, hyrtl's tandan; shaded triangles, mouth almighty; solid triangles, sleepy cod; open squares, hardyhead; shaded squares, mullet; solid squares, Butler's grunter (Daly), Jenkin's grunter (Fitzroy); X, glassfish; —, goby; +, barramundi; ⋇, archerfish (Daly), giant cod (Fitzroy); zp, zooplankton. Best-fit lines are shown for regression slopes significantly different from zero, with numbers that correspond to taxa in Table 3.

sions of fish $\delta^{13}C$ vs. biofilm $\delta^{13}C$ with nonzero slopes may therefore represent an underestimate of fish movement, as some species may be recent arrivals at refugial sites but continue feeding and growing through the dry season, resulting in isotopic turnover and equilibrium with local prey (Maruyama *et al.* 2001).

The isotopic mismatch between fishes and local biofilm in many cases likely reflects a combination of factors. Given the high degree of food web connectivity in these systems (Jardine *et al.* in press), the lack of correlation between fish $\delta^{13}C$ and biofilm $\delta^{13}C$ must largely be driven by the consumption of prey from other locations (e.g. the floodplain). Of the 528 fish values, 271 (51%) fell within the mean ± 1 SD (−22·8 ± 2·6‰ SD, Fig. 6) for wet season epiphyton measured in consecutive years on the Mitchell River floodplain (Jardine *et al.* in press). This $\delta^{13}C$ value for floodplain

epiphyton is consistent with measured values for attached microalgae from other Australian tropical floodplains: Magela Creek in the Northern Territory (−22·9 ± 0·4‰ S.D and −24·4 ± 0·7‰ SD in each of 2 years, S.E. Bunn, unpublished data) and the Flinders River in Queensland (−18·7 ± 0·3‰ SD, T.D. Jardine, unpublished data). These values are typical of moderately productive and partially CO_2 limited systems (Finlay 2004) and suggests that periphyton growing on tropical floodplains are generally ^{13}C-enriched relative to dry-season in-channel biofilm. This observation is useful for interpreting isotope data from other studies in tropical floodplain systems where only dry season sampling was conducted (e.g. Roach *et al.* 2009).

While phytoplankton also may have contributed to fish biomass, this source was only available in isolated waterholes and a few larger main channel sites. Furthermore, zooplank-

Table 3. Slopes and correlation coefficients for $\delta^{13}C$ in biofilm vs. $\delta^{13}C$ in fishes from three tropical rivers of northern Australia sampled early in the dry season

Taxa	Daly River Slope	r	n	Mitchell River Slope	r	n	Fitzroy River Slope	r	n	All rivers Slope	r	n
1 – Bony bream (*Nematolosa erebi*)	0·49[b]	0·87	7	0·62[d]	0·79	5	1·28[d]	0·70	6	0·76[a]	0·71	18
2 – Spangled perch (*Leiopotherapon unicolor*)	0·03[c]	0·05	20	0·19[c]	0·47	12	0·97[a]	0·66	18	0·18[c]	0·26	54
3 – Rainbowfish (*Melanotaenia splendida*)	0·07[c]	0·16	23	0·28[b]	0·73	15	0·91[a]	0·70	14	0·26[b]	0·45	53
4 – Hyrtl's tandan (*Neosilurus hyrtlii*)	0·03[c]	0·05	16	0·56[c]	0·85	6	0·70[d]	0·54	12	0·24[b]	0·36	35
5 – Goby (*Glossogobius aureus*)	0·11[d]	0·07	7				0·81[d]	0·56	12	0·57[a]	0·51	20
6 – Giant cod (*Oxyeleotris selheimi*)	−0·09[c]	−0·35	10				1·19[a]	0·85	7	0·22[c]	0·35	17
7 – Mouth almighty (*Glossamia aprion*)	−0·10[c]	0·33	10				1·25[a]	0·90	5	0·17[c]	0·31	19
8 – Glassfish (*Ambassis* spp.)	0·52[d]	0·65	7				1·19[a]	0·82	10	0·66[a]	0·61	18
9 – Barred grunter (*Amniataba percoides*)	0·28[c]	0·40	18	0·36[b]	0·89	5				0·45[b]	0·59	26
10 – Sooty grunter (*Hephaestus fuliginosus*)	0·14[c]	0·22	15	0·87[c]	0·71	6				0·21[c]	0·33	22
11 – Sleepy cod (*Oxyeleotris lineolatus*)	−0·15[c]	−0·32	16	0·09[d]	0·09	7				−0·11[c]	−0·17	24
12 – Barramundi (*Lates calcarifer*)	−0·09[c]	−0·52	9							−0·15[c]	−0·26	14
13 – Longtom (*Strongylura krefftii*)	0·03[c]	0·15	6							0·08[c]	0·14	11
14 – Archerfish (*Toxotes chatareus*)	−0·16[c]	−0·43	5							0·18[c]	0·30	11
15 – Northern trout gudgeon (*Mogurnda mogurnda*)	0·11[c]	0·27	9							0·07[c]	0·16	14
16 – Hardyhead (*Craterocephalus* spp.)	0·73[a]	0·77	10									
17 – Mullet (*Liza* spp.)	0·05[c]	0·22	6									
18 – Butler's grunter (*Syncomistes butleri*)	0·44[c]	0·72	7									
19 – Jenkin's grunter (*Hephaestus jenkensi*)							1·22[a]	0·75	10			
All species	0·13	0·18		0·42	0·65		1·06	0·72		0·25	0·31	

Superscripts correspond to scenarios in Fig. 1 (a, local biofilm dominant; b, mixed; c, alternate sources; d, unresolved) and denote whether slopes were significantly different ($P < 0.05$) from 0 and 1.
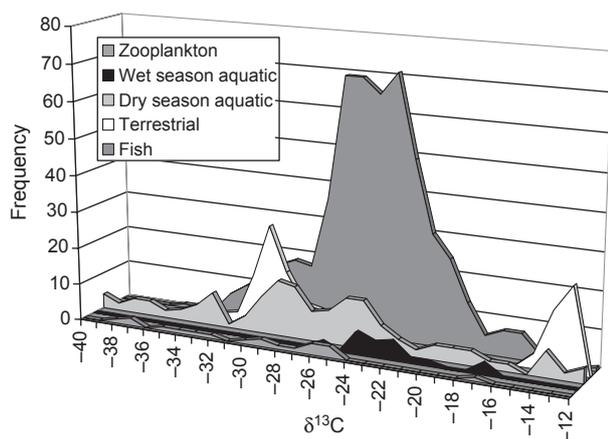

Fig. 6. Histogram of $\delta^{13}C$ values (absolute frequency) for fish and available food sources in rivers of the wet–dry tropics in northern Australia. Terrestrial sources include leaf litter, grasses, sedges and emergent and floating macrophytes. Dry season aquatic sources include biofilm, filamentous algae, charophytes and submerged macrophytes. Wet season aquatic sources are attached algal samples taken from seasonally inundated areas (i.e. floodplain).

ton (as a surrogate for phytoplankton) were ^{13}C-depleted relative to biofilm (Fig. 4), consistent with known trends in waterbodies (France 1995), and thus cannot account for fish that were out of phase with biofilm, such as those in the Daly River, because most fish were ^{13}C-enriched relative to both plankton and biofilm (147 of 207 fish analysed, Fig. 5). Combining plankton $\delta^{13}C$ with biofilm $\delta^{13}C$ to form a mean value for local sources generated slopes (rainbowfish = 0·23,

spangled perch = 0·19, hyrtl's tandan = 0·23, bony bream = 0·74) that did not differ from those calculated from biofilm alone, suggesting that the external source of carbon had $\delta^{13}C$ that was more different from biofilm than plankton and biofilm were from each other (mean difference = 1·9‰).

The variation observed among catchments in consumer–resource coupling could also be owing to the differences in terrestrial prey availability. Some terapontid grunters, including those sampled in the current study (*L. unicolor*, *Amniataba percoides*, *H. fulginosus*, *H. carbo*, *H. jenkinsi*), exhibit ontogenetic shifts towards more terrestrial prey as they age (Davis *et al.* 2010). While the proportion of terrestrial material in the diet of these species never exceeds 50% (Davis *et al.* 2010; Table 1), and terrestrial insects feature little in the diet of all but a few species (e.g. *T. chatareus*) elsewhere in the tropics during the dry season (Pusey, Kennard & Arthington 2004; Pusey *et al.* 2010), it is possible that the availability and consumption of terrestrial prey may be slightly elevated during the wet season (Balcombe *et al.* 2005; Rayner *et al.* 2010), particularly in those catchments where flood duration is long and allows for greater interaction at the aquatic-terrestrial interface (Junk, Bayley & Sparks 1989). In the Daly River, stable isotope sampling was conducted largely in smaller tributaries where edge effects are most likely and contributions from riparian insects to fish diets could be high (Nakano & Murakami 2001; Baxter, Fausch & Saunders 2005). Indeed, by analysing patterns of consumer–resource coupling in the two most common fishes (spangled perch and rainbowfish) in all sites across catchments, links to local biofilm were weaker in tributary sites

(spangled perch slope = 0·09, rainbowfish slope = 0·14) compared to main channels (spangled perch = 0·28, rainbowfish slope = 0·13) and waterholes (spangled perch slope = 0·22, rainbowfish slope = 0·34). This is similar to the trends observed for the three most common invertebrate taxa and likely reflects the gradient in perimeter-to-area ratios from high (tributaries) to low (waterholes) as well as the effects of riparian shading on algal production (Davies, Bunn & Hamilton 2008). However, within tributaries, trends among the three catchments remained for the two species, with the Fitzroy tributaries having the highest slopes for both spangled perch (slope = 0·86) and rainbowfish (slope = 0·45), and the Daly (spangled perch slope = 0·17, rainbowfish slope = 0·19), and the Mitchell (spangled perch slope = 0·06, rainbowfish slope = 0·14) having weakest links between fishes and biofilm. This reaffirms that variation in the relationship between fish and their diets is largely controlled by hydrological variability and connectivity.

The varying degree of connectivity also has implications for the exploitation of nonfish migrant prey. Large prawns (*Macrobrachium rosenbergii*) are often abundant in these systems and they serve as prey for many large-bodied fishes such as barramundi (Pusey, Kennard & Arthington 2004). These prawns featured prominently in the diet of many of the fish species included in this study (Table 1). *M. rosenbergii* is migratory, moving from brackish water as larvae into freshwater locations as adults and sub-adults (Short 2004), thus transporting organic matter from the lower reaches of rivers into headwaters, likely feeding while in transit and thereby delivering an isotope ratio to predatory fish that is out of phase with local resources. Prawns in the Daly and Mitchell Rivers had slopes (0·21 and 0·25 respectively) that were not significantly different from zero but those from the Fitzroy were tightly linked to local sources (slope = 1·00), suggesting limited hydrological connectivity in the Fitzroy restricts upstream–downstream movements by this species.

All of the observations reported here suggest that local effects of consumers on their prey will be strongest in isolated waterholes, both in-channel and on the floodplains. Conversely, permanently flowing reaches with extensive riparian cover should be the locations where consumer effects are weakest because of (i) the ability of consumers to move out of the local area to forage in other habitat patches (e.g. floodplains) and (ii) the availability of riparian insects and migratory prey. Our findings support both mechanisms, although the evidence was stronger for the first. An important direction for future work in these and other wet–dry tropical systems is to understand whether food consumption and growth rates vary with season. While many of these species have a distribution that is restricted to tropical locations where they clearly feed and grow best during the high-temperature wet season (e.g. barramundi, Robins *et al.* 2006), others are found across broad latitudinal ranges (e.g. spangled perch), suggesting a broader thermal tolerance and possible asynchrony between flooding, peak temperatures, productivity and fish growth (Welcomme & Halls 2003; Winemiller 2003).

Direct measurements of growth rates across seasons would be very useful in further understanding where consumer–resource coupling is likely to be strongest. If growth of the most common and abundant fishes is limited during the cooler months of the dry season (Yang & Dudgeon 2009), then consumer control of resources is less likely to have local effects in refugial habitats (tributaries, main channels, waterholes) unless considerable maintenance feeding occurs. Instead, potential top-down control may be higher in the wet season but modulated by high flows and associated scouring of the benthos within river channels (Douglas, Bunn & Davies 2005). This leaves slow-flowing, seasonally inundated floodplain habitats as candidates for a high degree of consumer control, as overall productivity in these areas is high because of higher nutrient availability (Junk, Bayley & Sparks 1989); while resources are dispersed during this time, scouring from turbulent flows is absent. Further testing of these processes could illuminate the dynamic nature of these wet–dry systems and reveal the key foraging areas for a highly diverse fauna.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article.

Table S1. Characteristics of 67 sites from three catchments (Daly River, Northern Territory, Fitzroy River, Western Australia, Mitchell River, Queensland) where fishes, invertebrates and primary sources were sampled for stable carbon isotope analysis in the early dry season.

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