Title: Dynamic stability in dry season food webs within tropical floodplain rivers.

Running head: Macroinvertebrate food webs in Australia's wet-dry tropics

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Abstract

Debate exists about the effects of hydrological variation on food web dynamics and the relative importance of different sources of organic carbon fuelling food webs in floodplain rivers. Stable carbon isotope analyses and ecological stoichiometry were used to determine the basal sources in dry season macroinvertebrate food webs in two floodplain river systems of Australia's wet-dry tropics that have contrasting flow regimes. Algae, associated with phytoplankton and biofilm, were the primary food source, potentially contributing > 55% organic carbon to the biomass of a wide range of primary and secondary consumers. However, many consumers assimilated other sources in addition to algae, e.g. detritus from local C₃ riparian vegetation. Food webs were characterised by substantial flexibility in the number and types of sources identified as important, which was indicative of generalist feeding strategies. These findings suggest 'dynamic stability' in the food webs, which imparts resilience against natural disturbances like flow regime seasonality and variation in hydrological connectivity. This adaptation may be characteristic of macroinvertebrate assemblages in highly seasonal river systems or in those with high levels of flow variability.

Additional key words:

Algae, terrestrial detritus, carbon: nitrogen, macroinvertebrates, hydrological connectivity, Gulf of Carpentaria

Introduction

Food web analysis helps improve our understanding of ecosystem function by revealing the key sources of organic matter that fuel metazoan consumers (Thorp *et al.* 1998). In river systems, a number of conceptual models emphasise the relative importance of different forms and origins of organic matter in driving aquatic food webs, depending upon on the type of system for which each model was developed (e.g. Vannote *et al.* 1980; Junk *et al.* 1989; Thorp and Delong 1994). Despite the disparate predictions from

these large-river models, there is growing acceptance that algae are the primary source of organic carbon fuelling metazoan food webs in riverine ecosystems the world over (see Thorp *et al.* 2006), supporting concepts outlined in the revised riverine productivity model (Thorp and DeLong 2002). This model emphasises the importance of bioavailable algae to riverine consumers despite the large amounts of terrestrial detritus often present; although a system may be strongly heterotrophic, the aquatic macro-consumers can be largely dependent on autotrophic sources (Lewis *et al.* 2001). Even in highly turbid waterholes of Cooper Creek, a central Australian floodplain river, where in-stream primary production is typically light-limited (e.g. Fellows *et al.* 2007; 2009), algae along littoral zone margins have been shown to provide the bulk of energy for higher trophic levels (Bunn *et al.* 2003).

Based on these studies, and the international literature on tropical river ecosystems, algae have recently been proposed to be the primary driver of aquatic food webs within floodplain river systems in Australia's wet-dry tropics (Douglas *et al.* 2005). These rivers have highly seasonal flow regimes but also experience substantial levels of non-seasonal flow variability, creating spatiotemporal variation in hydrological connectivity (Finlayson and McMahon 1988). They are among the most anthropogenically undeveloped aquatic ecosystems in the southern hemisphere and have large-scale interactions with both the marine and terrestrial environment (Woinarski *et al.* 2007). However, there is much interest in the future water resource and urban development potential of these systems (e.g. DNRW 2007), as is the case for many tropical rivers (Pringle 2001; Junk 2002; Moulton and Wantzen 2006). In addition, there are significant gaps in our understanding of how these rivers, and their food webs, function (Hamilton and Gerkhe 2005). Moreover, recent studies that have specifically investigated the effects of hydrological connectivity on food webs within floodplain rivers suggest that the effects are spatially inconsistent (e.g. Roach *et al.* 2009). Consequently, there is a pressing need to improve our understanding of food web processes and the effects of variation in hydrological connectivity acting within Australia's northern river systems.

Guided by principles outlined in Douglas *et al.* (2005), we therefore investigated the relative importance of algae and other sources of organic carbon to macroinvertebrate food webs in waterbodies within the lower, freshwater sections of two river systems in

the wet-dry tropics, the Gregory and Flinders, across two consecutive dry seasons using stable isotope and stoichiometric analyses. Specifically, we hypothesised that (1) much of the dry season macroinvertebrate biomass would be derived from algae, particularly algae associated with littoral zones, e.g. biofilm; (2) in lotic waterbodies with dense and complex riparian zones, however, the macroinvertebrate biomass was likely to be derived from both local and terrestrial sources of organic carbon; and (3) variation in hydrological connectivity among waterbodies would be associated with variation in these general pathways of carbon transfer from basal sources through to consumers.

Materials and methods

Study area and sampling regime

Australia's wet-dry tropics and the study region (*c.* 17.8-18.9°S and 139.2-140.9°E) within the remote Gregory and Flinders river systems are described by Leigh and Sheldon (2008; 2009). Briefly, these two systems are north of the Tropic of Capricorn and flow through savannah and dry forest country for which the main land use is low density cattle grazing (Fig. 1). The lower, freshwater and floodplain regions of these systems undergo an annual cycle of monsoonal rains, high flows and flooding during 'wet' months (~ November-April) followed by 'dry' months (~ May-October) where little rain falls and surface flows tend to cease. However, two distinct flow regime types have been described for rivers in the region—the more regular 'tropical' rivers, an example being the clear-flowing, perennial and aquifer-fed Gregory river system, and the more ephemeral 'dryland' rivers like the Flinders, where main channels and floodplains reduce to a mosaic of disconnected, turbid waterholes during the dry season (Leigh and Sheldon 2008).

Six waterbodies were sampled in the Gregory and five in the Flinders river systems during the 2005 dry season (in August). Two waterbodies in each river system were re-sampled the following dry season (in September, 2006) (Fig. 1; Table 1). All waterbodies were in the lower freshwater sections of the rivers and classified as either lotic or lentic, which represented their hydrological connectivity at the time of sampling (Table 1). In general, lotic waterbodies sampled in the Gregory river system tended to be deeper (2.5 ± 0.8 m) and to have lower pH (8.3 ± 0.1), lower concentrations of suspended nitrogen (0.18 ± 0.02 mg N L⁻¹) and phosphorus (0.012 ± 0.003 mg P L⁻¹),

total solids ($3.8 \pm 0.5 \text{ mg L}^{-1}$) and chlorophyll *a* ($0.5 \pm 0.1 \text{ } \mu\text{g L}^{-1}$) than lentic waterbodies ($0.8 \pm 0.2 \text{ m}$, $8.5 \pm 0.1 \text{ pH}$, $0.79 \pm 0.07 \text{ mg N L}^{-1}$, $0.136 \pm 0.049 \text{ mg P L}^{-1}$, $118 \pm 55 \text{ mg TSS L}^{-1}$, $12.5 \pm 2.7 \text{ } \mu\text{g Chl } a \text{ L}^{-1}$) or sites sampled in the Flinders river system ($0.8 \pm 0.2 \text{ m}$, $8.6 \pm 0.1 \text{ pH}$, $0.74 \pm 0.08 \text{ mg N L}^{-1}$, $0.134 \pm 0.052 \text{ mg P L}^{-1}$, $123 \pm 57 \text{ mg TSS L}^{-1}$, $12.1 \pm 3.5 \text{ } \mu\text{g Chl } a \text{ L}^{-1}$) (mean $\pm$ SE; Leigh and Sheldon 2009). Lotic waterbodies in the Gregory system also had more abundant and diverse vegetation in littoral zones, whereas lentic waterbodies and sites in the Flinders system tended to have greater proportions of bare sediment and snags.

Collection of samples for stable isotope analysis

Basal sources comprised suspended fine particulate organic material in the water column (hereafter seston); biofilm attached to plants, woody debris and cobbles in littoral zones; filamentous algal mats and colonial algal scum when present in littoral zones in noticeable quantities; macroalgae (*Chara* and *Nitella* spp.); leaves or blades collected from the dominant riparian plant species (trees, shrubs and grasses); submerged (*Potamogeton*, *Ottelia* and *Myriophyllum* spp.) and emergent (*Eleocharis* sp.) aquatic macrophytes; and benthic detritus collected from the littoral zone. Detritus was sorted into coarse benthic organic matter (CBOM, $> 1000 \text{ } \mu\text{m}$) and fine benthic organic matter (FBOM, $250\text{-}1000 \text{ } \mu\text{m}$) using test sieves (ISO 3310-1 Endecotts) and site water. Epiphytes were removed from aquatic vegetation via agitation in distilled water prior to sample storage. Large plant, woody debris or cobble samples were brushed gently with a clean toothbrush and washed with distilled water to dislodge biofilm; smaller samples were placed whole in a sealed bag with distilled water and shaken vigorously. Seston samples were collected by filtering known volumes of surface water onto pre-combusted, glass-fibre filter papers (Whatman). In general, triplicate samples of each basal source were collected from each site. However, the sampling effort was doubled within each of the four sites sampled in 2006, as many sources showed wide ranges in their stable isotope ratios. Duplicate sets of seston samples were also collected for analysis of chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) following standard methods (APHA 1989). All samples were frozen until analysed in the laboratory.

Zooplankton were collected during the 2005 dry season by towing a $250\text{-}\mu\text{m}$ plankton net through the near-surface water column; however, this technique did not capture enough animals for stable isotope analysis. Therefore, during the 2006 dry season, a

150- μ m Patalas-Schindler collection box was repeatedly pulled up through the water profile until adequate numbers of zooplankton were collected from each site, from both mid-channel and littoral zone locations. Aquatic macroinvertebrates were collected with a 500- μ m dipnet, swept proportionally over the different habitats present at each site (including snags, leaf packs, backwaters, aquatic macrophytes, algal mats and bare littoral areas) for at least 20 seconds. Collections were placed into white sorting trays from which the less-mobile taxa, which included both primary and secondary consumers, were picked by hand. Mussels (*Velesunio* sp.) were collected by hand from shallow benthic zones. Macroinvertebrates were sorted to Order and morphotaxa in the field to isolate predators and facilitate laboratory identification, which was performed down to the lowest taxonomic resolution possible. Gut voidance was facilitated by keeping invertebrates in aerated water and out of the heat for up to 24 h before being frozen.

Laboratory preparation and stable isotope analysis

Plants, algae, benthic organic matter, zooplankton and macroinvertebrate samples were rinsed thoroughly in distilled water, and examined under a dissecting microscope to remove foreign material. Non-dietary traces of carbonate in seston, macroalgae, FBOM and crustacean samples were removed via acid treatment (Bunn *et al.* 1995). Seston samples (on Whatman GFFs) were acid-treated via fumigation using the method outlined in Hamilton *et al.* (2005). Macroinvertebrates were grouped into similar size classes within each taxon and prepared samples consisted of 1–20 individuals depending on their size and mass requirements for analysis. Multiple samples of each taxon group collected from each site were prepared when there were sufficient numbers of individuals.

All samples were dried (60°C for at least 24 h) and ground to homogenise the contents, using either a mortar and pestle or an electric ball-mill grinder (Retsch MM200, Haan, Germany), as dictated by sample coarseness. Ground samples were analysed for percentage organic carbon (C) and nitrogen (N) and stable C isotope ratios ($^{13}\text{C}/^{12}\text{C}$) via combustion and mass spectrometry using a Eurovector EA 3000 (Milan, Italy) inlet with a GV Isoprime (Manchester, UK) mass spectrometer. Stable isotope values of samples ($\delta^{13}\text{C}$) were calculated as parts per thousand (‰) relative to the Vienna Pee Dee Belemnite standard. Lipid correction was not performed on macroinvertebrate $\delta^{13}\text{C}$

values as variation in lipid content among whole-body macroinvertebrate samples may lead to similar interpretations for both corrected and uncorrected data (Logan *et al.* 2008). Machine precision ranged from 0.0-0.3‰ for seston samples and from 0.0-0.1‰ for all other sample types.

Supplementary analyses to establish basal source origins

Source origins (live versus detrital; terrestrial versus aquatic; local versus transported) needed to be established to explore our hypotheses about macroinvertebrate consumers and their primary sources of organic carbon. Prior to stable isotope analyses, we had attempted to separate the live algal and mixed detrital components within seston and biofilm samples using the density-based separation method of Hamilton *et al.* (2005). The organic C content of each sample was compared with that of chlorophyll *a* (C:Chl mass ratios) as an adjunct method of estimating the relative proportions of live algae versus detrital organic matter (cf. Legendre and Michaud 1999). In general, the lower the C:Chl ratio, the greater the algal compared with detrital (aquatic or terrestrial) component within the sample (Hamilton *et al.* 2005). Unfortunately, it was not clear, based on the resulting $\delta^{13}\text{C}$ values and C:Chl ratios of our separated and unseparated samples, that the separation was successful (Leigh 2008). Therefore, we used $\delta^{13}\text{C}$ values of unseparated biofilm and seston samples in all subsequent analyses.

Percentage organic C and N values were used to calculate molar C:N ratios of basal source samples to help distinguish terrestrially derived organic matter from that of in-stream primary producers (aquatic sources) as well as local versus transported origins. Aquatic sources, especially phytoplankton, tend to have C:N ratios much lower (14:1 molar ratio; 12:1 mass ratio) than terrestrial sources (50-60:1 molar ratio; 45-50:1 mass ratio) (Wetzel 2001) and C:N ratios of organic material generally increase during decomposition (Kendall *et al.* 2001). Therefore we expected that transported sources would become increasingly refractory and decomposed with distance travelled downstream, showing an increase in their C:N ratios. Also, C:N ratios provided insight into the nutritional quality of basal sources for macroinvertebrate consumers; large differences between source and consumer C:N ratios generally imply a greater metabolic demand on the consumer than if the source has a more comparable C:N ratio (Frost *et al.* 2002).

Variations in $\delta^{13}\text{C}$, C:N and C:Chl data were compared among all basal sources, among site types and between years, based on their ranges of values and site means. A non-parametric Mann-Whitney-*U* test was used on untransformed data from the 2005 dry season to test for differences in $\delta^{13}\text{C}$ values of basal sources between river systems and between lotic and lentic sites. Pearson's correlation coefficients were used to explore the amount of spatial variation in $\delta^{13}\text{C}$ values of particular basal sources (CBOM, FBOM, biofilm and seston) that could be explained by the variation in their potential end-member sources (riparian vegetation and/or biofilm). The amount of spatial variation in $\delta^{13}\text{C}$ values for both primary and secondary consumers that could be explained by each basal source type was also explored in this manner. Only basal sources found throughout the study region were used in these analyses and consumers that had $\delta^{13}\text{C}$ values outside the range of basal source values were excluded. Pearson's correlation was used because relationships between variables were linear. All correlations were based on site means, as sample replicates were not matched among sources or between sources and consumers. This produced an acknowledged but unavoidable increase in the degree of uncertainty in the R^2 values. Statistical analyses were performed in SAS (Version 8, 2002).

Macroinvertebrate food web analysis and hypothesis testing

We used the IsoSource mixing model program (Phillips and Gregg 2003) and mean $\delta^{13}\text{C}$ values from each site, year and sample type to calculate the range of percentage contributions of each source to each consumer's $\delta^{13}\text{C}$ value, based on increments of 2%, that maintained mass balance within a tolerance of 0.2‰. We used $\delta^{13}\text{C}$ values only and a trophic enrichment factor of 0‰ because (1) our main aim was to determine the relative importance of organic carbon sources to macroinvertebrate consumers in the study region, and (2) food webs in the study region have not been previously investigated and thus the use of nitrogen isotope ratios in mixing models would require assumptions about trophic enrichment that may have been inappropriate (cf. Bunn *et al.* 2003; Melville and Connolly 2005; Benstead *et al.* 2006).

Source importance (the potential contribution of each basal source to the biomass of each consumer) was assessed using the 1st and 99th percentiles of IsoSource solution ranges; assuming all potential sources are sampled, a low 'maximum' (99th percentile) indicates a source is unlikely to be important, a high 'minimum' (1st percentile)

indicates a source is likely to be important, and a small range between the 1st and 99th percentiles ('1-99 range') indicates the estimate of a source's contribution is well constrained (Benstead *et al.* 2006). Differences in each source's minimum or maximum contributions between groups of waterbodies and consumers (Gregory v. Flinders river systems, lotic v. lentic sites, 2005 v. 2006 dry seasons, primary v. secondary consumers) were also explored statistically using the Mann-Whitney *U* test.

Results

Basal source origins and variations among $\delta^{13}\text{C}$, C:N and C:Chl values

Mean site $\delta^{13}\text{C}$, C:N and C:Chl values of the different basal sources, along with spatial patterns of variation among site types, were similar in both dry seasons (2005 and 2006; see Accessory Publication), but indicated different sources of origin and food quality (summarised below for the 2005 dataset only, unless indicated otherwise).

Comparatively, riparian plants were ^{13}C -depleted (mean site values for C_3 plants ranged from -29.2 to -32.6‰) or ^{13}C -enriched (C_4 plants ranged from -13.1 to -14.4‰). CBOM $\delta^{13}\text{C}$ values (-28.3 to -31.4‰) tended to match those of C_3 plants collected from corresponding sites, rather than C_4 plants. Spatial variation in mean site $\delta^{13}\text{C}$ values of C_3 plants explained 47% of the variation in CBOM values. Plant fragments identified within CBOM samples tended to match the dominant C_3 plants present within riparian zones on a site-by-site basis.

Mean $\delta^{13}\text{C}$ values of FBOM had a comparatively wide range among sites (-22.3 to -30.1‰) and, for some sites (especially in the Flinders system), were more similar to biofilm than CBOM values (see Accessory Publication). Only 14% and 16% of the spatial variation in FBOM $\delta^{13}\text{C}$ values could be explained by the variation in terrestrial C_3 plant and CBOM values, respectively, whereas 78% was explained by the variation in biofilm values. However, it was likely that FBOM was a mix of terrestrial and aquatic organic material, as FBOM samples had mean site C:N ratios between those of CBOM (> 45) and biofilm (< 18) and the C:N ratios of both FBOM and CBOM showed similar patterns of variation among sites (Fig. 2). $\delta^{13}\text{C}$ values of CBOM and FBOM were significantly ^{13}C -depleted in the Gregory compared with the Flinders river system (CBOM, $U_{16,15} = 300.5$, $P = 0.0175$; FBOM, $U_{15,15} = 306.5$, $P = 0.0023$) as well as in lotic compared with lentic sites (CBOM, $U_{16,15} = 331.0$, $P = 0.0003$; FBOM, $U_{15,15} = 168.0$, $P = 0.0079$).

Biofilm $\delta^{13}\text{C}$ values were significantly ^{13}C -depleted in the Gregory compared with the Flinders river system ($U_{14,11} = 94.5$, $P = 0.0085$). However, no statistical difference was found between lotic and lentic sites ($P > 0.05$). Mean site $\delta^{13}\text{C}$ values of biofilm ranged from -24.0 to -28.9‰ and less than 1% of the spatial variation in these values was explained by variation in the values of riparian C_3 plants. Mean site C:N ratios of biofilm were low (< 18), indicative of an aquatic rather than terrestrial origin.

For seston, mean site $\delta^{13}\text{C}$ values ranged from -24.9 to -29.1‰, with substantial variation within some sites (see Accessory Publication). No statistical differences were found between river systems or states of flow ($P > 0.05$). Seston values did not follow patterns of variation seen in riparian vegetation (or even in biofilm), which explained less than 1% of the variation in seston $\delta^{13}\text{C}$. In general, these findings were similar for the 2006 dry season. Low C:N molar ratios suggested an aquatic origin was likely for seston and C:Chl ratios indicated substantial amounts of detritus (site means all $>> 150$), i.e. seston mainly comprised of detrital and live phytoplankton (Fig. 2).

$\delta^{13}\text{C}$ values of sources that had the potential to originate from upstream (CBOM, FBOM and seston) did not become enriched in a consistent downstream direction for sites connected by surface flow at the time of sampling (GUm, GMmB and GDm in 2005; Fig.3). Mean site C:N ratios of CBOM and FBOM samples decreased in value downstream (as did local riparian vegetation), whereas C:N ratios of seston samples were comparatively constant (Fig. 3).

Variation in $\delta^{13}\text{C}$ and C:N values of basal sources and macroinvertebrate consumers

Spatial variation in the mean site $\delta^{13}\text{C}$ values of FBOM, seston and biofilm explained the greatest amounts of variation in mean site $\delta^{13}\text{C}$ values of consumers. However, the amounts of variation explained depended on the consumer group (primary or secondary) and year/s analysed (Fig. 4). For the combined 2005 and 2006 dataset, FBOM explained the greatest amount of variation in primary (43%) and secondary (50%) consumer $\delta^{13}\text{C}$ values among basal sources. This was followed by biofilm, which explained 43% and 39% of the variation in primary and secondary consumers respectively. In 2005, biofilm explained 42% of the variation in $\delta^{13}\text{C}$ values for primary consumers and 69% for secondary consumers. In 2006, seston explained 100% of the variation in $\delta^{13}\text{C}$ values

for primary consumers and 98% for secondary consumers (however, these correlations were based on 4 sites only). For all other combinations of basal source, year and consumer group, R^2 values from the Pearson correlations were low (0.02–0.11). Consumer C:N ratios were low (< 9) and had varying degrees of mismatch with basal source ratios. The greatest mismatch was with CBOM, which had the highest mean site ratios among basal sources (all > 45).

Macroinvertebrate food webs: mixing model results

$\delta^{13}\text{C}$ values and IsoSource mixing models were used to determine the potential contributions of basal sources to the assimilated diets of 66 out of the 88 consumer taxa collected from sites sampled during the 2005 and 2006 dry seasons (Tables 2 and 3; Fig. 5). Solutions were found for 61 consumers, which included zooplankton collected from 3 sites, 28 primary and 29 secondary macroinvertebrates. No solutions were found for consumers collected from FUm or FUo during the 2005 dry season. These and the 22 consumers not included in the analyses had $\delta^{13}\text{C}$ values outside the range of values of the available basal sources. FBOM was not included in mixing models as this was likely to be a mixture of CBOM and biofilm.

Ranges of percentage contributions from mixing model solutions tended to be wide (not well-constrained) for most basal sources. However, within the ‘1-99 range’ of solutions, seston had the highest minima (0–92%) and maxima (4–100%) compared with other sources found consistently throughout the study region (CBOM and biofilm). In addition, seston attained high maximum ($> 55\%$) contributions for 61% of the 61 consumers analysed and only attained low maximum ($< 35\%$) contributions for 13%. CBOM and biofilm had the next highest ‘1-99 ranges’: 0–74% to 4–98% and 0–24% to 0–94% respectively. Although filamentous algae (0–44% to 8–74%), macroalgae (0–80% to 4–98%) and algal scum (0–94% to 16–100%) were likely to be important for some consumers, these sources were not present at all sites (filamentous algae were at 2 sites only, macroalgae at 7 and algal scum at 3). Non-emergent (0–2% to 0–54%) and emergent (0–4% to 30–56%) macrophytes had the lowest ‘1-99 ranges’ of solutions and were present at only a few sites (non-emergents at 4 sites, emergents at 1).

Seston made significantly greater maximum contributions to consumers in 2006 than in 2005 ($U_{32,29} = 724.5$, $P = 0.0118$), whereas maximum contributions from biofilm ($U_{32,27}$

= 990.5, $P = 0.0061$) and macroalgae ($U_{18,20} = 278.0$, $P = 0.0336$) were greater in 2005. In 2006, seston and CBOM both made high maximum contributions ($> 55\%$) to the majority of consumers in GUm (lotic) and GUo (lentic). Minimum contributions from biofilm and macroalgae were significantly greater in lentic than lotic sites (biofilm: $U_{25,34} = 818.0$, $P = 0.0175$; macroalgae: $U_{7,31} = 175.5$, $P = 0.0136$). Maximum contributions from biofilm were significantly greater in the Flinders than the Gregory river system ($U_{18,41} = 673.5$, $P = 0.0325$), whereas maximum contributions from CBOM were greater in the Gregory ($U_{18,43} = 340.0$, $P = 0.0006$). Seston made high maximum contributions ($> 55\%$) to more primary than secondary consumers. However, 78% of primary consumers and 72% of secondary consumers had high maximum contributions ($> 55\%$) from more than one basal source type.

Discussion

Sources of organic carbon fuelling macroinvertebrate consumers

The dry season macroinvertebrate food webs in the Gregory and Flinders river systems appeared to be governed by principles outlined for river systems in Australia's wet-dry tropics (Douglas *et al.* 2005) and to function most similarly to the revised riverine productivity model (Thorp and Delong 2002). Algae provided the primary source of organic carbon to the consumer biomass, local sources of organic carbon were of greater importance than sources transported from elsewhere, and consumers assimilated organic carbon across the broad range of basal sources that were available to them. These findings add to the body of evidence that supports the dependence of metazoan consumers within floodplain river systems on algal production (e.g. Lewis *et al.* 2001; Bunn *et al.* 2003; Cotner *et al.* 2006).

The majority of basal sources available to the macroinvertebrate consumers in the study region were locally produced and aquatic in origin. The main exception to this basal source autochthony was CBOM, which was derived from local C_3 riparian vegetation. Although high C:Chl ratios indicated that seston contained a substantial amount of detrital material, low C:N ratios indicated that this was unlikely to have been terrestrially derived or transported from upstream (cf. Hamilton *et al.* 2005). Rather, the detrital content most likely originated from the phytoplankton biomass, as has been shown to occur in tropical and temperate rivers elsewhere (reviewed in Thorp *et al.* 2006). We assume, however, that the living fraction was preferentially assimilated by

the macroinvertebrate consumers. Dependence on this fraction of seston has been demonstrated in the Upper Mississippi River by a food web study that successfully separated the living from detrital fractions (Delong and Thorp 2006).

Algae were the most important sources of organic carbon to the dry-season macroinvertebrates across our study region. This supported our first hypothesis. However, the relative importance of seston, i.e. planktonic algae, was unexpected, despite being a major tenet of the riverine productivity model (Thorp and Delong 1994, 2002). We had instead hypothesised that the macroinvertebrates would rely most heavily on algae within littoral-zone biofilm as their source of organic carbon. Firstly, attached forms of algae have recently been proposed as playing a key role in riverine food webs in Australia's wet-dry tropics (Douglas *et al.* 2005). Secondly, floodplain rivers and waterholes in this region share similar hydrological and ecological characteristics (e.g. flow variability and macroinvertebrate patterns of diversity and composition) with those of Australia's central, dryland river systems (Leigh and Sheldon 2008, 2009). In these systems, attached forms of algae are considered to be the primary source of organic carbon for metazoan consumers (Bunn *et al.* 2003; Balcombe *et al.* 2005).

However, biofilm was still a potentially important source of organic carbon for many of the consumers across our study region. Biofilm potentially provided over 55% of organic carbon to 44% of the consumers analysed in mixing models. In addition, spatial variation in $\delta^{13}\text{C}$ values of biofilm and FBOM explained much of the variation in consumer values. Fine particulate organic material in river systems is often considered to be a mix of algae and terrestrial detritus (e.g. Bunn *et al.* 2003; Li and Dudgeon 2008). For our study, the majority of spatial variation in FBOM $\delta^{13}\text{C}$ values was explained by the variation observed in biofilm, with comparatively little variation attributed to terrestrial sources of organic carbon. This indicated that although the sampled FBOM was a mixture of terrestrially and aquatically derived material, it was likely to be dominated by algal carbon. Furthermore, when other algal sources (colonial algal scum, macroalgae and filamentous algae) were present within sites, they potentially contributed a high percentage of their organic carbon to the resident macroinvertebrate taxa.

We had hypothesised that local terrestrial detritus would be an important source of carbon for consumers specifically within lotic sites that had dense and complex riparian vegetation, like many sites in the Gregory river system. These sites would have greater potential for local riparian litterfall such that the CBOM would be more labile, and thus, a more likely source of organic carbon than the CBOM from sites with sparse vegetation. The maximum percent contribution from CBOM carbon to consumers within the Gregory river system was significantly higher than the contribution to consumers within the Flinders. However, CBOM was also an important source of carbon for consumers in both systems. Therefore, CBOM appeared to be important as a source of organic carbon regardless of the riparian characteristics or flow status of sites in which the consumers resided.

Despite the general, and relatively high, assimilation of CBOM throughout the study region, C:N ratios of this source were high. In comparison with the other basal sources available to consumers, this suggested that the nutritional quality of CBOM was one of the poorest (Frost *et al.* 2002; Fry 2006). Aquatic macroinvertebrates assimilate organic material with high C:N ratios, even as their primary source of organic carbon when other sources with higher nutritional value are available (Reid *et al.* 2008). However, in the present study, terrestrial sources like CBOM appeared to supplement the macroinvertebrates' diet rather than form their primary food source.

Food webs and hydrological connectivity

Within the dry season, the lotic or lentic nature of waterbodies was expected to cause corresponding changes in macroinvertebrate food web structure. However, variations in the importance of different basal sources to macroinvertebrate consumers did not correlate consistently with the variation seen in basal source $\delta^{13}\text{C}$ values among waterbody types. Variation existed in source $\delta^{13}\text{C}$ values between lotic and lentic sites (lentic sites having comparatively ^{13}C -enriched CBOM values), and between the Gregory and Flinders river systems (CBOM and biofilm both being comparatively ^{13}C -enriched in the Flinders). Based on mixing model solutions, however, the only significant differences in minimum and maximum contributions of organic carbon to consumer diets within lentic versus lotic sites were for biofilm and macroalgae, but not CBOM. In addition, biofilm made significantly higher maximum contributions to the

consumer biomass in the Flinders river system. However, the maximum contribution of CBOM carbon to consumer diets was higher in Gregory River waterbodies.

Furthermore, consumers in lotic and lentic sites did not display distinct preferences in their assimilation of basal sources; there was considerable variability in the array of sources that were most important to consumer diets in both site types. Specifically, mixing model results showed that, across the study region, a high proportion of primary (78%) and secondary consumers (72%) were likely to have assimilated organic carbon from more than one basal source type. This, along with the lack of correlation in patterns of variation among site types between $\delta^{13}\text{C}$ values of sources and source importance to consumers, suggests that the dry season food webs were not being driven to the same extent by hydrological connectivity as has previously been shown to occur for macroinvertebrate biodiversity in the study region (Leigh and Sheldon 2009). Rather, the high incidence of generalist feeding found within these dry season food webs suggests that the macroinvertebrate taxa possess substantial flexibility in their assimilation of food sources (Mihuc 1997). Thus, their food webs may exhibit 'dynamic stability' (*sensu* Woodward and Hildrew 2002). This implies that the food webs would be somewhat resilient against changes (especially short-term ones) that restructure food resources (Tomanova *et al.* 2006), as long as production of palatable algae in seston or biofilm was not severely disrupted (cf. Brodie and Mitchell 2005; Douglas *et al.* 2005). This would explain why variation in hydrological connectivity did not greatly affect relative source importance across the study region; the dynamically stable food webs were likely to be buffered against flow-related perturbations in food source variety and availability.

Given that the biomass of predatory fish and other vertebrates that reside in the studied river systems is fuelled by that of the sampled macroinvertebrate taxa (see Pusey *et al.* 2004), the dynamic stability and resilience proposed to exist in the macroinvertebrate food webs likely extends to higher trophic levels. Whether this resilience would remain in the face of severe and sustained deviation from the region's natural flow variability, nutrient status and channel geomorphology is unknown but unlikely. Such change has been linked to declines in biodiversity, water quality and habitat connectivity (Woodward and Hildrew 2002; Dudgeon *et al.* 2006; Rooney *et al.* 2006) and is likely

to disturb organic carbon production and the exchange between aquatic and terrestrial food webs (Lynch *et al.* 2002; Baxter *et al.* 2005; Leigh 2008).

Synthesis and prospects

Our research has demonstrated a degree of ‘dynamic stability’ and hence ‘resilience’ in the food webs of two river systems in Australia’s wet-dry tropics. Given the hydrological variability of these rivers and the previous descriptions of associated variability in pattern (macroinvertebrates: Marshall *et al.* 2006, Leigh and Sheldon 2009; and fish: Arthington *et al.* 2005) it is interesting to find some stability, albeit dynamic, in ecological function. However, our findings are restricted to dry season conditions and further research will be required to establish whether our conclusions describe aquatic food web processes over longer time periods, including the wet season when it is likely that floodplain production provides a large and bioavailable source of organic carbon for the metazoan consumers (Junk *et al.* 1989; Burford *et al.* 2008). In addition, waterbody-scaled isotopic enrichment studies, selected fatty acid analyses, and controlled feeding experiments that are specific to the basal sources and consumers found within the study region may better distinguish among source isotopic signatures and address limitations posed by wide-ranged solutions from mixing model predictions (Vander Zanden and Rasmussen 2001; Lau *et al.* 2008). Finally, future studies on tropical river systems over broader hydrological cycles, exploring both pattern and process, will not only add to a greater understanding of food web dynamics within riverine ecosystems but also of the resilience of such systems to broader hydrological and potentially climatic change.

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References

- APHA (American Public Health Association) (1989). 'Standard Methods for the Examination of Water and Wastewater.' (APHA-AWWA-WEF: Washington, D. C.)
- Arthington, A.H., Balcombe, S.R., Wilson, G.A., Thoms, M.C., and Marshall, J. (2005). Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research* **56**, 25-35.
- Balcombe, S.R., Bunn, S.E., McKenzie-Smith, F.J., and Davies, P.M. (2005). Variability of fish diets between dry and flood periods in an arid zone floodplain river. *Journal of Fish Biology* **67**, 1552-1567.
- Baxter, C.V., Fausch, K.D., and Saunders, W.C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* **50**, 201-220.
- Benstead, J.P., March, J.G., Fry, B., Ewel, K.C., and Pringle, C.M. (2006). Testing IsoSource: stable isotope analysis of a tropical fishery with diverse organic matter sources. *Ecology* **87**, 326-333.
- Brodie, J., and Mitchell, A. (2005). Nutrients in Australian tropical rivers: changes with agricultural development and implications for receiving environments. *Marine and Freshwater Research* **56**, 303-316.
- Bunn, S.E., Davies, P.M., and Winning, M. (2003). Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology* **48**, 619-635.
- Bunn, S.E., Loneragan, N.R., and Kempster, M.A. (1995). Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: implications for food-web studies using multiple stable isotopes. *Limnology and Oceanography* **40**, 622-625.
- Burford, M.A., Cook, A.J., Fellows, C.S., Balcombe, S.R., and Bunn, S.E. (2008). Sources of carbon fuelling production in an arid floodplain river. *Marine and Freshwater Research* **59**, 224-234.
- Cotner, J.B., Montoya, J.V., Roelke, D.L., and Winemiller, K.O. (2006). Seasonally variable riverine production in the Venezuelan llanos. *Journal of the North American Benthological Society* **25**, 171-184.
- Delong, M., and Thorp, J. (2006). Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. *Oecologia* **147**, 76-85.
- DNRW (Department of Natural Resources and Water) (2007). Water Resource (Gulf) Plan 2007. Department of Natural Resources and Water, Brisbane.
- Douglas, M.M., Bunn, S.E., and Davies, P.M. (2005). River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. *Marine and Freshwater Research* **56**, 329-342.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Knowler, D., *et al.* (2006). Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews* **81**, 163-182.
- Fellows, C., Wos, M., Pollard, P., and Bunn, S. (2007). Ecosystem metabolism in a dryland river waterhole. *Marine and Freshwater Research* **58**, 250-262.

- Fellows, C.S., Bunn, S.E., Sheldon, F., and Beard, N.J. (2009). Benthic metabolism in two turbid dryland rivers. *Freshwater Biology* **54**, 236-253.
- Finlayson, B.L., and McMahon, T.A. (1988). Australia v. the world: a comparative analysis of streamflow characteristics. In 'Fluvial Geomorphology of Australia'. (Ed. R.F. Warner) pp. 17-40. (Academic Press: Sydney.)
- Frost, P.C., Stelzer, R.S., Lamberti, G.A., and Elser, J.J. (2002). Ecological stoichiometry of trophic interactions in the benthos: understanding the role of C:N:P ratios in lentic and lotic habitats. *Journal of the North American Benthological Society* **21**, 515-528.
- Fry, B. (2006). 'Stable Isotope Ecology.' (Springer: New York.)
- Hamilton, S.K., and Gehrke, P.C. (2005). Australia's tropical river systems: current scientific understanding and critical knowledge gaps for sustainable management. *Marine and Freshwater Research* **56**, 243-252.
- Hamilton, S.K., Sippel, S.J., and Bunn, S.E. (2005). Separation of algae from detritus for stable isotope or ecological stoichiometry studies using density fractionation in colloidal silica. *Limnology and Oceanography: Methods* **3**, 149-157.
- Junk, W.J. (2002). Long-term environmental trends and the future of tropical wetlands. *Environmental Conservation* **29**, 414-435.
- Junk, W.J., Bayley, P.B., and Sparks, R.E. (1989). The flood pulse concept in river-floodplain systems. *Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences* **106**, 110-127.
- Kendall, C., Silva, S.R., and Kelly, V.J. (2001). Carbon and nitrogen isotopic compositions of particulate organic matter in four large river systems across the United States. *Hydrological Processes* **15**, 1301-1346.
- Lau, D.C.P., Leung, K.M.Y., and Dudgeon, D. (2008). Experimental dietary manipulations and concurrent use of assimilation-based analyses for elucidation of consumer-resource relationships in tropical streams. *Marine and Freshwater Research* **59**, 963-970.
- Legendre, L., and Michaud, J. (1999). Chlorophyll *a* to estimate the particulate organic carbon available as food to large zooplankton in the euphotic zone of oceans. *Journal of Plankton Research* **21**, 2067-2083.
- Leigh, C. (2008). Floodplain river function in Australia's wet/dry tropics, with specific reference to aquatic macroinvertebrates and the Gulf of Carpentaria. PhD thesis. Griffith University, Nathan, Queensland.
- Leigh, C., and Sheldon, F. (2008). Hydrological changes and ecological impacts associated with water resource development in large floodplain rivers in the Australian tropics. *River Research and Applications* **24**, 1251-1270.
- Leigh, C., and Sheldon, F. (2009). Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet /dry tropics. *Freshwater Biology* **54**, 549-571.
- Lewis, W.M., Jr., Hamilton, S.K., Rodriguez, M.A., Saunders, J.F., III, and Lasi, M.A. (2001). Foodweb analysis of the Orinoco floodplain based on production estimates and stable isotope data. *Journal of the North American Benthological Society* **20**, 241-254.
- Li, A.O.Y., and Dudgeon, D. (2008). Food resources of shredders and other benthic macroinvertebrates in relation to shading conditions in tropical Hong Kong streams. *Freshwater Biology* **53**, 2011-2025.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., *et al.* (2008). Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of

- chemical extraction and modelling methods. *Journal of Animal Ecology* **77**, 838-846.
- Lynch, R.J., Bunn, S.E., and Catterall, C.P. (2002). Adult aquatic insects: potential contributors to riparian food webs in Australia's wet-dry tropics. *Austral Ecology* **27**, 515-526.
- Marshall, J.C., Sheldon, F., Thoms, M., and Choy, S. (2006). The macroinvertebrate fauna of an Australian dryland river: spatial and temporal patterns and environmental relationships. *Marine and Freshwater Research* **57**, 61-74.
- Melville, A.J., and Connolly, R.M. (2005). Food webs supporting fish over subtropical mudflats are based on transported organic matter not in situ microalgae. *Marine Biology* **148**, 363-371.
- Mihuc, T.B. (1997). The functional trophic role of lotic primary consumers: generalist versus specialist strategies. *Freshwater Biology* **37**, 455-462.
- Moulton, T.P., and Wantzen, K.M. (2006). Conservation of tropical streams - special questions or conventional paradigms? *Aquatic Conservation-Marine and Freshwater Ecosystems* **16**, 659-663.
- Phillips, D.L., and Gregg, J.W. (2003). Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**, 261-269.
- Pringle, C.M. (2001). Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecological Applications* **11**, 981-998.
- Pusey, B.J., Kennard, M.J., and Arthington, A.H. (2004). 'Freshwater Fishes of North-Eastern Australia.' (CSIRO Publishing: Collingwood, Victoria.)
- Reid, D.J., Quinn, G.P., Lake, P.S., and Reich, P. (2008). Terrestrial detritus supports the food webs in lowland intermittent streams of south-eastern Australia: a stable isotope study. *Freshwater Biology* **53**, 2036-2050.
- Rooney, N., McCann, K., Gellner, G., and Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265-269.
- Thorp, J.H., and Delong, M.D. (1994). The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* **70**, 305-308.
- Thorp, J.H., and Delong, M.D. (2002). Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos* **96**, 543-550.
- Thorp, J.H., Delong, M.D., Greenwood, K.S., and Casper, A.F. (1998). Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia* **117**, 551-563.
- Thorp, J.H., Thoms, M.C., and Delong, M.D. (2006). The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* **22**, 123-147.
- Tomanova, S., Goitia, E., and Helesic, J. (2006). Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams. *Hydrobiologia* **556**, 251-264.
- Vander Zanden, J.M., and Rasmussen, J.B. (2001). Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography* **46**, 2061-2066.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.
- Wetzel, R.G. (2001). 'Limnology: Lake and River Ecosystems.' (Academic Press: San Diego.)

- Woinarski, J., Mackey, B., Nix, H., and Traill, B. (2007). 'The Nature of Northern Australia: Natural Values, Ecological Processes and Future Prospects. '(ANU E Press: Canberra.)
- Woodward, G., and Hildrew, A.G. (2002). Food web structure in riverine landscapes. *Freshwater Biology* **47**, 777-798.

Table 1: Waterbodies sampled in the study area during the 2005 and 2006 dry seasons, with site codes and information on river system, relative longitudinal and lateral positions and flow status at the time of sampling. Sites sampled in both dry seasons are underlined; otherwise sites were sampled in 2005 only.

Code	System	Longitudinal position	Lateral position	Flow status
GDm	Gregory	Downstream	Main channel	Lotic
GDo	Gregory	Downstream	Off-channel	Lotic
GMmB	Gregory	Midstream	Main channel	Lotic
GMmG	Gregory	Midstream	Main channel	Lotic
<u>GUm</u>	Gregory	Upstream	Main channel	Lotic
<u>GUo</u>	Gregory	Upstream	Off-channel	Lentic
FDm	Flinders	Downstream	Main channel	Lotic
FDo	Flinders	Downstream	Off-channel	Lentic
FMm	Flinders	Midstream	Main channel	Lentic
<u>FUm</u>	Flinders	Upstream	Main channel	Lentic
<u>FUo</u>	Flinders	Upstream	Off-channel	Lentic

Table 2: 1st-99th percentile ranges of the contribution (%) of basal sources (excluding FBOM) to *primary consumer* diets in the study region during the 2005 and 2006 dry seasons, determined using IsoSource mixing models based on $\delta^{13}\text{C}$ values. Ranges with 99th percentiles > 55% (high maximum contributions) are highlighted in bold, and < 35% (low maximum contributions) are italicised; those with 1st percentiles > 40% (high minimum contributions) are underlined.

Year	Site	Flow status	Consumer	Group	Seston (A)	CBOM (T)	Biofilm (A)	Algal scum (A)	Macroalgae (A)	Filamentous algae (A)	Aquatic (non-emergent) macrophytes (A)	Emergent macrophytes (A)
2005	FDm	Lotic	<i>Caridina</i> spp.	Decapoda	0-50	0-34	0-60	8-52	0-80	-	-	-
	FDo	Lentic	<i>Caridina</i> spp.	Decapoda	0-74	0-40	24-74	-	-	-	-	-
	FMm	Lentic	<i>Velesunio</i> sp.	Insecta	0-66	0-48	0-64	30-46	-	-	-	-
	FMm	Lentic	Leptoceridae	Insecta	0-34	0-26	0-34	62-72	-	-	-	-
	GDm	Lotic	<i>Caridina</i> spp.	Decapoda	0-44	0-92	0-60	-	-	2-50	-	-
	GDo	Lotic	Gastropoda	Mollusca	0-62	0-48	0-58	-	0-68	-	0-44	0-32
	GDo	Lotic	Leptoceridae	Insecta	0-64	0-44	0-60	-	0-70	-	0-46	0-30
	GMmB	Lentic	<i>Caridina</i> spp.	Decapoda	0-10	0-18	0-4	-	80-98	-	0-2	-
	GMmB	Lentic	Gastropoda	Mollusca	0-52	0-46	0-84	-	0-38	-	2-48	-
	GMmG	Lentic	<i>Caridina</i> spp.	Decapoda	0-48	0-70	0-58	-	0-40	-	0-52	-
	GMmG	Lentic	Gastropoda	Mollusca	0-44	0-76	0-54	-	0-44	-	0-48	-
	GUm	Lentic	<i>Caridina</i> spp.	Decapoda	18-72	0-32	0-66	-	0-70	0-16	-	-
	GUm	Lentic	<i>Velesunio</i> sp.	Mollusca	0-24	0-50	0-32	-	0-32	44-70	-	-
	GUo	Lentic	<i>Velesunio</i> sp.	Mollusca	0-22	74-86	nc	-	-	-	-	-
	FUm	Lentic	<i>Caridina</i> spp.	Decapoda	0-42	0-32	0-94	-	2-64	-	-	-
2006	FUm	Lentic	Leptoceridae	Insecta	0-40	0-30	0-92	-	6-66	-	-	-
	FUm	Lentic	<i>Velesunio</i> sp.	Mollusca	0-64	0-48	0-68	-	0-46	-	-	-
	FUm	Lentic	Zooplankton	Zooplankton	0-84	0-62	0-48	-	0-32	-	-	-
	FUo	Lentic	<i>Angrobia</i> sp.	Mollusca	0-92	2-80	0-52	0-16	-	-	-	-
	FUo	Lentic	Caenidae	Insecta	0-48	0-40	0-58	38-56	-	-	-	-
	GUm	Lentic	Caenidae	Insecta	0-64	0-62	0-44	-	0-48	0-74	0-16	-
	GUm	Lentic	Zooplankton	Zooplankton	0-64	0-62	0-44	-	0-48	0-74	0-16	-
	GUm	Lentic	Baetidae	Insecta	0-90	0-90	0-12	-	0-12	0-26	0-4	-
	GUm	Lentic	Atyidae	Decapoda	0-92	6-98	0-4	-	0-4	0-10	0-0	-
	GUm	Lentic	Nymphulinae	Insecta	0-56	0-54	0-56	-	0-62	0-66	0-22	-
	GUm	Lentic	<i>Thiara (Plotiopsis)</i> sp.	Mollusca	0-60	0-58	0-50	-	0-54	0-70	0-18	-
	GUo	Lentic	<i>Velesunio</i> sp.	Mollusca	46-94	0-52	0-10	-	-	-	-	-
	GUo	Lentic	Caenidae	Insecta	0-78	0-98	0-26	-	-	-	-	-
	GUo	Lentic	<i>Amerianna</i> sp.	Mollusca	0-72	0-92	6-32	-	-	-	-	-
	GUo	Lentic	Chironominae	Insecta	0-64	0-82	16-40	-	-	-	-	-
	GUo	Lentic	Leptoceridae	Insecta	0-58	0-74	24-46	-	-	-	-	-
	GUo	Lentic	Zooplankton	Zooplankton	38-92	0-60	0-12	-	-	-	-	-

A, aquatically derived sources of organic carbon; T, terrestrially derived. -, not present; nc, not collected.

Table 3: 1st-99th percentile ranges of the contribution (%) of basal sources (excluding FBOM) to *secondary consumer* diets in the study region during the 2005 and 2006 dry seasons, determined using IsoSource mixing models based on $\delta^{13}\text{C}$ values. Ranges with 99th percentiles > 55% (high maximum contributions) are highlighted in bold, and < 35% (low maximum contributions) are italicised; those with 1st percentiles > 40% (high minimum contributions) are underlined.

Year	Site	Flow status	Consumer	Group	Seston (A)	CBOM (T)	Biofilm (A)	Algal scum (A)	Macroalgae (A)	Filamentous algae (A)	Aquatic (non-emergent) macrophytes (A)	Emergent macrophytes (A)
2005	FDm	Lotic	Odonata	Insecta	<i>0-34</i>	<i>0-22</i>	<i>0-40</i>	40-70	<i>0-52</i>	-	-	-
	FMm	Lentic	Odonata	Insecta	0-82	0-60	0-80	<i>10-32</i>	-	-	-	-
	GDm	Lotic	<i>Macrobrachium</i> sp.	Decapoda	0-64	0-56	0-88	-	-	<i>0-30</i>	-	-
	GDm	Lotic	Odonata	Insecta	<i>0-48</i>	0-88	0-66	-	-	<i>0-46</i>	-	-
	GDo	Lotic	<i>Macrobrachium</i> sp.	Decapoda	0-64	<i>0-44</i>	0-60	-	0-70	-	<i>0-46</i>	<i>0-30</i>
	GDo	Lotic	Odonata	Insecta	<i>0-38</i>	0-80	<i>0-36</i>	-	<i>0-42</i>	-	<i>0-26</i>	4-56
	GMmB	Lotic	<i>Cherax quadricarinatus</i>	Decapoda	0-60	<i>0-54</i>	0-74	-	<i>0-46</i>	-	<i>0-40</i>	-
	GMmB	Lotic	Odonata	Insecta	0-60	0-86	<i>0-26</i>	-	2-76	-	<i>0-14</i>	-
	GMmG	Lotic	<i>Macrobrachium</i> sp.	Insecta	<i>0-48</i>	0-72	0-56	-	<i>0-40</i>	-	<i>0-50</i>	-
	GMmG	Lotic	Odonata	Insecta	<i>0-50</i>	0-66	0-60	-	<i>0-38</i>	-	<i>0-54</i>	-
	GUm	Lotic	<i>Cherax quadricarinatus</i>	Decapoda	54-86	<i>0-18</i>	<i>0-36</i>	-	<i>0-40</i>	<i>0-8</i>	-	-
	GUm	Lotic	<i>Macrobrachium</i> sp.	Decapoda	18-72	<i>0-32</i>	0-66	-	0-70	<i>0-16</i>	-	-
	GUm	Lotic	Odonata	Insecta	18-72	<i>0-32</i>	0-66	-	0-70	<i>0-16</i>	-	-
	GUo	Lentic	Odonata	Insecta	<i>0-30</i>	64-78	nc	-	-	-	-	-
	FUm	Lentic	Coenagrionidae	Insecta	<i>0-50</i>	<i>0-38</i>	0-84	-	0-56	-	-	-
2006	FUm	Lentic	Hydracarina	Hydracarina	0-86	0-64	<i>0-46</i>	-	<i>0-30</i>	-	-	-
	FUm	Lentic	Libellulidae	Insecta	<i>0-38</i>	<i>0-28</i>	0-90	-	8-68	-	-	-
	FUo	Lentic	<i>Holthuisana</i> sp.	Decapoda	<i>0-12</i>	<i>0-10</i>	<i>0-16</i>	82-90	-	-	-	-
	FUo	Lentic	Libellulidae	Insecta	<i>0-36</i>	<i>0-30</i>	<i>0-44</i>	54-68	-	-	-	-
	FUo	Lentic	Tabanidae	Insecta	<i>0-4</i>	<i>0-4</i>	<i>0-6</i>	94-100	-	-	-	-
	GUm	Lotic	<i>Macrobrachium</i> sp.	Decapoda	<i>0-48</i>	<i>0-46</i>	0-74	-	0-70	0-56	<i>2-32</i>	-
	GUm	Lotic	Protoneuridae	Insecta	0-80	0-78	<i>0-22</i>	-	<i>0-26</i>	<i>0-50</i>	<i>0-8</i>	-
	GUm	Lotic	Coenagrionidae	Insecta	0-94	2-96	<i>0-6</i>	-	<i>0-6</i>	<i>0-14</i>	<i>0-2</i>	-
	GUm	Lotic	Gomphidae	Insecta	0-86	0-84	<i>0-16</i>	-	<i>0-18</i>	<i>0-38</i>	<i>0-6</i>	-
	GUm	Lotic	Libellulidae	Insecta	0-72	0-70	<i>0-30</i>	-	<i>0-34</i>	0-64	<i>0-12</i>	-
	GUm	Lotic	Tabanidae	Insecta	0-58	0-56	<i>0-52</i>	-	0-58	0-70	<i>0-20</i>	-
	GUo	Lentic	Libellulidae	Insecta	74-100	<i>0-26</i>	<i>0-6</i>	-	-	-	-	-
	GUo	Lentic	Tanypodinae	Insecta	92-100	<i>0-8</i>	<i>0-2</i>	-	-	-	-	-
	GUo	Lentic	<i>Oecetis</i> sp.	Insecta	0-82	0-98	<i>0-22</i>	-	-	-	-	-

A, aquatically derived sources of organic carbon; T, terrestrially derived. -, not present; nc, not collected.

Figure captions

Figure 1: Study area in the southern Gulf of Carpentaria, showing location of sites sampled in the lower Gregory and Flinders river systems during the 2005 and 2006 dry seasons. Waterbody abbreviations refer to the river system (G, Gregory; F, Flinders), river section (D, downstream; M, mid; U, upstream) and lateral position (m, main channel; o, off-channel) of each site (see Table 1 for more detail). Modified from Leigh and Sheldon (2009).

Figure 2: Bi-plot of mean site $\delta^{13}\text{C}$ values and molar C:N ratios of sources collected from the study region during the 2005 dry season, with the two most distinct sources (biofilm representing aquatic sources, and CBOM representing terrestrial sources) shown as dark, closed symbols. Typical molar C:N ratios of aquatic and terrestrially-derived organic carbon in fresh waters (Wetzel 2001) are indicated by the broken line and box, respectively.

Figure 3: Means for a) $\delta^{13}\text{C}$ values and b) C:N molar ratios (with ± 1 standard error bars) of CBOM, FBOM and seston (sources with the potential to originate and be transported from upstream), in comparison with local riparian vegetation (C:N ratios only), for sites that follow a downstream continuum and were linked by surface water flow during the 2005 dry season.

Figure 4: Correlations in site mean $\delta^{13}\text{C}$ values (‰) between basal sources and macroinvertebrate consumers in the study region during the 2005 and 2006 dry seasons, showing linear correlation trend lines and R^2 values for a-b) FBOM, c-d) biofilm, and e-f) seston versus primary and secondary consumers.

Figure 5: Minimum and maximum percent contributions from basal sources (excluding FBOM) to consumer diets within waterbodies (11 sampled in 2005, 4 re-sampled in 2006) in the study region during the dry season, calculated with IsoSource mixing models on $\delta^{13}\text{C}$ data. The total number of taxa potentially assimilating each basal source is given in parentheses. Y-axes are scaled differently for the different basal sources.

Figure 2

Figure 3

Figure 4

60 **Figure 5**

Accessory Publication: Mean $\delta^{13}\text{C}$ values (‰) of basal sources for samples collected from the study region during the 2005 and 2006 dry seasons (standard errors, and number of replicates, are given in parentheses).

	GDm	GDo	GMmB	GMmG	GUm	GUm	GUo	GUo	FDm	FDo	FMm	FUm	Fum	FUo	FUo
	2005	2005	2005	2005	2005	2006	2005	2006	2005	2005	2005	2005	2006	2005	2006
Seston	-26.6 (0.2, 3)	-27.6 (0.2, 3)	-29.1 (0.8, 3)	-26.7 (0.3, 3)	-24.9 (0.7, 2)	-30.8 (0.3, 6)	-26.4 (2.0, 3)	-30.6 (0.1, 6)	-25.7 (2.2, 3)	-29.1 (2.6, 3)	-26.1 (0.6, 3)	-27.7 (0.1, 3)	-28.6 (0.1, 6)	-26.3 (0.4, 2)	-27.6 (0.1, 6)
FBOM	-29.8 (0.2, 2)	-30.1 (0.5, 2)	-28.3 (0.0, 3)	-29.0 (0.1, 3)	-29.5 (0.2, 2)	-29.0 (0.2, 6)	-24.1 (1.1, 3)	-26.7 (0.2, 6)	-22.3 (0.9, 3)	-28.3 (0.1, 3)	-26.7 (0.3, 3)	-24.2 (0.4, 3)	-23.4 (0.7, 6)	-26.6 (0.2, 3)	-25.8 (0.3, 6)
CBOM	-31.1 (0.4, 2)	-31.3 (0.5, 3)	-29.9 (0.3, 3)	-30.7 (0.4, 3)	-31.4 (0.5, 2)	-31.0 (0.3, 6)	-29.7 (0.5, 3)	-29.5 (0.1, 6)	-30.7 (0.3, 3)	-29.9 (0.1, 3)	-29.8 (0.2, 3)	-29.9 (0.8, 3)	-31.5 (0.4, 5)	-28.3 (0.7, 3)	-29.2 (0.2, 6)
Biofilm	-28.9 (0.1, 3)	-27.2 (1.6, 3)	-26.3 (0.5, 2)	-27.9 (0.1, 2)	-28.2 (-, 1)	-27.1 (0.4, 6)	-	-25.6 (0.3, 5)	-24.1 (1.6, 3)	-28.1 (0.6, 3)	-26.3 (0.4, 3)	-24.0 (0.9, 3)	-23.5 (0.5, 6)	-24.7 (1.0, 2)	-26.2 (0.4, 6)
Filamentous algae	-35.0 (0.9, 2)	-	-	-	-37.6 (1.8, 3)	-29.2 (2.5, 2)	-	-	-	-	-	-	-	-	-
Algal scum	-	-	-	-	-	-	-	-	-14.7 (0.1, 2)	-	-15.7 (0.2, 2)	-	-	-	-19.6 (1.5, 3)
Macroalgae *	-	-28.3 (-, 1)	-31.4 (-, 1)	-33.7 (-, 1)	-28.0 (-, 1)	-27.5 (0.6, 4)	-	-	-21.7 (-, 1)	-	-	-	-19.6 (1.3, 3)	-	-
Aquatic macrophytes (non-emergent)	-	-25.0 (1.9, 3)	-22.2 (-, 1)	-27.2 (1.8, 2)	-	-20.7 (-, 1)	-	-	-	-	-	-	-	-	-
Emergent macrophytes	-	-34.2 (-, 1)	-	-	-	-	-	-	-	-	-	-	-	-	-
Riparian vegetation (C ₃)	-32.1 (0.8, 4)	-31.9 (1.2, 2)	-30.6 (0.5, 2)	-32.6 (1.6, 2)	-31.4 (0.7, 3)	-29.7 (0.3, 6)	-29.6 (0.7, 2)	-30.2 (0.3, 5)	-30.9 (-, 1)	-29.2 (0.6, 2)	-31.2 (-, 1)	-31.6 (-, 1)	-29.6 (0.5, 2)	-29.6 (0.5, 2)	-29.2 (0.5, 3)
Riparian vegetation (C ₄)	-	-13.5 (-, 1)	-	-	-14.4 (-, 1)	-13.9 (-, 1)	-	-14.3 (1.2, 2)	-13.4 (-, 1)	-14.1 (-, 1)	-13.1 (-, 1)	-13.9 (0.3, 2)	-	-	-15.2 (-, 1)

* *Chara* sp. only at Gregory sites; *Chara* and *Nitella* spp. at FDM; *Nitella* sp. only at FUM.