Trophic structure of benthic resources and consumers varies across a regulated floodplain wetland

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Abstract. Riverine food webs are often laterally disconnected (i.e. between watercourses) in regulated floodplain wetlands for prolonged periods. We compared the trophic structure of benthic resources and consumers (crustaceans and fish) of the three watercourses in a regulated floodplain wetland (the Gwydir Wetlands, Australia) that shared the same source water but were laterally disconnected. The crustaceans *Cherax destructor* (yabby), *Macrobrachium australiense* (freshwater prawn), the exotic fish *Cyprinus carpio* (European carp) and *Carassius auratus* (goldfish) showed significantly different δ^{13}C values among the watercourses, suggesting spatial differences in primary carbon sources. Trophic positions were estimated by using δ^{15}N values of benthic organic matter as the base of the food web in each watercourse. The estimated trophic positions and gut contents showed differences in trophic positions and feeding behaviours of consumers between watercourses, in particular for *Melanotaenia fluviatilis* (Murray–Darling rainbowfish) and *M. australiense*. Our findings suggest that the observed spatial variation in trophic structure appears to be largely related to the spatial differences in the extent and type of riparian vegetation (i.e. allochthonous carbon source) across the floodplain that most likely constituted part of the benthic resources.

Additional keywords: allochthonous carbon source, food webs, riparian vegetation, river regulation, spatial segregation, stable isotopes.

Introduction

Floodplain wetlands provide habitats for many species of terrestrial and aquatic biota (Junk *et al.* 1989; Bayley 1991; Junk and Wantzen 2004). River regulation has increased the spatial and temporal extent of lateral disconnection between watercourses in the wetlands (Kingsford 2000; Frazier and Page 2006; Powell *et al.* 2008). Aquatic food webs in regulated floodplain wetlands are confined within watercourses for prolonged periods. Under such environmental conditions, the structure of aquatic food webs is most likely influenced by in-channel conditions (e.g. hydrology, habitat size and complexity) and surrounding geomorphic settings (e.g. riparian vegetation) specific to the watercourses (Tockner *et al.* 2000; Thorp *et al.* 2006; Zeug and Winemiller 2008). This may lead to spatial differences in trophic structure across a regulated floodplain wetland.

The major aquatic consumers of floodplain wetlands include native and exotic fish, reptiles, amphibians and invertebrates. Freshwater crustaceans break down leaf matter and in the case of omnivorous and carnivorous species regulate prey populations (Momot 1995; Usio 2000). *Cherax destructor* ('yabby') is the most abundant and widespread freshwater crayfish in Australia (Jones and Obst 2000). The natural diet of yabbies may include either plant material and detritus or small fish (Bunn and Boon 1993; Beatty 2006). The freshwater palaemonid prawn *Macrobrachium australiense* is another widespread freshwater crustacean in Australia (Murphy and Austin 2004). This species is an indiscriminate scavenger and browser, known to feed on bacteria and biofilm (Lee and Fielder 1982; Burns and Walker 2000). Fish often regulate prey populations including plants, herbivores and other predators (Hall *et al.* 1970; Thorp 1986; Power 1990). In Australia, the trophic ecology of freshwater fish has been studied in relation to the food sources sustaining populations (Medeiros 2004; Burford *et al.* 2008), dietary overlaps between native and exotic species (Pen and Potter 1991; Pen *et al.* 1993), flow conditions (Balcombe *et al.* 2005; Sternberg *et al.* 2008) and fish passage obstruction in regulated rivers (Baumgartner 2007).

Stable carbon and nitrogen isotope analysis is a useful technique in food web research (Peterson and Fry 1987; Fry 1991; Post 2002). Carbon isotopes indicate the sources of organic carbon for consumers and their cycling through an ecosystem, with important distinctions in carbon isotope values among key primary producers, including C_3 and C_4 plants (Smith and Epstein 1971), and less distinctly, between benthic and pelagic algae (France 1995; Finlay *et al.* 1999). Nitrogen isotopes are used to indicate the trophic position of consumers. In Australian wetlands, stable isotopes have been used to identify not only the sources of organic carbon in floodplain waterholes (Bunn and Boon 1993; Bunn *et al.* 2003) and rivers (Bunn *et al.* 2003; Burford *et al.* 2008) but also the contribution of aquatic and riparian plants to shredder communities (Deegan and Ganf 2008).

In the present study, we used stable isotopes and gut contents to examine the trophic structure of benthic resources and consumers (crustaceans and fish) among watercourses in a regulated floodplain wetland that shared the same source water but were spatially segregated. We tested the prediction that the trophic structure of benthic resources and consumers varies significantly among watercourses. Under river regulation, riverine food webs are affected by riverscape resources such as autochthonous autotrophs and heterotophs, and riparian

vegetation. We expected that the spatial variation in the trophic structure would reflect the variation in the extent and type of riverscape resources across the ecosystem.

Materials and methods

Study area

Our study area is the Gwydir Wetlands ($\sim$102 100 ha), an ecologically important floodplain wetland system in the northern Murray–Darling Basin of New South Wales, Australia (Fig. 1). The wetlands support threatened wetland plants and native fish (Wilson *et al.* 2009, 2010) and provide significant breeding sites for colonially nesting waterbirds (Kingsford 2000; Spencer and Allman 2009), although the wetlands are located within a highly developed agricultural landscape dominated by irrigated crop production, dryland cropping, and cattle and sheep grazing. Annual average rainfall of the Gwydir Wetlands is <450 mm year^{-1} (Keyte 1994).

Regulated flows into the wetlands are released via the Gwydir River from Copeton Dam for irrigation, stock and domestic and environmental purposes. The Gwydir River diverges into the following three major watercourses near Moree: the Gingham Watercourse, Lower Gwydir River and Mehi River (Fig. 1). The Mehi River generally has the highest
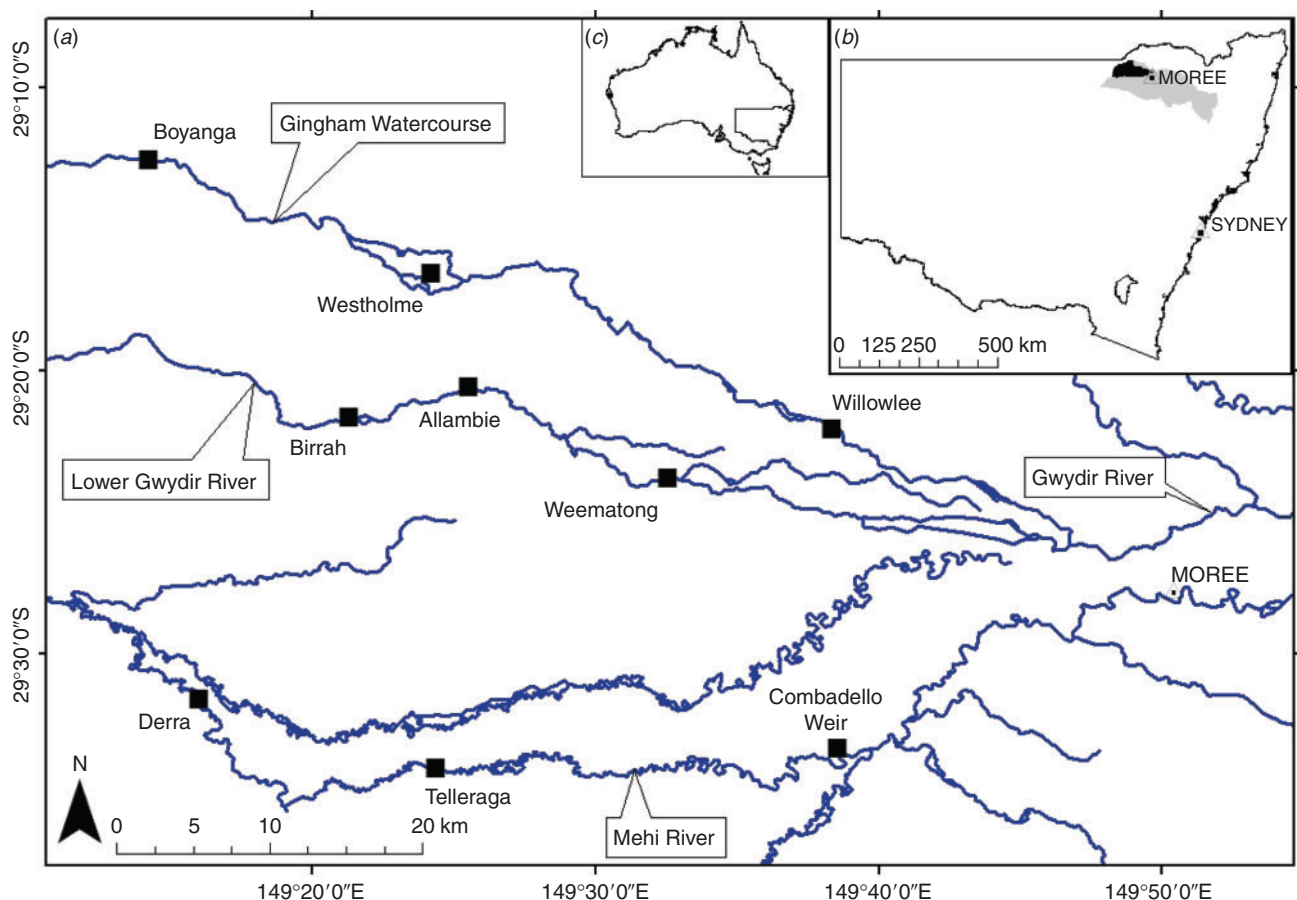

Fig. 1. (*a*) Location of nine sampling sites (■) in (*b*) the Gwydir Wetlands (blackened area) in the Gwydir catchment (light grey area) in New South Wales, (*c*) Australia.
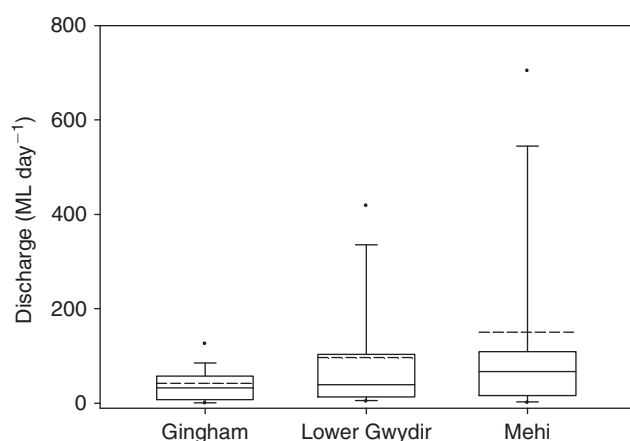
Fig. 2. Box-and-whisker plots of daily discharge (ML day^{-1}) for the 12 months preceding field sampling in the Gingham Watercourse, Lower Gwydir River and Mehi River in the Gwydir Wetlands. Lower and upper whiskers indicate 5th and 95th percentiles and mean discharge rates are indicated by dashed line.

discharge of the three watercourses (median daily discharge rate in the 12 months preceding sampling: 66.8 ML day^{-1}), followed by the Lower Gwydir River (39.3 ML day^{-1}) and the Gingham Watercourse (33.2 ML day^{-1}) (Fig. 2). Summer flows for agricultural purposes dominated the hydrograph 12 months before our field sampling (late March to early May 2007). The Lower Gwydir River also received an environmental contingency allowance (ECA) flow in December 2006, and all three watercourses had a small increase in discharge following rainfall in early March 2007.

The Gingham Watercourse has experienced a major decrease in the extent of its riparian woodland cover (*Acacia stenophylla*, *Eucalyptus coolabah* and *E. camaldulensis*) across recent decades (McCosker and Duggin 1993), However, despite clearing across floodplain areas, riparian tree coverage along the immediate riparian zones of the Lower Gwydir and Mehi Rivers remains largely intact. The Mehi River also has a higher degree of in-channel habitat complexity (e.g. coarse woody debris and variable water depths) than the other two watercourses. The Gwydir Wetlands have a native fish fauna numerically dominated by *Nematalosa erebi* (bony bream), *Leiopotherapon unicolor* (spangled perch) and *Hypseleotris* spp. (carp gudgeons) (Spencer *et al.* 2008; Wilson *et al.* 2009). The exotic *Cyprinus carpio* (European carp) represents more than 50% of the fish biomass in the wetlands. Other exotic fish species include *Carassius auratus* (goldfish) and *Gambusia holbrooki* (plague minnow) (Wilson *et al.* 2009, 2010).

Field sampling

Three sampling sites were chosen along each of the Gingham Watercourse ('Willowlee', 'Westholme', 'Boyanga'), Lower Gwydir River ('Weematong', 'Allambie', 'Birrah') and Mehi River (downstream of Combadello Weir, 'Telleraga', 'Derra') (Fig. 1). Sampling was carried out at all sites from late March to early April 2007, before an ECA release in the Gingham Watercourse. Freshwater prawns (*Macrobrachium australiense*), yabby (*Cherax destructor*) and fish were sampled by fyke

netting for an average duration of 18 h in each location. Two large fyke nets (12-mm stretched mesh, 1.1-m diameter, 7.5-m wings) and two small fyke nets (2-mm mesh, 0.4-m diameter, 1.2-m wings) were set at each site, one of each size class facing upstream and one downstream. Nets were set in the late afternoon and retrieved the following morning. We recognise that gut contents for some of the species may have included food items that had been consumed while in the nets. Duplicate samples of benthic (0–5 cm depth) sediment organic matter (SOM) were collected at each site with a hand-corer at a water depth of < 1 m. Fresh leaf samples were also collected from dominant aquatic plants (*Typha domingensis*, *Persicaria decipiens* and *Eichhornia crassipes*), riparian trees (*Acacia stenophylla*, *Eucalyptus camaldulensis* and *Eucalyptus coolabah*) and floodplain groundcover plants (*Muehlenbeckia florulenta*, *Juncus aridicola* and *Phyla canescens*). All samples were immediately frozen and kept at −20°C until laboratory preparation and analysis.

Sample preparation

Consumer and plant specimens collected at each site were pooled within each watercourse. A maximum of five similar-sized adult specimens of each species (cf. Mazumder *et al.* 2008) were selected from each watercourse for stable isotope analyses (Table 1). On thawing, a small portion of dorsal muscle tissue was taken from each fish. For the crustaceans, the samples of tail muscle tissue were placed in a Petri dish, bathed in 0.1 N HCl for 1 h (Polunin *et al.* 2001) and rinsed with Milli-Q water to remove calcium carbonates within the animal's newly developing shell. Benthic sediment samples were rinsed with Milli-Q water through a series of sieves (1000, 500 and 250 μm). Material retained on each of the 500-μm mesh, 250-μm mesh and collection basin (i.e. < 250 μm) was subsampled for the analysis of carbon (bathed in 0.1 N HCl for 1 h) and nitrogen (unbathed) (e.g. Bunn *et al.* 1995). Leaf samples were rinsed with Milli-Q water before drying and grinding. All samples were oven-dried at 60°C for 24 h. After drying, samples were ground to a fine powder with a mortar and pestle.

Stable isotope measurements

Powder for each sample was analysed with a continuous flow stable-isotope mass spectrometer (GV Instruments IsoPrime EA/IRMS, Manchester, UK) at the Institute for Environmental Research, the Australian Nuclear Science and Technology Organisation. All isotopic values were reported in the notation: δ^{13}C or δ^{15}N = $[(X_{sample}/X_{standard}) - 1]$ in parts per thousand (‰), where X is ^{13}C/^{12}C or ^{15}N/^{14}N. Pee Dee Belemnite and N$_2$ in air were used as international standards for δ^{13}C and δ^{15}N, respectively.

Gut content analysis

An analysis of gut contents was conducted on 1–11 specimens (mode $n = 3$) of each crustacean and fish species, from which the muscle tissues had already been taken for stable isotope analysis (total $n = 75$). The entire digestive tract was removed from each specimen and the contents examined at magnifications of ×100 to ×320. Items were identified to the finest level of taxonomy possible (order level in general) and recorded in terms of presence/absence.

Table 1. Sediment organic matter (SOM) and aquatic consumer species analysed from the Gingham Watercourse, Lower Gywdir River and Mehi River in the Gwydir Wetlands
Feeding-group classifications follow the adult-fish feeding groups in Kennard *et al.* (2001). *Exotic species

Common name	Scientific name	Feeding group	No. of samples analysed		
			Gingham	Lower Gwydir	Mehi
SOM (×3 size fractions)			6 (18)	6 (18)	6 (18)
Freshwater prawn	*Macrobrachium australiense*	Indiscriminate scavenger and browser	5	5	5
Yabby	*Cherax destructor*	Detritivore and omnivore	5	5	5
Bony bream	*Nematalosa erebi*	Microphagic detritivore and zooplanktivore	5	5	5
Spangled perch	*Leiopotherapon unicolor*	Macrophagic carnivore	5	4	5
Carp gudgeon	*Hypseleotris* spp.	Microphagic carnivore	–	2	5
Murray–Darling rainbowfish	*Melanotaenia fluviatilis*	Microphagic carnivore	1	5	4
Eel-tailed catfish	*Tandanus tandanus*	Macrophagic carnivore	1	–	–
Golden perch	*Macquaria ambigua*	Macrophagic carnivore	–	–	1
Australian smelt	*Retropinna semoni*	Microphagic carnivore	–	–	1
European carp	*Cyprinus carpio**	Microphagic omnivore	5	3	5
Goldfish	*Carassius auratus**	Microphagic omnivore	5	5	–
Gambusia	*Gambusia holbrooki**	Aquatic and terrestrial insectivore	–	–	3

Data analysis

The C : N mass ratio was calculated for each stable isotope sample. If an overall mean C : N ratio was >3.5 for a species, a lipid-normalisation equation (Post *et al.* 2007) was applied to $\delta^{13}C$ values for that species, as follows:

$$\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N \quad (1)$$

Trophic position (TPO) was calculated following Post (2002):

$$TPO = \lambda + (\delta^{15}N_{organism} - \delta^{15}N_{base\ of\ food\ web})/3.4 \quad (2)$$

where λ is the trophic position of the organism used to estimate $\delta^{15}N_{base\ of\ food\ web}$.

In the present study, SOM (all size classes pooled) was assumed as the most likely basal trophic resource (i.e. $\lambda = 1$), and so the formula used to identify trophic position for each individual was:

$$TPO = 1 + (\delta^{15}N_{organism} - water\ course\ mean\ \delta^{15}N_{SOM})/3.4 \quad (3)$$

Comparison of SOM and consumer $\delta^{13}C$ values among the watercourses was made using one-way analysis of variance (ANOVA), or Welch's F-test if homogeneity of sample variance was rejected on the basis of the Levene's test ($\alpha = 0.05$). When one-way ANOVA or Welch's F-test provided significant results, Tukey's pairwise comparisons were used to compare each pair of means. Student's t-test or Welch t-test (for samples with heterogeneous variance) was used if samples were present only in two watercourses. All statistical procedures were carried out using PAST (version 1.82) software (Hammer *et al.* 2001).

Results

Plants

The plant species showed little variation in $\delta^{13}C$ both within and among species, with mean ($\pm$s.d.) values ranging from

Table 2. Mean and standard deviation (s.d.) of $\delta^{13}C$ and $\delta^{15}N$ values for common plant species in the Gwydir Wetlands

Species (no. of samples)	$\delta^{13}C$		$\delta^{15}N$	
	Mean	s.d.	Mean	s.d.
Aquatic				
Typha domingensis (8)	−29.6	1.1	7.2	0.8
Persicaria decipiens (8)	−30.5	0.8	9.0	1.6
Eichhornia crassipes (2)	−29.3	0.0	6.0	0.9
Riparian trees				
Acacia stenophylla (12)	−29.9	1.4	−0.9	2.3
Eucalyptus camaldulensis (12)	−29.1	1.4	3.6	1.3
Eucalyptus coolabah (6)	−30.2	1.1	2.7	1.3
Floodplain groundcover				
Muehlenbeckia florulenta (8)	−28.5	1.8	6.3	2.4
Juncus aridicola (6)	−27.1	1.5	5.1	1.6
Phyla canescens (6)	−29.3	0.9	8.6	3.8

$-30.5 \pm 0.8‰$ (*P. decipiens*) to $-27.1 \pm 1.5‰$ (*J. aridicola*). In contrast, $\delta^{15}N$ ratios were considerably more depleted among riparian tree species ($-0.9 \pm 2.3‰$ to $3.6 \pm 1.3‰$) than aquatic ($6.0 \pm 0.9‰$ to $9.0 \pm 1.6‰$) and floodplain groundcover species ($5.1 \pm 1.6‰$ to $8.6 \pm 3.8‰$) (Table 2).

Sediment organic matter (SOM)

Among the watercourses, the mean ($\pm$s.d.) $\delta^{13}C$ values of three size classes of SOM varied from $-26.1 \pm 1.4‰$ to $-24.5 \pm 0.8‰$ (size class: $<250\ \mu m$), $-26.0 \pm 1.3‰$ to $-25.0 \pm 0.6‰$ ($250–500\ \mu m$), and $-25.8 \pm 1.5‰$ to $-23.8 \pm 5.4‰$ ($500–1000\ \mu m$). There was no significant difference in the mean $\delta^{13}C$ values of each size class of SOM among the watercourses ($P > 0.094$). The mean ($\pm$s.d.) $\delta^{15}N$ values of three size classes of SOM varied from $3.9 \pm 1.2‰$ to $5.3 \pm 2.9‰$ ($<250\ \mu m$), $4.1 \pm 2.0‰$ to $4.6 \pm 0.8‰$ ($250–500\ \mu m$), and $4.0 \pm 1.6‰$ to $5.2 \pm 1.4‰$ ($500–1000\ \mu m$).

The overall mean ($\pm$s.d.) values of $\delta^{13}C$ and $\delta^{15}N$ of SOM in each watercourse were -25.2 ± 3.4‰ and 4.4 ± 1.3‰ in the Gingham Watercourse, -25.7 ± 1.3‰ and 4.7 ± 2.0‰ in the Lower Gwydir River, and -24.9 ± 0.7‰ and 4.1 ± 1.9‰ in the Mehi River (Fig. 3).

Lipid normalisation among consumers

Lipid normalisation on $\delta^{13}C$ was required only for the crustaceans *C. destructor* (mean muscle tissue C : N = 3.59, max = 3.79) and *M. australiense* (mean C : N = 3.55, max = 3.97). Normalisation increased $\delta^{13}C$ values only slightly for *M. australiense* (mean change = 0.21‰).

Crustaceans

The mean ($\pm$s.d.) $\delta^{13}C$ value (-21.0 ± 0.6‰) of *C. destructor* in the Mehi River was significantly more enriched than that in the Gingham Watercourse (by 2.7‰) and Lower Gwydir River (by 3.7‰) ($P < 0.001$). Mean $\delta^{13}C$ values of *C. destructor* and SOM were relatively closer in the Gingham and Lower Gwydir than those in the Mehi (Fig. 3). *C. destructor* was the consumer most depleted in $\delta^{15}N$ (≤ 8.4‰) in each watercourse. This was especially the case in the Mehi River, where the mean $\delta^{15}N$ value of *C. destructor* was >2‰ more depleted than that of the other consumer species examined in the watercourse. *C. destructor* held the lowest trophic position (range: 1.8–2.4) among consumers in each watercourse (Fig. 4).

The mean ($\pm$s.d.) $\delta^{13}C$ value (-25.2 ± 0.3‰) of *M. australiense* in the Lower Gwydir River was similar to that in the Gingham Watercourse whereas it was significantly more depleted than the mean $\delta^{13}C$ value (-23.4 ± 1.0‰) in the Mehi River ($P = 0.002$). The mean $\delta^{13}C$ value of *M. australiense* was close to that of SOM (<1.5‰ trophic fractionation) in each watercourse. The trophic position of *M. australiense* (range: 2.5–3.4) was higher than that of some of the fish species examined in each watercourse (Fig. 4). Food items in the guts of *C. destructor* and *M. australiense* were difficult to identify because the items were highly macerated. Between the two crustacean species, however, the occurrence of algae was more frequent in the guts of *C. destructor*, whereas invertebrate fragments and unidentified animal material were more frequent in the guts of *M. australiense* (Table 3).

Native fish

Nematalosa erebi was more depleted in the mean $\delta^{13}C$ values (≤ -27.2‰) than most other consumer species examined and displayed the largest variation in the mean $\delta^{13}C$ values (Fig. 3). There was some variation in its trophic position both within and among watercourses (range: 2.3–2.9) (Fig. 4). This fish species also held a trophic position within the range of the exotic species *Cyprinus carpio* and *Carassius auratus* (Fig. 4). Gut contents of *N. erebi* were distinct from those of the other fish species analysed, containing plant material, sediment and benthic diatoms (i.e. *Aulacoseira*, *Nitzschia*, *Melosira*, *Surirella*, *Cymbella*, *Cyclotella*, *Cocconeis* and *Eunotia*) in all watercourses (Table 3).

The mean $\delta^{13}C$ values of *Leiopotherapon unicolor* varied little (-25.8‰ to -25.3‰) and did not differ significantly among the watercourses. There was, however, relatively large
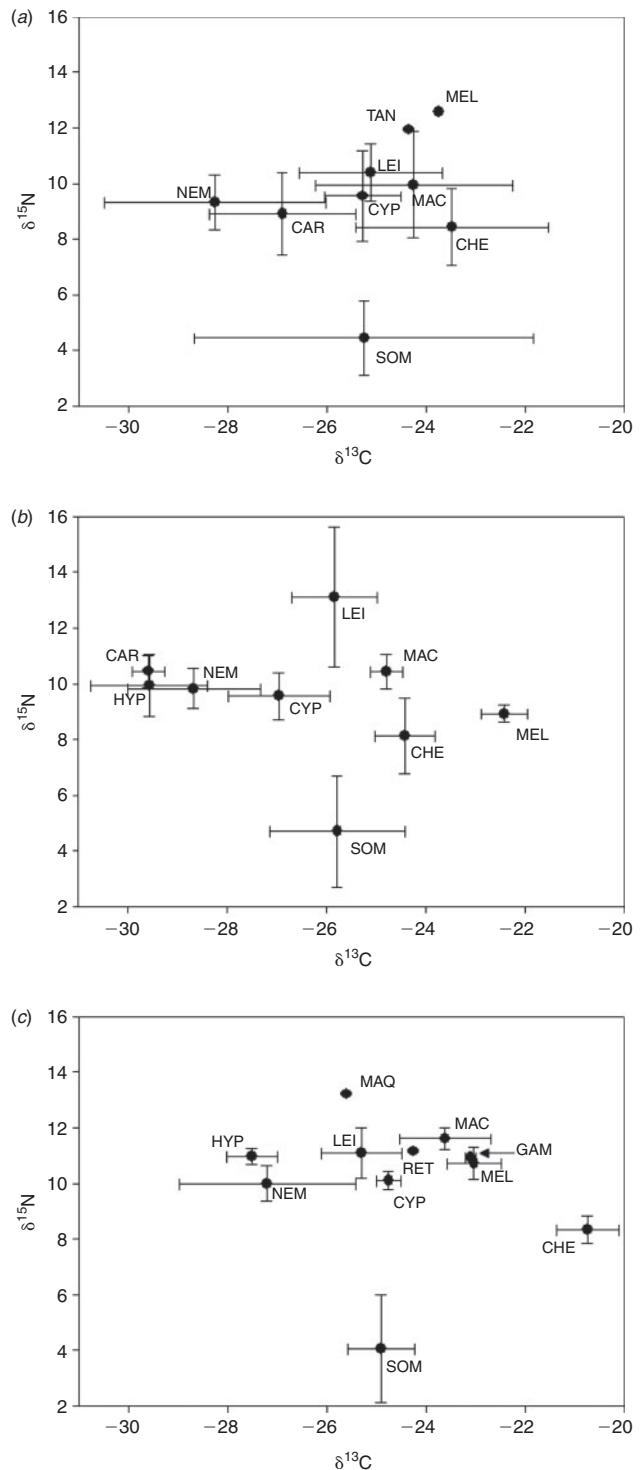
Fig. 3. Mean ($\pm$s.d.) $\delta^{13}C$ and $\delta^{15}N$ values of sediment organic matter (SOM) and aquatic consumer species in the Gwydir Wetlands. (*a*) Gingham Watercourse, (*b*) Lower Gwydir River and (*c*) Mehi River. Error bars indicate a standard deviation. SOM, sediment organic matter; MAC, *Macrobrachium australiense*; CHE, *Cherax destructor*; NEM, *Nematalosa erebi*; LEI, *Leiopotherapon unicolor*; HYP, *Hypseleotris* spp.; MEL, *Melanotaenia fluviatilis*; TAN, *Tandanus tandanus*; MAQ, *Macquaria ambigua*; RET, *Retropinna semoni*; CYP, *Cyprinus carpio*; CAR, *Carassius auratus*; and GAM, *Gambusia holbrooki*.

Fig. 4. Trophic positions (mean ± s.d.) of aquatic consumer species from the Gingham Watercourse, Lower Gwydir River and Mehi River in the Gwydir Wetlands. Species are shown from lowest (left) to highest (right) on the basis of their overall mean trophic position across all locations.
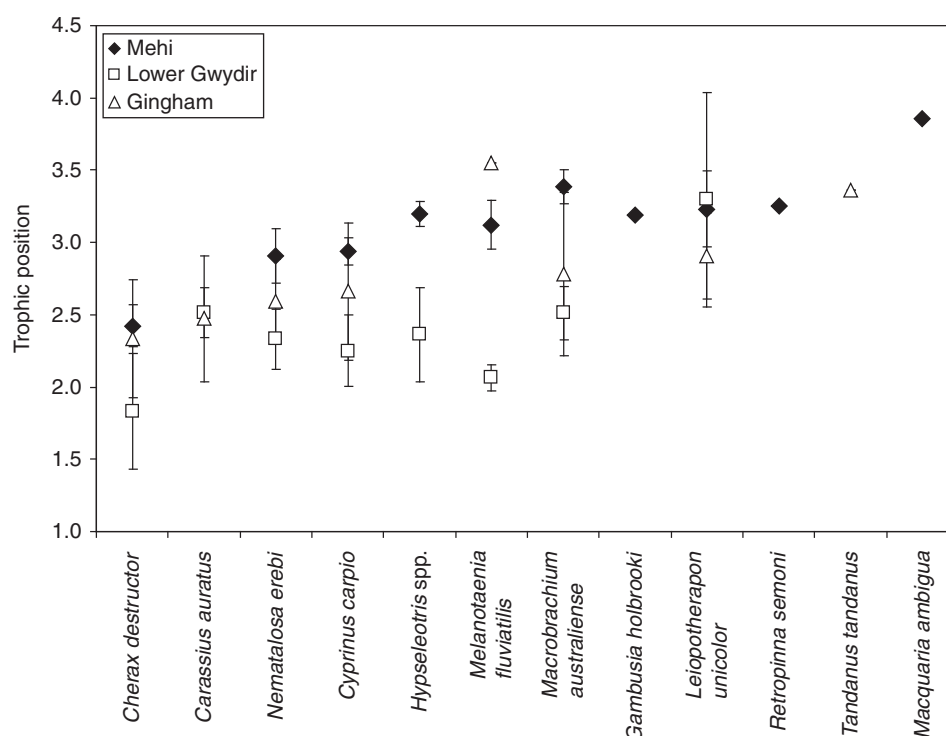
variation in the mean δ^{15}N values (from 10.4‰ in the Gingham to 13.1‰ in the Lower Gwydir) and trophic position of *L. unicolor* among the watercourses. Although fish, crustaceans and aquatic insects were common items in the guts, filamentous green algae were found only in the Gingham samples.

Hypseleotris spp. had the most depleted mean δ^{13}C value ($\leq$ −27.5‰) among all fish species examined. In the Mehi River, *Hypseleotris* spp. had a mean δ^{15}N value and trophic position (3.2) similar to those of four other fish species (*L. unicolor*, *R. semoni*, *G. holbrooki* and *M. fluviatilis*), although the mean δ^{13}C value of *Hypseleotris* spp. was distinct from them (Fig. 3). Gut contents of *Hypseleotris* spp. comprised fish, prawns, aquatic insects and zooplankton (Table 3).

Melanotaenia fluviatilis was the species most enriched in the δ^{13}C value among all fish species examined in each watercourse (Fig. 3). The mean δ^{15}N value for *M. fluviatilis* varied among the watercourses, ranging from 8.9‰ in the Lower Gwydir to 12.6‰ in the Gingham. The trophic position of *M. fluviatilis* varied among the watercourses, ranging from 2.1 in the Lower Gwydir to 3.5 in the Gingham (Fig. 4). Gut contents from the Lower Gwydir and Mehi specimens comprised aquatic insects and zooplankton, whereas the single Gingham sample contained algae and plant detritus (Table 3).

Only a single specimen was analysed for *R. semoni* (body length: 46 mm, Mehi River), *T. tandanus* (320 mm, Gingham Watercourse) and *M. ambigua* (243 mm, Mehi River). The samples indicated relatively high trophic positions of 3.3, 3.4 and 3.9, respectively (Fig. 4). The single *T. tandanus* gut contained prawns, yabbies, aquatic insects, plant detritus and

gravel. The gut of *M. ambigua* contained prawns and aquatic insects, whereas that of *R. semoni* contained several invertebrate taxa (Table 3).

Exotic fish

The δ^{13}C value (mean ± s.d.: −27.0 ± 1.0‰) of *C. carpio* in the Lower Gwydir River was significantly ($P = 0.01$) more depleted than those in the Gingham Watercourse (−25.3 ± 0.8‰) and Mehi River (−24.8 ± 0.2‰). In the Gingham and Mehi, the δ^{13}C value of *C. carpio* was less variable than that of the other fish species present (Fig. 3). *Carassius auratus* was also significantly more depleted in δ^{13}C in the Lower Gwydir River (−29.6 ± 0.3‰) than in the Gingham (−26.9 ± 1.5‰) (Fig. 3). The trophic positions of *C. carpio* and *C. auratus* were, however, both relatively low ($\leq$2.9) in each watercourse (Fig. 4). Gut contents (animal remains, microinvertebrates, algae and plant detritus) of *C. carpio* and *C. auratus* were also similar with each other within and among the watercourses. *Gambusia holbrooki* found only in the Mehi River (trophic position: 3.2) showed little variation in δ^{13}C and δ^{15}N values (−23.1 ± 0.1‰ and 10.9 ± 0.1‰), and in the gut contents, including only invertebrates (Table 3).

Discussion

Sources of carbon for aquatic consumers

On the basis of the similarity of δ^{13}C values between the source and consumers, and the estimated trophic position of consumers, SOM seems to be a primary source of carbon for *C. destructor* and to a lesser extent for *M. australiense* in the Gwydir

Table 3.   Summary of gut content analyses for aquatic consumer species from the Gingham Watercourse (GIN), Lower Gwydir River (GWY) and Mehi River (MEH) in the Gwydir Wetlands

Results represent the number of guts in which each food item was present

Location (no. of guts analysed)	Macrobrachium australiense			Cherax destructor			Nematalosa erebi			Leiopotherapon unicolor			Hypseleotris spp.		Melanotaenia fluviatilis			Tandanus tandanus	Macquaria ambigua	Retropinna semoni	Cyprinus carpio			Carassius auratus		Gambusia holbrooki
	GIN (3)	GWY (3)	MEH (3)	GIN (3)	GWY (3)	MEH (2)	GIN (3)	GWY (3)	MEH (3)	GIN (11)	GWY (3)	MEH (2)	GWY (2)	MEH (3)	GIN (1)	GWY (3)	MEH (3)	GIN (1)	MEH (1)	MEH (1)	GIN (3)	GWY (3)	MEH (3)	GIN (3)	GWY (3)	MEH (3)
Fish																										
Unidentified										3			1													
Unidentified fragments			1							4																
Macroinvertebrates																										
Macrobrachium sp.										1	1	1		1				1	1							
Macrobrachium sp. (fragments)				2		1				2	1			2				1	1							
Cherax destructor (fragments)																		1								
Isopoda (Cirolanidae)																		1								
Mollusca (bivalve fragments)																		1								
Nematoda																				1						1
Coleoptera										2						1	3		1	1						1
Ephemeroptera																				1						
Hemiptera										7	1			1		3	1									
Diptera										1				1			1	1								
Unidentified animal material																										
Invertebrate fragments	3	2		2						4	2	1	1			1		1	1	1	1					1
Animal material	1	2			1					1	1								1							
Eggs							1														1	1	3	1	1	
Microinvertebrates																										
Ostracoda																									1	
Cyclopoida													1			2	2				1	3	3		2	1
Calanoida																				1		1			1	
Cladocera									2				1				2				2	1	3		1	2
Rotifera (Lecane bulla)									1																	
Protozoa																								1	1	
Algae																										
Diatoms				2	1	2	3	3	3						1						1			1	1	
Green algae				2	2	2	2	3	3	8					1								3	2	2	
Dinoflagellates						1			1																	
Unidentified algae					2	2																				
Other																										
Plant detritus	3	2	3	3	3	2	2	2	1	1					1			1			3	3	3	3	3	
Sediment/gravel	3		3	3	3	1	2	3	3									1			3	3	3	3	3	

Wetlands. The similarity of $\delta^{13}C$ values and comparable variability between the SOM and most fish species within the Gingham Watercourse also suggests that SOM constituted an important source of carbon in this channel. However, the highly depleted $\delta^{13}C$ value of several consumers (especially *Hypseleotris* spp., *N. erebi* and *C. auratus*) relative to SOM in each watercourse clearly indicates that the aquatic food webs of the Gwydir Wetlands are supported by multiple primary carbon sources.

The stable isotopes of the riparian C_3 plants in the Gwydir Wetlands all showed highly depleted $\delta^{13}C$ values relative to SOM. The corresponding highly depleted $\delta^{13}C$ values in some consumers suggest that they were supported by carbon sources derived from C_3 plants. The stable isotope values of SOM reflect a combination of the signatures of various organic components including benthic algae, bacteria, fungi, and animal detritus and perhaps microinvertebrates. Gut content analyses of the Gwydir consumers confirmed that diverse items (fish, invertebrates, benthic algae, and plant and animal detritus) were ingested by the consumers to varying degrees. Although the specific organic components of SOM were not examined, it is highly likely that the C_3 plant material also constituted an important component of SOM in each watercourse. This is because the observed range of $\delta^{13}C$ values from the C_3 plant community overlapped with that of SOM.

It appears that species of riparian trees (*E. camaldulensis* and *E. coolabah*) and floodplain groundcover (*M. florulenta* and *J. aridicola*) may have contributed more to SOM in the Gwydir Wetlands than did the aquatic plant species because their $\delta^{15}N$ values were closer to those of SOM than were those of the aquatic plant species. This is consistent with a current model of floodplain wetlands that the allochthonous source of carbon in the form of riparian plant detritus and leachate can dominate the carbon pools of floodplain rivers (Baldwin 1999; Robertson *et al.* 1999; Howitt *et al.* 2008). In the Gwydir Wetlands, the contribution of plant material to SOM may have been more pronounced in the Lower Gwydir River, where consumer taxa (*N. erebi*, *Hypseleotris* spp. and *C. carpio*) showed more depleted $\delta^{13}C$ than in the other two watercourses.

Feeding behaviours of aquatic consumers

The $\delta^{13}C$ values of *C. destructor* in the Gingham Watercourse and Lower Gwydir River were closely aligned to SOM. This is similar to the findings of Bunn and Boon (1993) who classified *Cherax* as a detritivore in floodplain lakes, on the basis of stable isotope analyses. However, the more enriched carbon signature of *C. destructor* in the Mehi River suggests that this species may also have used benthic algae or detritus from unsampled C_4 plants (see Smith and Epstein 1971). This is because the gut contents of *C. destructor* in the Mehi River included benthic diatoms, green algae and plant detritus. On the other hand, *M. australiense* was both a browser and a scavenger (*sensu* Lee and Fielder 1983), as indicated by a relatively high trophic position and the animal material found in the guts.

Nematalosa erebi is one of the most abundant fish within the Gwydir Wetlands (Spencer *et al.* 2008). Gut contents and low $\delta^{15}N$ values showed that this species was primarily a herbivore/

detritivore, as classified by Harris (1995), with bottom sediment-feeding apparent in the watercourses. This species is known to change its diet according to the availability of food associated with different flow regimes (Sternberg *et al.* 2008). It was not possible in the present study to demonstrate clearly whether such dietary changes occurred among the watercourses, although some animal components (zooplankton) were found only in the guts of *N. erebi* from the higher-flow Mehi River. *Leiopotherapon unicolor* showed distinctly more enriched $\delta^{13}C$ values than the other two dominant native fish in the Gwydir Wetlands (*N. erebi* and *Hypseleotris* spp.). This suggests that a different trophic pathway supports *L. unicolor*. The species also exhibited the greatest range in trophic positions among the consumers, suggesting a broader food niche. Trophic positions of the small predatory fish species *Hypseleotris* spp., *M. fluviatilis*, *R. semoni* and the exotic *G. holbrooki* were very similar in the Mehi River, although there seemed to be two distinct food-source pathways among them. One is utilised by *Hypseleotris* spp. that had relatively depleted $\delta^{13}C$ values of about $-27‰$ to $-28‰$, and appears to be driven by C_3 vegetation. The other is utilised by *M. fluviatilis*, *R. semoni* and the exotic *G. holbrooki* that had $\delta^{13}C$ values of about $-22.5‰$ to $-25‰$, and is most likely driven by benthic algae (i.e. autochthonous primary producers). The close alignment in $\delta^{13}C$ values of *M. fluviatilis*, *R. semoni* and *G. holbrooki* also suggests the potential for food competition among these species. The remaining native fish species analysed in the present study were numerically minor components of the fish community, each having an overall abundance $<2\%$ of all fish in the Gwydir Wetlands (Wilson *et al.* 2009). The feeding behaviour of *M. fluviatilis* has been described as both omnivorous (Harris 1995) and carnivorous (Kennard *et al.* 2001), with the present study suggesting primarily omnivorous feeding in the Lower Gwydir River and carnivorous feeding in the Mehi and Gingham, although only a single specimen was examined for the Gingham. Further sampling of this species is necessary to confirm such variable feeding behaviour.

The exotic *C. carpio* and *C. auratus* were the only fish species with a significant difference in $\delta^{13}C$ values (i.e. primary carbon sources) among the watercourses. The trophic overlap between *C. carpio*, *C. auratus* and the native *L. unicolor* was relatively large in the Gingham Watercourse where *L. unicolor* is most abundant, whereas the trophic overlap between the native *N. erebi* and both *C. carpio* and *C. auratus* was relatively large in the Lower Gwydir River where *N. erebi* is most abundant (Wilson *et al.* 2009). Such patterns may simply indicate that the exotic fish species changed their feeding behaviours to eat the most readily available food items within each watercourse, although it is unclear whether this is exerting a significant competitive pressure for food on the native fish species. The gut content of *L. unicolor* was completely different from the gut content of the exotic fish species for all watercourses. Further detailed studies of the food-resource availability (both quantity and quality) are necessary to determine whether *C. carpio* and *C. auratus* are indeed in food-resource competition with *L. unicolor* and *N. erebi*. The *C. carpio* in particular has been implicated in the decline of native fish populations in Australia (Koehn 2004).

Spatial variation in the trophic structure among watercourses

The observed spatial variation in the trophic structure of benthic resources and consumers among the watercourses during periods of low flow appears to be largely related to the spatial differences in the extent and type of the riparian vegetation community (i.e. allochthonous carbon source) across the floodplain. The fish assemblages at sites along the Lower Gwydir and Mehi Rivers with the most extensive coverage of δ^{13}C-depleted riparian trees were dominated by δ^{13}C-depleted consumers (*N. erebi* and *Hypseleotris* spp.). In the Gingham Watercourse, where riparian tree coverage is much lower (or in many places absent), the more δ^{13}C-enriched *L. unicolor* dominated the fish community. The presence of fringing riparian vegetation affects the structure and function of riverine food webs in two important ways. First, riparian tree species such as *Eucalyptus coolabah* and *E. camaldulensis* drop large amounts of leaf litter into river channels and support detritivorous, δ^{13}C-depleted food chains (Robertson *et al.* 1999). Second, shading by the riparian tree species decreases in-channel solar radiation and limits in-channel autotrophic production (Boston and Hill 1991; Thorp and Delong 1994).

A study of invertebrate shredders in riverine stretches of varying riparian tree coverage found a stoichiometric mismatch between primary sources and consumers in stretches without riparian trees (Deegan and Ganf 2008). This highlights the need for further research to determine the impact of riparian vegetation on carbon and nutrient dynamics in aquatic food webs of floodplain wetland ecosystems (Junk *et al.* 1989; Baldwin 1999; Zeug and Winemiller 2008). The widespread clearance of vegetation in the riverine landscapes of regulated floodplain wetlands including the Gwydir Wetlands (Bowen and Simpson 2009) is likely to have reduced the inputs of allochthonous sources of carbon and nutrients into channels, compared with autochthonous sources. Vegetation clearance would also modify and restrict aquatic habitats during prolonged low-flow periods when there is little or no connectivity among the watercourses.

We still have little understanding of the long-term ecological implications of such floodplain modifications for the structure and function of food webs in regulated floodplain wetlands. Because river regulation restricts the lateral connectivity, riverine food webs may be highly susceptible to changes in the habitat structure and water-flow patterns in the riverscape, independent of the floodscape (Ward *et al.* 2002; Junk and Wantzen 2004; Thorp *et al.* 2006). Further monitoring of the trophic structure and its variation should provide valuable insights into consequences of future management intervention.

Acknowledgements

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