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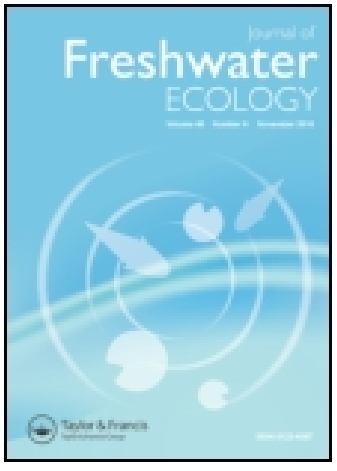

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The effects of dams on longitudinal variation in river food webs

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The effects of dams on longitudinal variation in river food webs

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We examined the effects of two dams on longitudinal variation of riverine food webs using stable isotope and gut contents analyses along four rivers in the Hunter Valley in eastern Australia. Longitudinal ^{15}N enrichment was observed in most invertebrate taxa and food sources but significant longitudinal variation was rare for ^{13}C, and composition of gut contents of invertebrate taxa did not vary significantly with longitudinal position. Most invertebrates and food sources were more ^{15}N-enriched at sites immediately downstream of the dams than expected from their upstream longitudinal position, a result not mirrored by gut contents and ^{13}C. Enrichment of ^{15}N downstream may be attributed to altered water quality as a result of impoundment but further research is necessary to elucidate whether physico-chemical riverine processes or trophic mechanisms are responsible. Our observations regarding the influence of dams on isotope ratios are contrary to the few existing studies, suggesting the small volumes relative to annual inflows of dams in the present study limit downstream impacts by maintaining aspects of flow variability.

Keywords: river regulation; tail waters; dams; water resource management; aquatic macroinvertebrates; stable isotopes

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Introduction

Understanding longitudinal variation in the contributions of different energy sources to river food webs is important for both ecological theory and river management (Gawne et al. 2007). The River Continuum Concept of Vannote et al. (1980) suggests that the dominant food resources for primary consumers vary in a predictable manner from headwater streams to large rivers. Many authors suggest that allochthonous carbon, derived from terrestrial inputs, is the major source of energy in forested headwater streams (e.g. Gessner et al. 1999; Reid et al. 2008) and that the contribution of autochthonous carbon increases with river size (Finlay 2001; Hadwen et al. 2010a). However, natural longitudinal patterns of energy flow can be disrupted by the presence of dams in a river system. The Serial Discontinuity Concept (Stanford & Ward 2001) stresses the recovery of ecosystem processes downstream of major longitudinal disruptions with the natural addition of tributary inputs. Nevertheless, downstream recovery can also take place without major tributary contributions (e.g. Growns et al. 2009).

Stable isotope analysis (SIA) has commonly been used to reconstruct food webs and energy flow from microbes, plants and detritus to primary and secondary consumers (Peterson & Fry 1987; Hershey et al. 2006). In many ecosystems, individual food sources

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have different ratios of ^{13}C:^{12}C and ^{15}N:^{14}N; therefore, food assimilation by animals can be inferred from the isotopic signatures of their tissues (Fry 1991). However, when sources have similar or overlapping isotope ratios it can be difficult to estimate their relative contributions. Gut contents analysis (GCA) is also frequently used to investigate diets by revealing the food ingested during a short period prior to sampling (e.g. Whitledge & Rabeni 1997; Mantel et al. 2004; Li & Dudgeon 2008), whereas SIA can indicate which prey items are assimilated in the medium to long term (Perga & Gerdeaux 2005). Therefore, the two techniques are complementary means of assessing trophic linkages (Post 2002).

The effects of dams on the structure and function of river food webs are poorly known (Power & Dietrich 2002) and although some studies have investigated the effects, they show contrasting results. Angradi (1993) observed enrichment of ^{13}C and depletion of ^{15}N in epilithon, enrichment of ^{13}C and ^{15}N in seston and a primary consumer, and enrichment of ^{15}N in macrophytes compared to a nearby unregulated tributary. It was suggested that the changes in $\delta^{13}C$ were due to a decreasing contribution of phytoplankton with downstream distance, but they could offer no explanation for the enrichment of ^{15}N in macrophytes. In contrast, Angradi (1994) observed depletion of ^{13}C and ^{15}N in seston in a downstream direction and no longitudinal variation in the isotopic composition of amphipods or fish for 25 km. Shannon et al. (2001) observed enrichment of ^{13}C in benthic algae, macroinvertebrates and fish up to 350 km downstream of Glen Canyon Dam but no longitudinal trends in $\delta^{15}N$ for the same groups. Doi et al. (2008) used isotope signatures of phytoplankton to suggest that they contributed to the downstream food webs for up to 10 km. Overall, while these studies evaluated differences in energy flow between regulated and unregulated rivers, they did not generally account for potential longitudinal patterns in stable isotope composition. Therefore, in order to evaluate natural variability aside from the effect of dams at various downstream locations, it is important to account for longitudinal variation in food-web dynamics simultaneously in regulated and natural, unregulated rivers.

In this study, we predicted that the presence of dams would affect invertebrate diets and the isotopic composition of invertebrates, and potential food sources in two regulated rivers. To assess this we used both SIA and GCA to determine the effects of dams on the longitudinal variation in $\delta^{13}C$ and $\delta^{15}N$ isotopic composition of food sources, primary consumers (and their gut contents) and invertebrate predators in regulated and unregulated rivers. We compared sites immediately downstream of dams with two unregulated rivers and unregulated sites upstream of the dams to determine whether dams influenced longitudinal variation in food-web dynamics.

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Methods

Study sites

We studied four tributaries of the Hunter River in New South Wales, Australia: the Allyn, the Chichester, the Paterson and the Williams rivers (Figure 1). These rivers rise on the Barrington Plateau at approximately 1500 m altitude and flow in a generally southeasterly direction. The region has primarily Carboniferous sedimentary and volcanic geology and a warm temperate climate (mean annual temperature of 18°C), with median annual rainfall of 1061–1278 mm concentrated in the austral summer (~40% falling in January–March) but with high inter-annual variability. The upper reaches of each river lie in relatively undisturbed catchments in either a national park or state forest, whereas grazing and dairy

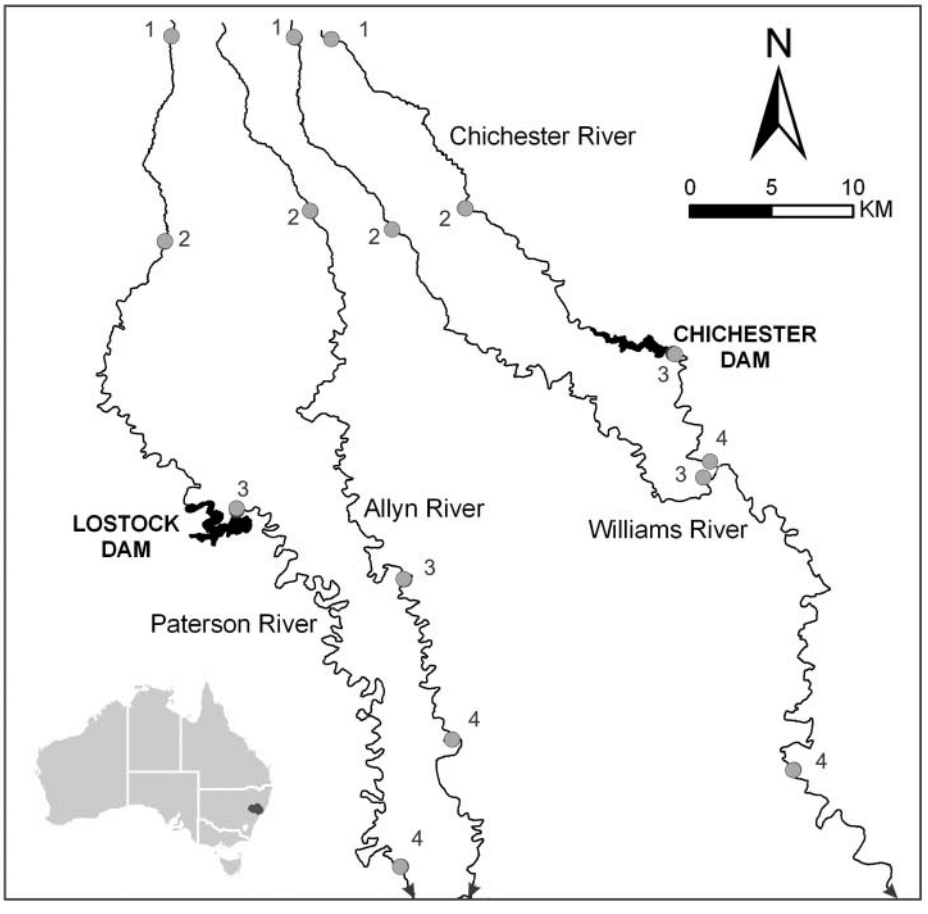

Figure 1. Location of collection sites; numbers indicate reaches referred to in the text.

production are the major land uses along the lower reaches. The riparian vegetation in the lower reaches is dominated by native species including river bottlebrush (*Callistemon sieberi*), river oak (*Casuarina cunninghamiana*) and spiky mat rush (*Lomandra* spp.) as well as exotic species including willows (*Salix* spp.) and giant reed (*Arundo donax*).

Two dams were included in the study: Chichester Dam (built in 1921, 43 m height, 21×10^6 m^3 capacity) on the Chichester River which supplies water for domestic consumption and Lostock Dam (1971, 38 m height, 20×10^6 m^3 capacity) on the Paterson River which supplies water for agricultural purposes (mainly irrigation). Both dams have a small operational capacity relative to annual inflow volume, so storage levels rarely fall below 80% and spills are frequent. They can develop thermal and oxygen stratification (particularly in summer because of their depth and consistently high storage levels) and discharge cold water to downstream river reaches through hypolimnetic outlets.

Four sites, each a 100 m reach, were chosen on each of the Chichester, the Paterson and the Williams rivers and three on the Allyn River (Table 1, Figure 1). One site was selected in the sub-alpine headwaters of each river at 1300 to 1480 m altitude, except for the Allyn River where difficult terrain prevented access. A second site was established within the national park or state forest on the slope reaches of each river at 240–350 m.

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Table 1. Characteristics of sites identified in Figure 1.

River	Reach number	Longitude	Latitude	Altitude (m)	Distance from source (km)	Catchment area (km^2)	Median annual discharge ($x10^6$ m^3)*
Allyn	2	151° 30′ E	32° 10′ S	310	17	56	9.1
Allyn	3	151° 33′ E	32° 22′ S	90	52	241	27.2
Allyn	4	151° 34′ E	32° 27′ S	37	66	292	39.6
Chichester	1	151° 30′ E	32° 4′ S	1300	5	8	0.9
Chichester	2	151° 35′ E	32° 10′ S	240	15	60	9.1
Chichester	3 (Dam)	151° 42′ E	32° 14′ S	143	35	204	30.0
Chichester	4	151° 43′ E	32° 18′ S	85	44	232	32.5
Paterson	1	151° 25′ E	32° 4′ S	1480	2	2	0.7
Paterson	2	151° 25′ E	32° 11′ S	350	19	52	7.4
Paterson	3 (Dam)	151° 27′ E	32° 20′ S	141	51	260	25.2
Paterson	4	151° 33′ E	32° 31′ S	25	107	453	28.7
Williams	1	151° 29′ E	32° 4′ S	1360	3	3	1.4
Williams	2	151° 32′ E	32° 10′ S	340	17	46	7.0
Williams	3	151° 43′ E	32° 18′ S	90	51	203	24.4
Williams	4	151° 46′ E	32° 28′ S	36	82	720	82.3

*Modelled data from Stein et al. (2007).

A third site was located immediately downstream of the Chichester and Lostock dams on the Chichester and the Paterson rivers, respectively, and at similar altitudes on the Allyn and the Williams rivers. A fourth site was established on each river at the most downstream accessible location with both pools and riffles. The fourth site on the Williams River was considered to be unaffected by the Chichester Dam because 80% of its catchment area was unregulated.

Field sampling

We collected invertebrates and potential food sources at each site between November 2008 and March 2009. All sites were only sampled once between those months and all material was collected on the same day at each site. New leaf growth of the dominant riparian vegetation was collected by hand. Biofilm samples were collected from the pools and riffles by scrubbing rocks in a 10-L bucket filled with filtered river water and the resulting suspension being filtered through a 250-μm mesh sieve with biofilm retained by a 25-μm mesh net. Benthic organic matter was collected by washing sediment with river water and retaining organic material on graded sieves as coarse particulate organic matter (CPOM, 2–5 mm) and fine particulate organic matter (FPOM, 0.25–2 mm). Samples of filamentous algae, if present, were collected by hand from rocks.

Macroinvertebrates were collected from pools and riffles at each site with a 250-μm mesh dip net and by handpicking from rocks taken from the river bed. Representatives of the most abundant taxa at each site were immediately preserved in ethanol for GCA. Samples for SIA were stored in plastic zip-lock bags and immediately placed on ice for at least 8 hours. This procedure allowed the invertebrates to void their guts, removing unassimilated material. Samples were frozen at -20°C upon return to the laboratory prior until further processing.

Gut contents analysis

GCA followed the methods of Chessman (1986). Preserved invertebrates were identified to the lowest possible taxon using keys in Hawking (2000) and dissected individually under a stereomicroscope. A maximum of 10 individuals per taxa per site were examined, selected where possible to span a range of body sizes. Each specimen was washed with distilled water and, if necessary, adhering debris was removed with a small brush and forceps. Invertebrates were then dried with tissue and the thorax and abdomen were slit with fine forceps and needles. The anterior half of the digestive tract was removed, and its contents were expelled into a droplet of distilled water on a microscope slide and distributed as uniformly as practical. A cover slip was placed over the droplet which was then scanned at magnifications of 100x–400x under a compound microscope.

Food items were classified into seven categories: unidentifiable fine organics, fungi, planktonic algae, non-filamentous benthic algae (mostly diatoms), filamentous algae, plant material (wood and leaf fragments) and animals (invertebrate fragments). Inorganic material was not included in the analysis. The food categories observed in each digestive tract were ranked in the order of increasing abundance, assessed subjectively according to the area of the slide covered. Points were then awarded to each category by expressing its rank as a proportion of the sum of the ranks of all categories in the same specimen. The gut contents of 503 invertebrates from 30 taxa were examined but several of these were collected from only one or a few sites. Sixteen taxa were sufficiently abundant and distributed amongst enough sites to be included in the analysis (Table 2).

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Table 2. Average percentage (±1 S.E.) of the total points for seven food categories in 16 invertebrate taxa.

Family	Taxon	Total number of individuals	No. of sites	Unidentifiable fine organic material	Benthic algae	Planktonic algae	Filamentous algae	Fungi	Vascular plant material	Animal matter
Aytidae	*Paratya australiensis*	82	11	70.6 ± 2.2	21.9 ± 1.8	–	2.8 ± 0.8	0.2 ± 0.2	4.5 ± 1.1	0.1 ± 0.1
Baetidae	*Edmundsiops* spp.	35	5	47.1 ± 3.1	46.7 ± 3.3	–	6.2 ± 1.9	–	–	–
Hydropsychidae	*Asmicridea* AV1	23	6	23.5 ± 2.7	24.2 ± 3.6	–	19.9 ± 3.2	0.3 ± 0.3	9.3 ± 2.7	22.9 ± 4.3
	Cheumatopsyche AV1	10	1	24.1 ± 4.1	17.6 ± 1.7	–	10.1 ± 2.5	1.0 ± 1.0	26.9 ± 2.6	20.4 ± 3.6
	Cheumatopsyche AV2	10	1	43.7 ± 4.4	29.7 ± 2.4	–	17.7 ± 4.7	–	7.0 ± 3.6	2.0 ± 2.0
	Cheumatopsyche AV6	35	4	31.8 ± 2.6	21.5 ± 1.9	0.9 ± 0.0	16.3 ± 1.8	–	16.0 ± 2.7	13.5 ± 2.5
	Diplectrona AV3	18	3	18.3 ± 1.3	1.1 ± 0.6	–	3.7 ± 1.5	1.1 ± 1.1	41.9 ± 3.0	33.9 ± 2.4
Leptoceridae	*Notalina spira*	12	5	22.5 ± 2.2	34.4 ± 4.7	–	27.8 ± 6.5	0.8 ± 0.8	11.1 ± 5.4	3.3 ± 3.3
	Triplectides altenogus	4	2	32.5 ± 0.8	9.2 ± 5.3	–	–	2.5 ± 2.5	55.8 ± 6.6	–
	Triplectides australicus	56	8	19.0 ± 1.6	13.8 ± 2.0	–	16.8 ± 3.5	4.2 ± 1.3	46.2 ± 3.4	–
	Triplectides AV10	4	2	33.3 ± 0	4.2 ± 4.2	–	4.2 ± 4.2	–	58.3 ± 4.8	–
	Triplectides ciuskus	14	3	27.4 ± 2.8	4.8 ± 3.2	–	–	2.4 ± 2.4	65.5 ± 3.3	–
	Triplectides parvus	18	4	22.6 ± 3.3	14.6 ± 4.0	–	1.9 ± 1.3	0.4 ± 0.4	60.6 ± 6.0	–
	Triplectides similis	13	3	25.1 ± 7.2	–	–	6.2 ± 4.0	6.7 ± 3.6	40.8 ± 8.1	21.3 ± 9.0
Leptophlebiidae	*Austrophlebioides* spp.	102	11	51.0 ± 2.0	39.9 ± 2.0	–	5.1 ± 1.0	0.5 ± 0.4	3.0 ± 0.8	0.5 ± 0.3
	Nousia spp.	22	8	57.6 ± 4.7	15.2 ± 5.0	–	0.5 ± 0.5	6.8 ± 2.4	20.0 ± 3.5	–

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Stable isotope analysis

Leptocerid cases and shrimp exoskeletons were removed prior to isotope analysis. All samples were dried at 60°C for 24–48 hours, ground to a powder with a glass rod and porcelain dish, and pelletised in tin capsules. Pelletised samples were analysed for stable isotopes with a continuous flow-isotope ratio mass spectrometer (Eurovector EA3000, Milan, Italy) at Griffith University, Brisbane, Australia. The ratios (R) of the heavy isotope ^{13}C to the light isotopes ^{12}C and ^{15}N to ^{14}N were expressed in parts per thousand, relative to standards (Pee Dee belemnite limestone and atmospheric nitrogen, respectively) in delta notation according to the following equation:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1]^{*}1000$$

Spatial patterns in consumer stable isotopes were analysed for the following invertebrate taxa or groups: *Paratya australiensis*, Hydropsychidae, Leptoceridae, Ephemeroptera nymphs and predators (Gyrinidae, Odonata and Megaloptera).

Statistical analysis

Differences in the gut contents between the selected taxa were tested with analysis of similarities (ANOSIM) and the Bray–Curtis dissimilarity measure (Clarke 1993) in the PRIMER program (Clarke & Gorley 2006). This was done in order to group those with similar diets for longitudinal analysis, which was necessary because of the patchy distributions of individual species. Dietary items that contributed most to significant differences were identified with similarity percentages (SIMPER) in PRIMER.

We used linear regression to assess the longitudinal changes in the importance of the gut contents of common species or groups of species with similar diets. The gut contents data (points per food category) were averaged for all individuals of a species or group at each site. Principal components analysis was used to summarise the variability in the gut contents across all sites, excluding those immediately downstream of the dams. The first principal component of the gut contents for each species or group was regressed against the distance of each site from the source of the river. If a significant longitudinal relationship was not observed, ANOSIM was used to test whether the gut contents of invertebrates collected immediately downstream of the dams were significantly different from those at the remaining sites.

Longitudinal changes in $\delta^{13}C$ and $\delta^{15}N$ of the invertebrate groups and potential food were also assessed with linear regression. The $\delta^{13}C$ or $\delta^{15}N$ values of the invertebrate groups and food at each site, excluding the sites downstream of the dams, were regressed on distance from the source of the river. If a significant relationship was observed between the distance from the source and $\delta^{13}C$ or $\delta^{15}N$ of an invertebrate group or food; the data were plotted with 95% confidence limits. We inferred that the dams affected the isotopic composition if the $\delta^{13}C$ or $\delta^{15}N$ values lay outside the confidence limits of the regression line. Where no significant longitudinal variation could be established we compared the $\delta^{13}C$ or $\delta^{15}N$ values between the sites immediately downstream of the dams and the remaining sites with one-way analysis of variance.

The contribution of potential food sources to primary consumers was assessed for each river reach and sites below the dams using the MixSIR mixing model (Semmens & Moore 2008). This algorithm carries out Bayesian analysis using sampling importance resampling and is able to explicitly account for uncertainty in the isotope source and

fractionation values (Moore & Semmens 2008; Semmens et al. 2009; Jackson et al. 2009). Fractionation constants were estimated from the literature and were set at 0.4 ± 1.20 ‰ ($\mu \pm$ S.D.) and 2.3 ± 1.61 ‰ for δ^{13}C and δ^{15}N, respectively (McCutchan et al. 2003).

Results

Gut contents analysis

The shrimp *Paratya australiensis* was collected at all sites except those in reaches 1 and 2 on the Chichester River and reach 1 on the Paterson and the Williams rivers (Table 2). Its gut contents consisted mainly of unidentifiable organic matter and unicellular benthic algae and contained small amounts of the remaining food types, excluding planktonic algae (Table 2). The first principal component explained 60% of the variation of the shrimp diet data and there was no significant longitudinal trend in the gut contents of *P. australiensis* (linear regression, $F < 1.0$, $p > 0.10$) and no difference between the sites immediately downstream of the dams and the remaining sites (ANOSIM, rho $= -0.07$, $p = 0.82$).

The baetid mayfly nymph *Edmundsiops* spp. was collected from all four rivers but only at five sites (Table 2). Its gut contents consisted mainly of unidentifiable organic matter and unicellular benthic algae, but a small amount of filamentous algae was also present (Table 2). The gut contents of *Edmundsiops* spp. were similar to those of the leptophlebid mayfly *Austrophlebioides* spp. at sites not immediately below the dams (rho $= -0.04$, $p = 0.71$), but significantly different from those of the leptophlebiid mayfly *Nousia* spp. (rho $= 0.37$, $p = 0.003$). The gut contents of the two leptophlebiid species were also significantly different (rho $= 0.41$, $p < 0.001$). SIMPER analysis identified that unicellular benthic algae (38%), unidentified fine organic material (26%) and vascular plant material (22%) contributed to the dissimilarity between *Austrophlebioides* spp. and *Nousia* spp. The gut contents of *Austrophlebioides* spp. contained more unicellular benthic algae and unidentified fine organic material and less vascular plant material than *Nousia* spp. Therefore, *Edmundsiops* spp. and *Austrophlebioides* spp. but not *Nousia* spp. were combined to allow sufficiently wide spatial representation for analysis of patterns in the mayfly diets. The first principal component explained 85% of the variation of the diet data and there was no significant longitudinal change in the gut contents of *Edmundsiops* spp. plus *Austrophlebioides* spp. ($F = 0.12$, $p > 0.10$) and no difference between the sites immediately downstream of the dams and the remaining sites (rho $= -0.10$, $p = 0.97$).

Hydropsychid caddisflies occurred at approximately half of the sites (Table 2), with gut contents differing significantly among species (rho $= 0.30$, $p < 0.001$). Pair-wise comparisons indicated that the gut contents of *Diplectrona* spp. were significantly different from those of the remaining species. SIMPER analysis identified that vascular plant material (28%), animal fragments (21%) and unicellular benthic algae (21%) contributed to the dissimilarity between the gut contents of *Diplectrona* spp. and the other species. The gut contents of *Diplectrona* spp. contained more animal and vascular plant material and less unicellular benthic algae. With combined data for all species except *Diplectrona* spp., the first principal component explained 87% of the variation of the diet data and there was no significant longitudinal trend in the gut contents ($F = 0.34$, $p > 0.10$) and no difference between sites immediately downstream of dams and the remaining sites (rho $=$ 0.04, $p = 0.12$).

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Leptocerid caddisflies were collected from all reaches except the headwater sites (Table 2). There was no significant difference in the gut contents of the species (rho = 0.08, $p = 0.06$). The first principal component explained 66% of the variation of the diet data but there was no significant longitudinal pattern in the gut contents of all the species combined ($F = 1.7$, $p > 0.10$) or difference between sites immediately downstream of dams and the remaining sites (rho = −0.06, $p = 0.83$).

Stable isotopes

Significant longitudinal changes were observed in δ^{13}C of *P. australiensis* and FPOM (Figure 2) but not in the other invertebrate groups and potential food sources. The δ^{13}C values of *P. australiensis* decreased with increasing distance from the source ($F = 18.4$, $p < 0.01$) whereas those of FPOM increased with increasing distance from the source ($F = 11.1$, $p < 0.01$). The δ^{13}C values of *P. australiensis* in reaches 3 and 4 downstream of the dams fell outside the confidence limits of the regression but in different directions, indicating no consistent dam effects. There were also no consistent dam effects on the δ^{13}C values for FPOM at the downstream sites. The δ^{13}C value for the filamentous algae was significantly higher downstream of the Lostock Dam than at the remaining sites ($F = 11.8$, $p < 0.05$, Figure 2) but δ^{13}C values of other invertebrates and food sources did not differ significantly between the dam and no-dam sites ($F < 2.0$, $p > 0.05$).

δ^{15}N values increased with increasing distance from the water source for all invertebrate groups, CPOM, riparian plants, pool biofilm and filamentous algae ($F > 17.0$,

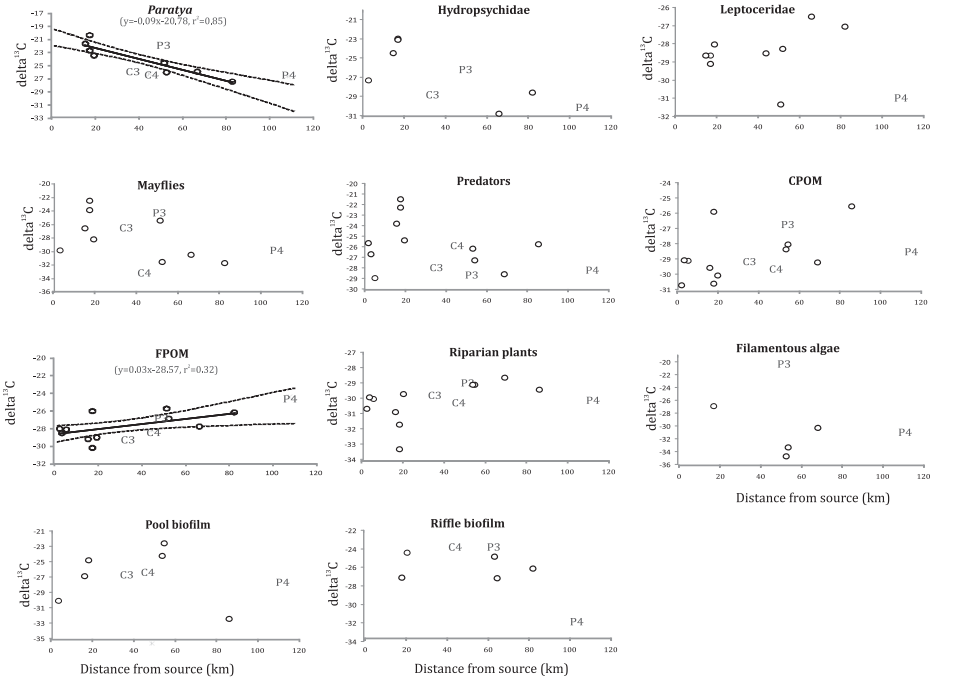

Figure 2. Scatterplots of mean δ^{13}C values against the distance from the source. Regression lines with lower and upper 95th percentile confidence limits are shown for significant relationships. C3, P3, C4 and P4 refer to reaches 3 and 4 on the Chichester and the Paterson rivers, respectively.

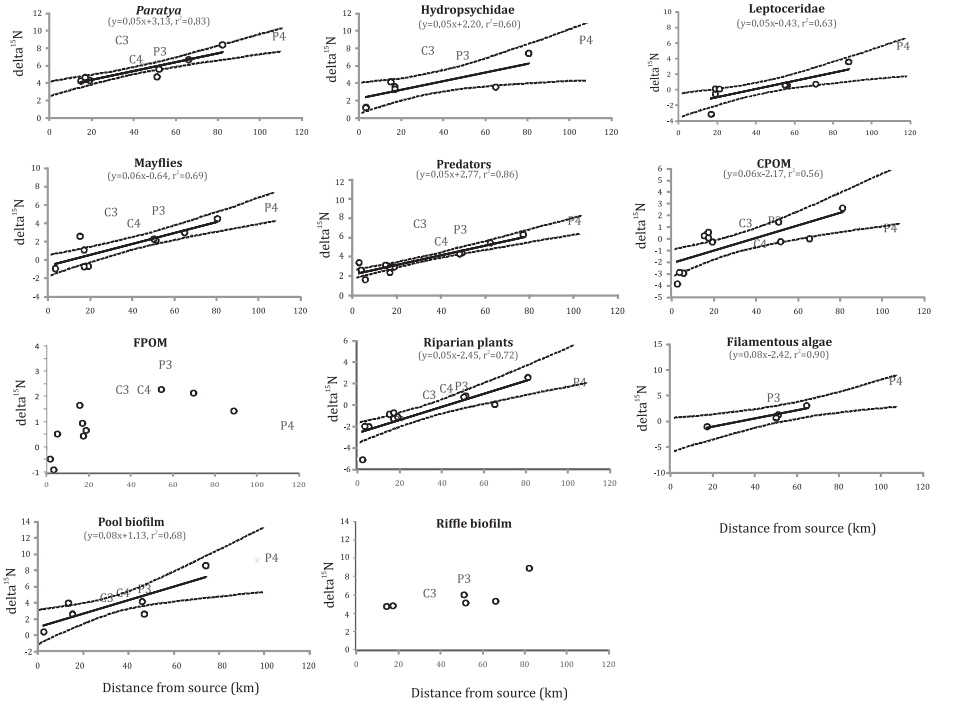

Figure 3. Scatterplots of mean δ^{15}N values against the distance from the source. Regression lines with lower and upper 95th percentile confidence limits are shown for significant relationships. C3, P3, C4 and P4 refer to reaches 3 and 4 on the Chichester and the Paterson rivers, respectively.

$p < 0.01$, Figure 3). The δ^{15}N values at reaches 3 and 4 on the Chichester River and reach 3 on the Paterson River, all within 9 km of the dams, lay above the regression confidence limits, implying significantly higher δ^{15}N, in all cases except CPOM and pool biofilm. In contrast, the δ^{15}N values of those biota and potential food sources at reach 4 on the Paterson River, 56 km from the dam, fell within the confidence limits, implying the dam effect had no effect this far downstream. The δ^{15}N values of FPOM were significantly higher at the dam sites than elsewhere ($F = 6.1$, $p < 0.05$, Figure 2). In contrast, there was no significant difference in the δ^{15}N values of riffle biofilms between dam and no-dam sites ($F = 0.7$, $p > 0.10$).

Mixing model

The contribution of the autochthonous sources (filamentous algae and biofilms) to the diet of *P. australiensis* decreased with increasing river size and was similar at dam sites compared with the same river section (section 3) on the unregulated rivers (Figure 4). Similarly, allochthonous contributions to the diet of mayflies increased with increasing river size, principally due to a decrease in the filamentous algae contributions. However, the contribution of the food sources at sites downstream of the dams was different from the same section of river on the unregulated rivers. There were no consistent longitudinal patterns in the contributions of the various food sources for either Leptoceridae or Hydropsychidae.

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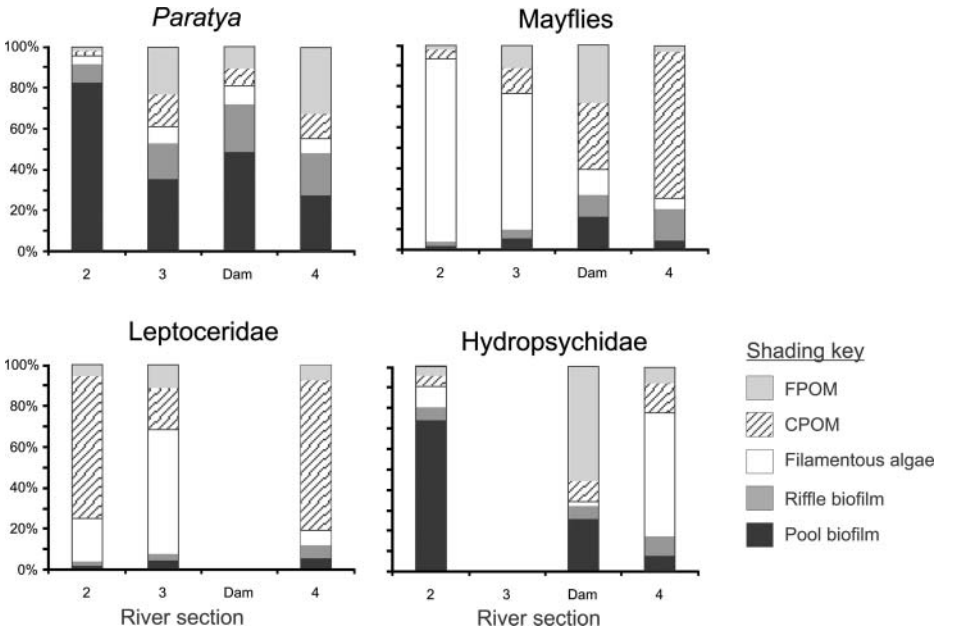

Figure 4. Median percent contribution of five potential food sources to the diets of four primary consumers in three separate river sections and sites immediately downstream of dams.

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Discussion

Most invertebrate groups and potential food sources in our study rivers had significant longitudinal trends in δ^{15}N and there was ^{15}N enrichment downstream of the dams that exceeded expectations from the dams' longitudinal position relative to other sites. The observation of enrichment is supported by Maxwell (2010), who observed enrichment of ^{15}N in biofilm downstream of the Chichester and Lostock dams. The processes that govern the ratios of nitrogen isotopes are complex (Hoegberg 1997; Nestler et al. 2011) but increased anthropogenic nitrogen inputs to aquatic systems often result in enrichment of ^{15}N in biota (e.g. Costanzo et al. 2001). Consequently, the longitudinal ^{15}N enrichment in our rivers may have been the result of increased agricultural land-use in their lower reaches. However, this mechanism is unlikely as Miyajima et al. (2009) found no effect of land use or geology on longitudinal ^{15}N enrichment of suspended particulate nitrogen or nitrates. Udy and Bunn (2001) found ^{15}N enrichment of aquatic macrophytes but not riparian plants at sites with greater catchment clearing. Our results for riparian plants are also in contrast with previous findings for terrestrial plants, which generally show δ^{15}N depletion with decreasing altitude (e.g. Sah & Brumme 2003; Liu & Wang 2010).

Longitudinal changes in δ^{15}N may be caused by several mechanisms, including isotope fractionation during in-stream nitrogen removal by denitrification and assimilation, in-stream nitrification generating isotopically different nitrogen relative to upstream sites, and external loading of isotopically different nitrogen from upstream sources (Miyajima et al. 2009). Information on these processes is not available for the four rivers in the present study and, consequently, the mechanisms underlying their longitudinal ^{15}N enrichment require further investigation. Many studies suggest that dams are net exporters of nitrogen and other authors have also demonstrated enriched ^{15}N in the biota

downstream of dams (Moore et al. 1992; Xu et al. 2005; Beutel 2006; Duda et al. 2010). It is likely that the enrichment of ^{15}N that we observed downstream of the dams is due to reservoir processes releasing isotopically enriched nitrogen compounds to downstream reaches.

In contrast to our results for $\delta^{15}N$, we could not detect systematic longitudinal variation in the $\delta^{13}C$ values of the majority of invertebrates and potential food sources or effects of dams on these variables. The lack of spatial variation in $\delta^{13}C$ is supported by our observed lack of spatial variation in the gut contents of the primary invertebrate consumers. However, we observed a decreasing contribution of autochthonous food sources to the diet of *P. australiensis*, which was supported by a trend of ^{13}C depletion with increasing distance from source. The lack of longitudinal variation in $\delta^{13}C$ values in the majority of invertebrates, CPOM, FPOM and riparian plants is consistent with the findings of Finlay (2001) and Hadwen et al. (2010a). However, the lack of longitudinal trends in $\delta^{13}C$ of epilithon in the present study is in agreement with the findings of Hadwen et al. (2010a) but in contrast to those of Finlay (2001). The absence of longitudinal trends in biofilm $\delta^{13}C$ in our rivers may have been due to high variability in the $\delta^{13}C$ values among species of algae and other biota that make up the biofilm (Hadwen et al. 2010b). An alternative explanation is that the factors that influence fractionation of $\delta^{13}C$ by algae, such as carbon supply and photosynthetic rates, may be too spatially or temporally (sampling took place over several months) variable across our rivers to generate consistent longitudinal patterns.

The minimal influence of dams on the $\delta^{13}C$ values of potential food sources and biota in this study is in contrast to other studies that have demonstrated enrichment or depletion of ^{13}C in biota downstream of dams (Angradi 1993, 1994; Shannon et al. 2001; Doi et al. 2008). The influence of the Lostock and Chichester dams on downstream $\delta^{13}C$ values may be minor because they are small dams that spill frequently with hypolimnetic water that is infrequently released. The effects of dams on river hydrology and, therefore, ecology, vary according to the structural features of the impoundment, the purpose of the dam and how it is operated (Armitage 1984; Finlayson et al. 1994). The lack of a consistent effect of dams on ^{13}C in the literature may reflect differing management of the dams in previous studies. However, the inconsistent effect suggests that there may be numerous mechanisms operating to influence carbon isotope dynamics and therefore $\delta^{13}C$ values of biota.

In conclusion, longitudinal increases in ^{15}N enrichment were observed from the headwaters to the lowland reaches of our study rivers in the majority of invertebrate groups and potential food sources, but little systematic spatial variation in gut contents or $\delta^{13}C$ signatures was noted. Additionally, most invertebrate groups and food sources were ^{15}N enriched immediately downstream of the dams, but the impoundment of water did not appear to influence either the gut contents of primary consumers or $\delta^{13}C$ signatures of invertebrates and potential food. The observed ^{15}N enrichment downstream of the dams was most likely due to the effects of reservoir processes on water chemistry and further research is required to elucidate the mechanisms responsible for the observed longitudinal trends in $\delta^{15}N$. Our observations regarding the influence of dams on isotope composition and energy flow are contrary to the few previous similar studies, perhaps because the dams in the present study have small operational capacities relative to annual inflows, resulting in reduced downstream impacts of regulated flow regimes relative to the size of the reservoirs in the other studies. We recommend that future studies incorporate multiple dams of different sizes or operational rules to test this hypothesis.

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