

The loss of aquatic and riparian plant communities: Implications for their consumers in a riverine food web

BRIAN M. DEEGAN* AND GEORGE G. GANF

School of Earth and Environmental Science, University of Adelaide, Adelaide, SA 5005, Australia

(Email: brian.deegan@adelaide.edu.au)

Abstract Human induced alterations to rivers and streams have resulted in significant changes to the structure and diversity of riparian and aquatic plant communities. These changes will impact on the dynamics of riverine carbon cycles and food web structure and function. Here we investigate the principal sources of organic carbon supporting local shredder communities across a gradient in different levels of anthropogenic development along riverine reaches, in South Australia. In forested/wooded reaches with minimum to limited development, semi-emergent macrophytes were the principal sources of organic carbon supporting the local shredder communities. However, in developed reaches, coarse particulate organic matter and filamentous algae were the principal food sources. The C:N ratios of the food sources in developed reaches were higher than those of their consumers indicating a stoichiometric mismatch. This imbalanced consumer-resource nutrient ratio in those developed reaches is likely to impose constraints on the growth and reproduction of their aquatic shredder communities with probable knock-on effects to higher trophic levels.

Key words: aquatic macrophyte, ecological stoichiometry, organic carbon, shredder, stable isotope.

INTRODUCTION

Identifying the principal food sources of aquatic invertebrates provides the basis for the understanding and management of riverine communities (Finlay 2001). However, as a consequence of anthropogenic alterations in land use, river regulation and water abstraction, primary producer communities and sources of organic carbon for invertebrate consumers have changed (Biggs 1996; Blanch *et al.* 1999; Blanch *et al.* 2000; Baattrup-Pedersen *et al.* 2005). For example, the Darling, Murray, Napean, Hawkesbury and Swan Rivers in Australia have changed from clear water – macrophyte dominated ecosystems to turbid, plankton dominated systems (Harris 2001; Scheffer *et al.* 2001). Other lotic ecosystems, particularly the more ephemeral systems, either have a significantly reduced biodiversity (i.e. the loss of many aquatic and riparian plant species and their replacement by more terrestrial species) or a substantial microbenthos community, as a result of anthropogenic alterations (Sheldon & Walker 1997; Burns & Walker 2000a; Burns & Walker 2000b). These alterations in the primary producer communities will impact on the dynamics of organic carbon cycles (Robertson *et al.* 1999) and food web structure and function (Ward & Stanford 1983; Hicks 1997; Harris 1999a).

Stable isotopes can be used to trace the origin and movement of energy and nutrients from primary producers/autotrophs to consumers (Connolly *et al.* 2005). The stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) differ among autotrophs (Fry 1984; Bouillon *et al.* 2002) and these ratios, the isotopic signatures, are taken on by the consumers and reflected in their tissues at whatever trophic level they occur (Fry & Sherr 1984; Wada *et al.* 1991; Boon & Bunn 1994; Peterson 1999). Routine analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provide information on the carbon to nitrogen ratios of the source material. These ratios may be interpreted stoichiometrically and may provide additional information about the suitability of the food source, and the consequences of elemental imbalances between consumers and their food sources (Frost *et al.* 2005). The concept of ecological stoichiometry recognizes that freshwater primary invertebrate consumers have conservative C:N ratios of 4–10:1 (mean 6.3) (Elser *et al.* 2000a). In contrast, potential food sources have C:N ratios that range from <5 to >70 (mean 10.2:1) (Elser *et al.* 2000a). In general, terrestrial food sources have higher C:N (mean 36:1) ratios than their freshwater counterparts. Higher C:N ratios will result in increased consumption rates and reduced food assimilation efficiencies, which ultimately translates into reduced growth and survivorship by primary consumers (Tuchman *et al.* 2003).

Rural areas close to major cities have undergone major anthropogenic development in land use that is accompanied by major shifts in the composition of

*Corresponding author.

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both riparian and aquatic vegetation. An example is the Mt Lofty Ranges in South Australia where many native plant species are in decline and agricultural practises have caused a loss of the riparian zone (Holmes & Iversen 1976; Kraehenbuehl 1996). Changes in hydrology have resulted in the loss of aquatic macrophytes (Holmes & Iversen 1976). A consequence of a shift away from aquatic and riparian to terrestrial plants is that it may force invertebrate consumers to rely upon food sources with a relatively high C:N ratio compared with their body tissue.

The first aim of this study was to determine the principal sources of organic carbon supporting local primary consumers (shredder communities) across riverine reaches with different levels of anthropogenic development. The results are reported as ranges of minimum and maximum contributions (Benstead *et al.* 2006) and are not unique solutions but the best statistical estimates derived from the mixing model of Phillips and Gregg (2003). The second aim was to investigate how closely the C:N ratios in the principal food sources aligned with the C:N ratios in the shredders and to examine whether there was a mismatch between the two. Reaches with minimum anthropogenic influences were wooded or forested and it was hypothesized that in those reaches allochthonous carbon sources together with aquatic macrophytes would be the principal food source for local primary consumers (Vannote *et al.* 1980; Bunn 1993; Cummins *et al.* 1995; Hicks 1997). Primary consumers inhabiting reaches devoid of riparian vegetation and aquatic macrophytes (significant anthropogenic alterations) would feed on a nutritively inferior carbon source.

MATERIALS AND METHODS

Selection of study sites

Deterioration in stream habitat (Biggs 1996; Maddock 1999) and the displacement of riparian and aquatic vegetation (Merritt & Cooper 2000; Pettit *et al.* 2001; Baron *et al.* 2002) is dependent on the level of anthropogenic development both along an identified stream reach and also owing to alterations to the stream hydrology (Poff *et al.* 1997). This will inevitably lead to spatial variation in the distribution of both primary sources of organic carbon and their consumers. To reduce this effect of spatial variation in deciphering food webs (Boon & Bunn 1994) and to examine the effect of anthropogenic influences on carbon dynamics and food web structure and function within a lotic ecosystem, all study reaches were chosen along the Finnis River system (Fig. 1).

The Finnis River is located approximately 50 km south of Adelaide, South Australia, in the Eastern Mount Lofty Ranges, which flows in a south-easterly direction before entering Lake Alexandrina. Rainfall in this catchment varies from 850 mm in the north-western highlands to less than 450 mm on the south-eastern side at the confluence with Lake Alexandrina. Major land use in the catchment includes broad scale grazing (64% of total area), intensive grazing (12%), forestry and protected areas (21%), vines (2.6%), horticulture and floriculture (Savadamuthu 2003). In recent years, increasing development has put much pressure on the available water, through the increased use of farm dams and ground water extraction. As a consequence a once variable hydraulic regime has now been replaced by a significantly reduced and relatively stable regime (Savadamuthu 2003).

Study sites were chosen to reflect three categories of anthropogenic development; Minimal, Modest and Widespread, which were determined by the continuity of overstorey canopy cover along the river banks, the continuity of the understorey and its structural complexity as determined by the ratio of native species to exotic pasture grasses and the dominance of aquatic in-stream *versus* terrestrial vegetation at each site (Ladson *et al.* 1999; Jansen & Robertson 2001). Each site was a 100 m riverine reach and three representative reaches of each category were selected. Those reaches classified as minimal (Sites 40, 18 and 22) were surrounded by extensive native forest/woodland, the understoreys were dominated by native species, with an abundance of riparian and aquatic species present in-stream, and with no indications of agricultural development or grazing by livestock. The sites with modest development (Sites 48, 17 and 27) had a reduced canopy cover (between 30% and 60% relative to the minimal sites), had an altered understorey cover (between 30% and 60% of species were native compared with the minimal sites) and were subject to some grazing by livestock. The widespread sites (Sites 36, 44 and 30) were devoid of canopy cover, the understoreys were dominated by pasture grasses (>90%) and were mostly devoid of any riparian/aquatic in-stream vegetation cover (<10%), and were subject to intensive grazing. To account for stream order all sites were classified as either fourth or fifth order streams.

Sampling protocol and collection of primary sources and consumers

A pilot study (27 and 28 March 2005), sampled three sites that ranged from widespread (36), to moderate (48) to minimal (40) anthropogenic development. A more extensive study between 31 October and 2 November, 2005, sampled all nine sites (Fig. 1). To reduce the influence of macroinvertebrate drift

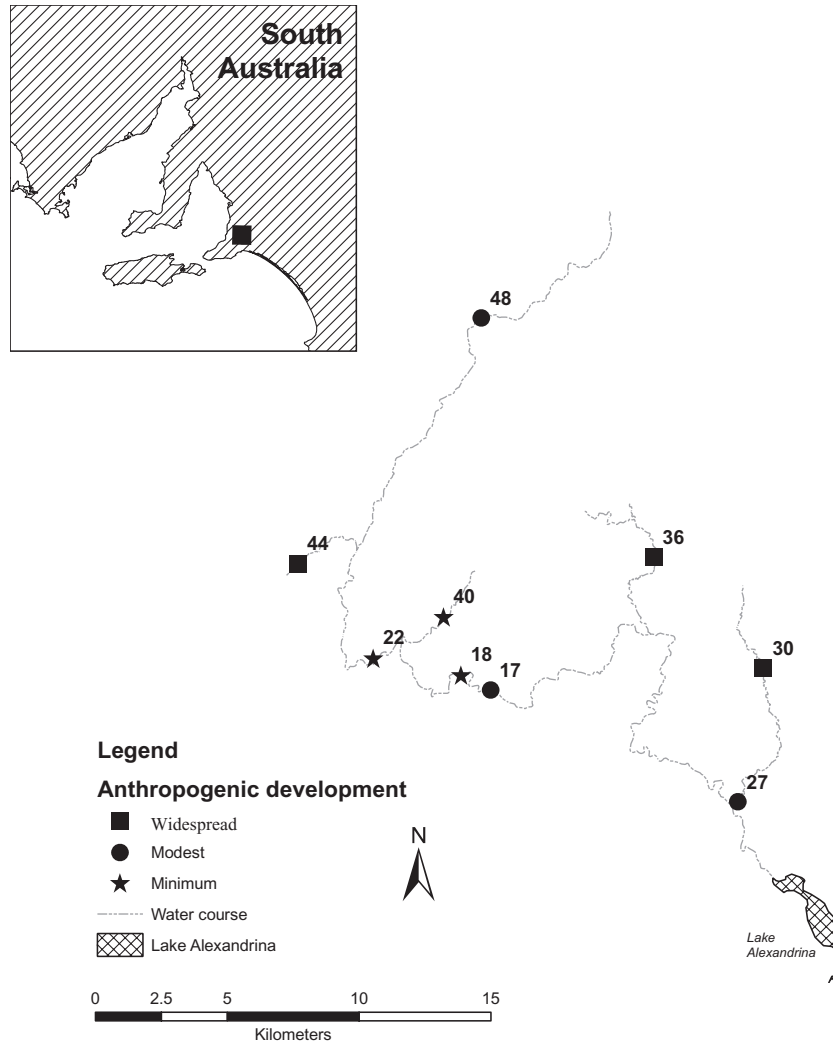


Fig. 1. Map of the Finnis River indicating each of the study sites and their degree of anthropogenic development.

sampling only occurred after flow had been low for at least 7 days prior to sampling. The protocol for the pilot study was to collect specimens of macroinvertebrate shredders and the three most dominant macrophytes species from each site (Table 1). This was used as an indication of the role aquatic macrophytes played in the nutrition of shredder communities. For the more extensive study, the protocol was to collect specimens of shredders and all potential primary sources, both terrestrial and aquatic. To reduce the effect of habitat type (e.g. riffles, pool and edge), only pool habitats (with still or slow flowing water) were sampled within each selected site. Three replicate pool habitats each with a surface area of approximately 10 m² were sampled within each site and the samples collected were pooled for each site. Three replicate samples of each of the primary sources of organic carbon (plant species and coarse particulate organic matter, CPOM) were randomly collected from the same location as the

macroinvertebrates sampled. Macroinvertebrates were collected using a kick-net (250 µm mesh) and immediately stored in 70% ethanol (Jardine *et al.* 2003). Plant samples were refrigerated immediately and then frozen as soon as possible (same day) and stored for isotope analysis.

Sample preparation and analysis

Macroinvertebrates were identified (Hawking & Smith 1997; Gooderham & Tsyrlin 2002; Dean *et al.* 2004) and only those macroinvertebrates classified as shredders were analysed. The two orders of macroinvertebrates classified as shredders were Trichoptera – *Triplectides* sp. and Amphipoda – *Austrogammarus* spp., *Paramelitidae* spp., *Corophiidae* spp., and *Neoniphargidae* spp. These genera are restricted to still or slow-flowing riverine patches where organic matter

Table 1. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of three dominant macrophytes and two primary consumers (corrected for fractionation) at sites indicative of Widespread, Moderate and Minimum anthropogenic development

Site	Isotope	Corrected primary sources			Consumers	
		<i>C. vaginatus</i>	<i>R. nasturtium-aquaticum</i>	<i>P. australis</i>	Trichoptera	Amphipoda
Widespread	$\delta^{13}\text{C}$	-27.4 (0.5)	-29.4 (0.8)	-27.3 (0.6)	-29.4 (3.2)	-28.4 (1.4)
	$\delta^{15}\text{N}$	10.6 (0.8)	8.1 (0.2)	11.0 (0.2)	7.8 (0.0)	8.1 (0.4)
Moderate	$\delta^{13}\text{C}$	-24.2 (0.5)	-29.8 (0.4)	-27.0 (1.1)	-30.5 (0.8)	-28.7 (1.1)
	$\delta^{15}\text{N}$	10.3 (0.6)	6.7 (0.8)	10.5 (0.3)	7.8 (0.4)	8.2 (0.4)
Minimal	$\delta^{13}\text{C}$	-30.0 (0.3)	-27.3 (0.5)	-29.4 (0.3)	-25.1 (0.9)	-26.8 (0.9)
	$\delta^{15}\text{N}$	9.1 (0.2)	10.0 (0.1)	5.9 (0.1)	6.3 (0.2)	8.3 (0.0)

Standard deviations in brackets. See Table 2 for the full forms of the abbreviated species names.

accumulates (Gooderham & Tsyrlin 2002). For each site, the shredders were separated into two orders (Trichoptera and Amphipoda) and these two orders were analysed separately. All plant and animal materials were washed in distilled water to remove epiphytes. Samples were oven-dried at 60°C for 36–48 h and then ground to a fine powder-like consistency using a mortar and pestle.

Dried, ground samples were oxidized at high temperatures and the resultant CO_2 and N_2 were analysed for percentage C, N and stable isotopes ratios with a Tracermass ion ratio mass spectrometer and Roboprep preparation system manufactured in 1997 by Europa PDZ, UK. Ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were expressed as parts per thousands (‰) difference between the sample and conventional standards (Vienna Pee Dee belemnite for C and atmospheric N_2 for N; Gorokhova *et al.* 2005) where:

$$\delta\text{X}(\text{‰}) = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1) \times 1000$$

Where X = ^{13}C or ^{15}N and R = $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

Repeated analyses of homogeneous material yielded SD of 0.1‰ and 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Modelling feasible source mixtures to explain shredder nutrition

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated for both the consumers and the primary sources at each site. To overcome the problem that not all primary sources (plant species) were represented at all sites, the plant species were pooled into groups of similar life form (Table 2) and the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values calculated for individual species were pooled for each vegetation grouping across sites with the same level of development (Phillips *et al.* 2005). This enabled a

Table 2. Plant species are grouped based on similar life forms

Group	Species of similar life form
1	CPOM
2 (Riparian)	Riparian leaves, Riparian grasses, <i>Plantago major</i> , <i>Anagallis arvensis</i> , <i>Zantedeschia aethiopica</i>
3 (Semi-emergent)	<i>Persicaria decipiens</i> , <i>Cotula coronopifolia</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Crassula helmsii</i> , <i>Callitriche stagnalis</i> , <i>Triglochin procerum</i>
4 (Emergent)	<i>Cyperus vaginatus</i> , <i>Juncus pallidus</i> , <i>Baumea juncea</i> , <i>Typha domingensis</i> , <i>Phragmites australis</i> , <i>Eleocharis pusilla</i>
5 (Submerged)	<i>Myriophyllum simulans</i> , <i>Ranunculus amphitrichus</i> , <i>Batrachium trichophyllum</i> , <i>Potamogeton crispus</i>
6 (Algal)	Filamentous algae, <i>Chara</i> sp.

CPOM, coarse particulate organic matter.

comparison between sites of differing levels of development even when there were different primary sources collected from each site.

In determining the relative contributions of different food sources to an animal's diet, a number of different mixing model procedures can be used. In general, the proportional contribution of $n + 1$ different sources can be uniquely determined by the use of n different isotope system tracers (e.g. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) with linear mixing models based on mass balance equations. Often, however, the number of potential sources exceeds $n + 1$, which prevents finding a unique solution. When no definitive solution exists, there is a method that is informative in determining bounds for the contributions of each source – IsoSource model (Phillips & Gregg 2003).

The pooled values were used in the IsoSource model of Phillips and Gregg (2003) to calculate feasible combinations of primary source material (vegetation groupings) that could explain the consumer signatures. This method examined all possible combinations of each primary source potential contribution (0–100%) in small increments (here 1%) when the number of primary sources per site were either 6 or 7, and 2% when the number of primary sources were 8 (Phillips & Gregg 2003). Combinations that added to within 0.01‰ of the consumer signature were considered feasible solutions (Melville & Connolly 2003; Connolly *et al.* 2005). As recommended by Phillips and Gregg (2003), results are reported as the distribution of feasible solutions for each primary source. The median contribution and the 1 and 99 percentile range is given, rather than the full range, which is sensitive to small numbers of observations on the tails of the distribution (Phillips & Gregg 2003). All feasible source mixture modelling is presented for each vegetation group across each level of anthropogenic development (Minimal to Widespread), and individually for each site and its primary sources during the second sampling period. Interpretation of these potential contributions (1 (minima) and 99 (maxima) percentile range) deserves some discussion here. According to Benstead *et al.* (2006), low maxima are least ambiguous and therefore most useful; they indicate that the organic matter source can be rejected as important. Relatively high minima indicate that the source may be important, if all likely sources have been included in the analysis. Large ranges between minima and maxima are clearly not informative, unless the minima is relatively high, and small ranges represent relatively well constrained estimates of the source contribution (Benstead *et al.* 2006).

To account for fractionation, we used a correction based on the most recently reported average fractionation increase of 0.3‰ for carbon isotopes and 2.2‰ for nitrogen isotopes per trophic level for consumers that were raised on plant and algal diets (McCutchan *et al.* 2003).

RESULTS

Pilot study

Because not all possible food sources were collected and analysed it would be misleading to use geometric or mixing model procedures to quantify the contributions of these food sources to the diets of Amphipoda and Trichoptera. Examination of the results shows there is an overlap of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between two plant species and the consumers sampled (Table 1). It

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Table 3. Distribution of feasible contributions to Amphipoda nutrition presented for each vegetation grouping across each category of anthropogenic development (Minimal to Widespread)

Vegetation groupings	Anthropogenic development (%)		
	Minimal	Modest	Widespread
Group 1	0–13 (4)	0–5 (1)	20–53 (38)
Group 2	2–25 (8)	0–3 (1)	0–31 (8)
Group 3	57–72 (67)	65–97 (88)	0–49 (14)
Group 4	0–27 (8)	0–24 (6)	0–48 (13)
Group 5	7–12 (11)	0–11 (4)	0–29 (8)
Group 6		0–2 (0)	0–23 (11)

Ranges: 1 and 99 percentiles. Median in brackets.

appears that *Rorippa nasturtium-aquaticum* was a contributor to the diets of both Amphipoda and Trichoptera at site 36, widespread and *Potamogeton crispus* was a contributor to the diets of Trichoptera at site 48, modest (Table 1).

Modelled feasible source mixtures to explain shredder nutrition

In the riverine reaches with widespread agricultural development (Sites 36, 44 and 30) and little or no understorey and canopy cover, group 1 (CPOM) formed the main dietary component of Amphipoda (20–53%) (Table 3). The feasible contributions to Amphipoda nutrition from each of the individual primary sources modelled for each of the widely developed sites further support this observation (Table 4). It clearly shows CPOM was the main dietary component of Amphipoda across sites with widespread developments, with contributions of between 19–32% (site 36) and 49–65% (site 30). The balance of their diet was generally distributed evenly across vegetation groups 2–6 (Table 3) depending on the species present at individual sites (Table 4). For Trichoptera (only recorded at site 36), group 6 formed the main dietary component (48–64%) followed by group 1 (2–22%) (Table 5). This observation was reflected in the contributions from each of the individual primary sources modelled at site 36 (Table 4). The remaining aquatic and terrestrial plant species modelled played significantly reduced roles in the diet of Trichoptera.

Along reaches with modest development, group 3 species were the major nutritive source for Amphipoda accounting for 65–97% of total intake (Table 3). This observation was further supported by modelling the feasible contributions of each individual primary source from each reach with modest developments (Table 6). *Callitriche stagnalis* (6–56%), *Ranunculus amphitrichus* (0–30%), *Crassula helmsii* (0–72%) and

Table 4. Distribution of feasible contributions to shredder nutrition from primary sources collected from sites with widespread anthropogenic developments based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Site	Consumer	Primary sources (%)					
		CPOM	Riparian grasses	<i>C. vaginatus</i>	<i>P. australis</i>	<i>R. nasturtium-aquaticum</i>	Filamentous algae
36	Amphipoda	19–32 (24)	0–47 (12)	0–39 (10)	0–36 (9)	0–41 (10)	17–33 (25)
	Trichoptera	32–36 (33)	0–14 (3)	0–11 (3)	0–9 (2)	0–12 (3)	50–54 (52)
44	Amphipoda	CPOM	Riparian grasses	<i>E. pusilla</i>	<i>C. stagnalis</i>	<i>Z. aethiopica</i>	<i>B. trichophyllum</i>
		11–46 (36)	0–27 (7)	0–57 (15)	0–23 (6)	20–29 (25)	0–26 (7)
30	Amphipoda	CPOM	<i>C. coronopifolia</i>	<i>C. vaginatus</i>	<i>C. stagnalis</i>	Filamentous algae 1	Filamentous algae 2
		49–65 (61)	0–18 (4)	0–9 (2)	0–18 (4)	2–19 (13)	0–44 (10)

Ranges: 1 and 99 percentiles. Median in brackets. See Table 2 for the full forms of the abbreviated species names. CPOM, coarse particulate organic matter.

Table 5. Distribution of feasible contributions to Trichoptera nutrition presented for each vegetation grouping across each category of anthropogenic development (Minimal to Widespread)

Vegetation groupings	Anthropogenic development (%)		
	Minimum	Modest	Widespread
Group 1	0–27 (10)	0–8 (3)	2–22 (13)
Group 2	0–28 (11)	0–5 (1)	0–19 (5)
Group 3	31–64 (48)	47–91 (78)	0–35 (9)
Group 4	1–59 (25)	0–34 (10)	0–28 (7)
Group 5	0–6 (4)	0–17 (7)	0–17 (4)
Group 6		0–3 (0)	48–64 (57)

Ranges: 1 and 99 percentiles. Median in brackets.

Triglochin procerum (0–26%) formed the main dietary components of Amphipoda at site 48. At site 17, *C. helmsii* and *T. procerum* (0–41% and 0–38%, respectively) formed the main dietary components, while at site 27, *Cotula coronopifolia*, *R. nasturtium-aquaticum* and *C. helmsii* (0–55%, 0–48% and 0–47%) formed the principal energy sources supporting Amphipoda. All of these species belong to vegetation group 3. Group 3 species were also the main source of nutrition for Trichoptera (47–91%; Table 5) in each of these reaches (Table 6), except at site 27 where the major dietary component for Trichoptera was *Typha domingensis* (36–76%; group 4), followed by group 3 species (Table 6).

In the riverine reaches with minimal anthropogenic influences, with extensive canopy and understorey cover, and no agricultural development, group 3 species again formed the main dietary components of Amphipoda (57–72%; Table 3). However, the feasible contribution made by individual primary sources modelled for each of the minimum reaches did not

support this observation (Table 7). Riparian grasses made up a considerable proportion of the Amphipoda diets at sites 40, 18 and 22 (18–64%, 39–46% and 0–68%, respectively; Table 7), but these contributions were not reflected in group 2's contribution to Amphipoda diet (Table 3). Similar observations were made for Trichoptera across the sites with minimum influences (Table 5) but less pronounced (Table 7). In general, the results from the vegetation groupings and subsequent modelling (Table 5) hold true but are site specific (Table 7), i.e. the primary sources present at individual sites and their availability to consumers. At site 40 group 4 (*T. domingensis*; 44–66%) was the main nutritional source followed by group 2 and then group 3. Group 2 (particularly Riparian grasses; 36–46%) made up the main dietary components followed closely by group 3 (*T. procerum* 23–38%) at site 18 and finally group 3 formed the main dietary components for Trichoptera at site 22, followed by groups 4 and 2 (Table 7).

C:N ratios found in primary sources and their primary consumers

The C:N ratio found in the primary sources varied considerably between sites with the same level of development and between sites of different levels of development (Tables 8–10). For example, CPOM ranged from 23.3 to 39.7 in sites with widespread anthropogenic developments (Table 8), from 24.7 to 47.0 in sites with modest developments (Table 9), and from 43.1 to 59.4 in sites with minimal developments (Table 10). This was also true for primary producers; *C. stagnalis* had a C:N ratio of 7.6 at site 48 (Table 9) and ratios of 10.6 and 11.9 at sites 44 and 30 (Table 8). *Cyperus vaginatus* had a C:N ratio of 25.0

Table 6. Distribution of feasible contributions to shredder nutrition from primary sources collected from sites with modest anthropogenic developments based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Site	Consumer	Primary sources (%)									
		CPOM	Riparian leaves	<i>C. stagnalis</i>	<i>R. amphitrichus</i>	<i>C. helmsii</i>	<i>T. procerum</i>	<i>T. domingensis</i>	<i>P. crispus</i>		
48	Amphipoda	0-22 (4)	0-16 (2)	6-56 (36)	0-30 (10)	0-72 (16)	0-26 (6)	0-30 (6)	0-24 (10)		
	Trichoptera	0-22 (4)	0-16 (4)	0-36 (16)	0-56 (18)	0-50 (14)	0-28 (6)	0-30 (6)	0-44 (24)		
17	Amphipoda	0-43 (15)	0-27 (10)	21-33 (16)	0-48 (13)	0-41 (18)	0-38 (20)				
	Trichoptera	0-20 (8)	0-12 (5)	9-20 (14)	0-76 (21)	0-64 (22)	0-60 (20)				
27	Amphipoda	0-37 (12)	0-21 (7)	0-55 (17)	0-48 (17)	0-47 (13)	0-15 (5)	0-53 (17)			
	Trichoptera	0-28 (12)	0-11 (3)	0-30 (8)	0-28 (8)	0-26 (6)	0-6 (1)	36-76 (57)			

Ranges: 1 and 99 percentiles. Median in brackets. See Table 2 for the full forms of the abbreviated species names. CPOM, coarse particulate organic matter.

Table 7. Distribution of feasible contributions to shredder nutrition from primary sources collected from sites with minimal anthropogenic developments based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Site	Consumer	Primary sources (%)									
		CPOM	Riparian leaves	Riparian grasses	<i>T. procerum</i>	<i>A. arvensis</i>	<i>P. major</i>	<i>T. domingensis</i>	<i>P. decipiens</i>		
40	Amphipoda	0-12 (2)	0-12 (2)	18-64 (50)	0-26 (8)	0-62 (14)	0-14 (4)	0-18 (4)	0-28 (8)		
	Trichoptera	0-32 (10)	0-32 (16)	0-6 (0)	0-16 (4)	0-8 (2)	0-20 (4)	44-66 (56)	0-18 (4)		
18	Amphipoda	0-9 (2)	0-7 (1)	39-46 (43)	33-43 (39)	0-19 (4)	0-19 (4)	0-16 (3)			
	Trichoptera	0-12 (2)	0-9 (2)	36-46 (42)	23-38 (32)	0-27 (6)	0-27 (6)	0-22 (5)			
22	Amphipoda	0-22 (4)	0-16 (4)	0-68 (18)	0-52 (14)	0-26 (6)	0-60 (12)	0-52 (24)	0-18 (4)		
	Trichoptera	0-22 (4)	0-16 (4)	0-66 (16)	0-50 (12)	0-26 (6)	0-58 (12)	0-54 (24)	0-20 (6)		

Ranges: 1 and 99 percentiles. Median in brackets. See Table 2 for the full forms of the abbreviated species names. CPOM, coarse particulate organic matter.

Table 8. Mean C:N ratios of consumers and primary sources collected from sites of with widespread anthropogenic developments

Site	Consumer		Primary sources					
	Amphipoda	Trichoptera	CPOM	Riparian grasses	<i>C. vaginatus</i>	<i>P. australis</i>	<i>R. nasturtium-aquaticum</i>	Filamentous algae
36	4.8 (0.0)	5.4 (0.1)	23.3 (1.1)	9.3 (0.5)	25.0 (2.0)	11.9 (0.2)	7.9 (1.2)	7.7 (0.5)
	Amphipoda		CPOM	Riparian grasses	<i>E. pusilla</i>	<i>C. stagnalis</i>	<i>Z. aethiopica</i>	<i>B. trichophyllum</i>
44	4.9 (0.1)		26.7 (1.5)	9.4 (0.2)	18.8 (0.6)	10.6 (0.3)	13.1 (2.2)	10.8 (0.3)
	Amphipoda		CPOM	<i>C. coronopifolia</i>	<i>C. vaginatus</i>	<i>C. stagnalis</i>	Filamentous algae 1	Filamentous algae 2
30	5.0 (0.0)		39.7 (4.5)	16.3 (2.1)	42.5 (5.8)	11.9 (0.5)	15.3 (0.3)	22.5 (0.2)

Standard deviation in brackets. See Table 2 for the full forms of the abbreviated species names. CPOM: coarse particulate organic matter.

Table 9. Mean C:N ratios of consumers and primary sources collected from sites with modest anthropogenic developments

Site	Consumer		Primary sources							
	Amphipoda	Trichoptera	CPOM	Riparian leaves	<i>C. stagnalis</i>	<i>R. amphitrichus</i>	<i>C. helmsii</i>	<i>T. procerum</i>	<i>T. domingensis</i>	<i>P. crispus</i>
48	5.0 (0.1)	4.7 (0.0)	24.7 (1.2)	34.9 (3.4)	7.6 (0.3)	9.8 (0.3)	11.4 (0.4)	7.8 (0.1)	11.0 (0.3)	7.3 (0.3)
	Amphipoda	Trichoptera	CPOM	Riparian leaves	Riparian grasses	<i>C. vaginatus</i>	<i>C. helmsii</i>	<i>T. procerum</i>		
17	4.7 (0.2)	5.7 (0.3)	47.0 (1.5)	17.5 (0.4)	14.6 (0.5)	27.4 (0.9)	14.9 (0.2)	9.1 (0.2)		
	Amphipoda	Trichoptera	CPOM	Riparian leaves	<i>C. coronopifolia</i>	<i>R. nasturtium-aquaticum</i>	<i>C. helmsii</i>	<i>Chara</i> sp.	<i>T. domingensis</i>	
27	4.8 (0.1)	5.4 (0.3)	46.6 (2.6)	26.7 (0.5)	12.0 (0.8)	6.9 (0.2)	11.8 (0.7)	10.1 (0.3)	14.0 (0.2)	

Standard deviation in brackets. See Table 2 for the full forms of the abbreviated species names. CPOM, coarse particulate organic matter.

Table 10. Mean C:N ratios of consumers and primary sources collected from sites with minimal anthropogenic developments

Site	Consumer			Primary sources						
	Amphipoda	Trichoptera	CPOM	Riparian leaves	Riparian grasses	<i>T. procerum</i>	<i>A. arvensis</i>	<i>P. major</i>	<i>T. domingensis</i>	<i>P. decipiens</i>
40	4.7 (0.2)	4.9 (0.1)	47.4 (1.7)	18.4 (0.6)	15.4 (0.5)	7.1 (0.1)	12.7 (0.3)	21.0 (1.0)	15.1 (0.1)	8.5 (0.0)
18	4.5 (0.1)	Trichoptera	CPOM	Riparian leaves	Riparian grasses	<i>T. procerum</i>	<i>C. vaginatus</i>	<i>J. pallidus</i>	<i>B. juncea</i>	
		5.0 (0.2)	59.4 (1.7)	29.2 (0.9)	21.8 (1.3)	8.7 (0.3)	50.1 (2.2)	44.0 (1.2)	48.8 (2.0)	
22	4.6 (0.1)	Trichoptera	CPOM	Riparian leaves	Riparian grasses	<i>T. procerum</i>	<i>C. vaginatus</i>	<i>J. pallidus</i>	<i>C. helmsii</i>	<i>M. simulans</i>
		5.7 (0.2)	43.1 (1.8)	45.2 (2.3)	10.6 (1.0)	8.8 (0.1)	25.3 (0.7)	27.7 (0.5)	14.3 (0.2)	13.4 (0.8)

Standard deviation in brackets. See Table 2 for the full forms of the abbreviated species names. CPOM, coarse particulate organic matter.

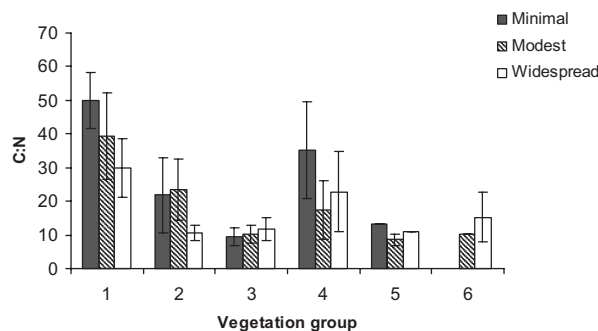


Fig. 2. Mean C:N ratios for each of the vegetation groupings across each level of anthropogenic development (Minimal to Widespread).

and 42.5 at sites 36 and 30, respectively (Table 8), a ratio of 27.4 at site 17 (Table 9), and a ratio of 50.1 at site 18 (Table 10). The primary consumers, however, were very much homeostatic in their C:N ratios, regardless of the level of anthropogenic development across the site. Amphipoda ranged from 4.5 to 5.0 and Trichoptera from 4.7 to 5.7 between sites of the same and different levels of development (Tables 8–10). In general, the mean C:N ratio for each of the vegetation groupings shows that group 3 had the lowest C:N ratio while group 1 had the highest across each level of development (Fig. 2).

DISCUSSION

In undisturbed forested riverine reaches with minimum anthropogenic alterations, riparian vegetation has a controlling influence on ecosystem function by reducing solar radiation and therefore limiting in-stream primary production (Boston & Hill 1991; Cummins *et al.* 1995). As a result, food webs in forested/wooded streams are thought to be largely dependent on terrestrial allochthonous material (Vannote *et al.* 1980; Bunn 1993; Cummins *et al.* 1995; Hicks 1997). However, in this study semi-emergent macrophytes (local in-stream primary production) were found to be the major energy sources supporting the local shredder communities along forested riverine reaches.

Reaches with less shading (limited clearance and grazing by livestock) have increased solar radiation, and increased nutrient inputs owing to anthropogenic influences in the catchments that often results in enhanced in-stream primary production (submerged and emergent macrophytes; Brookes 1994; Bunn *et al.* 1998). It is reasonable to assume that the increased in-stream primary productivity would play an even greater role in the nutrition of local shredder communities. Shredder communities found in these reaches have a greater nutritional dependence on suc-

culent semi-emergent macrophytes in comparison to those found in reaches with minimum anthropogenic alterations.

Those reaches subjected to widespread clearance have experienced changes to their fluvial geomorphology and bank erosion, leading to river channelization. These channelized rivers are often deeply incised and it is this incision and lowering of the streambed that leads to a lowering of the water table in the riparian zone, leading to the loss of longitudinal and lateral hydrological connectivity (Amoros & Bornette 2002). This loss can result in significant alterations to primary producer communities and hence to riverine carbon cycles (Walker *et al.* 1997), which will alter food web structure and function (Ward & Stanford 1983; Hicks 1997; Harris 1999b). The principal energy sources supporting the local shredder communities found in these developed reaches were CPOM and filamentous algae.

Nutritional constraints as a result of anthropogenic alterations

The factors that influence the nutrient ratios in the leaves of primary producers and leaf litter (CPOM) are not consistent. Large variations in the C:N ratios of autotrophs occurs within and between ecosystems (Elser *et al.* 2000a). The C:N ratio found in the primary sources varied considerably among sites with the same level of development and between sites with differing levels of development. Reasons for this discrepancy have been attributed to differences in resorption efficiency, nutrient availability and plant homeostatic regulation (Aerts 1996; Gusewell 2004). However, regardless of the level of development across a broad range of food qualities and physiochemical environmental conditions (Cross *et al.* 2005), the primary macroinvertebrate consumers were relatively homeostatic in their C:N ratios and this is in accordance with other studies (Elser *et al.* 2000b; Cross *et al.* 2003, 2005; Frost *et al.* 2003).

The elemental composition of autotrophs is often out of balance with the nutritional demands of herbivorous animals (Elser *et al.* 2000a). Emergent aquatic macrophytes tend to be carbon-rich owing to a requirement for a carbon-based strengthening frame, whereas most herbivores and decomposers (animals, bacteria and fungi) found in aquatic systems have a much lower C:N ratio (Elser *et al.* 2000a), as was the case for the shredder communities in this study. This suggests that elemental imbalances between food resources and consumer requirements may be common in these systems (Cross *et al.* 2005). Many consumers selectively feed on high energy (high C) or high nutritive food resources or a specific combination thereof (Plath & Boersma 2001). Both Amphipoda

and Trichoptera selectively fed on vegetation group 3 across sites with modest to minimum anthropogenic developments. This vegetation group contained the lowest C:N ratio (Fig. 2) and therefore the highest nutritional content. In degraded riverine reaches there are limited food resources available, hence vegetation group 1 (CPOM) formed the main dietary components of Amphipoda even though it had the highest C:N ratio. At site 36, vegetation group 6 (filamentous algae) was the main dietary component of Trichoptera owing to its availability and its low C:N ratio in comparison to the other primary sources available. The imbalanced consumer-resource nutrient ratios in these degraded riverine reaches are likely to impose constraints on the growth and reproduction of their aquatic shredder communities with probable knock-on effects to higher trophic levels (Plath & Boersma 2001; Frost & Elser 2002; Frost *et al.* 2002; Tuchman *et al.* 2002, 2003; Cross *et al.* 2003; Brookes *et al.* 2005; Tibbets & Molles 2005).

The concept of a stoichiometric resource optima (Elser *et al.* 2005) predicts that primary consumers may respond positively or negatively to low C:N ratios in food resources depending on the elemental requirements of the consumers and their physiological responses (e.g. ingestion and assimilation) to increases in food nutrient concentrations. Anthropogenic alterations and modifications in catchments leading to increased nutrient inputs, outputs and retention times with in aquatic ecosystems can alter the stoichiometric relationships between consumer and food resources, which will have profound consequences for riverine carbon cycles and on aquatic food-web structure and function (Ward & Stanford 1983; Hicks 1997; Walker *et al.* 1997; Harris 1999b, 2001; Scheffer *et al.* 2001; Frost *et al.* 2005).

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