

# Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams

L. E. ENGLAND AND A. D. ROSEMOND

*Institute of Ecology, University of Georgia, Athens, GA, U.S.A.*

## SUMMARY

1. We assessed the impacts of deforestation on the energy base of headwater food webs in seven headwater streams in the Upper Chattahoochee basin, GA, U.S.A where percentage forest in catchments ranged from 82 to 96%. We measured terrestrial organic matter standing crop and determined consumer (crayfish and insectivorous fish) dependence on terrestrial versus aquatic energy sources via gut content and stable isotope analyses.
2. Standing crop of coarse particulate organic matter (CPOM) declined with deforestation at large scales (i.e. catchment deforestation and riparian deforestation at the entire stream network scale). Terrestrial plant matter, the dominant component of crayfish guts, declined in crayfish guts with reductions in CPOM standing crop and with deforestation.
3. Crayfish and insectivorous fish  $\delta^{13}\text{C}$  showed enrichment trends with deforestation, indicating isotopic divergence from CPOM, the most  $^{13}\text{C}$ -depleted basal resource, with reductions in catchment and riparian forest cover. Crayfish  $\delta^{13}\text{C}$  also exhibited enrichment with decreased instream CPOM standing crop.
4. A concentration-dependent mixing model was used to calculate the relative dependence of crayfish and fish on terrestrial versus aquatic basal resources. Results suggested that both allochthonous CPOM and autochthonous production were important basal resources. Consumer dependence on CPOM decreased with reductions in canopy cover.
5. Our data suggest the importance of forest cover to headwater food webs at multiple scales, and that relatively low levels of riparian deforestation along headwater streams can lead to reductions in stream food web dependence on terrestrial subsidies.

*Keywords:* allochthonous resources, deforestation, food web subsidies, riparian buffers, stable isotopes, terrestrial-aquatic linkages

## Introduction

Riparian forests influence physical, chemical, and biological dimensions of streams and mediate a number of terrestrial-aquatic linkages (Karr & Schlosser, 1978; Gregory *et al.*, 1991; Sweeney, 1992). Strong connectivity between adjacent terrestrial and aquatic ecosystems can result in reciprocal subsidies (*sensu* Nakano & Murakami, 2001). In headwater streams, aquatic insect emergence may be the primary stream-to-forest subsidy, while forest-to-stream fluxes

include nutrients, dissolved and fine particulate organic carbon, coarse detritus and debris, and terrestrial arthropods (Polis, Anderson & Holt, 1997; Sabo & Power, 2002). These allochthonous resources can have potentially large impacts on the productivity of receiving systems (Polis & Hurd, 1996; Nakano, Miyasaka & Kuhara, 1999; Wallace *et al.*, 1999), but are donor-controlled (Polis *et al.*, 1997) and consequently may depend on the condition of the donor system. The critical role of terrestrial detritus in the food webs of forested headwater streams was recently defined on a large-scale through a long-term exclusion of leaf litter to a montane stream in the south-eastern U.S. Exclusion of riparian inputs in this study resulted in lower productivity of both primary and higher order

---

Correspondence: L. E. England, 923 O'Sheridan Street, Madison, WI 53715, U.S.A.

E-mail: lengland@uga.edu

consumers, indicating dependence on terrestrial subsidies by multiple trophic levels (Wallace *et al.*, 1999).

The River Continuum Concept (RCC, Vannote *et al.*, 1980) asserts that headwater food webs are largely supported by inputs of allochthonous detritus that become less important as autochthonous production increases downstream. This results in a longitudinal gradient in terrestrial subsidies of aquatic food webs in river networks. This prediction is based on relatively higher canopy cover in headwaters, which results in higher allochthonous detrital inputs per area of streambed (Webster *et al.*, 1990) and low autochthonous production because of light limitation (Minshall *et al.*, 1983; Feminella, Power & Resh, 1989, but see Winterbourn, Rounick & Cowie, 1981 for an example of a different pattern). While some of the RCC's longitudinal linkage predictions have been supported for river systems in relatively undisturbed catchments (e.g. Rosi-Marshall & Wallace, 2002), today's landscapes are more commonly mosaics of various anthropogenic land uses. The question of how anthropogenic alteration of catchments and riparian corridors affects the energy-base continuum within river systems remains essentially unanswered. Further, although the impacts of catchment clearcuts (Webster *et al.*, 1990) and exclusion of all detrital inputs have been studied (Wallace *et al.*, 1999), it is unclear how gradients in landscape alteration affect the magnitude of allochthonous inputs to streams, and how potential gradients in allochthonous resource availability impact stream food webs.

Stable isotopes (mainly of C and N) have been employed extensively as food web tracers (Rounick & Winterbourne, 1986; Peterson & Fry, 1987) and have been useful in establishing the relative importance of terrestrial versus aquatic energy sources in supporting stream food webs in systems where these basal resources have distinct isotopic signatures (Rounick, Winterbourne & Lyon, 1982; Rosenfeld & Roff, 1992; Finlay, 2001). However, most research in this area has focused on undisturbed lotic systems (Bunn *et al.*, 1989; Hamilton, Lewis & Sippel, 1992; Rosenfeld & Roff, 1992; Thorp *et al.*, 1998; Finlay, 2001; Lewis *et al.*, 2001) or comparisons of forest versus pasture, grassland, or clear cut streams (Rounick *et al.*, 1982; Hicks, 1997; Parkyn, Collier & Hicks, 2001). Here, we used variation in stable isotopes of C and N to assess effects of gradients in deforestation on stream food webs.

On current landscapes, riparian forests are commonly narrow, discontinuous corridors of vegetation along streams ('buffers') embedded within catchment matrices of anthropogenic land use patches and forested patches in various stages of recovery from both anthropogenic and natural disturbance (Malanson, 1993; Yarnell, 1998). Ecologists are just beginning to examine the effects of such disturbance on food web structure and dynamics (Power & Dietrich, 2002). The focus of the present research was to assess, using gut contents and stable isotope analyses, how gradients in catchment and riparian deforestation affected (i) the availability of terrestrial organic matter in headwater streams and (ii) the dependence of headwater stream food webs on terrestrial energy sources. We determined relationships between forest cover, standing crop of allochthonous detritus and isotopic signatures of top consumers. Study streams encompassed a relatively narrow range in riparian forest cover within catchments that were predominantly forested; thus our results are indicative of the impacts of relatively subtle forest cover changes. We assessed forest cover at multiple scales, from reach to catchment, to determine the scale(s) of deforestation impacts on headwater food webs.

## Methods

### *Land use assessment*

Seven study streams (Fig. 1) were selected from the Upper Chattahoochee River Basin, GA, U.S.A. based on a suite of criteria including catchment area, elevation, gradient, and access (Table 1). High resolution (1–2 m resolution, National Aerial Photography Program, United States Geological Survey) colour-infrared aerial photographs of study catchments (March 1999) were digitised, georeferenced and rectified for analysis using ERDAS Imagine® 8.4 (ERDAS®, Atlanta, GA, U.S.A.). Catchment boundaries were delineated and land-cover types in study catchments were classified with the supervised classification procedure described in the ERDAS Imagine® Tour Guides™ (1999). Classification resulted in a thematic raster layer that allowed determination of percentages of each land-cover type, including forest cover, impervious cover, and agricultural cover.

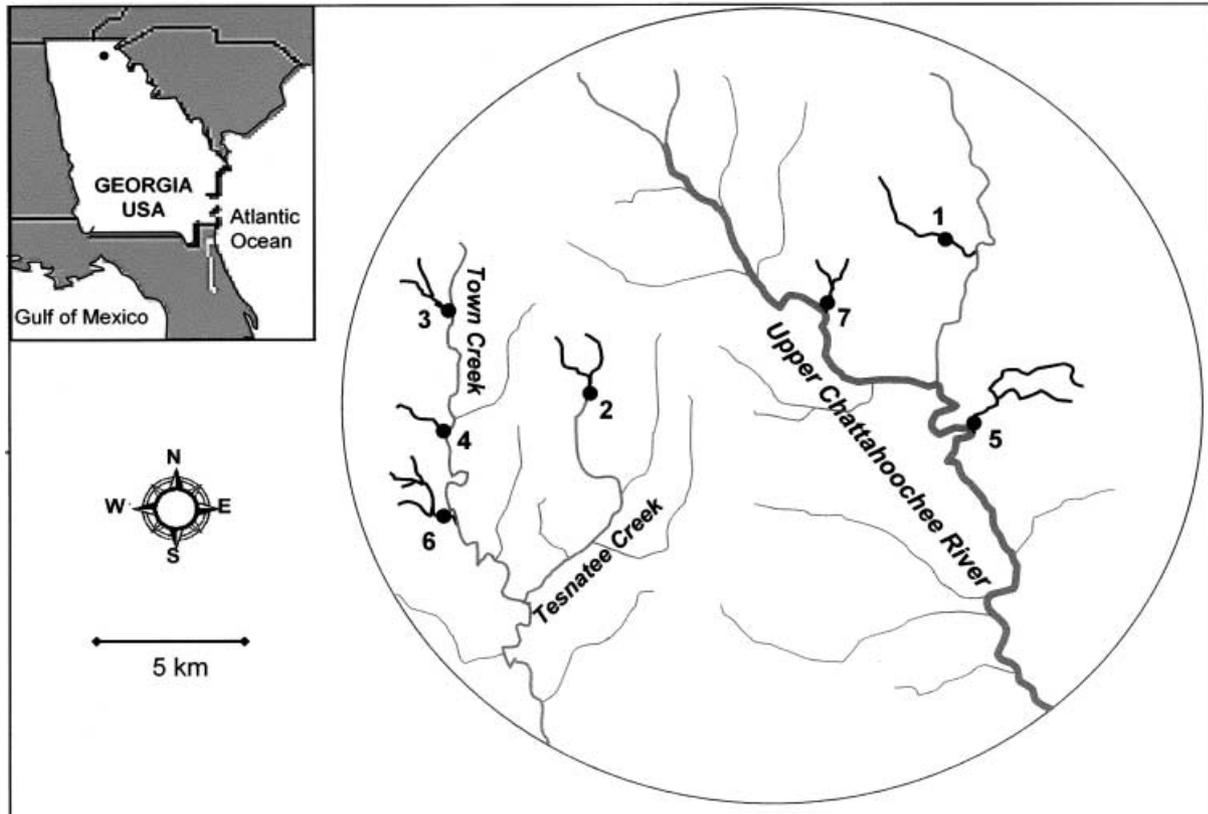


Fig. 1 Map of study stream locations (1–7 in order from most to least forested catchments) in the Upper Chattahoochee River basin, GA, U.S.A. All study sites are within the Blue Ridge physiographic province at the southernmost extent of the Appalachian Mountains. Town Creek flows into Tesnatee Creek, which flows into the Chestatee River and eventually into the Upper Chattahoochee River. 1 = York Creek, 2 = Cathey Creek, 3 = Town tributary 3, 4 = Town tributary 2, 5 = Maudin Mill Creek, 6 = Town tributary 1, 7 = Bell's Creek.

To assess riparian land-cover, 100 ft buffers (100 ft = 30.48 m, buffer laws in the U.S. are typically written using imperial units) were delineated around study streams throughout the entire upstream networks and land-cover within the buffers was determined from the land-cover raster layers. All gaps in forest cover within the 30.48 m buffer were digitally measured (Fig. 2) and these data were used to calculate several riparian forest cover metrics (Table 1). Continuity of stream canopy cover (CONTIN-CC) and riparian buffers (CONTIN-BW) was calculated as the per cent stream length with a buffer wider than 0 and 30.48 m, respectively. Mean buffer width (MBW) was calculated for multiple scales: (100 m local reach, 1000 m of network above study site, and entire stream network above study site) using the following weighted-average formula:

$$\text{MBW} = \frac{\sum L_{\text{BG}} \times W_{\text{BG}} + 100 (L_{\text{TS}} \times 2 - \sum L_{\text{BG}})}{L_{\text{TS}} \times 2} \quad (1)$$

$L_{\text{BG}}$  = length of buffer gap,  $W_{\text{BG}}$  = buffer width at gap,  $L_{\text{TS}}$  = total stream length.

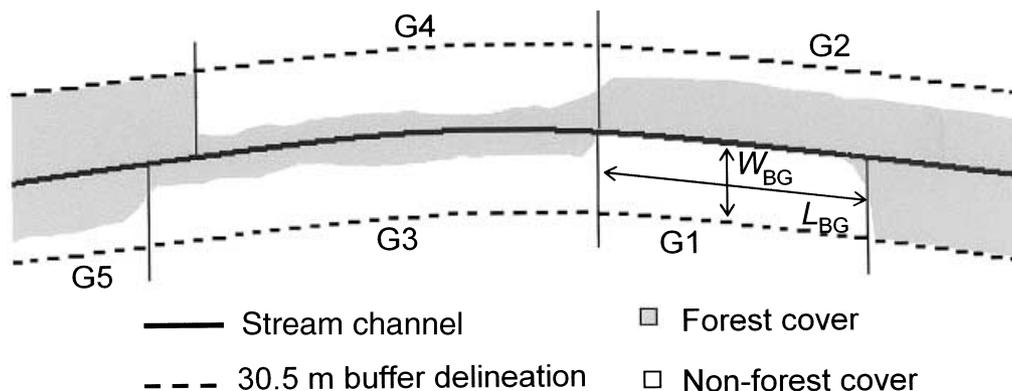
Stream canopy cover was determined for each study reach by averaging spherical densitometer measurements at five points along each study reach.

#### *Availability of allochthonous resources*

Benthic coarse particulate organic matter (CPOM) was quantified in the autumn (November 2000) and the following spring (May 2001). A 1-m<sup>2</sup> plot, assembled from polyvinyl chloride (PVC) pipe and divided into four quadrants, was used to survey CPOM coverage of the streambed in randomly chosen plot locations to ensure that the proportion of different habitats

**Table 1** Summary site characteristics and land-cover for streams studied in the Upper Chattahoochee River basin, GA, U.S.A. Includes physical characteristics and results of land-cover classification of study catchments and riparian buffers. Streams are ordered left to right by catchment forest cover. Mean width and depth ( $\pm 1$  SE) are based on 10 and 50 measurements, respectively

Site characteristics and land-cover	Abbreviation	Stream						
		1	2	3	4	5	6	7
<b>Site characteristics</b>								
Mean width (m)		3.6	2.1	1.5	1.2	4.7	2.0	2.2
SE		0.23	0.12	0.07	0.05	0.32	0.11	0.11
Mean depth (m)		0.12	0.12	0.10	0.11	0.19	0.13	0.11
SE		0.09	0.014	0.08	0.07	0.14	0.09	0.011
Gradient ( $\text{m m}^{-1}$ )		0.006	0.015	0.016	0.014	0.015	0.013	0.013
Elevation (m)		499	517	533	482	431	465	432
Catchment area ( $\text{km}^2$ )		3.90	2.67	1.85	1.94	7.17	3.21	2.37
<b>Land-cover</b>								
Canopy cover (%)	CC	81.4	85.3	87.7	81.9	77.2	85.5	88.7
Mean buffer width (m)								
100 m reach	MBW-100	25.8	28.2	21.6	30.5	28.7	27.9	29.7
1000 m reach	MBW-1000	29.0	21.8	24.6	28.3	24.8	22.9	10.3
Entire network	MBW-NET	29.4	27.9	26.2	28.2	26.8	25.5	17.3
Continuity of:								
Canopy cover (%)	CONTIN-CC	100.0	97.6	96.4	100.0	95.0	95.3	63.2
Buffer >30.5 m (%)	CONTIN-BW	92.5	86.2	79.1	84.5	81.2	77.5	52.3
Catchment % forest	FWS	96.3	94.3	91.2	90.6	89.8	88.4	82.5



**Fig. 2** Schematic illustrating how buffer gap measurements were made along a hypothetical stream reach. Areas within the 30.5 m buffer delineation without forest cover were considered buffer gaps, shown as white areas. The two sides of each stream were analysed separately as forest cover often varied considerably from one side to the other. For each gap (here G1–G5), a gap width ( $W_{BG}$ ) and length ( $L_{BG}$ ) were measured. Gaps along the entire stream network above the sample reach were measured and these data were used to calculate riparian forest cover width and continuity metrics at multiple scales.

(% riffle, % pool and % run) in measured plots reflected the proportions of these habitats throughout the streambed. Percent coverage by CPOM for each of the four quadrants was visually estimated to the nearest 10% at 30 1-m<sup>2</sup> plots in each stream, and the quadrants were classified as riffle, run, or pool habitat. At every other survey plot ( $n = 15/\text{stream}$ ), all CPOM within the plot was collected by hand and rinsed in

stream water to remove sediment particles. CPOM samples were oven dried at 40 °C and weighed to determine dry mass of CPOM per m<sup>2</sup> of streambed. A sum of habitat-specific CPOM standing crop ( $\text{g m}^{-2}$ ) weighted by the percentage of streambed area in each habitat type (i.e. pool, riffle, or run) was calculated for autumn and overall (autumn/spring average). Standing crop of large woody debris (LWD  $\geq 10$  cm diam-

eter, >1 m length) was assessed once in November 2000. All LWD within the sample reach was measured (diameter and length) in order to estimate planar area of LWD habitat.

#### *Natural abundance stable isotopes and food web energy base*

To assess the relative importance of aquatic versus terrestrial energy sources to consumers in these headwater streams, we determined carbon and nitrogen isotope signatures for basal food web resources of terrestrial and aquatic origin and top consumers (crayfish and insectivorous fish). All food web components were sampled for isotopic analyses in the autumn of 2001. Three replicates of allochthonous (CPOM) and autochthonous (epilithic biofilm) basal resources as well as seston were sampled from each study stream. CPOM was collected from natural leaf accumulations in study streams and oven dried at 40 °C. We chose to sample conditioned leaf litter over leached leaf litter because it provides a stronger representation of what stream consumers actually obtain from this basal resource. For seston, we collected and filtered 4–5 L of stream water and the resulting filters were oven dried at 40 °C. Epilithon was sampled by taking epilithic scrapings of median-sized cobbles from riffles with similar flow velocity in all study streams to minimize isotopic variation due to flow (Finlay, Power & Cabana, 1999). We chose to sample riffle habitats because this is where the dominant herbivores, *Stenonema spp.*, feed and are thus the habitats that contribute the most algae to food webs in these streams.

We attempted to isolate algae from other epilithon components using a density-gradient centrifugation technique that relies on differential densities of epilithic biofilm components (Hamilton *et al.*, 1992). However, because of low algal biomass and a high proportion of diatoms (which have a high density relative to other algae) in these heavily shaded streams, effective algal isolation (evaluated by microscopic examination) with this technique was achieved for just two samples, hereafter 'pure algal' samples. Therefore, we considered Finlay's (2001) alternative approach of using an herbivore as an isotopic proxy for algae, which has been successful in getting strong (nearly 1 : 1) relationships between isolated epilithic algal  $\delta^{13}\text{C}$  and herbivore  $\delta^{13}\text{C}$  across a wide range in

stream size (Finlay, 2001). We sampled the predominant herbivore in our streams, heptageniid mayflies (*Stenonema spp.*), for isotope analysis and regarded these herbivores as 'algae samplers'. We conducted gut analysis to evaluate how well they sample algae and thus their potential to serve as an algal proxy (see gut content analysis below). For each study stream, three riffles were sampled and 5–10 individuals for each of three size classes (0–5, 5–10 and 10–15 mm) were collected and frozen. Individuals within a size class were combined, their guts were removed, and remaining tissue was oven dried at 40 °C.

In sampling consumers for isotope analyses, we focused on top trophic levels since they are isotopic integrators of lower trophic levels and thus may be used to infer food web changes. We sampled crayfish (*Cambarus sp.*), which are omnivores that feed on terrestrial detritus and aquatic insects, often in varying proportions with age (Momot, Gowing & Jones, 1978; Hury & Wallace, 1987; Whitley & Rabeni, 1997; Parkyn *et al.*, 2001). We also sampled the six most common species of insectivorous fishes in the study streams [Alabama hog sucker *Hypentelium etowanum* (Jordan), bandfin shiner *Luxilus zonistius* (Jordan), blackbanded darter *Percina nigrofasciata* (Agassiz), bluehead chub *Nocomis leptoccephalus* (Girard), mottled sculpin *Cottus bairdi* (Girard), and yellowfin shiner *Notropis lutipinnis* (Jordan and Brayton)]. A subset of these six species was present at each study site. Insectivorous fish (five individuals for each species present) and crayfish (six to 10 individuals, total carapace length measured) were collected from study streams via electroshocking. Specimens were returned to the laboratory on ice. In the laboratory, tail muscle tissue (crayfish) and caudal-peduncle muscle tissue (fish) was removed for isotope analysis and oven-dried at 40 °C.

All dried samples were ground, weighed, and analysed using a Finnigan Delta C mass spectrometer linked with a Carlo Erba 1500 CHN analyser. Standard methods for reporting isotopic composition were followed (DeNiro & Epstein, 1978; Rounick & Winterbourne, 1986).

#### *Gut content analyses*

As crayfish feed directly on terrestrial leaf litter (unlike the insectivorous fish sampled), we analysed crayfish gut contents to test whether the diet of these omnivores

varied with riparian deforestation. Crayfish collected for isotope analyses were also used for gut content analyses in which we measured the relative proportion (by area, using microscopy) of different classes of food particles found in crayfish guts. Crayfish guts were dissected and gut content slides were prepared following standard protocol (Cummins, 1973; Hall, Wallace & Eggert, 2000). Slides were viewed at  $100\times$  magnification using an Olympus BX40 phase-contrast compound microscope, and digital images of 20–30 randomly chosen microscope fields per slide were taken with a video camera. Image analysis software, Image-Pro® Plus 3.0.1 (Media Cybernetics, Silver Spring, MD, U.S.A.), was then used to analyse digital images by identifying and digitally measuring the area of 50 food particles per slide, as is standard for this type of diet analysis (Cummins, 1973; Hall *et al.*, 2000). Particles were classified as plant matter (leaf and wood material), algae (diatoms and filamentous forms), animal material (invertebrates), or amorphous detritus (no cellular structure), and the percentage of area contributed by each of these classes was calculated for individual crayfish.

Previous work has shown that *Stenonema* larvae may derive large portions of their carbon from bacteria (Edwards & Meyer, 1990; Hall & Meyer, 1998). Thus, to evaluate the potential use of *Stenonema* as an isotopic proxy for algae, we analysed *Stenonema* gut contents to determine how much of their assimilated carbon could potentially be attributed to algae. *Stenonema* (five to 10 individuals) from three riffles were sampled in each study stream and preserved in formalin. Guts for individuals from the same riffle were combined onto one slide for analysis following the above methods, but these slides were viewed under  $400\times$  magnification. Food particles were classified as diatoms, filamentous algae, or amorphous detritus, and the percentage of area contributed by each of these classes was calculated. To determine the actual proportion of carbon derived from each food source, these percentages were corrected using assimilation efficiencies from the literature: 10% for amorphous detritus and 30% for diatoms and filamentous algae (Benke & Wallace, 1980; Hall *et al.*, 2000).

#### Data analysis and mixing model

We used regression analysis to determine whether there were relationships between riparian and catch-

ment land-cover and allochthonous standing crop or the contribution of allochthonous resources to food webs (via gut content and isotopic analyses). Assumptions of normality were tested using Shapiro–Wilks tests for all data (land-cover and dependent variables, e.g. isotopic signatures, per cent plant matter in guts), and non-normal data were transformed prior to statistical analysis (percentage data were arcsin-squareroot transformed and network-scale mean buffer width was cosine transformed). Crayfish gut data were also analysed for relationships with total carapace length to test for diet changes with age that have been previously shown (e.g. Whittledge & Rabeni, 1997; Parkyn *et al.*, 2001). We interpreted trends of consumer  $\delta^{13}\text{C}$  enrichment (increasing  $\delta^{13}\text{C}$ ) as indicating divergence from terrestrial detritus signatures, as CPOM was the most  $^{13}\text{C}$  depleted (i.e. most negative) food web component.

We used a mixing model to determine the percentage contribution of allochthonous sources to fish and crayfish diets. We first determined whether basal resources were significantly different from each other. Analysis of variance (ANOVA) coupled with Ryan's Q test (Day & Quinn, 1989) and a Kramer correction for unequal sample size, was used to determine differences among basal resources in isotopic composition. Multiple analysis of variance (MANOVA) was used to determine whether basal resources differed in bivariate (i.e. dual isotope, C and N) space. We then used a concentration-dependent, dual isotope (C and N) mixing model developed by Phillips & Koch (2002), which calculates the relative importance of food sources in a consumer's diet while accounting for differences in C and N content of food sources. Most published models assume that the proportions of C and N a consumer obtains from a food source are identical, but when food sources differ substantially in C and N content (e.g. leaf litter versus algae) this assumption is not valid (Phillips & Koch, 2002). We used this mixing model to compare the importance of terrestrial (represented by CPOM isotope data for each site) versus aquatic (algae, represented by 'adjusted epilithon' isotope data, see Results for rationale) basal resources in supporting crayfish and insectivorous fishes. Consumer isotopic signatures were corrected for trophic fractionation using the product of trophic level and fractionation values ( $0.4\text{‰}$   $\delta^{13}\text{C}$  and  $3.4\text{‰}$   $\delta^{15}\text{N}$ , Post, 2002). Trophic levels used in these calculations were 1.6 for crayfish ( $1\times\%$

plant matter in guts  $\times$  (assimilation efficiency for plant matter + 2)  $\times$  % insect matter in guts  $\times$  assimilation for insect matter) and 2 for insectivorous fish. CPOM C and N content values came from elemental composition analysis that was coupled with isotope analysis. For algae, we used N content of 4% (Pandian & Marian, 1986) and then calculated C content (26.5%) using the Redfield ratio of 106 C : 16 N (Wetzel, 2001). Regression was then used to determine whether forest cover on multiple scales could explain variation in consumer dependence on CPOM (mixing model results). All statistical tests were performed using SAS® 8.02 (SAS Institute, Cary, NC, U.S.A.).

## Results

### *Catchment and riparian forest cover*

Study catchments were predominantly forested (82–96%), while agricultural and impervious cover made up relatively small percentages (Table 1). The sites comprised a gradient in riparian forest cover that varied with the scale of analysis; that is the ranking of streams from most to least forested depended on scale. Mean buffer width ranged from 10.4 to 30.5 m across all scales. Local canopy cover was relatively high at all sites (77–89%), while continuity of canopy cover throughout stream networks (CONTIN-CC) was somewhat more variable (63–100%). In general,

streams had relatively high forest cover across all scales and metrics, thus relationships between forest cover and food web analyses are indicative of impacts of relatively subtle changes in forest cover.

### *Allochthonous resources, crayfish gut contents, and consumer carbon isotopes across sites*

Standing crops of allochthonous resources varied across sites (Table 2). Habitat-weighted CPOM standing crop in November (25.3–206.2 g m<sup>-2</sup>) was more variable than in May (20.8–84.6 g m<sup>-2</sup>). LWD (planar area of wood per m of stream) was absent in one study reach and was as high as 0.118 m<sup>2</sup> m<sup>-1</sup> in another study reach (Table 2). Plant matter (leaf and woody material) was the predominant component of crayfish guts at all sites followed by animal matter and amorphous detritus (Table 2); both diatoms and filamentous algae were rarely found and made up <1% of crayfish gut contents at all sites. Regression results indicated that proportions of various food items in crayfish gut contents were not related to carapace length ( $P > 0.05$ ,  $n = 62$ , length range: 1.2–3.9 cm), indicating no significant feeding shifts over this size range. Consumer carbon isotopic signatures fell within narrow ranges (Table 2). Crayfish  $\delta^{13}\text{C}$  values (–24.8 to –23.8‰) were slightly depleted compared to insectivorous fish  $\delta^{13}\text{C}$  (–24.5 to –22.7‰).

**Table 2** Results of food web analyses: allochthonous resource standing crops, crayfish gut contents, and consumer carbon isotope signatures. Habitat weighted CPOM measurements are sums of habitat-specific CPOM standing crops weighted by the percentage of streambed area in each habitat type (pool, riffle, or run). LWD is measured in planar area of wood per metre length of stream. In crayfish gut contents, some diatoms and filamentous algae were found, but data are not shown because they made up <1% by area in all cases. Streams are ordered by catchment forest cover (FWS)

Food web analyses	Stream						
	1	2	3	4	5	6	7
Allochthonous resources							
Habitat-weighted CPOM							
Autumn (g m <sup>-2</sup> )	184.2	160.9	206.2	69.5	128	91.9	25.3
Spring (g m <sup>-2</sup> )	33.2	42.1	23.3	44.9	84.6	52.4	20.8
Overall (g m <sup>-2</sup> )	101.5	96.5	93.1	50.7	105.6	73.6	23.0
LWD planar area (m <sup>2</sup> m <sup>-1</sup> )	0.118	0.036	0.046	0.032	0.0	0.024	0.084
Crayfish gut contents							
% Plant matter	74.2	76.4	81.3	39.1	62.2	51.1	44.4
SE	6.2	3.8	6.0	9.3	8.4	9.4	6.8
% Animal matter	15.4	14.8	11.4	26.0	6.0	38.9	32.8
SE	5.1	3.8	6.4	6.3	5.6	10.0	6.9
% Amorphous detritus	10.4	8.8	7.3	34.5	30.5	10.0	22.7
SE	1.6	1.1	2.0	5.6	5.4	1.9	3.9
Consumer $\delta^{13}\text{C}$							
Crayfish (‰)	–24.7	–24.8	–24.5	–24.6	–23.8	–24.3	–24.2
SE	0.27	0.20	0.15	0.09	0.21	0.13	0.10
Insectivorous fish (‰)	–24.4	–24.0	–23.6	–24.5	–22.7	–23.3	–23.7
SE	0.25	0.19	0.36	0.23	0.22	0.27	0.49

*Relationships between forest cover and food web analyses: regression results*

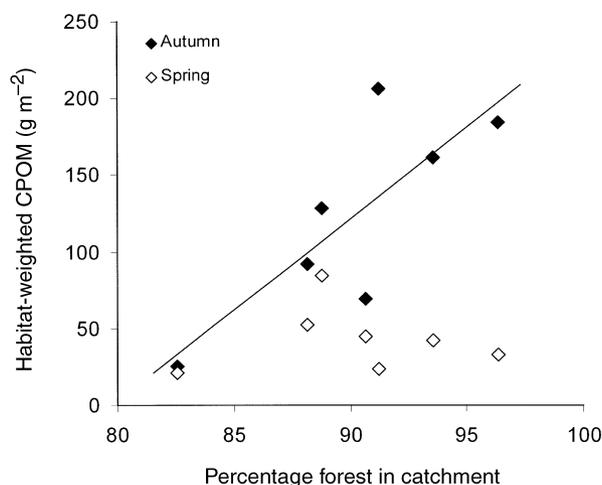
Allochthonous resource availability varied with forest cover (Table 3). Habitat-weighted CPOM standing crop was positively related to both catchment and network-scale riparian forest cover. Autumn CPOM standing crop declined from nearly 200 to about 25 g m<sup>-2</sup> (Fig. 3) over a narrow range in watershed deforestation, from 96 to 82% forest cover. CPOM standing crop was also positively related to network-scale buffer width and riparian continuity variables (CONTIN-CC and CONTIN-BW, Table 1), but was not related to local scale riparian variables (Table 3). Spring CPOM standing crop was not related to measures of forest cover ( $P > 0.05$ ). LWD standing crop was not related to any forest cover variable. However, the least forested stream (7) had among the highest LWD standing crop of streams studied. This stream has highly unstable banks and nearly all of the wood in this stream comes from mass wasting of banks and bank trees; we documented several new fallen bank trees during the course of the study (L.E. England, unpublished data). We suggest that a different mechanism (bank instability) explains the LWD standing crop at this particular site compared to the remaining six streams, for which LWD standing crop was positively related to catchment forest cover (Table 3).

The proportion of plant matter in crayfish guts was positively related to CPOM standing crop in autumn when crayfish were collected (Fig. 4), but not to overall or spring CPOM standing crop ( $P > 0.05$ ). An opposite, but weak, relationship was seen with the proportion of animal matter in crayfish guts, which declined with increasing CPOM standing crop ( $P < 0.01$ ,  $R^2 = 0.12$ ), while consumption of amorphous detritus did not vary with CPOM standing crop ( $P > 0.05$ ). The proportion of plant matter in crayfish guts was also positively related to catchment forest cover and network-scale riparian forest cover variables (Table 3). The percentage of *Stenonema* gut contents composed of algae (mostly diatoms but some filamentous algae) ranged from 23.9 to 58.4% and averaged  $36.1 \pm 3.4\%$  while amorphous detritus averaged  $63.9 \pm 3.4\%$  (mean  $\pm$  SE,  $n = 62$ ) in study streams. Percentage of algae in *Stenonema* guts was negatively, though weakly, related to canopy cover ( $P < 0.05$ ,  $R^2 = 0.21$ ), but not to any other riparian forest cover variable ( $P > 0.05$ ). By applying assimilation efficiency corrections to gut content percentages, we determined that algae contributed 62.8% while amorphous detritus contributed 37.2% of organic matter assimilated by *Stenonema* in study streams.

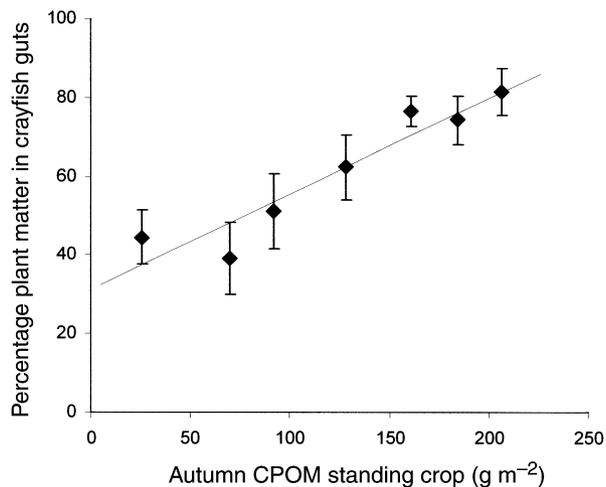
Generally, crayfish and insectivorous fish  $\delta^{13}\text{C}$  were negatively related to forest cover, indicating more positive signatures (divergence from CPOM  $\delta^{13}\text{C}$ ) with reductions in forest cover (Table 3). Crayfish

**Table 3** Results of simple linear regression between forest cover variables and food web analyses. Direction of effect for relationships is noted by (+) or (-) followed by the coefficient of determination,  $R^2$ . Significant  $P$ -values are indicated by asterisk (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ), and non-significant results are indicated by ns. Percent variables were arcsin-squareroot transformed and network mean buffer width was cosine transformed to meet assumptions of normality for regression analyses. Only 6 sites were used for LWD analyses; see Results for rationale. Negative relationships between consumer  $\delta^{13}\text{C}$  and land use variables indicate isotopic divergence from terrestrial CPOM  $\delta^{13}\text{C}$  with increasing catchment or riparian deforestation

Dependent variables	Local scale riparian			Stream network-scale riparian			Catchment scale % forest
	Canopy cover	Mean buffer width : stream length			Continuity of		
		100 m	1000 m	Network	Canopy	Buffer >30.5 m	
Allochthonous resources							
CPOM standing crop							
Overall	ns	ns	ns	(+)0.21***	(+)0.46*	(+)0.58*	(+)0.46*
Autumn	ns	ns	ns	(+)0.38***	ns	ns	(+)0.60*
LWD planar area	ns	ns	ns	ns	ns	ns	(+)0.76*
Crayfish gut contents							
% Plant matter	ns	ns	(+)0.06*	(+)0.09*	(+)0.06*	(+)0.11**	(+)0.16**
Consumer $\delta^{13}\text{C}$							
Crayfish	ns	ns	ns	(-)0.23*	(-)0.09*	(-)0.09*	(-)0.15**
Insectivorous fish	(-)0.07*	ns	ns	(-)0.15***	(-)0.05*	ns	(-)0.08**

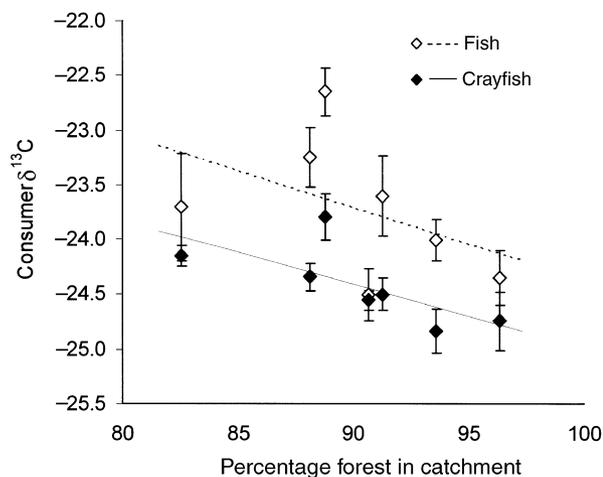


**Fig. 3** Linear regression results showing that autumn CPOM standing crop was positively related to catchment forest cover ( $P < 0.05$ ,  $R^2 = 0.60$ , line indicates significant regression) while spring CPOM standing crop was not. CPOM standing crop variables are sums of habitat-specific CPOM standing crop weighted by the per cent streambed area in each habitat type (pool/riffle/run). Percentage variables are graphed untransformed for ease in visual interpretation, but statistics apply to arcsin-squareroot transformed data.



**Fig. 4** Linear regression results for crayfish gut contents showing that as CPOM availability increased, crayfish consumed more plant matter ( $P < 0.0001$ ,  $R^2 = 0.28$ ). Error bars are  $\pm 1$  SE and line indicates significant regression. Percentage variables are graphed untransformed for ease in visual interpretation, but statistics apply to arcsin-squareroot transformed data.

$\delta^{13}\text{C}$  was negatively related to CPOM standing crop and large scale forest cover variables: catchment forest cover and network-scale riparian forest cover width and continuity (Fig. 5 and Table 3). Local scale



**Fig. 5** Linear regression results showing that consumer  $\delta^{13}\text{C}$  signatures were negatively related to catchment forest cover. Examined in terms of increasing deforestation, consumer  $\delta^{13}\text{C}$  showed significant enrichment trends. This indicates consumer divergence from  $\delta^{13}\text{C}$  of terrestrial CPOM, the most depleted food web component (mean CPOM  $\delta^{13}\text{C} = -28.57$ ) with deforestation. Consumer  $\delta^{13}\text{C}$  also showed enrichment with network scale riparian forest cover (Table 3). Error bars are  $\pm 1$  SE and lines indicate significant regressions (crayfish:  $P < 0.01$ ,  $R^2 = 0.15$ , fish:  $P < 0.01$ ,  $R^2 = 0.008$ ).

riparian variables were not predictive of short-term (gut contents) or long-term ( $\delta^{13}\text{C}$ ) measures of crayfish diets. Isotopic signatures of insectivorous fish species were combined into one consumer category because ANOVA showed no significant differences in isotopic signatures among species ( $P = 0.1$ ,  $n = 96$ , d.f. = 5,  $F = 1.92$ ,  $\beta = 0.37$ ). Similar to crayfish, insectivorous fish  $\delta^{13}\text{C}$  showed significant negative relationships with catchment forest cover (Fig. 5) and network-scale riparian buffer width and continuity of canopy cover (Table 3). In addition to relationships with catchment forest cover, fish  $\delta^{13}\text{C}$  was also negatively related to local canopy cover (Table 3). In general, relationships between consumer  $\delta^{13}\text{C}$  and forest cover variables had low  $R^2$  values.

#### Consumer terrestrial dependence: mixing model results

Carbon and nitrogen isotopic signatures differed among basal resources (Table 4). Terrestrial CPOM was the most  $\delta^{13}\text{C}$  depleted while seston was the least depleted of the basal resources sampled (Table 4). Basal resource type was a significant effect in ANOVA (blocked by stream) for both  $\delta^{13}\text{C}$  ( $P < 0.0001$ , d.f. = 2,  $F = 96.47$ ) and  $\delta^{15}\text{N}$  ( $P < 0.0001$ , d.f. = 2,  $F = 53.2$ ),

**Table 4** Stable carbon (A) and nitrogen (B) isotope signatures of basal resources (site mean  $\pm$  1 SE). Epilithon data are *Stenonema* signatures corrected for trophic fractionation. 'Pure algal' are two samples for which algal isolation was successful using density gradient centrifugation. Using ANOVA blocked by stream, we determined that basal resource type (not including pure algal because of inadequate sample size) was a significant effect for  $\delta^{13}\text{C}$  ( $P < 0.0001$ , d.f. = 2,  $F = 96.5$ ) and  $\delta^{15}\text{N}$  ( $P < 0.0001$ , d.f. = 2,  $F = 53.2$ ). Ryan's Q multiple comparisons test showed that these three basal resources were isotopically distinct from each other for both C and N isotopes (a, b, c, denotes groupings from this test). ND = no data because of analytical error

Stream	Basal resource			Pure algal
	CPOM	Epilithon	Seston	
(A) $\delta^{13}\text{C}$				
1	$-29.17 \pm 0.15$	$-27.13 \pm 0.79$	$-22.88 \pm 0.87$	-24.19
2	$-27.84 \pm 0.07$	$-28.76 \pm 0.26$	$-24.60 \pm 0.55$	
3	$-27.23 \pm 0.10$	$-27.55 \pm 0.30$	$-23.24 \pm 0.47$	
4	$-28.33 \pm 0.29$	$-27.04 \pm 0.28$	$-23.15 \pm 0.38$	
5	$-29.25 \pm 0.16$	$-26.65 \pm 0.22$	$-25.95 \pm 0.19$	-24.73
6	$-28.75 \pm 0.30$	$-28.43 \pm 0.33$	$-23.93 \pm 0.43$	
7	$-29.52 \pm 0.28$	$-29.82 \pm 0.27$	$-21.76 \pm 1.17$	
Mean	$-28.57 \pm 0.19$	$-27.84 \pm 0.23$	$-23.64 \pm 0.25$	-24.46
	a	b	c	
(B) $\delta^{15}\text{N}$				
1	$-1.47 \pm 0.10$	$1.89 \pm 0.16$	$6.23 \pm 3.74$	2.71
2	$-1.01 \pm 0.42$	$3.90 \pm 0.28$	ND	
3	$-0.47 \pm 0.68$	$2.01 \pm 0.33$	$7.48 \pm 1.29$	
4	$1.30 \pm 0.56$	$6.54 \pm 0.53$	$6.35 \pm 2.24$	
5	$-0.67 \pm 0.62$	$4.24 \pm 0.09$	ND	6.27
6	$-2.60 \pm 0.62$	$3.04 \pm 0.25$	$7.40 \pm 2.97$	
7	$-0.63 \pm 0.35$	$1.41 \pm 0.10$	$5.25 \pm 1.82$	
Mean	$-0.79 \pm 0.29$	$3.25 \pm 0.28$	$6.54 \pm 0.99$	4.49
	a	b	c	

while stream was not significant for either ( $P > 0.05$ ). Ryan's Q multiple comparisons test separated each basal resource (CPOM, epilithon, and seston) as an isotopically distinct group for both C and N isotopes. In addition, MANOVA, used to determine if basal resources differed in dual isotope (C and N) bivariate space, showed a significant effect of basal resource type (Wilk's Lambda statistic  $P < 0.0001$ ). Though algal isolation by density gradient centrifugation was not consistent for all samples, successful isolation was achieved for two samples. These two 'pure algal' samples were several ‰ enriched in  $^{13}\text{C}$  relative to CPOM (Table 4). Therefore, although epilithon values (determined from *Stenonema*) were only slightly enriched relative to CPOM, we inferred that instream primary production resources were generally more

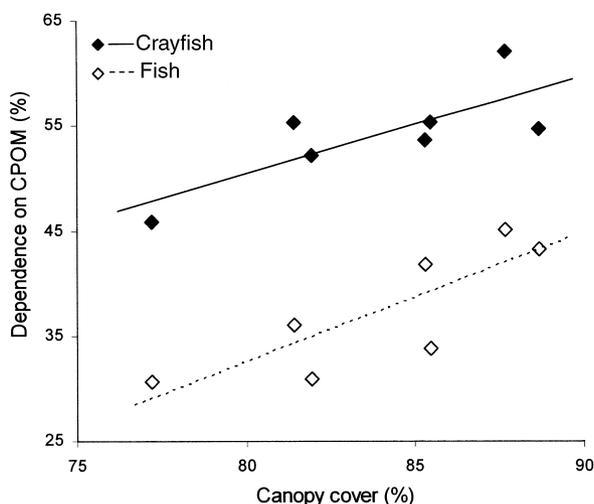
$^{13}\text{C}$  enriched than CPOM in these streams. Seston  $\delta^{13}\text{C}$  was most similar to the 'pure algal' samples (Table 4), suggesting a large algal component in seston or other processes that resulted in relatively enriched  $\delta^{13}\text{C}$  values.

As epilithon isotope signatures (inferred from herbivore signatures) were quite different from pure algal signatures (Table 4) and because crude estimates of dependence on algae by herbivores indicated incomplete reliance (Table 3 and assimilation estimates above), we did not use herbivores as an algal proxy in mixing model calculations. Instead, we used 'adjusted epilithon' signatures to represent instream primary production. Mean isotopic differences between the two pure algal signatures and respective epilithon signatures (a difference of 2.43  $\delta^{13}\text{C}$  and 1.43  $\delta^{15}\text{N}$ ) were used as correction factors to adjust epilithon data for all sites. Adjusted epilithon data represented the algal component of epilithon in mixing model calculations. Although this approach allows for potential inaccuracies, it includes techniques that combine for an unbiased estimate of primary producer signatures that is an improvement over the traditional approach of using undifferentiated epilithon samples to represent algal production in isotope mixing models.

Model results showed that both terrestrial and aquatic basal food web resources were important in these headwater streams (Fig. 6). Crayfish showed somewhat higher dependence on CPOM (45–62%) than insectivorous fish (30–45%), with a mean of approximately 46% terrestrial dependence for both consumer groups. The only forest cover variable that was significantly related to consumer dependence on CPOM was the most local scale riparian variable, canopy cover. Regression results showed that canopy cover explained 59 and 69% of the variation in terrestrial dependence for crayfish and insectivorous fish, respectively (Fig. 6).

## Discussion

Our data suggest that riparian deforestation, even over a narrow range, can result in decreased terrestrial support of headwater stream food webs. Two lines of evidence from our data support this conclusion. First, consumer  $\delta^{13}\text{C}$  diverged from the terrestrial signal with increasing deforestation (regression results). Secondly, dependence of consumers on ter-



**Fig. 6** Terrestrial dependence of consumers as a function of local riparian canopy cover. Both top consumer categories showed decreasing dependence on CPOM as a basal resource with reductions in canopy cover (crayfish:  $P = 0.04$ ,  $R^2 = 0.59$ , fish:  $P = 0.02$ ,  $R^2 = 0.69$ ). Dependence on CPOM was calculated using an isotopic mixing model in which dependence on CPOM and dependence on algae add up to 100%. Percentage variables are graphed untransformed here for ease in visual interpretation, but statistics apply to arcsin-squareroot transformed data.

restrial CPOM decreased with local riparian deforestation (mixing model results).

Reductions in forest cover were associated with top consumer  $^{13}\text{C}$  enrichment and divergence from terrestrial carbon  $\delta^{13}\text{C}$ , the most depleted food web component. This trend suggests a decreased reliance on terrestrial subsidies with deforestation. Although these relationships were relatively weak, it is notable that significant relationships were observed between large-scale landscape patterns and fine scale isotope patterns. Diminishing terrestrial support of stream food webs with deforestation may be because of reductions in the availability of terrestrial resources (as observed for CPOM and LWD) in these streams. Consequently there may be shifts in consumption patterns to an increased dependence on autochthonous resources that are relatively  $^{13}\text{C}$  enriched (epilithon, algae, and seston). We have also documented a decline in the abundance of macroinvertebrate shredders with reductions in CPOM availability in these streams (L.E. England & A.D. Rosemond, unpublished data). Reductions in shredders, which serve as a conduit for detrital carbon support of higher trophic levels, may partially account for the reduced terrestrial support of fishes and crayfish that we observed.

These food web changes were more related to forest cover at stream network and catchment scales, rather than local reach scales.

In contrast, consumer dependence on CPOM (mixing model results) was related only to the most local riparian variable, canopy cover, suggesting that multiple scales of forest cover were driving food web changes. Different forest cover scales (catchment versus local) may influence different food web pathways (heterotrophic versus autotrophic). Specifically, our data indicate that large-scale forest cover influenced food webs through heterotrophic pathways by controlling detrital standing crops. In contrast, local canopy cover did not influence standing crop of allochthonous materials, but was inversely related to the proportion of algae in *Stenonema* guts. This result, although only representative of one taxon, supports the hypothesis that local riparian canopy cover may have influenced these food webs through autotrophic pathways via increased algal availability.

The relative dependence on instream primary production by consumers (mean of 54%) was high given that conventional stream theory predicts dominance by terrestrial support in headwaters with dense forest canopies. A number of recent stable isotope analyses of aquatic food webs also report that the contribution of instream production to higher trophic levels was unexpectedly large given low algal biomass (Rosenfeld & Roff, 1992; France, 1995; Bunn, Davies & Kellaway, 1997; Thorp *et al.*, 1998; Bunn, Davies & Mosisch, 1999; Lewis *et al.*, 2001; McCutchan & Lewis, 2002; Thorp & Delong, 2002). Thus, even in systems where carbon budgets are dominated by allochthonous materials such as headwater streams (Fisher & Likens, 1973) and floodplain rivers (Lewis *et al.*, 2001), autochthonous resources may be important because of high nutritional quality and assimilation efficiency (Cummins, 1974; Rosenfeld & Roff, 1992).

Stream food web enrichment in  $^{13}\text{C}$  with increasing catchment area has been demonstrated for several food web components (algae, herbivores, collectors, and fish, Finlay, 2001). In general, increasing catchment area is associated with reduced terrestrial inputs per unit area of stream bed (Vannote *et al.*, 1980) and increased algal productivity, which may lead to  $^{13}\text{C}$  enriched algal communities (Finlay, 2001). Due to the intentionally narrow range in catchment area studied, we did not find strong relationships between carbon isotopes and catchment area. However, our results

suggest that deforestation may lead to food webs that function more like downstream reaches. Specifically, CPOM standing crop declined and consumer isotopic signatures indicated less dependence on terrestrial food resources with increasing deforestation. These findings bear out a prediction of the River Continuum Concept that human impacts may alter the degree of autotrophy or heterotrophy of a stream, potentially resulting in longitudinal shifts in the continuum (Vannote *et al.*, 1980). Apparent river continuum shifts with deforestation have been shown for stream community structure (e.g. Scott & Helfman, 2001). Our study provides some evidence that apparent continuum shifts with reductions in forest cover may also occur in the support of stream food webs.

The findings of this research suggest the importance of forest cover to headwater food webs at multiple scales ranging from local canopy cover to catchment forest cover. Multiple-scale analyses are becoming more prevalent in stream research due to the recognition that processes governing stream and riparian structure and function may be hierarchically arranged (Allan & Johnson, 1997; Johnson & Covich, 1997; Poole, 2002). However, many multiple-scale analyses lack the resolution in spatial data to make comparisons of the relative importance of local versus landscape scales. With a given spatial resolution, land-cover classification error is inversely proportional to size of the landscape feature being analysed. Thus when using coarse resolution images (e.g. 30 m Landsat TM), catchment land cover data will be much more accurate than riparian land cover data, making it difficult to compare the predictive ability of land-cover across different scales. One strength of this study is the high resolution of spatial data (1–2 m), which is more appropriate for comparing the strength of relationships between land use and instream responses across multiple spatial scales.

Previous work has highlighted the importance of riparian subsidies in maintaining secondary production of headwater streams draining forested catchments (Wallace *et al.*, 1999). Our study showed that moderate levels of riparian deforestation (reductions in canopy cover and riparian buffer width and continuity) can lead to reduced dependence of headwater food webs on terrestrial subsidies. Headwater streams, which make up nearly 75% of stream miles in the United States (Leopold, Wolman & Miller, 1964), play vital roles within the continuum, and are

tightly linked in several ways to downstream systems (Webster *et al.*, 1999; Meyer & Wallace, 2001; Peterson *et al.*, 2001; Gomi, Sidle & Richardson, 2002). It is unknown how altered headwater food webs may affect downstream linkages and potentially fragment the river continuum. Our data suggest that catchment forest cover, in addition to riparian cover, is related to the availability and retention of allochthonous resources in headwater streams. Thus, protection of both riparian and catchment forest cover, not just narrow riparian buffers, may be warranted in order to preserve terrestrial-aquatic linkages that are important in supporting native headwater stream food webs and their role within the continuum of river systems.

### Acknowledgments

Funding for this study was provided by a U.S. Environmental Protection Agency STAR (Science to Achieve Results) Fellowship grant (U-91595501-0) with additional support by the University of Georgia River Basin Science and Policy Center's Trout Stream Buffer Study. We are grateful to K. Jones, M. Scott, B. England, and S. Madritch for field assistance and J. Benstead, W. Cross, J. Greenwood, K. Schofield, W. Bumback, and T. Maddox for assistance with laboratory and image analyses. Comments from J. Benstead, G. Poole, W. Cross, B. Hall, M. Madritch, C. Anderson, J. Greenwood, and two anonymous reviewers greatly improved this manuscript.

### References

- Allan J.D. & Johnson L.B. (1997) Catchment-scale analysis of aquatic ecosystems. *Freshwater Biology*, **37**, 107–111.
- Benke A.C. & Wallace J.B. (1980) Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology*, **61**, 108–118.
- Bunn S.E., Barton D.R., Hynes H.B.N., Power G. & Pope M.A. (1989) Stable isotope analysis of carbon flow in a tundra river system. *Canadian Journal of Fisheries and Aquatic Science*, **46**, 1769–1775.
- Bunn S.E., Davies P.M. & Kellaway D.M. (1997) Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. *Marine and Freshwater Research*, **48**, 173–179.
- Bunn S.E., Davies P.M. & Mosisch T.D. (1999) Ecosystem measures of river health and their response to riparian

- and catchment degradation. *Freshwater Biology*, **41**, 333–345.
- Cummins K.W. (1973) Trophic relations of aquatic insects. *Annual Review of Entomology*, **18**, 183–206.
- Cummins K.W. (1974) Structure and function of stream ecosystems. *Bioscience*, **24**, 631–641.
- Day R.W. & Quinn G.P. (1989) Comparisons of treatment after an analysis of variance in ecology. *Ecological Monographs*, **59**, 433–463.
- DeNiro M.J. & Epstein S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, **42**, 495–506.
- Edwards R.T. & Meyer J.L. (1990) Bacterivory by deposit-feeding mayfly larvae (*Stenonema* spp). *Freshwater Biology*, **24**, 453–462.
- Feminella J.W., Power M.E. & Resh V.H. (1989) Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology*, **22**, 445–457.
- Finlay J.C. (2001) Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology*, **82**, 1052–1064.
- Finlay J.C., Power M.E. & Cabana G. (1999) Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. *Limnology and Oceanography*, **44**, 1198–1203.
- Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs*, **43**, 421–439.
- France R. (1995) Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 651–656.
- Gomi T., Sidle R.C. & Richardson J.S. (2002) Understanding processes and downstream linkages of headwater systems. *BioScience*, **52**, 905–916.
- Gregory S.V., Swanson F.J., McKee W.A. & Cummins K.W. (1991) An ecosystem perspective of riparian zones. *BioScience*, **41**, 540–551.
- Hall R.O. & Meyer J.L. (1998) The trophic significance of bacteria in a detritus-based stream food web. *Ecology*, **79**, 1995–2012.
- Hall R.O., Wallace J.B. & Eggert S.L. (2000) Organic matter flow in stream food webs with reduced detrital resource base. *Ecology*, **81**, 3445–3463.
- Hamilton S.K., Lewis W.M. & Sippel S.J. (1992) Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia*, **89**, 324–330.
- Hicks B.J. (1997) Food webs in forest and pasture streams in the Waikato region, New Zealand: a study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. *New Zealand Journal of Marine and Freshwater Research*, **31**, 651–664.
- Huryn A.D. & Wallace J.B. (1987) Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology*, **18**, 277–286.
- Johnson S.L. & Covich A.P. (1997) Scales of distribution of riparian forests and distributions of suspended detritus in a prairie river. *Freshwater Biology*, **37**, 163–175.
- Karr J.R. & Schlosser I.J. (1978) Water resources and the land-water interface. *Science*, **201**, 229–234.
- Leopold L.B., Wolman M.G. & Miller J.P. (1964) *Fluvial Processes in Geomorphology*. Freeman and Co., San Francisco, CA, USA.
- Lewis W.M., Hamilton S.K., Rodriguez M.A., Saunders J.F. & Lasi M.A. (2001) Food web analysis of the Orinoco floodplain based on production estimates and stable isotope data. *Journal of the North American Benthological Society*, **20**, 241–254.
- Malanson G.P. (1993) *Riparian Landscapes*. Cambridge University Press, Cambridge, U.K.
- McCutchan J. & Lewis W.M. (2002) Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography*, **47**, 742–752.
- Meyer J.L. & Wallace J.B. (2001) Lost linkages and lotic ecology: rediscovering small streams. In: *Ecology: Achievement and Challenge* (Eds M.C. Press, N.J. Huntly & S. Levin), pp. 295–317. Blackwell Scientific, Oxford, UK.
- Minshall G.W., Petersen R.C., Cummins K.W., Bott T.L., Sedell J.R., Cushing C.E. & Vannote R.L. (1983) Interbiome comparison of stream ecosystems dynamics. *Ecological Monographs*, **53**, 1–25.
- Momot W.T., Gowing H. & Jones P.D. (1978) The dynamics of crayfish and their role in ecosystems. *American Midland Naturalist*, **99**, 10–35.
- Nakano S. & Murakami M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences*, **98**, 166–170.
- Nakano S., Miyasaka H. & Kuhara N. (1999) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, **80**, 2435–2441.
- Pandian T.J. & Marian M.P. (1986) An indirect procedure for the estimation of assimilation efficiency of aquatic insects. *Freshwater Biology*, **16**, 93–98.
- Parkyn S.M., Collier K.J. & Hicks B.J. (2001) New Zealand stream crayfish: functional omnivores but trophic predators. *Freshwater Biology*, **46**, 641–652.
- Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.

- Peterson B.J., Wollheim W.M., Mulholland P.J. *et al.* (2001) Control of Nitrogen Export from Watersheds by Headwater Streams. *Science*, **292**, 86–90.
- Phillips D.L. & Koch P.L. (2002) Incorporating concentration dependence in stable isotope mixing models. *Oecologia*, **130**.
- Polis G.A. & Hurd S.D. (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*, **147**, 396–423.
- Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.
- Poole G.C. (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology*, **47**, 641–660.
- Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703–718.
- Power M.E. & Dietrich W.E. (2002) Food webs in river networks. *Ecological Research*, **17**, 451–471.
- Rosenfeld J.S. & Roff J.C. (1992) Examination of the carbon base in southern Ontario streams using stable isotopes. *Journal of the North American Benthological Society*, **11**, 1–10.
- Rosi-Marshall E.J. & Wallace J.B. (2002) Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, **47**, 129–141.
- Rounick J.S. & Winterbourne M.J. (1986) Stable carbon isotopes and carbon flow in ecosystems. *BioScience*, **36**, 171–177.
- Rounick J.S., Winterbourne M.J. & Lyon G.L. (1982) Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. *Oikos*, **39**, 191–198.
- Sabo J.L. & Power M.E. (2002) River-catchment exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*, **83**, 1860–1869.
- Scott M.C. & Helfman G.S. (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, **26**, 6–15.
- Sweeney B.W. (1992) Streamside forests and the physical, chemical, and trophic characteristics of Piedmont streams in Eastern North America. *Water Science and Technology*, **26**, 2653–2673.
- Thorp J.H. & Delong M.D. (2002) Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*, **96**, 543–550.
- Thorp J.H., Delong M.D., Greenwood K.S. & Casper A.F. (1998) Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia*, **117**, 551–563.
- Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science*, **37**, 130–137.
- Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1999) Effects of resource limitation on a detrital-based system. *Ecological Monographs*, **69**, 409–442.
- Webster J.R., Golladay S.W., Benfield E.F., D'Angelo D.J. & Peters G.T. (1990) Effects of forest disturbance on particulate organic matter budgets of small streams. *Journal of the North American Benthological Society*, **9**, 120–140.
- Webster J.R., Benfield E.F., Ehrman T.P., Schaeffer M.A., Tank J.L., Hutchens J.J. & D'Angelo D.J. (1999) What happens to allochthonous material that autumns into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology*, **41**, 687–705.
- Wetzel R.G. (2001) *Limnology: Lake and River Ecosystems*, 3rd edn. Academic Press, San Diego, CA, U.S.A.
- Whitledge G.W. & Rabeni C.F. (1997) Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Canadian Journal of Fisheries and Aquatic Science*, **54**, 2555–2563.
- Winterbourn M.J., Rounick J.S., & Cowie B. (1981) Are New Zealand ecosystems really different? *New Zealand Journal of Marine and Freshwater Research*, **15**, 321–328.
- Yarnell S.L. (1998) *The Southern Appalachians: A History of the Landscape*. Report SRS-18 of the Southern Research Station, U.S. Forest Service, U.S. Department of Agriculture, Asheville, NC, U.S.A.

(Manuscript accepted 5 March 2004)