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Linkages Between Trophic Variability and Distribution of Pteronarcys spp. (Plecoptera: Pteronarcyidae) Along a Stream Continuum

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ABSTRACT.—*Pteronarcys* stoneflies, which are traditionally considered shredders in eastern North America, inhabit second- through seventh-order streams in the Little Tennessee River (LTR) drainage basin. Because very little coarse allochthonous particulate organic matter occurs in the relatively large (sixth- and seventh-order) LTR, we analyzed the gut contents of five individuals from each of five sites and two dates (August and December) (n = 50) along a fourth- through seventh-order stretch of this stream continuum. Pteronarcids consumed significantly different percentages of some food items between sampling dates. *Pteronarcys* progressively consumed significantly more diatoms (from <1% of gut contents at stream order 4 to 46% at stream order 7) and significantly less detrital material (from >90% of gut contents at stream order 4 to ca. 50% at stream order 7) from fourth- to seventh-order sites, and the amount of *Pteronarcys* production attributable to each of these food items shifted significantly along the stream continuum. This diet shift raised the obvious question: Does the shift reflect changing *Pteronarcys* species composition or is only one species present throughout the continuum? We conducted an allozyme electrophoretic analysis on 62 pteronarcids from the LTR drainage basin using five diagnostic gene loci for eastern USA *Pteronarcys* species. We determined that three apparent species occur along this continuum. *Pteronarcys* species A inhabits the upstream sites (fourth- through sixth-order), *Pteronarcys* species C the downstream sites (sixth- and seventh-order), and *Pteronarcys* species B the mid-reach site where A and C co-occur (sixth-order). Based on their diet and distribution, *Pteronarcys* sp. A and *P.* sp. C exhibit different patterns of food consumption along the continuum, with the former consuming mainly detritus and the latter consuming detritus and diatoms.

INTRODUCTION

The concept of functional feeding groups (FFGs) among stream macroinvertebrates (sensu Merritt and Cummins, 1996) is an important tenet of stream ecology. Although FFG classifications are often linked to the type of food an organism consumes (*e.g.,* shredders—vascular plant tissue, collectors—fine particulate organic matter [FPOM]), FFGs are primarily based on the macroinvertebrate's mode of food acquisition (sensu Cummins, 1987). For example, filter feeders that obtain the majority of their production from animal consumption (*e.g.,* Benke and Wallace, 1980) are nonetheless placed in the filter feeder, and not the predator, FFG. The River Continuum Concept (RCC) (Vannote *et al.,* 1980) is

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largely linked to the concept of FFGs. The RCC predicts that shredders will have their highest biomass in forested headwater streams (roughly stream orders 1–3) due to the relatively high input of allochthonous coarse particulate organic matter (CPOM). As the amount of CPOM in a stream decreases with increasing stream size, shredders will likewise progressively decrease from headwaters to medium sized streams (orders 4–6) to larger rivers (orders >6).

Some aquatic insects are known to change their diet because of differential instar preferences (Crosby, 1975; Fuller and Stewart, 1979) or changing food availability (Richardson and Gaufin, 1971; Lechleitner and Kondratieff, 1983). As Cummins (1973) suggests, many taxa are trophic generalists that are greatly influenced by local food availability. Because FFGs are tied to a consumer's food, trophic shifting and generalism can distort relative FFG biomasses. Hence, ''blind faith'' assumptions of an organism's FFG based solely on published classifications (*e.g.,* Merritt and Cummins, 1996) may refute the RCCs predictions. The fact that FFGs are primarily founded at the generic and not at the species level (*see* Merritt and Cummins, 1996) can also skew the RCCs predictions because some species may not feed like the majority of their congeners and therefore should not be placed in the same FFG. These potential problems must be considered whenever doing system level comparisons of FFGs, especially when observed biomass and production of specific taxa do not coincide with RCC predictions.

Pteronarcys spp. (Plecoptera: Pteronarcyidae) are large stoneflies generally characterized as CPOM shredders (McDiffett, 1970; Merritt and Cummins, 1996), although Angradi (1993) observed *Pteronarcys californica* (Newport) feeding primarily on FPOM. In addition to detritus, some species consume varying amounts of animal material and algae (Richardson and Gaufin, 1971; Shapas and Hilsenhoff, 1976; Lechleitner and Kondratieff, 1983; Freilich, 1991). Therefore, the genus has additionally been characterized as facultative predators and scrapers (Merritt and Cummins, 1996). *Pteronarcys* occurs from second- through seventh-order streams in the Little Tennessee River (LTR) drainage basin in western North Carolina, constituting a fairly large percentage of the invertebrate biomass through this range (<1–47%, Grubaugh *et al.,* 1996). *Pteronarcys* displays its highest biomass in the seventh-order LTR (Grubaugh *et al.,* 1996), which has very little allochthonous CPOM standing crop (*see* below). Greater biomass of this ''shredder'' taxon at downstream sites is inconsistent with RCC predictions. Our objective is to investigate whether: (1) *Pteronarcys* exclusively shreds allochthonous material throughout the drainage basin, which would disagree with the RCC at the medium and large order stream sites (collecting stations 5b–7, *see* below), or (2) their diet shifts with stream order, possibly as the result of a species composition change along the continuum.

METHODS

Study sites.—The study was conducted along a 35-km section of a river continuum in the Blue Ridge province of the southern Appalachian Mountains. The continuum includes Ball Creek at the Coweeta Hydrologic Laboratory, Coweeta Creek, and the LTR upstream of Fontana Reservoir. Five sampling sites were established along the fourth- through seventh-order reaches of the continuum and are numbered by stream order, with site 5a upstream of 5b. Geomorphic parameters and thermal regime change with stream order along the continuum (Table 1). At the uppermost sites (4 and 5a; Lower Ball Creek and Coweeta Creek, respectively, at the Coweeta Hydrologic Laboratory), an extensive canopy of mixed hardwoods and rhododendron (*Rhododendron maximum* L.) effectively shades the stream year-round. Stream width is narrow (5.5 m and 7.2 m, respectively), allochthonous inputs are prevalent, and leaf packs and debris dams are common within the stream channel.

TABLE 1.—Physical parameters of the study sites along the Little Tennessee River drainage basin (from Grubaugh *et al.,* 1996)

	Station number				
	4	5a	5b	6	7
Stream order	4	5	5	6	7
Stream width (m)	5.5	7.2	13	25	60
Catchment area (ha)	690	1548	3052	36,260	83,660
Distance from headwater (km)	2.6	4.8	8.2	14.2	38.7
Elevation (m asl)	690	671	642	620	597
Slope (%)	7.0	2.9	0.43	0.05	0.14
Annual degree-days	3937	4078	4322	4763	4922

Farther downstream (site 5b; Coweeta Creek at the Coweeta Creek campground), canopy cover diminishes as the stream widens (13 m). Leaf packs become a less common feature of the channel. Large cobble is colonized by the submerged macrophyte *Podostemum ceratophyllum* (Michaux). At the lowermost sites (6 and 7; Little Tennessee River at Prentiss and Iotla, respectively), the stream channel becomes much wider (25 and 60 m, respectively) and the canopy cover becomes a minor feature of stream area. Leaf packs and debris dams are sparse and occur only in small slackwater areas along the shore. Bedrock, boulder and cobble substrata are extensively colonized by thick stands of *P. ceratophyllum* at both downstream sites.

Dietary analysis.—Pteronarcys nymphs at all sites were collected with a kicknet (1-mm-mesh opening) on 25 August and 13 December 1993, and were preserved in Kahle's solution (Wiggins, 1996). The foreguts of five similar sized individuals from each site and date were dissected (after Cummins, 1973). A sample of each animal's gut contents was individually sonicated in a beaker for 30 sec and was then drawn down under vacuum onto a 0.45 μm pore Metricel membrane filter. The filters were dried at 60 C for 20 min and then cleared with several drops of immersion oil. Each filter was permanently mounted on a slide with a drop of Permount® and a cover slip. Slides were scanned at 100× to identify food items as either animal material, amorphous detritus, vascular plant detritus, diatoms, or filamentous algae. Projected areas of individual food particles within each category were measured by digitizing 10 randomly selected fields of view for each insect using a SummaSketch® digitizer interfaced to a desktop computer. Total area of diatoms consumed was obtained by digitizing 100 diatoms at 200× and converting that measurement to a mean size at 100×. The total number of diatoms was then counted at 100× and multiplied by the mean size. Although the amorphous detritus category is a catchall for all unrecognizable organic matter (Shapas and Hilsenhoff, 1976), in this study it is presumed to be dominated by allochthonous material. Therefore, this, along with vascular plant detritus, will hereafter be combined as detrital material.

Projected areas of particles were used to calculate proportions of the various food types in the guts from each site and date. A Mann-Whitney nonparametric one-way analysis of variance (ANOVA) was run on SYSTAT Version 5.2 (SYSTAT, Inc., 1992) to determine whether the percentage of each of the four food categories differed between collection dates for each site. A Jonckheere-Terpstra test for ordered alternatives (Daniel, 1978) was performed to test the *a priori* hypotheses that the amount of detrital material consumed progressively decreased while the amount of diatoms consumed progressively increased at higher order sites.

TABLE 2.—Procedure for calculating production attributed to various food types for *Pteronarcys* individuals collected in December from station 6

Food type	% in foregut		Assimilation efficiency (AE)[1]		Net production efficiency (NPE)[2]		Relative amount to production	Production attributed to food type (%)
Animal	1.5	×	0.70	×	0.342	=	0.36	7.8
Detrital material	88.3	×	0.106[2]	×	0.342	=	3.20	69.4
Diatoms	10.0	×	0.30	×	0.342	=	1.03	22.3
Filamentous algae	0.2	×	0.30	×	0.342	=	0.02	0.4

[1] From Benke and Wallace (1980) unless otherwise noted
[2] From McDiffett (1970)

The amount of production attributable to each food type was computed for each site and date (*see* Table 2 for an example of this procedure). We did not calculate assimilation efficiency (AE) or net production efficiency (NPE) for these pteronarcids and have assumed these numbers to be similar to those published for other aquatic insects. The AE of detrital material was taken from McDiffett's (1970) calculations for *Pteronarcys scotti* Ricker. AEs for all other food items were taken from Benke and Wallace (1980) while NPE was also taken from McDiffett's (1970) calculations for *P. scotti*.

Species identification.—Although several dichotomous keys exist for *Pteronarcys* spp. nymphs (Ricker, 1952; Tarter, 1976; Surdick and Kim, 1976), none are applicable to all potential species inhabiting the LTR drainage basin and free of subjective couplets. Therefore, we conducted an allozyme electrophoretic analysis on individuals from each site in order to definitively identify the number of species inhabiting the LTR continuum. A total of 62 nymphs (≥10/site) were collected from the five sites and analyzed at five presumptive allozyme loci: *Aat-1, Aat-2, Dia, Mdh,* and *Pgm*. These loci were chosen because Wright and White (1992 and M. M. White, Ohio University, pers. comm.) found them to be diagnostic and therefore good characters to discriminate among the five *Pteronarcys* species (*Pteronarcys biloba* Newman, *P. dorsata* (Say), *P. pictetii* Hagen, *P. proteus* Newman and *P. scotti*) which potentially occur in the LTR drainage basin.

Pteronarcids were collected on 5 November 1995 from cobble riffle habitats at each site using a kicknet (1-mm-mesh opening). Live individuals were transported back to the laboratory on ice and then stored at −80 C until electrophoretic analysis. Thin thoracic slices from each stonefly (≈8 μl) were placed in individual 1.5-ml microcentrifuge tubes and crushed in 8 μl of crushing buffer (10 ml diH_2O, 1 mg NADP, 10 μl β-mercaptoethanol) using a glass rod. The samples were then centrifuged at 10,000 rpm for 90 sec. Electrophoresis was performed on cellulose acetate plates using the method of Hebert and Beaton (1993). All gels were run at room temperature (≈25 C) at 200 V for 30 min. The electrophoretic running conditions and stain recipes for each enzyme are listed in Table 3. Allelic designations were confirmed by running presumed homologues side by side on the same gel (*i.e.,* line-up gels, sensu Richardson *et al.,* 1986). Alleles and loci (for *Aat*) were numbered by decreasing electrophoretic mobility.

The criteria used to determine reproductive isolation, and therefore species distinctness, was the presence of differentially fixed alleles between *Pteronarcys* individuals. If two groups of individuals are fixed for different alleles at a locus, then we can assume there is no gene flow between them and they are therefore "good" species, as defined by the biological species concept. Allele frequencies were calculated for all presumptive loci and species.

TABLE 3.—Enzyme systems used to discriminate biochemically *Pteronarcys* spp. from the Little Tennessee River drianage basin, with buffer and stain recipe references

E.C. no.	Name	Symbol	# of scorable loci	Quaternary structure	Reference for buffer system[1]	Stain recipe[2]
2.6.1.1	Aspartate aminotransferase	AAT	1	dimeric	B	1
1.6.2.2	Diaphorase	DIA	1	monomeric	B	2
1.1.1.37	Malate dehydrogenase	MDH	1	dimeric	B[3,4]	1
5.4.2.2	Phosphoglucomutase	PGM	1	monomeric	D[4]	1

[1] See Richardson *et al.* (1986) for buffer recipes; continuous buffer system unless otherwise noted
[2] 1 = Hebert and Beaton (1993), 2 = Richardson *et al.* (1986)
[3] Soak in D buffer
[4] Do not add $MgCl_2$ to D buffer

Deviations from Hardy-Weinberg equilibrium expected allele frequencies were measured using the χ^2 goodness-of-fit test. All calculations were performed by BIOSYS-1 (Version 1.6, Swofford and Selander, 1981).

Voucher specimens from both the dietary analysis and the species identification are stored in the University of Georgia Natural History Museum.

RESULTS

Dietary analysis.—A total >7700 food particles were digitized or counted for the 50 individuals sampled in this study. Overall, 80.0% of gut contents was comprised of detrital material, 13.3% of diatoms, 5.8% of animal material and 1.0% of filamentous algae. All sampled animals contained detrital material, 76% contained animal material, 70% contained diatoms and 32% contained filamentous algae. At sites 4, 5a and 5b, pteronarcids consumed a significantly lower percentage of detrital material ($P \leq 0.05$) and a significantly higher percentage of animal material in August than in December (Table 4). Pteronarcids

TABLE 4.—Percentage of foregut food contents of *Pteronarcys* individuals in the Little Tennessee River drainage basin [* indicates values which are significantly different ($P \leq 0.05$) between dates at each station]

Station	Collecting date	No. guts examined	Animal	Detrital material	Diatoms	Filamentous algae
4	August, 1993	5	6.3*	93.1*	0.6	0.0
4	December, 1993	5	0.4*	99.5*	0.1	0.0
5a	August, 1993	5	8.7*	90.4*	0.7	0.1
5a	December, 1993	5	0.5*	99.2*	0.2	0.1
5b	August, 1993	5	14.0*	84.0*	2.0*	0.0
5b	December, 1993	5	2.2*	97.5*	0.1*	0.1
6	August, 1993	5	38.4	55.8	5.4	0.3
6	December, 1993	5	1.5	88.3	10.0	0.2
7	August, 1993	5	4.0	74.3	21.2	0.4*
7	December, 1993	5	1.2	41.7	52.8	4.3*

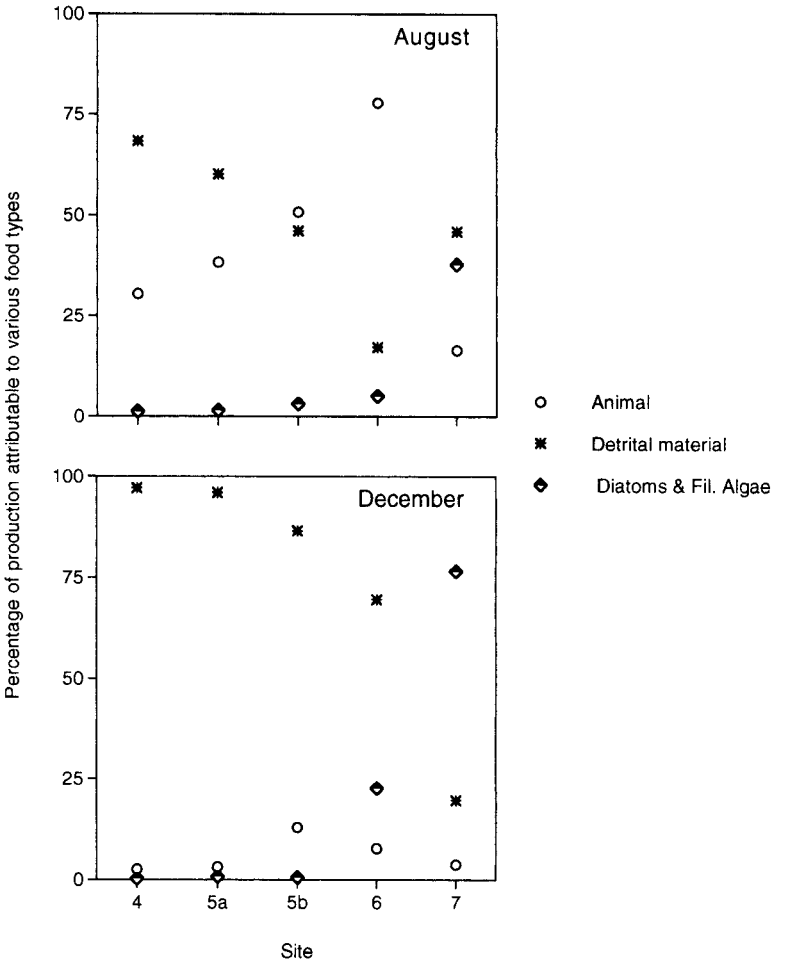

FIG. 1.—Percentage of *Pteronarcys* production in the Little Tennessee River drainage basin attributable to animal material, algae and detritus, respectively, in August and December

also consumed a significantly higher percentage of diatoms and a significantly lower percentage filamentous algae in August than in December at sites 5b and 7, respectively (Table 4).

On each date, *Pteronarcys* significantly consumed progressively more diatoms with increasing stream size (August, $P < 0.005$; December, $P < 0.005$) while significantly consuming progressively less detrital material (August, $P = 0.005$; December, $P < 0.005$) (Table 4). Detritus accounted for >90% of their diet at site 4 and ca. 50% at site 7, while diatoms accounted for <1% of their diet at site 4 and 46% at site 7 (the latter three values are means for all individuals as none of these food items were consumed at significantly different proportions between dates). In August, detritus was responsible for more of *Pteronarcys'* production than algae at every site (Fig. 1). In December, detritus was responsible for >85% of the production at upstream sites (4, 5a and 5b) and algae were responsible for >75% of production at the downstream site 7 (Fig. 1). Although animal material contributed little

TABLE 5.—Sample sizes and allele frequencies at each collecting station and locus for each putative *Pteronarcys* species collected from the Little Tennessee River drainage basin

	Station				
	4	5a	5b	6	7
P. sp. A					
(N)	11	10	10	3	
Aat-2					
1	1.000	1.000	1.000	1.000	
Dia					
2	1.000	1.000	1.000	1.000	
Pgm					
1			0.050		
2	0.091	0.150	0.250	0.500	
3	0.909	0.800	0.650	0.500	
4		0.050	0.050		
P. sp. B					
(N)				2	
Aat-2					
2				1.000	
Dia					
2				1.000	
Pgm					
3				1.000	
P. sp. C					
(N)				8	18
Aat-2					
1				0.625	0.361
2				0.375	0.639
Dia					
1				1.000	1.000
Pgm					
3				0.063	0.028
4					0.028
5				0.938	0.944

to *Pteronarcys* production in December (Fig. 1), in August animals accounted for >25% of production at sites 4 and 5a, ca. 50% of production at site 5b and > 75% of production at site 6 (Fig. 1).

Allozyme analysis.—Among the five presumptive loci examined, *Mdh* was monomorphic while *Aat-1* was not consistently scorable. These two loci were therefore not included in the analysis. The genotypes of all 62 assayed individuals were resolved for the other three loci, however. These loci were very informative, suggesting that three putative species [*Pteronarcys* species A (=*P. scotti,* we suspect), *Pteronarcys* species B (=*P. biloba,* we suspect), and *Pteronarcys* species C (=*P. dorsata* or *P. pictetii,* we suspect)] exist within the LTR drainage basin. Each species had one fixed allelic difference with each other species (Table 5), thereby indicating reproductive isolation among the three taxa. Also, no observed allele frequencies deviated significantly from Hardy-Weinberg expectations for any species ($P > 0.05$) (which is not the case when *P.* sp. B individuals are lumped into *P.* sp. A), suggesting

that each population within the LTR continuum is panmictic and each species is real. Although these taxa could be genetically divergent populations of the same species, we feel it is more parsimonious to consider them distinct species instead of trying to explain why one species is divided into three sympatric reproductively isolated subpopulations. For *P.* sp. A, the frequency of allele 2 at *Pgm* progressively increased down the stream continuum while the frequency of allele 3 progressively decreased (Table 5), which may suggest clinal variation, and therefore likely selection, at this locus.

Of the 62 pteronarcids collected, 34 were *Pteronarcys* sp. A, two were *P.* sp. B, and 26 were *P.* sp. C. *Pteronarcys* sp. A was the exclusive taxon at sites 4, 5a and 5b, with additional individuals occurring at site 6 (Table 5). *Pteronarcys* sp. B was only collected from site 6. *Pteronarcys* sp. C also occurred at site 6 and was the exclusive taxon at site 7.

DISCUSSION

We anticipated identifying the *Pteronarcys* individuals from the LTR drainage basin by comparing our observed genotypes to those Wright and White (1992) found in their comprehensive biochemical systematic analysis of *Pteronarcys* spp. (White, pers. comm.). Unfortunately, positive identifications were impossible because the suite of genotypes from the three LTR drainage basin species did not coincide with the genotypes of any three species (out of the potential five species known from western North Carolina) Wright and White observed. This failure can probably be attributed to one of four phenomena: (1) we may not have encountered the same genotypes Wright and White observed due to sampling error caused by relatively small sample sizes (n = 12 per species in their study, n = 2 for *P.* sp. B in our study), (2) differential resolution of alleles may have resulted from our use of different support media or buffers (*i.e.,* electromorph splittings; *see* Richardson *et al.,* 1986), (3) one or more of these three species may exhibit geographic population genetic differences (*i.e.,* different populations have different genotypes) due to limited gene flow or differential selection, or (4) one or more of these species may be represented by more than one morphologically identical yet reproductively isolated species (*i.e.,* cryptic species), essentially meaning that Wright and White (1992) did not assay all *Pteronarcys* species. Numerous aquatic insects exhibit significant intraspecific allelic differences which suggest either limited gene flow or differential selection (Sweeney *et al.,* 1987; Funk *et al.,* 1988; Sweeney *et al.,* 1991; Jackson and Resh, 1992), and several cryptic aquatic insect species have been discovered using genetic markers (Funk *et al.,* 1988; Sweeney and Funk, 1991; Jackson and Resh, 1992). Wright and White (1992) similarly found substantial allozyme differences between two *P. biloba* populations, thereby suggesting this too may represent either geographic genetic differentiation or a species complex with one or more cryptic species. Therefore, one of these two explanations is likely the reason our observed genotypes did not coincide with Wright and White's. A thorough analysis of *Pteronarcys* spp. population genetic structures over a large geographic range may resolve this discrepancy and aid in future biochemical identifications. Such a study could also: (1) clarify the amount of gene flow and thus the dispersal capabilities of these taxa, and (2) confirm whether a cline exists at the *Pgm* locus for *P.* sp. A and accurately define its location (*e.g.,* is it controlled by longitudinal stream gradients or latitudinal gradients?).

Although the dietary analysis and the species analysis were conducted on different animals 2 yr apart, each shows a changing trend through the LTR continuum which may be linked. Specifically, the *Pteronarcys* community apparently shifts through the LTR continuum, and this shift may be coupled with a change in food consumption. If this is the case, *P.* sp. A individuals predominantly consumed detritus in the upper reaches of the continuum (sites 4, 5a and 5b), where leaf packs and debris dams are prevalent, whereas *P.* sp. C

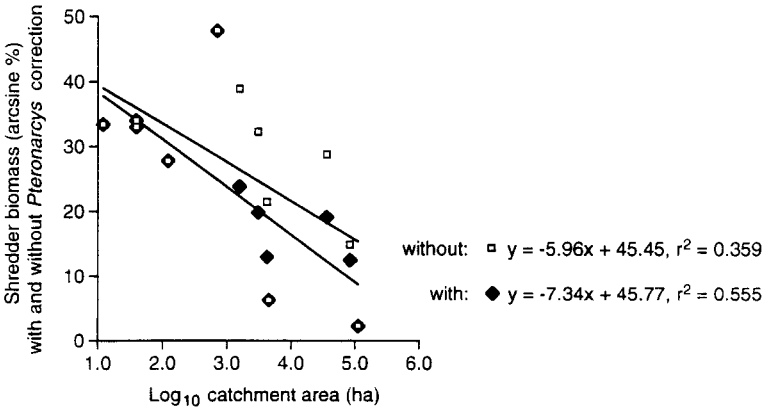

FIG. 2.—Shredder biomass based on assumption that all *Pteronarcys* spp. are detritivore-shredders (open squares) plotted against drainage basin area for various sites in the Little Tennessee River basin versus shredder biomass adjusted for proportion of *Pteronarcys* spp. guts containing detritus at various locations (dark diamonds)

individuals consumed mixed amounts of detritus and diatoms in the low reaches (site 7), where the canopy cover is minimal and we assume the diatom abundance is relatively high (Minshall, 1978). The distributions of *P.* sp. A and *P.* sp. C may be influenced by the availability of each of these food resources, or each species may simply be opportunistic omnivores, both able to shift their diet as available food resources change. However, the latter seems to be the most likely explanation because pteronarcids throughout the continuum fed on more animal material in August, presumably when allochthonous CPOM is relatively scarce, yet they consume very little animal material shortly after leaf fall in December. For future studies, this question could be addressed by conducting dietary and allozyme analyses on the same individuals.

Pteronarcys in the LTR drainage basin had its highest biomass at the downstream site 7 (Grubaugh *et al.,* 1996), which also corresponds to its highest ingestion of diatoms. Diatoms have a greater AE than detrital material (Benke and Wallace, 1980), which suggests higher food quality in the lower reaches of this continuum than in the upper reaches. However, we are uncertain whether *P.* sp. C individuals scrape diatoms at this site or whether they coincidentally consume attached algae while shredding *Podostemum* and/or CPOM.

"Shredder" biomass in mid- and downstream reaches of the Coweeta Creek, LTR continuum is dominated by *Pteronarcys* spp. (Grubaugh *et al.,* 1996). Although the proportional contribution of shredders to total invertebrate biomass decreases along this gradient, shredder biomass remained higher than would be anticipated based on the RCC predictions of Vannote *et al.* (1980). *Pteronarcys* biomass was adjusted and reassigned to the "shredder" category based only on the portion of detrital material found in their guts (using the mean of all individuals combined), assuming that detritus was from shredding activities. The downstream decrease in shredder biomass with increasing stream size was much more evident and provided a much better fit to the data after biomasses were adjusted based on *Pteronarcys* gut contents (Fig. 2). Our results clearly show both longitudinal changes in food resources and sequential shifts in *Pteronarcys* species along the LTR continuum, as well as a temporal shift in animal consumption at the three uppermost sites. Similarly, Lechleitner and Kondratieff (1983) found that *P. dorsata* in the Little River (Virginia) shifted their diets

temporally, from detritus in winter to algae in summer, as food resources changed. These results underscore the need for caution when assigning functional feeding groups without examining patterns of food consumption. Although FFG assignment based on dietary analysis alone can be misleading or uninformative (*e.g.,* Palmer *et al.,* 1993), fine-grained resolution of feeding habits may be required in some cases for omnivorous species which occur over a broad spectrum of stream sizes with different energy bases. Such resolution is very important with taxa such as *Pteronarcys* which often comprise a large portion of benthic biomass.

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