

## NOTES

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### Grazer–diatom size relationships in an epiphytic community

**Abstract**—We investigated the animal–food size relationships of an invertebrate grazer community that feeds on the epiphytic diatoms of mosses in a Québec stream. The relationship between invertebrate head width and maximum size of ingested diatoms was significant ( $r^2 = 0.57$ ,  $n = 82$ ,  $p < 0.00001$ ). This relationship did not differ significantly among widely different taxa of insects, crustaceans, and worms. The comparison of our results with relationships developed in the laboratory for zooplankton and benthos indicated that artificial particles or simplified algal assemblages underestimate the size range of algae ingested by grazers. The examination of the size distribution of the ingested diatoms and of those available in the environment showed that grazers fed preferentially on different diatom size classes in accordance with their head width. Concepts of resource partitioning, optimal foraging, and size efficiency proposed for other habitat types are relevant to stream invertebrate communities. This recognition should facilitate the study of algal–grazer interactions in streams.

The relationship between the size of an animal and the food it ingests has long been a central topic in ecology. Several predation and competition theories, such as niche, optimal foraging, and resource partitioning, often explicitly quantify food in terms of its size. Animal–food size relationships have been studied in terrestrial as well as aquatic systems (Burns 1968; Vézina 1985). In planktonic communities, predator–prey size relationships have been demonstrated for piscivorous and planktivorous fish and for zooplankton. These relationships form the basis of the size efficiency hypothesis that has been so influential in theoretical and applied limnology (Brooks and Dodson 1965). The surprising regularities in plankton size distributions observed across several orders of magnitude in oceans and lakes are generally attributed to a consistent animal–food size relationship between trophic levels (Sheldon et al. 1972). Such allometric relationships have received little attention in the context of benthic communities. An application of theories elaborated for planktonic communities might facilitate the study of the notoriously complex benthic communities.

Previous studies of benthic invertebrate herbivory have focused mostly on one or a few populations of large grazers that are easily manipulated in the laboratory or, more rarely, in natural streams (*see* review in Steinman 1996). Such studies show the effect of these grazers on periphyton but provide little information about natural communities in which invertebrates range widely in size and taxonomy. Benthic grazers have been traditionally considered generalists rather than specialist feeders (Cummins 1973; Mihuc 1997), but some evidence suggests that they might select algae on the basis of size, life form, chemical composition, or a combi-

nation of factors (Peterson 1987; Steinman 1996; Hamels et al. 2004).

In this study, we have analyzed the size range of epiphytic diatoms consumed by a grazer community associated with aquatic moss in a Québec stream. The technique we used to examine their gut contents involved the oxidation of organic matter, which allowed the analysis of particles ingested by small grazers without dissection. This technique, however, limits observations to diatoms. For this reason, we chose an epiphytic community in which diatoms represented >90% of total algal density and biomass.

In this paper, we assess the application of ecological theories on predator–prey size to a benthic system. In particular, we test whether (1) there is a relationship between the size of ingested diatoms and grazer size, (2) this relation differs according to grazer taxon, and (3) grazers feed selectively on diatoms as a function of their size. We then compare our results to grazer–prey size relationships observed for planktonic communities.

**Materials and methods**—Diatoms and grazers were collected from a second-order stream, Ruisseau Pin Rouge, which is 80 km north of Montréal in the Laurentians Mountains (45°59'N, 74°1'W). This stream is oligomesotrophic with slightly acid, colored, low-conductivity water (Cattaneo et al. 2004). The aquatic moss *Fontinalis dalecaerlica* grows profusely on the side of large boulders, where it forms a habitat for periphyton and invertebrates. This study is based on quantitative samples of moss with their epiphytic algae and invertebrates that were collected along a 100-m-long run in May 1998 to study the effects of varying discharge on stream communities (Cattaneo et al. 2004). We analyzed the gut content of invertebrates belonging to the main grazer taxa found in the moss. Chironomids were the most abundant grazers (Table 1). Individuals were macerated in concave slides with 30% hydrogen peroxide for 3–24 h depending on size and cuticle texture and then mounted in Hoyer's mounting medium (Humason 1967). After mounting, grazers were identified to genus (Wiederholm 1983; Merritt and Cummins 1996). The maceration procedure enabled observation of the diatoms contained in the gut. We counted and identified the ingested diatoms to genus or species (Table 2) and then measured their greatest axial length dimension (GALD) to the nearest 1  $\mu\text{m}$  under a microscope ( $\times 400$ ) connected to an image analysis system (Image Pro Plus, version 4.1 for Windows, Media Cybernetics). When >100 diatoms were present in a gut, we analyzed a subsample. Only grazers with at least 10 diatoms present in the gut were used in the analysis. We chose head width as a de-

Table 1. Taxonomy and size range of the grazer community studied.

		Number studied	Head width ( $\mu\text{m}$ )
Diptera/Chironomidae			
Chironominae			
Chironomini	<i>Paratendipes</i>	3	65–95
	<i>Polypedilum</i>	1	375
Tanytarsini			
	<i>Micropsectra</i>	4	75–370
	<i>Tanytarsus</i>	5	205–315
Orthoclaadiinae			
	<i>Corynoneura</i>	1	370
	<i>Cricotopus</i>	11	280–750
	<i>Eukiefferiella</i>	3	150–240
	<i>Limnophyes</i>	3	125–230
	<i>Nanocladius</i>	1	230
	<i>Orthoclaadius</i>	3	125–155
	<i>Tvetenia</i>	1	180
	Unidentified	1	330
Tanypodinae			
	<i>Meropelopia</i>	6	315–890
	<i>Nilotanypus</i>	7	200–330
Coleoptera			
Psephenidae			
	<i>Ectopria</i>	1	265
Elmidae			
	<i>Promoresia</i>	7	155–335
Ephemeroptera			
Baetidae			
	<i>Baetis</i>	3	85–150
Ephemerellidae			
	<i>Eurylophella</i>	2	190–265
Leptophlebiidae			
	<i>Paraleptophlebia</i>	1	300
Plecoptera			
Leuctridae			
	<i>Leuctra</i>	2	205–335
Trichoptera			
Hydroptilidae			
	<i>Hydroptila</i>	3	205–280
Copepoda			
		5	80–85
Oligochaeta			
		8	70–340
Total		82	

scriptor of grazer size because the head of insect larvae is the most sclerotized part of the body and thus is most likely to represent a constraint on food size. For oligochaetes and copepods, which have poorly defined heads, body width was used as a proxy for head width. Measurements of head width were made to the nearest 0.01 mm.

To estimate the diatom taxa and size range available to grazers, we analyzed nine quantitative samples of algae associated with the moss (Cattaneo et al. 2004). The algae suspended during sampling and the moss itself were treated with 30% hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) following the method of Battarbee (1986). Permanent mounts of clean diatoms were made with Naphrax (Northern Biological Supplies). Each slide was then examined at  $\times 400$ , and at least 100 diatoms were counted, identified to genus or species, and measured with an image analysis system. Because a grazer's ability to ingest colonial algae is likely to depend on the dimensions of the whole colony, colonial algae were considered to be large single cells. Diatom composition varied little among replicates. Consequently, samples were pooled to calculate the relative abundance of different diatom taxa within the community.

Table 2. Diatoms observed in the grazer gut and in the stream. Percent abundance refers to the total diatom density on the aquatic mosses.

	Diatom	Mean GALD ( $\mu\text{m}$ )	Abundance (%)
Centrophycidae	<i>Cyclotella</i> spp.	10	5.7
Pennatophycidae			
Fragilariiales			
	<i>Tabellaria fenestrata</i>	43	10.8
	<i>Tabellaria flocculosa</i>	21	25.4
	<i>Diatoma</i> sp.	14	0.1
	<i>Meridion circulare</i>	39	0.9
	<i>Fragilaria</i> spp.	22	13.5
	<i>Synedra ulna</i>	174	14.1
Monoraphidae	<i>Achnantes</i> spp.	13	12.1
Biraphidae			
	<i>Stauroneis</i> sp.	25	0.4
	<i>Navicula</i> spp.	18	0.8
	<i>Pinnularia</i> spp.	32	0.8
	<i>Cymbella</i> spp.	31	3.4
	<i>Gomphonema</i> spp.	36	2.4
	<i>Surirella</i> spp.	42	0.3
Others			9.3

We analyzed the relationship between grazer and diatom size by simple regression. Regression residuals were examined to test for differences among taxa (Kruskal–Wallis non-parametric one-way analysis of variance). Residuals were grouped by tribe for chironomids and by order for other invertebrates to attain reasonable statistical power ( $n \geq 3$ ). Therefore, we excluded the Plecoptera ( $n = 2$ ) from our analysis. All analyses were performed with Statistix (Analytical Software).

We grouped diatoms and grazers in size classes on the basis of GALD and head width, respectively, to assess diatom size selection. Selection was estimated for each grazer size class with the  $E^*$  electivity index (Vanderploeg and Scavia 1979). This index, which ranges from +1 to -1 with 0 indicating random feeding, is calculated as

$$E_i^* = [W_i - (1/n)]/[W_i + (1/n)] \quad (1)$$

where  $n$  is the number of available items and  $W_i = (r_i/p_i)/\sum_i r_i/p_i$ , where  $r_i$  is the proportion of food  $i$  in the diet, and  $p_i$  is the proportion of food  $i$  in the environment.

Comparison of our results with existing grazer–food size relationships required some transformations to standardize the grazer body size description. We recalculated the equation of chironomids fed pollen grains by McLachlan et al. (1978) with the original data presented by Brennan (1976). Chironomid size, expressed as mentum width ( $M$ ) was converted to head width ( $H$ ) with the use of chironomid photographs from Simpson and Bode (1980) ( $H = M \times 3.3$ ). Published allometric food relationships for zooplankton are based on body length. We therefore converted *Daphnia* body length ( $L$ ) to body width ( $W$ ) according to data provided by Swift and Fedorenko (1975) ( $W = L/3.6$ ). Because cladoceran feeding appendages and mouthparts are located in the abdomen, body width is assumed to be functionally equivalent to the head width of other invertebrates. We chose to

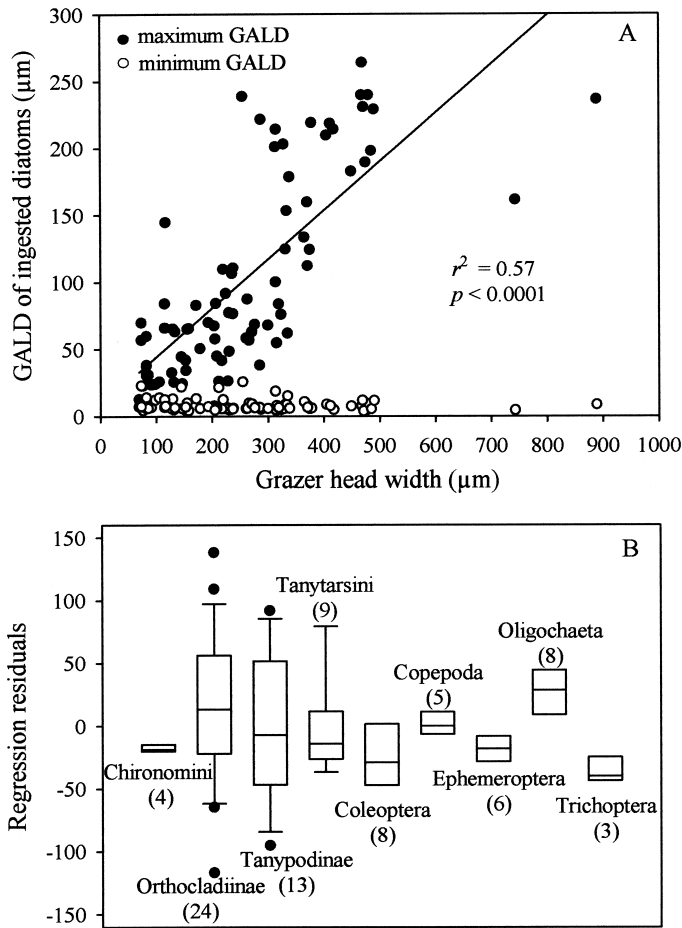


Fig. 1. (A) Relationship between minimum or maximum Gald of ingested diatoms ( $\mu\text{m}$ ) and grazer head width ( $\mu\text{m}$ ) observed for an invertebrate community feeding on epiphytic algae in a Québec stream. (B) Box plots of the residuals of the regression between maximum Gald ( $\mu\text{m}$ ) and grazer head width ( $\mu\text{m}$ ) for all taxa studied in the community (except Plecoptera, for which only two replicates were available). The number of replicates for each taxon is indicated in brackets.

base our plankton–benthos comparison on grazer width rather than length for the following reasons. First, Pearre (1980) suggested that width was a better measurement of size than length for feeding studies. Second, the oval shape of the Cladocera is clearly different from the elongated shape of benthic grazers; thus, a body length comparison would lead to the overestimation of the relative size of benthic invertebrates.

**Results**—The relationship between invertebrate head width and maximum size of ingested diatoms was significant for the grazer community associated with moss in the Pin Rouge stream. This relationship is described by Eq. 2,

$$Y = 7.79 + 0.36X$$

$$R^2 = 0.57, \quad n = 82, \quad p < 0.00001 \quad (2)$$

where  $X$  = grazer head width ( $\mu\text{m}$ ) and  $Y$  = maximum Gald of ingested diatoms ( $\mu\text{m}$ ).

Grazer size was not related to minimum size of ingested

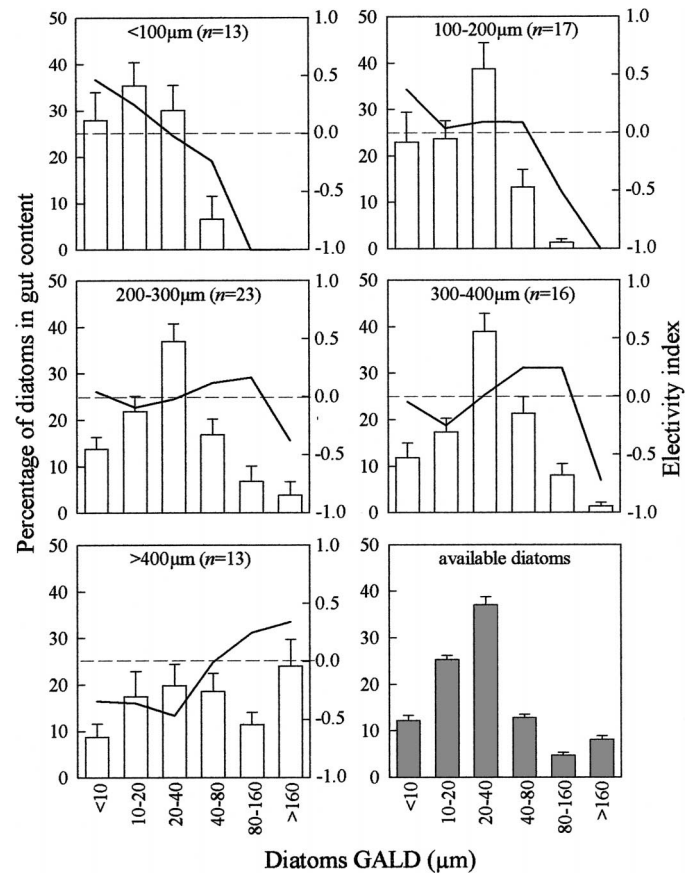


Fig. 2. Size distribution of diatoms ingested by grazers of different size classes on the basis of head width (white bars) and diatoms available in the Pin Rouge stream (grey bars). Bars represent mean values ( $\pm 1$  SE), with  $n$  indicated in each panel. Continuous lines represent changes in grazer electivity index across diatom size classes. Dashed lines indicating the absence of selection are traced as reference.

diatoms, which remained nearly constant across the grazer size gradient (Fig. 1A). Consequently, the size range of ingested diatoms was broader for large than for small grazers.

We examined the residuals of Eq. 2 to test whether the grazer–diatom size relationship differed among grazer taxa (Fig. 1B). A nonparametric comparison of mean ranks of regression residuals by taxon showed no significant pairwise differences (rejection level = 0.05).

The size distribution of the ingested diatoms varied between invertebrate size classes (Fig. 2). The proportion of large diatoms in the gut increased with grazer size. Using information about the size distribution of diatoms in the environment, we calculated electivity indices to ascertain whether grazers fed selectively on specific diatom size classes. Grazers fed unselectively on the intermediate diatom size class (20–40  $\mu\text{m}$ ), which was the most common in the environment and in the guts. Only the largest invertebrates (head width  $> 400\mu\text{m}$ ) showed negative selection for diatoms in this size range. The smallest diatom size class ( $< 10\mu\text{m}$ ) was selected positively by small grazers (head width  $< 200\mu\text{m}$ ) and negatively by those with head width  $> 400\mu\text{m}$ . Conversely, the largest diatoms ( $> 160\mu\text{m}$ ) were pos-

itively selected only by grazers with head width  $> 400 \mu\text{m}$ . As a result, clear size selection was observed only for the smallest and largest grazers, whereas grazers of intermediate size (head width ranging between 200 and  $400 \mu\text{m}$ ) ingested the different diatom size classes in roughly the same proportion they occurred in the stream.

**Discussion**—Herbivory in streams has usually been studied in experimental settings and single-grazer communities. In this study, however, we considered an entire grazer community feeding in situ on natural food. Consequently, natural levels of competition and facilitation between different taxa and sizes probably affected grazer diet. Diatoms provided an ideal model in our study because their frustules are not digested and they are therefore as easily identified, counted, and measured as plastic beads but with the advantage of representing the natural resource. We also chose a habitat in which a large size range of diatoms occurred and represented the main algal resource for primary consumers. Because our technique involved organic material destruction, we could not ascertain whether ingested or available diatoms were living or dead to test for differential digestion of various algal taxa (e.g., Peterson 1987).

We compared the relationship we observed with those presented in the literature for other aquatic communities. Relations between animal and food size in terrestrial ecosystems are usually calculated for predators (Vézina 1985) and thus do not always apply to other trophic groups because plants are often larger than herbivores. Several relationships between grazer length and maximum size of ingested particles have been developed for zooplankton. The studies of Burns (1968) and De Mott (1995) were based on cladocerans, mostly *Daphnia* spp., feeding on plastic beads or *Eudorina* colonies in the laboratory. To our knowledge, the only attempt to develop a similar relationship for benthic grazers was a laboratory experiment with chironomids (*Eukiefferiella* sp., *Rheotanytarsus pentapoda*, and *Synorthocladius semivirens*), which were fed pollen grains of various diameters (Brennan 1976 reported in McLachlan et al. 1978).

Equations developed for plankton differ slightly in slope and intercept. The relationship from *Daphnia* feeding on *Eudorina* (De Mott 1995) has a higher slope than that developed for cladocerans feeding on plastic beads (Burns 1968; Fig. 3). The relationship for chironomids feeding on pollen grains also agrees well with those developed for cladocerans. The diatom–grazer relationship observed in our study, however, has a higher intercept and slope than all the others. The discrepancy between the results of these different studies does not appear related to the different habitat, plankton versus benthos, because the chironomid equation of Brennan (1976) and the zooplankton equations are in close agreement. A possible explanation for the difference is that the shape and nature of food particles affect the capture ability of consumers. The *Eudorina* colonies, plastic beads, and pollen used in the laboratory experiments were spherical, whereas the diatoms available to stream grazers were generally elongated (pennate). A spherical particle with the same GALD of an elongated diatom might be too large to fit in the grazer mouth because diatoms are engulfed lengthwise (Edlund and Francis 1999; our observations). Intuitive-

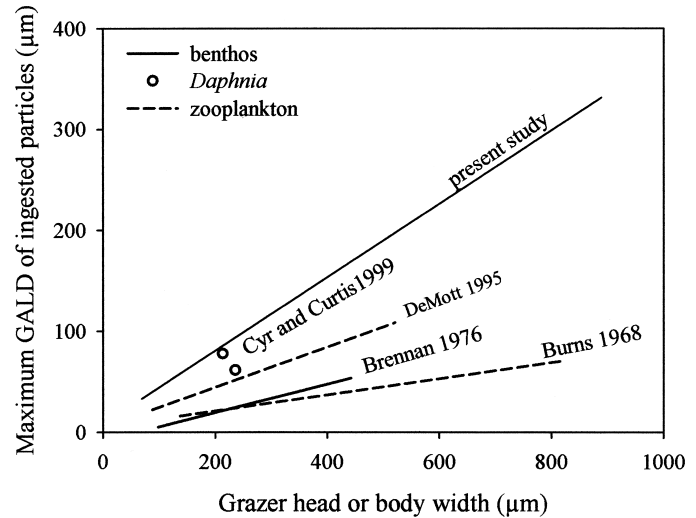


Fig. 3. Comparison of relationships between grazer body width ( $X$ ,  $\mu\text{m}$ ) and maximum GALD of ingested particles ( $Y$ ,  $\mu\text{m}$ ) observed for benthos and plankton. The equations presented are: present study,  $Y = 0.36X + 7.79$ ; Brennan (1976),  $Y = 0.14X - 8.94$ ; Burns (1968),  $Y = 0.08X + 4.87$ ; DeMott (1995),  $Y = 0.11X + 9.35$ . Circles indicate field measurements by Cyr and Curtis (1999) on *Daphnia*-dominated communities. Transformations used in these equations are detailed in the *Materials and Methods* section.

ly, such ingestion behavior suggests that diatom width rather than length sets the size of edible food particles. However, grazer size was related to diatom GALD ( $r = 0.65$ ,  $p = 0.02$ ) but not to diatom width ( $r = 0.28$ ,  $p = 0.37$ ) in a preliminary analysis of chironomid gut content ( $n = 12$ ; data not shown). The seizing and handling of an elongated diatom could be problematic for a small grazer, even if the particle is narrow enough to be readily engulfed. We suggest that GALD probably summarizes the size limits for both handling and ingestion and therefore represents a simple and effective parameter to describe food for consumption studies. Cyr and Curtis (1999) reported an inconsistency between laboratory results with artificial particles and field observation of maximum algal size ingested by *Daphnia*-dominated communities (Fig. 3). These authors reported zooplankton grazing on both *Ceratium* (mean GALD  $237 \mu\text{m}$ ) and *Oscillatoria* (mean GALD  $146 \mu\text{m}$ ), which greatly exceed the size range predicted by plankton-based equations but are within the size range of diatoms ingested by grazers in our study. Laboratory studies with simplified assemblages of one or a few algal species or with particles (beads or pollen grains) thus appear to underestimate the size of algae actually available to zooplankton (Cyr and Curtis 1999) and benthos. The prediction of grazing selectivity will require the development of more realistic models based on natural food size and shape.

Studies of terrestrial (Vézina 1985) and aquatic communities (Hall et al. 1976; Scharf et al. 2000) suggest that maximum prey size increases with predator size, whereas minimum size remains constant or increases slightly. This pattern is probably the result of an increased behavioral and morphological capability to capture and swallow large prey combined with the ongoing encounter and capture of small prey.

Because large organisms can consume a wider range of prey size than small ones, they have a competitive advantage, which is explained by the “size efficiency hypothesis” proposed for plankton communities (Brooks and Dodson 1965). Our results indicate that this hypothesis could also be relevant to benthic communities. In our study, large grazers tended to feed on a broader range of diatom sizes than small grazers.

Surprisingly, the grazer–diatom size relationship did not vary significantly among the different taxa of benthic grazers we examined. Numerous feeding modes and mouthpart morphologies are found within benthic herbivores (Allan 1995). The grazer community we studied comprised invertebrates considered scrapers and collectors. The scrapers (Coleoptera, Trichoptera, and some Ephemeroptera) presumably fed primarily on attached algae by scraping mineral or organic surfaces with specialized mouthparts, whereas the collectors (Chironomidae, Oligochaeta, and some Ephemeroptera) presumably filtered or gathered particles that were suspended or loosely attached (Merritt and Cummins 1996). The consistency in the grazer–diatom size relationship observed among grazers with such different feeding mechanisms suggests that head width sets a crucial mechanical constraint on the size of ingested food. This mechanical control apparently transcends taxonomy and habitat, being confirmed in both the plankton and the benthos.

If grazer width constrains the maximum size of ingested particles, it does not necessarily follow that grazers actively select diatoms of a specific size range. Such selectivity can only be assessed by comparing diatoms present in the gut to those available in the environment. In our study, size selection for the smallest and the largest grazers was evident. Large grazers were free from mechanical constraints, limiting the range of available diatoms. Their selection for the largest diatoms, mostly represented by *Synedra ulna*, follows the prediction of the optimal foraging hypothesis, which states that consumers tend to choose the most profitable food, which is often a compromise between the largest and the most available sizes (Krebs 1978). Small grazers selected for small diatoms, mostly *Cyclotella* sp. and *Achnanthes minutissima*, likely because not all diatoms were available because of small mouth size. By concentrating on small diatoms, competition with other grazers was also probably reduced.

Feeding selectivity by the benthos is much debated. In a recent review, Mihuc (1997) concluded that generalized feeding behavior is a common strategy among primary consumer in streams. There are several examples of grazers selecting algae on the basis of their size, however. Several experimental studies have shown that some grazers select for large diatoms (Steinman 1996). Selection toward large pennate diatoms has also been reported for late instar larvae of chironomids (Marker et al. 1986; Edlund and Francis 1999), whereas early instars favor small diatoms (Pinder 1992). Grazer selection has also been reported to be a function of algal physiognomy (Steinman 1996) or chemical cues (Hamels et al. 2004). Such selective feeding behavior is probably more widespread than generally assumed.

When a guild of organisms exploits the same limited resource, partitioning according to size might allow the co-

existence of different taxa (Shoener 1974). No general review of resource partitioning among stream invertebrates yet exists (Allan 1995). Filter-feeding caddisfly larvae provide an example of coexistence mediated by resource partitioning among individuals as a function of net mesh size (Malas and Wallace 1977). In this study, we provide circumstantial evidence for resource partitioning on the basis of diatom size for a guild of grazers. Our study of a natural community of grazers feeding on epiphytic diatoms showed that theories on herbivory developed in terrestrial and planktonic systems are relevant to the benthos.

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