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# Size structure of the metazoan community in a Piedmont stream

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**Abstract.** We characterized the size structure of virtually the entire metazoan community in a fourth order, sandy-bottomed Piedmont stream during late summer. Our study, the first to sample across all habitat types and sizes of metazoans in an aquatic ecosystem, indicates that at the community level, stream size spectra may be bimodal for the benthos or trimodal when fish are included. Animals spanning 10 orders of magnitude in dry mass (from gastrotrichs to fish) were quantitatively collected from nine habitat types. The bimodal benthic size spectrum was characterized by a meiofaunal component (mostly oligochaetes and micro-crustacea) and a macrobenthic component (mostly the introduced asiatic clam, *Corbicula fluminea*). Insects contributed little to overall standing crop. Size-specific contribution to whole-community metabolism was assessed using allometric equations for respiration, and we found a distinctly bimodal distribution across the entire metazoan size range, with peaks in the meiofaunal and benthic macrofaunal size ranges. Our bimodal benthic size spectrum is similar to that observed for marine benthos but not to other freshwater benthic systems, possibly because the entire range of habitat types and/or animal sizes were not sampled in the latter. Numerous factors may influence size spectra in stream ecosystems, including local geomorphic (habitat) conditions, water level fluctuations, species introductions, and predation processes.

**Key words:** Body size – Size spectrum – Community structure – Energy flow – Aquatic ecology

One goal of community ecology is to construct generalizations about the structure and functioning of assemblages of organisms across different ecosystems (e.g., Diamond and Case 1986; Cole et al. 1991). Achieving this goal is not easy because it is difficult to compare communities that vary in taxonomic composition, evolutionary history, and/or environmental constraints. Nontaxonomic approaches represent one possible solution to this problem, but selection of appropriate measures is critical. Since organism body size constrains many ecological processes and influences community organization, size distribution represents a fundamental property that can be used to compare communities (e.g., Schoener 1986). Body size often influences energy flow and trophic structure, so abundance and biomass of differentially-sized animals should reflect size-specific allocation of total community resources (Peters 1983b), and this allocation may vary within and among ecosystems characterized by different abiotic and biotic constraints. If general patterns of community organization can be revealed by comparing size structures among ecosystems, then a cataloging of size spectra for different ecosystems is a necessary first step for constructing testable hypotheses in a comparative framework.

Size spectra were first characterized for certain size ranges of marine plankton (Sheldon and Parsons 1967; Sheldon et al. 1972). Total biomass in pelagic communities is often distributed relatively equitably among size classes in both marine systems (e.g., Sheldon et al. 1977) and in freshwater systems (Peters 1983a; Sprules and Munawar 1986; Duarte et al. 1987; Ahrens and Peters 1991a). These relatively flat size spectra have been explained theoretically as resulting from a uniform proportional transfer of energy across trophic levels in pelagic systems (Kerr 1974; Borgmann 1982), where predation may impose a correspondence between body size and trophic level (Borgmann 1987). Thus, although successively higher trophic levels comprise fewer (and larger) organisms, slower rates of biomass turnover result in similar standing crops among levels. However, exceptions to flat pelagic size spectra do occur, and these

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may reflect littoral (benthic) influences (Sheldon et al. 1977; Sprules et al. 1983; Boudreau and Dickie 1992) or lake trophic status (Strayer 1991; see Ahrens and Peters 1991a).

In benthic communities, size spectra often deviate strongly from flatness, both in marine (Schwinghammer 1981; Warwick 1984; Gerlach et al. 1985; Warwick and Joint 1987) and freshwater systems (Strayer 1986, 1991; Hanson et al. 1989; Hanson 1990; Morin and Nadon 1991). Furthermore, the shape of the size spectrum may vary markedly among ecosystems. For example, Schwinghammer (1981) found a bimodal size spectrum for marine benthos and suggested that there were distinct "meiofaunal" and "macrofaunal" components in the benthic community. By contrast, Strayer (1986) found a unimodal size spectrum in a freshwater lacustrine benthic community, which suggested no distinct "meiofaunal" component. Variation in shape among size spectra may reflect inherent differences in evolutionary history, trophic level organization, and/or environmental constraints on community membership. However, observed size structure may also reflect arbitrary delineation of the habitats and organisms included in the surveyed "community" (cf. Strayer 1991). To date, freshwater studies have included only a subset of metazoan size ranges and/or available habitat types in surveys of both lentic systems (e.g., Strayer 1986; Hanson et al. 1989; Hanson 1990; Tokeshi 1990) and lotic systems (Morin and Nadon 1991; Cattaneo 1993). Hence, meaningful generalizations about the size structure of freshwater benthic communities (particularly stream communities) have not been possible.

Our study of a stream community's size spectrum addressed three primary objectives. First, we characterized the size structure for an entire metazoan community in a temperate Piedmont stream by sampling all habitat types and all animal body sizes (meiofauna to fish) because such a comprehensive description is lacking for streams. Second, we evaluated the relative contributions of different size classes to whole community metabolism using well-established allometric relationships to assess whether energy flow is dominated by particular sizes of animals. Third, we generated a "snapshot" of a community level pattern in a stream to explore whether size spectra can provide useful insights for comparing lotic to marine and lentic communities. Although community patterns based on single surveys must be interpreted cautiously (Wiens 1981), such one-time "snapshot" samplings have proven useful in providing insightful descriptions of size spectra in other aquatic systems (Warwick and Joint 1987).

## Methods

The study was done in August 1991 in Goose Creek, a fourth order Piedmont stream in northern VA, USA. This system has been described in detail elsewhere (Palmer 1990; Palmer et al. 1992b; Vadas 1992). We surveyed a representative 2380 m$^2$ section of wetted channel along a ca. 100 m stream reach, where we identified nine microhabitat types in three major categories (Table 1). The areal coverage of the streambed for each habitat type was mapped to provide information on proportional distribution. During the summer of 1991, water levels in Goose Creek dropped to very low levels, so that at the time of our sampling, most water movement through riffles was hyporheic.

**Table 1.** Relative proportions of nine microhabit types classified according to major habitat categories for a 2380 m$^2$ section of Goose Creek. Mineral sediment and water column categories add to 100%, but organic structured habitats do not because some stream bottom was only bare sediment

| *Category* | *Microhabitat type* | *% of total* |
|---|---|---|
| Mineral sediment | Sandy channel | 82 |
| | Silty channel | 3 |
| | Riffle bottom | 14 |
| | Rocky bank | 1 |
| Organic structure | Algal filaments | 60 |
| | Macrophytes | 2 |
| | Debris dams | 1 |
| Water column | Non-riffle | 86 |
| | Riffle | 14 |

Numerous sampling techniques were used, depending on habitat type and size of animals sampled. Among the mineral sediment habitats, sandy channels were sampled with 5.31 cm$^2$ cores ($n$ = 2) for macrofauna and meiofauna. Cores were taken to a depth of 50 cm, which represents the average extent of the hyporheic zone in Goose Creek (Palmer 1990). Additionally, 1600 cm$^2$ cores were taken for burrowing clams ($n$ = 2). In sandy channels covered by filamentous algal carpets, 5.31 cm$^2$ cores were also taken for meiofauna ($n$ = 2). Silty channel areas were also sampled with 5.31 cm$^2$ cores ($n$ = 2) to a depth where anoxic conditions occurred. A 250 µm mesh kick net was used to sample macroinvertebrates from 1 m$^2$ sections ($n$ = 2) of shoreline areas with larger cobble/boulder substrate covered with silt (hereafter "rocky bank"). Meiofauna were not sampled in the rocky bank area, but were estimated from data collected for silty channel samples. Riffle habitat consisted of sediment ranging from silt to small boulders. Macrobenthos were collected using a 250 µm, 0.1 m$^2$ Surber sampler ($n$ = 2). Meiofauna were collected from a 237 cm$^2$ area by scraping rocks and suspending sediment from a depth of 5 cm and collecting material in a 44 µm mesh net ($n$ = 3).

We refer to three-dimensional habitats extending from the sediment into the water column as structured organic habitats (e.g., algae, debris dams, macrophytes). We estimated the surface area of streambed covered by structured habitat types rather than the actual surface area of available habitat (e.g., leaf surface area). Algal filaments were sampled directly by placing plastic cores (5.31 cm$^2$) over the algae and down to the streambed, then sliding a sharp flat plate under the core at the sediment surface. The sandy sediment beneath the algae was also sampled with a 5.31 cm$^2$ core and added to the sandy channel component. Macrophyte beds (mostly *Elodea* sp.) were sampled for macrofauna and meiofauna by collecting plants within a 102 cm$^2$ area. Debris dams, collections of woody material and leaves along the stream margin, posed particular sampling problems. We took "grab" samples (i.e., representative collections of twigs and leaves) by placing plastic bags over the twigs/leaves and breaking the "sample" off in the bag. The fraction of the entire dam sampled in this manner was estimated based on previous survey work (Palmer et al. 1992a).

Organisms in the water column (nekton) were sampled both in the riffle area and in the remainder of the stream ("non-riffle"). Large fish occupied only the non-riffle area and these were sampled using an electric seine and 5 mm mesh dip nets (see methodology of Angermeier et al. 1991). Species and total lengths were recorded in the field for larger fish, which were released alive. Smaller fish were fixed in 10% formalin and transferred to 70% ethanol before identification and measurement. Fish were seined from two separate pools (combined area = 3030 $m^2$) downstream of the 2380 $m^2$ section to prevent disturbance to ongoing research in the upstream area. Data were adjusted to reflect area in the 2380 $m^2$ section. Surface-dwelling insects and young-of-year fish were estimated by observing and counting individuals over the entire riffle area (two passes) and over 1260 $m^2$ of the downstream pool area (one pass). Drifting invertebrates were not sampled because streamflow was negligible and because diurnal drift densities in Goose Creek are characteristically $<0.1\%$ of benthic invertebrate densities (Palmer 1992).

In the field, all sampled material was stored in formalin. In the laboratory, all samples were passed through 44 μm sieves (meiofauna) or 250 μm sieves (macrofauna) and animals were sorted from sediments and identified to lowest practicable taxon. Insects were typically identified to family or genus, except for early instars, which could only be identified to order. Micro-metazoans were generally identified to lowest practicable taxon (e.g., Gastrotricha, Cladocera, Oligochaeta, etc.). Previous work in Goose Creek has shown that a 44 μm mesh size captures $>90\%$ of the metazoans that could theoretically pass through (Palmer, unpubl. data).

Methods for determining biomass varied between taxa. For fish, the wet mass of each individual was determined from species-specific length-mass regressions for Virginia fishes (P.L. Angermeier, unpub. data). Frog tadpoles collected in the field were returned to the lab, where individual lengths were recorded and a wet mass-length regression determined. Dry mass for aquatic vertebrates was estimated by multiplying wet mass by the conversion factor of 0.26 (Carlander 1977).

A length-dry mass regression was derived for most macrobenthic taxa. Animals were dried at 105° C for 24 h and weighed individually to the nearest 1 mg on a Fisher Scientific balance. Before drying and weighing, clams and snails were measured (shell length) and then placed in 12% $H_2SO_4$ to dissolve the mineral portions of their shells (T. McMahon, University of Texas at Arlington, pers. comm.). Macrofauna too small to weigh individually were treated in one of two ways. Abundant animals were visually sorted into similar size classes (two to four) and an average weight determined for each size class (e.g., chironomids, oligochaetes, amphipods, turbellarians). Animals that were too scarce to pool for average weights were measured and their masses determined from published length-mass relationships (see Smock 1980; Meyer 1989). Generic, familial or ordinal level equations were chosen, depending on the degree of taxonomic resolution available for the identified invertebrates. Meiofaunal-sized animals were assigned characteristic weights derived from the literature (Strayer 1984, see refs. in Palmer et al. 1992b). Meiofaunal-sized mollusca were subsampled

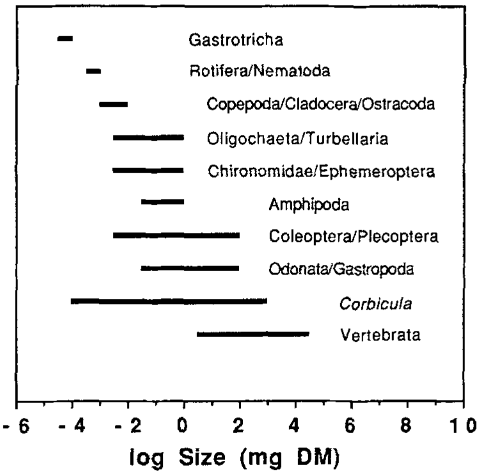

Fig. 1. Range of body sizes (mg dry mass [DM]) of dominant metazoans collected in Goose Creek

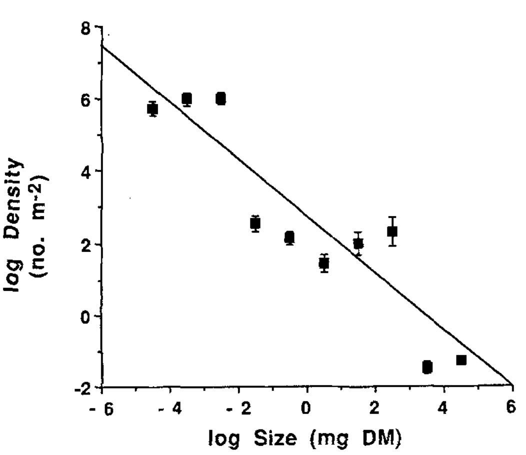

Fig. 2. Population density scaling for all metazoans collected from 2380 $m^2$ of wetted channel in Goose Creek. Points represent data pooled in log10 intervals across all nine habitat types depending on relative abundance of habitat (see Table 1). All points shown with error bars of ±2 SE. The regression equation is $\log(D) = 2.95-0.824 \log(\text{Size})$. SE of the slope = 0.126. $r^2 = 0.84$

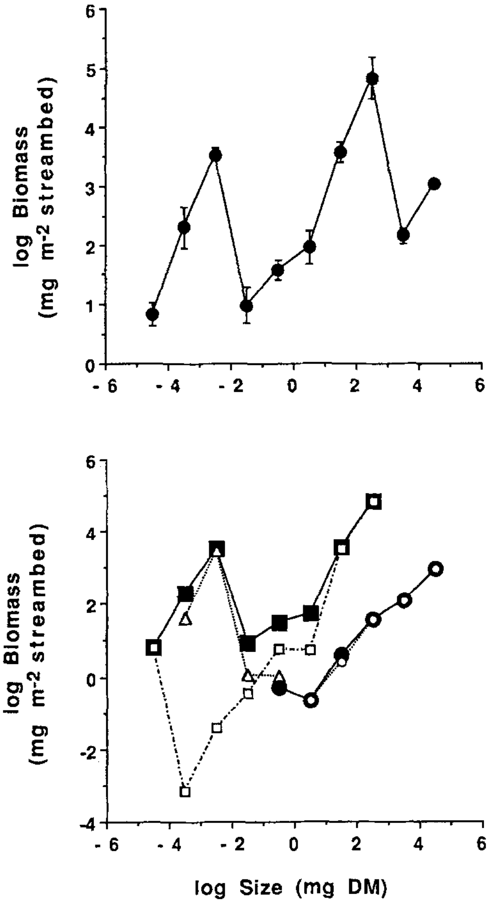

Fig. 3. Upper panel: Biomass size spectrum for all metazoans collected from 2380 $m^2$ of wetted channel in Goose Creek. Points represent data pooled in log10 intervals across all nine habitat types depending on relative abundance of habitat (see Table 1). All points shown with error bars of ±2 SE. *Lower panel:* Biomass size spectra for various community components. The benthic size spectrum (closed squares) is comprised mostly of oligochaeta/micro-crustacea (open triangles) and *Corbicula fluminea* (open squares), while the nektonic size spectrum (closed circles) consists mostly of fish (open circles)

for average shell length and weights were extrapolated from the length-mass regressions derived from the larger, individually-weighed specimens.

Data from all taxa were grouped into log10 size (mg) intervals such that abundance and biomass of animals in these intervals was determined for each habitat type and for the entire stream (i.e., weighted by relative contribution of each habitat type).

Size-specific contribution to community energy flow was assessed as a first approximation by using the following allometrically-scaled estimate of animal respiration (Robinson et al. 1983):

$$R_p = B*R$$

where Rp is population respiration rate (Watts $km^{-2}$), B is biomass (kg $km^{-2}$) and R is specific standard metabolic rate (Watts $kg^{-2}$). R is temperature dependent and scaled according to body size as follows:

$$R = 0.071*e^{0.051T}*W^{-0.24}$$

where W is body size (kg). We used log10 size class interval for W in this equation and set T = 26° C. This allometric relationship is appropriately applied to invertebrates and poikilotherms (Peters 1983b; Peters and Wassenberg 1983; Ahrens and Peters 1991b).

## Results

We identified 50 taxa of benthic invertebrates and 23 species of fish in this study. The size ranges of dominant animals varied over 10 orders of magnitude (Fig. 1). Total faunal abundance declined with body size both in individual habitat types and for the stream as a whole, i.e., when the relative contribution of each habitat type to the total 2380 $m^2$ of streambed was taken into account (Fig. 2).

The size spectrum for the whole animal community in Goose Creek was multi-modal (Fig. 3). Obvious biomass peaks occurred in the meiofaunal size range ($10^{-3}$ to $10^{-2}$ mg) and in the benthic macrofaunal size range ($10^2$ to $10^3$ mg). A third peak comprised exclusively of fish was also suggested for the largest size class (Fig. 3). The meiofaunal peak was comprised mostly of oligochaetes and micro-crustacea, while the larger macrofaunal peak was dominated by the asiatic clam, *Corbicula fluminea* (Figs. 3, 4). A conspicuous trough in size range occurred for benthic insects ($10^{-2}$–$10^2$ mg) and a suggested trough also occurred in the $10^4$ mg range occupied by fish. The three observed biomass peaks were found to be statistically distinct. At the $\alpha = 0.10$ level, each peak was comprised by a single size class category. At the $\alpha = 0.05$ level, both the meiofaunal and the macrobenthic peaks were comprised of two size class categories rather than just one, but the fish peak ($10^4$–$10^5$ mg) remained distinct (see Fig. 3).

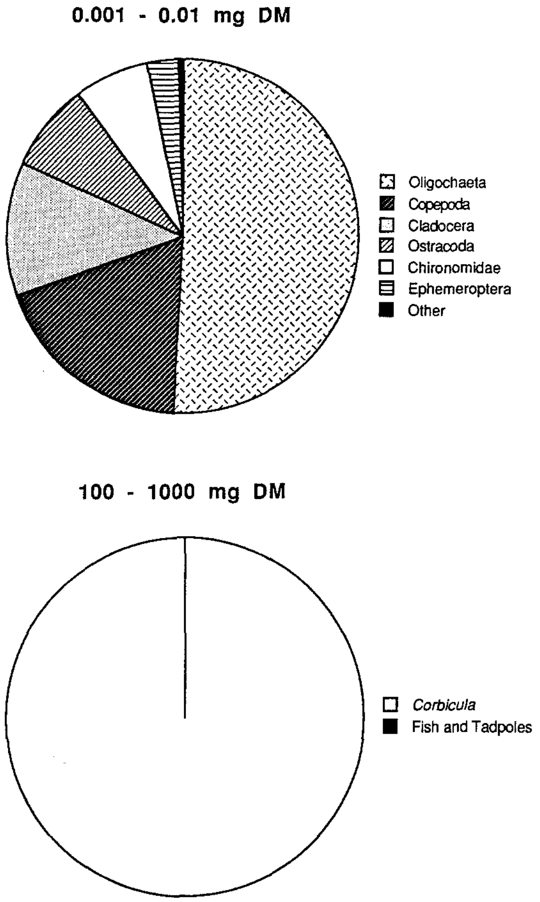

**Fig. 4.** Taxonomic composition of dominant organisms comprising the two largest biomass peaks in Fig. 3

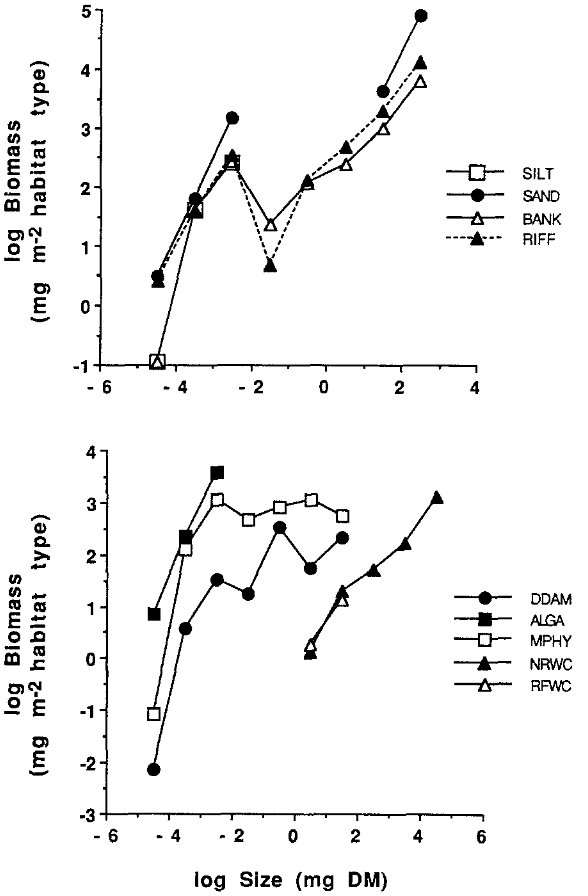

**Fig. 5.** Biomass size spectra for all metazoans collected in each of nine habitat types (see Table 1). Points represent data pooled in log10 intervals within each habitat type. Habitat abbreviations are SILT (silty channel), SAND (sandy channel), BANK (rocky bank), RIFF (riffle bottom), DDAM (debris dam), ALGA (algal filaments), MPHY (macrohpytes), NRWC (non-riffle water column), and RFWC (riffle water column)

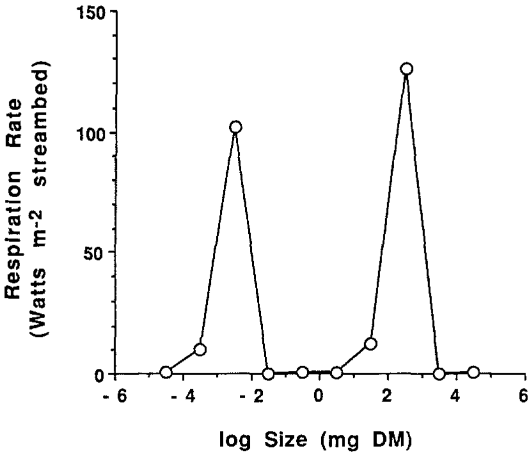

**Fig. 6.** Estimated size-specific metabolism for entire metazoan community in Goose Creek. Points represent data pooled in log10 intervals across all nine habitat types depending on relative abundance of habitat (see Table 1). Data from Fig. 3 are used in the following equation: $R_p = B*R$, where $R = 0.071*e^{0.051T}*W^{-0.24}$ (Robinson et al. 1983)

The size spectra for individual habitat types revealed several patterns (Fig. 5). In small-grained sedimentary habitats (sandy and silty channel), biomass increased from $10^{-4}$ to $10^{-2}$ mg DM, beyond which no larger metazoans occurred, with exception of sand which supported a high biomass of *Corbicula*. Riffle bottom and rocky bank habitats showed very similar curves that tended to increase over a wide size range, but with a weak local peak at the large meiofaunal size range. In both these habitat types, *Corbicula* exclusively comprised the biomass in the two largest size classes. Structured organic habitats like macrophytes and debris dams supported a wide size range of animals but did not show a bimodal curve. Animal size on algal filaments did not exceed large meiofauna. Small fish and adult gyrinid beetles were the only swimming animals observed in the riffle water column habitat. The non-riffle water column habitat contained animals ranging in size from young-of-year fish to neustonic insects to frog tadpoles to large fish (Fig. 5).

Estimated community-wide metabolism in Goose Creek was dominated by two benthic components: oligochaetes/micro-crustacea and *Corbicula* (Fig. 6). Metabolism of all other size categories, including large fish, was at least an order of magnitude smaller and thus made a negligible contribution to metazoan metabolism at system-wide scale. The bimodality of the metabolism curve remains even if the estimates for benthic meiofaunal respiration are overestimated by a factor of 3–5 (cf. Banse and Mosher 1980; Banse 1982).

## Discussion

Our study is the first to sample across all habitat types and size ranges of stream metazoans, and our community-wide results indicate a bimodal size spectrum for benthic organisms, and a trimodal size spectrum when nektonic organisms (mostly fish) are included. A bimodal benthic size structure was seen for mineral substrate habitats that supported a wide range of animal sizes (sandy channel, riffle bottom, rocky bank) but not on structured organic substrates (macrophytes, debris dams, algae) and not for water column habitats. Estimates of stream-wide metabolism in Goose Creek also showed a clear bimodality, with meiofauna and the bivalve *Corbicula fluminea* dominating energy flow, but with fish making relatively little contribution.

Stream ecologists have only recently begun to assess the potential contribution of meiofaunal-sized animals to the dynamics of lotic systems (e.g., Meyer 1990), and previous freshwater studies have rarely assessed the relative contributions of meiofauna and macrofauna to community biomass or productivity (e.g., Strayer and Likens 1986). In the only published stream study to date, Morin and Nadon (1991) argued that meiofaunal contribution to community metabolism was negligible across several Canadian streams in stony habitats, but they suggested their results might not be applicable in depositional habitats with hyporheic organisms (such as occur in Goose Creek). Cattaneo (1993) also examined size spectra on stream rocks and found that inclusion of protozoa and benthic algae resulted in a flat biomass curve in the size range up to small insects. However, the meiofaunal-sized metazoans that contributed to our observed meiofaunal biomass peak were rare to absent in her collections (especially micro-crustaceans and small oligochaets). Our multiple-habitat study clearly suggests that meiofaunal-sized animals cannot be discounted if one wishes to assess community size structure and whole-system energy flow.

The biomass peak in the large meiofauna size range is suggestive of a biomass "sink"; however, this is unlikely given that meiofauna such as oligochaetes and micro-crustaceans may be subject to intense predation (Strayer and Likens 1986; O'Doherty 1988; Coull 1990; Vadas 1990) and have high turnover rates. Because most of the meiofaunal biomass is tied up in sandy habitats where larger invertebrate predators are rare, energy flow and trophic structure in Goose Creek may be directly influenced by physical habitat structure. We do not know the extent to which energy "cycles" within the meiofauna in sandy habitats or whether significant energy is transferred to predators residing in other habitat types (e.g., fish in water column, as has been reported in the marine literature (e.g., Gee 1989; Coull 1990)).

The great contribution of *Corbicula fluminea* to community biomass is perhaps not surprising because this exotic species has often attained impressive densities elsewhere (> 1000 $m^{-2}$, McMahon 1983; > 3000 g $m^{-2}$, Cohen et al. 1984) and typically live for 2–4 year (Hornbach 1992). In general, bivalves are slow-growing and long-lived and presumably have a low susceptibility to predation (but see Neves and Odum 1989); therefore, they might be expected to represent a biomass "sink" (Schwinghammer 1981). In the absence of *Corbicula*, community size structure in Goose Creek might change substantially (see Fig. 3). For example, it is possible that native unionid mussels, presently uncommon in Goose Creek, could experience a compensatory increase in abundance were *Corbicula* not present, as has been speculatively suggested elsewhere (McMahon 1982). *Corbicula* is presumably at a competitive advantage over native unionid and sphaerid mussels because it has a much higher seston filtration rate than do the native taxa (Mattice 1979; Lauritsen 1986) and because it can feed directly on sedimentary detritus (T. McMahon, pers. comm.). At least one freshwater benthic study has shown that unionid mussels can significantly influence community size structure (Hanson et al. 1989). Many examples exist of changes in lotic community composition following introduction of exotic species (see Allan and Flecker 1993), but the extent to which exotics may alter community size structure and energy flow are presently unknown.

An interesting result of this study is that benthic insects contributed little to overall biomass and community metabolism. The paucity of riffle habitat in Goose Creek may explain this result, because riffles typically support high benthic insect production (Ward 1992). Alternatively, we sampled this system during a period of typically low macrobenthic biomass (August) and others have shown that community size structure can vary seasonally (Hanson et al. 1989; Tokeshi 1990), as aquatic insect life stages switch from aquatic to terrestrial forms and as invertebrates grow larger. Further, we sampled during an exceptionally dry year when mortality in riffles occurred, presumably in response to flow cessation and habitat shrinkage (N.L. Poff, pers. obs.). Had ambient conditions been less stressful, benthic insect contribution to whole-system biomass could have been greater, but it is not clear that the observed "insect trough" would disappear regardless of sampling time because small larval insects overlap with the "meiofaunal" size class (see Fig. 1).

Fish biomass in the largest size class approached that of the large meiofauna and thus gave the impression of a third biomass peak in the whole-community size spectrum, an intriguing pattern that merits further attention. Fish biomass clearly increased unimodally with increasing body size (see Fig. 3); however, late summer mortality associated with flow cessation may have reduced biomass of small fish, either through environmental stress or through predation by larger fish or avian predators (Vadas 1992). For example, late-summer minnow abundance was previously documented to be an order of magnitude higher under more normal (higher) flows, even when a less complete sampling method than electroseining was used (Vadas 1991). However, any effects of differential mortality of small fishes on the overall shape of the fish size spectrum could be counterbalanced by potential emigration of large fish in response to low flow.

Interestingly, the whole-stream, bimodal benthic biomass curve is similar to Schwinghammer's (1981) and Warwick and Joint's (1987) bimodal marine benthic curves, but not to Strayer's (1986) unimodal lacustrine curve, which was generated for a system where metazoans exceeding $10^{-3}$ mg in dry mass were very rare (Strayer 1991). The benthic size spectrum for Goose Creek is superficially similar to that recorded by Hanson et al. (1989) for a littoral benthic community with abundant unionid mussels. However, because they did not sample in the meiofaunal size range, direct comparison with our lotic size spectrum is not possible. Strayer (1991) argued that differences in selective forces and species richness of large macrobenthos imply that any striking similarities in lacustrine and marine benthic size spectra are likely to be only fortuitous, not homologous. Given the shared evolutionary history of the freshwater fauna, one might expect lotic systems to have size spectra more similar to lentic than to marine systems. Significantly, streams such as Goose Creek share some important environmental selective forces with some marine systems. For example, Goose Creek is dominated by sandy habitats, and the pattern observed for the whole community largely reflects the pattern seen in the sandy channel. Sandy habitats in Goose Creek are frequently disturbed by scouring floods (Palmer 1990; Palmer et al. 1992b), an environmental instability that may limit the biomass of nonmolluscan macroinvertebrates (Ward 1992). In marine systems, storm-induced sediment disturbance may also exert size-selective mortality to favor a bimodal size structure (Schwinghammer 1983).

We suggest, therefore, that just as size spectra may vary among lake systems depending on trophic conditions (Strayer 1991; see Ahrens and Peters 1991a), the extent to which the bimodality in biomass and community metabolism found for the Goose Creek benthic community will hold in other streams will probably depend on dominant environmental selective factors, among which we posit geomorphology and disturbance to be significant. By contrast, low-gradient streams with high macrofaunal production on woody debris (e.g., Benke et al. 1984) or high-gradient streams with coarser sediments and more extensive riffle habitat for benthic insects may not be characterized by bimodal benthic size spectra. In streams, unlike lakes, exogenous disturbances are generally important structuring features (Resh et al. 1988), but marked differences in disturbance regimes occur among streams depending on hydrologic and geomorphologic conditions (Poff and Ward 1989). Characterizing size spectra among many different streams may provide a useful functional (i.e., nontaxonomic) framework for assessing how community structure reflects local environmental selective forces and thus offer a useful lotic community typology (cf. Schoener 1986). More broadly, patterns may emerge that will provide a basis for comparing streams with other types of ecosystems (cf. Fisher and Grimm 1991).

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