

Taxonomic and Size Structures of Aquatic Macroinvertebrate Assemblages in Different Habitats of Tropical Streams, Costa Rica

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(Accepted March 12, 2008)

Romina E. Principe (2008) Taxonomic and size structures of aquatic macroinvertebrate assemblages in different habitats of tropical streams, Costa Rica. *Zoological Studies* 47(5): 525-534. Taxonomic and size structures of macroinvertebrate assemblages associated with different habitats of tropical streams of Costa Rica were analyzed. Surber samples were taken in riffle and run habitats in 2 streams. Invertebrates were identified and measured, and the biomass was estimated. The taxonomic richness and total abundance were higher in riffle habitats. Correspondence analysis showed a clear separation between riffle and run samples. The IndVal method identified the characteristic assemblages in each habitat type. Tricladida, Hydrachnidia, Leptophlebiidae, Hydropsychidae, *Simulium* sp., Corynoneurini, Orthocladiinae, and Empididae showed significant indicator values for riffle habitats; whereas *Bivalvia*, Tanyptodinae, and Chironomini were the characteristic taxa from runs. The length-frequency distribution of riffles differed from that in runs in both streams as measured by Kolmogorov-Smirnov tests. The largest organisms were found in run habitats, with macroinvertebrates belonging to the 1st size class being the most abundant in riffles. Although larger organisms were found in runs, differences in total biomass between habitats were not observed due to the high number of small invertebrates collected in riffles. The size spectrum for the entire benthic community showed that the total biomass was relatively equitably distributed among the size classes, although a peak was suggested for medium size classes. When the size spectrum was separately analyzed in each habitat, a peak was also suggested in riffles. Differences in the physical attributes of riffles and runs were clearly reflected in the taxonomic composition of the size spectra. Patterns observed in taxonomic and size structures may indicate different ecological functioning at the habitat level in the tropical streams studied.
<http://zoolstud.sinica.edu.tw/Journals/47.5/525.pdf>

Key words: Benthos, Size spectra, Organism distribution, Community structure, Lotic ecosystem.

The distribution of the benthic community may be explained as an adjustment between hydrological conditions and life history of the populations (Statzner et al. 1997). The distribution of organisms changes in relation to hydrological and geomorphological conditions at different spatial scales: drainage, reach, and habitat (Hildrew 1996, Maddock 1999). Information about benthic assemblages associated with particular habitats is essential in order to assess environmental changes and to understand ecological segregation within multispecies communities (Bisson et al. 1982). Quantification of habitat use provides a basis for

predicting biotic responses to changes in habitat availability (Hawkins et al. 1993).

The study of community size structure is important since organism body size constrains many ecological processes that influence community organization (Schoener 1986). Body size influences an organism's energetic requirements, its potential resource exploitation, and its susceptibility to predation (Schmid et al. 2000). Thus, the abundances and biomass values of differentially sized animals should reflect size-specific allocation of total community resources (Peters 1983), and this allocation may vary among

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habitats characterized by different abiotic and biotic constraints (White et al. 2007).

In aquatic ecology, size distribution research has focused on the size spectrum which is the concentration of individuals or biomass in logarithmic size classes and the variation in concentrations among classes (Schwinghamer 1981, Poff et al. 1993, White et al. 2007). Considerable research has been carried out on invertebrate size structure in fluvial systems (Poff et al. 1993, Morin et al. 2001, Solomini et al. 2001, Principe and Corigliano 2006), and the distribution of benthic macroinvertebrates in different habitats has been studied in tropical systems (Ramírez et al. 1998, Fenoglio et al. 2004, Ramírez and Hernández-Cruz 2004). In stream ecology, data on the size structure of macroinvertebrates are available for temperate streams, whereas they are actually lacking for tropical streams. Virtually all concepts and ideas in stream ecology have been formulated based primarily on studies in temperate streams. Consequently, tropical streams provide an opportunity to examine the generality of these concepts since the fauna in these lotic systems has developed under very different set of environmental variables (e.g., temperature, rainfall, photoperiod, and seasonal variation).

Physical and life history traits of species are reflected in their body size and may control species composition and relative abundances, thereby indirectly influencing community function (Robson et al. 2005). Thus, knowing the distribution of body sizes in a community should provide useful information about its ecological properties relative to comparable communities elsewhere. In this study, taxonomic and size structures of macroinvertebrate assemblages associated with different habitats of 2 tropical streams were analyzed. Habitat preferences of macroinvertebrate taxa were evaluated, and the size spectrum was constructed for each habitat type. Recognizing patterns in body mass structure can provide clues about the underlying processes affecting the community in streams of a tropical rainforest.

MATERIALS AND METHODS

This study was conducted at the La Selva Biological Station (10°26'N, 84°01'W), which is owned and operated by the Organization for Tropical Studies (Heredia, Costa Rica). La Selva is on the Caribbean slope of Costa Rica, near

sea level (at an elevation of 35 m). Mean annual rainfall at La Selva averages 4 m, with a drier season from Dec. to Mar. (Sanford et al. 1994). Sampling took place during Mar. 2005 in 2 streams located in a transitional secondary forest. The studied streams were of 3rd order (stream 1) and 2nd order (stream 2) and drain into the Sarapiquí River, which joins the Puerto Viejo and drains into the San Juan River on the border between Costa Rica and Nicaragua.

The channel width was 3 m in stream 1 and 2 m in stream 2. In each stream, 4 Surber samples (0.09 m², 300 µm mesh size) were taken from riffles and 4 from runs following a stratified sampling design. According to Gordon et al. (1994), riffles have coarse bed materials and shallow fast-moving water, and the term, run, is given to an intermediate category between riffles and pools, in which the flow is less turbulent than in riffles but moves faster than in pools. In the studied streams, runs were also characterized by fine substrate, mainly of fine sand, silt, and clay. In riffle habitats, stones from the sampling area (enclosed by the frame of the sampler) were taken and scrubbed to remove invertebrates which were swept into the net by the current. Once the stones had been removed, the bottom sediments were stirred up to a depth of about 10 cm. In runs, sediments from the sampling area were disturbed to the same depth as that in riffles.

Conductivity, pH, and temperature were measured in each stream. Current velocity, depth, and type of substrate were assessed in each habitat sampled. The surface current velocity was obtained by timing a bobber (the average of 3 times). Average depth was calculated over 3 measurements in each habitat with a calibrated stick. The dominant substrate types were assessed by visual estimation (Gordon et al. 1994). In the laboratory, organisms were sorted, identified to the lowest possible taxonomic level, counted, and preserved in 70% ethanol.

In this paper, the term, taxonomic richness, is used instead of species richness (Malmquist et al. 2000), because not all of the identifications were made to the same taxonomic level. Richness was measured by considering the number of different taxa recorded, and the Shannon diversity index and evenness index were calculated using natural logarithms. Mann-Whitney tests were performed in order to compare the diversity, evenness, richness, and macroinvertebrate abundance between habitats.

A correspondence analysis of samples and

taxa was carried out using the statistical package, CANOCO (Ter Braak and Smilauer 1999). Log (y+1)-transformed abundance data were used. Differences in the correspondence analysis scores among assemblages from different habitats were evaluated by the *t*-test. The indicator value method (IndVal) proposed by Dufrene and Legendre (1997) was used to identify the characteristic taxa of riffles and runs. This analysis was performed using PC-Ord for Windows 4.25 (McCune and Mefford 1999).

Macroinvertebrates in all samples were measured to the nearest 0.5 mm in a stereo microscope, and their masses were determined from length-mass relationships (Smock 1980, Meyer 1989). Order-level equations from Smock (1980) were used for insects, and equations from Meyer (1989) were used for non-insect invertebrates. All individuals were sized along the longest dimension. Cerci, anal gills, and antennae were not considered in this length measurement. Differences in the length-frequency distribution between riffle and run assemblages were assessed with the Kolmogorov-Smirnov test, which is sensitive to differences in the general shapes of the distributions of 2 populations (Seigel and Castellan 1988). Mann-Whitney tests were conducted to compare the total biomass between the 2 streams and habitat types. Size data from all taxa were grouped into log₁₀ size (mg) intervals, and biomass in these intervals was determined for each habitat type and for the entire benthic community (riffle + run) in each stream. Differences in biomass among the intervals were assessed by analysis of variance (ANOVA).

RESULTS

Habitats showed different physical attributes. Riffle habitats were characterized by a coarse substrate composed mainly of cobbles. The average depth was 0.15 m, average current velocity was 0.6 m/s, and superficial flow was turbulent. Run habitats were composed of fine substrate of sand, silt, and clay. The average depth was 0.20 m, average current velocity was 0.3 m/s, and superficial flow was smooth. Water temperature varied around 25°C in stream 1 and 23°C in stream 2. Conductivity was 17.7 µS/cm in stream 1 and 25.2 µS/cm in stream 2; pH was 6.5 in both streams.

In total, 36 macroinvertebrate taxa were identified (Table 1). The most common taxon was

Diptera; *Simulium* sp. was the dominant taxon in riffles, while chironomids from the subfamilies Tanypodinae and Chironominae were the main taxa in runs. Ephemeropterans were neither frequent nor abundant and were collected mainly in riffle habitats. Odonata had a frequency of occurrence of < 10%; Gomphidae and Libellulidae were mainly associated with run habitats, and the Coenagrionidae was collected only in riffles. The Hydropsychidae was the most frequent Trichoptera (50%) and was found only in riffle habitats. Elmidae larvae were the most frequent and abundant Coleoptera, and were found in both habitat types. Non-insect taxa were not abundant in riffles; Tricladida and Hydrachnidia were the most frequent non-insect taxa in that habitat. In runs, Oligochaeta was the most frequent and abundant non-insect taxon, followed by Bivalvia and Gastropoda.

Richness per sample ranged from 7 to 17. From a total of 36 taxa, 31 were found in riffles and 23 in runs. In stream 1, diversity and evenness did not show differences between habitats (Mann-Whitney: diversity, $W = 20$, $p = 0.6860$; evenness, $W = 12$, $p = 0.1140$), and richness and total abundance were higher in riffle habitats (Fig. 1) (Mann-Whitney: richness, $W = 26$, $p = 0.0290$; abundance, $W = 26$, $p = 0.0290$). In stream 2, all community attributes differed between riffles and runs (Mann-Whitney: diversity, $W = 10$, $p = 0.0290$; evenness, $W = 10$, $p = 0.0290$; richness, $W = 26$, $p = 0.0290$; abundance, $W = 26$, $p = 0.0290$). The highest diversity and evenness were found in run habitats, whereas the highest richness and total abundance were in riffles (Fig. 1).

The results of the correspondence analysis showed that 67% of species abundance was accounted by the first 4 ordination axes (eigenvalues for axis 1: 0.372, axis 2: 0.155, axis 3: 0.128, and axis 4: 0.070; total inertia: 1.083). Axis 1 showed a clear separation between riffle and run samples (Fig. 2). Ordination scores of riffle samples significantly differed from those of run samples, as measured by the *t*-test ($t = -3.71$, $p = 0.0075$). Tricladida, Hydrachnidia, Leptophlebiidae, Hydropsychidae, *Simulium* sp., Corynoneurini, Orthocladiinae, and Empididae showed significant indicator values for riffle habitats (Table 1) and were closely associated with riffle samples in the correspondence analysis (Fig. 2). On the other hand, Bivalvia, Tanypodinae, and Chironomini were the characteristic taxa from run habitats, since they presented significant indicator values (Table 1) and were clustered in relation to

Table 1. List of aquatic macroinvertebrates collected from riffles and runs in the studied streams with corresponding indicator values (IVs) for each habitat type. Monte Carlo tests were used to assess the significance of the observed maximum IVs for each taxon. The highest IVs and significant p values are in bold

Taxa		Riffle	Run	p value
Platyhelminthes				
Tricladida		62.5	0.0	0.032*
Mollusca				
Gastropoda		2.0	41.7	0.239 ^{ns}
Bivalvia		0.0	62.5	0.031*
Annelida				
Oligochaeta		4.0	55.4	0.125 ^{ns}
Hirudinea		12.5	0.0	1.000 ^{ns}
Arthropoda				
Hydrachnidia		87.5	0.0	0.005**
Crustacea				
Brachyryncha		12.5	0.0	1.000 ^{ns}
Insecta				
Plecoptera				
Perlidae	<i>Anacroneuria</i> sp.	37.5	0.0	0.193 ^{ns}
Ephemeroptera				
Baetidae		20.8	2.0	0.727 ^{ns}
Caenidae	<i>Caenis</i> sp.	6.2	6.0	1.000 ^{ns}
Leptohyphidae	<i>Tricorythodes</i> sp.	44.4	1.0	0.124 ^{ns}
Leptophlebiidae		86.4	0.0	0.005**
Odonata				
Coenagrionidae		12.5	0.0	1.000 ^{ns}
Ghompidae		0.0	12.5	1.000 ^{ns}
Libellulidae		6.2	6.0	1.000 ^{ns}
Heteroptera		12.5	0.0	1.000 ^{ns}
Trichoptera				
Hydropsychidae		100.0	0.0	0.001***
Philopotamidae		12.5	0.0	1.000 ^{ns}
Hydroptilidae		50.0	0.0	0.091 ^{ns}
Coleoptera				
Dytiscidae		12.5	0.0	1.000 ^{ns}
Dryopidae		12.5	0.0	1.000 ^{ns}
Elmidae		40.5	23.0	0.575 ^{ns}
Diptera				
Tipulidae		16.7	4.0	1.000 ^{ns}
Simuliidae	<i>Simulium</i> sp.	99.8	0.0	0.001***
Ceratopogonidae	Species 1	27.0	28.1	1.000 ^{ns}
	Species 2	32.5	2.0	0.457 ^{ns}
Chironomidae				
Chironomini		21.0	79.1	0.039*
Tanytarsini		69.2	27.0	0.137 ^{ns}
Tanypodinae		7.0	86.7	0.013*
Corynoneurini		97.1	1.0	0.001***
Orthoclauiini		80.9	14.0	0.007**
Stratiomyidae		0.0	12.5	1.000 ^{ns}
Empididae		79.0	2.0	0.018*
Dixidae		0.0	12.5	1.000 ^{ns}
Syrphidae		12.5	0.0	1.000 ^{ns}
Muscidae		0.0	12.5	1.000 ^{ns}

Indicator value method; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, non significant.

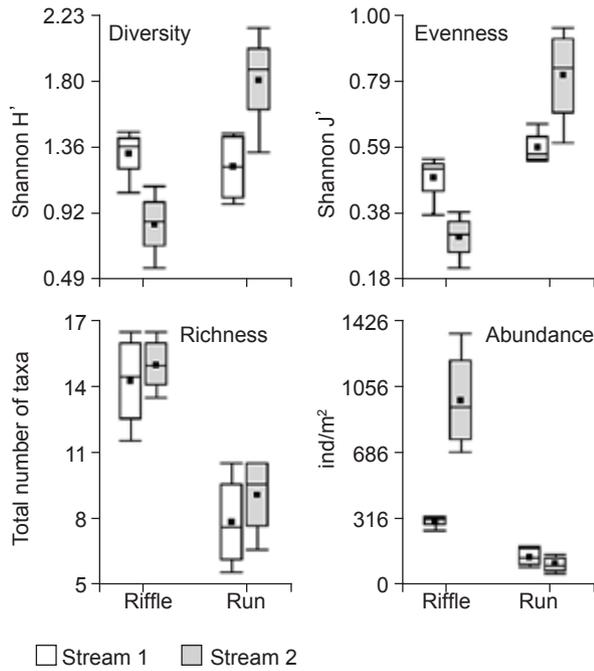


Fig. 1. Box plots for diversity, evenness, taxonomic richness, and total macroinvertebrate abundance in riffles and runs of the studied streams.

run samples in the correspondence analysis (Fig. 2).

In total, 3,656 individuals were measured. The length-frequency distribution in riffles differed from that in runs in both streams (Fig. 3) (Kolmogorov-Smirnov: stream 1, $D = 1.59$, $p < 0.0100$; stream 2, $D = 1.20$, $p < 0.0100$). The largest individuals were found in run habitats (Oligochaeta, Gomphidae, Libellulidae, Elmidae larvae, and large chironomids). In riffles, macroinvertebrates belonging to the 1st size class (Hydropsychidae, Hydrachnida, and small Chironomidae and Simuliidae larvae) were the most abundant.

Total macroinvertebrate biomass did not differ between streams (Mann-Whitney: $W = 75$, $p = 0.5050$) or between riffles and runs in each stream (Mann-Whitney: stream 1, $W = 18$, $p = 0.9000$; stream 2, $W = 23$, $p = 0.2000$). The size spectrum determined for the entire benthic community showed that total biomass was relatively equitably distributed among the size classes (Fig. 4), although a peak was suggested in medium size classes (ANOVA: stream 1, $F = 12.75$, $p < 0.0001$;

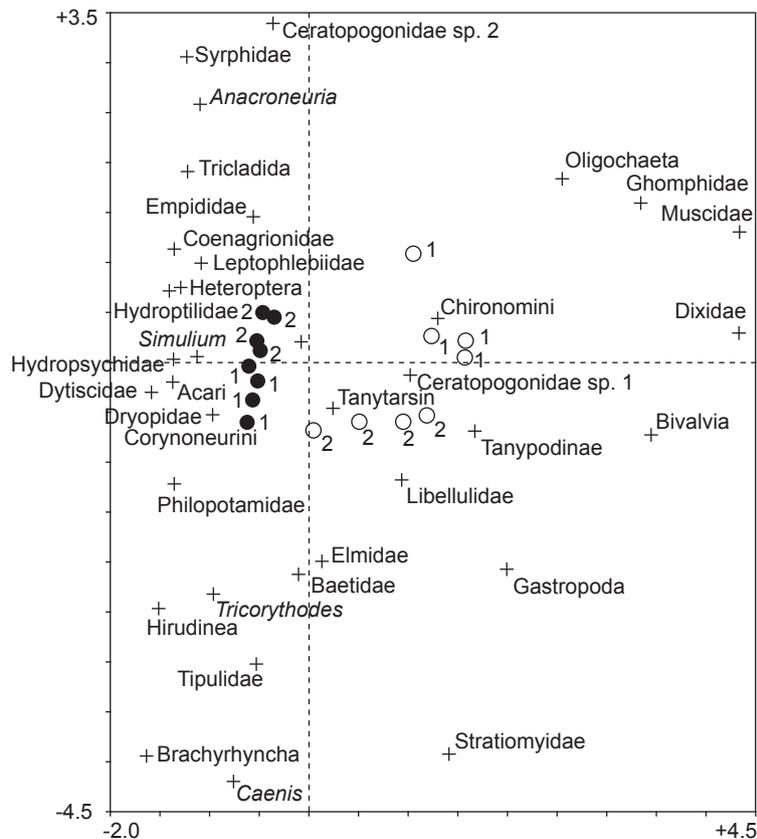


Fig. 2. Correspondence analysis (CA) ordination of benthic samples (circles) and taxa (crosses) in the studied streams (1 and 2). Open circles correspond to run samples, and closed circles correspond to riffle samples.

stream 2, $F = 12.50$, $p < 0.0001$). When the size spectrum was separately analyzed in each habitat, a peak was also suggested in riffles in medium size classes (ANOVA: riffle in stream 1, $F = 12.24$, $p < 0.0001$; run in stream 1, $F = 8.13$, $p < 0.0004$; riffle in stream 2, $F = 27.69$, $p < 0.0001$; run in

stream 2, $F = 8.76$, $p < 0.0002$).

In riffle habitats, medium size classes were mainly comprised of *Simulium* sp., Chironomidae from the tribes Orthoclaudiini and Corynoneurini, Trichoptera, and Ephemeroptera (Fig. 5). In runs, medium size classes were mainly composed of

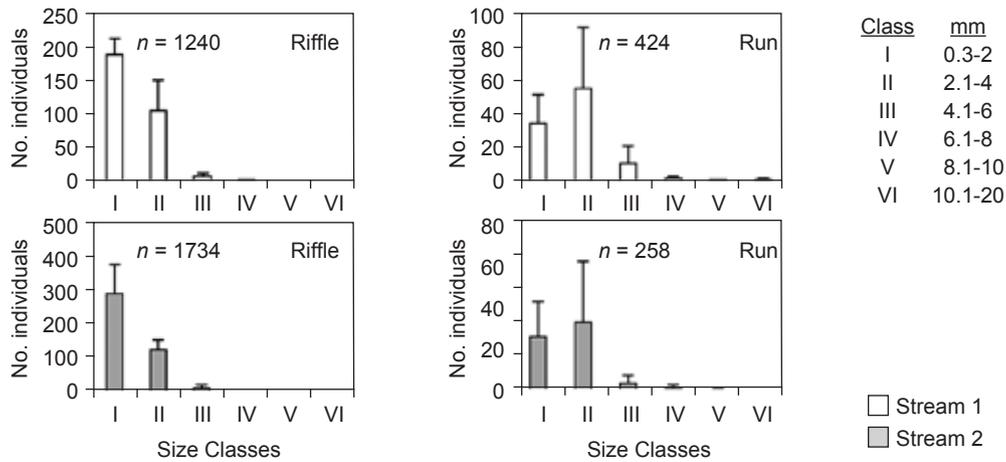


Fig. 3. Length-frequency distributions of macroinvertebrates from riffles and runs of the studied streams.

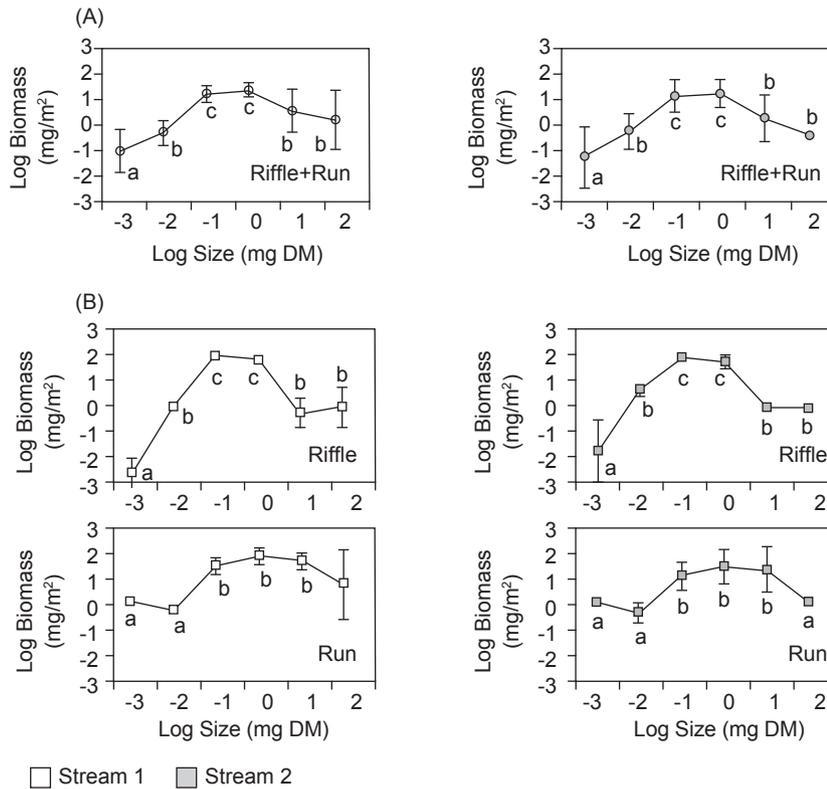


Fig. 4. Biomass size spectra of macroinvertebrates collected in riffles and runs of the studied streams. In the upper panel (A), the size spectra for the entire benthic community (benthic samples pooled together) are shown. In the lower panel (B), the size spectra for riffle and run samples are shown separately. Different letters indicate significant differences among classes tested by ANOVA (SNK test). DM, dry mass.

Oligochaeta, Elmidae larvae, and Tanypodinae and Chironomini. The largest size classes presented higher biomass in runs than in riffles, and were comprised of Oligochaeta, Elmidae, Chironomidae larvae, Gomphidae and Libellulidae.

DISCUSSION

Macroinvertebrate community structure has been found to differ among stream habitats by many authors (Ramírez et al. 1998, Armitage and Cannan 1999, Tickner et al. 2000, Baptista et al. 2001, Bonada et al. 2006, Principe et al. 2007). Some studies reported the lowest values of richness and diversity in habitats characterized by fine substrate (Armitage and Cannan 1999, Tickner et al. 2000, Fenoglio et al. 2004), while the highest values were found in the most heterogeneous environments (Beisel et al. 2000, Principe and Corigliano 2006). The highest richness was also found in the most complex habitat units in this study (i.e., riffles), but the highest diversity was registered in relatively homogeneous habitats (i.e., runs), due to the high evenness of the assemblages living in runs. Heterogeneous

environments potentially offer a great number of niches for invertebrates. These habitat units are preferred by a lot of species because they offer refugia and adequate conditions for feeding, since the probability of predation decreases. On the other hand, in habitats with finer substrates, the instability of the substrate and the low organic matter availability lead to a low richness (Hawkins 1984).

Results for macroinvertebrate total abundances are quite contradictory, since some authors have found the lowest values in riffle habitats (Baptista et al. 2001, Principe et al. 2007), while others have reported the lowest abundance for habitats characterized by fine substrates such as pools and runs (Armitage and Cannan 1999, Tickner et al. 2000); which is in agreement with the results of this study. In tropical streams, patches of fine substrate can be subjected to higher predation by fish and shrimp (Pringle 1996), and it has been demonstrated that this activity results in low abundances of insects in these habitat units (Pringle and Hamazaki 1998). Furthermore, chironomids were the main taxa in runs of the studied streams. These taxa were reported to be the least affected by activities of fish and shrimp,

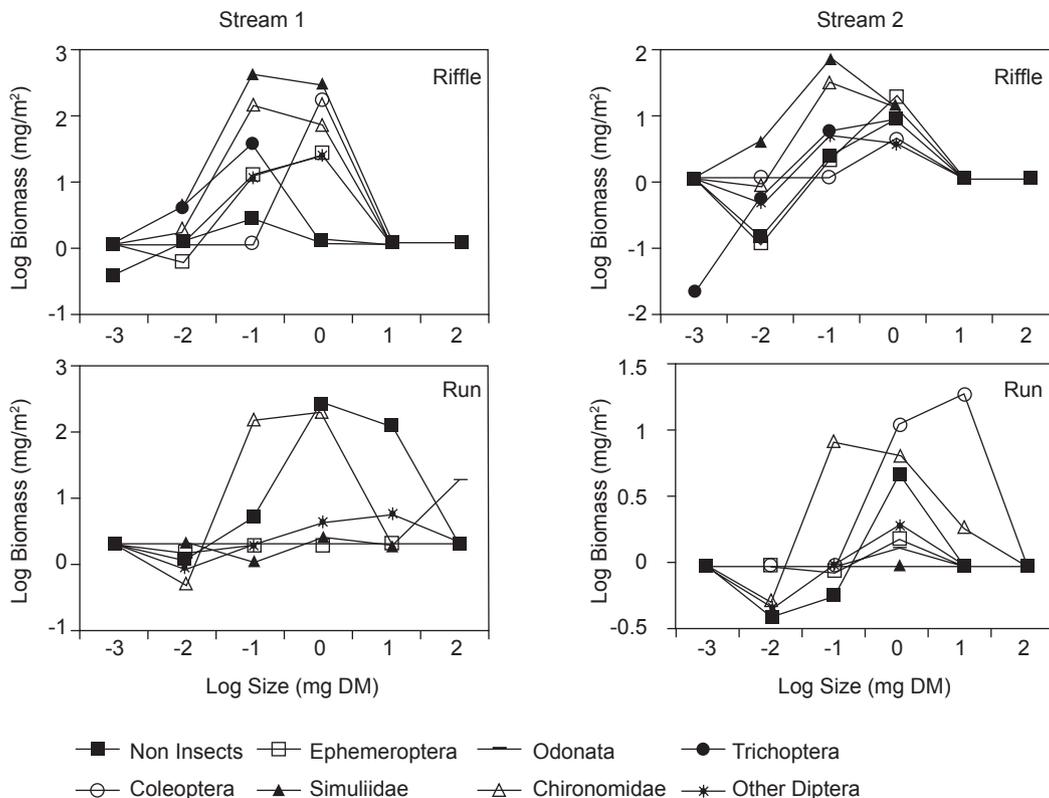


Fig. 5. Biomass size spectra considering the biomass of the main community taxocenes in each size class. DM, dry mass.

suggesting that their ability to build retreats and bury themselves provides protection against macroconsumers (Pringle and Hamazaki 1998, Rosemond et al. 1998).

Each habitat unit of a lotic system is associated with a particular macroinvertebrate assemblage whose composition is mainly determined by substrate and flow type (Ramírez et al. 1998, Beisel et al. 2000, Tickner et al. 2000). In this study, the correspondence analysis clearly separated groups of samples from different habitats. This suggests that different stream habitats may play different roles in overall community dynamics (Ramírez and Pringle 1998) and that resources may be patchily distributed. The IndVal method allowed the identification of characteristic assemblages in each habitat type. All significant indicator taxa for riffles presented indicator values of > 60% demonstrating high affinities for this habitat type. On the other hand, the Chironominae, Tanyptodinae, and Bivalvia were the characteristic taxa of runs. Species of the subfamily Chironominae are adapted to living in soft sediments and are better able to tolerate lower oxygen concentrations that occur in habitats with this type of substrate (Pinder 1995). Some genera of the Tanyptodinae have also been reported to prefer fine substrates (Fittkau and Roback 1983), and most freshwater Bivalvia live in sandy or silty substrates (Ageitos de Castellanos and Landoni 1995).

The length-frequency distribution of riffles differed from that in runs. Although larger organisms were found in run habitats, differences in total biomass between these 2 habitats were not observed due to the high number of small invertebrates collected in riffles. The largest invertebrates collected in runs were Oligochaeta, Gomphidae, Libellulidae, and large chironomids. These taxa are less affected by predation because they bury themselves, and they do not have to spend as much energy as invertebrates living in riffles, which have to spend more energy to avoid being displaced by the current and in grazing for resources. Alternatively, riffles have been reported to be habitats for small species and nurseries for young life stages (Power 1987, Winfield 1990).

Before discussing biomass patterns in the size spectra, the potential bias that may have been introduced when length-mass relationships based on data from different sites are used must be taken into account. This procedure can introduce some bias due to differences in the physical-chemical environment, trophic conditions, or

genetics (Benke et al. 1999, Gonzalez et al. 2002). Various authors have suggested that regressions developed for the same taxa but from different geographic regions may have different length-mass relations, and recommended caution in their application (Smock 1980, Meyer 1989, Burgherr and Meyer 1997, González et al. 2002). However, Benke et al. (1999) argued that in cases where different investigators developed equations for the same taxa in different regions, it is possible that investigator-related biases in weighing or measurement rather than geographic location could have been responsible for the differences. As I am aware of the potential bias, I made comparisons between habitats within the study and analyzed patterns with the same bias. I discuss the obtained results comparing them with those found in similar works, although I recognize that different patterns may be found in tropical streams. Further studies in the region will produce increased knowledge of the patterns of size distributions and elucidate any differences if they exist. The elaboration of regression equations for tropical stream invertebrates becomes essential in order to obtain more-accurate comparisons and decrease this potential source of error.

The biomass distribution of the entire benthic community was approximately unimodal in the studied streams. In riffles, the size spectra were also unimodal, whereas nearly flat spectra were found in runs. Benthic stream communities usually exhibit an irregular size spectrum (Poff et al. 1993, Bourassa and Morin 1995, Morin et al. 2001, Solomini et al. 2001), and although several authors have analyzed the response of size distribution to spatial factors, there has been no satisfactory theory explaining the characteristic shape of the size spectra that encompasses all habitat types (Stead et al. 2005). Moreover, most pattern-seeking studies have not yet been able to describe the general connection between community characteristics and patterns in body size in a consistent way (Robson et al., 2005). Body size distributions are dynamic, and are not characterized by 1 pattern or category (Allen et al. 2006), therefore White et al. (2007) pointed out that the general variability and complexity of the size spectra across groups make it hard to draw general conclusions about these relationships.

The length-frequency distribution and the shape of the size spectrum differed between habitats, which differed in substrate and flow type. In addition, differences in the physical attributes of riffles and runs were clearly reflected in the

taxonomic composition of the size spectra. Several authors have investigated the response of size distributions to variations in substratum particle size. Some found a low influence of substrate on the shape of the size spectra (Bourassa and Morin 1995, Solomini et al. 2001), whereas others reported opposite results (Poff et al. 1993). Variations in shape among the size spectra may reflect inherent differences in evolutionary histories, trophic level organization, and/or environmental constraints on community membership (Poff et al. 1993). Holling (1992) stated that a range of mechanisms may be responsible for the observed body-size distributions, with different mechanisms operating at different spatial and temporal scales. The variability in the results found in studies about size distribution in different geographical regions, ratifies the importance of considering local characteristics and makes so far the elaboration of theoretical generalizations in relation to this concept difficult. Patterns observed in taxonomic and size structures in riffles and runs may indicate that different intra- and interspecific relationships may act in each habitat as factors structuring the macroinvertebrate benthic community. Therefore, the ecological functioning may be considered to differ at the habitat level in the studied tropical streams.

Acknowledgments: I thank Mónica Springer for providing some of the taxonomic keys used for identifying macroinvertebrates, Minor Hidalgo for his help with field and laboratory materials, and Alejandro Muñoz for helpful assistance. María Corigliano, Ana Oberto, and Daniela Gomez provided very useful comments on the manuscript. MINAE (Costa Rica) extended collecting permits. The study was supported by a fellowship from the Organization for Tropical Studies. I would also like to thank 2 anonymous reviewers for their helpful comments and suggestions.

REFERENCES

- Ageitos de Castellanos ZJ, NA Landoni. 1995. Mollusca Pelecypoda y Gastropoda. In EC Lopretto, G Tell, eds. Ecosistemas de aguas continentales. Metodologías para su estudio. Tomo II. La Plata, Argentina: Ediciones Sur, pp. 759-781.
- Allen CR, AS Garmestani, TD Havlicek, PA Marquet, GD Peterson, C Restrepo, CA Stow, BE Weeks. 2006. Patterns in body mass distributions: sifting among alternative hypotheses. *Ecol. Lett.* **9**: 630-643.
- Armitage PD, CE Cannan. 1999. Annual changes in summer patterns of mesohabitat distribution and associated macroinvertebrate assemblages. *Hydrol. Process.* **14**: 3161-3179.
- Baptista DF, DF Buss, LFM Dorville, JL Nessimian. 2001. Diversity and habitat preference of aquatic insects along the longitudinal gradient of the Macaé River basin, Rio de Janeiro, Brazil. *Rev. Brasil. Biol.* **61**: 249-258.
- Beisel JN, P Usseglio-Polatera, JC Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* **422/423**: 163-171.
- Benke AC, AD Huryn, LA Smock, JB Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J. North Am. Benthol. Soc.* **18**: 308-343.
- Bisson PA, JL Nielsen, RA Palmason, LE Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. In NB Armantrout, ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: American Fisheries Society, Western Division, pp. 62-73.
- Bonada N, M Rieradevall, N Prat, VH Resh. 2006. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. *J. North Am. Benthol. Soc.* **25**: 32-43.
- Bourassa N, A Morin. 1995. Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *J. North Am. Benthol. Soc.* **14**: 393-403.
- Burgherr P, El Meyer. 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Arch. Hydrobiol.* **139**: 101-112.
- Dufrene M, P Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* **67**: 345-366.
- Fenoglio S, T Bo, M Cucco. 2004. Small-scale macroinvertebrate distribution in a riffle of a Neotropical rainforest stream (Río Bartola, Nicaragua). *Caribb. J. Sci.* **40**: 253-257.
- Fittkau EJ, SS Roback. 1983. The larvae of Tanytopodinae (Diptera: Chironomidae) of the Holarctic region - keys and diagnoses. In T Wiederholm, ed. Chironomidae of the Holarctic Region: keys and diagnoses. Part 1. Larvae. *Entomol. Scand.* **19 (Supplement)**: 1-457.
- González JM, A Basaguren, J Pozo. 2002. Size-mass relationships of stream invertebrates in a northern Spain stream. *Hydrobiologia* **489**: 131-137.
- Gordon ND, TA McMahon, LB Finlayson. 1994. Stream hydrology, an introduction for ecologists. New York: J Wiley.
- Hawkins CP. 1984. Substrate associations and longitudinal distributions in species of Ephemerellidae (Ephemeroptera: Insecta) from western Oregon. *Freshw. Invertebr. Biol.* **3**: 181-188.
- Hawkins CP, JL Kershner, PA Bisson, MD Bryant, LM Decker, SV Gregory, DA McCullough, CK Overton, GH Reeves, RJ Steedman, MK Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* **18**: 3-12.
- Hildrew AG. 1996. Whole river ecology: spatial scale and heterogeneity in the ecology of running waters. *Arch. Hydrobiol.* **113**: 25-43.
- Holling CS. 1992. Cross-scale morphology, geometry, and

- dynamics of ecosystems. *Ecol. Monogr.* **62**: 447-502.
- Maddock I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biol.* **41**: 373-391.
- Malmquist HL, T Antonsson, G Gudbergsson, S Skúlason, SS Snorrason. 2000. Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Iceland lakes. *Verh. Int. Verein. Limnol.* **27**: 121-127.
- McCune B, MJ Mefford. 1999. *Multivariate analysis of ecological data*. Vers. 4.25. Gleneden Beach, OR: MjM Software.
- Meyer E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. *Arch. Hydrobiol.* **117**: 191-203.
- Morin A, N Bourassa, A Cattaneo. 2001. Use of size spectra and empirical models to evaluate trophic relationships in streams. *Limnol. Oceanogr.* **46**: 935-940.
- Peters RH. 1983. *The ecological implications of body size*. Cambridge, UK: Cambridge Univ. Press.
- Pinder LCV. 1995. The habitats of Chironomidae larvae. *In* P Armitage, PS Cranston, LCV Pinder, eds. *The Chironomidae. The biology and ecology of non-biting midges*. London: Chapman and Hall, pp.107-135.
- Poff LN, MA Palmer, PL Angermeier, RL Vadas, CC Hakenkamp, A Bely, P Arensburger, AP Martin. 1993. Size structure of the metazoan community in a piedmont stream. *Oecologia* **95**: 202-209.
- Power ME. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. *In* WC Kerfoot, A Sih, eds. *Predation, direct and indirect impacts on aquatic communities*. Dartmouth: Univ. of New England, pp. 333-351.
- Principe RE, MC Corigliano. 2006. Benthic, drifting and marginal macroinvertebrate assemblages in a lowland river: temporal and spatial variations and size structure. *Hydrobiologia* **553**: 303-317.
- Principe RE, GB Raffaini, CM Gualdoni, AM Oberto, MC Corigliano. 2007. Do hydraulic units define macroinvertebrate assemblages in mountain streams of central Argentina? *Limnologia* **37**: 323-336.
- Pringle CM. 1996. Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. *Freshwater Biol.* **35**: 125-140.
- Pringle CM, T Hamazaki. 1998. The role of omnivory in a Neotropical stream: separating diurnal and nocturnal effects. *Ecology* **79**: 269-280.
- Ramírez A, LR Hernández-Cruz. 2004. Aquatic insect assemblages in shrimp-dominated tropical streams, Puerto Rico. *Biotropica* **36**: 259-266.
- Ramírez A, P Paaby, CM Pringle, G Agüero. 1998. Effect of habitat type on benthic macroinvertebrates in two lowland tropical streams, Costa Rica. *Rev. Biol. Trop.* **46**: 201-213.
- Ramírez A, CM Pringle. 1998. Structure and production of a benthic insect assemblage in a Neotropical stream. *J. North Am. Benthol. Soc.* **17**: 443-463.
- Robson BJ, LA Barmuta, PG Fairweather. 2005. Methodological and conceptual issues in the search for a relationship between animal body-size distributions and benthic habitat architecture. *Mar. Freshwater Res.* **56**: 1-11.
- Rosemond AD, CM Pringle, A Ramírez. 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. *Freshwater Biol.* **39**: 515-523.
- Sanford RL, P Paaby, JC Luvall, E Phillips. 1994. Climate, geomorphology and aquatic systems. *In* LA McDade, KS Bawa, HA Hespeneide, GS Hartshorn, eds. *La Selva: ecology and natural history of a Neotropical rainforest*. Chicago, IL: Univ. of Chicago, pp. 19-33.
- Schmid PE, M Tokeshi, JM Schmid-Araya. 2000. Relation between population density and body size in stream communities. *Ecology* **298**: 1757-1570.
- Schoener TW. 1986. Overview: kinds of ecological communities – ecology becomes pluralistic. *In* J Diamond, J Caset, eds. *Community ecology*. New York: Harper and Row, pp. 467-479.
- Schwinghamer P. 1981. Characteristic size distributions of integral benthic communities. *Can. J. Fish. Aquat. Sci.* **38**: 1255-1263.
- Siegel S, NJ Castellan Jr. 1988. *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill.
- Smock LA. 1980. Relationships between body size and biomass of aquatic insect. *Freshw. Biol.* **10**: 375-383.
- Solomini AG, A Benvenuti, R D'Olimpio, M De Cicco, G Carchini. 2001. Size structure of benthic invertebrate assemblages in a Mediterranean river. *J. North Am. Benthol. Soc.* **20**: 421-431.
- Statzner B, K Hoppenhaus, MF Arens, P Richoux. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biol.* **38**: 100-135.
- Stead TK, JM Schmid-Araya, PE Schimd, AG Hildrew. 2005. The distribution of body size in a stream community: one system, many patterns. *J. Anim. Ecol.* **74**: 475-487.
- Ter Braak C/JF, P Smilauer. 1999. *CANOCO for Windows (vers. 4.02) – a FORTRAN program for canonical community ordination*. Wageningen, The Netherlands: Centre for Biometry Wageningen.
- Tickner D, PD Armitage, MA Bickerton, KA Hall. 2000. Assessing stream quality using information on mesohabitat distribution and character. *Aquat. Conserv.* **10**: 170-196.
- White EP, SKM Ernest, AJ Kerkhoff, BJ Enquist. 2007. Relationships between body size and abundance in ecology. *Trends Ecol. Evol.* **22**: 323-330.
- Winfield IJ. 1990. Predation pressure from above, observations on the activities of piscivorous birds at a shallow eutrophic lake. *Hydrobiologia* **191**: 223-231.