Verh. Internat. Verein. Limnol.	27	1485–1488	Stuttgart, November 2000

Distribution and abundance patterns of macroinvertebrates in a mountain stream: an analysis along multiple environmental gradients

F. Richard Hauer, Jack A. Stanford, J. Joseph Giersch and Winsor H. Lowe

Introduction

Current velocity, substratum size, fluid dynamics, seston quantity and quality, and thermal regimes have been suggested as major abiotic gradients that affect the distribution and abundance of lotic macroinvertebrates (e.g. WALLACE et al. 1977, HILDREW & EDINGTON 1979, ALSTAD 1982, THORP et al. 1986, STATZNER et al. 1988). STANFORD et al. (1988) attributed changes in thermal regimes associated with discontinuities in a river system resulting from river regulation as the primary mechanism influencing the distribution of hydropsychid caddisflies. HALL et al. (1992) hypothesized that the distribution of plants and animals was the consequence of energy balances (i.e. gains vs. losses) across multiple environmental gradients. Since environmental gradients operate at different spatial and temporal scales, the distribution and abundance of organisms appear at distinct spatial and temporal scales. For example, well-defined spatial distributions are readily apparent in plant communities distributed along elevation and moisture gradients (WHITTICKER 1967)

We conducted a detailed spatial analysis of current velocity, substratum size, sestonic carbon and nitrogen, thermal regimes, and changing abundance of dominant species of the macroinvertebrate community along a mountain stream gradient. Herein, we demonstrate that macroinvertebrate distribution and abundance are highly correlated with specific stream elevation and thermal characteristics.

Study site

McDonald Creek is a fourth-order stream draining ~400 km^2 of Glacier National Park in northwest Montana, U.S.A. and has a mean annual discharge of 16.4 m^3 s^{-1}. Basin and stream channel morphology is greatly influenced by the sedimentary bedrock and glacial history of the area. Maximum elevation in the drainage is 2,912 m on the continental divide along the eastern border of the catchment. Lake McDonald, a glacial lake on the valley floor near the catchment terminus, is at an elevation of 961 m.

Methods

To determine the relationships, if any, between the distribution and abundance of macroinvertebrates and various abiotic stream gradients, we collected data at eight sampling sites located sequentially along a 1,500-m elevation and 36 km longitudinal stream gradient of McDonald Creek. Benthic samples were collected monthly during summer and fall and once during early spring after ice out, but prior to snowmelt runoff. Abundances of mayflies, stoneflies and caddisflies at each site were summarized from the annual means of the monthly quantitative collections. Samples were made using the modified kick-net procedure specifically designed for large cobble substratum (HAUER & STANFORD 1981). We also collected seasonal seston samples that were analyzed for carbon and nitrogen content. Current velocity and substratum size were determined at each of the sampling locations. Small, computerized thermograph recorders were installed near the thalweg at each sample site to collect hourly temperature data over the annual hydrographic cycle.

Results

Temperatures increased significantly along the elevation and longitudinal stream gradient as a function of annual degree-days ($P < 0.01$; $r^2 = 0.96$), maximum summer temperature ($P < 0.01$; $r^2 = 0.92$), and mean summer temperature ($P < 0.01$; $r^2 = 0.91$) (Fig. 1). In contrast, sestonic carbon and nitrogen concentrations (Fig. 2) as well as current velocity and substratum size (Fig. 3) were highly variable between sites and were not correlated with either stream elevation or the longitudinal gra-

0368-0770/00/0027-01485 $ 1.00

dient.

The macroinvertebrates displayed distinct trends in abundance and limits to their range along the stream gradient. Among the mayflies, stoneflies and caddisflies, 27 species occurred abundantly at one or more of the sampling sites. Some species occurred most frequently in the headwater sites. Other species achieved maximum abundance among central reach sites, while other species occurred most commonly, and some exclusively, at the lowest, downstream sites (Fig. 4). Further analyses of these abundance data revealed that most species occurred within well-defined, normal-shaped, Gaussian density patterns. Among these mountain stream macroinvertebrates, the well-defined distribution patterns along the elevation and longitudinal gradient were highly recognizable. Species achieved maximum abundance within central reaches of their range.

A predictable species replacement along the stream gradient occurred commonly among similar taxonomic and functional groups. For example, three species of the mayfly genus *Epeorus* occurred abundantly among different sites along the stream length of McDonald Creek. *E. grandis* occurred most abundantly at the most headwater sites, *E. deceptivus* occurred most abundantly at the central reach sites, while *E. longimanus* occurred most abundantly at the three most downstream sites. Among the preda-

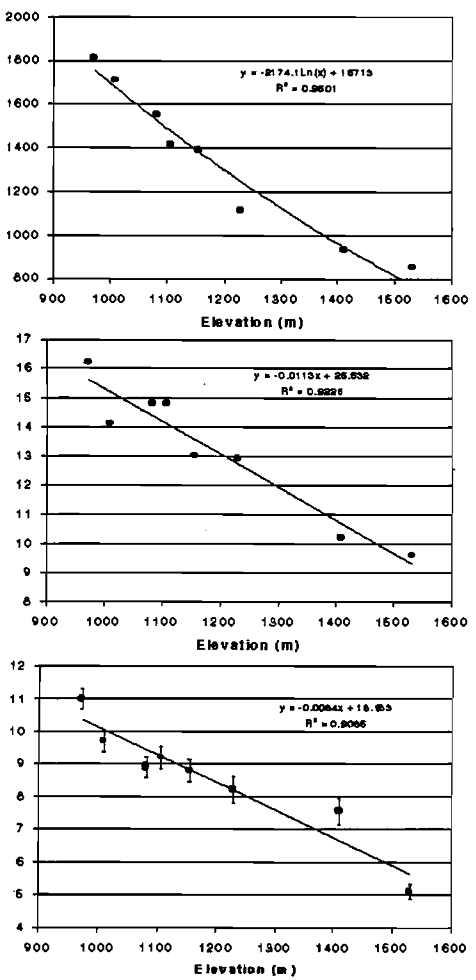

Fig. 1. Relationship between elevation and the annual degree-days (top panel), maximum summer temperature (middle panel), and mean summer temperature (lower panel; error bars ± 1 S.E.) along the McDonald Creek stream gradient.

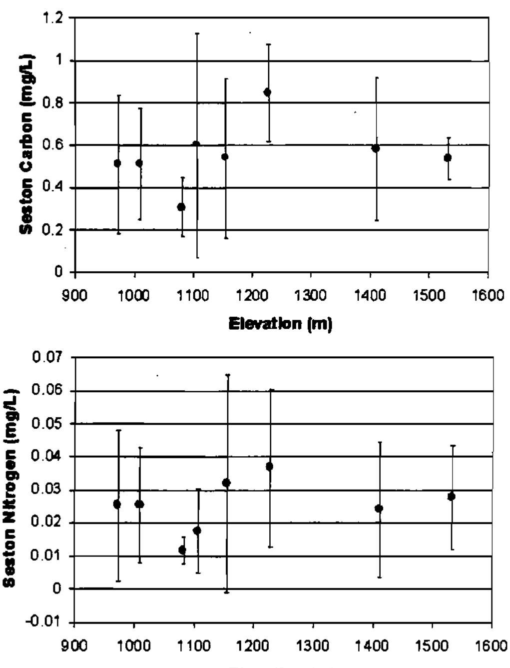

Fig. 2. Relationship between elevation and sestonic carbon (top panel; error bars ± 1 S.E.) and sestonic nitrogen (lower panel; error bars ± 1 S.E.) along the McDonald Creek stream gradient.

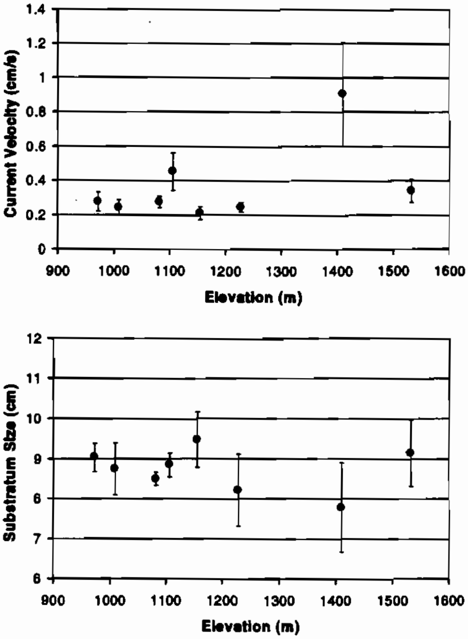

Fig. 3. Relationship between elevation and current velocity (top panel; error bars ± 1 S.E.) and substratum size (lower panel; error bars ± 1 S.E.) along the McDonald Creek stream gradient.

ceous stoneflies, *Setvena bradleyi* occurred abundantly at the most upstream sites while *Doroneuria theodora* were most abundant at the lower sites. Patterns of species replacement were perhaps most clearly seen among the net-spinning, hydropsychid caddisflies, in which *Parapsyche elsis* occurred most abundantly at upstream sites and was replaced in dominance by *Arctopsyche grandis* at the most downstream sites.

Discussion

There were two major questions in this study. The first was whether the distribution and abundance patterns among similar species and across taxonomic groups were distinguishable and predictable, and the second was whether there were any environmental gradients other than stream size or elevation that could account for species-specific distribution patterns. Indeed, macroinvertebrate distributions demonstrated patterns of abundance that were consistent for species distributed across a spatially predictable environmental gradient. Current velocity, substratum size and the quantity and quality of trophic resources have all been suggested as mechanisms controlling landscape level distribution and abundance patterns of stream invertebrates. However, we found only temperature, expressed as annual degree-days and maximum and mean summer temperatures as the variables occurring as corollary gradients.

Hall et al. (1992) provided an ideal theoretical framework to interpret the results of this study. Species with distinctly different rates of energy losses or gains across an environmental gradient will respond with different energy efficiencies. In the central regions of a species' distribution, energy efficiencies across gradients are maximized; however, at the extreme ends of the distribution, energy inefficiencies are limiting. In this study, temperature is the primary environmental gradient along a predictable spatial gradient, namely stream size and elevation. For example, we observed *Parapsyche elsis* in upstream reaches, whereas *Arctopsyche grandis*, which is functionally almost identical to *P. elsis*, was the dominant net-spinning caddisfly in downstream reaches. Although we observed these species distributed spatially either in upstream segments or downstream segments, these species are rather responding to thermally mediated spatial distributions and species-specific controls of metabolism. This relationship, demonstrated for these species, can be applied among all macroinvertebrate species such that distribution and abundance patterns along the elevation and longitudinal stream gradient can largely be attributed to species-specific bioenergetics under the spatial control of a predictable thermal gradient.

We conclude that the lack of a significant longitudinal gradient in flow velocity, substratum and seston and the highly significant thermal gradient support the hypotheses of Hall et al. (1992) regarding a bioenergetic model structuring present distribution and abundance patterns of stream macroinvertebrates. Regardless of the specific bioenergetic mechanisms producing distribution and abundance patterns,

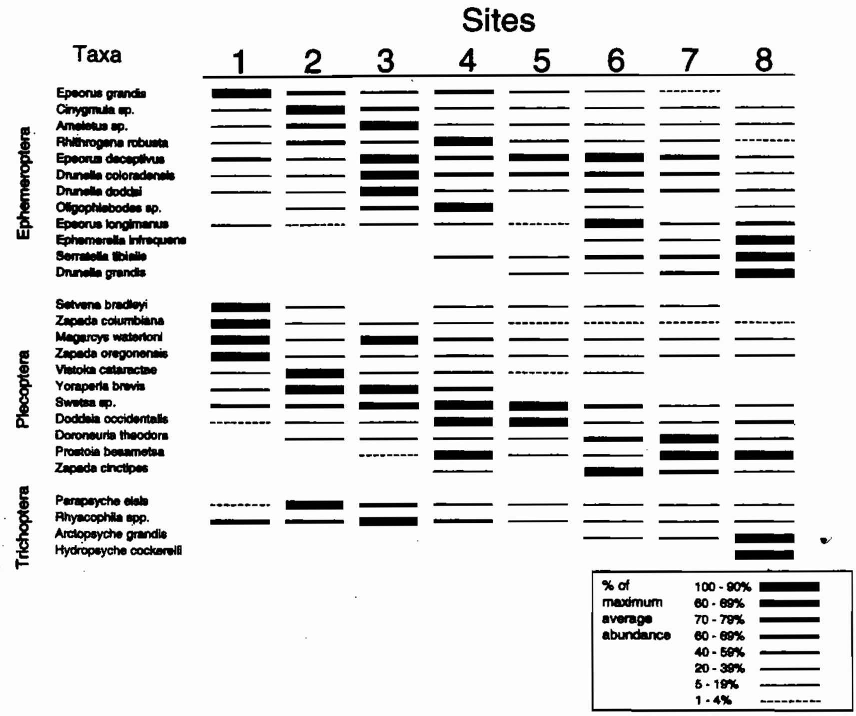

Fig. 4. Relative species abundance at each sampling site expressed as a percentage of the annual means. Percentages were calculated as a function of maximum site abundance.

this study underscores the value of macroinvertebrates as ideal indicators of thermal modification that may be associated with change in land use, riparian vegetation or climate change.

Acknowledgments

Funding was provided by a grant from the Global Change Program of the Biological Resources Division, U.S. Geological Survey and the U.S. National Park Service.

References

Alstad, D. N., 1982: Current speed and filtration rate link caddisfly phylogeny and distributional patterns on a stream gradient. – *Science* 216: 533–534.

Hall, C. A. S., Stanford, J. A. & Hauer, F. R., 1992: The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. – *Oikos* 65: 377–390.

Hauer, F. R. & Stanford, J. A., 1981: Larval specialization and phenotypic variation in *Arctopsyche grandis* (Trichoptera: *Hydropsychidae*. – *Ecology* 62: 645–653.

Hildrew, A. G. & Edington, J. M., 1979: Factors facilitating the coexistence of hydropsychid caddis larvae (Trichoptera) in the same river system. – *J. Anim. Ecol.* 48: 557–576.

Stanford, J. A., Hauer, F. R. & Ward, J. V., 1988: Discontinuities in a river ecosystem. – *Verh. Internat. Verein. Limnol.* 23: 1114–1118.

Statzner, B., Gore, J. A. & Resh, V. H., 1988: Hydraulic stream ecology: Observed patterns and potential applications. – *J. N. Am. Benthol. Soc.* 7: 307–360.

Thorp, J. H., Wallace, J. B. & Georgian, T. J., 1986: Untangling the web of caddisfly evolution and distribution. – *Oikos* 47: 253–256.

Wallace, J. B., Webster, J. R. & Woodall, W. R., 1977: The role of filter feeders in flowing waters. – *Arch. Hydrobiol.* 79: 506–532.

Authors' address:

F. Richard Hauer, Jack A. Stanford, J. Joseph Giersch, Winsor H. Lowe, Flathead Lake Biological Station, The University of Montana, 311 Bio Station Lane, Polson, Montana 59860-9659, USA.