

Dynamics of Lotic Ecosystems

Edited by

Thomas D. Fontaine, III
Savannah River Ecology Laboratory
University of Georgia

Steven M. Bartell
Environmental Sciences Division
Oak Ridge National Laboratory



ANN ARBOR SCIENCE
THE BUTTERWORTH GROUP

WILSON JOURNAL
OF LOTS AND LOTS

Copyright © 1983 by Ann Arbor Science Publishers
230 Collingwood, P.O. Box 1425, Ann Arbor, Michigan 48106

Library of Congress Catalog Card Number 82-048641
ISBN 0-250-40612-8

Manufactured in the United States of America
All Rights Reserved

Butterworths, Ltd., Borough Green, Sevenoaks
Kent TN15 8PH, England

15. BIOTIC INTERACTIONS OR ABIOTIC LIMITATIONS? A MODEL OF LOTIC COMMUNITY STRUCTURE

Barbara L. Peckarsky

Entomology Department
Cornell University
Ithaca, New York

Rocky Mountain Biological Lab
Crested Butte, Colorado

ABSTRACT

The relative roles of biological interactions and physical-chemical factors in structuring benthic stream communities have not been established. It is proposed that the relative importance of physical-chemical factors, predation, and competition depends on the physical harshness and resultant potential secondary productivity of each particular stream. If streams are placed on a gradient from harsh to benign physical conditions, harsher streams may be characterized by unfavorable ranges of diel and seasonal fluctuation of such factors as current, depth, substrate shifts, temperature, and availability of habitable space. Biological interactions may be relatively unimportant if harsh physical conditions eliminate predators and maintain prey populations at low numbers. As streams become more benign, biological interactions may increase in importance as a result of the release of physical limitations on species distributions. Predation may override competition in benign streams where predators are not excluded by physical conditions, where prey have effective defenses, or where prey cannot find spatial refuge from preda-

tors. Competition may dominate as a determinant of species distribution within prey refuges, in systems where prey defenses are effective, or within moderately harsh systems where predator populations do not reach levels high enough to exert sufficient pressure on prey populations. Data from a Wisconsin and a Colorado stream are presented in support of this hypothesis.

INTRODUCTION

I have previously reported on experiments designed to determine the role of biological factors, such as benthic density (Peckarsky, 1979b; 1981), food (Peckarsky, 1980a; Peckarsky and Dodson, 1980b), predation (Peckarsky and Dodson, 1980a), and competition (Peckarsky and Dodson, 1980b) on habitat choice by stream invertebrates. These experiments established that biological variables can have a significant influence on benthic community structure in streams. Biological factors were manipulated in cages with nearly constant physical factors, such as temperature, current velocity, and substrate, since investigators have shown that these variables may also be important determinants of distributions of invertebrates in streams (Cummins and Lauff, 1969; Minshall and Minshall, 1977; Rabeni and Minshall, 1977).

A remaining problem is to sort out the relative roles of all these factors in determining the distribution and abundance of stream invertebrates. Stream ecologists have been unsuccessful in solving this problem for a number of reasons. First, most of the evidence available is correlative. Only recently have experimental manipulations allowed us to answer questions of cause and effect. Also, manipulations have generally been simple, testing one factor at a time. More elaborate experiments are needed to test interactions among various factors. Another important restriction is that we suffer from the "my stream" syndrome; most of us concentrate on a very limited range of conditions. Because we do not incorporate a broad spatial perspective into our thinking, we limit our ability to generalize about lotic community dynamics. We also must encompass a broader temporal concept of the stream ecosystem. Processes dominating stream dynamics during one season may differ widely from those during another. It is this temporal and spatial perspective that is lacking in contemporary stream theory.

This paper has two purposes: first, to report the results of experiments conducted during several seasons in a Wisconsin and a Colorado stream to measure the effects of certain physical variables on the colonization of cages by invertebrates and, second, to propose a conceptual model that

defines conditions under which physical-chemical and biological factors (predation and competition) may operate to influence invertebrate community structure in streams. The model incorporates data from all experiments conducted in the two streams and from other reports in the literature.

Physical variables tested in this study were chosen on the basis of reports in the literature of their significance in determining distributions of stream benthos and their suitability to manipulation within stainless-steel-screen cages (Peckarsky, 1979b). The specific hypotheses tested were that colonization of habitat by stream benthos differs with distance from the stream bank, current velocity, depth within the substrate, and substrate heterogeneity.

Bishop and Hynes (1969) observed that benthic invertebrates colonized traps by moving upstream within the substrate. Colonization rates were higher adjacent to the stream banks in winter and in more midstream areas in the summer. Differences were not statistically significant, however. Hayden and Clifford (1974) noted the migration of the mayfly *Leptophlebia cupida* along the stream banks during all seasons, presumably because of lower current velocity. Elliott (1971) also found upstream movement to be highest near stream banks where discharge was low and stones smaller. Cummins (1964) observed that some caddis flies inhabit stream margins during early instars and migrate to center stream in later life stages because of changes in food requirements and case-building materials.

Allen's paradox (Allen, 1951) that trout consumed more invertebrates than the production measured by biologists sparked a quest for missing benthos. The hyporheic zone has been suggested as a potential reservoir of invertebrates not detected by conventional surface-sampling techniques (Bishop, 1973; Hynes, 1974; Williams and Hynes, 1974). Williams and Hynes measured maximum benthic density at a depth of 10 to 20 cm within the substrate of the Speed River, Ontario. Poole and Stewart (1976), however, found maxima at 0 to 10 cm in the Brazos River, Texas. Bishop and Hynes (1969) observed higher colonization of invertebrates at lower levels in the substrate (9 cm deep), whereas others (Hayden and Clifford, 1974) found upstream migration to occur at the substrate surface.

The quality of the substrate has been tested directly as an important determinant of habitat selection by stream invertebrates. Substrate type (Hildrew et al., 1980; Thorup, 1966), particle size (Reice, 1980; Williams and Mundie, 1978), and heterogeneity (Hart, 1979; Williams, 1980) have been documented as causal factors of the distribution and abundance of stream benthos.

MATERIALS AND METHODS

Sites

Experiments were conducted in two third-order streams, Otter Creek, Sauk County, Wisconsin, and the East River, Gunnison County, Colorado, from 1976 to 1978. Dates of experiments, ranges of current velocity, water depth, and maximum/minimum water temperatures are shown in Table 1 for each trial. The substrate at the sites of both streams consisted of coarse cobble material interspersed with finer stones and gravel. Otter Creek substrate was generally more heterogeneous, with particle sizes ranging from fine sand to boulders 1 m in diameter. The high-elevation (3100 m) East River is a generally larger stream, but sampling sites were chosen within an area where the stream divided into two or three smaller channels with depth and width similar to Otter Creek. Otter Creek receives allochthonous input from extensive deciduous riparian vegetation, whereas the East River, sparsely bordered by willows (*Salix* spp.) and various conifers, receives less detrital input. (See Peckarsky, 1979a; 1979b; 1980a, for more complete descriptions of the streams.)

Experimental Design

Transects

Cages were buried along perpendicular stream transects on four dates in Otter Creek and two dates in the East River (Table 1). Four cages were buried at each transect at similar depth within the substrate and at approximately 0.5-m intervals from the stream bank to center stream and covered with approximately 5 to 10 cm of substrate material. Twelve cages along three transects were used in all trials, except the last trial in each stream, for which 16 cages allowed four replicate transects. Transects were at least 18 m apart.

Substrate was standardized among cages as follows: All cages received 15 stones, four <5 cm, six <7.5 cm, three <10 cm, and two <12.5 cm in largest diameter (determined by passing them through graduated hose clamps). Texture classes were qualitatively determined according to the ratio of smooth to rough faces (>1, smooth; approximately 1, intermediate; and <1, rough).

Table 1. Physical Data on the Two Streams During Trials

Site and Date*	Trial	Number of cages buried	Current, † cm/s	Depth, ‡ cm	Temperature, § °C
Otter Creek	Oct. 29–Nov. 1, 1976	12	0.18–0.21	13.2	5.6/3.3
	May 23–26, 1977	12	0.29–0.24	11.5	19.4/15.0
	Oct. 7–11, 1977	12	0.23–0.36	17.8	11.1/7.2
East River	May 26–30, 1978	16	0.45–0.44	18.2	18.3/15.0
	Aug. 1–5, 1977	12	0.22–0.22	9.4	17.7/7.2
	Aug. 2–5, 1978	16	0.33–0.27	13.3	15.0/4.4
Otter Creek	Sept. 17–20, 1976	12	0.18–0.18	5.0	14.4/11.7
	Apr. 29–May 2, 1977	12	0.41–0.37	13.9	14.4/10.0
	Sept. 30–Oct. 4, 1977	12	0.26–0.26	8.8	7.8/13.3
East River	Apr. 24–28, 1977	16	1.10–0.88	25.2	6.1/12.8
	July 20–23, 1977	12	0.29–0.36	1.5	18.3/10.0
	July 24–27, 1978	16	0.81–0.65	8.9	15.0/5.0
Otter Creek	June 20–23, 1977	12	0.18–0.21	14.0	17.8/13.3
	Sept. 27–30, 1977	12	0.21–0.24	16.3	15.0/11.7
	June 6–9, 1978	16	0.24–0.20	14.5	16.7/11.2
East River	Aug. 14–17, 1977	12	0.20–0.23	6.3	18.9/11.1
	July 6–9, 1979	16	1.64–1.32	30.6	12.8/3.3

*Burial and retrieval dates.

†Average current velocity on burial and retrieval dates.

‡Average depth to top of upper cage.

§Maximum/minimum water temperature over sampling period.

Depth

Pairs of cages were buried stacked vertically within the substrate of both streams (Figure 1). Six replicate pairs were used for all except the last trial in each stream, for which eight replicate pairs of cages were buried. The top cage was flush with the surface of the substrate at a depth of 0 to 10 cm; the lower cage was at a depth of 10 to 20 cm beneath the surface of the substrate. Substrates were standardized as described above.

Substrate

Pairs of directly adjacent cages were buried. One of each pair contained the heterogeneous substrate described; the other contained 10 10-cm stones of intermediate texture. Cages were covered with 5 to 10 cm of natural substrate.

All cages were oriented to receive active colonizers walking or swimming upstream and were buried for 3 to 4 days (see Table 1), a duration chosen to maximize numbers of trails and yet allow adequate numbers of colonizing insects for statistical comparison between experimentals and controls at each date (Peckarsky, 1979b). The short-term nature of these experiments precludes investigation of longer-term effects. Current velocity was measured at each cage with a Marsh-McBirney model 201 current meter, and water depth to the top of the upper cage was recorded.

Statistical comparisons between paired replicates were made with a Wilcoxon Sign Rank Test (depth and substrate), and Spearman Rank

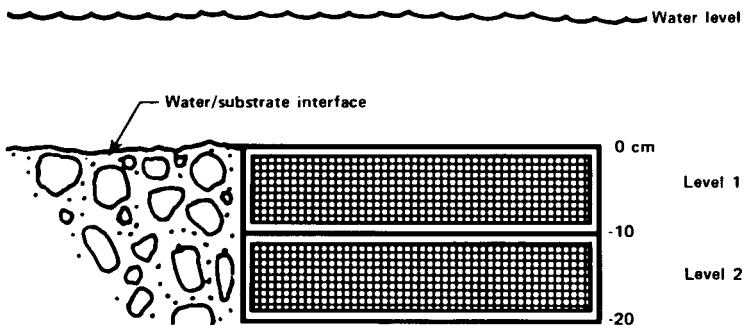


Figure 1. Schematic representation of cage orientation for depth experiment.

Correlation coefficients were calculated to determine associations between number of invertebrates per cage and distance to the closest stream bank or current velocity (transects).

RESULTS

Transects

No association was shown between total number of invertebrates per cage and distance from the stream bank for fall or spring trials in Otter Creek or for summer 1978 trials in the East River. In the summer of 1977, however, a larger number of invertebrates colonized cages in the center stream than cages closer to the banks (Figure 2a). Analysis of 22 common taxa in Otter Creek and 14 in the East River showed that no Otter Creek taxa differentially colonized cages at different distances from the stream bank on any dates (Table 2). *Cinygmula* sp. (Figure 2b) and Turbellaria (Figure 2c) preferentially colonized cages in the center of the East River during the summer of 1977.

Total invertebrates and 22 individual taxa also showed no differential colonization of cages at different current velocities for any trial in Otter Creek. During the summer of 1977, total invertebrates (Figure 3a) and *Cinygmula* sp. (Figure 3b) preferentially colonized cages at higher current velocity. Chloroperlidae spp. preferentially colonized cages at lower current velocities (Figure 3c). No such associations were shown for summer 1978 trials in the East River. Spearman Rank Correlation Coefficients were also calculated on the current velocity vs. distance to nearest stream bank for each trial. No significant associations were obtained.

Depth

The median number of invertebrates colonizing cages at the two different depth strata in both streams is shown in Figure 4. There was no significant difference between the number retrieved at 0 to 10 and 10 to 20 cm depths for any trial in Otter Creek, and there were no consistent seasonal trends (Figure 4a). However, more total numbers of invertebrates colonized the upper cage (0 to 10 cm) during both summers in the East River (Figure 4b, $P < 0.05$). Table 2 summarizes the data for 23 taxa in Otter Creek and 18 taxa in the East River. Several species showed preferences for the upper or lower strata in both streams. For example, the perlodid stonefly *Isoperla cotta*, the ephemereid mayfly, *Ephemera subvaria*, the limnophilid caddisfly, *Pycnopsyche* sp., and the black

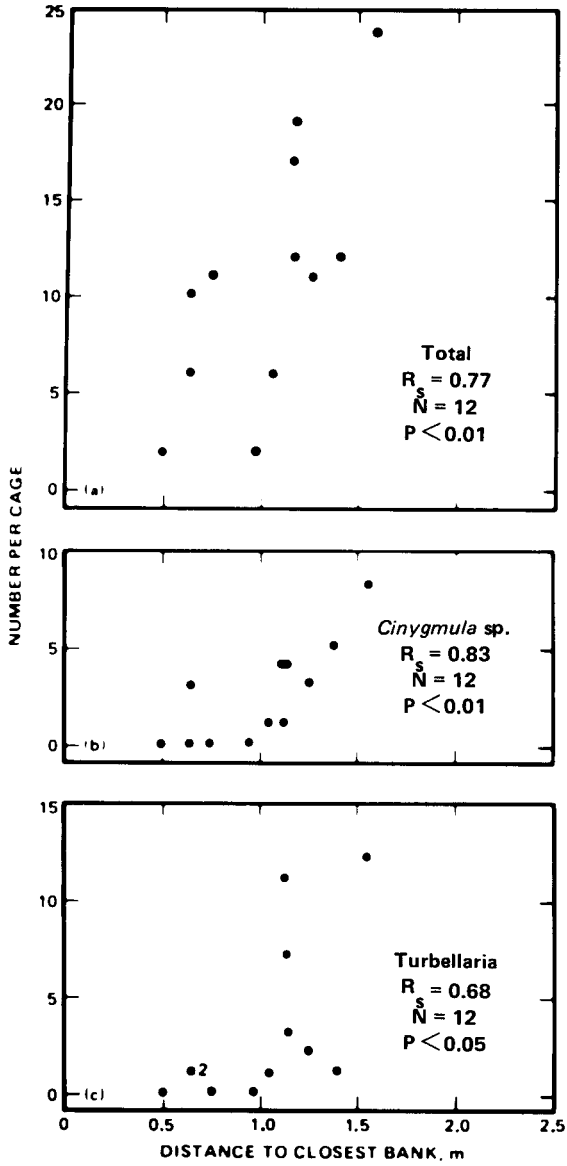


Figure 2. Numbers of invertebrates colonizing cages at different distances from the stream bank. East River, summer 1977.

Table 2. Taxa Analyzed Separately for Transect and Depth Experiments

Species	Transects†	Depth§	
		Number at 0-10 cm	Number at 10-20 cm
Otter Creek			
<i>Baetis phoebus</i>	+	19	12
<i>Ephemera subvaria</i>	+	19**	6
<i>Heptagenia hebe</i>	+	1	15***
<i>Stenonema fuscum</i>	+	11	33***
<i>Paraleptophlebia</i> sp.	+	14	24
<i>Paracapnia angulata</i>	+	2	6
<i>Amphinemura delosa</i>	+	10	21
<i>Acroneuria lycorias</i>	+	2	6
<i>Isoperla cotta</i>	+	58*	33
<i>Taeniopteryx nivalis</i>	+		
<i>Micrasema rusticum</i>	+	26	24
<i>Glossosoma</i> sp.	+	6	1
<i>Hydropsychidae slossonae</i>	+	16	23
<i>Lepidostoma</i> sp.	+	8	17
<i>Mystacides</i> sp.	+	4	2
<i>Oceceis</i> sp.		5	5
<i>Pycnopsyche</i> sp.		17*	4
Limnephilidae spp.			
<i>Optioservus fastidius</i>	+	9	6
<i>Nigronia serricornis</i>	+	2	4
<i>Sialis</i> sp.		1	2
<i>Atherix variegata</i>	+		
Chironomidae spp.	+	45	43
<i>Prosimulium tuberosum</i>	+	40**	6
<i>Antocha</i> sp.		2	5
<i>Tipula</i> sp.		4	6
Minnows	+		
Total		355	348
East River			
<i>Baetis bicaudatus</i>	+	57	15
<i>Ephemera infrequens</i>	+	6	2
<i>Cinygmula</i> sp.	+	138*	60
<i>Epeorus longimanis</i>		5	0
<i>Rhiithrogena hageni</i>		4	2
<i>Paraleptophlebia vaciva</i>		0	4
<i>Ameletus velox</i>	+	20	10
Chloroperlidae spp.	+	29	74**
<i>Zapada haysi</i>	+	3	1
<i>Kogotus modestus</i>	+	16*	8
<i>Pteronarcella badia</i>	+	4	6
<i>Arctopsyche grandis</i>	+	1	0
<i>Rhyacophila tucula</i>		0	1
<i>R. valuma</i>		4	0
<i>Heterlimnius</i> sp.	+	4	2
Chironomidae spp.	+	22	15
<i>Prosimulium</i> sp.	+	35**	4
Hydrachnellae spp.		2	3
Turbellaria spp.	+	9	19
Total		353*	241

†A plus (+) indicates that taxa were analyzed separately in transect experiments.

§Asterisks represent conventional levels of significance. Absence of data indicates that taxa were not individually analyzed for depth experiments.

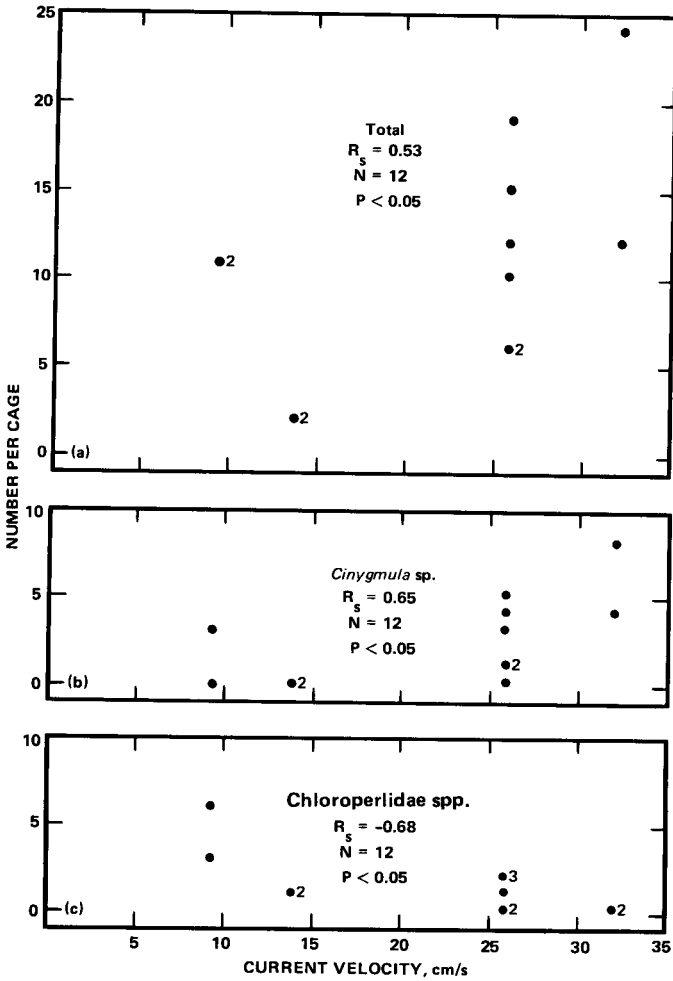


Figure 3. Numbers of invertebrates colonizing cages at different current velocities, East River, summer 1977.

fly, *Prosimulium magnum* preferred the upper cages, and the heptageniid mayflies *Heptagenia hebe* and *Stenonema fuscum* preferred the lower cages in Otter Creek. In the East River the perlodid stonefly *Kogotus modestus*, the heptageniid, *Cinygmula* sp., and *Prosimulium* sp. colonized upper cages significantly more abundantly, and Chloroperlidae spp. appeared in greater numbers in lower cages. Others, such as the baetid mayfly *B. bicaudatus* in the East River showed nonsignificant trends

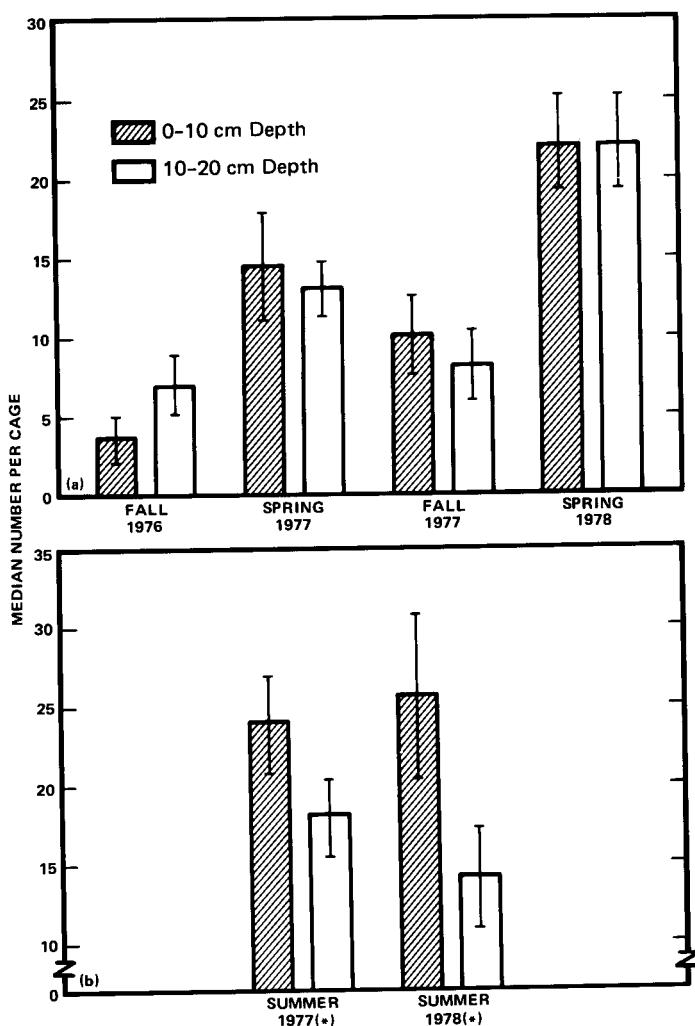


Figure 4. Number of invertebrates ($\bar{x} \pm SE$) colonizing cages at different depths in the substrate. (a) Otter Creek. (b) East River. Asterisk (*) indicates $P < 0.05$ level of significance.

toward one stratum; a few were found in almost equal numbers in upper and lower cages (see Table 2).

Substrate Heterogeneity

As shown in Figure 5, most trials produced no significant differences in median species richness and median numbers of individuals between

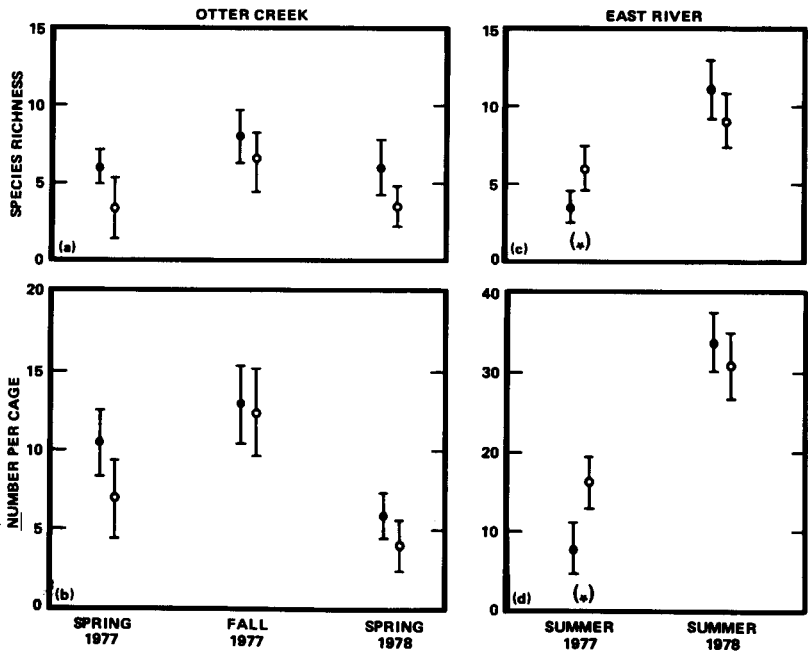


Figure 5. Species richness (a)(c) and median number of individuals (b)(d) per cage ($\bar{x} \pm SE$) with homogeneous and heterogeneous substrates. ●, Homogeneous substrate. ○, Heterogeneous substrate. Asterisk (*) indicates $P < 0.05$ level of significance.

paired cages with homogeneous and heterogeneous substrates. However, both species richness and number of individuals were significantly higher in cages with heterogeneous substrate during the summer of 1977 in the East River (Figures 5c and 5d, $P < 0.05$).

DISCUSSION

The physical factors tested did not show any overwhelming effects on the colonization of substrate-filled cages in either stream. The only factor that significantly influenced Otter Creek benthos was depth within the substrate. Although total numbers of invertebrates were nearly equal in upper and lower cages, several species consistently appeared in one stratum or the other. *Isoperla cotta*, a somewhat stout stonefly predator; *E. subvaria*, an herbivorous mayfly; *Pycnopsyche* sp., a very large leaf shredder; and *P. magnum*, the filter-feeding black fly larva, preferred the upper cages. These insects might be restricted to upper substrate strata by

their large size or by food requirements. Simuliids, for example, attach to the substrate surface and filter seston from the water column. Large leaf material and periphyton are more abundant at the substrate surface for leaf shredders and grazers, such as *Pyncnopsyche* sp. and *E. subvaria*. The dorsoventrally flattened heptageniids, *H. hebe* and *S. fuscum*, inhabit interstitial spaces quite easily and would be expected to reside on unexposed substrate as long as current and oxygen conditions were adequate (Wiley and Kohler, 1980).

Physical parameters also did not produce consistent effects on colonization of East River benthos in summer 1978 trials. The only factor having significant influence was depth within the substrate. More total numbers and numbers of several individual taxa appeared in the upper cages than in the lower cages. The large stonefly predator *K. modestus* may have been restricted from foraging at lower levels by its size. *Baetis bicaudatus* and *A. velox* tended to colonize upper cages more readily, although differences were not statistically significant. Both mayflies are excellent swimmers (Gilpin and Brusven, 1970), and baetids have been documented to remain on exposed substrate surfaces (Wiley and Kohler, 1980) and commonly enter the water column (Hughes, 1966; Peckarsky, 1980b). Simuliids, again, were found almost exclusively in the upper cages because of the nature of their filter-feeding habits. *Cinygmula* sp., a dorsoventrally flattened mayfly, might be expected to inhabit deeper strata, like the Otter Creek heptageniids. Gilpin and Brusven (1970) reported this mayfly to be most abundant in moderate to fast riffles, however, and to be absent from mud and silt substrates. Perhaps its respiratory requirements restrict it to upper substrate levels.

The only trials in which physical effects were consistently important determinants of species distributions and abundances were those of summer 1977 in the East River. Very low snowfall during the winter of 1976-1977 resulted in drought conditions in Colorado. The East River had extremely low water depth and current velocity and unusually high temperatures during the following summer (Table 1) in comparison with all other summers in my experience (Peckarsky, 1979a).

Invertebrates colonized cages in center stream and at higher current velocities than those at the periphery of the stream or at low current velocities. Benthos concentrated at the upper substrate strata in preference to 10- to 20-cm depths within the substrate. A significantly greater number of species and individuals were recovered from heterogeneous substrates as opposed to homogeneous substrates. These results suggest that suitable habitat space may have been limiting during the summer of 1977.

The high-temperature-low-flow regime could have produced respira-

tory stress for invertebrates adapted to cooler, more rapid current conditions. Higher densities of benthos would be expected in center stream, at high current velocity, and in upper cages under such potential stress. Organisms should choose their habitat to minimize respiratory stress (Wiley and Kohler, 1980). Presumably, during "normal flow" conditions in other seasons, the cages along the entire stream transect and range of current velocities tested provided adequate oxygen conditions for the benthos.

The results of the substrate experiments were not consistent with those of most other similar studies, except in the summer of 1977. Williams (1980) showed that a significantly higher number of taxa colonized heterogeneous than homogeneous substrates. Wene and Wickloff (1940) demonstrated that the number of insects on heterogeneous substrates increased by 26%. Hart (1979) concluded that spatial heterogeneity or substrate complexity provide greater resource availability and lead to increased numbers of species and individuals. Wise and Molles (1979), however, found greater numbers of species on small gravel and greater numbers of individuals on large gravel than on a heterogeneous mixture of the two sizes.

Reice (1980) and Hart (1979) suggested that the available surface area of substrate is an important variable determining the resultant diversity of stream invertebrate communities. I did not determine surface area of substrates used in this experiment. It is reasonable to assume that the intermediate-textured stones of homogeneous size (10 cm) offered a surface area comparable to that of the heterogeneous substrate. Alternatively, the short-term experiment might not have allowed enough time to detect substrate preferences. The inconsistency of the results for summer 1977 might, again, be due to peculiarities of the current-temperature-depth regime and the interaction with the substrates provided rather than to the substrate alone.

THE MODEL

An attempt was made to incorporate the data from these experiments and others on biological interactions conducted in both streams into a general model of lotic community structure. The basic idea is not original in ecology; it was developed by Menge (1976) in interpreting data on the organization of the marine rocky intertidal invertebrate community. The high intertidal is a physically harsh habitat tolerated by few species and is structured directly by physical factors, such as wave action and frequent desiccation. The low intertidal is relatively benign, supporting large

populations of starfish predators, whose feeding constitutes the dominant influence on prey community structure. In the middle intertidal zone, conditions become sufficiently harsh to limit populations of starfishes, and thus prey populations are effectively released from regulatory control by predators. This zone constitutes a refuge from predation but allows prey populations to increase to a level where resources (space) are limited; thus competitive interactions become the dominant process organizing the invertebrate community.

Can such a model be applied to streams? Results of experiments on factors determining invertebrate distributions in the two widely differing stream systems tested here showed that the importance of invertebrate predation, competition, and physical factors was not the same in both streams (Peckarsky, 1979a; Peckarsky and Dodson, 1980b). I have attempted to compare conditions of relative harshness between the two streams to determine whether the concept developed by Menge has application to stream ecosystems.

I identified several problems in applying a harsh-to-benign gradient to stream ecosystems. Streams, unlike the marine rocky intertidal, do not exist in a spatial or temporal continuum from harsh to benign physical conditions. Hypotheses become very difficult to test experimentally, since we cannot readily identify conditions that are harsh to stream invertebrates. The following is a working definition of a harsh habitat; it will be subject to subsequent modification, but it provides potential schemes for ranking habitats in terms of a continuum of harsh-to-benign conditions for comparative purposes. "Harsh" is a set of physical-chemical conditions that impose physiological problems for many stream invertebrates. These might include manmade perturbations, such as acid mine drainage, channelization, and stream regulation, to which many species have not evolved adaptive mechanisms. Natural harshness may be imposed by seasonal and diel fluctuations that are unpredictable or hazardous to stream species or by extreme lack of seasonal fluctuations, as in a spring ecosystem, which presents problems to insects whose life cycles depend on proximal cues involving temperature fluctuations. Therefore a benign stream is not necessarily one lacking in disturbance or fluctuations but one that could potentially support a highly productive consumer community. Alternatively, streams may be placed relatively on a two-dimensional scale, such as oligotrophic ↔ eutrophic, tolerable ↔ intolerable, moderate ↔ erratic or extreme.

Comparative physical-chemical and biological data measured during 3 years of study of the East River and Otter Creek are presented qualitatively in Table 3. They support the contention that the East River can be ranked as a harsher stream than Otter Creek, by the previous definition.

Table 3. Comparisons between the East River, Colorado, and Otter Creek, Wisconsin

Parameter	East River, Colorado	Otter Creek, Wisconsin
Elevation	3100 m	300 m
Substrate	More homogeneous	More heterogeneous
Current velocity	Higher absolute, more seasonal and diel fluctuation	Lower absolute, less seasonal and diel fluctuation
Temperature	More diel fluctuation	Less diel fluctuation
	Similar seasonal fluctuation	
Depth, width	More seasonal and diel fluctuation	Generally smaller and shallower, less fluctuation
Habitable space	More temporal fluctuation	Less temporal fluctuation
Abiotic fluctuations	Greater	Fewer
Environmental predictability (?)	Less	Greater
Food, primary productivity	Low allochthonous input, autotrophic, more oligotrophic	High allochthonous input, heterotrophic, more eutrophic
Biotic diversity	Lower	Higher
Density of invertebrates (?)	Higher	Lower
Invertebrate predators	Fewer species, less dense	More species, more dense
Vertebrate predators	Four trout species	Many—trout, minnows, amphibians, snakes

This ranking is based on relative biological productivity, as well as physical-chemical factors (Sander, 1968). Question marks appear when ranking is uncertain. (More complete descriptions appear in Peckarsky, 1979a; 1979b). Similar comparisons have been made between temperate and tropical streams (Stout and Vandermeer, 1975; Fox, 1977).

Otter Creek provides suitable habitat for a wide range of invertebrates. Predation by large stoneflies has been shown to exert a significant influence on benthic distributions in this stream (Peckarsky, 1980b; Peckarsky and Dodson, 1980a; 1980b). In an interactive experiment to test the relative effects of predation and competition, access to cages by predators eliminated or reduced to insignificant the effect of the presence of competitors on colonization by mayflies. Only in cages offering a refuge from predation (by restrictive mesh size) was a competitive effect measured (Peckarsky and Dodson, 1980b). In the present study the physical factors tested had little influence on habitat choice by benthos. The results of these single-factor and interactive experiments are consistent with the hypothesis that invertebrate predation is the most important factor structuring communities of stream benthos in the benign, temperate, woodland stream.

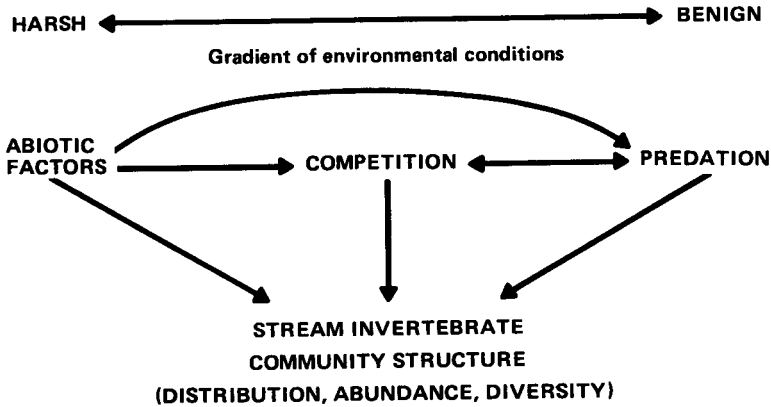


Figure 6. Conceptual model of stream community structure. (See text for explanation.)

The results of identical experiments in the harsher, high-altitude stream were different. Experiments on predation effects produced variable results in the East River (Peckarsky and Dodson, 1980a). During the summer of 1977, the unusually low-discharge-high-temperature regime could be considered harsh, producing stressful conditions for the benthos. Effects of predation were not significant during this summer. This was also the only summer in which physical factors were significant determinants of benthic distributions. The interactive experiment testing the effects of predation and competition showed that competition had the predominant influence over colonization of cages by prey (Peckarsky and Dodson, 1980b). Access to cages by predators did not override the effects of the presence of competitors in determining habitat choice by prey. These results are consistent with the hypothesis that in "normal" seasons the East River supports lower populations of invertebrate predators, which, thus, exert lower predation pressure on prey. Conditions are favorable enough, however, to support prey populations dense enough to compete for potentially limited habitable space or, perhaps, a limited allochthonous food source (Peckarsky, 1980a). Competition was the dominant biological factor structuring the benthic communities in the East River. Under the unusually stressful drought conditions of 1977, physical factors were also significant determinants of benthic distributions.

A model of lotic community structure incorporating the results of these experiments is given in Figure 6. In summary, when physical conditions are benign enough to support a large invertebrate predator population, effects of predation may maintain prey populations at levels low enough to minimize competition for limited habitable space (or, in some cases,

food). When some factor (such as differential physical-chemical harshness, differential vertebrate predation, prey defenses, or the existence of refuges from predators) reduces the effectiveness of invertebrate predators, competition for limited habitable space or food may result. When physical-chemical conditions become so harsh that physiological tolerance by prey populations is difficult, biological interactions are probably unimportant in determining stream community structure, and chance dispersal (Harrison, 1980), and the physical factors themselves may directly structure the insect community. These conditions might be present in highly stressed streams, such as heavy-metal- or nutrient-polluted streams, streams with acid stress, or intermittent streams.

Stout (1981) showed that abiotic factors control populations of insects in extremely harsh streams in Costa Rica. Matthews and Hill (1980) suggested that habitat partitioning among species of stream fishes is evident only when environmental conditions are relatively mild in a stream in central Oklahoma. Closely related species converged to similar habitats when physical-chemical conditions were rigorous. Matthews and Hill documented the importance of physical-chemical factors in regulating distributions of stream fishes under unstable conditions. Kraemer (1979) suggested that harsh conditions in altered rivers eliminated competitors of the introduced Asiatic clam (*Corbicula*), but, in more benign, unaltered streams, competition was prevalent between *Corbicula* and the native Unionidae.

These studies provide preliminary evidence of the generality of this model, but complete experiments must be designed to test interactive effects of physical-chemical and biological parameters on community structure of stream invertebrates. Rigorous tests of this model will require such hypothesis testing under a wide range of controlled environmental conditions.

ACKNOWLEDGMENTS

I thank Stan Dodson, Rosemary Mackay, Andy Sheldon, John Neess, James Ward, Manuel Molles, Seth Reice, Chuck Hawkins, the Cornell Ecology Group, Bill Matthews, and Bill Matter for critical comments and valuable discussions of these ideas. Stan Dodson and Dick Gange designed and built the cages; Beth French edited the manuscript; and Steve Horn and Cheryl Hughes prepared the illustrations. Leanne Mumpy and Steve Horn provided laboratory and field assistance. Jo Ann Hayes was an expert stone measurer and found more 10-cm stones than anyone else. The experiments were supported by an NSF Doctoral

Dissertation Grant, a National Academy of Sciences Grant, and University of Wisconsin Graduate Research grants. Research was conducted in partial fulfillment of a Ph.D. degree at the University of Wisconsin, Madison.

REFERENCES

- Allen, K. R., 1951, The Horokiwi Stream, *N.Z. Mar. Dep. Fish. Bull.*, 10.
- Bishop, J. E., 1973, Observations on the Vertical Distribution of the Benthos in a Malaysian Stream, *Freshwater Biol.*, 3: 147-156.
- , and H. B. N. Hynes, 1969, Upstream Movements of Benthic Invertebrates in Speed River, Ontario, *J. Fish. Res. Board Can.*, 26: 279-298.
- Cummins, K. W., 1964, Factors Limiting the Microdistribution of Larvae of Caddisflies, *Pycnopsyche lepida* (Hagen) and *P. guttifer* (Walker) in a Michigan Stream, *Ecol. Monogr.*, 34: 271-295.
- , and G. H. Lauff, 1969, The Influence of Substrate Particle Size on the Microdistribution of Stream Macrobenthos, *Hydrobiologia*, 34: 145-181.
- Elliott, J. M., 1971, Upstream Movements of Benthic Invertebrates in a Lake District Stream, *J. Anim. Ecol.*, 40: 235-252.
- Fox, L. R., 1977, Species Richness in Streams: An Alternative Mechanism, *Am. Nat.*, 111: 1017-1021.
- Gilpin, B. R., and M. A. Brusven, 1970, Food Habits and Ecology of Mayflies of the St. Marie's River in Idaho, *Melandaria*, 4: 20-40.
- Harrison, R. G., 1980, Dispersal Polymorphisms in Insects, *Annu. Rev. Ecol. Systemat.*, 11: 95-118.
- Hart, D. D., 1979, Diversity in Stream Insects: Regulation by Rock Size and Microspatial Complexity, *Verh. Internat. Verein. Limnol.*, 20: 1376-1381.
- Hayden, W., and H. F. Clifford, 1974, Seasonal Movements of the Mayfly *Leptophlebia cupida* (Say) in a Brown-Water Stream of Alberta, Canada, *Am. Mid. Nat.*, 91: 90-102.
- Hildrew, A. G., C. R. Townsend, and J. Henderson, 1980, Interactions Between Larval Size, Microdistribution and Substrate in the Stoneflies of an Iron-Rich Stream, *Oikos*, 35: 387-396.
- Hughes, D. A., 1966, On the Dorsal Light Response of a Mayfly Nymph, *Anim. Behav.*, 14: 13-16.
- Hynes, H. B. N., 1974, Further Studies on the Distribution of Stream Animals Within the Substrate, *Limnol. Oceanogr.*, 19: 92-99.
- Kraemer, L. R., 1979, *Corbicula* (Bivalvia: Sphaeriacea) vs. Indigenous Mussels (Bivalvia: Unionacea) in U.S. rivers: A Hard Case for Interspecific Competition? *Am. Zool.*, 19: 1085-1096.
- Matthews, W. J., and L. G. Hill, 1980, Habitat Partitioning in the Fish Community of a Southwestern River, *Southwest. Nat.*, 25: 51-66.

- Menge, B. A., 1976, Organization of the New England Rocky Interstitial Community: Role of Predation, Competition, and Environmental Heterogeneity, *Ecol. Monogr.*, 46: 355-393.
- Minshall, G. W., and J. N. Minshall, 1977, Microdistribution of Benthic Invertebrates in a Rocky Mountain (U.S.A.) Stream, *Hydrobiologia*, 55: 231-249.
- Peckarsky, B. L., 1979a, Experimental Manipulations Involving the Determinants of the Spatial Distribution of Benthic Invertebrates Within the Substrate of Stony Streams, Ph.D. Thesis, University of Wisconsin, Madison.
- , 1979b, Biological Interactions as Determinants of Distributions of Benthic Invertebrates Within the Substrate of Stony Streams, *Limnol. Oceanogr.*, 24: 59-68.
- , 1980a, Influence of Detritus upon Colonization of Stream Invertebrates, *Can. J. Fish. Aquat. Sci.*, 37: 957-963.
- , 1980b, Predator-Prey Interactions Between Stoneflies and Mayflies: Behavioral Observations, *Ecology*, 61: 932-943.
- , 1981, Reply to Comment by Sell, *Limnol. Oceanogr.*, 26: 982-987.
- , and S. I. Dodson, 1980a, Do Stonefly Predators Influence Benthic Distributions in Streams? *Ecology*, 61: 1275-1282.
- , and S. I. Dodson, 1980b, An Experimental Analysis of Biological Factors Contributing to Stream Community Structure, *Ecology*, 61: 1283-1290.
- Poole, W. L., and K. W. Stewart, 1976, The Vertical Distribution of Macrobenthos Within the Substratum of the Brazos River, Texas, *Hydrobiologia*, 50: 151-160.
- Rabeni, C. F., and G. W. Minshall, 1977, Factors Affecting Microdistribution of Stream Benthic Insects, *Oikos*, 29: 33-43.
- Reice, S. R., 1980, The Role of Substratum in Benthic Macroinvertebrate Microdistribution and Litter Decomposition in a Woodland Stream, *Ecology*, 61: 580-590.
- Sanders, H. L., 1968, Marine Benthic Diversity: A Comparative Study, *Am. Nat.*, 102: 243-282.
- Stout, J., 1981, How Abiotic Factors Affect the Distribution of Two Species of Tropical Predaceous Aquatic Bugs (Family: Naucoridae), *Ecology*, 62: 1170-1178.
- , and J. Vandermeer, 1975, Comparisons of Species Richness for Stream-Inhabiting Insects in Tropical and Mid-Latitude Streams, *Am. Nat.*, 109: 263-280.
- Thorup, J., 1966, *Substrate Type and Its Value as a Basis for the Delimitation of Bottom Fauna Communities in Running Waters*, Special Publication No. 4. Pymatuning Laboratory of Ecology, University of Pittsburgh.
- Wene, G., and E. L. Wickloff, 1940, Modification of Stream Bottom and Its Effect on the Insect Fauna. *Can. Entom.*, 72: 131-135.
- Wiley, M. J., and S. L. Kohler, 1980, Positioning Change of Mayfly Nymphs Due to Behavioral Regulation of Oxygen Consumption, *Can. J. Zool.*, 58: 618-622.

- Williams, D. D., 1980, Some Relationships Between Stream Benthos and Substrate Heterogeneity, *Limnol. Oceanogr.*, 25: 166-171.
- _____, and H. B. N. Hynes, 1974, The Occurrence of Benthos Deep in the Substratum of a Stream, *Freshwater Biol.*, 4: 233-256.
- _____, and J. H. Mundie, 1978, Substrate Size Selection by Stream Invertebrates and the Influence of Sand, *Limnol. Oceanogr.*, 23: 1030-1033.
- Wise, D. H., and M. C. Molles, Jr., 1979, Colonization of Artificial Substrates by Stream Insects: Influence of Substrate Size and Diversity, *Hydrobiologia*, 65: 69-74.