Bernard Hachmöller, Barfüsserstrasse 42, 3550 Marburg, West Germany

Robin A. Matthews, Huxley College of Environmental Studies, Western Washington University,
Bellingham, Washington 98225, U.S.A.

and

David F. Brakke, Biology Department, University of Wisconsin, Eau Claire,
Wisconsin 57401, U.S.A.

Effects of Riparian Community Structure, Sediment Size, and Water Quality on the Macroinvertebrate Communities in a Small, Suburban Stream

Abstract

We studied the relationships between benthic macroinvertebrates, water quality, sediment characteristics, and riparian community structure in Padden Creek, a second-order stream in Bellingham, Washington, to look for patterns in the macroinvertebrate community structure between upstream and downstream sites. Padden Creek was sampled at four sites; one site was densely forested and relatively unpolluted, while the remaining sites were affected to various degrees by channelization, deforestation, and nonpoint source pollution. We measured water quality (including nutrients), sediment structure, riparian vegetation, and benthic macroinvertebrate densities at each site between 14 May and 1 October 1989. Many taxa were more abundant at the undisturbed, forested upstream site (Site 1), especially pollution intolerant mayflies, stoneflies, and caddisflies. At Site 2, where the surrounding forest had been cleared, there was a decrease in the density of shredders, predators, and collector-filterers, and an increase in scrapers. At Sites 3 and 4, where the stream is affected by organic pollution, there were fewer representatives from pollution intolerant orders (Ephemeroptera, Plecoptera, and Trichoptera) and many more non-insect taxa (e.g., oligochaetes and gastropods). Thus, the effects of channelization, deforestation, and pollution resulted in major changes in the structure of macroinvertebrate communities at downstream sites, suggesting that such riparian alterations imitate similar urbanization effects of higher-order rivers.

Introduction

Dense riparian vegetation influences the trophic structure of headwater streams by shading (which decreases autotrophic production) and by providing a large input of allochthonous detritus in the form of coarse particulate organic matter (CPOM). This loading, in turn, is reflected in the functional feeding group composition of benthic macroinvertebrates. Headwater sections of streams are typically populated by a large proportion of macroinvertebrate shredders, which shifts to higher proportions of scrapers in midreaches and collectors in lower reaches of river systems (Vannote *et al.* 1980, Hawkins and Sedell 1981). Other factors besides organic matter also affect the community structure of benthic macroinvertebrates, including changes in water quality, land use alterations, and changes in substrate characteristics (Hawkes 1979, Newbold *et al.* 1980, Williams 1980, Molles 1982, Kondratieff *et al.* 1984, Minshall 1984).

Padden Creek is a small, second-order stream that is typical of many urban streams in that portions of its watershed have been impacted by channelization, deforestation, and non-point source pollution. Our objectives were to evaluate the effects of changes in water quality, riparian community structure, and sediment size on the macroinvertebrate taxonomic structure and functional group composition in Padden Creek. In doing so, we hoped to illustrate some of the influences of urban development on stream biota.

Study Sites

Padden Creek begins as a lake outlet and flows 4.72 km from Lake Padden (elevation 136 m) to the marine waters of Bellingham Bay. The watershed, which occupies a total area of 15.5 km^2, includes Connelly Creek, the only tributary, and two small inlets of Lake Padden (Figure 1).

We studied four sites in Padden Creek, which are described in Table 1. Site 1 was surrounded by dense, second-growth forest, and had a rocky, diverse substrate. Site 2 had a comparatively open canopy due to urbanization and a homogeneous substrate due to channelization of the stream. Connelly Creek enters between Sites 2 and 3, and was the major source of nutrient pollution into the creek. Site 3 was in a park (Fairhaven Park), which

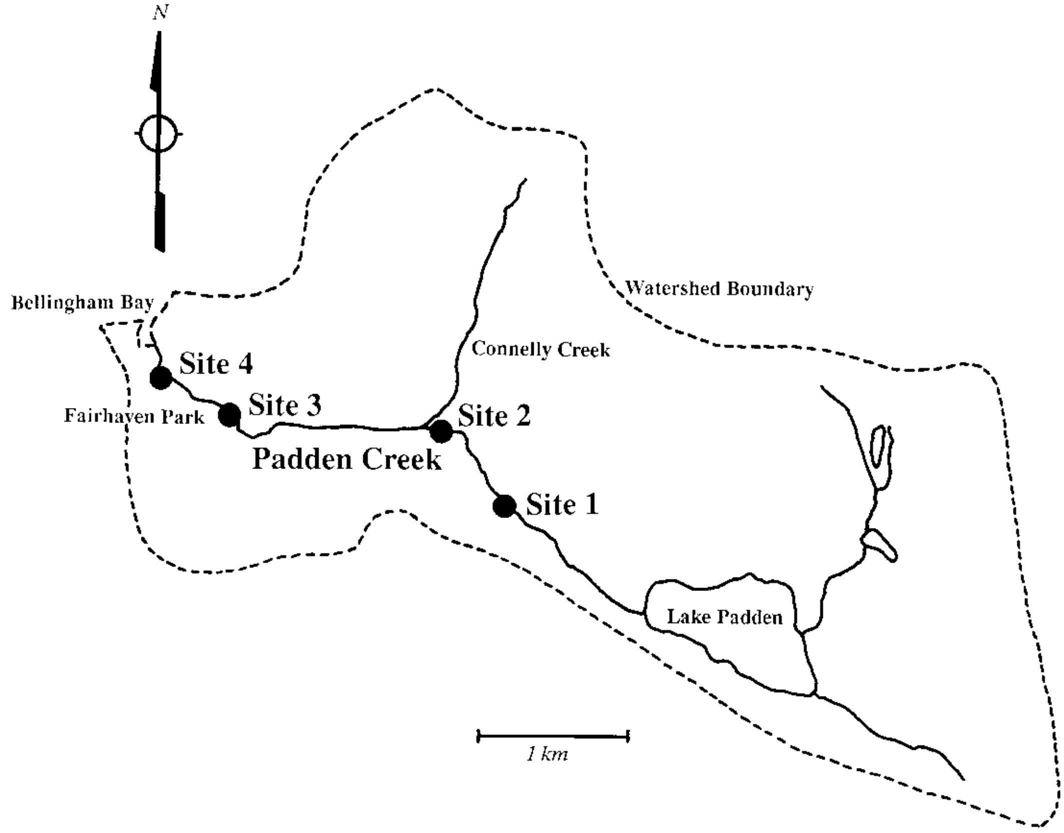

Figure 1. Padden Creek sampling sites and watershed description.

TABLE 1. Descriptions of Padden Creek sampling sites.

Factor	Site 1	Site 2	Site 3	Site 4
nutrient concentrations	low-moderate	low-moderate	elevated	elevated
riparian vegetation	second-growth coniferous forest	alder, gaps in canopy	park-like vegetation	freshwater wetland
stream velocity	fast-flowing	fast-flowing	fast-flowing	slow-flowing
substrate	diverse cobble-pebble	uniform cobble-pebble	diverse pebble-sand	diverse pebble-sand
stream gradient	61 m/km	19 m/km	8 m/km	11 m/km

was forested and had a diverse substrate, but had poor water quality. Site 4 was located near the mouth of Padden Creek in a freshwater wetland, and was characterized by poor water quality, high turbidity, and a fine-grained substrate.

Methods

Four sites were sampled along the stream, as shown in Figure 1. The riparian vegetation was sampled on 14 April and 14 August, 1988. All tree species and common understory species in the riparian zone were identified, and the dominant tree species were determined by canopy cover. Stream sediment samples were collected on 10 August from a 929 cm^2 (1 ft^2) area to a depth of about 7.5 cm. The sediment samples were oven dried, sieved, and weighed to determine sediment size fractions (Minshall 1984). Water samples were collected approximately monthly between 14 May and 1 October, 1988 at each Padden Creek site and from Connelly Creek where it joins Padden Creek. Water temperature was measured in the field. Laboratory analyses (pH, alkalinity, conductivity, turbidity, ammonia, nitrite/nitrate, soluble reactive phosphate, and total phosphorus) were done by the Institute for Watershed Studies (Western Washington University) using standard EPA protocols (EPA 1983).

Benthic macroinvertebrate samples were collected monthly between 14 May and 1 October using a Surber sampler (1 mm mesh size). Ten replicates were collected at each site on each date. The macroinvertebrates were preserved (in the field) in 10% formalin, sorted, and identified to the lowest practical taxonomic unit. Representative taxa were preserved in 70% ethanol. Macroinvertebrate densities were calculated for each taxa as the average number of individuals per square meter (n = 10 per site and taxa). In addition to the quantitative samples, insect emergence was noted, and log debris and larger rocks were sampled qualitatively. The qualitative data were not used in the calculations of macroinvertebrate densities, but were added to the taxonomic list.

Results and Discussion

Riparian Community, Stream Substrate, and Water Quality

Site 1 is dominated by dense, second-growth, coniferous forest about 90-100 years in age. The most common tree species include western hemlock (*Tsuga heterophylla*), red alder (*alnus rubra*), western red cedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). The understory contains many hydrophytes such as devil's club (*Oplopanax horridum*) and skunk cabbage (*Lysichitum americanum*) that indicate water saturation of the soils near the creek. Other common understory species include vine maple (*Acer circinatum*), salmonberry (*Rubus spectabilis*), and sword fern (*Polysitchum munitum*). The riparian community at Site 2 is disturbed, and consists primarily of young alders and willows (*Salix* spp.) on one or both sides of the creek, as well as blackberries (*Rubus* spp.) and reed canary grass (*Phalaris arundinacea*). The forest at Site 3 in Fairhaven Park has a much more open canopy and understory than Site 1. The dominant tree species at Site 3 are bigleaf maple and red alder. Shrubs dominate the understory, especially snowberry (*Symphoricarpus albus*), ocean spray (*Holodiscus discolor*), and Indian plum (*Osmaronia cerasiformis*), indicating drier conditions than at Site 1. In the wetland area at Site 4, willows and alders form a dense canopy that overshadows much of the creek. Parts of the wetland are characterized by emergent aquatic species such as cattail (*Typha latifolia*) and bullrush (*Scirpus silvaticus*).

The gradient of a stream is one of the major factors controlling stream velocity and sediment size (Richards 1982). As the stream gradient decreases downstream, the mean sediment size usually decreases. Accordingly, the particle size in the riffles of Padden Creek shifted from a mixture of cobbles and pebbles upstream to mostly smaller pebbles downstream (Figure 2). At the same time, the weight of the fine sediment fraction (granule to sand) increased downstream. The only major exception to this was at Site 2. At this site the stream is channelized, which creates a more uniform stream velocity, particularly when viewed horizontally across the stream channel. As a result, the sediment structure at Site 2 is relatively uniform.

Because Padden Creek was at least partly shaded at all sampling sites, stream temperatures were consistently low. The highest temperature in Padden Creek (15.8°C) was measured downstream from the inflow of Connelly Creek on 24 August. Connelly Creek was not shaded at the sampling site and had noticeably higher water temperatures than Padden Creek (Table 2). Similarly, the values for pH, alkalinity and conductivity in Connelly Creek were much higher than at Sites 1 and 2 in Padden Creek. The influence of Connelly Creek can be seen at Sites 3 and 4, where the pH, alkalinity, and conductivity values are intermediate between those for Connelly Creek and the upstream sites of Padden Creek.

Ammonia concentrations were about the same at Site 3 as at Sites 1 and 2, and only slightly elevated at Site 4, even though ammonia inputs from Connelly Creek were high. Ammonia is usually transformed rapidly in streams to nitrate (Hynes 1974), suggesting that the elevated nitrite/nitrate concentrations at Sites 3 and 4 were probably caused by both ammonia and nitrite/nitrate inputs from Connelly Creek. Soluble reactive phosphorus concentrations were higher at Sites 3 and 4; however, total phosphorus concentrations were not.

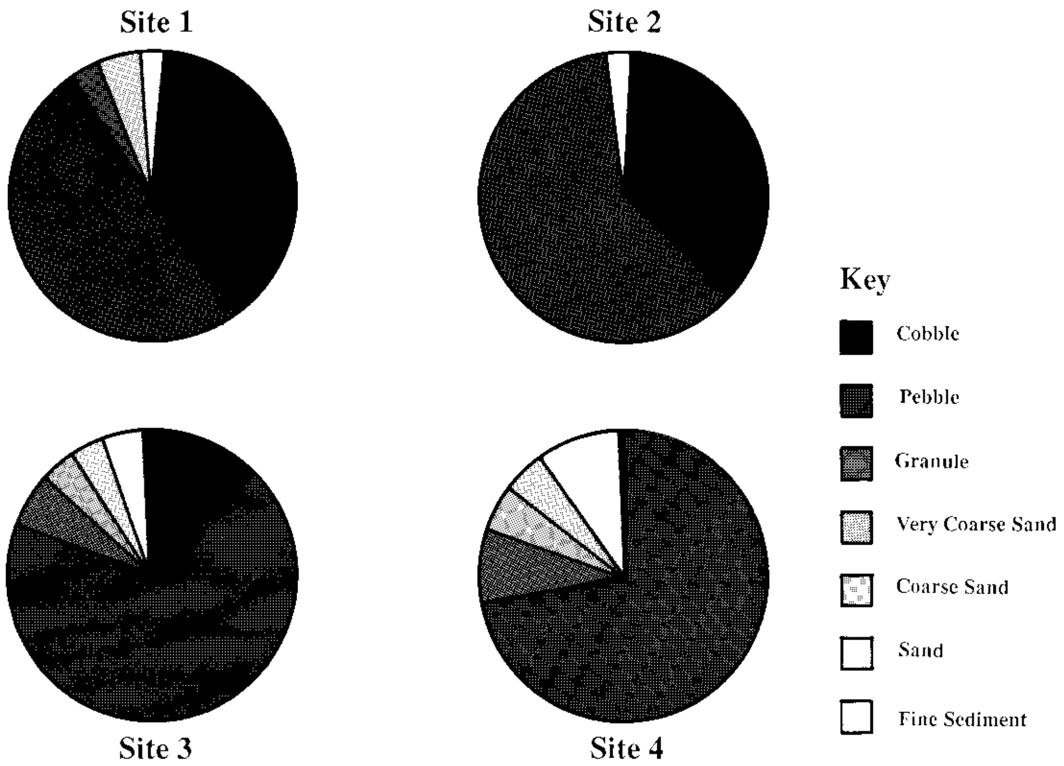

Figure 2. Padden Creek sediment size distribution (by percent of total weight). 10 August, 1988.

TABLE 2. Water quality data from Padden Creek and Connelly Creek.[1]

Parameter	Padden Creek—Data Ranges (Average)				Connelly Creek
	Site 1	Site 2	Site 3	Site 4	
Temperature (°C)	11.5-14.4	12.0-14.5	12.0-15.0	11.5-14.0	14.0-18.5
pH	7.43-7.70 (7.57)	7.47-7.59 (7.53)	7.70-7.84 (7.79)	7.76-7.91 (7.86)	7.85-8.53 (8.10)
Alkalinity (mg CaCO$_3$/L)	24.8-31.1 (28.7)	25.1-36.1 (32.2)	45.0-63.3 (55.3)	39.4-66.4 (56.1)	79.9-133.4 (99.8)
Conductivity (μS/cm)	96-109 (104)	97-113 (108)	134-175 (161)	136-184 (167)	218-353 (263)
Turbidity (NTU's)	3.1-6.3 (4.8)	2.8-7.3 (4.1)	2.7-4.8 (3.8)	3.1-4.7 (3.9)	2.8-5.4 (4.0)
Ammonia (μg N/L)	<2-33.7 (10.0)	<2.-19.7 (8.5)	<2-23.3 (6.8)	<2-28.9 (17.4)	12.1-556.5 (252.3)
Nitrite/Nitrate (μg N/L)	108.7-412.6 (280.4)	101.6-382.1 (267.3)	203.9-706.9 (393.8)	196.6-759.9 (392.0)	246.8-571.1 (417.4)
Sol. Phosphate (μg P/L)	5.0-14.4 (9.9)	6.1-13.6 (10.9)	13.2-29.5 (22.6)	14.3-28.7 (22.1)	22.5-45.7 (32.9)
T. Phosphorus (μg/L)	19.5-73.4 (28.0)	19.3-55.2 (39.8)	27.5-40.1 (34.1)	23.5-36.7 (33.6)	42.4-70.1 (52.8)

[1] The Padden Creek samples were collected from 14 May-1 October, 1988 (n = 5); Connelly Creek samples were collected from 21 June-1 October, 1988 (n = 4).

The exact sources of pollution to Connelly Creek have not been identified, but they are most likely the result of nonpoint source agricultural and residential runoff. The periodically high ammonia concentrations suggest agricultural runoff or faulty septic tanks. Along Connelly Creek, there are septic tanks as well as an intensively used agricultural area where manure is spread on the fields.

Benthic Macroinvertebrate Populations

We collected a total of 71 taxa from Padden Creek (the Padden Creek taxa list is available upon request from the authors), of which 21 taxa were defined as "common" (representing at least 1% of the total density at any site). Because downstream drift can affect interpretations of taxa distribution data, especially for rare taxa (Waters 1972), most of our discussion is restricted to the common taxa. Uncommon taxa that are especially sensitive to changes in the environment or those with special habitat demands are also discussed.

Many mayflies, stoneflies, and caddisflies preferred Sites 1 and 2. These three groups together made up 62-67 percent of the macroinvertebrate densities at the upstream sites, but only 40 percent at Site 3 and 26 percent at Site 4. Mayflies, stoneflies, and caddisflies are generally intolerant of pollution, especially the heptageniid mayflies and most stoneflies. Many other stream studies have reported similar patterns, i.e., decreases in mayflies, stoneflies, and caddisflies in polluted sections (e.g. Hynes 1970a, 1970b; Hawkes 1979; Wiederholm 1984).

A few mayfly genera, such as *Baetis* and *Paraleptophlebia*, are widespread and include species that can tolerate moderate pollution (Merritt and Cummins 1984). These two genera were relatively abundant at all four sites in Padden Creek. Some non-insect groups, on the other hand, actually prefer organically-enriched streams. In Padden Creek, these included amphipods, annelids, and molluscs; all of which were more common in the downstream sites. This distribution was especially true for the molluscs, which were not found at Site 1.

Many of the uncommon taxa also preferred Site 1. These included the stoneflies *Pteronarcys, Perlomyia, Despaxia augusta, Calineuria californica*, and *Hesperoperla pacifica;* the mayflies *Cinygma* and *Rhithrogena;* the caddisflies *Allocosmoecus partitus, Apatania sorex, Ecclisomyia, Neophylax*, and *Lepidostoma;* and the aquatic beetles *Hydrochus squamifer* and *Lara avara.*

Many predatory taxa also preferred Site 1, including the large, predatory stoneflies, *Hesperoperla pacifica* and *Calineuria californica.* These stoneflies consume large percentages of the standing crop of benthic invertebrates (Siegfried and Knight 1976). At Site 2, where the large stoneflies were absent, the medium-sized stonefly *Skwala* appeared to be the major invertebrate predator. At Sites 3 and 4, the largest insect predators were alderflies (*Sialis*). The filter-feeding *Parapsyche*, common at Site 3, may also be predatory. The predacious aquatic beetles *Agabinus sculpturellus, Agabus*, and *Hydrovatus* were among the few invertebrates with an apparent preference for Site 4. Species belonging to this family are very adaptable, and some of them occur in slow-flowing streams and lentic habitats (Usinger 1971). They may prefer Site 4 because the stream velocity is relatively slow and pool areas are relatively large.

Distribution of Hydropsychidae

The caddisfly family Hydropsychidae includes species that can tolerate moderate pollution (Hawkes 1979, Wiederholm 1984). In Padden Creek, this family showed a distinct longitudinal distribution pattern: *Hydropsyche* was more common at the upper sites and *Parapsyche* was more common downstream.

The longitudinal distribution of Hydropsychidae has been the subject of several studies in the eastern United States (Gordon and Wallace 1975, Wiggins and Mackay 1978). Most studies show that *Parapsyche* are found mostly in the upper headwater streams, while species of *Hydropsyche*, although widely distributed, tend to prefer downstream sections of rivers. These distributions are usually explained by differences in morphology: *Parapsyche* is a big caddisfly, having a coarse net that enables it to catch coarse particulate organic matter (CPOM), the major food source in headwater streams. Conversely, *Hydropsyche* larvae are small and build nets with a smaller mesh size than *Parapsyche* in order to feed on fine particulate organic matter (FPOM).

Our data could reflect the influence of Lake Padden, which has an epilimnetic outfall and probably adds FPOM to the upper section of the creek, thus favoring *Hydropsyche.* However, it is also possible that the *Hydropsyche* species inhabiting Padden

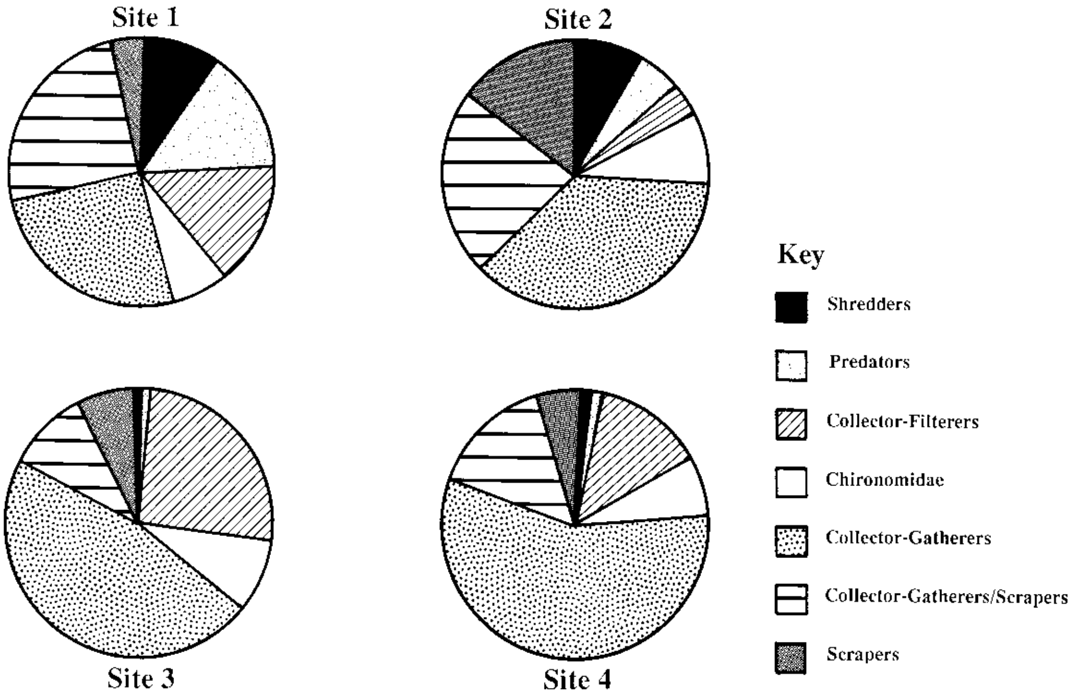

Figure 3. Padden Creek macroinvertebrate functional group distributions (percent of total density), 14 May-1 October, 1988.

Creek are less tolerant to organic enrichment than *Parapsyche* so that they are confined to the relatively unpolluted upstream portions of the creek.

Macroinvertebrate Functional Groups

Figure 3 summarizes the functional group percentages for the common taxa in Padden Creek (based on Merritt and Cummins 1984). Chironomid larvae were classified separately because species of Chironomidae belong to several different functional groups. Some mayflies are able to feed both as collector-gatherers and as scrapers; these taxa were classified as collector-gatherers/scrapers.

According to the River Continuum Concept (Vannote *et al.* 1980), Padden Creek is a headwater stream, characterized by a closed forest canopy, with its primary energy source coming from allochthonous organic matter in form of CPOM. Shredders, who feed on CPOM, should be abundant, while scrapers and collectors (who feed on periphyton and FPOM), should be less abundant. Although shredder densities were relatively low in Padden Creek compared to headwater streams sampled in western Oregon (Hawkins and Sedell 1981), shredders were proportionately more abundant at Site 1 than at the other Padden Creek sites. Padden Creek also is undoubtedly influenced by inputs of FPOM from Lake Padden, which probably caused the relatively high collector-gatherer and collector-filterer densities at all sites. The collectors were mainly represented by the filter-feeding caddisfly *Hydropsyche*, which was common at Site 1, and oligochaetes (collector-gatherers), which were common at all sites. Studies in England (Armitage 1978) and in Colorado (Ward and Short 1978) in creeks downstream from reservoirs also showed elevated populations of oligochaetes.

At Site 2, collector-gatherers and scrapers were the dominant functional groups. Predator and collector-filterer densities were much lower than at Site 1. Shredder densities and the number of shredder taxa were also slightly lower at Site 2 than at Site 1. The changes observed between Site 1 and Site 2 probably were caused by channelization, which reduced substrate heterogeneity (see Figure 2), and by deforestation, which increased the amount of light reaching the stream bed and changed the character of the riparian vegetation.

Minshall (1984) and Williams (1980) report that species diversity generally increases with substrate heterogeneity. At Site 2, where the substrate was fairly homogeneous, there was a general reduction in species diversity, especially for predators and collector-filterers, from that found at Site 1. In an experiment with artificial substrates in a third-order stream in Ontario (Williams 1980), all predators showed a significant preference for areas having highly heterogeneous substrates.

Compared to Sites 1 and 2, Sites 3 and 4 had very unbalanced distributions of functional groups. Predator and shredder populations were greatly reduced at Sites 3 and 4, while collector-filterers were increased at Site 3 and collector-gatherers were increased at Site 4. Scraper populations had similar densities to those at Site 1, but consisted of different taxa. These differences probably were correlated with the decrease in substrate size and slower stream velocities at Site 4, which favors collector-gatherers more than filter-feeders. In addition, the changes in water quality may have contributed to shifts toward relatively tolerant taxa at Sites 3 and 4. Similar patterns are described by Wiederholm (1984), who reported that the expected longitudinal (downstream) succession of macroinvertebrate functional groups is altered in nutrient-enriched streams because of the change in algal flora and increase in detritus input caused by eutrophication.

Conclusions

Many Padden Creek taxa, especially mayflies, stoneflies, and caddisflies, were more abundant at Site 1, which was densely forested, had a heterogeneous substrate, and was relatively unpolluted. The downstream sites, which were affected by channelization, deforestation, pollution, and natural decreases in sediment size and stream velocity, were populated mostly by tolerant taxa and had a greater proportion of non-insect taxa than the upstream sites.

All macroinvertebrate functional groups were well represented at Site 1. The relatively high density of shredders at that site suggests that CPOM was a major food source. In addition, the addition of FPOM from Lake Padden resulted in large numbers of collector-gatherers and collector-filterers at all sites. Channelization at Site 2 caused a decrease in the number and density of predators and collector-filterers. Because the riparian forest was partly cleared at this site, the number of shredder taxa also was decreased. Scraper densities, on the other hand, increased because as more light reached the stream, algal productivity probably increased. Relatively tolerant insect and non-insect taxa, most of which were collector-filterers and collector-gatherers, dominated Sites 3 and 4, where pollution from Connelly Creek and reduced sediment size and stream velocity may have been major factors influencing the macroinvertebrate community structure. Shredders and predators were very uncommon at both downstream sites.

Our study showed that changes in water quality, substrate characteristics and land use are associated with longitudinal zonation of the benthic invertebrate community in Padden Creek. Because of interactions between these factors and the biota, the importance of each single factor cannot easily be quantified. However, there was a general tendency for channelization and deforestation to mimic the habitat found in mid-reach rivers, resulting, at Site 2, in a greater density of scrapers than would normally be expected in a headwater stream. Similarly, at Sites 3 and 4, the combined effects of deforestation, nutrient inputs, and natural decreases in the stream velocity and substrate size created a habitat similar to that found in lower reaches of rivers, resulting in a macroinvertebrate community dominated by collector-gatherers and collector-filterers.

This study was relatively qualitative in nature, being limited by time, funding, and lack of a preexisting data base on the stream. Its primary purpose was to collect baseline data on the macroinvertebrate taxa in Padden Creek, and to look for general longitudinal trends. These objectives were met, despite the design constraints, suggesting that stream ecosystem studies are not restricted to multiyear, externally-funded projects. Land-use changes along streams are commonplace, and increased development pressure will likely result in additional changes along stream courses in the Pacific Northwest. Further research should emphasize appropriate biological and chemical sampling that may lead to a comprehensive monitoring of impacts on streams. Our study suggests that very meaningful information can be gained from short-term sampling along stream gradients to assess impacts of land use patterns.

Acknowledgments

We would like to thank Dr. Gerald Kraft, Biology Department, Western Washington University, for assistance with the taxonomic identifications, and the Institute for Watershed Studies for laboratory analyses for this study.

Literature Cited

Armitage, P. D. 1978. Downstream changes in the composition, number and biomass of bottom fauna in the Tees below Cow Green Reservoir and in an unregulated tributary Maize Beck, in the first five years after impoundment. Hydrobiol. 58:145-156.

EPA. 1983. Methods for Chemical Analysis of Water and Wastes. EPA-600/4-79-020. U.S. Environmental Protection Agency, Cincinnati, Ohio.

Franklin, J. and C. Dyrness. 1988. Natural Vegetation of Oregon and Washington. 2nd ed. Oregon State University Press, Corvallis.

Gordon, A. E. and J. B. Wallace. 1975. Distribution of the family Hydropsychidae in the Savannah River basin of North Carolina, South Carolina and Georgia. Hydrobiol. 46:405-423.

Hawkes, H. A. 1979. Invertebrates as indicators of river quality. *In* A. James and L. Evison (eds.) Biological Indicators of Water Quality. John Wiley and Sons. New York. Pp. 2-1 to 2-45.

Hawkins, C. P. and J. R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology 62:387-397.

Hynes, H. B. N. 1970a. The Ecology of Running Water. University of Toronto Press. Toronto.

Hynes, H. B. N. 1970b. The ecology of stream insects. Ann. Rev. Entomol. 15:25-39.

Hynes, H. B. N. 1974. The Biology of Polluted Waters. University of Toronto Press. Toronto.

Kondratieff, P. F., R. A. Matthews, and A. L. Buikema. 1984. A stressed stream ecosystem: macroinvertebrate community integrity and microbial trophic response. Hydrobiol. 111:81-91.

Merritt, R. W. and K. W. Cummins. 1984. An Introduction to the Aquatic Insects of North America. 2nd ed. Kendall/Hunt Publ. Co., Dubuque, Iowa.

Received 25 January 1990
Accepted for publication 13 August 1990

Minshall, G. W. 1984. Aquatic insect-substratum relationships. *In* V. H. Resh and D. M. Rosenberg (eds.) The Ecology of Aquatic Insects. Praeger Publ., New York. Pp. 358-400.

Molles, M. C. 1982. Trichopteran communities of streams associated with aspen and conifer forest: long-term structural change. Ecology 63:1-6.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37:1076-1085.

Richards, K. 1982. Rivers. Form and Process in Alluvial Channels. Methuin & Co. Ltd., New York.

Siegfried, C. A. and A. W. Knight. 1976. Trophic relations of *Calineuria californica* in a Sierra foothill stream. Environ. Entomol. 5:575-581.

Usinger, P. L. 1971. Aquatic Insects of California. University of California Press. Berkeley.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Ward, J. W. and R. A. Short. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, USA. Verh. Int. Verein Limnol. 20:1382-1387.

Waters, T. F. 1972. The drift of stream insects. Ann. Rev. Entomol. 17:253-272.

Wiederholm, T. 1984. Responses of aquatic insects to environmental pollution. *In* V. H. Resh and D. M. Rosenberg (eds.) The Ecology of Aquatic Insects. Praeger Publ., New York. Pp. 508-557.

Wiggins, G. B. and R. J. Mackay. 1978. Some relationships between systematics and trophic ecology in nearctic aquatic insects, with special reference to Trichoptera. Ecology 59:1211-1220.

Williams, D. D. 1980. Some relationships between stream benthos and substrate heterogeneity. Limnol. Oceanogr. 25:166-172.