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ENVIRONMENTAL RESEARCH BRIEF

Habitat Structure and Fish Communities of Warmwater Streams

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Introduction

The basic goal of clean water legislation passed in the last two decades is restoration and maintenance of the chemical, physical, and biological integrity of the nation's waters. The mechanisms required to reach this goal are not entirely obvious. Early efforts concentrated on physical and/or chemical pollution; however, a broader perspective is required.[1,2] Based on the authors' work over the past decade, five major sets of variables that impact the structure of stream communities (Figure 1) have been identified.

Most research on the role of physical habitat characteristics in the regulation of fish community structure has concentrated on cold water systems, with emphasis on salmonids. The significance of physical habitat in warmwater streams has been largely ignored by water resource planners. Even studies that describe physical habitat of streams rarely examine the cause and effect interactions of habitat structure, availability of food resources, and other factors that shape fish communities.

With this background in mind, a research program was initiated to evaluate the role of physical habitat in regulating the structure of fish communities in warmwater streams in east central Illinois. The study combined an empirical approach involving observations of fish in relatively natural conditions with studies of stream areas subjected to extensive modifications by human society. Finally, several experimental field and laboratory studies were designed to clarify aspects of fish community dynamics. This research brief is a summary of several journal articles published and in review. Complete citations for those articles can be found at the end of this brief.

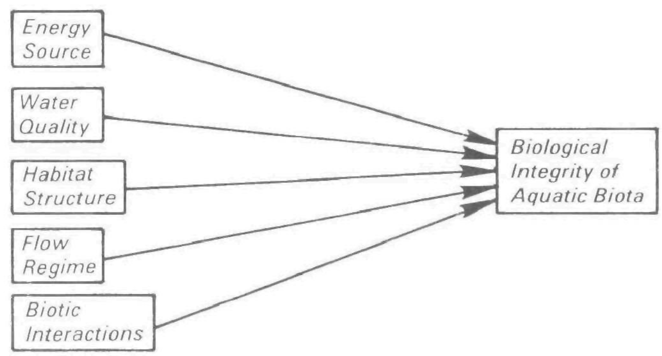

Figure 1. *Primary variables that affect the structural and functional integrity of an aquatic biota.*

Fish Communities Along Physical Habitat Gradients—Natural Gradients

Two habitat gradients (upstream to downstream and riffle to pool) were investigated in Jordan Creek in Vermilion

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County, Illinois.[3] Several major patterns were identified—from the diversity of the fish community to the apparent dominant processes regulating community organization along each of these gradients (Table 1).

The major attributes of physical habitat measured in this study were habitat diversity and habitat volume. Habitat diversity is a complex integration of depth, current velocity, and substrate attributes. Habitat volume is measured as stream area times mean depth for a study region. Both habitat diversity and habitat volume increased from upstream to downstream and riffle to pool habitats. Temporal variation in habitat diversity was greater in upstream areas and habitat volume tended to vary more over time in upstream and riffle areas. Seasonal and year-to-year variation in rainfall also caused variation in habitats, especially volume.

Benthic insect density in Jordan Creek was high from autumn (Oct-Nov) through spring (May-June). Following emergence of adults in late spring, invertebrate densities were low in summer in areas with riparian vegetation. Insect availability, as indicated by drift samples, increased along a gradient from silt-sand to gravel-rock substrates. Potential food availability for top carnivore fish peaked in late summer and early fall with increased numbers and biomass of young-of-the-year fish.

Although habitat diversity was significantly ($p < .05$) correlated with fish species diversity, the relationship between the two variables varied as a result of seasonal migration by fishes. These seasonal migrations were tied to changing flow conditions, food availability, and the search for suitable spawning and nursery areas. As a result, the utility of the habitat/ fish diversity relationship as a predictive model varied seasonally. In addition, the precision of the relationship was lowest in more variable upstream and riffle habitats.

Younger fish (age classes 0-II) were found primarily in shallow, temporally variable areas upstream and in riffles. Relative growth rates were highest during summer but they did not increase (relative to spring) as much as expected from seasonal increases in water temperature. Centrarchids had substantially higher growth rates than cyprinids during early life stages. Net production for age 0-II fish was highest in upstream and riffle areas because those areas supported high densities of young, generalized insectivores. Net production of insectivore-piscivores was highest in downstream and pool habitats. Stream reaches with large, stable pools and raceways produced fewer fish due to shifts in age structure toward fewer, large individuals (age III+) with slower relative growth rates. Temporal variation in reproductive success and survival of younger age groups (0-I) was associated with variation in peak flows. Finally,

Table 1. Summary of Relative Characteristics of Habitat Structure and Fish Organization Along Two Physical Gradients in a Headwater Stream

Characteristics	Relative Position on Gradient: Downstream or Pool Environment	Relative Position on Gradient: Upstream or Riffle Environment
1. Habitat Structure	Deep, temporally stable	Shallow, temporally variable
2. Fish Community Structure		
a. Species richness	High	Low
b. Age structure	Old fish	Young fish
c. Size composition	Large fish	Small fish
d. Dominant trophic group(s)	Insectivore-piscivores Benthic insectivores	Generalized insectivores
3. Fish Community Function		
a. Net production	Low	High
b. Absolute and relative growth rates of age 0-I of the dominant trophic group(s)	High	Low
4. Seasonal and annual stability of community attributes; i.e., species richness, trophic structure, age structure, and production	High	Low
5. Hypothesized dominant processes regulating community organization	Competitive exclusion and predation	Recolonization dynamics, effects of gradual changes in the physical environment on competitive interactions, and temporal variation in reproductive success

variation in peak flow was a major factor determining spatial and temporal variation in production.

Therefore, spatial shifts in physical conditions from shallow, temporally variable areas (upstream and riffles) to deeper, more stable areas (downstream and pools) result in consistent spatial changes in community structure (Table 1). The ultimate mechanisms responsible for these changes were not precisely documented, although they clearly vary from headwater to downstream or riffle to pool. We hypothesize that in shallow, unstable habitats, recolonization dynamics, the effect of gradual changes in physical conditions on competitive interactions, and temporal variation in reproductive success are more important than competitive exclusion and predation as determinants of community organization (Table 1).

Fish Communities Along Physical Habitat Gradients—Human Disturbance

We assessed the impact of channel straightening and removal of riparian vegetation on trophic structure, reproductive success, and growth rates of fishes in relatively natural (Jordan Creek - JC) and modified (Big Ditch - BD) headwater streams.[4] Shallow habitats and organic substrates (diatoms and/or filamentous algae) were more common in BD (not shaded by riparian vegetation) than JC (shaded) during low flow periods in summer. Insect densities in JC were highest in late spring, declining to low levels by late summer. Insect densities in BD were high throughout summer.

Fish species in JC were predominantly benthic insectivores and insectivore-piscivores, and trophic structure, age structure, and biomass of the fish community were stable between years and seasons. Recruits made up a small and stable portion of community biomass and were primarily insectivore-piscivores and generalized insectivores. Younger age classes occupied shallow riffle habitats.

In contrast, trophic structure and recruits in BD were predominantly generalized insectivores, omnivores, and herbivore-detritivores. Omnivores and herbivore-detritivores were primarily mid-river species (quillback and gizzard shad). Considerable seasonal and annual variation in trophic structure, total biomass, and age structure occurred in BD associated with annual fluctuations in flow regime, abundance of organic substrates, and reproductive success of mid-river species. Younger age classes had higher summer growth rates in BD than JC.

The effects of alteration of headwater streams are evident when placed in the context of the stream continuum concept which suggests that interactions between physical environment and the organic energy base result in a relatively predictable pattern of lotic community structure and function from headwaters to downstream areas. The critical effect of stream alterations in the context of this concept is that alterations create a shallow, temporally variable physical environment typical of headwater areas where most recruitment occurs. Yet, at the same time, the alterations shift the energy base toward autotrophic processes which are more typical of mid-river habitats. As a result, mid-river omnivores and herbivore-detritivores dominate recruitment in modified headwaters. Reduced availability of benthic invertebrates and altered habitat conditions result in declining abundance of insectivores and carnivores due to lowered reproductive success. The authors conclude that land use and channelization activities in headwater streams have played a major role in the shift in recent decades of many large river communities in the midwestern United States from dominance by insectivore and insectivore-piscivore fishes to omnivores and herbivore-detritivores.[5]

Physical Habitat and Fish Assemblages in Divided Streams

Two 35-m sections of Jordan Creek were divided in half longitudinally with 6mm mesh hardware cloth supported by steel posts.[6] On one side of each section, all cover features (logs, limbs) were removed from in or near the water. On the other side, a continuous series of similar objects was secured along the stream. In July and September, samples of the biomass of fish were 4.8 to 9.4 times as high in the areas with structurally complex habitats (Table 2). Further, larger fish, and especially top predators, tended to select the structured habitat. In this case we know that water quality was the same in the structured and unstructured sides of the stream, yet the numbers of fish are markedly different. These improved habitat conditions seem to provide two things: habitat for small fish including a diversity of substrates for food organisms and hiding places

Table 2. Fish and Invertebrate Densities and Fish Biomass in Adjacent Sides of a Stream Split with 6mm Mesh Hardware Cloth

	July 1979		September 1979	
	No Cover	Cover	No Cover	Cover
Fish				
Number of individuals	34	46	4	73
Number >120mm TL	2	28	2	17
Total biomass (gms)	170	1606	284	1366
Benthos				
Number/0.1 m²	92	383	39	219

(cover) from which large fish can prey on smaller species. This emphasizes the importance of habitat structure as a determinant of biotic conditions in a stream.

Woody Debris in Warmwater Streams

The importance of woody debris to the structure and function of a warmwater stream ecosystem was examined by removing woody debris from a series of stream reaches. Experimental reaches were compared with unaltered reaches over a 2-year period.[7]

At initiation of the experiments (June 1980), altered and unaltered sites were similar with respect to depth profiles, current regimes, and standing stock of organic litter (Figure 2). Water depth declined in all sites through the summer and autumn due to lack of precipitation, but shifts toward shallow depths were especially pronounced in altered sites due to the filling of pools by unstable substrates (Figure 2). In addition, the abundance of organic litter on the stream bottom declined markedly in altered sites but remained relatively constant in unaltered sites.[6] Litter abundance declined in altered sites due to burial by shifting substrate and the absence of retention structures. In June 1981, depth profiles, current regimes, and organic litter abundances for unaltered sites were similar to those in June 1980. In altered sites, however, deep areas were not re-established, currents were faster, and organic debris was only one-third as abundant as the previous year (Figure 2). Seasonal shifts in depth, current and litter abundance in 1981 were similar to those observed in 1980, though less pronounced due to the uncommonly stable flows that occurred through the summer of 1981. In reaches of Jordan Creek with stable (rocky) substrates, removal of woody debris had less impact on stream structure and function than in reaches with unstable (silt-sand) substrates.

Fish were also monitored throughout the experimental period to evaluate effects of habitat changes on the fish community.[7] In June 1980, mean fish biomass was similar ($p > .05$) between groups of altered and unaltered sites (Figure 3) but by October 1981 mean biomass in unaltered sites (1833gm/35m) was significantly ($p < .05$) greater than that found in altered sites. Declines in fish abundance

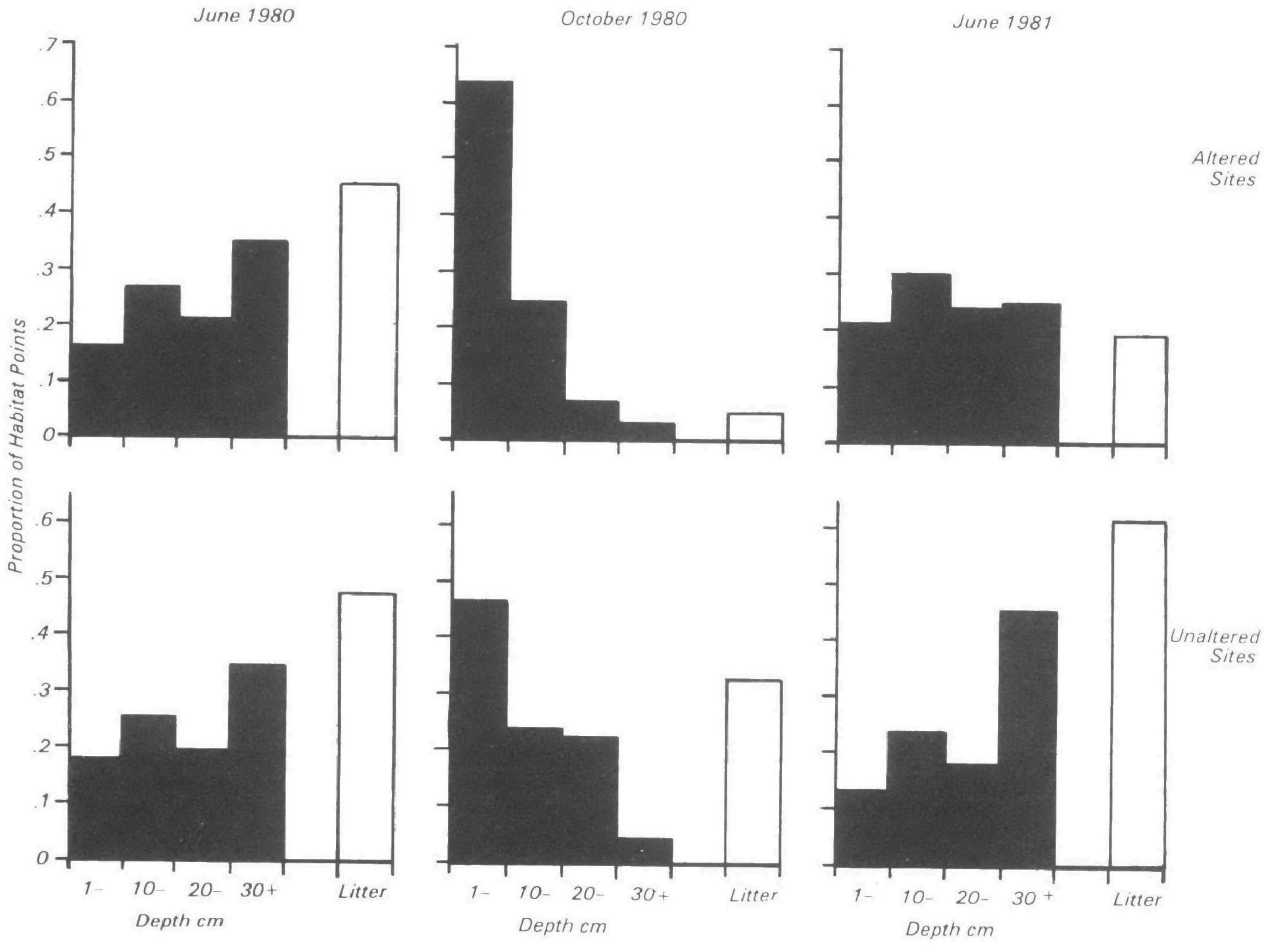

Figure 2. Depth frequency distribution and litter abundance in unaltered and altered (woody debris removed) reaches of Jordan Creek. Debris was removed in July 1980.

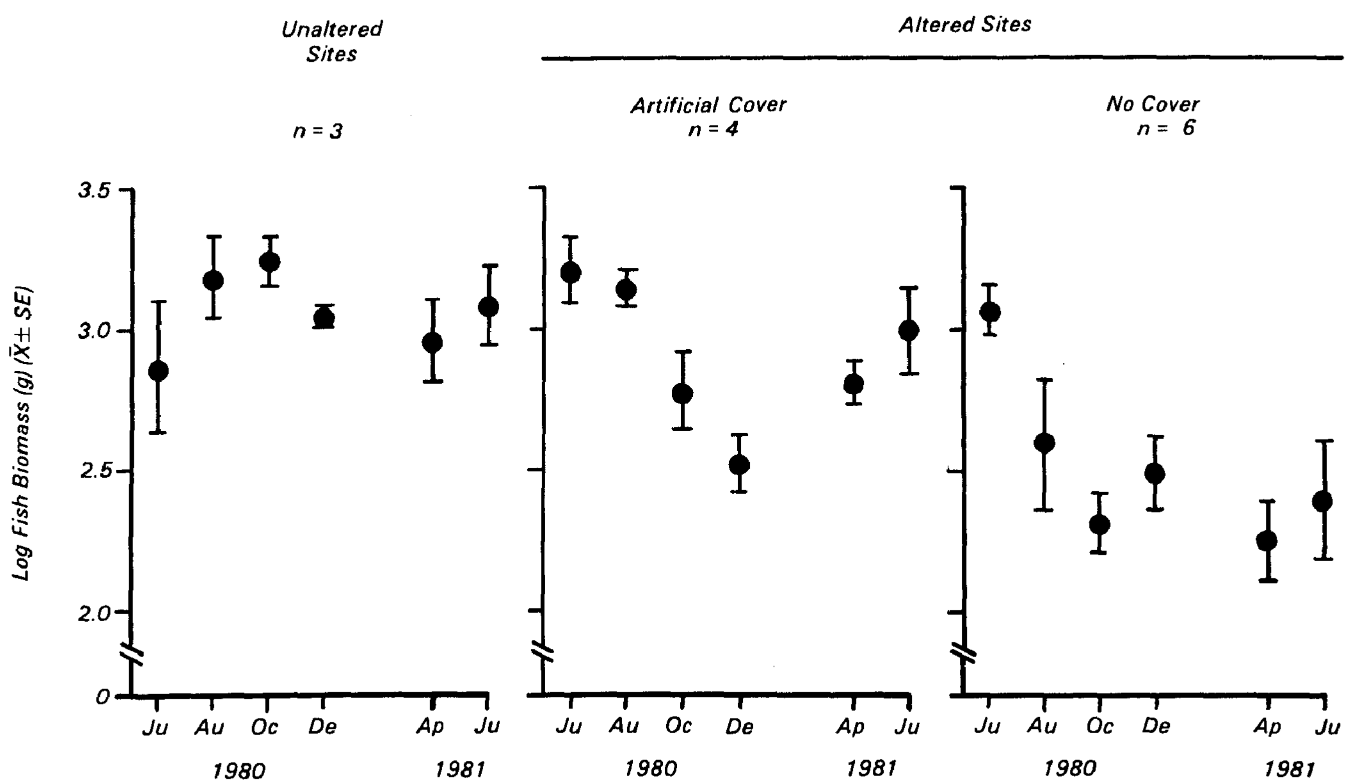

Figure 3. *Biomass (estimates from a multiple regression model) of fish captured in experimental sites of upper Jordan Creek during a year of cover manipulation.*

through the summer were less striking in altered sites where artificial cover structures were provided than in altered sites with no cover. Furthermore, fish biomass in altered sites (coefficient of variation = 81%, N = 10) was more variable than that observed in unaltered sites (CV = 41%, N = 3), suggesting that use of altered sites by fish was more transitory than their use of unaltered sites. Differences in fish biomass between altered and unaltered sites were less pronounced in 1981 than in 1980, presumably because stable flows resulted in good habitat quality throughout the drainage.

Losses of deep areas in altered sites had greatest impact on large fish (>35 g), their abundance being lower in altered than unaltered sites. Distributions of small fish (<40 mm total length) among sites were variable. Small cyprinids tended to be most numerous in altered sites, while small centrachids tended to be most numerous in unaltered sites.

These experiments illustrate the interactions of physical and biological processes that occur in stream ecosystems. Woody debris has several important functions in Jordan Creek. It affects channel hydraulics and so maintains depth, current, and substrate diversity. It acts as a stable substrate for retaining organic material and supporting macroinvertebrates. These functions, in addition to providing cover, are essential to maintaining habitat quality for fish. In streams with unstable substrates (silt, sand), woody debris may be the most important attribute of physical habitat in determining ecosystem structure and function.

Effects of Fish Consumption On Food Availability

Paired screen exclosures were erected to assess the impact of fish consumption on benthic invertebrate abundance and size distribution.[8] One exclosure (closed) excluded fish from a section (0.54 m^2) of stream bottom, while the other (open) permitted fish to enter and exit freely. Exclosures were set up for 4-week periods in upstream (silt-sand substrates) and downstream (gravel-pebble substrates) reaches of Jordan Creek. Closed exclosures from upstream sites supported greater densities of invertebrates than open enclosures (Table 3). These density differences were largely due to the greater abundance of chironomid larvae and copepods, both of which are important food items for Jordan Creek fish. In addition, large invertebrates (at least 4.7mm long), which are generally preferred by fish, were more abundant in closed exclosures than open ones. Data from downstream exclosures indicated that fish consumption had no effect on invertebrate abundance or size frequency. These results suggest that the potential for competition for food among stream fishes is greatest in upstream areas. If so, stream modifications such as removal of riparian vegetation or woody debris, which may have dramatic effects on invertebrate availability, can be expected to have greatest impact on upstream fish populations. Competition for food among fish in upstream areas may be a common phenomenon, particularly during summer. Thus, disturbances that further destabilize food resources may ultimately contribute to instability in fish community structure.

Table 3. Invertebrate Densities (No./0.0116m²) from Paired Exclosures in Jordan Creek. Open Exclosures were Accessible to Fish, While Closed Ones were Not

Pair	Month	Open	Closed
1	June	72	108
2	June	11	93
3	June	11	34
4	September	77	84
5	September	51	191
6	September	140	210

Effects of Cover and Current on Predation Rate

A series of experiments were conducted in a laboratory stream to examine the influence of habitat variables on predator-prey interactions among fishes.[9] Several hypotheses were tested: 1) fish seek cover to avoid predators; 2) presence of cover decreases predation rates; 3) fish seek cover to avoid current. Experiments included various combinations (presence or absence) of prey, predators, cover, and current.

Small fish (4 species) were attracted to cover (plastic plants) in the absence of current, but not in the presence of current (4-15 cm/s). In addition, small fish were more strongly attracted to cover when predators (large fish) were absent than when predators were present. The presence of predators also inhibited activity (swimming) of small fish. Small centrarchids exhibited stronger associations with cover than did small cyprinids.

Presence of cover did not affect average predation rates suffered by small fish in these experiments, though rates were more variable in the presence of cover. However, centrachids suffered higher mortalities in experiments without current than in those with current.

In conclusion, these experiments indicate that small fish may effectively alter their habitat use so as to avoid predators. Furthermore, predation on fish by other fish may be more important to community organization in non-turbulent (i.e. lentic) environments than in turbulent (i.e. lotic) ones.

Conclusion

Overall, the study results clearly show that factors limiting biotic integrity in warmwater stream ecosystems are not restricted to water quality. Indeed, physical habitat is a major determinant of biotic integrity. The role of physical habitat conditions includes direct effects on fish abundances as well as indirect effects resulting from complex interactions with channel hydraulics, availability of food (both primary and secondary production), and susceptibility to predators. The interactions of these and other variables are exceedingly complex and require that water resource planners consider factors in addition to water quality (physical and chemical attributes) in efforts to restore and maintain biotic integrity.

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