

The Mechanisms of Species Interactions
and Community Organization in Fish

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Werner, Earl E. 1984. pp. 360-382 in Strong, Donald R., Daniel Simberloff, Lawrence G. Abele, and Anne B. Thistle (Editors). Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, New Jersey.

Factors determining Community Structure

I. Introduction

- A. No consensus on methodology appropriate to the study of ecological communities
- B. Resource partitioning patterns among coexisting species have been used to indicate the role of competition in organizing ecological communities
- C. What is needed is a better understanding of the mechanisms of species interactions to develop a better theory for predicting patterns

II. Approach of Werner (1984) in studying fish communities to determine Community Structure

- A. Show the occurrence of competition and its effect on sunfish
- B. Perform laboratory experiments designed to explore the mechanisms of the competitive effects
- C. Examine interactions between size-structured populations
- D. Predict behavior when foraging profitability or growth and predation risk are conflicting constraints

III. Species Interactions

- A. Niche Segregation (Figure 21.1 & 21.2)
 1. Depth of water
 2. Distance from shore
 3. Stratification in the water column
 4. Food size
 5. Feeding times
- B. Habitat Types Available
 1. Vegetation
 - a. green sunfish
 2. Open Waters (plankton)
 - a. bluegill
 3. Benthic (sediment feeder)
 - a. pumpkinseed
- C. Foraging Efficiency-Shifting Patterns (Figure 21.4)
 1. Green sunfish - most effective of three in vegetation
 2. Pumpkinseed - First to shift - most effective of the remaining two in feeding on sediment
 3. Bluegill - compared with the pumpkinseed, as effective at feeding in the vegetation but much less so at feeding on the sediments

IV. Body Size Plan and Foraging Efficiency

A. Gross morphology (Figure 21.5 - page 1)

1. Mouth

2. Body Shape

B. Foraging Efficiency (Figure 21.6)

1. Feeding on large prey items

2. Feeding on small prey items

3. Pursuit time (Figure 21.7)

V. Population Structure and Ontogenetic Niche Shifts

A. Bluegill vs. largemouth bass

B. Size frequency distribution of prey vs. body size

1. Net energy intake (Figure 21.11)

2. Net energy intake from food taken in different habitats (Figure 21.12)

VI. Conclusions from Werner (1984)

A. Competition

B. Predation

C. Problems with current theories

Karr, J.R. 1981. Assessment of biotic integrity using fish communities.
Fisheries 6(6): 21-27.

BACKGROUND

- I. Other methods of monitoring the quality of water resource systems.
 - A. Acute toxicity tests and chemical monitoring
 1. Neglects naturally occurring geographic variation of contaminants
 2. Unknown synergistic or sublethal effects of various contaminants
 3. Miss short-term events
 4. Miss man-induced perturbations
 5. Can't measure all factors of biotic integrity
 - B. Diversity indices
 1. Dependent on sample size
 2. Neglects individual tolerance of species
 3. Doesn't consider community structure
 - C. Biotic indices (diatoms, macroinvertebrates)
 1. Difficult identifying, sorting
 2. Difficult for general public

WHY USE FISH COMMUNITIES

- I. Advantages of fish
 - A. Life history information
 - B. Variety of trophic levels; top of aquatic food web
 - C. Easy identification
 - D. Public understanding
 - E. Evaluates acute and chronic effects
- II. Disadvantages of fish
 - A. Fish mobility
 - B. Variable selectivity and efficiency of gear
 - C. Labor intensive sampling

INDEX OF BIOTIC INTEGRITY

I. Classification criteria

A. Species composition and richness

1. Total number of fish species
2. Number of individuals in a sample
3. Darter species
4. Sunfish species
5. Sucker species
6. Intolerant species
7. Proportion as green sunfish

B. Ecological factors

1. Proportion as omnivores
2. Proportion as insectivorous cyprinids
3. Proportion as top carnivores
4. Proportion as hybrids
5. Proportion with disease

II. Classification process

A. Sampling

1. Fish sample is a balanced representation at the sample site
2. Sample site is representative of the larger geographic area of interest
3. Data analysis by a trained biologist familiar with local fish fauna

B. Assignment of value to each metric

1. (-)=1; (0)=3; (+)=5

C. Class assignment

1. Table

SIGNIFICANCE OF IBI

- I. Includes both aspects of diversity (richness, evenness) on an individual bases.
- II. Combines numerical and functional components of community structure
- III. Allows regional adaptation of index for stream management

DISCUSSION

- I. How would the IBI need to be adopted to provide accurate assessment of Colorado's warm and cold water streams?
- II. Would the IBI be sensitive to non-organic pollution?
- III. What are other possible metrics?
- IV. Could macroinvertebrates be used in the IBI?
- V. For Hal Copeland: What good are aquatic invertebrates?

Prouwer, J.E. and J.H. Zed

Table 5B.1. Various diversity indices computed for hypothetical situations of N individuals distributed among s species, with n_i individuals in the i th species. Data sets A, B, and C have identical values of N and s . Set D has the same s and species distribution as A, but with a larger N . Set E has the same N and evenness as set A, but a smaller s .

	hypothetical set of data				
	A	B	C	D	E
n_1	10	29	91	100	20
n_2	10	19	1	100	20
n_3	10	14	1	100	20
n_4	10	11	1	100	20
n_5	10	9	1	100	20
n_6	10	7	1	100	
n_7	10	5	1	100	
n_8	10	3	1	100	
n_9	10	2	1	100	
n_{10}	10	1	1	100	
s , number of species	10	10	10	10	5
N , number of individuals	100	100	100	1000	100
D_a , Margalef diversity	4.50	4.50	4.50	3.00	2.00
D_b , Menhinick diversity	1.00	1.00	1.00	0.32	0.50
λ , Simpson dominance	0.09	0.16	0.83	0.10	0.19
D_s , Simpson diversity	0.91	0.84	0.17	0.90	0.81
d_s , inverse of λ	11.00	6.23	1.21	10.09	5.21
H , Brillouin diversity	0.92	0.79	0.18	0.99	0.66
H' , Shannon diversity	1.00	0.86	0.22	1.00	0.70
D_{max} , maximum D_s	0.91	0.91	0.91	0.90	0.81
E_s , evenness, using D_s	1.00	0.92	0.19	1.00	1.00
d_{max} , maximum d_s	11.00	11.00	11.00	10.09	5.21
e_s , evenness, using d_s	1.00	0.57	0.11	1.00	1.00
H_{max} , maximum H	0.92	0.92	0.92	0.99	0.66
J , evenness, using H	1.00	0.86	0.20	1.00	1.00
$1 - J$, dominance, using H	0.0	0.14	0.80	0.0	0.0
H_{max}' , maximum H'	1.00	1.00	1.00	1.00	0.70
J' , evenness, using H'	1.00	0.86	0.22	1.00	1.00
$1 - J'$, dominance, using H'	0.0	0.14	0.78	0.0	0.0

Table 1. Biotic integrity classes used in assessment of fish communities along with general descriptions of their attributes.

Class	Index	Attributes
Excellent	57-60	Comparable to the best situations without influence of man; all regionally expected species for the habitat and stream size, including the most intolerant forms, are present with full array of age and sex classes; balanced trophic structure.
Good	48-52	Species richness somewhat below expectation, especially due to loss of most intolerant forms; some species with less than optimal abundances or size distribution; trophic structure shows some signs of stress.
Fair	39-44	Signs of additional deterioration include fewer intolerant forms, more skewed trophic structure (e.g., increasing frequency of omnivores); older age classes of top predators may be rare.
Poor	28-35	Dominated by omnivores, pollution-tolerant forms, and habitat generalists; few top carnivores; growth rates and condition factors commonly depressed; hybrids and diseased fish often present.
Very Poor	1-23	Few fish present, mostly introduced or very tolerant forms; hybrids common; disease, parasites, fin damage, and other anomalies regular.
No Fish		Repetitive sampling fails to turn up any fish.

INDEX OF BIOTIC INTEGRITY: REGIONAL USE

(Fausch et al 1984.)

TABLE 1.—Metrics used in assessment of fish communities. (Modified from Karr 1981.)

Category	Metric	Scoring criteria		
		5 (best)	3	1 (worst)
Species richness and composition	Total number of fish species	Varies with stream size and region		
	Number and identity of darter species			
	Number and identity of sunfish species			
	Number and identity of sucker species			
	Number and identity of intolerant species*			
Trophic composition	Proportion of individuals as green sunfish	<5%	5-20%	>20%
	Proportion of individuals as omnivores ^b	<20%	20-45%	>45%
	Proportion of individuals as insectivorous cyprinids	>45%	20-45%	<20%
Fish abundance and condition	Proportion of individuals as top carnivores ^c	>5%	1-5%	<1%
	Number of individuals in sample	Varies with stream size		
	Proportion of individuals as hybrids	0	0-1%	>1%
	Proportion of individuals with disease, tumors, fin damage, and other anomalies	0	0-1%	>1%

* Criteria for Salt Creek were: no intolerant species = 1, one or more intolerant species = 5.

^b Omnivores are species with diets composed of more than 25% plant material, the rest being animal material (Schlosser 1982).

^c Criteria for Chicago area streams and Red River were weighted by stream order.

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LIFE HISTORY AND ECOLOGY OF ENDEMIC FISH INHABITING THE UPPER COLORADO RIVER SYSTEM

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Numerous water development projects have been completed, others are in progress, and still others are contemplated for the upper Colorado River basin. The Utah Cooperative Fishery Research Unit has studied the fish of the upper Colorado River basin since 1963 and has documented the decline in abundance of several of the indigenous species. In most areas, only large adult specimens of the Colorado squawfish (Ptychocheilus lucius), humpback chub (Gila cypha), bonytail chub (Gila elegans) and humpback sucker (Xyrauchen texanus) are found, indicating a lack of reproductive success. Man-made changes of the river environment have been responsible for the reduction in several endemic species. Our present study is focused on the life history and ecology of the Colorado squawfish and humpback sucker and will provide insights into defining "critical habitat" as specified by the Endangered Species Act of 1973 and subsequently further specified in the Federal Register. This information will obviously be needed to protect some of these threatened and endangered species from extinction.

Our recent efforts were concentrated on the Yampa River of Northwestern Colorado because it is the last major river in the Colorado River basin that remains relatively uninfluenced by man's activities, and still maintains populations of squawfish and humpback suckers. Both species migrate to spawn and are found seasonally in the Yampa River.

Humpback suckers appear in the mouth of the Yampa in late fall and remain there until late spring. During the winter, the lack of access to the river prevented us from sampling. However, we believe that the humpback suckers remain in this area over winter. Other fish move upstream from the Green in the spring to join the fish already on the spawning area. In 1975 and 1976 spawning humpback suckers were found using a gravel bar about 1/4 mile upstream in the Yampa. Flannelmouth suckers (Catostomus latipinnis) spawn in the same areas at the same time and hybridization between these two species has been documented. No evidence of successful reproduction by humpback suckers has been found, but larval and juvenile flannelmouth suckers are abundant in the Green and Yampa Rivers. Only adult humpback suckers have been captured, even though collections were made with small-mesh seines that would have been effective for the younger individuals.

Colorado squawfish enter the Yampa River during mid-July to late August and migrate upstream to spawning sites. Last summer (1975), one area was located that has been tentatively identified as a spawning site. This area is a riffle about 1 mile downstream from the mouth of Cross Mountain Gorge. No actual observations of spawning were made, but ripe males and females that were judged to be spent were collected in the area. No evidence of successful reproduction has been found recently in the Yampa River or in the Green River above the confluence with the Yampa. However, young of the

year were rather common in this area about 10 years earlier. It appears that the primary importance of the Yampa River is not only as habitat for endangered or threatened species, but as a modifying influence on the Green River below its confluence with the Yampa.

The status of these endemic species is threatened by several factors including high dams with their resulting reservoirs and cold tailwaters and competition with introduced species. The dams are constructed in canyon areas that provided the habitat for these species by altering flow patterns, lowering mean temperatures, and reducing turbidity. Based on the impact of other dams in the basin, it is safe to assume that any kind of impoundment on the Yampa River would not only eliminate those endangered or threatened fishes still using the river, but could also eliminate populations in the Green River. This could be very important to the continued survival of the Colorado squawfish in particular, since the only evidence of successful reproduction in recent years has been in the Green about 30 miles below the mouth of the Yampa, and in Desolation Canyon above the confluence of the Green and Colorado Rivers. Squawfish, humpback suckers and humpback chubs are still existing in the Colorado River, but their future fate is uncertain.

This study has made it evident that much more knowledge is needed before a successful attempt can be made to save these endemic fish. The inaccessibility of many stretches of river has made sampling difficult, and therefore adequate knowledge of the distribution of these animals is still lacking. It also emphasizes the importance of life history information of other fishes that are still common - such as the flannelmouth sucker and roundtail chub - since the development of the upper Colorado River basin may also affect the status of these unique species. R. Miller has stated that 74% of the native fish are endemic to only the Colorado River and its major tributaries, and any further reduction in this exceptional fauna would be a great loss.

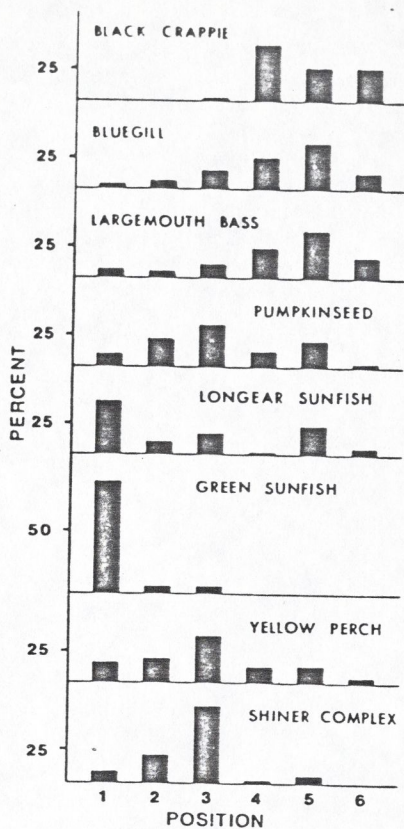


Fig. 21.1. Average midsummer relative abundance (percent of total numbers) with respect to distance from shore for eight common species in Lawrence Lake (Barry County), Michigan. Positions are equally spaced in the littoral zone from <0.5 m deep (position 1) to the deepest extent of the littoral zone (ca. 5 m, position 6). See Werner *et al.* (1977) for details.

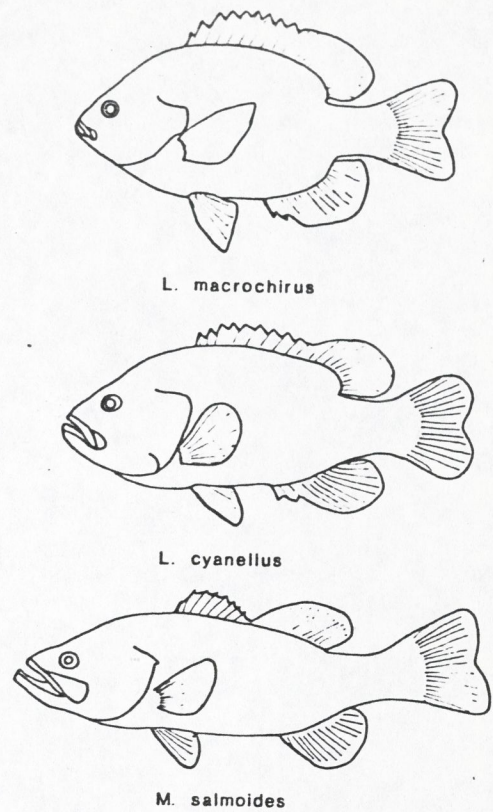


Fig. 21.5. Schematic of the body plan for the bluegill (*L. macrochirus*), the green sunfish (*L. cyanellus*), and the largemouth bass (*M. salmoides*).

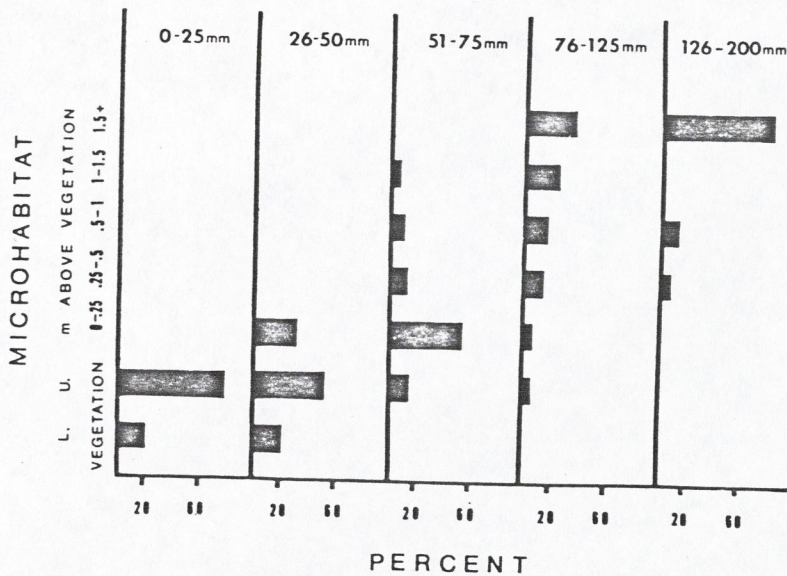


Fig. 21.2. Vertical distribution of five size classes of bluegills in Lawrence Lake, Michigan (percent of total numbers in each size class). L and U refer to the lower and upper one-half of the standing vegetation (ca 0.5 m tall). Data are the average of six transect counts in July and August.

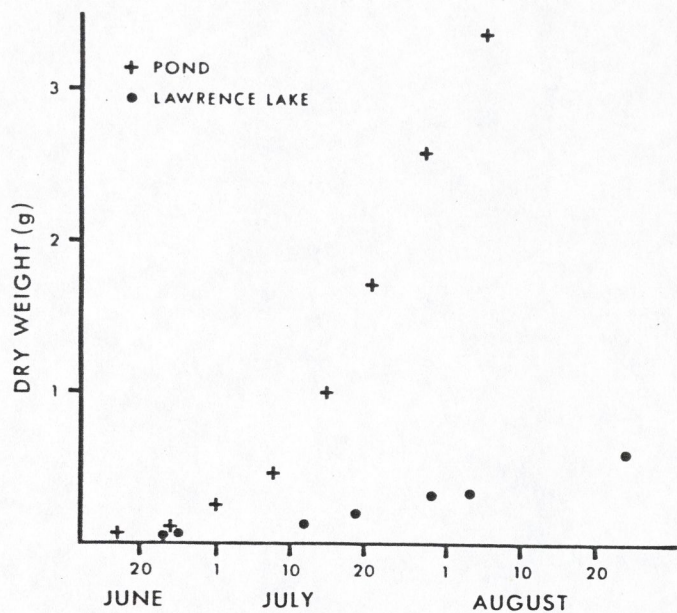


Fig. 21.3. Growth of cohorts of young-of-the-year largemouth bass (*Micropterus salmoides*) in a natural lake (Lawrence Lake, Michigan) and experimental ponds. Densities stocked in the ponds were considerably higher than those extant in the natural lake but no other species were present in the ponds.

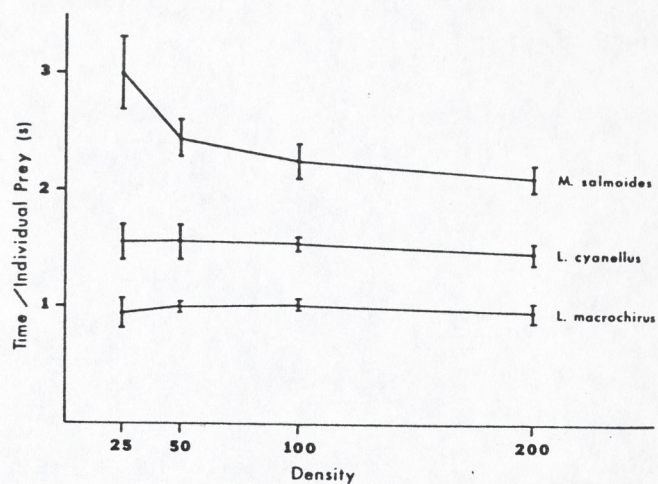


Fig. 21.6. Average time (\pm SE) required per capture of individual *Daphnia magna* (mean size of 3.6 ± 0.05 mm) by the largemouth bass (*M. salmoides*), green sunfish (*L. cyanellus*), and bluegill (*L. macrochirus*). Density is number of prey introduced into 110-liter aquaria. See Werner (1977) for details.

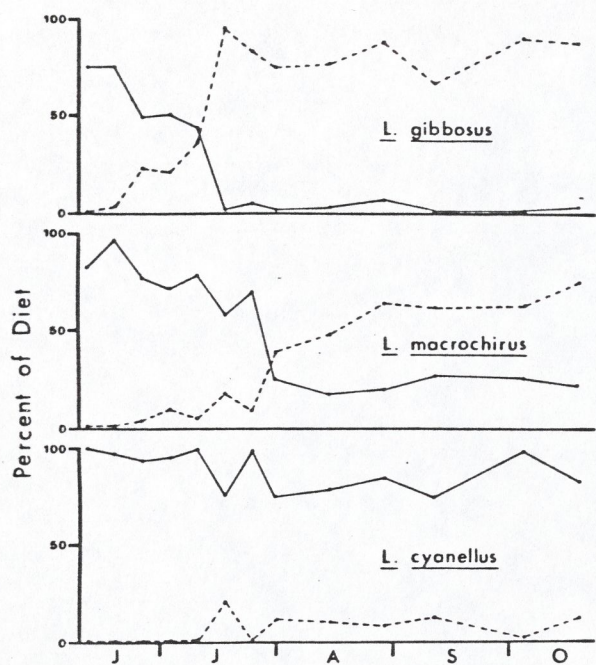


Fig. 21.4. Percent of the diet (by dry weight) comprised by vegetation prey (solid lines) and sediment prey (dashed lines) over the season for the pumpkinseed (*L. gibbosus*), bluegill (*L. macrochirus*), and green sunfish (*L. cyanellus*), respectively. Points are averages for 10 fish on each date. Plots do not total 100% because small amounts of prey were due to species that were not habitat-specific. See Werner and Hall (1979) for details.

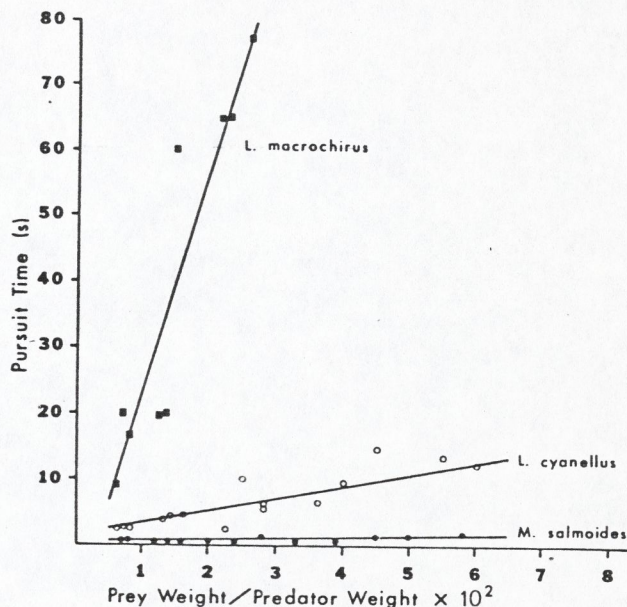


Fig. 21.7. Pursuit time required per capture of small fish by the bluegill (*L. macrochirus*), green sunfish (*L. cyanellus*), and largemouth bass (*M. salmoides*) plotted against the ratio of prey to predator weight. Regressions fit by least squares. See Werner (1977) for details.

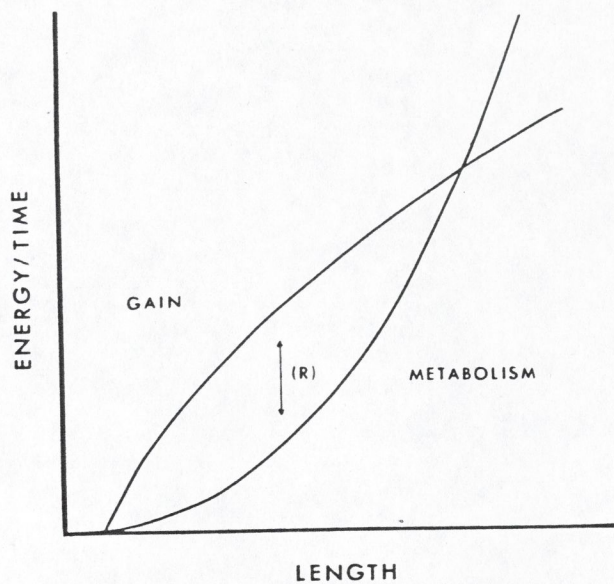


Fig. 21.11. Hypothetical curves for the relation between fish length and metabolic expenditures and foraging gain in a habitat. Curves are patterned after results of the laboratory experiments with bluegills. R is the net energy available for growth and reproduction.

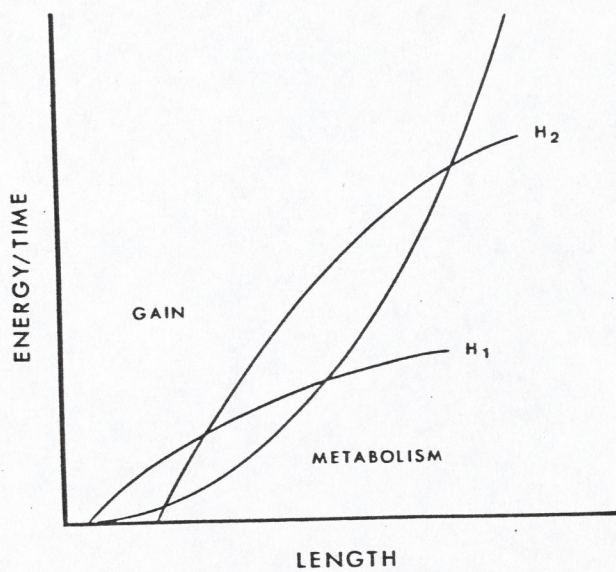


Fig. 21.12. Same as Figure 21.11 except that two habitats are compared. Habitat 2 (H_2) has larger prey than habitat 1 (H_1).

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Growth Decline in Subyearling Brook Trout (*Salvelinus fontinalis*) after Emergence of Rainbow Trout (*Salmo gairdneri*)

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In a tributary of Lake Superior, brook trout (*Salvelinus fontinalis*) subyearlings, after emergence in April, initially gained length at 0.51 mm/d and weight at a specific growth rate per day (G) of 0.058. After the emergence of larval rainbow trout (*Salmo gairdneri*) in June, however, length increments of brook trout declined to 0.05 mm/d and G was reduced to 0.005. During August, brook trout growth rebounded somewhat (0.12 mm/d; $G = 0.008$). Rainbow trout subyearlings, by contrast, grew at relatively constant rates of 0.42 mm/d and G of 0.040, from emergence until September. By late August, mean weights of brook and rainbow trout, 2026 and 2282 mg, respectively, did not differ significantly. Stream positions occupied by brook trout, characterized by flows of less than 20 cm/s and depths of less than 40 cm, did not change over the first summer. During June and July, stream positions of rainbow trout subyearlings coincided with those of brook trout. During August, however, rainbow trout moved to faster waters (>20 cm/s). The taxonomic composition of the diets of the two species did not differ. Mean width of food items consumed was linearly correlated with the total length of the fish ($r = 0.97$). The range of sizes of items eaten by the two species overlapped considerably by mid-June. For brook trout, mean food size increased, and amount consumed decreased, after the emergence of rainbow trout larvae. Growth reduction during the first summer, an outcome of interspecific competition for food and space, may result in increased overwintering mortality of fish at high latitudes, and be a mechanism by which brook trout are excluded by rainbow trout.

Dans un tributaire du lac Supérieur, des ombles de fontaine (*Salvelinus fontinalis*) de moins de un an ont, après leur éclosion en avril, crû d'abord à un taux de 0,51 mm/jour et augmenté de poids à un taux de croissance spécifique par jour (G) de 0,058. Cependant, après l'apparition des larves de truite arc-en-ciel (*Salmo gairdneri*) en juin, l'augmentation de longueur des ombles de fontaine est tombée à 0,05 mm/jour et G a diminué jusqu'à 0,005. En août, la croissance des ombles de fontaine s'est élevée quelque peu (0,12 mm/jour; $G = 0,008$). Par contre, les truites arc-en-ciel de moins de un an se sont développées à des taux relativement constants de 0,42 mm/jour et de 0,040 (G), de leur éclosion jusqu'en septembre. À la fin d'août, le poids moyen des ombles de fontaine et des truites arc-en-ciel, respectivement de 2026 et de 2282 mg, ne différait pas sensiblement. Les emplacements occupés par les ombles de fontaine dans le cours d'eau, caractérisés par des débits inférieurs à 20 cm/s et des profondeurs ne dépassant pas 40 cm, n'ont pas changé au cours du premier été. En juin et en juillet, les emplacements occupés par les truites arc-en-ciel de moins de un an dans le cours d'eau coïncidaient avec ceux des ombles de fontaine. Cependant, en août, les truites arc-en-ciel se sont rendues dans des eaux plus rapides (>20 cm/s). La composition taxonomique des proies ingérées par les deux espèces ne différait pas. Il y avait une corrélation linéaire entre la largeur moyenne des proies ingérées et la longueur totale des poissons ($r = 0,97$). À la mi-juin, les échelles de taille des proies consommées par les deux espèces se chevauchaient considérablement. Pour l'omble de fontaine, la taille moyenne des proies a augmenté et la quantité ingurgitée a diminué après la sortie des larves de truites arc-en-ciel. La réduction de la croissance au cours du premier été, résultat de la concurrence interspécifique pour l'espace et la nourriture, peut entraîner une mortalité plus importante des poissons pendant l'hiver à des latitudes élevées et constituer un mécanisme par lequel les ombles de fontaine sont écartés par les truites arc-en-ciel.

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The introduction of exotics has often led to displacement or elimination of indigenous species with similar niches (Kelly et al. 1980; Li and Moyle 1981). Competitive advantages, thought to be responsible for such exclusions, are seldom fixed or constant, but vary with season, developmental stage, and environmental fluctuations (Spiller 1984a; Abrams 1980; Chesson and Warner 1981). Thus, critical periods may exist when competition between given species is intense and reduction mechanisms functional. Studies conducted at other times or on other developmental stages may fail

to detect any interaction, or even show reverse dominance (Spiller 1984b).

Brook trout (*Salvelinus fontinalis*) have lost ground since the introduction of rainbow trout (*Salmo gairdneri*) to eastern North America in the 1800s (Power 1980). Often, after the two species have become sympatric, the brook trout has been virtually eliminated (King 1937, 1942; Kelly et al. 1980; Larson and Moore 1985). Although competition has been routinely invoked as a cause of the exclusion of brook trout (King 1937, 1942; Balon 1980; Power 1980; Waters 1983; Larson and

Moore 1985), a competitive mechanism capable of causing exclusion has not been demonstrated.

For brook and rainbow trout, spatial overlap in habitat is likely maximal during the first summer. Recently emerged rainbow trout occupy a wide range of microhabitats, including shallow waters at stream margins and riffles (Hartman 1965). During their first year, they move to habitats with faster waters and coarser substrates (Everest and Chapman 1972). In contrast, brook trout utilize slower waters throughout their lives (Gibson 1973; Cunjak and Green 1984). Subyearling brook trout feed on stream drift (Lord 1933; Griffith 1974) as do subyearling rainbow trout (Jenkins et al. 1970; Johnson and Ringle 1980).

Competition may alter growth rates. Removal of a competitor may increase growth in remaining species (Gibson and Dickson 1984; Moore et al. 1983); addition of a competitor may decrease growth in species already present (Hanson and Leggett 1985). Poor growth during the first summer of life has been correlated with elevated overwintering mortality of fish at high latitudes (Toneys and Coble 1979, 1980; Oliver and Holey 1979; Hunt 1969). Thus, competitive effects on growth during early life could regulate adult abundance (Gutreuter and Anderson 1985), and cause exclusion of species.

I hypothesized that a critical period of competition would occur during the first months of coexistence, and that during this period the growth rate of brook trout would be depressed, thus reducing their survivorship through the first winter.

Study Site

This hypothesis was tested in a tributary of Lake Superior, the Goulais River, located 30 km north of Sault Ste. Marie, Ontario. Rainbow trout were originally stocked in eastern Lake Superior in 1895 (MacKay 1963). Stocking of rainbow trout in the Goulais River has occurred during the past 20 yr (O. Wohlgenuth, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont., pers. comm.). Anecdotal evidence suggests that brook trout were abundant in the Goulais prior to the introduction of rainbow trout. Recent studies have shown that rainbow trout are now substantially more abundant in all parts of the river accessible to them, and that brook trout are rare in most of that area (Ontario Ministry of Natural Resources, Sault Ste. Marie District, unpubl. data). Brook trout larvae were found to be abundant, however, at a site in the Goulais about 80 km from Lake Superior. This was also a spawning site for rainbow trout.

The study site was 500 m in length; river width ranged from 36 to 88 m, but was 50% emergent gravel bars at its widest point. Major substrates were gravel, rubble, cobble, and angular rock. Secondary channels and backwaters occur on each side of the river and between the extensive gravel bars. Overhanging vegetation and fallen trees shaded approximately 30% of the banks; the remainder were bare gravel-cobble bars. Water depth and velocities varied seasonally and in response to rainfall. During June approximately 50% of the area was less than 60 cm deep and had flows of less than 20 cm/s (deepest zones were 200 cm, fastest water was 100 cm/s). Water quality characteristics in June were pH 7.1, alkalinity 9.2 mg/L, oxygen 9.3 mg/L, color nil, and clarity to substrate at all points. Water temperatures ranged from 4°C in April to 18°C in August, but decreased as much as 5° subsequent to precipitation events.

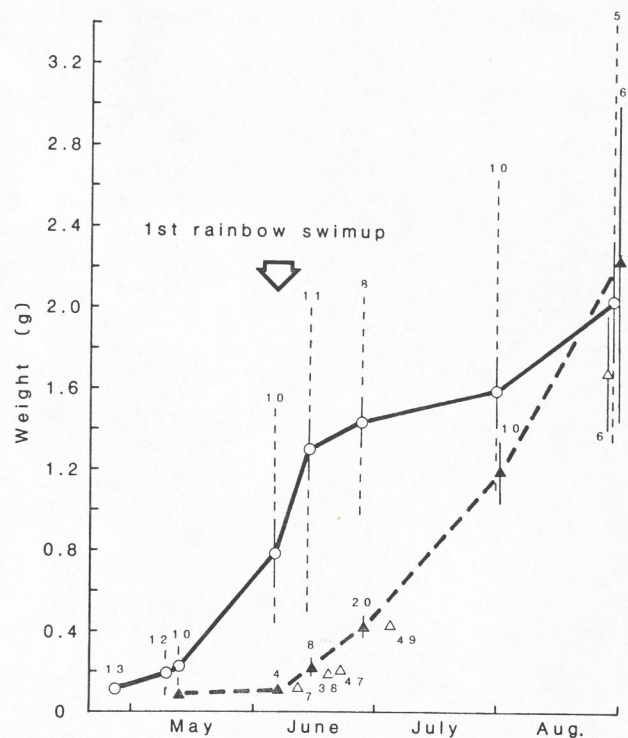


FIG. 1. Growth in weight (mean \pm SE) of sympatric brook trout (O) and rainbow trout (▲) and allopatric rainbow trout (Δ) subyearlings in the Goulais River during 1984. Broken vertical lines are ranges for data of sympatric brook trout. Numbers indicate *n*.

Methods

Sampling was conducted during 1984. Fish were collected by a two- or three-person crew with a Smith-Root 12-V DC backpack electrofisher and hand-held catching nets. All areas with depths of less than 1 m were sampled at the study site and at six other sites on the river. Brook trout subyearlings were present only at the study site; rainbow trout subyearlings were present at all sites. Brook trout subyearlings and yearlings and rainbow trout yearlings were collected from April 28 to August 30. Rainbow trout subyearlings were collected from May 13, at which time they were still in the gravel, until August 30. Densities of subyearlings were calculated from the number of fish electroshocked and the total area sampled. No error term can be assigned to estimates so calculated. Fish were stored in 10% Formalin. Total weight (milligrams) and length (millimetres) were determined for each individual. A correction factor of 1.035 was applied to length data because of shrinkage during storage (Wagner 1975). Changes in weight were assessed by the specific growth rate (*G*), defined as the change in the natural logarithm of weight per day of the growth interval. Stomach contents were examined and frequency of occurrence and estimates of wet weight (percent by volume of each item \times total weight) for each diet item were determined.

Depth of water (centimetres), surface flow (centimetres per second), and substrate type (sand, gravel (0.5–5 cm diameter)), cobble-rubble (>5–20 cm), or boulders (>20 cm) were recorded for each site where a fish was observed.

Statistical comparisons were made with analysis of variance and significance declared if $P < 0.05$, unless otherwise indicated.

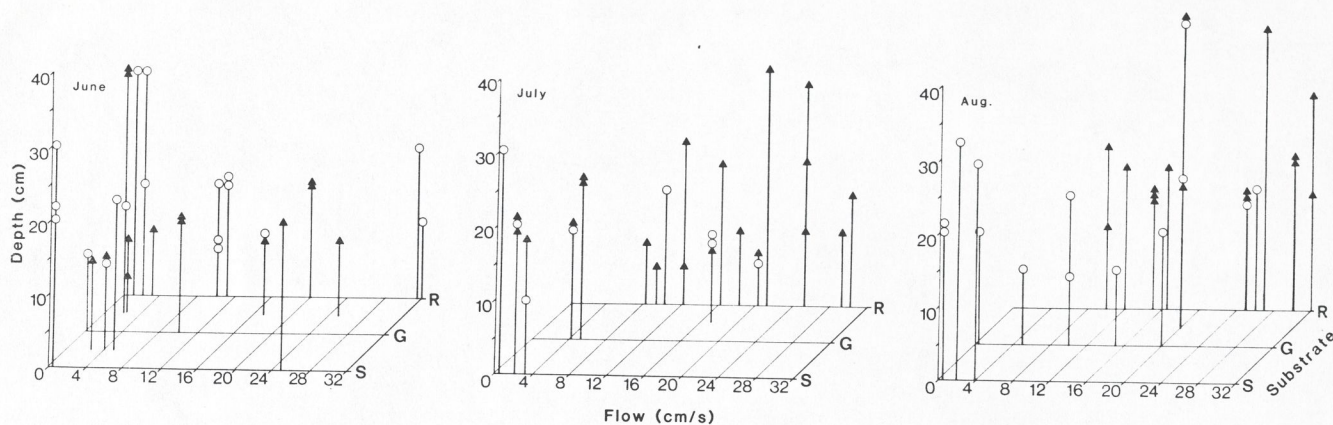


FIG. 2. Depth, surface flow, and substrate (S = sand, G = gravel, R = cobble-rubble) at sites occupied during June, July, and August by subyearling brook trout (○) and rainbow trout (▲).

Results

During April and early May, free swimming brook trout larvae were numerous (density $0.5/m^2$) at the study site. Densities declined to less than $0.3/m^2$ in mid-May after a major flooding event caused by heavy rains. Free-swimming rainbow trout larvae were first observed on June 6, and by mid-June were abundant (density $0.5/m^2$). There was no indication that numbers of brook trout decreased in relation to the emergence of rainbow trout. By late August, the densities of brook and rainbow trout subyearlings were 0.2 and $0.3/m^2$, respectively. At the other sites, densities of allopatric subyearling rainbow trout ranged from 0.1 to $1.2/m^2$ in June and early July. Density declined to $0.4/m^2$ by late August at the site with the highest density in June; no other sites were sampled at that time.

On April 28, brook trout larvae had a mean weight of 80 mg (Fig. 1). Growth was rapid until mid-June, when mean weight was 1304 mg. The value of G over this interval was 0.058 and increments in total length averaged 0.51 mm/d. From late-June until the end of July, however, growth virtually ceased; G declined to 0.005 and mean daily length increments decreased to 0.05 mm. During August, growth rebounded marginally, but G increased only to 0.008 and length gains increased only to 0.12 mm/d.

On June 6 at the study site, rainbow trout larvae had a mean weight of 80 mg (Fig. 1). Growth was uninterrupted and relatively uniform until September. Over this period, G was 0.040 and gains in total length averaged 0.42 mm/d. At the other sites, mean weights of allopatric rainbow trout subyearlings were consistently below the growth curve indicated at the study site.

Brook trout were significantly heavier than rainbow trout until the end of July; by September, however, mean weights, 2026 and 2282 mg, respectively, did not differ significantly. Yearling brook and rainbow trout did not differ significantly in weight; means were 11.2 ($n = 4$) and 11.6 g ($n = 16$), respectively. Sample sizes of yearlings were too small to permit within-year analysis of growth.

During April and May, brook trout subyearlings were observed only in waters having depths of less than 20 cm and surface flows less than 15 cm/s. From June to late August, surface flows and depths of stream positions where brook trout were observed did not change significantly (Fig. 2). During June, July, and August, brook trout occupied positions characterized by mean (\pm SE) surface flows of 9 ± 3 , 9 ± 3 , and 11

± 3 cm/s, respectively, and mean depths of 16 ± 2 , 15 ± 3 , and 19 ± 2 cm, respectively. Proportions of substrate types for sites occupied by brook trout changed significantly between June and August (chi square = 11.47 , $df = 2$); during June, 69% of positions were over cobble-rubble whereas during August, 73% were over sand or gravel.

The stream positions occupied by rainbow trout during June were in close proximity to those of brook trout; mean (\pm SE) surface flow and depth of rainbow trout positions were 10 ± 3 cm/s and 14 ± 4 cm, respectively (Fig. 2). During July, some rainbow trout were observed in faster waters (>20 cm/s) with coarser substrates, but surface flows and depths (mean \pm SE of 14 ± 2 cm/s and 16 ± 2 cm, respectively) did not differ significantly from those of brook trout. By late August, however, an increased proportion of rainbow trout occupied sites in waters with greater surface flows (mean \pm SE of 21 ± 2 cm/s) than sites occupied by brook trout.

Allopatric rainbow trout subyearlings occupied positions during June and July with depth, flow, and substrate characteristics similar to those at the study site. Mean (\pm SE (n)) depths were 18 ± 1 (69) and 19 ± 1 cm (57), respectively; flows were 6 ± 1 (69) and 15 ± 2 cm/s (57), respectively; substrates were primarily cobble-rubble. By late August, as at the study site, rainbow trout subyearlings occupied positions with higher surface flows (34 ± 5 cm/s (6)), similar depths (20 ± 1 (6)), and coarser substrates (4 of 6 over rubble-boulders) as compared with positions occupied during June and July.

Yearling brook trout were found in deeper (mean \pm SE of 36 ± 6 cm), but not faster (mean \pm SE of 15 ± 5 cm/s) water than were subyearlings. In each case, yearling positions were associated with overhanging banks. Yearling rainbow trout were found in significantly deeper (mean \pm SE of 25 ± 4 cm) and faster (mean \pm SE of 30 ± 6 cm/s) water than were subyearlings of either species or yearling brook trout. Yearling rainbow trout occupied positions near the cover of boulders in midstream bed as well as under shaded bank areas.

The taxonomic composition of the diets of the two species differed little; both fed primarily on subadult aquatic dipterans, trichopterans, and ephemeropterans and adult insects of various orders (Table 1). Mean width of food items consumed was linearly related to the total length of the fish, regardless of species ($r = 0.97$, for combined data) (Fig. 3). When rainbow trout larvae emerged, however, the mean size of food items of brook trout temporarily increased above that predicted by the food size-fish size regression (Fig. 4). The range of sizes of

TABLE 1. Stomach contents of subyearling brook trout, before and after the emergence of rainbow trout, and subyearling rainbow trout, in sympatry with brook trout and in allopatry at other sites, from the Goulais River, May to August 1984 (*n* in parentheses; %f = frequency of occurrence, expressed as percentage; %wt = percent of total wet weight; tr = trace).

	Brook trout				Rainbow trout			
	Pre-rainbow (45)		With rainbow (34)		Sympatric (48)		Allopatric (138)	
	%f	%wt	%f	%wt	%f	%wt	%f	%wt
Adult Insecta	42	19	41	22	40	39	3	5
Subadult								
Ephemeroptera	44	33	30	30	20	21	60	51
Tricoptera	39	24	38	14	18	6	10	5
Diptera	42	19	29	10	53	25	62	34
<i>Catostomus</i> spp. and Cyprinid fry			12	16	1	tr	3	5
Collembola	10	4	2	tr	8	2	1	tr
Ostracoda	3	tr			10	2		
Copepoda					1	tr		
Arachnida					12	5		
Hirudinea			1	2				
Amphipoda			8	5	1	tr		
Nematoda					1	tr		
Hydracarina			2	1	1	tr	1	tr
Tardigrada	18	tr						

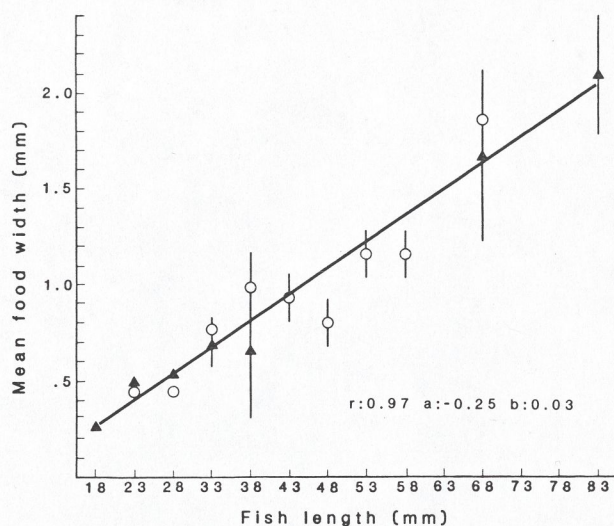


FIG. 3. Width of food items (mean \pm SE) found in stomachs of sub-yearling brook trout (○) and rainbow trout (▲) in relation to total length of fish.

items eaten by the two species overlapped considerably by mid-June, and mean food sizes by late June were not significantly different. The minimum size of food items was the same for both species and did not change during the first summer.

The quantity of food in the stomachs of brook trout, expressed as percent of body weight, declined significantly after the emergence of rainbow trout larvae from 3.1 (*n* = 45) to 1.4 (*n* = 19). During August, the stomach contents of brook trout increased significantly to 5.5% (*n* = 15) of body weight. At the study site, and at the other sites under allopatric conditions, rainbow trout stomach contents were 2.5 (*n* = 48) and 2.2% (*n* = 150) of body weight, respectively, and did not vary significantly among months.

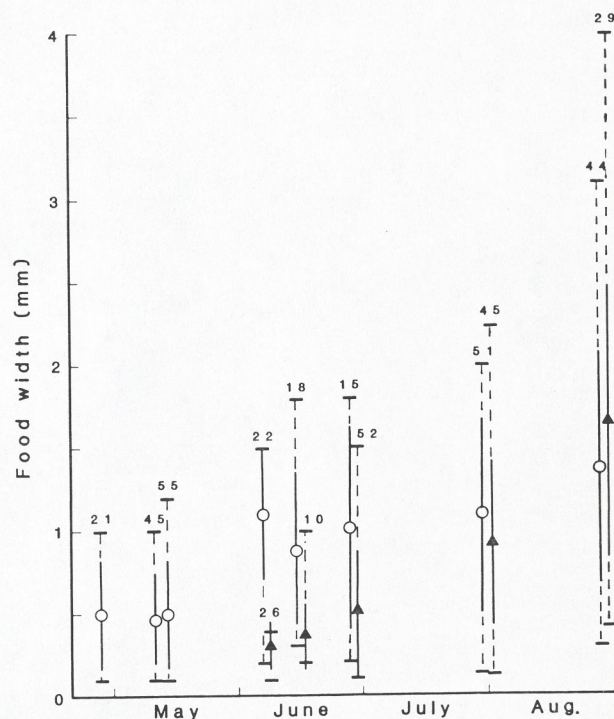


FIG. 4. Width of food items (mean \pm SE) found in stomachs of sub-yearling brook trout (○) and rainbow trout (▲) of specific ages. Broken vertical lines are ranges. Numbers indicate *n*.

Discussion

Prior to the emergence of rainbow trout from the gravel, brook trout growth was typical of the species at this latitude. Sub-yearling brook trout typically gain length at a rate of 0.45 mm/d over the growth season (Power 1980). Data in Carlander (1969) indicate that specific growth rates (per day) of

0.03–0.04 are typical of subyearling brook trout. In three Michigan rivers, at sites that contained fair to large populations of naturally spawned brook trout, subyearlings increased in length linearly from May until September, illustrating growth ranges thought typical of latitudes similar to our study site (Cooper 1953) (Fig. 5). Cooper attributed growth differences among subyearlings from these three rivers to differences in food availability; temperatures at the three sites were similar to each other and to those in the Goulais River during the present study.

Subsequent to the emergence of rainbow trout, the growth of brook trout declined to well below typical rates. The only available data on growth of subyearling brook and rainbow trout in sympatry in other systems were given by Whitworth and Strange (1983). Using their data, I calculated that average gains in length for brook trout were >0.5 mm/d prior to the emergence of rainbow trout, but decreased to 0.25 mm/d after their emergence. In contrast, rainbow trout grew at >0.7 mm/d (assuming late May emergence at an average size of 25 mm). These calculations should be interpreted with some caution, however, since the fish included in the calculations were from several areas of a river in which productivity may have been unequal and the proportions of the two species varied considerably. Nevertheless, the apparent decline in growth of brook trout after the emergence of rainbow trout is remarkably similar to that found in this study.

Rainbow trout were somewhat smaller at sites where brook trout were absent. Over 80% of the fish included in these data are from sites where densities in June were higher than at the study site. Although productivity was not quantified during the present work and between-site comparison is made with caution, it is possible that the lesser growth reflects intraspecific competition and is density dependent.

Stream space and food are inextricably linked and are competed for by stream salmonids (Chapman 1966; Slaney and Northcote 1974; Fausch and White 1981). Thus, species whose spatial distributions differ are less likely to compete for food. Brook trout have been sympatric with Atlantic salmon (*Salmo salar*) in coastal rivers of eastern North America since at least the last ice age. These species exhibit behavior which minimizes competition (Gibson and Dickson 1984; Gibson and Power 1975). Predictably, growth of subyearling brook trout did not decline after the emergence of salmon 2–3 wk later in two rivers in Nova Scotia (Randall 1982).

By contrast, no spatial segregation of indigenous brook trout and exotic rainbow trout was apparent during June and July. The greater rheophilic abilities of the rainbow trout were not apparent until juveniles reached a length of approximately 40 mm. Prior to their attainment of this size, the potential exists for competition for food or space between these two species. The general field observations of Larson and Moore (1985) that habitat use by subyearlings of these species was very similar supports these conclusions. Cunjak and Green (1983) argued that in Newfoundland streams, subyearling rainbow trout occupied faster water than did subyearling brook trout. However, their argument does not address the critical period of the first 1–2 mo of coexistence, as it is based on a comparison of mean flows at sites occupied by these species between April and October.

Other species of salmonids have been shown to exhibit similar divergences in niche overlap with age. Under controlled laboratory conditions, rainbow trout and coho salmon (*Oncorhynchus kisutch*) subyearlings utilized space, depth, and cur-

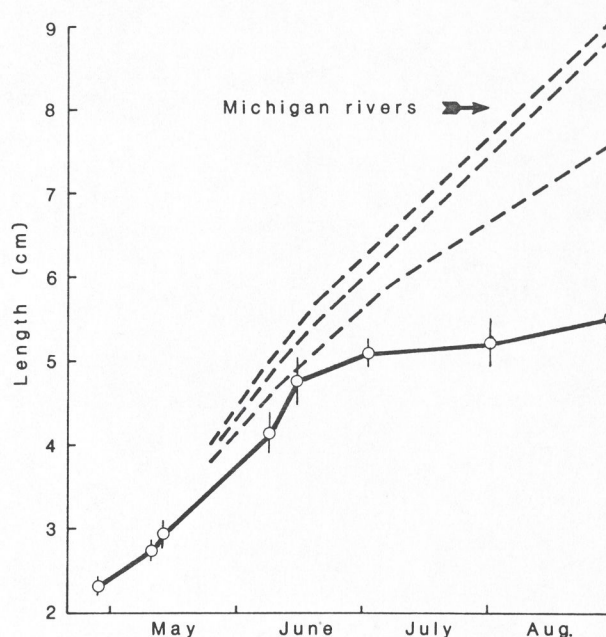


FIG. 5. Growth in length (mean \pm SE) of brook trout in the Goulais River during 1984 (O) and in three northern Michigan rivers (data from Cooper 1953).

rent in the same manner after emergence of trout larvae, but progressively diverged in utilization patterns during their first year (Hartman 1965).

The decreased growth of brook trout, linked with evidence of dietary and spatial overlap demonstrated in this study, is strong evidence of competition between these species during their first summer. My data suggest that during June and July, when the more abundant rainbow trout cooccurred with brook trout, rainbow trout removed smaller food items in the stream drift which were previously available to the brook trout. Brook trout then fed on remaining items that had sizes nearer the upper range available to them. This restriction of diet resulted in brook trout consuming less food. By late August, when rainbow trout had moved to sites with greater flows, brook trout had greater access to available food, and their stomach contents increased accordingly. In contrast, feeding by rainbow trout did not appear to be affected by the presence of brook trout. Stomach content data reported here are similar to those in the literature (Lord 1933; Jenkins et al. 1970; Johnson 1981).

Behavioral interactions may reduce foraging efficiency (Brown 1945; Stauffer 1977a). Thus, energy and time expenditures by brook trout, in attempts to extirpate rainbow trout larvae from established territories, may have contributed to a decline in the magnitude and metabolic efficiency of feeding. Laboratory observations have indicated that subyearling rainbow trout are more aggressive than subyearling brook trout (unpublished data). Thus, although smaller initially, the more numerous rainbow trout may have been capable of reducing or even preventing feeding by brook trout. These findings call into question the long-held axiom that greater size equals dominance (Newman 1956; Chapman 1966). My work shows that smaller individuals, especially in larger numbers, may attain dominance and eventually larger size.

The low numbers of yearling brook trout encountered during this study point to high levels of winter mortality related to poor first year growth. Applying my data to Hunt's (1969) regression of survival as a function of first summer growth of brook

trout in a Wisconsin stream indicates that few Goulais River brook trout would survive their first winter. These findings suggest that at high latitudes, growth reduction during the first summer may be a major determinant of relative population sizes of competing species.

Brook trout abundance is almost certainly dependent on the relative abundance of potential competitors. Rainbow trout abundance varies widely, for reasons not entirely understood. Beneficial abiotic factors and spawning site requirements may differ between brook trout and rainbow trout (Seegrist and Gard 1972). Where conditions are highly suitable for rainbow trout, brook trout may be eliminated. In five similar tributaries of Lake Superior in Michigan, three rivers with average densities of subyearling rainbow trout of 0.4, 0.6, and 0.8/m² sustained extant brook trout populations. Two rivers having average densities of subyearling rainbow trout of 1.8 and 2.6/m² contained no brook trout (Stauffer 1977b). Cunjak and Green (1983) found that abundances of brook trout were severalfold less in Newfoundland streams where rainbow trout were present than where they were absent. Larson and Moore (1985) showed that brook and rainbow trout have reciprocal abundances in Appalachian streams. For these similar salmonids, and others such as the brown trout (*Salmo trutta*), a total potential biomass may exist. Interactions such as I have demonstrated, mediated by a myriad of environmental factors, determine the proportion of each species. The difficulty for brook trout appears to be that over much of its native range, sites where it can remain abundant in the presence of rainbow trout are limited.

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Stream Fish Communities Revisited:
A Case of Mistaken Identity

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An extensive array of tools is available to help ecologists study community structure. Increasingly, we rely on the more abstract of these tools, e.g., mathematical models of varying complexity and multivariate statistical techniques, which are useful and often appropriate. However, an equally important tool, a thorough knowledge of the natural histories of organisms found in the community under study, is sometimes applied carelessly. This concern was gently raised by Stearns (1985), but the effect of misapplying natural history may not always be so benign.

Recently, Herbold (1984) reanalyzed fish abundance data from one Indiana stream site that had been the subject of a controversial paper by Grossman et al. (1982). To elicit greater structural detail in this community, Herbold calculated rank and absolute correlation coefficients among the 18 most abundant species. He used data from all 27 samples taken April-November over a 12-year period (Whitaker 1976; Grossman et al. 1982). Using recurrent group analysis on these correlations, Herbold distinguished two covarying groups which he labeled as riffle-dwelling and pool-dwelling species (hereafter referred to as Groups A and B, respectively; Fig. 1). Herbold confirmed these groups with a principal components analysis.

Herbold apparently realized (p. 561) the importance of a thorough knowledge of the natural history of each species in studies that delineate groups or guilds as the units of study. Furthermore, he emphasized (p. 564) that the natural histories of these fishes provide additional support for analyzing them as two different units. While we do not necessarily disagree with his

two-group interpretation, we feel: (1) that these groups cannot be properly referred to as riffle- and pool-dwellers if natural history information is indeed used; (2) that the within-group structure is more complex than described; and (3) that some of his conclusions about community structure and persistence are open to question. We have not reanalyzed Herbold's data as that is not the thrust of our response [see Grossman et al. (in press) for a reanalysis].

referring to something
in press
asking readers
to "see"
something
they cannot!

After reviewing several regional fish textbooks (Cross 1967; Scott and Crossman 1973; Eddy and Underhill 1974; Pflieger 1975; Smith 1979; Lee et al. 1980; Trautman 1981; Becker 1983), particularly those works concentrating on the region around Indiana, we find no justification for labeling Group A as riffle-dwelling and Group B as pool-dwelling. Four of the six species in Group B are darters (Etheostoma blennioides, E. caeruleum, E. flabellare, E. nigrum), one is a sucker (Hypentelium nigricans), and one is a madtom (Noturus miurus). With the possible exceptions of the madtom and E. nigrum, all species in this group "typically" inhabit riffles or riffle-like areas especially when feeding or breeding. Little is known about the madtom, but it apparently inhabits both pools and riffles throughout its range (Cross 1967; Pflieger 1971). On the other hand, the fishes of Group A (all members of the minnow family, Cyprinidae) are quite diverse in their habitat utilization. Six species (Notropis chrysocephalus, N. spilopterus, N. stramineus, Ericymba buccata, Campostoma anomalum, Semotilus atromaculatus) are commonly found in both pools and riffles; however, they appear to occur most often in pools. Only one species (Phenacobius

mirabilis) can be considered a true riffle-dweller, and two species (N. ^{copies}umbratilis, Pimephales notatus) are primarily pool-dwellers. Schlosser (1982) studied a small stream in Illinois with a similar species composition. His segregation of species into habitat guilds provides empirical evidence that corroborates our interpretation of the regional fish texts.^{2, confusing} Because of the flexibility in habitat use for most of these species and Herbold's mislabeling of Groups A and B, we feel that any conclusions drawn by him about his groups cannot describe the structure or persistence of pool- and riffle-dwelling fishes.

textbooks?
as in
beginning
of this
paragraph (p. 2)

Herbold also described Group A as resident species and Group B as the opportunistic non-resident species. However, only E. blennioides (Group B) was present in all collections. One measure of residency is frequency of occurrence (= ^{i.e.,} percentage of all samples where a given species is found). The mean frequencies of occurrence for Group A ($\bar{x} = 87.3\%$) and Group B (85.1%)^{be consistent} are very similar. Additionally, the mean coefficient of variation for abundance (coefficient of variation defined as standard deviation of a species' abundance divided by mean abundance for ^a that species) is larger for Group A than Group B [1.88 vs 1.31, respectively, as calculated by Rahel et al. (1984) for autumn samples only]. It is also not evident from plots of relative abundance (Fig. 2) and total abundance (Fig. 3) that either group is more resident, except that Group A species are relatively more abundant and perhaps more variable. Thus, there seems to be little justification for describing Group A as resident and Group B as non-resident and opportunistic.

Herbold based his conclusions about residency, for the most part, on the fact that six species of Group A showed significant correlations with total abundances of all other fishes, while significant correlations are lacking in Group B. It is unclear why these correlations (or lack thereof) should demonstrate residency. The opposite could be argued; that some resident species may be found at fairly constant, if low levels, while the total population fluctuates around them. Also, the most abundant species were minnows (Group A) that often occur in mixed-species schools. It is not surprising then to find these species' abundances correlated with total numbers of all other species. ^{awk}

The question of persistence for these covarying groups was addressed by Herbold using Kendall's coefficient of concordance, W . He found that Group A was persistent and Group B was non-persistent. Rahel et al. (1984) presented a strong case against the use of W as a measure of persistence because it depends on the arbitrary choice of assemblage size. We also find that subtle differences in abundance equate to large differences in ranks. For example, in four samples (June 1965, July 1967, September 1965, and September 1966) abundances of the six Group B species are less than or equal to 10 and differences among the abundance values amount to no more than 8 [Appendix 2 of Grossman et al. (1982)]. To ascribe rank differences to these minor abundance differences does not reflect biological reality. Compounding the issue is the inability to accurately census riffles with seines, especially gravel/rock riffles (sensu Whitaker 1976). It is perhaps an appropriate alternative, as Yant et al. (1984) point out, to have as the null

strange order, not chronological

again (see) the impossible

hypothesis that there is no variation in species presence among sampling times [but see Grossman et al. (in press)]. We suggest Cochran's Q-test as an appropriate test for persistence when presence/absence time series data are available (Green 1979; p. 189). Cochran's Q is a distribution-free test that is not dependent upon species assemblage size nor does it require the assumptions of the method used by Yant et al. (1984) in addressing the same question. For both Group A ($p > 0.5$) and Group B ($p < 0.1$) we fail to reject the null hypothesis.

What then can be said about either of these two covarying groups? One could be tempted to simply reverse Herbold's designations and refer to Group A as largely pool-dwelling and Group B as riffle-dwelling. Herbold's designation of the niche diversification model and the intermediate disturbance hypothesis as conforming to patterns observed in Groups A and B, respectively, would now make more intuitive sense and correspond to Schlosser's (1982) work on the riffle to pool habitat gradient in stream fishes. However, we are not in favor of these labels either, because they simplify an underlying situation that is much more complex. In our opinion, Group A is best described as the minnow component of the community and Group B as the darter/sucker component.

The correlation between spring rainfall and abundances of some Group A fishes (Herbold 1984) may reflect conditions that affect minnow recruitment. Schlosser's (in press) analysis of fish community structure in Jordan Creek, Illinois, over two years of above and below normal flows demonstrates the importance of age structure and recruitment to stream fish communities. Between-year

differences in stream flow appeared to affect juvenile abundance of some minnows (notably P. notatus and N. chrysocephalus) and sunfishes while juvenile abundance of darters and suckers appeared less affected. The adult portion of the community remained fairly constant. In light of this, the differences between Herbold's two groups may represent recruitment variability between taxonomic groups with varying life history strategies.

Finally, we agree with Herbold that the natural histories of Group A fishes show a fairly strong niche diversification based on gross trophic considerations. However, we feel that Group B fishes, although all are "bottom" feeders, also partition the environment albeit in more subtle manners. For example, E. blennioides and E. caeruleum show responses to fluctuations in discharge related to subtle differences in microhabitat use that appear to be critical ecological factors determining their relative abundances and spatial distributions (Schlosser and Toth, 1984).

Studies of stream fish communities can make substantial contributions to our understanding of community structure and function. We were motivated to respond to Herbold's (1984) paper because of detractors that diminish any contribution: (1) failure to use adequate autecological information in studies of this type; and (2) our concern that sweeping generalizations of observed results not become firmly entrenched as central dogma concerning stream fish communities.

FINAL NOTE

There appear to be a number of internal inconsistencies in Herbold's paper. For example, the significant correlations marked in Table 2 do not agree with the numbers reported in the text (p. 564). When we tried to reconstruct Figure 1 from Table 2 we were unable to get the same results. Also, if Table 3 represents the correct results of the principal components analysis then the fourth component consists of Lepomis macrochirus and two group B species NOT associated with it in Figure 1, unlike what the text reports (p. 564). As stated earlier, we are not interested in recalculating Herbold's analysis. But, we feel that these inconsistencies should be noted, should anyone else care to shake hands with the tar baby first constructed by Brers Grossman, Moyle, and Whitaker.

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Figure 1. Species associations indicated by Kendall's τ , modified from Herbold's (1984) Fig. 1. All species within rectangles are significantly correlated ($p < 0.05$) with all other species within the rectangle. Lines between rectangles represent the number of significant correlations between the species within one rectangle and the species within another (see also our Final Note).

Figure 2. Box plots representing log transformed abundances of the 18 most abundant fish species from 27 samples (Appendix 2 of Grossman et al. 1982). The box plots include median (\emptyset), interquartile range (height of main box), 10%tile and 90%tile (narrow box), and range (vertical line). Numbers (on abscissa) represent species' labels as used by Herbold (1984) and in our Fig. 1.

Figure 3. Box plots representing relative abundances of the 18 most abundant fish species from 27 samples (Appendix 2 of Grossman et al. 1982). Figure format as in Fig. 2.

Figure 1

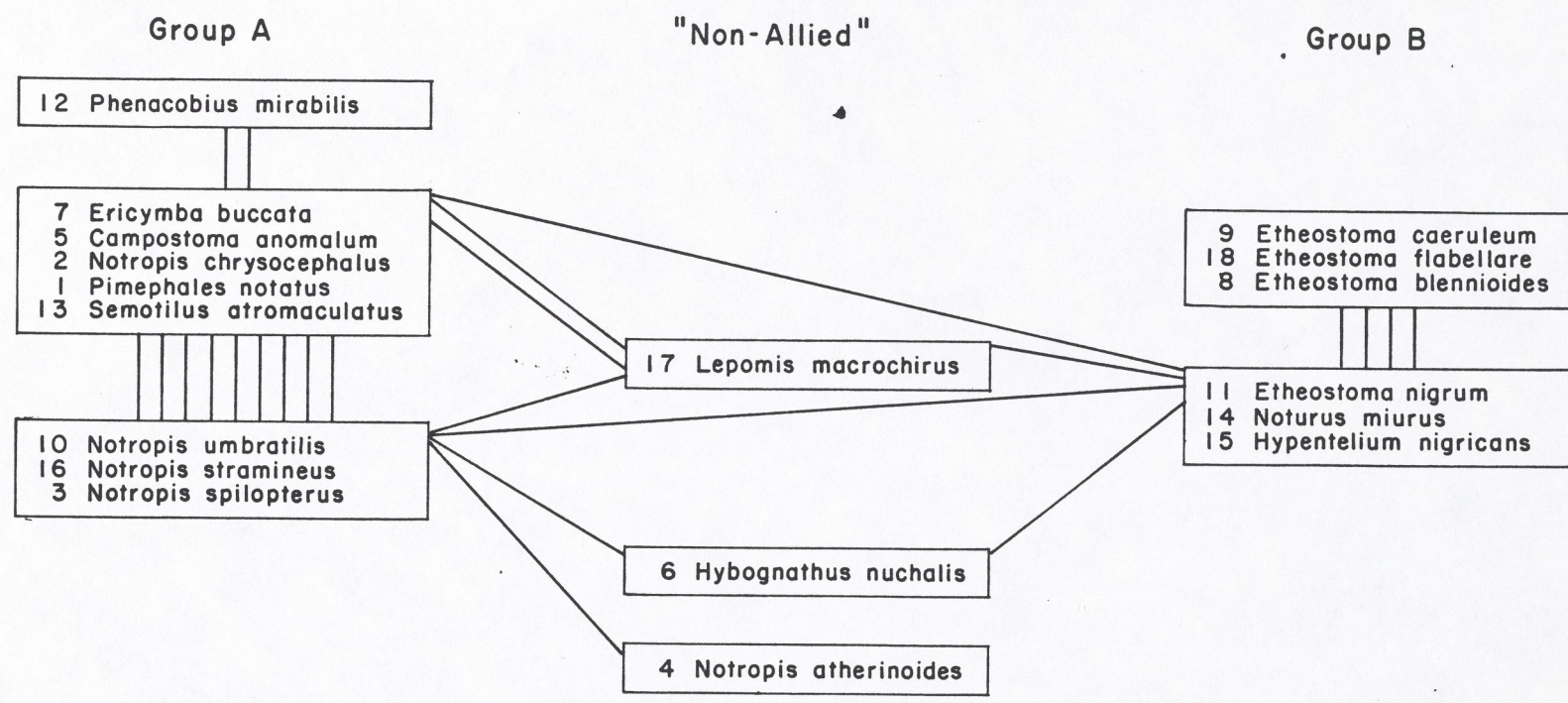


Figure 2

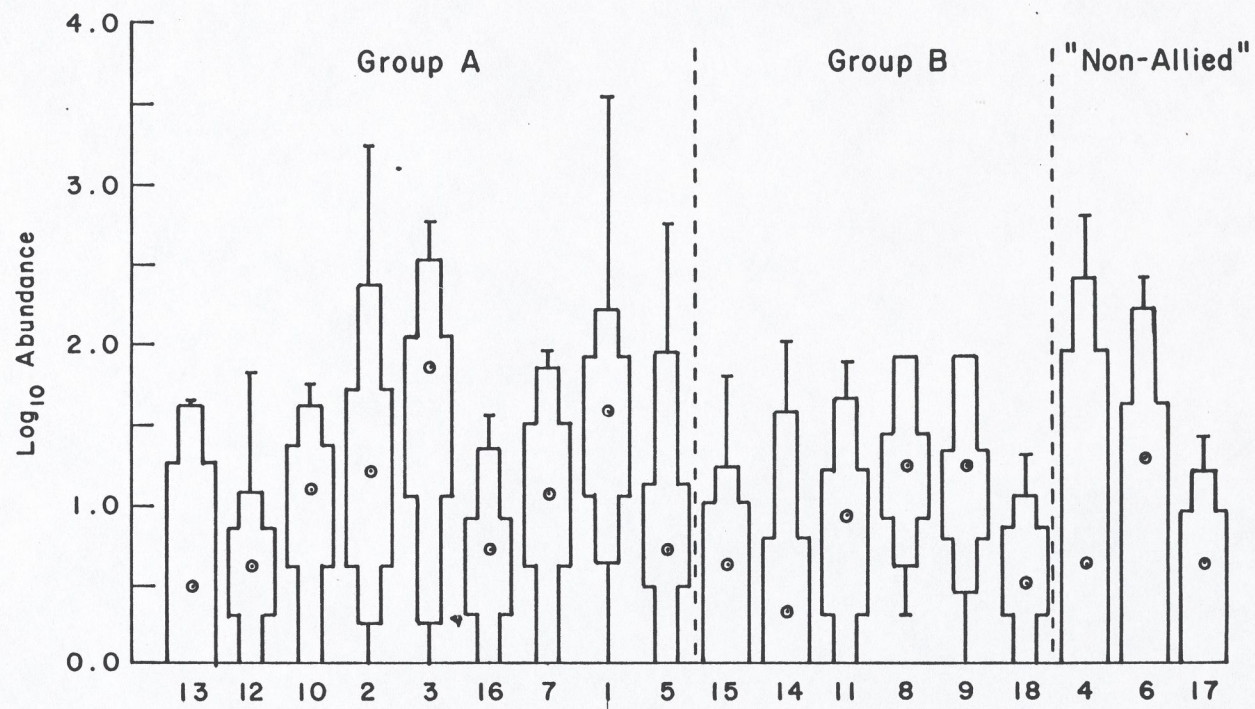
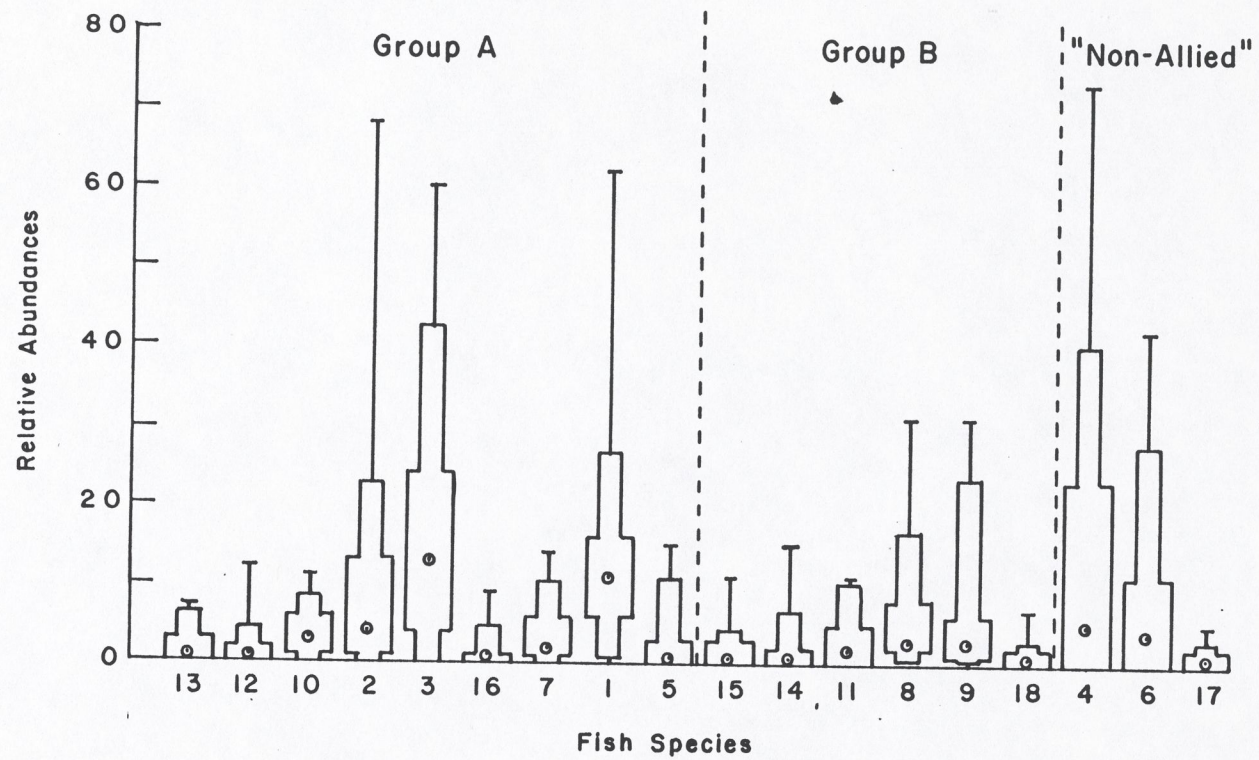


Figure 3.



PREDATION AND SPECIES REPLACEMENT IN
AMERICAN SOUTHWESTERN FISHES:
A CASE STUDY

GARY K. MEFFE

ABSTRACT.—Declines in distribution and abundance of native fishes of the American Southwest have been noted for decades, but mechanisms leading to these losses are unclear. The Sonoran topminnow (*Poeciliopsis occidentalis*) was studied to determine mechanisms leading to local extirpation, as a model of southwestern fish extinctions. Although habitat destruction is the cause of several population losses, interactions with introduced mosquitofish (*Gambusia affinis*) are responsible for reduction of topminnows through much of their native range. A series of laboratory and field experiments indicated that predation of juvenile topminnows by mosquitofish is a major factor in decline of the species. For lack of evidence, introduced parasites or diseases, hybridization, physiological stress, and resource competition are all dismissed as probable mechanisms of extirpation.

Local extinction of native species is a common result of introduction of exotic organisms, and man-induced range extensions are a major threat to the integrity of natural communities (Elton, 1958). Despite potentially disastrous effects of introduced fishes on native communities (e.g., Miller, 1961; Zaret and Paine, 1973), little is known of mechanisms by which intruders replace natives. Although hypotheses such as competition, predation, and habitat alteration abound, few have been tested. Here, I report an experimental analysis of mechanisms involved in replacement of a native Sonoran Desert fish by a non-native species, and discuss losses of other southwestern fishes via exotics.

The Sonoran topminnow, *Poeciliopsis occidentalis* (Baird and Girard), is a small (<50 mm) poeciliid fish native to the Gila River drainage of southern Arizona and several major drainages in northwestern mainland Mexico (Rosen and Bailey, 1963; Hendrickson et al., 1981). It formerly occurred in most aquatic habitats throughout this region, including stream margins, springs, and marshes. In the past four decades, distribution of *P. occidentalis* has narrowed to the extent that it now occurs in the United States only in a few isolated streams, springs, or segments of creeks in southern Arizona, and is listed as endangered (U.S. Department of the Interior, 1980). Various aspects of Sonoran topminnow life history are extensively documented elsewhere (Minckley, 1973; Schoenherr, 1974, 1977, 1981; Constantz, 1974, 1975, 1979, 1980; Minckley et al., 1977; Gerking and Plantz, 1980; Meffe et al., 1983).

The mosquitofish, *Gambusia affinis* (Baird and Girard), is a poeciliid native to temperate and semi-tropical regions of the eastern and central United States (Rosen and Bailey, 1963) and is widely introduced through much of the world. First brought into Arizona about 1926 for mosquito control (Miller and Lowe, 1964), it is presently ubiquitous and has replaced the Sonoran topminnow throughout much of its former range (reviewed by Meffe et al., 1983). On a local scale, replacement occurs from four months

to several years after colonization, although long-term coexistence may also occur. On a geographic scale, topminnows have declined only in the zone of overlap of these two species (Meffe et al., 1983). In northwestern Mexico, where *G. affinis* has only recently colonized a few localities, *P. occidentalis* remains abundant (Hendrickson et al., 1981).

HYPOTHESES.—Although several topminnow populations have been extirpated by habitat destruction (Miller, 1961; Minckley and Deacon, 1968; Minckley, 1973; McNatt, 1979; Meffe et al., 1983), many others have been lost with no apparent environmental change other than introduction of mosquitofish. It is unlikely that subtle physical or chemical fluctuations contributed to decline of this species, as the fish can tolerate a wide range of conditions (Schoenherr, 1974; Meffe et al., 1983). These observations suggest that interaction with *G. affinis* is a major factor in local extirpation of *P. occidentalis*. Specific mechanisms of replacement are not known, although several hypotheses were advanced (Miller, 1961; Minckley, 1973; Schoenherr, 1974, 1981). The more plausible of these are summarized below, and I present experimental evidence for predation as a major cause of topminnow losses.

Parasites and Disease.—Introduced organisms may harbor parasites or diseases that can decimate native species (Elton, 1958, and references therein), and transfer of parasites to native fishes by introduced fish vectors has been documented in some instances (Hoffman, 1970; Bauer and Hoffman, 1976; Deacon, 1979). In the present case no new parasites or diseases of *P. occidentalis* are evident and the fish appears healthy where sympatric with introduced species. Mpoame (1981) found only the nematode *Camallanus* sp. infecting *P. occidentalis*, with no evidence that parasites of introduced fishes affected any native Arizona species. Therefore, hypotheses suggesting decline of Sonoran topminnows through introduction of parasites or diseases are not supported.

Hybridization.—There is no evidence that *P. occidentalis* and *G. affinis* hybridize. Hybrids were not observed in the field or laboratory (Schoenherr, 1974; Meffe, pers. observ.), and conspecific mate choice fidelity was high in laboratory observations (Schoenherr, 1981).

Competition.—Because topminnows and mosquitofish are morphologically similar (Minckley, 1973), and competition is generally greatest among similar species (Darwin, 1859; Gause, 1934; Miller, 1967), one might predict intense interspecific resource competition; however, none can be demonstrated between *P. occidentalis* and *G. affinis* (Schoenherr, 1981; Meffe et al., 1983). The mosquitofish is largely a piscivore/insectivore (Harrington and Harrington, 1961; Myers, 1965), while topminnows feed primarily on detritus and vegetation, with insect larvae and amphipod crustaceans important in the diet of some populations (Minckley, 1973; Deacon and Minckley, 1974; Schoenherr, 1974; Constantz, 1976; Gerking and Plantz, 1980). Food choice also seems little influenced by sympatry (Schoenherr, 1981). Additionally, trophic morphologies are quite different. Mosquitofish have strong, conical teeth, firmly attached to the jaw, and a gut length about 0.69 times standard length (SL), whereas Sonoran

topminnows have elongate, spatulate teeth, more weakly attached to the jaw, and a gut length 1.5 to 2.0 times SL (Schoenherr, 1981; Meffe et al., 1983). These trophic morphologies are characteristic of a carnivore and an herbivore/detritivore, respectively (Al-Hussaini, 1949; Barrington, 1957; Lagler et al., 1977). Furthermore, there is no evidence that food is limiting in highly productive desert habitats (Schreiber and Minckley, 1981), and growth rates also appear unaffected in sympatry (Schoenherr, 1981). Competition hypotheses therefore appear unsupported.

Predation.—Predation was suggested as a major factor in decline of Sonoran topminnows (Minckley, 1973; Minckley et al., 1977; Schoenherr, 1981; Meffe et al., 1983), yet the hypothesis was not adequately tested. *Gambusia affinis* is a known piscivore and its introduction was correlated with population reductions of more than 20 species of fishes (Schoenherr, 1981). It eats *P. occidentalis* in the field and laboratory (Minckley, 1973; Schoenherr, 1981; Meffe et al., 1983) and is potentially capable of exerting predation pressure on the species. I tested the hypothesis that predation on juveniles causes local extinction of Sonoran topminnows.

Physiological Stress.—Schoenherr (1981), through observations of these two fishes in aquaria and an experimental pond, and with concordant observations by P. Winkler (in Schoenherr, 1981), concluded that mosquitofish physiologically stress topminnow adults by constant aggression. This resulted in reduced fecundity, cessation of feeding, and increased mortality of *P. occidentalis* when sympatric with *G. affinis*. I tested Schoenherr's hypothesis through examination of those parameters in a controlled laboratory experiment, and at a field site with natural experimental and control groups.

MATERIALS AND METHODS.—*Laboratory Coexistence Study.*—I examined impacts of predation by *G. affinis* on population size of *P. occidentalis* under non-competitive conditions. The null hypothesis is that there is no difference in topminnow population growth rates, and hence recruitment, when in allopatry or sympatry with mosquitofish.

Sympatric and allopatric populations of each species were established in 75.0 and 37.5 l aquaria, respectively. Six replicates of each were in simple habitats (sand substrate only) and 6 in complex habitats (sand, rocks, and submergent vegetation [*Vesicularia* sp., Hypnacea]). Eight females and four males of either or both species were stocked on 16 July 1981, at a density of 320 fish/m³ (natural densities vary widely from a few individuals to several hundred fish per m³). Topminnows were taken from a natural spring-seep in southern Arizona (Meffe et al., 1982) and mosquitofish were from an artificial pond at Arizona State University (ASU).

Fish were fed powdered trout chow twice daily, with frozen brine shrimp substituted three times weekly. Fish were fed to excess, thus eliminating food competition. Populations were counted at regular intervals for a total of 63 weeks and dead fish were removed and preserved in 10% formalin. Adult females were dissected as they died, and mature ova and embryos (= fertility) counted.

Field coexistence study.—The above design was repeated in a natural habitat, a small spring run near Bylas, Arizona (habitat descriptions are in Meffe, 1983a, and Meffe and Marsh, 1983), employing the same null hypothesis. Open-bottomed cages of 15 mm-mesh hardware cloth lined with nylon window screening were sunk into the substrate on 24 June 1981. Three allopatric (1,200 cm²) and three sympatric (2,400 cm²) covered cages were used. Seven female and three male topminnows were stocked in the former, and seven males and three females of both species were placed in the latter. All fish were collected *in situ*, and stocked at densities of 1 fish/120 cm² surface area (water depth = 3-10 cm). Only natural food was available. Individuals in each cage were counted 5, 13, and 24 days after stocking.

Fin damage analysis.—A characteristic result of interaction of these two poeciliids is damage to topminnow caudal fins, a direct result of mosquitofish aggression (Meffe et al., 1983). This was quantified in a laboratory experiment and at Bylas. The null hypothesis was that there would be no difference in fin damage frequency in allopatry or sympatry. Caudal fins were examined and scored for no damage (intact, rounded fin) or damage (shredded fin, missing tissue). Laboratory fish were held allopatrically or sympatrically in 37.5 or 75.0 l aquaria at constant densities for 52 days before examination. The field sympatric sample was compared with a 1968 collection (ASU museum) made prior to mosquitofish colonization.

Stress analysis.—To test the physiological stress hypothesis of Schoenherr (1981), I established 37.5 and 75.0 l aquaria in April 1982 and stocked 15 females and 5 males of either or both species, respectively. After 12 weeks, all surviving *P. occidentalis* were preserved in 10% formalin for three days, then transferred to 70% ethyl alcohol for a week. Standard lengths (nearest 0.1 mm) and wet weights (nearest 0.1 μ g) of the ovary and somatic tissue were measured for all females. Ovaries were dissected and numbers of embryos and mature ova counted. This experiment was repeated in August 1982. Additionally, wild topminnows were collected from two pools of Sharp Spring, Santa Cruz County, Arizona (Meffe et al., 1982) in June 1980, one sympatric with, and one allopatric to, mosquitofish. Fish were frozen on dry ice, transferred to a laboratory freezer, and analyzed as above within a month of collection.

RESULTS.—*Laboratory Coexistence Study.*—Allopatric populations of *P. occidentalis* successfully reproduced and grew in laboratory aquaria, whereas those sympatric with *G. affinis* had no net recruitment and steadily declined (Fig. 1). Population growth in simple and complex sympatric tanks was statistically indistinguishable, and these were combined in analysis.

In allopatry, *P. occidentalis* populations grew rapidly, stabilized, then began a slow, long-term decline (Fig. 1). The decline is attributed to toxic waste accumulations in aquaria; in particular, soluble reactive phosphate concentration toward the end of the experiment was 3.43 mg/l, compared with values in topminnow natural habitats ranging between 0.00 and 0.10 mg/l (Meffe et al., 1983). Dead and moribund fish, particularly juveniles, were common in the latter half of the experiment in allopatric tanks.

Despite these toxicity problems, topminnow populations all grew in the absence of mosquitofish. In contrast, there was no successful recruitment by *P. occidentalis* in presence of the introduced predator. Newborn fish were repeatedly observed in aquaria, but never survived more than a day; several were seen being eaten by female mosquitofish. Analysis of all *P. occidentalis* females that died before the decline phase revealed that most were gravid (42/51 allopatric [82.4%]; 36/42 sympatric [85.7%]), and that there was no significant difference in fertility between the two groups (allopatric: \bar{X} = 6.66, SD = 8.02; sympatric: \bar{X} = 5.95, SD = 4.36; t = 0.517, P = .6063). Topminnows in sympatry with mosquitofish therefore reproduced normally, but all offspring were eaten. There was no difference in mean number of topminnow adults surviving at the end of the 63 week experiment (allopatric: \bar{X} = 0.83, SD = 0.84; sympatric: \bar{X} = 2.33, SD = 2.39; t = 2.055, P = .0606), indicating their survival was not reduced by mosquitofish.

There was similarly no recruitment of *G. affinis* in any experimental unit. Females were fertile (allopatric: \bar{X} = 24.4, SD = 19.0, n = 18; sympatric: \bar{X} = 31.1, SD = 31.1, n = 23), but cannibalism was so severe that no juveniles escaped in these restricted aquarium habitats, even with vegetation as a refugium. In nature, refugia for the neonates of both species

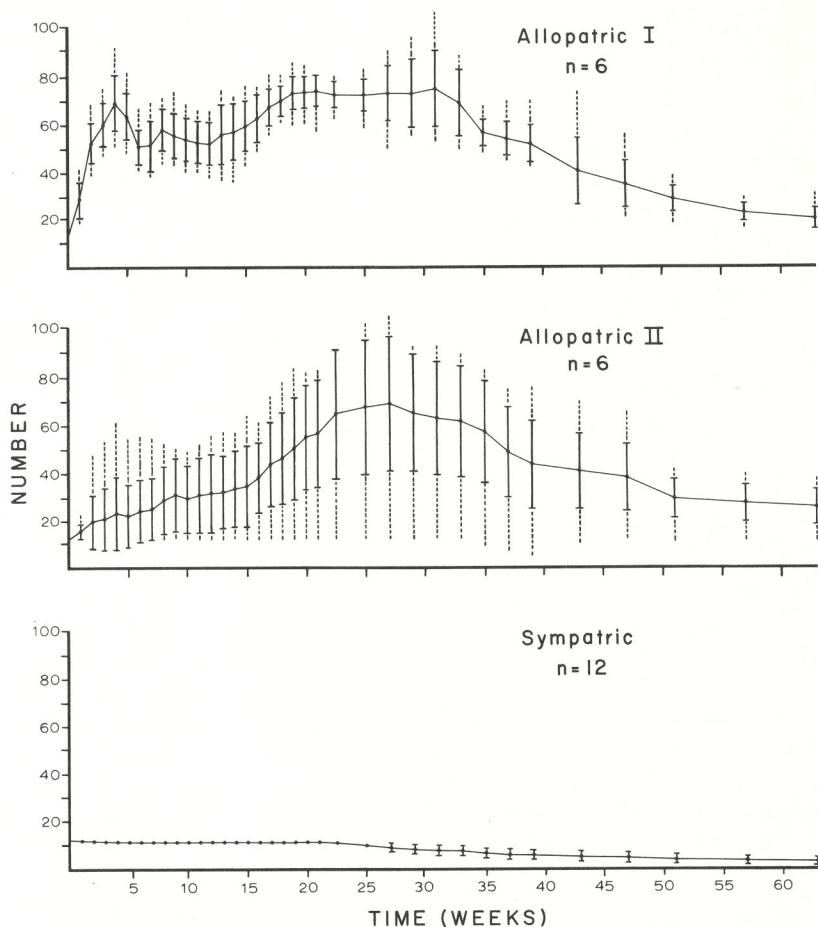


FIG. 1.—Results of laboratory coexistence study. Plotted is mean number of *P. occidentalis*, plus or minus two standard errors (solid lines) with range indicated (broken lines), versus time. Allopatric I is a complex habitat and allopatric II is a simple habitat; both habitats were combined for *P. occidentalis* sympatric with *G. affinis*.

are quantitatively and qualitatively different, especially with the presence of shallow areas inaccessible to adults. Since mosquitofish obviously recruit well in nature, predation rates in this experiment were probably artifactual. However, it does illustrate the potential extent to which mosquitofish predation may limit population growth, and suggests that this effect is partly a function of habitat size and structure.

Field Coexistence Study.—There was no recruitment of topminnows in sympatric field cages, and all three populations became extinct between days 13 and 24 (Fig. 2). Surviving adults were physically damaged in the first two weeks, and all were eaten by the end of the experiment. Allopatric cage populations all experienced successful recruitment and were extant at the end of the 24 day experiment (Fig. 2).

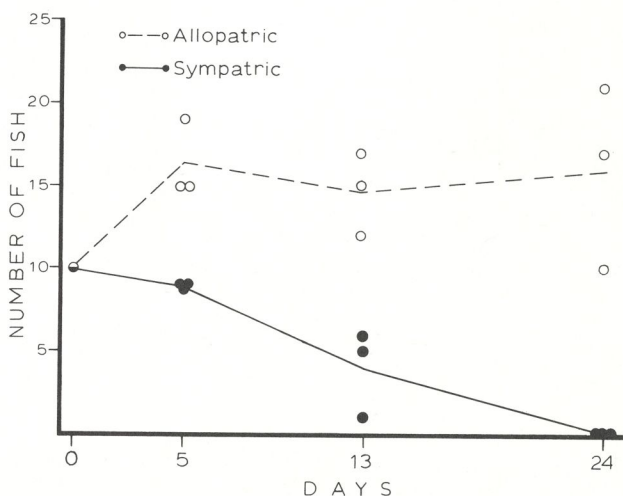


FIG. 2.—Results of field coexistence study. Plotted is individual population sizes of *P. occidentalis* versus time for populations allopatric to, and sympatric with, *G. affinis*. Lines connect population means.

Fin Damage Analysis.—In the native population at Bylas Springs, 122 of 178 (68.5%) topminnows examined from October 1980 to March 1982 had slight to heavy caudal fin damage. Forty-two topminnows collected in 1968, before mosquitofish colonization, had no damage. Over 100 topminnows examined between March and July, 1981 from an adjacent spring lacking mosquitofish exhibited <1% fin damage.

Similar damage appeared on laboratory topminnows coexisting with mosquitofish. After 52 days in aquaria, 73 of 130 (56.2%) topminnows held with *G. affinis* had damaged fins, while none of 144 held in allopatry was damaged. There was also a slight, but significant decrease in mean survival of populations of 12 topminnows adults when in sympatry (allopatric: $\bar{X} = 11.92$, $SD = 0.29$; sympatric: $\bar{X} = 10.92$, $SD = 0.90$; $t = 3.664$, $P = .0029$). When the species were placed together, mosquitofish females immediately became aggressive, and chased and bit topminnows. Within 15 minutes some fish were damaged; most were attacked within an hour. Mosquitofish did not generally act aggressively toward one another, and no fin damage was observed on that species.

Stress Analysis.—Topminnows sympatric with mosquitofish in the first laboratory stress experiment were significantly lighter in somatic weight, and produced fewer embryos and mature ova, than did allopatric individuals (Fig. 3, Table 1). In the second trial, significant differences appeared in ovary weight and fertility (Fig. 4, Table 1). There was no detectable effect of sympatry versus allopatry on total weight or ovary weight in the field (Fig. 5, Table 1) and trends (regression slopes) were in the opposite direction of laboratory results. There was a significant difference in fertility between allopatric and sympatric field populations, but again in the opposite direction of that seen in the laboratory.

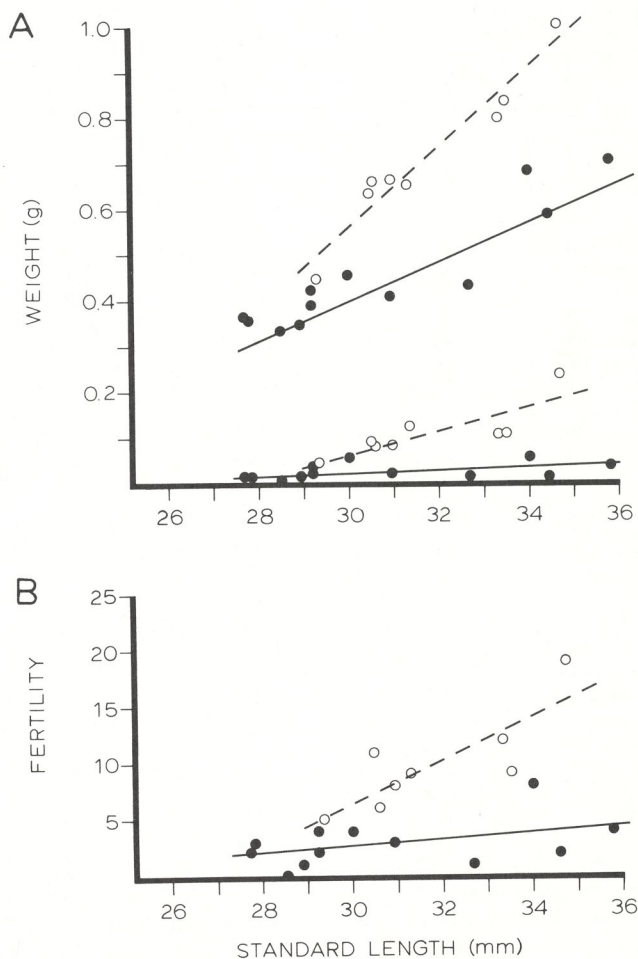


FIG. 3.—Results of laboratory stress analysis I. A) Plotted is wet body weight (upper regressions) and wet ovary weight (lower regressions) versus standard length for allopatric (○ - ○) and sympatric (● - ●) Sonoran topminnow populations. B) Plotted is fertility versus standard length for allopatric (○ - ○) and sympatric (● - ●) Sonoran topminnow populations.

DISCUSSION.—Available data suggest that replacement of *P. occidentalis* by *G. affinis* is primarily due to predation on juveniles, with stress responses in adults potentially playing a minor role. Other hypotheses, such as resource competition, hybridization, parasitism, or disease, are rejected for lack of supportive evidence.

Predation on topminnows by mosquitofish was repeatedly observed in the laboratory and the field. In both experimental settings, the native species did not recruit successfully when in sympatry with mosquitofish. A possible stress response, expressed as lighter, less-fecund female topminnows, was inconsistently observed in laboratory experiments. Since similar results

TABLE 1.—Regression statistics for stress studies. m = slope; b = Y -intercept; r = Pearson's product-moment correlation coefficient; F_s = sample statistic of F distribution; P = level of significance for test of relationship between dependent and independent variable. Regression comparisons = tests of difference between two analogous regression lines (e.g., lab sympatric vs. lab allopatric ovary weight). * = statistically significant relationship.

Parameters	m	b	r	F_s	P	Regression comparisons
LAB I						
I. Sympatric (n=12)						
Somatic weight	.042	-.860	.910	48.0	<.001*	$P < .05^*$
Ovary weight	.002	-.034	.329	1.2	<.5	$.2 > P > .1$
Fertility	.312	-6.75	.416	2.1	<.25	$P < .01^*$
II. Allopatric (n=8)						
Somatic weight	.087	-2.05	.968	88.7	<.001*	—
Ovary weight	.025	-.687	.820	12.4	<.025*	—
Fertility	1.90	-50.6	.809	11.4	<.025*	—
LAB II						
I. Sympatric (n=10)						
Somatic weight	.086	-1.88	.983	226.1	<.001*	$P > .1$
Ovary weight	.002	-0.05	.452	2.1	<.25	$P < .05^*$
Fertility	.178	-4.44	.359	1.2	<.50	$P < .05^*$
II. Allopatric (n=9)						
Somatic weight	.097	-2.14	.994	572.4	<.001*	—
Ovary weight	.014	-.366	.771	10.3	<.025*	—
Fertility	1.07	-23.4	.829	15.4	<.01*	—
FIELD						
I. Sympatric (n=20)						
Somatic weight	.102	-2.46	.939	140.3	<.001*	$P > .9$
Ovary weight	.035	-.979	.863	52.3	<.001*	$P > .9$
Fertility	2.53	-62.8	.896	32.1	<.001*	$P < .05^*$
II. Allopatric (n=20)						
Somatic weight	.060	-1.15	.938	133.0	<.001*	—
Ovary weight	.009	-.145	.425	4.0	.05 < P < .1	—
Fertility	1.38	-27.0	.822	15.4	<.005*	—

could not be demonstrated in nature, this may reflect the artifact of topminnows unable to escape harassment in the laboratory. The observation that *P. occidentalis* stops feeding in the presence of *G. affinis*, retreats to a hiding place, and dies (Schoenherr, 1981), was not supported here. In laboratory aquaria, little species segregation was found, and topminnows always fed despite frequent attacks from mosquitofish. Surface and underwater field observations confirmed the lack of segregation, and quantitative (Schoenherr, 1981) and qualitative (Meffe, unpubl. data) gut content analyses argue against cessation of feeding. However, a stress response demonstrated in the laboratory indicates at least a potential for contributing to species replacement in spatially restricted habitats in nature, such as small, isolated pools.

Further support for the predation hypothesis is provided by qualitative observations at Bylas. This formerly "pure topminnow" locality was colonized by mosquitofish in winter 1978-79, and numbers of the native poeciliid declined precipitously over the next two years (Meffe et al., 1983; Meffe, 1983a). In March 1982, with topminnows nearly extirpated, a live stock of *P. occidentalis* was removed and the spring was poisoned with the

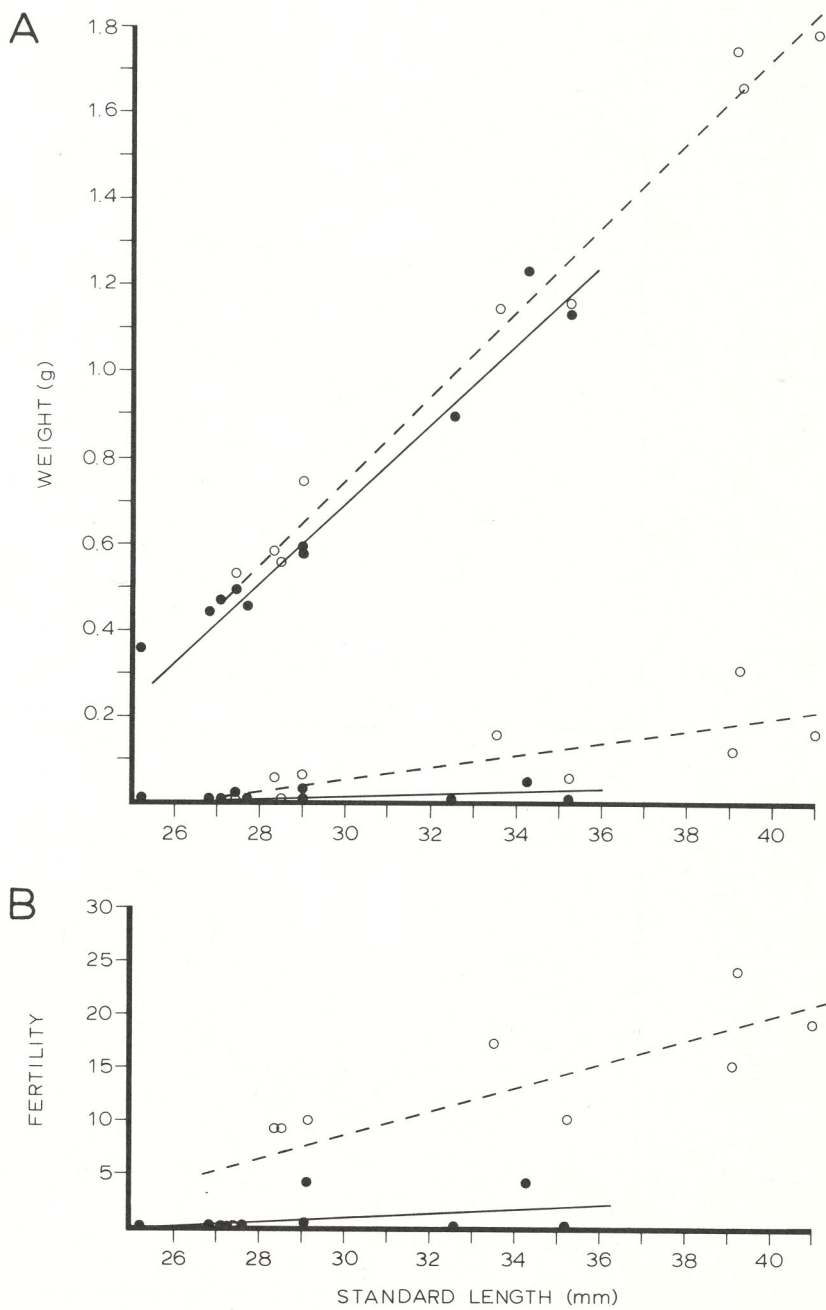


FIG. 4.—Results of laboratory stress analysis II. Symbols as in Figure 3.

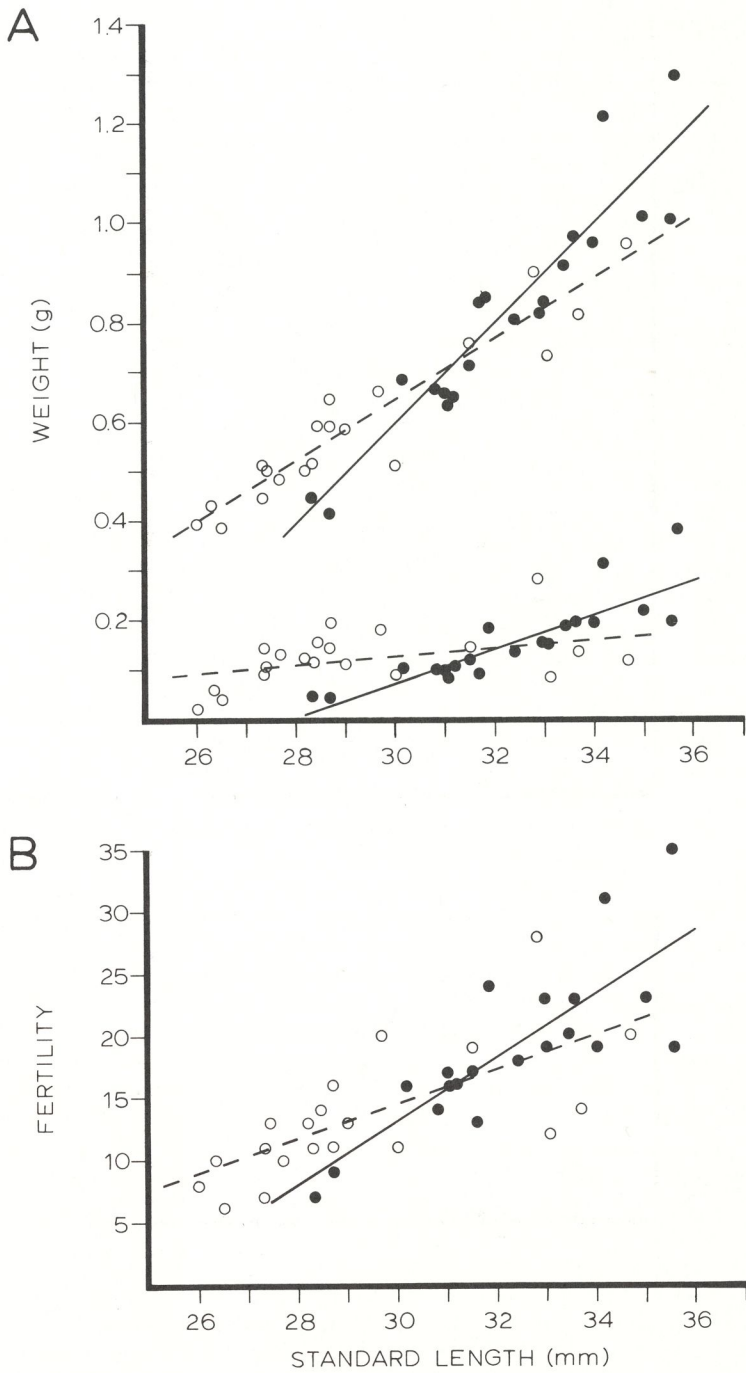


FIG. 5.—Results of field stress analysis. Symbols as in Figure 3.

piscicide Antimycin A. It was subsequently re-stocked with the original *P. occidentalis* (Meffe, 1983a). Before removal of *G. affinis*, juvenile topminnows numbered in the tens of individuals in each of two spring sources. Three weeks after re-stocking there were hundreds of juvenile topminnows at densities higher than I had ever observed, suggesting a previously large impact of predation on population recruitment.

Kitching and Ebling (1967), paraphrased by Simberloff (1981), proposed four criteria for establishing that predation is responsible for the absence of a species from an area. All four are met by this interaction:

1) "One must know, by prevention of predation, that physical factors are not limiting". This is obviously true in this case, since *P. occidentalis* formerly occupied habitats where *G. affinis* now prevails. Several of these habitats have not been physically altered other than through colonization by mosquitofish (Meffe et al., 1983).

2) "The geographical patterns of the predator and the putative prey must be complementary". These poeciliids, with allopatric natural ranges, meet this criterion (Rosen and Bailey, 1963).

3) "One must demonstrate, through laboratory, or preferably, field observations, the occurrence of predation". Both sets of observations have repeatedly been made (Minckley, 1973; Meffe et al., 1983; Minckley, pers. comm; and present study).

4) "Conduct transplant experiments in which the predator has been observed to eat the putative prey". This criterion has been satisfied numerous times, both in the present laboratory and field experiments, and by introduction of mosquitofish into natural habitats throughout Arizona, with subsequent predation on, and extinction of, topminnows.

Although predation is deemed important, rates and outcomes are obviously affected by other parameters such as alternative foods available for *G. affinis*, juvenile and adult densities, and particularly, environmental heterogeneity. Coexistence of predator and prey due to increased habitat complexity was proposed theoretically (Roff, 1974a,b; Hilborn, 1975; Levin, 1976; Hastings, 1977) and demonstrated empirically in fishes (Cooper and Crowder, 1979; Fraser and Cerri, 1982; Crowder and Cooper, 1982). I do not have data that address heterogeneity, but the most rapid elimination of topminnows occurred in the smallest, simplest habitats, such as field cages, laboratory aquaria, a 0.004 ha experimental pond (Schoenherr, 1974), and larger artificial ponds (Meffe et al., 1983). Long-term coexistence (up to 18 years) occurs in large, spatially and temporally more complex systems. The Santa Cruz River, which has several tributary springs that serve as repopulation centers, and Sharp Spring, with 18 separate sub-units (pools) connected by a complex marsh network, and with periodic floods, both have supported coexisting populations for long periods (Minckley et al., 1977; Meffe et al., 1982, 1983; Meffe, 1983b).

A common approach to studying predation is to analyze gut contents and infer population effects of cropping. No such analyses were conducted here, for several reasons. First, to observe full impact of predation on topminnow populations, it would be necessary to examine gut contents soon after initial colonization by mosquitofish, probably within the first few weeks.

At that time the highest concentration of juvenile prey would be available and the greatest intensity of predation would occur. Afterward, availability of juveniles would be reduced and few would be detected in gut analyses. Because no *G. affinis* were available from any locality directly after colonization, and intense cropping was recorded in all experiments, gut content analyses were deemed unlikely to provide further insight.

Second, there may generally be a low probability of finding juvenile fish in guts of these predators even under the best of circumstances. In the laboratory, fish were recognizable in gut contents for less than four hours after ingestion. If a single predation event occurred during each 16 hour daylength, an investigator would detect at most 4/16 or 25% of prey captures by gut analyses. Also, if predators greatly outnumber prey, as in several populations where *G. affinis* swarm by the thousands, then probability of detecting predation on young topminnows would be low.

Third, even if a predation rate is calculated, impact on the prey population is difficult to assess. A low predation rate may still have a large impact if the prey species has relatively low fecundity, as is the case here, or if predators are abundant. For example, Schoenherr (1974) studied a population of *G. affinis* soon after it colonized a *P. occidentalis* pond and reported that about 6% of mosquitofish diet (by volume) consisted of juvenile fish. Newborn topminnows average 1.336 μ g dry weight, and full-grown female mosquitofish are approximately 0.55 g. Assuming a mosquitofish ingests four times its weight per year (a conservative estimate [S. D. Gerking, pers. comm.]), a single female would consume about 100 topminnow juveniles per year. Since topminnow brood sizes range from about 5 to 15 individuals, with 2 to 5 broods per year (Constantz, 1974; Schoenherr, 1974), a single female mosquitofish could easily consume all offspring of a single topminnow in one season at this relatively low predation rate. Even "rare" predation on topminnows could decimate their populations.

Other examples of fishes being limited by piscivorous fishes were presented (summarized in Stroud and Clepper, 1979), but complete extirpation appears to be most prevalent where a new predator is introduced (e.g., Zaret and Paine, 1973). Rapid elimination of a prey species in these situations may reflect an evolution in communities with few or different natural predators. Consequently, there may be an absence of morphological or behavioral "anti-predator traits" in native species appropriate in avoiding new types of piscivores (Miller, 1961; Smith, 1978; Hobson, 1979; Stein, 1979).

"Naivete" of other prey taxa, due to evolution in predator-poor environments, was suggested as relevant to their declines (Simpson, 1950, 1953; Eckhardt, 1972), and may be a major factor in predation of native western fishes. As a group, these organisms evolved in habitats with few predaceous fishes. For example, in an area covering 325,000 km² of the southwest, including parts of the Chihuahuan, Sonoran, Mojave, and Great Basin deserts, there are 37 native inland fishes (Lee et al., 1980), of which only four (10.8%) are known piscivores. One (*Elops affinis*) is primarily marine, venturing periodically only into the lower Colorado River, and

another (*Ptychocheilus lucius*) is restricted as adults to deeper waters (>1m) of larger rivers (Minckley, 1973). Only the facultatively piscivorous chubs *Gila robusta* and *G. intermedia* interacted with spring or small-stream species on a regular basis, and even they are usually restricted to deeper waters (Minckley, 1973). In contrast, of at least 57 introduced fishes established in this region, 26 (45.6%) are piscivorous, including such voracious egg, juvenile, or adult predators as largemouth (*Micropterus salmoides*) and smallmouth (*M. dolomieu*) bass, several catfishes (*Ictalurus* spp.), carp (*Cyprinus carpio*), and mosquitofish (Minckley, 1973). This increase in predator load (2, to at least 28 species) is compounded by the fact that several introduced predators are small enough to gain access to shallow backwaters and marshes which formerly provided refuge from larger piscivores (Minckley, 1983). This shift to predator-influenced communities occurred instantaneously on an evolutionary time scale, with little opportunity for native species to evolve appropriate behavioral responses. As a result, small, native western fishes may fall easy prey to this new suite of predators, as illustrated by the extinct Monkey Spring pupfish, *Cyprinodon* sp. This undescribed species from southern Arizona was eliminated from its only known locality in just a few months by largemouth bass predation (Minckley, 1973).

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Influence of Habitat Complexity on Resistance to Flooding and Resilience of Stream Fish Assemblages

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Abstract.—The structure of fish assemblages in five reaches of a high desert stream in north-central Oregon was determined by snorkeling before and after a summer flash flood and two spring floods. One reach in each of two other streams that were unaffected by the first flood was used as a reference system. Stream reaches varied in habitat complexity as measured by hydraulic retention. Following the floods, hydraulically complex stream reaches lost proportionately fewer fish, had generally higher fish diversities, and had higher fish assemblage similarity than hydraulically simple stream reaches. Fish assemblages were resilient, and certain species such as speckled dace *Rhinichthys osculus* were exceptionally good at recolonizing disturbed habitats. Successful recruitment of different fish species depended, in part, on flood timing. Young of the year of species that spawn in early spring (e.g., rainbow trout *Oncorhynchus mykiss*) were more negatively affected by early spring floods than summer floods. Species that spawn later in the season (e.g., cyprinids and catostomids) were more negatively affected by summer flooding. Higher fish diversities in hydraulically complex reaches (lower disturbance intensity) after floods support predictions of the intermediate-disturbance hypothesis and suggest that fish assemblage resistance may be related to overall habitat complexity in these small streams.

Flooding is one of the most important abiotic factors that structure biotic assemblages in streams (Resh et al. 1988). Many studies have shown that floods can alter both assemblage structure and abundance of fishes in stream reaches (Harrell 1978; Ross et al. 1985; Matthews 1986; Meffe and Minckley 1987; Fausch and Bramblett 1991; Lamberti et al. 1991). Different species or age-classes of a species vary considerably in vulnerability to flooding (Harrell 1978). For example, in an Arizona desert stream, the native Gila topminnow *Poeciliopsis occidentalis* survived floods better than the exotic western mosquitofish *Gambusia affinis* (Meffe 1984; Minckley and Meffe 1987). Benthic species such as sculpins (Cottidae) are vulnerable to crushing by bedload movement during spates and high flushing flows (Erman et al. 1988). Young-of-year fishes may be particularly vulnerable to floods because of their poor swimming ability and small size (Harvey 1987).

For example, young of year and eggs of trouts are affected more strongly by floods than are adults (Seegrist and Gard 1972; Hanson and Waters 1974).

Two components of species assemblage stability are resistance, the ability to resist change during a disturbance, and resilience, the ability of an assemblage to return to its predisturbance structure after a disturbance (Connell and Sousa 1983). In streams, physically complex habitats may be more stable (biotically structured) than simple habitats (abiotically structured) (Schlosser 1987). Certain channel units (e.g., deep pools with permanent structures) and stream reaches (e.g., broad, unconstrained reaches) may serve as refugia during or after floods (Tschapinski and Hartman 1983; Matthews 1986; Hill and Grossman 1987; Meffe and Minckley 1987; McMahon and Hartman 1989; Townsend 1989; Fausch and Bramblett 1991; Lamberti et al. 1991). Channel units are defined as pools, riffles, or runs with lengths greater than the average channel width; stream reaches are a series of connected channel units (Frissell et al. 1986; Gregory et al. 1991).

Habitat complexity can be defined as the diversity of different habitat types available to fishes and has been measured in various ways. The most

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common method is to compute a Shannon–Wiener diversity index for different categories of depth, current velocity, and substrate type (Gorman and Karr 1978; Schlosser 1982; Angermeier and Schlosser 1989). Fausch and Bramblett (1991) defined complex pools as those more than 1 m deep with coarse substrate (>64 mm in diameter) and cover from vegetation or undercut banks. In areas with dense forests, the amount and configuration of large woody debris have been used to measure habitat complexity (Tschaplinski and Hartman 1983). Conducting dye releases in 100-m reaches, Kaufmann (1987) found that hydraulic resistance and transient hydraulic storage were significantly correlated with measures of pool volume, channel morphometric variability, and volume of woody debris. Lamberti et al. (1989) also found that hydraulic retention was positively related to habitat complexity.

On 13 August 1988, 26 April 1989, and 10 May 1989, floods occurred in isolated areas of an eastern Oregon drainage. Before and after the floods, fishes were inventoried in reaches of varying habitat complexity. Habitat complexity was measured by hydraulic retention. We sought to answer whether habitat complexity and time of flooding affect the resistance and resilience of stream fish assemblages to flash floods.

Methods

Site description.—The John Day basin in the high desert of north-central Oregon (Figure 1) is the fourth largest drainage in Oregon (21,072 km²). It also is 1 of 42 free-flowing rivers longer than 200 km in the contiguous USA (Benke 1990). Peak stream discharges occur in late winter to early spring during snowmelt. Low water discharge typically occurs in late summer, punctuated by floods following thunderstorms.

Streams in the John Day basin were clustered according to their physical attributes so that physically similar streams could be compared (H. W. Li and others, unpublished data). Physical data on streams in the basin were taken from maps and examined by an agglomerative clustering procedure (Gauch 1982). Three streams were chosen for the present study because of their high physical similarity. Five stream reaches (RC1–RC5) about 150 m long in Rock Creek and one each in Fields (FC1) and Murderers creeks (MC1) were sampled (Table 1).

Thirteen fish species inhabited the study streams (Table 2). Rainbow trout, chinook salmon, mountain whitefish, mountain sucker, and torrent and paute sculpin are considered temperate steno-

therms; longnose dace and bridgelip sucker are temperate mesotherms; and chiselmouth, speckled dace, northern squawfish, redbreasted shiner, and largescale sucker are temperate eurytherms (Li et al. 1987). In Rock Creek, adult rainbow trout lay eggs in gravels during April, and young emerge from the gravels about 6–8 weeks later (Wydoski and Whitney 1979). The remaining species (except the mountain whitefish) spawn later in spring and summer and usually hatch in 2 weeks or less (Wydoski and Whitney 1979). Rainbow trout inhabit midwater and feed on drifting invertebrates; sculpins and longnose dace are benthic, inhabiting substrate interstices and feeding primarily on benthic invertebrates; the suckers are benthic herbivores or omnivores; chiselmouths are also omnivorous but occupy the water column; speckled dace are benthic insectivores that occupy the lower water column and streambed; and redbreasted shiners and northern squawfish are midwater insectivores, the latter becoming increasingly piscivorous when reaching 240 mm total length (Li et al. 1987).

Floods.—On 13 August 1988, between 1700 and 1730 hours, a severe thunderstorm in the Rock Creek drainage yielded 4.6 cm of water from melted hail (T. Fremd, U.S. National Park Service, personal communication). Water levels rose quickly above the active channel, washed large amounts of sediment (silt to large boulders) into the stream, destroyed small bridges, and blocked roads with debris. Water levels increased 5–10 times within minutes (Fremd, personal communication). Two days later, discharge in Rock Creek had returned to nearly normal levels. Fields Creek and Murderers Creek did not experience such flooding. The next spring, higher-than-normal rain showers triggered a series of even larger floods on 26 April and 10 May in all study streams (Ron Gaither, local resident, personal communication).

Sampling.—We snorkeled to count fish by species and size-class (adult, juvenile, young of year) in channel units representative of the stream reach once during each sampling period of 13 July–13 August 1988 (before the flash flood), 1–25 September 1988 (after the flash flood), 6–10 June 1989 (after spring floods), and 27 July–4 August 1989. For example, pool channel units were snorkeled in stream reaches dominated by pool channel units (RC5), and riffles and runs were snorkeled in stream reaches dominated by riffles and runs (RC2). Three to 15 representative channel units were inventoried in each reach. Two divers entered the downstream end of a channel unit and snorkeled upstream in lanes, counting fish and recording numbers on white Plexiglas slates. Snor-

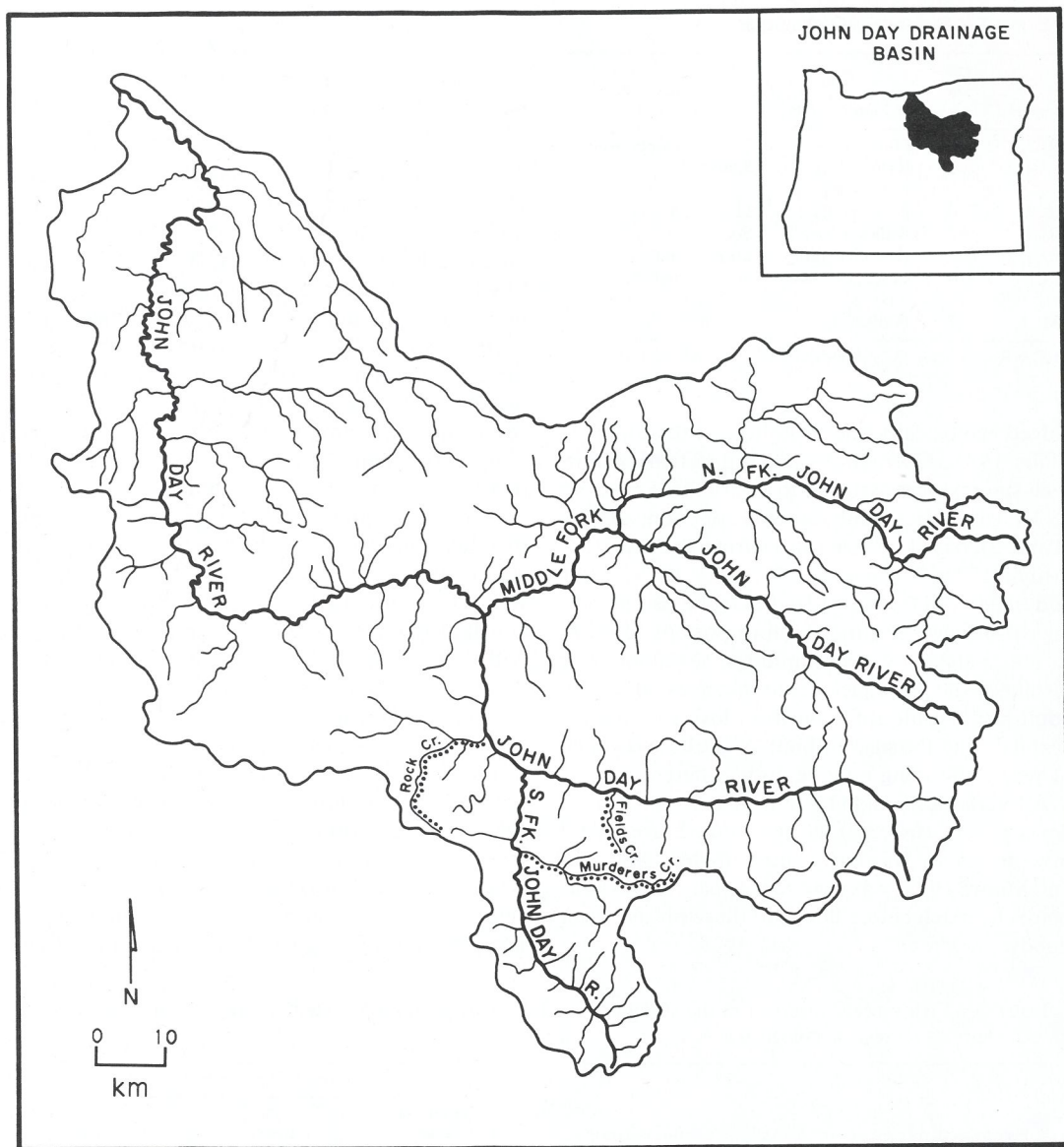


FIGURE 1.—Map of the study site in the John Day basin, north-central Oregon. Dotted lines indicate the streams studied.

keling was conducted between 1000 and 1600 hours. In three of the Rock Creek reaches, we snorkeled the same channel units twice to determine precision of our snorkeling technique. Precision was estimated by subtracting the second count from the first count and dividing the difference by the first count.

Water volumes snorkeled were calculated by multiplying the length, average width, and average depth of the channel unit sampled. One to five transects, depending upon the channel unit's size

and degree of homogeneity, were taken perpendicular to stream flow. Depths were taken at 1-m intervals along the transect, and widths were measured to the wetted edges.

Assemblage analysis.—Fish assemblages were compared between two dates, among three or more dates, and among reaches by species and ecological species diversity (H' ; Shannon and Weaver 1949), evenness (Pielou's J ; Peet 1974), species richness, and total fish density. Ecological species were defined as subsets of the species that were

TABLE 1.—Stream reach characteristics.

Reach ^a	Elevation (m)	Channel units	Protective substrate
RC5	795	Plunge pools	Large boulders, wood
RC4	761	Runs, riffles, shallow pools	Sparse
RC3	730	Runs, pools	Large boulders
RC2	690	Riffles, runs	Sparse
RC1	660	Cascades, pools	Large boulders
FC1	910	Cascades, riffles, pools	Wood, small boulders
MC1	927	Pools, runs	Sparse

^a RC = Rock Creek; FC = Fields Creek; MC = Murderers Creek.

judged ecologically and morphologically different (Polis 1984; Gorman 1988). Individuals within each species were assigned to one of three possible ecological species: adult, juvenile, or young of year (Table 2), based on size ranges from the literature (Moyle 1976; Wydoski and Whitney 1979; Sigler and Sigler 1987). We believe that the use of ecological species categories is an important addition to the analysis by taxonomic species alone. For instance, the ecological consequences of losing adult fish is quite different from losing young-of-year fish, and the susceptibility of adults and young of year to flooding may be quite different.

All variables listed above were calculated from density data (fish/m³) as determined from field inventories. A similarity index (SIMI; McIntire and Moore 1977) was used to compare fish assemblages by reach before floods to those present after floods:

$$\text{SIMI}(a,b) = \frac{\sum_{i=1}^S P_{ai}P_{bi}}{\left(\sum_{i=1}^S P_{ai}^2\right)\left(\sum_{i=1}^S P_{bi}^2\right)};$$

" P_{ai} and P_{bi} are the proportions of individuals represented by the i -th taxon in assemblages a and b respectively; and S is the total number of taxa in the assemblages" (McIntire and Moore 1977). The SIMI ranges from 0 to 1, 1 being complete assemblage similarity and 0 being no assemblage similarity. A similarity index was chosen instead of a rank correlation statistic because of the small number of species in the study reaches, which could result in a high probability of accepting the null hypothesis when it was false. The SIMI also uses density instead of ranks as input variables.

Habitat complexity.—We used the fluorescent dye rhodamine-WT (Replogle et al. 1976) to measure hydraulic retention. A known amount of dye was mixed into 15 L of water and released at a constant rate into a turbulent area of the stream with a steady-head dripper system. By visual observation, we determined that dye usually mixed completely with stream water within 10 m of the release point. A field fluorometer was used to monitor dye concentration at 100 m (in 1988) or 150 m (in 1989) downstream of the release point. Dye was released until an equilibrium level was reached (i.e., all water within the reach was equally labeled). Dye release was then halted, and concentration was monitored with the fluorometer until less than 2% of equilibrium concentrations

TABLE 2.—Fish species observed in the study area in John Day basin, north-central Oregon. Three size-classes for each species represent ecological species.

Family and species	Common name	Total length (mm)		
		Young of year	Juvenile	Adult
Salmonidae				
<i>Oncorhynchus mykiss</i>	Rainbow trout	<90	90–300	>300
<i>Oncorhynchus tshawytscha</i>	Chinook salmon	<90	90–140	>140
<i>Prosopium williamsoni</i>	Mountain whitefish	<90	90–220	>220
Cyprinidae				
<i>Acrocheilus alutaceus</i>	Chiselmouth	<45	45–130	>130
<i>Ptychocheilus oregonensis</i>	Northern squawfish	<70	70–240	>240
<i>Rhinichthys cataractae</i>	Longnose dace	<50	50–76	>76
<i>Rhinichthys osculus</i>	Speckled dace	<33	33–46	>46
<i>Richardsonius balteatus</i>	Redside shiner	<40	40–63	>63
Catostomidae				
<i>Catostomus columbianus</i>	Bridgelip sucker	<79	79–152	>152
<i>Catostomus macrocheilus</i>	Largescale sucker	<50	50–170	>170
<i>Catostomus platyrhynchus</i>	Mountain sucker	<38	38–127	>127
Cottidae				
<i>Cottus beldingi</i>	Paiute sculpin	<36	36–53	>53
<i>Cottus rhotheus</i>	Torrent sculpin	<38	38–53	>53

remained within the reach. From the dye-decay curve, movement of the water mass out of the reach can be described by

$$C_t = C_o e^{-kt};$$

C_o is the equilibrium dye concentration in the reach, C_t is the dye concentration in the reach after some interval t , and k is the instantaneous rate of dye decay (or instantaneous retention rate), and $1/k$ is the time that the "average" water molecule spends within the reach (Newbold et al. 1981).

From the dye accumulation and evacuation curves, 50% travel time (time required for the reach to evacuate 50% of its water mass as determined from dye decay) and 95% travel time (time required for the reach to evacuate 95% of its water mass) also were derived. Discharge within the reach also was determined with the dye dilution method (Replogle et al. 1976).

Dye releases were conducted 31 August–2 September 1988 for 100 m each of four Rock Creek sites (RC1, RC2, RC3A, and RC4), Murderers Creek (MC1), and Fields Creek (FC1). The dye release in RC3A was not in the same area as the fish inventory. From 1 to 3 August 1989, dye releases were repeated in all the above Rock Creek sites, except that the dye release in RC3 (RC3B) was in the same area as the fish inventory; dye was also released at site RC5 but not at sites MC1 and FC1. Dye releases were extended to 150 m in 1989 to encompass a larger proportion of the study reach.

Pearson's r was used to determine the relationship between hydraulic retention (50% travel time) and the absolute value of the change in fish density before and after the first flood. Proportions were arcsine-transformed to normalize the data.

Results

Retention

Relative patterns of dye retention were similar between years in Rock Creek reaches (Table 3). Reaches RC1, RC3, and RC5 were the most hydraulically retentive during 1989, and RC1 during 1988, as measured by 50 and 95% travel times. Hydraulic retention was lowest in both years in RC2 and RC4. Hydraulic retention in RC3 was not comparable between years because the dye releases were conducted in different reaches.

Variation in retention within Rock Creek reaches within a year was likely not affected by the small within-year differences in discharge, but between-year differences corresponded to changes in dis-

TABLE 3.—Hydraulic retention in 1988 (100-m reaches) and 1989 (150-m reaches) in Rock Creek (RC), Murderers Creek (MC), and Fields Creek (FC). 50% TT = 50% travel time; 95% TT = 95% travel time.

Site	50% TT (min)	95% TT (min)	Discharge (m ³ /s)
1988			
RC4	5	9	0.230
RC3A	6	9	0.218
RC2	6	9	0.268
RC1	10	20	0.276
MC1	29	73	0.041
FC1	23	37	0.011
1989			
RC5	10	16	0.087
RC4	8	12	0.079
RC3B	9	14	0.083
RC2	7	11	0.094
RC1	8	14	0.106

charge (Table 3). Rock Creek discharge in August 1988 was more than double the discharge in August 1989. Unretentive reaches (RC2 and RC4) had lower retention during 1988 than 1989, but the retentive reach (RC1) had lower retention during 1989 than 1988. The 1989 retention data were used in subsequent analyses because they incorporated a larger portion of the study reach, included the correct site within the RC3 reach, and included RC5.

The reference reaches in Murderers Creek and Fields Creek were more hydraulically retentive than any of the Rock Creek reaches (Table 3). This may be explained in part by the lower discharge, gradient, and water velocity of the reference sites, which in combination increased retention.

Fish Responses

The greatest change in total fish densities during the August 1988 flood were in hydraulically unretentive stream reaches (Table 4; $r = -0.87$, $N = 5$, $P < 0.05$). Change in adult fish densities corresponded to hydraulic retention ($r = -0.95$, $N = 5$, $P < 0.01$), although correlations between retention and changes in densities of juveniles and young of year were not statistically significant. With the exception of RC3, all fish densities in the Rock Creek stream reaches examined declined after the August 1988 flood. The increase in fish density in RC3 was largely due to a redistribution of rainbow trout and speckled dace following the flood (Table 5). Over the same time period, fish densities increased in the reference reaches, so changes in fish densities in Rock Creek were attributed to the flood (Table 4). Precision of snorkeling estimates for

TABLE 4.—Total, adult, juvenile, and young-of-year fish densities in reaches of Rock, Fields, and Murderers creeks during sampling dates in 1988 and 1989. Flooding occurred on 13 August 1988, 26 April 1989, and 10 May 1989. The "change" in fish density was the density of fish during July 1988 minus the density of fish during September 1988, divided by the density of fish during July 1988 (– = net loss; + = net gain).

Site	Density (fish/m ³)		Proportional change, 1988	Density (fish/m ³)	
	Jul 1988	Sep 1988		Jun 1989	Aug 1989
All fish					
RC5	4.95	4.27	-0.14	0.77	4.96
RC4	3.86	0.91	-0.76	1.36	5.49
RC3	3.92	4.78	+0.22	2.63	9.84
RC2	24.69	8.59	-0.65	0.58	10.20
RC1	4.54	2.03	-0.55	1.33	5.11
FC1	9.87	14.88	+0.51	1.69	5.04
MC1	8.69	9.40	+0.08	1.60	14.92
Adults					
RC5	2.92	2.52	-0.14	0.17	0.76
RC4	1.91	0.56	-0.71	0.37	1.13
RC3	2.32	1.23	-0.47	0.78	0.51
RC2	13.48	2.91	-0.78	0.27	1.02
RC1	2.54	0.66	-0.74	0.85	0.57
FC1	1.01	0.64	-0.37	0.17	0.28
MC1	3.79	4.74	+0.25	0.86	10.65
Juveniles					
RC5	1.24	1.19	-0.05	0.60	2.87
RC4	0.98	0.09	-0.91	0.99	3.11
RC3	0.96	1.88	+0.96	0.95	2.36
RC2	10.02	5.62	-0.44	0.28	2.26
RC1	1.36	0.88	-0.35	0.27	0.47
FC1	1.35	5.12	+2.81	1.52	0.99
MC1	1.81	4.28	+1.36	0.68	3.57
Young of year					
RC5	0.79	0.56	-0.28	0.00	1.33
RC4	0.97	0.26	-0.73	0.00	1.25
RC3	0.64	1.67	+1.61	0.91	6.97
RC2	1.19	0.07	-0.94	0.03	6.92
RC1	0.64	0.49	-0.23	0.20	4.07
FC1	7.51	9.12	+0.21	0.00	3.76
MC1	3.08	0.39	-0.87	0.05	0.70

total fish densities were -9.0, -0.3, and +6.6% for RC1, RC2, and RC4, respectively. In June 1989, fish densities in all stream reaches were far below the 1988 pre-flood densities, ranging from 2 to 67% of the July 1988 densities. Because of possible winter mortality or emigration it is difficult to know how many fish were lost in each stream reach as a result of the spring 1989 floods. Recolonization of the stream reaches was rapid, however, and by August 1989 fish densities were close to or above predisturbance levels.

Fish species differed in their response to flooding and in their ability to recolonize habitats following flooding (Table 5). Compared with other

TABLE 5.—Densities of rainbow trout, speckled dace, bridgelip sucker, young-of-year rainbow trout, and late-spawned young-of-year fish in Rock, Fields, and Murderers creeks on sampling dates in 1988 and 1989.

Site	Density (fish/m ³)			
	Jul 1988	Sep 1988	Jun 1989	Aug 1989
Rainbow trout				
RC5	1.85	1.42	0.42	1.29
RC4	1.54	0.22	0.67	1.13
RC3	0.37	1.10	0.09	0.44
RC2	0.58	0.07	0.04	0.00
RC1	0.27	0.10	0.01	0.00
FC1	8.74	12.00	1.47	4.47
MC1	0.93	0.89	0.34	1.88
Speckled dace				
RC5	1.68	1.39	0.06	2.32
RC4	1.76	0.52	0.45	3.62
RC3	2.33	2.98	1.56	6.84
RC2	7.32	0.89	0.27	6.84
RC1	2.09	0.56	0.20	1.89
FC1	0.11	0.00	0.00	0.00
MC1	4.82	1.86	0.66	5.96
Bridgelip sucker				
RC5	0.50	0.34	0.27	0.95
RC4	0.38	0.02	0.21	0.11
RC3	0.34	0.52	0.08	0.74
RC2	5.91	0.23	0.15	0.65
RC1	0.36	0.02	0.12	0.13
FC1	0.00	0.00	0.00	0.00
MC1	1.15	1.62	0.00	0.38
Young-of-year rainbow trout				
RC5	0.71	0.54	0.00	0.24
RC4	0.95	0.17	0.00	0.40
RC3	0.22	0.45	0.00	0.03
RC2	0.12	0.00	0.00	0.00
RC1	0.23	0.10	0.00	0.00
FC1	7.51	8.64	0.00	3.62
MC1	0.53	0.27	0.00	0.66
Late-spawned young-of-year fish				
RC5	0.07	0.03	0.00	1.09
RC4	0.02	0.09	0.00	0.84
RC3	0.42	1.21	0.91	6.94
RC2	1.07	0.07	0.03	6.92
RC1	0.41	0.39	0.20	4.07
FC1	0.00	0.48	0.00	0.14
MC1	2.55	0.12	0.05	0.05

species, speckled dace was the best at recolonization after habitats were disturbed, often returning to densities higher than predisturbance levels. Rainbow trout and bridgelip sucker were the less effective recolonizers after flood disturbance. Following all floods (August 1989), rainbow trout and bridgelip sucker occasionally exceeded predisturbance levels but most often failed either to recolonize some reaches or to recolonize stream reaches to predisturbance levels. Longnose dace were rare and were found in only three reaches before

the first flood. After the first flood, longnose dace were found in only one reach through August 1989.

Survival of young-of-year fish seemed to be related to timing of adult spawning and flooding. Young of year that had been spawned in late spring or early summer were more abundant in August 1989 than in September 1988 in all Rock Creek sites, whereas young rainbow trout (spawned in early spring) decreased in three out of four of the Rock Creek reaches that contained them (Table 5). During the same time period, young of year of species that spawn in late spring to early summer decreased in reference reaches, and young rainbow trout decreased in Fields Creek but increased in Murderers Creek.

Species diversity was generally higher in hydraulically retentive than in less retentive stream reaches after flooding (Table 6). Sites RC5 and RC1 had the highest diversity in Rock Creek in September 1988 and August 1989. Diversity in RC5 and RC1 increased following the first flood, as did that of the reference reaches. Site RC3 was the only exception to this pattern, which probably resulted from the addition of the already common speckled dace and the loss of four rare species (many represented by only one individual). After all floods, in August 1989, diversity decreased from 1988 levels in all reaches except for the reference reaches. There were no clear patterns observed for species evenness and richness. Ecological species diversity was highest in retentive habitats after the 1988 flood (Table 6). Ecological species diversity declined in RC4, RC3, and RC2 and increased slightly in RC5 and RC1 after that flood.

Assemblage similarity was quite high for all stream reaches across all sampling periods when compared with preflood assemblages, but was highest in RC5 or RC1, the most hydraulically retentive reaches (Table 6). Following the first flood, RC5 and RC3 were most similar to corresponding preflood assemblages. In August 1989, RC5, RC3, and RC1 were most similar to July 1988 assemblages. High SIMI values for RC4 may be the result of low densities of young of year, which are typically quite variable, and the presence of a high proportion of species that are good colonizers (Table 5). Assemblages in RC2 were consistently the least similar to predisturbance assemblages. Among the reference reaches, Fields Creek had a nearly identical fish assemblage throughout the study period (SIMI > 0.99). The relatively low SIMI value (following the first flood) for Murderers Creek largely resulted from immigration of reddsides shiners and northern squawfish

TABLE 6.—Diversity (Shannon–Wiener) for true species and ecological species and similarity index (SIMI) values for stream reaches in Rock Creek, Fields Creek, and Murderers Creek between sampling dates, 1988 and 1989. All SIMI values were calculated with the July 1988 sample as the standard against which assemblages at different times after the flood(s) were compared. July 1988 was before first flood; September 1988 was after first flood; June 1989 was after spring floods; August 1989 was 2 months after spring floods.

Site	Jul 1988	Sep 1988	Jun 1989	Aug 1989
Species diversity				
RC5	1.50	1.60	1.01	1.28
RC4	1.16	1.12	1.12	1.06
RC3	1.22	1.02	0.39	0.87
RC2	1.37	1.32	1.42	0.78
RC1	1.27	1.55	1.42	1.16
FC1	0.39	0.49	0.39	0.43
MC1	1.26	1.39	1.12	1.44
Ecological species diversity				
RC5	1.90	2.03	1.32	1.99
RC4	1.67	1.44	1.37	1.88
RC3	1.99	1.88	1.33	1.69
RC2	2.16	1.75	2.03	1.78
RC1	1.99	2.03	1.97	1.90
FC1	0.78	1.15	0.47	0.95
MC1	2.15	1.94	1.64	1.92
SIMI				
RC5	0.99	0.78	0.93	
RC4	0.92	0.96	0.90	
RC3	0.94	0.95	0.94	
RC2	0.63	0.72	0.63	
RC1	0.86	0.78	0.96	
FC1	0.99	1.00	1.00	
MC1	0.68	0.90	0.91	

and corresponding emigration or mortality of speckled dace.

Discussion

Dye retention was measured during summer base flow, but we believe that the relative differences between reaches was as great or greater during the floods. As discharge increases in complex reaches, the dead zone fraction (a measure of hydraulic retention) increases. In simple reaches the dead zone fraction decreases (Kaufmann 1987). This means that complex reaches become absolutely and relatively more complex than simple reaches as discharge increases. Our data support the above statement. Retention in RC2 and RC4 (simple reaches) was less, but retention in RC1 (a complex reach) was greater, during the high-discharge summer of 1988 than during the low-discharge summer of 1989 (Table 3).

Compared with other organisms, temperate stream fishes live in environments characterized

by high physical stress (Schoener 1987; Townsend 1989). Among temperate lotic ecosystems, desert streams are probably among the most physically unpredictable (Fisher 1982; Meffe and Minckley 1987; Poff and Ward 1989).

Because of the high level of disturbance in desert streams, the intermediate-disturbance hypothesis (Connell 1978) predicts that fish diversity should be low and that any reduction in the frequency or intensity of disturbance, or an increase in predictability (Resh et al. 1988) of disturbance, increases diversity. Horwitz (1978) found that species diversity was lowest in stream sections with the most discharge variability. In addition, increases in diversity downstream were greatest in streams with the greatest reduction in discharge variability downstream. Although flash floods may affect an entire stream, particular habitat types within the stream may be affected differentially: flood intensity should be lower in complex than in simple stream reaches because greater hydraulic roughness dissipates more of the power of the high discharges. Thus, species diversity after a flood should be higher in complex than in simple reaches.

In this study, flood effects were most profound in simple stream reaches, as demonstrated by the higher proportion of retained fishes in complex and reference reaches during the August 1988 flood. After the flood, species and ecological species diversities were generally higher in complex than in simple stream reaches. The low species diversity for one complex site (RC3) after the flood resulted from the loss of several rare species and the addition of speckled dace.

Community stability has been a controversial topic among ecologists (Schoener 1987). Two components of community stability are resistance and resilience to disturbance (Connell and Sousa 1983). Fish assemblages in complex stream reaches of Rock Creek were more resistant to the August 1988 flood and more resilient after the spring floods than fish assemblages in simple stream reaches. Similarities in assemblages before and after the August flood were generally higher among complex habitats than among simple habitats. Following fall emigration and a series of spring floods, fish assemblages in complex habitats during August 1989 were most similar to assemblages in the same stream reach before summer and spring floods.

The timing, frequency, and intensity of flooding can determine community structure through effects on recruitment and subsequent age-class structure. Species that minimize exposure of vul-

nerable life history stages to disturbance increase the probability of recruitment success (Seegrist and Gard 1972). Summer floods are detrimental to cyprinids and catostomids that spawn during the late spring and summer. Recruitment of the most abundant salmonid present in this study (rainbow trout) is most affected by flooding during the early spring, when the eggs are still in gravel.

Fish inhabiting the interstitial spaces of the substrate may be more vulnerable to floods than species in the water column. Erman et al. (1988) found that floods inflict high mortality on fish that live in interstitial spaces of streambed sediments, probably because they are crushed by bedload movement. We suspect that high frequency of floods and slow recolonization are responsible for the low density of fish that occupy interstitial spaces in Rock Creek substrates (e.g., sculpins and longnose dace). Furthermore, the August 1988 flood filled many of the interstitial spaces with silt and perhaps forced many surviving sculpins to the top of the silt, where they became more conspicuous to predators.

Streams that are dominated by floods should have fish species that are adept at recolonizing, that minimize exposure of vulnerable life history stages, and that occupy safe microhabitats during floods. Although rainbow trout and bridgelip suckers recolonized Rock Creek habitats well, speckled dace were especially effective at recolonization. After several floods during 1988–1989, densities of speckled dace increased to levels that equaled or surpassed those before the floods. During all sampling periods, the speckled dace was the dominant or codominant fish species in each Rock Creek reach. Speckled dace were highly vulnerable to floods in simple habitats but, because they occupied stream reaches of varying habitat complexity, many of them survived in complex habitats. The speckled dace seems to be a habitat generalist; all life history stages of this species were observed in all channel units (riffles, runs, and pools) in all of the stream reaches.

Because of seasonal movements of fish in Rock Creek, changes in fish numbers after the flood cannot be attributed solely to the flood. The increase in late-immigrating species such as chiselmouth and northern squawfish dampened the apparent effect of the summer flood in Rock Creek. Furthermore mortality of young-of-year suckers unrelated to the flood may have inflated the apparent effects of the flood. Despite a large emigration of speckled dace in Murderers Creek, we do not think that a similar emigration occurred in Rock Creek.

Murderers Creek is at higher elevation and gets colder earlier in late summer than does Rock Creek. We believe that temperature is a primary factor in fish emigration in these streams.

In conclusion, complex habitats are refuges for fishes during disturbances such as floods. In our study, the change in total fish density was lower after floods, assemblage diversity was greater, and assemblage similarity was higher in complex habitats than in simple habitats. Complex habitats may be sources of fish to colonize simple habitats after floods, but large-scale migrations of fishes from lowland tributaries or the main stem are probably the main sources of fish colonists. Fishes that are poor recolonizers, inhabit vulnerable habitats, or subject vulnerable life-history stages to floods should be rare (e.g., sculpins), and fishes that do the opposite should be abundant (e.g., speckled dace). Complex habitats should be protected to maintain diverse assemblages in disturbed streams.

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