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HABITAT SELECTION AND RESILIENCE OF STREAM
FISHES IN THE RED CEDAR RIVER WATERSHED,
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presented by

JO ANNE LATIMORE

has been accepted towards fulfillment
of the requirements for the

Doctoral degree in Fisheries and Wildlife

Major Professor's Signature

9 December 2005

Date

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HABITAT SELECTION AND RESILIENCE OF STREAM FISHES IN THE RED CEDAR RIVER WATERSHED, MICHIGAN

By

Jo Anne Latimore

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

HABITAT SELECTION AND RESILIENCE OF STREAM FISH IN THE RED CEDAR RIVER WATERSHED, MICHIGAN

By

Jo Anne Latimore

Resilience to disturbance is vital to the sustainability of ecological systems. However, determination of system resilience in the field is less than straightforward because of its dependence on the nature of the disturbance and on the choice of endpoints for system recovery. More frequently, we base assessments of ecological system health on measures of function, such as abundance, productivity, and biomass, and measures of structure, such as species richness and diversity, which are relatively simple to obtain in the field.

I conducted 14 experimental fish defaunations in 100-meter reaches of second- to fourth-order warmwater streams in the Red Cedar River watershed of lower Michigan. Stream habitat was left intact. I documented fish assemblage recovery in these reaches over the course of a month in order to describe the structure of recovering assemblages over time and to identify habitat or assemblage characteristics that influenced resilience. Fish assemblages recovered remarkably quickly, exhibiting high similarity to pre-disturbance structure within two days of defaunation. Pool habitat appeared to encourage recolonization, while pre-disturbance fish abundance was negatively related to abundance recovery. No relationship between resilience and multimetric indices commonly used to assess stream health, such as overall habitat quality or biotic integrity, was evident. Such metrics, although efficient in terms of cost and time, may not produce a complete picture of stream health.

The results of these experiments permitted an examination of the relationship between assemblage structure, function, and resilience as components of ecological health. There was no relationship between the pre-disturbance vigor or organization of the fish community and its resilience to disturbance. While I found that measuring post-disturbance changes in structure and abundance over time was useful in determining recovery, these resilience values are applicable only to one type of disturbance at one spatial and temporal scale. Although vigor and organization may serve as partial indicators of community health, a general model of the relationship of these variables to resilience would be invaluable for ecosystem conservation and management.

Finally, the structure of these defaunation experiments provided an opportunity to investigate habitat selection in a common stream fish, the creek chub (*Semotilus atromaculatus* Mitchill). Traditional methods of assessing habitat suitability rely on correlating habitat characteristics with the number of individuals occupying the habitat under natural conditions. Distribution is a behavioral phenomenon, however, and the majority of these correlations do not consider movement or density-dependent interactions that may influence the suitability of a particular habitat, and therefore, the dynamics of creek chub population recovery following to disturbance. In this study, I considered both the influence of physical habitat and density of conspecifics on distribution. Creek chubs preferred pools over runs, and runs over riffles. Alternative methods of measuring selection, including selection indices and immigration rates, revealed similar insights. Density of creek chubs in the study reaches, which ranged from zero immediately following defaunation to above pre-defaunation (natural) densities, had no apparent effect on habitat preferences.

ACKNOWLEDGMENTS

None of the research included here could have been accomplished without the invaluable assistance of a talented and energetic group of undergraduate technicians: Kelly DeGrandchamp, Janice Karcher, Kevin Mann, Colleen McLean, Cassandra Meier, Aaron Shultz, and Alfred Thomson. I truly hope I was able to share something in return. Fellow graduate students in the Department of Fisheries and Wildlife provided technical assistance, social support, and intellectual stimulation, especially Bryan Burroughs, Matt Klungle, Anita Morzillo, Sharon Johnson Schapel, Dave Thomas, and Brad Thompson. My faculty Guidance Committee held high standards and provided direction throughout the course of my program at Michigan State University: Mary Bremigan, Tom Coon, Scott Witter, and most outstandingly, my Major Professor, Dan Hayes, about whom I could never say enough.

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Finally, I express heartfelt appreciation for the support I have received as I worked toward this goal – at once a mission accomplished and an adventure just beginning – from my incomparable family: my parents, Terry and Nancy Latimore, my sister, Janet Latimore, and my husband, Ralph Kridner.

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CHAPTER 1

Fish assemblage resilience in experimentally defaunated warmwater stream reaches

Abstract

Resilience to disturbance is vital to the sustainability of ecological systems. Stream ecosystems are noted for their resiliency, due to the broad range of natural fluctuations in habitat and water conditions to which the biota is adapted. However, anthropogenic impacts can disturb stream systems by shifting habitat, flow, or water quality out of typical ranges or by introducing new stressors. We currently have limited knowledge of stream fish assemblage resilience, especially the short-term dynamics of recolonization following disturbance. I conducted 14 experimental fish defaunations in 100 m reaches of second- to fourth-order warmwater streams in the Red Cedar River watershed of lower Michigan. Stream habitat was left intact. I documented recovery in these reaches over the course of a month in order to describe the structure of recovering assemblages over time and to identify habitat or assemblage characteristics that influenced resilience. Assemblage structure was highly similar to the pre-disturbance state within two days of defaunation. Recovery of fish abundance was slower, but approached full recovery within one month at most sites. Pool habitat within the defaunated area appeared to encourage fish recolonization, while pre-disturbance fish abundance was negatively related to abundance recovery. No relationship was found between species richness and resilience. These results suggest that rapid colonization of undisturbed stream habitat may be a general property of warmwater fish assemblages in low-order streams. Interestingly, no relationship between resilience and multimetric

indices commonly used to assess stream health, such as overall habitat quality or biotic integrity, was evident. In fact, overall habitat quality as measured by the Qualitative Habitat Evaluation Index, designed to assess fish habitat, did not relate to pre-defaunation fish assemblage. Such metrics, although efficient in terms of cost and time, may not produce a complete picture of stream health.

Introduction

Resilience, or the ability to recover from disturbance (Holling 1973, Pimm 1984) is an important component of ecosystem sustainability. Contanza and Mageau (1999) emphasized this when they defined sustainability as the ability to maintain structure and function over time in the presence of disturbance. Stream ecosystems are noted for their resiliency (Resh et al. 1988), which is often attributed to biological adaptation to the broad fluctuations in flow (Fisher et al. 1982, Poff et al. 1997), temperature (Hawkins et al. 1997), and related variables that streams naturally exhibit (Wallace 1990, Yount and Niemi 1990). Human impacts within streams and their watersheds, however, often shift stream conditions outside the natural range of variation (Likens et al. 1970, Ward and Stanford 1983, Bain et al. 1988, Niemi et al. 1990, Kinsolving and Bain 1993, Li et al. 1994), or introduce new stresses to the system, such as exotic species (Pringle 1997) or pollutants (Krumholz and Minckley 1964). The severity of these disturbances may test the resiliency, and therefore the sustainability, of stream systems.

A substantial body of research exists on the impacts of disturbance on stream fishes (see Detenbeck et al. 1992 for a review), but it consists primarily of case studies with multiple ecological impacts and minimal pre-disturbance information. As such, we currently have limited knowledge of the patterns or mechanisms of stream fish resilience, or how resilience is affected by specific stream or assemblage characteristics. Experimental studies of resilience are replicable and also have the advantage of being able to manipulate single variables, thereby revealing the dynamics of recovery in a way not possible in the majority of case studies. A few experimental studies of stream fish response to disturbance have been conducted in which habitat is largely unchanged, but these studies have addressed resiliency over relatively long time intervals (e.g., re-sampling after one year). Most of these studies have shown substantial, if not always complete, recovery (Larimore et al. 1959; Gunning and Berra 1968,1969; Berra and Gunning 1970; Olmsted and Cloutman 1974; Meffe and Sheldon 1990; Ensign et al. 1997). Explorations of short-term dynamics are rare. Peterson and Bayley (1993) observed fish assemblages recovering from experimental defaunation in Midwestern warmwater streams over intervals of thirty minutes to six days in reaches 46-113 m in length and predicted near-complete recovery would occur within two weeks. In a similarly designed study, Sheldon and Meffe (1995) defaunated individual warmwater stream pools and observed recovery within one to two months. The former study also was designed to detect ecological factors that may influence recovery, but found that time since defaunation was the only predictor of the degree of colonization at a particular site.

Stream and fisheries management frequently depends on the use of multimetric indices that combine a number of variables that have been shown to relate to overall stream quality. These indices are typically straightforward, replicable, and cost little in terms of effort or resources, allowing many sites to be assessed quickly. For example, the quality of fish habitat in Midwestern streams is often measured using the Qualitative

Habitat Evaluation Index (QHEI; Rankin 1989). Stream fish assemblages are frequently assessed using an index of biotic integrity (IBI; Karr 1987). Resilience to disturbance is clearly a factor in stream integrity and sustainability, yet intentionally disturbing streams to determine resilience could be counterproductive and costly. Determining whether current methods for assessing streams reflect their ability to recover from disturbance (or learning how to modify them to do so) would be extremely valuable from a management standpoint.

I conducted replicable experimental defaunations in undisturbed habitat to address two major objectives. The first was to describe the rate at which fish assemblages rebound following this type of disturbance, and the structure of the assemblage over time as it recovered. An understanding of the rate and pattern of the recovery process provides a model for setting expectations for other recovering stream fish assemblages. I expand on the design of Peterson and Bayley (1983) by repeatedly observing the colonization process in 100 m reaches over a month's time. My second objective was to identify features of fish assemblages and stream habitat that influenced recovery. I considered not only individual stream and assemblage descriptors, but also multimetric indices commonly used to assess stream quality. Achieving this objective would allow us to identify less resilient systems where impacts should be avoided, and to determine whether current methods of stream assessment reflect the system's ability to recover from disturbance.

Methods

Fourteen fish removal experiments were conducted in twelve second- to third-order streams during the summers of 2001 and 2002. To maintain consistency in fish fauna, geology, and climatic effects, all work took place in the Red Cedar River watershed, Ingham and Livingston Counties, Michigan, USA (Figure 1). This warmwater system is characterized by low gradients (mean = 0.475 m/km; Horton 1969), glacial till geology, and a high percentage of agricultural land cover. Experimental sites

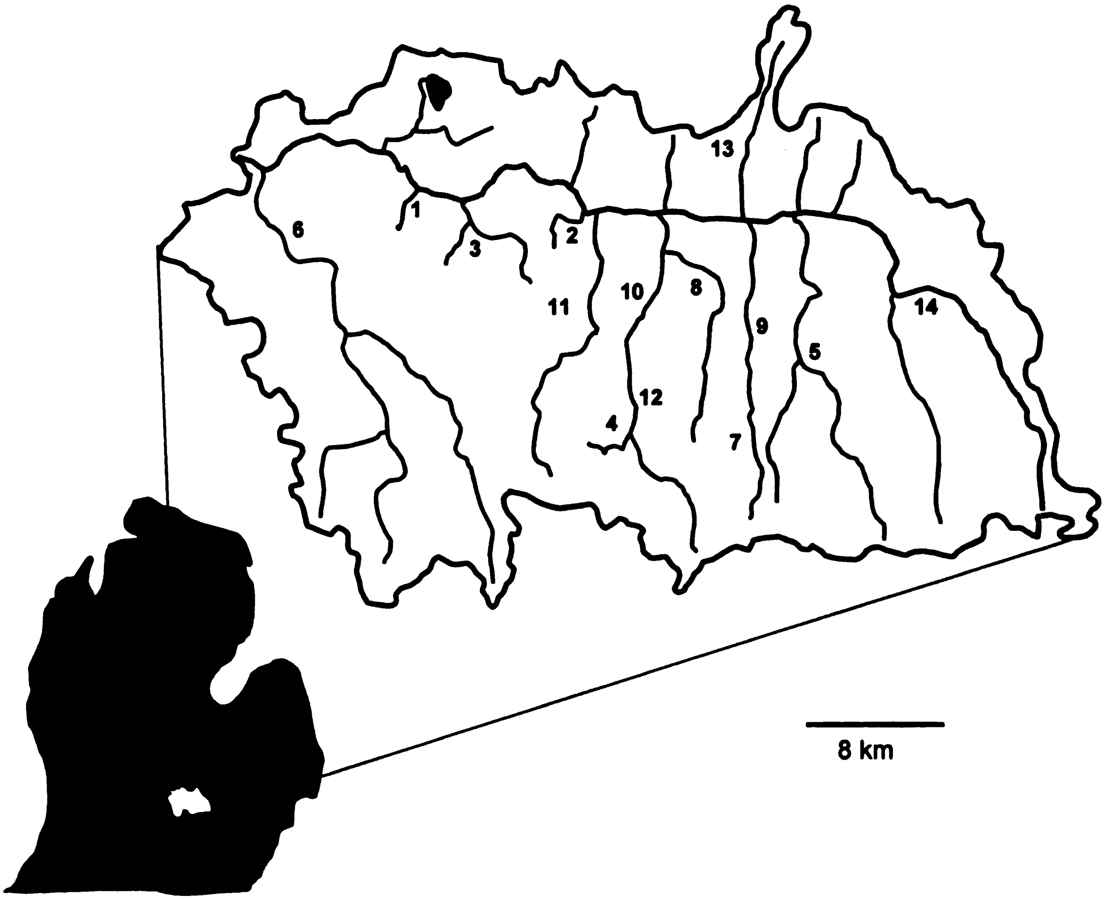


Figure 1. Locations of study sites in the Red Cedar River watershed, Ingham and Livingston Counties, Michigan. See Table 1 for study site descriptions.

were selected, using land use data (MDNR 2001) and field scouting, to include a range of stream sizes and habitat characteristics.

I characterized the habitat in each study reach prior to fish assemblage manipulation. First, approximately 100 meters of stream were delineated into channel units (pools, riffles, and runs; Dunne and Leopold 1978). The length of each unit was recorded, and a transect was established at the midpoint of the unit. At each transect, the wetted width, depth profile, and substrate composition using the pebble count method (Wolman 1954) were documented. Habitat quality of the study reach was assessed using the Qualitative Habitat Evaluation Index (QHEI), a subjective, multimetric stream fish habitat assessment index that includes substrate, in-stream cover, channel morphology, riparian zone quality and bank erosion, and pool and riffle quality (Rankin 1989).

Block nets (3-mm mesh) were temporarily installed at the upstream and downstream ends of the study reach during fish removal to prevent fish immigration or emigration. Fish were collected using a Smith-Root backpack-mounted or barge-mounted electrofishing unit, depending on stream depth. Fish were removed using a minimum of three electrofishing passes through the reach. If more than ten individuals were collected on the third pass, additional passes were conducted. The completeness of my removal method was confirmed at one site (site 5) by leaving block nets in place overnight following removal. The study reach was electrofished again the following day. Very few fish were found, all of which were small and the majority of which were young-of-the-year, which were excluded from all analyses in this study.

All fish collected from the study reach were identified to species, with the exception of young-of-the-year fish, which were excluded from analysis due to the difficulty of collection and identification. During removal, fish were held in large shaded holding containers filled with stream water and supplied with aeration. Following removal, all collected fish were released at stream sites within the watershed 2-10 km from the study reach to reduce the chance of their returning to the study site within the experimental period. Pre-defaunation fish assemblages were assessed using the Michigan Department of Environmental Quality's Procedure 51 scoring method (MDEQ 1997), which closely resembles the index of biotic integrity (IBI; Karr 1987) used in many Midwestern states.

Return trips were made to each study reach to determine the progress of recolonization of the defaunated reach. Pilot studies indicated that study reaches could recover within one week. Therefore, the first return trip took place within two days of fish removal. Return trip sampling consisted of a single electrofishing pass through the study reach. After identification, fish were returned to the channel unit from which they were collected to allow colonization to continue unimpeded. Subsequent return trips were made to each study reach at intervals of one week or less for at least a month.

Species richness (number of species present) and total number of fish collected were calculated for removal and recovery samples. Fish collections from the first electrofishing pass during the removal were used for comparison with return trip collections to standardize for collection effort. For analysis, any recovery sample that met or exceeded removal abundance or richness was considered 100% recovered for that parameter. By not assigning recovery values greater than 100%, I maintained a conservative estimate of across-watershed recovery rates.

Resilience was calculated in terms of fish abundance by comparing first-pass removal counts to return trip counts. I used Morisita's index of similarity ($I_{M;}$ Morisita 1959) to quantify assemblage resilience by comparing fish assemblage structure during recovery to the pre-disturbance state:

$$I_M = \frac{2\sum_{i=1}^{\infty} n_{1i} n_{2i}}{(\lambda_1 + \lambda_2) N_1 N_2}$$

Where n_i = the number of individuals of species i in a sample; and

N = the total number of individuals in a sample; and

$\lambda = \frac{\sum n_{1i}(n_{1i}-1)}{N_1(N_1-1)}$, based on Simpson's measure of diversity (Simpson 1949).

This index represents assemblage similarity based on relative abundance of species in the samples, so that proportionally similar assemblages of species score high regardless of the total number of individuals in the samples. In addition, its performance is less influenced by sample size than other similarity indices (Wolda 1981). Morisita's index ranges from zero (completely dissimilar) to slightly greater than one (complete similarity). Values of 0.70 or greater are generally taken to indicate a high degree of similarity (Matthews et al. 1988). Patterns of resilience were then related to habitat and assemblage descriptors, including the QHEI and Procedure 51, using simple linear regression.

Results

The 14 study sites, located in twelve separate tributaries of the Red Cedar River (Table 1), ranged in mean wetted width from 2.6 to 11.1 m and in mean depth from 0.11

Table 1. Stream habitat characteristics for the experimental sites. QHEI is the Qualitative Habitat Evaluation Index (range 0-90; Rankin 1989). Mean width and depth are reported in meters. Percent channel unit composition calculated as proportion of total site length.

Site	Site Name	QHEI	Mean Width	Mean Depth	% Pool	% Riffle	% Run
1	Dobie Road Tributary	63	3.5	0.25	33	49	18
2	Corwin Road Tributary	65	2.8	0.35	42	18	39
3	Sloan Creek	51	4.2	0.19	0	50	50
4	Doan Deer Creek	34	3.0	0.19	0	0	100
5	West Branch, Red Cedar River	18	7.2	0.38	0	0	100
6	Sycamore Creek	59	11.1	0.23	0	10	90
7	Kalamink Creek (Columbia Road)	21	4.3	0.11	0	0	100
8	Dietz Creek	16	3.6	0.22	0	0	100
9	Kalamink Creek (Van Orden Road)	63	3.9	0.19	23	21	57
10	Doan Creek (Noble Road)	53	6.4	0.26	26	32	43
11	Deer Creek	56	4.9	0.22	10	6	84
12	Doan Creek (Columbia Road)	56	4.4	0.35	28	0	72
13	Wolf Creek	44	2.6	0.22	0	12	88
14	East Branch, Red Cedar River	43	4.7	0.34	15	0	85

to 0.38 m. Substrate was predominantly sand (mean 40%, range 17-59%, of substrate material), followed by organic material and silt. The study sites varied from channelized, continuous runs to stable riffle-run sequences. Qualitative Habitat Evaluation Index (QHEI; Rankin 1989) values for the experimental sites ranged from 18 (poor) to 65 (excellent); the average was 46 (marginally acceptable).

Twenty-five species of fish were collected during the fish removals (Table 2 and 3). Dominant species were creek chub (*Semotilus atromaculatus*), blacknose dace (*Rhinichthys atratulus*), johnny darter (*Etheostoma nigrum*), brook stickleback (*Culaea inconstans*), bluntnose minnow (*Pimephales notatus*) and white sucker (*Catostomus commersoni*). Species richness in the study reaches during removal ranged from 5 to 16 (mean = 9.6, SE = 0.8). Total fish abundance within the 100-meter reaches ranged from 35 to 489 (mean = 246.0, SE = 40.0). Procedure 51 (MDEQ 1997) fish assemblage scores for the study reaches ranged from -8 (poor) to +3 (tending toward excellent; mean = -4.1, SE = 0.73).

I calculated species-specific recovery rates for the most abundant fish species. First, I considered the recovery rate during the first interval following removal (two to four days), by calculating the percentage of removal density recovered per day during that first interval. This first-interval recovery rate represents the maximum rate observed for each species, and ranged from 44% recovery/day (SE = 22%) for johnny darters to 9% recovery/day (SE = 1%) for rock bass (Figure 2). Second, I generated a pattern of density recovery over the duration of the one-month experimental period for each of these species by summing the number of individuals collected at each sampling interval for all experiments. While some species, such as the central mudminnow and the mottled

Table 2. Total fish collected during experimental fish removals, excluding young-of-the-year. Procedure 51 Score refers to the Michigan Department of Environmental Quality scoring method for stream fish assemblages (range -10 to 10; MDEQ 1997).

	Site														**Mean Across Sites**
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	
Blacknose Dace	8	160	228	33	67	5	30	31	8	4	11	20	59	27	**49.4**
Creek Chub	68	198	42	6	76	27	8	77	10	13	63	51	20	13	**48.0**
Johnny Darter	10	18	12	1	99	40	45	68	3	12	24	22	72	58	**34.6**
Brook Stickleback	9	54	146	0	51	7	39	8	0	2	3	0	99	0	**29.9**
Bluntnose Minnow	0	0	23	0	55	36	10	7	2	0	7	4	0	73	**15.5**
White Sucker	9	25	2	0	2	3	0	8	7	7	23	74	5	30	**13.9**
Mottled Sculpin	0	2	19	10	0	0	0	0	0	80	20	60	0	0	**13.6**
Rainbow Darter	0	0	14	0	23	130	0	0	0	0	1	0	0	0	**12.0**
Common Shiner	0	0	0	0	52	0	0	0	0	1	7	4	10	1	**5.4**
Blackside Darter	3	1	0	0	2	31	0	0	2	4	1	4	0	22	**5.0**
Central Mudminnow	0	3	0	0	0	0	26	13	2	0	0	0	6	14	**4.6**
Green Sunfish	0	0	0	0	7	2	0	0	0	0	5	4	0	43	**4.4**
Rock Bass	0	0	0	0	0	10	0	0	0	0	0	0	0	49	**4.2**
Central Stoneroller	0	2	2	0	7	7	0	4	0	1	2	24	0	0	**3.5**
Bluegill	1	2	1	1	0	3	0	0	1	0	1	0	0	0	**0.7**
Pugnose Minnow	0	0	0	0	0	6	0	0	0	0	0	0	0	0	**0.4**
Smallmouth Bass	0	0	0	0	0	4	0	0	0	0	0	0	0	0	**0.3**
Spottail Shiner	0	0	0	0	3	0	0	0	0	0	0	0	0	0	**0.2**
Black Bullhead	0	0	0	0	2	0	0	0	0	0	0	0	0	0	**0.1**
Brown Bullhead	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**0.1**
Emerald Shiner	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**0.1**
Northern Hog Sucker	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**0.1**
Pearl Dace	0	0	0	0	1	0	0	0	0	0	0	0	0	0	**0.1**
Rainbow Trout	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**0.1**
Species Richness:	**7**	**10**	**10**	**5**	**14**	**16**	**6**	**8**	**8**	**9**	**13**	**10**	**7**	**12**	
Total Catch:	**108**	**465**	**489**	**51**	**447**	**313**	**158**	**216**	**35**	**124**	**168**	**267**	**271**	**332**	
Procedure 51 Score:	**-6**	**-4**	**-4**	**-7**	**-2**	**3**	**-8**	**-6**	**-5**	**-4**	**-4**	**-6**	**-3**	**-2**	
Max. % Richness Recovery:	**100**	**70**	**92**	**100**	**73**	**89**	**100**	**100**	**100**	**100**	**80**	**100**	**63**	**100**	
Max. % Abundance Recovery:	**100**	**32**	**52**	**100**	**29**	**60**	**100**	**67**	**100**	**100**	**100**	**100**	**31**	**100**	

Table 3. Common and scientific names of all fish species collected in the course of fish removal experiments in the Red Cedar River watershed, Michigan, in 2001 and 2002.

Family	**Scientific Name**	**Common Name**
Catostomidae	*Catostomus commersoni*	White Sucker
	Hypentelium nigricans	Northern Hog Sucker
Centrarchidae	*Ambloplites rupestris*	Rock Bass
	Lepomis cyanellus	Green Sunfish
	Lepomis macrochirus	Bluegill
	Micropterus dolomieu	Smallmouth Bass
Cottidae	*Cottus bairdi*	Mottled Sculpin
Cyprinidae	*Campostoma anomalum*	Central Stoneroller
	Luxilus cornutus	Common Shiner
	Margariscus margarita	Pearl Dace
	Notropis atherinoides	Emerald Shiner
	Notropis hudsonius	Spottail Shiner
	Opsopoeodus emiliae	Pugnose Minnow
	Pimephales notatus	Bluntnose Minnow
	Rhinichthys atratulus	Blacknose Dace
	Semotilus atromaculatus	Creek Chub
Gasterosteidae	*Culaea inconstans*	Brook Stickleback
Ictaluridae	*Ameiurus melas*	Black Bullhead
	Ameiurus nebulosus	Brown Bullhead
Percidae	*Etheostoma caeruleum*	Rainbow Darter
	Etheostoma nigrum	Johnny Darter
	Percina maculata	Blackside Darter
Salmonidae	*Oncorhynchus mykiss*	Rainbow Trout
Umbridae	*Umbra limi*	Central Mudminnow

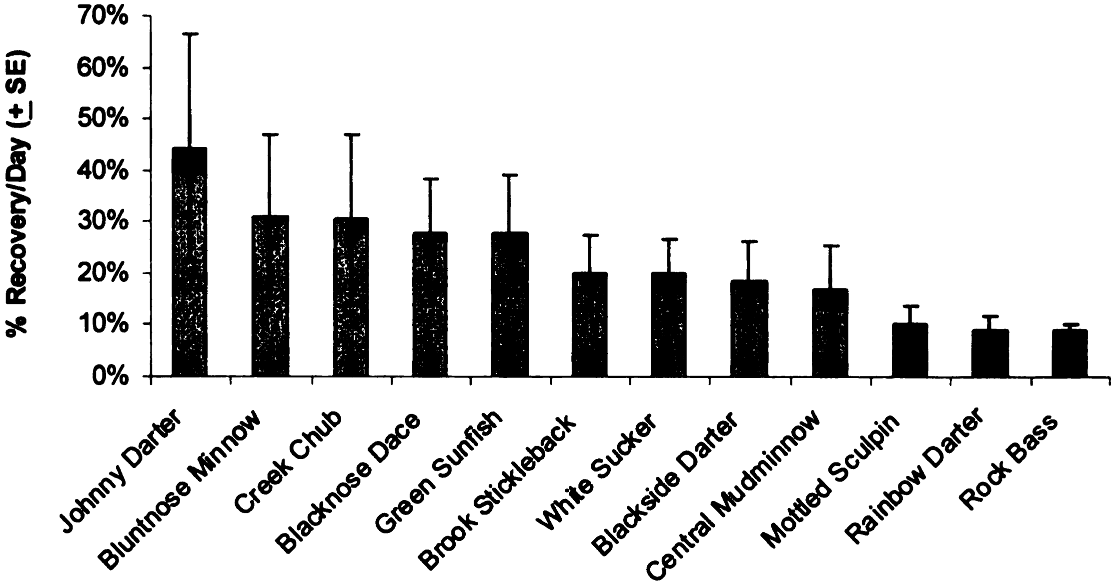


Figure 2. Recovery rates of fish species recolonizing defaunated stream reaches during the first sampling interval following fish removal (2-4 days), presented as the mean percentage of pre-removal density recovered per day for the most common species encountered.

sculpin, increased steadily and approached or reached recovery over a month's time, several other species did not (Figure 3). It is important to note that the apparent failure of creek chubs, white suckers, and blacknose dace to approach recovery is strongly influenced by the data from a single site (Site 2, Corwin Road Tributary). Likewise, the erratic patterns demonstrated by green sunfish, bluntnose minnows, and rock bass are partly the result of data from Site 14 (East Branch, Red Cedar River), where these species were abundant but which was not sampled on days 11 or 25.

Stream fish assemblage structure recovered rapidly at all sites (Figure 4). Within two days of disturbance, the mean level of Morisita's (1959) similarity (I_M) between removal assemblages and recovering assemblages across all streams was 0.83 (SE = 0.048), and the similarity of assemblages to pre-disturbance conditions remained high throughout the study. Species richness, a component of assemblage structure, followed a similar pattern. The number of fish in the experimental reaches took more time to recover (Figure 5). After two days, the mean level of numerical recovery across all streams was 38% (SE = 8%). Densities continued to increase throughout the one-month experimental period, averaging 69% (SE = 9%) recovery after 32 days.

I compared the QHEI scores of the study reaches to removal fish assemblages and the recovery of abundance and species richness to look at habitat influences on fish assemblage structure or recovery. In no case was there a significant relationship (Figures 6 and 7). However, in streams without distinct pool habitat, only two out of seven (29%) reached complete abundance recovery, while 6 out of 7 (86%) with pools did (Figure 8).

Pre-removal assemblage characteristics had variable effects on recovery. There

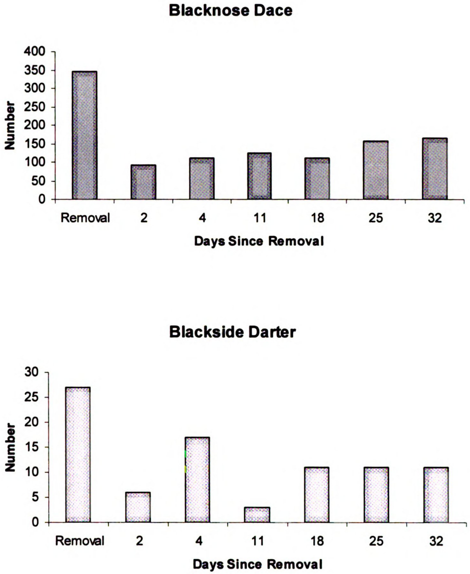
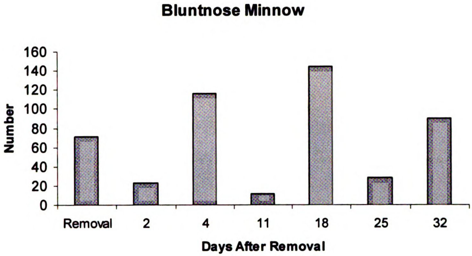
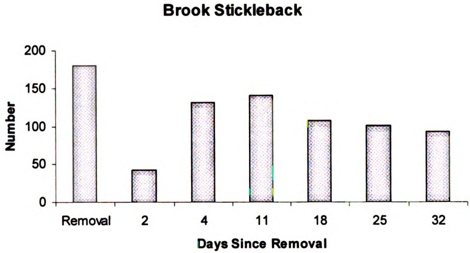


Figure 3. Species-specific patterns of density recovery over the course of the one-month recolonization period following defaunation, presented as the total number of individuals collected at all experimental sites for each sampling interval.



Bluntnose Minnow



Brook Stickleback

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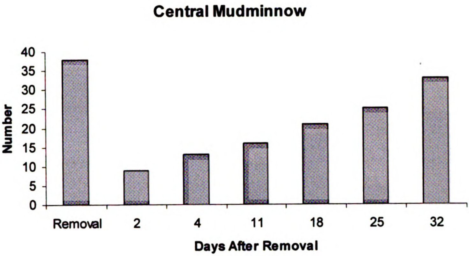

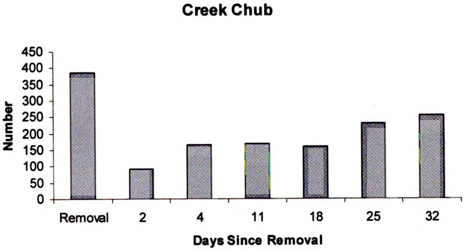

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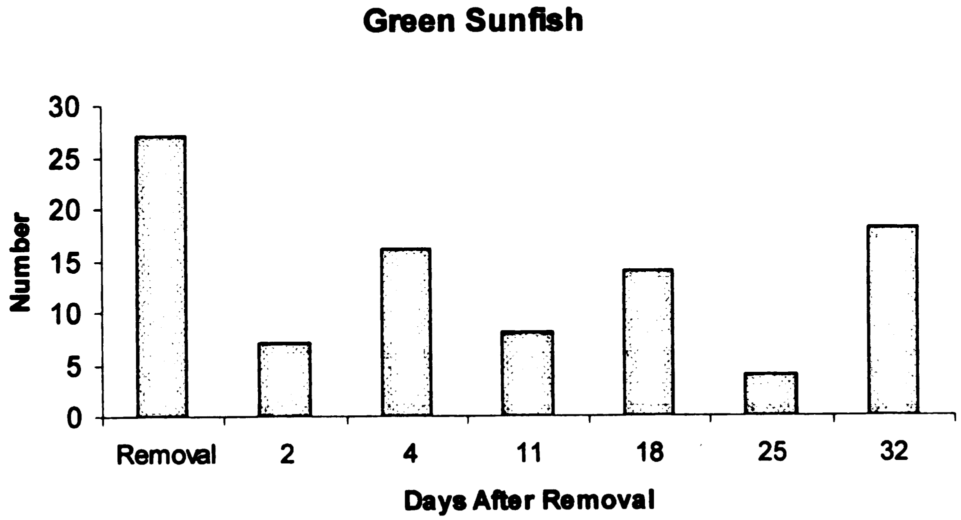


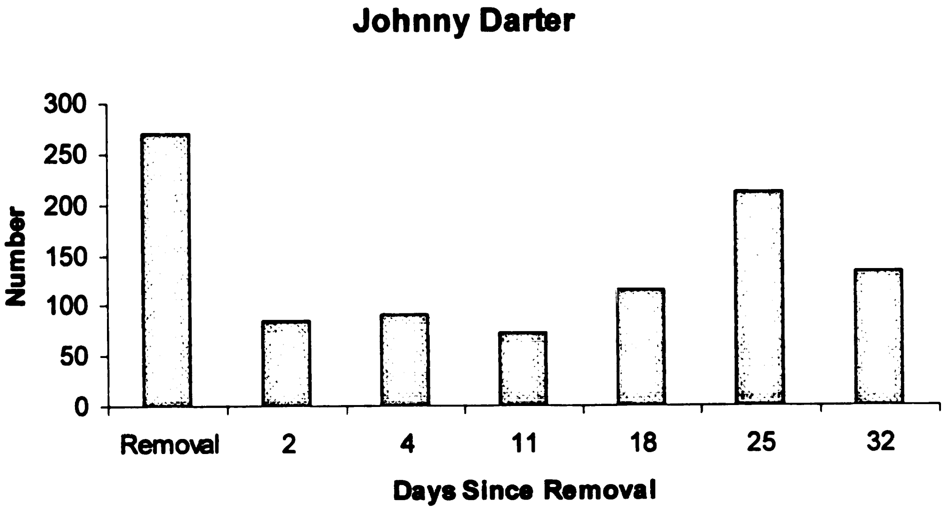
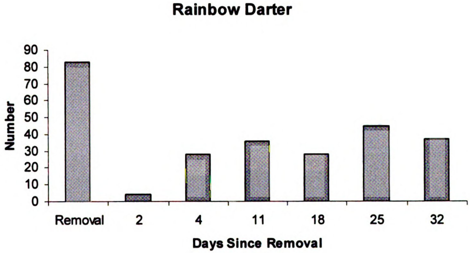


Figure 3 (cont'd).



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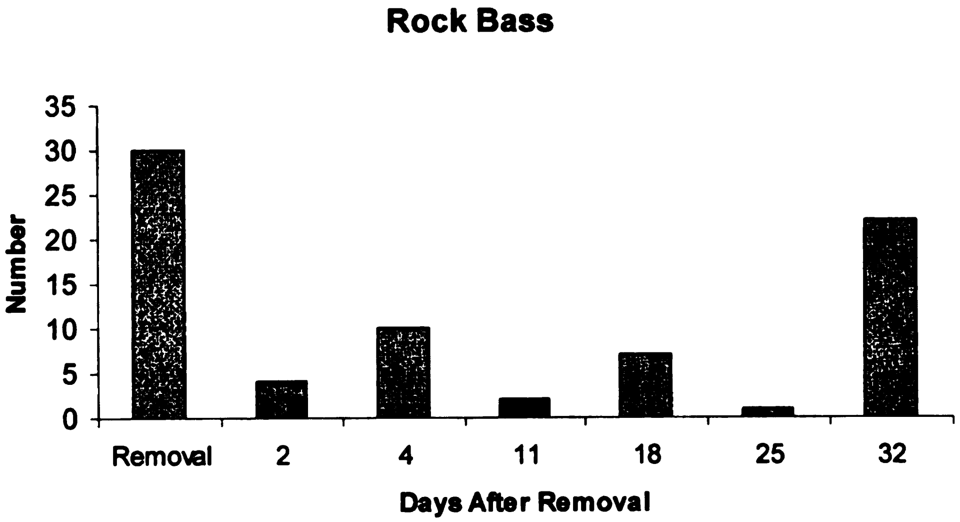
Rock Bass

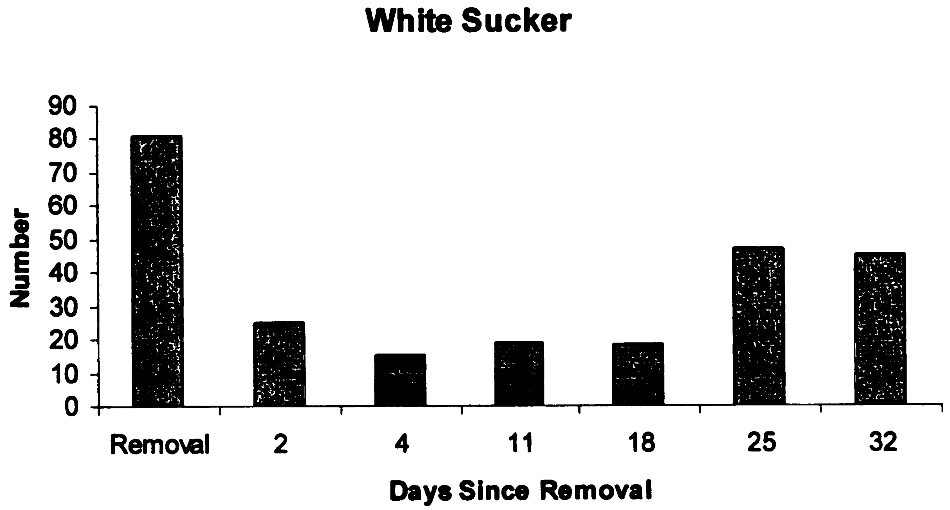
White Sucker

Figure 3 (cont'd).

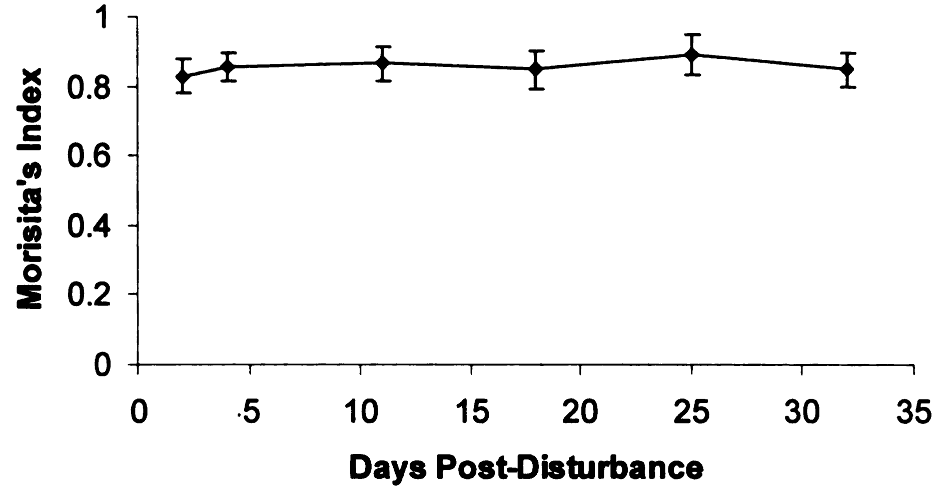

Figure 4. Morisita's (1959) similarity of fish assemblages sampled during the recovery period compared to pre-disturbance assemblages. Data points represent the mean value (±1 SE) across all 14 experimental stream reaches.

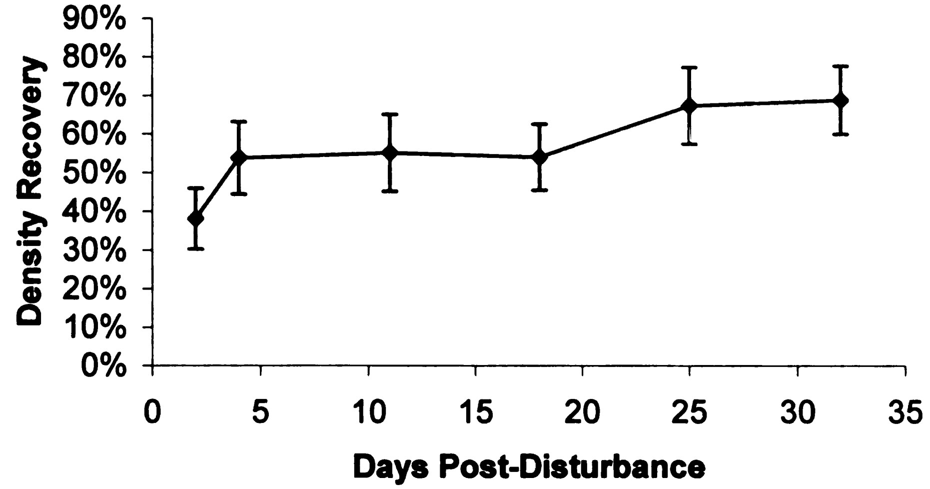

Figure 5. Mean level of fish density recovery (±1 SE) over time across all 14 experimental stream reaches.

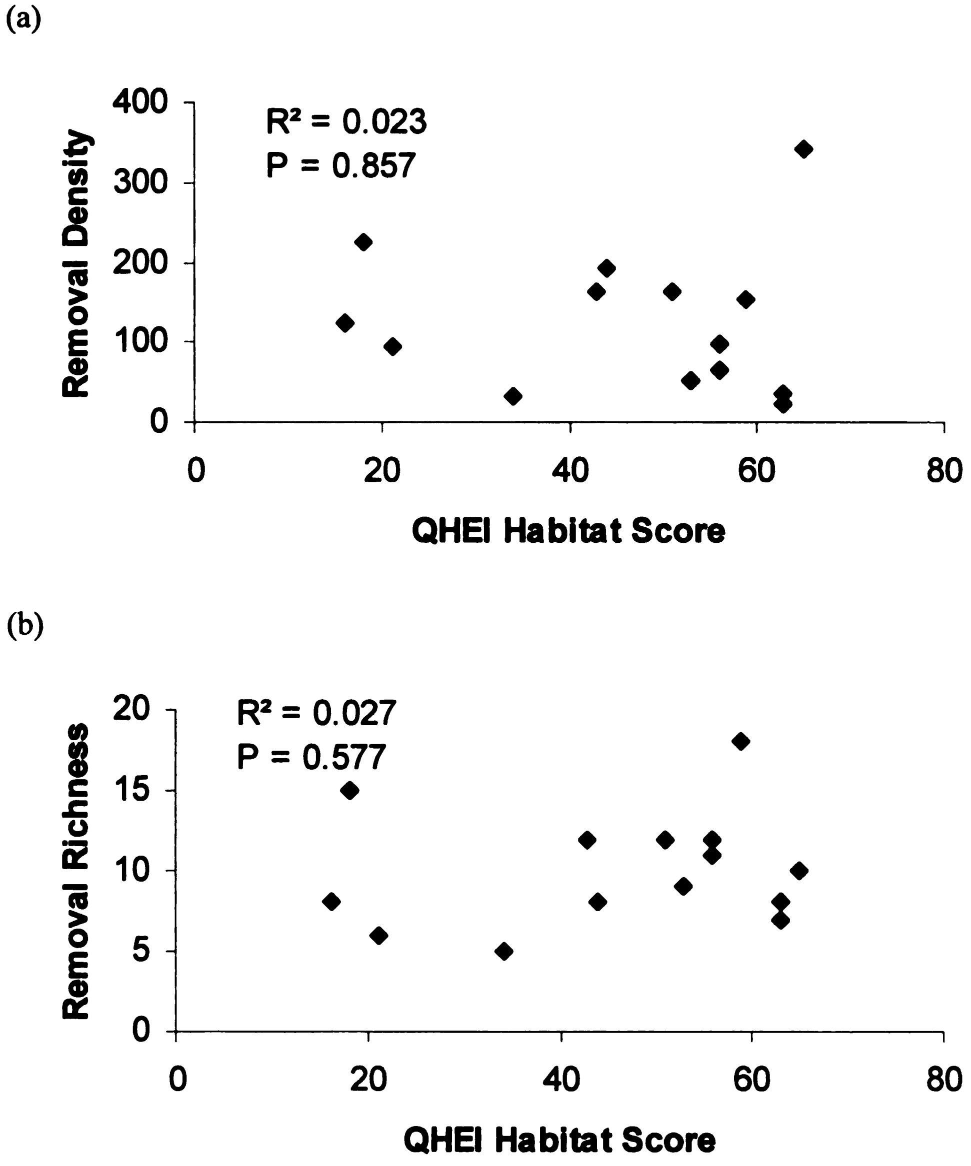

Figure 6. Pre-disturbance fish density(a) and species richness(b) in the 14 experimental stream reaches relative to the Qualitative Habitat Evaluation Index (QHEI; Rankin 1989).

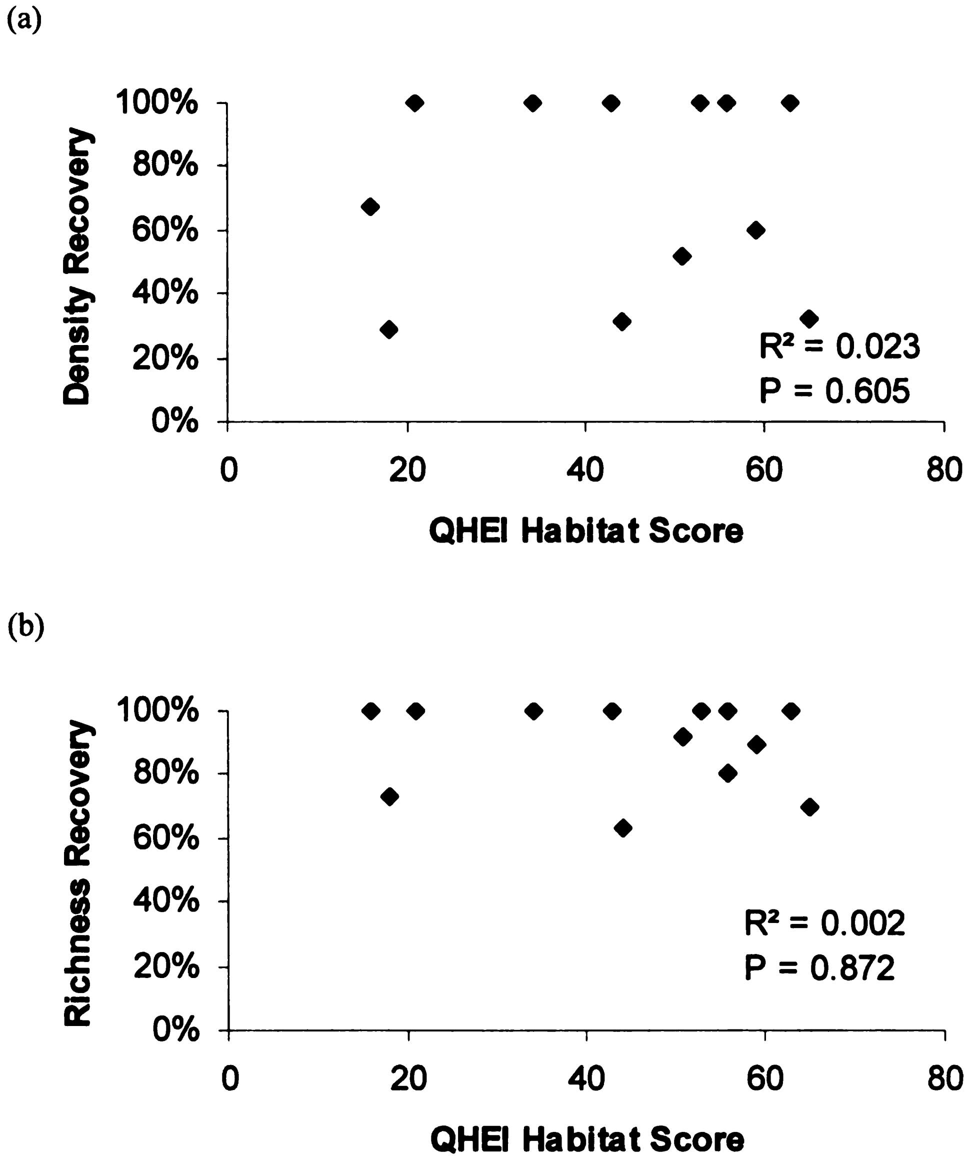

Figure 7. Maximum fish density(a) and maximum species richness(b) recovery in the 14 experimental stream reaches relative to Qualitative Habitat Evaluation Index (QHEI; Rankin 1989).

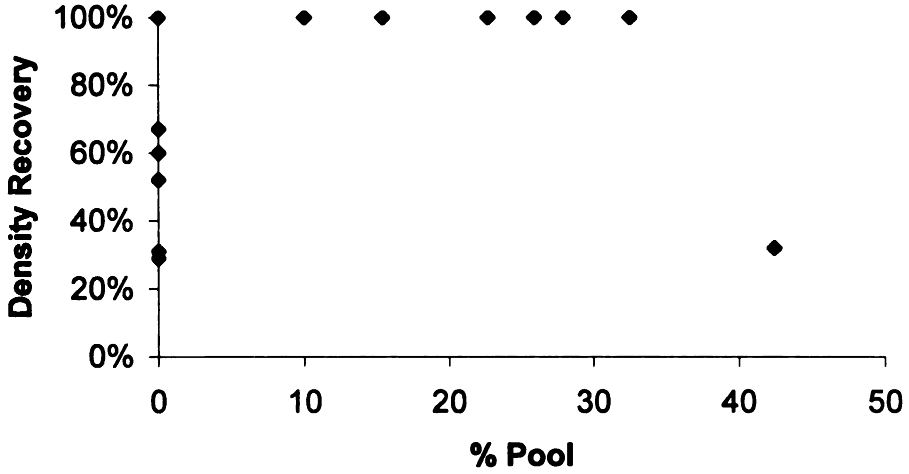

Figure 8. Maximum fish density recovery compared to the percentage of reach length as pool habitat in the 14 experimental stream reaches.

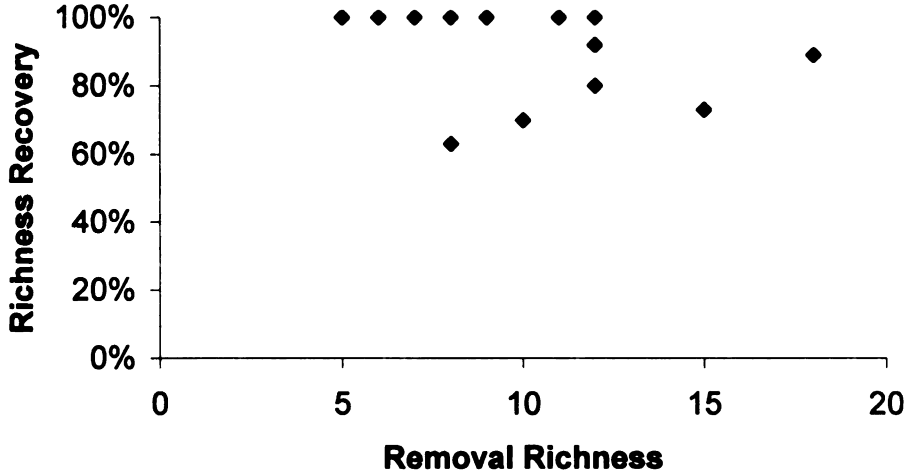

Figure 9. Level of maximum fish species richness recovery compared to the pre-disturbance richness of the 14 experimental stream reaches.

was no relationship between pre-removal species richness and richness recovery (Figure 9). Pre-removal fish abundance did appear to influence abundance recovery, however (Figure 10). Reaches with relatively low numbers of fish (≤100) were able to recover completely within the experimental period, while reaches with relatively high fish numbers (>175) generally did not recover numbers fully. Finally, Procedure 51 fish assemblage scores did not appear to relate to fish assemblage recovery (Figure 11).

Discussion

The sandy, low-gradient, and often channelized streams of the Red Cedar River watershed are typical of agricultural watersheds in Michigan and elsewhere in the Midwestern United States (Richards et al. 1996, Iowa State University 1997). Qualitative Habitat Evaluation Index (QHEI; Rankin 1989) values for the experimental stream reaches ranged from 18 to 65. Values below 45 (7 sites) indicate poor fish habitat, scores of 45-60 (6 sites) are average, and scores of 60-90 (3 sites) are considered excellent. This index suggests that the study reaches provided minimally acceptable fish habitat on average.

The fish assemblages observed in the experimental sites were dominated by species common in warmwater streams of the eastern United States (Trautman 1981). Five of the six numerically dominant species are tolerant of degraded stream quality (*Rhinichthys atratlulus*, blacknose dace; *Semotilus atromaculatus*, creek chub; *Etheostoma nigrum*, johnny darter; *Pimephales notatus*, bluntnose minnow; and *Catostomus commersoni*, white sucker) and four are omnivorous (creek chub, blacknose dace, bluntnose minnow, and white sucker; MDEQ 1997), indicating a generalist,

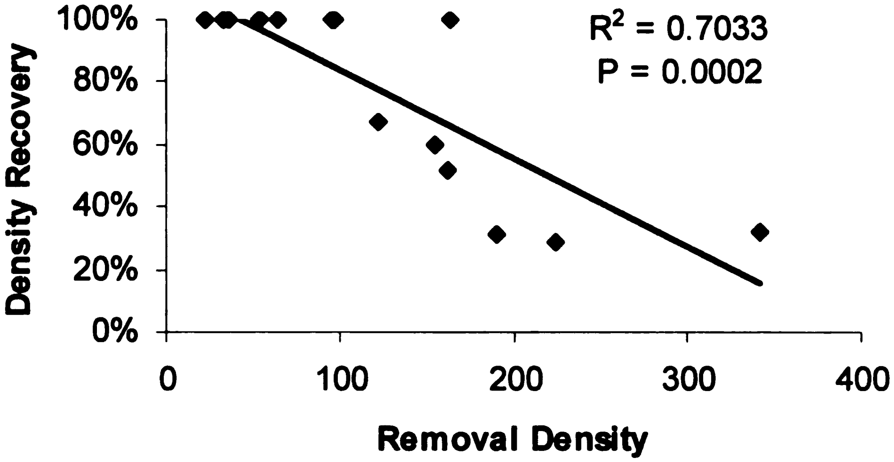

Figure 10. Level of maximum fish density recovery compared to the pre-disturbance density of the 14 experimental stream reaches.

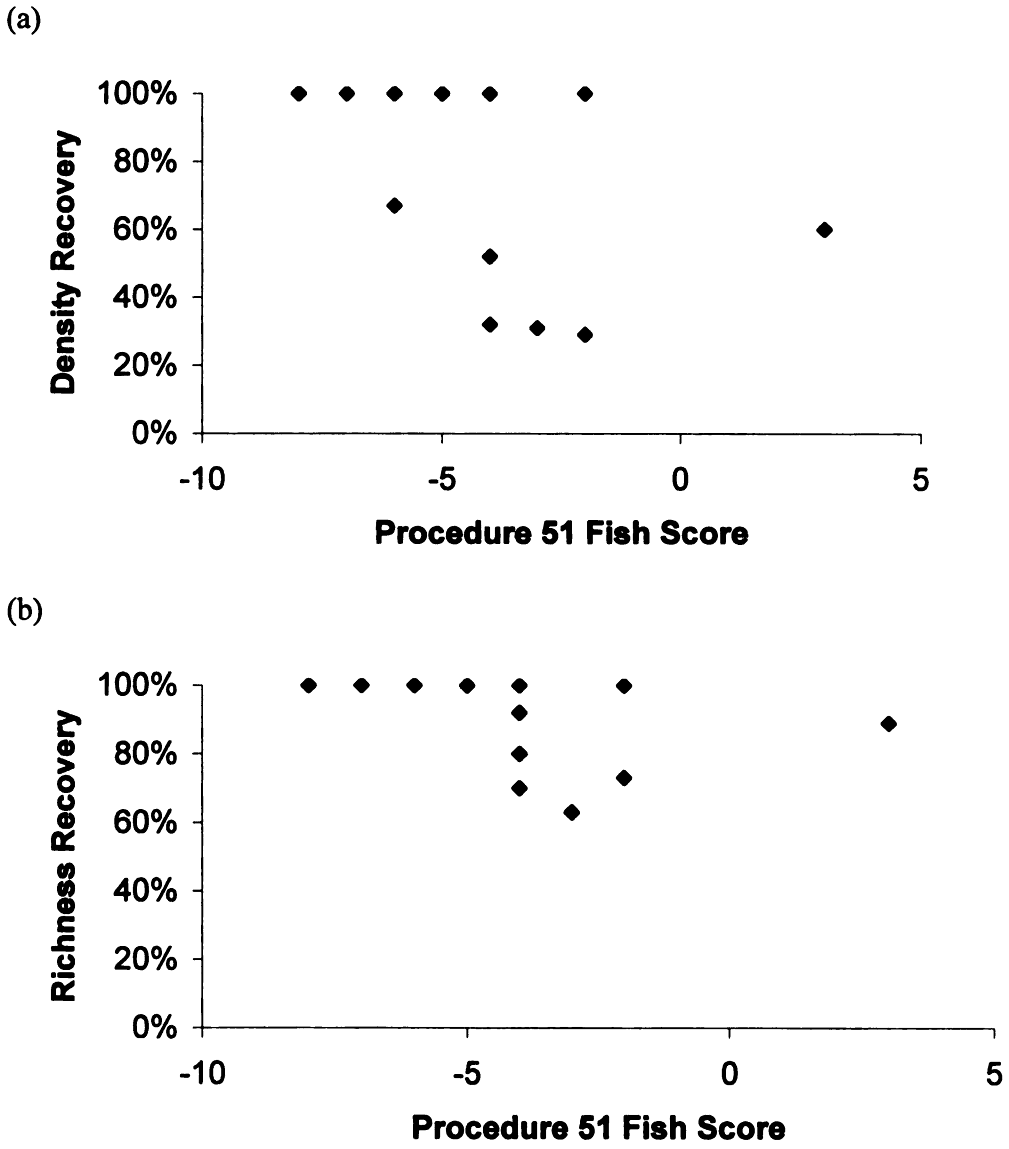

Figure 11. Procedure 51 fish assemblage scores (MDEQ 1997) compared to the level of maximum fish density recovery(a) and species richness recovery (b) in the 14 experimental stream reaches.

adaptable assemblage. The Michigan Department of Environmental Quality's (1997) Procedure 51 fish assemblage assessment can range from -10 to 10 for a particular site. A score of 5 or higher is "excellent", -5 or lower is "poor", and anything in between is "acceptable". Of the 14 experiment sites, six fish assemblages rated poor, eight were acceptable, and none was excellent. The generalist nature of the assemblages may reflect the quality of habitat available in the watershed and also suggests a degree of adaptation to disturbance. For example, the assemblages are dominated by cyprinids, a mobile group that appears to be able to rapidly colonize available habitats following disturbance (Storck and Momot 1981, Smithson and Johnston 1999, Larson et al. 2002). Indeed, creek chubs, blacknose dace, and bluntnose minnows were among the fastest-recovering species in the first few days following removal in these experiments.

Stream fish assemblages recovered rapidly from defaunation at the scale of this experimental disturbance, with recovering assemblages exhibiting highly similar structure to removal assemblages (mean I_M=0.83) within two days, regardless of any variation in recovery rates among species. Assemblage similarity greater than 0.70 is typically considered high (Matthews et al. 1988, Walser et al. 2000). The restricted movement paradigm (Gerking 1953) suggests that adult stream fish tend not to move from a home pool or restricted reach. However, recent studies have demonstrated that while many stream fish may remain in a home channel unit most of the time, regular exploratory trips are commonplace (Smithson and Johnston 1999, Larson et al. 2002). The speed of recovery in this study also suggests that a portion of the individuals of each species is mobile, rather than restricted in their movements.

I suspect that the lag in abundance recovery behind structural similarity is at least partly due to decreasing fish abundance throughout the vicinity of the experimental reaches as individuals dispersed into the empty habitat. Again, this trend suggests that a portion of each species is making exploratory trips outside of the home channel unit at any given time. By not assigning recovery values greater than 100% when individual samples did, in fact, occasionally exceed removal abundance, I maintained a conservative estimate of across-watershed recovery rates. Some portion of the detected lag in abundance recovery may be an artifact of this approach.

Prior studies of stream fish assemblage resilience have addressed long-term potential for recovery, typically returning to the disturbed site after a year (Gunning and Berra 1968,1969; Berra and Gunning 1970; Meffe and Sheldon 1990). Given my results, it is not surprising that these earlier researchers observed full or nearly full recovery. Peterson and Bayley (1993) suggested that assemblage recovery may occur much more quickly. They investigated the recovery of fish assemblages from experimental defaunation in Midwestern warmwater streams in reaches 46-113 m long at a time scale of 0.5-140 hours. The assemblages in these streams, which had several species in common with my sites, reached a proportional similarity index (Schoener 1968) of 0.70 in 60-140 hours (2.5-5.8 d) following defaunation and recovered a projected 90% of fish abundance within 100-270 h (4-11 d). Similarly, Sheldon and Meffe (1995) observed the recovery of fish assemblages in individual pools within 1 to 2 months. These results agree with the rapid colonization of available undisturbed stream habitat that I observed, suggesting that this may be a general property of warmwater fish assemblages in low-order streams.

Although fish assemblages generally recovered quickly, there was variation in the rate and completeness of recovery among streams, allowing me to investigate potential effects of habitat quality on fish assemblages and resilience. The QHEI was not related to pre-defaunation assemblage structure (species richness, fish abundance, or Procedure 51 score) or resilience in my streams. It is curious that the fish assemblage did not correlate to the QHEI because this index was designed to evaluate fish habitat in streams and indicate the quality of assemblage that the stream could support (Rankin 1989). The QHEI was created for Ohio warmwater streams similar to those in the Red Cedar River watershed of lower Michigan. Stauffer and Goldstein (1997) similarly found no relationship between QHEI and fish assemblage metrics (including IBI score, species diversity, species richness, evenness, and percent of total individuals within trophic groups) in a study of 18 prairie streams. While they noted that the QHEI was developed for streams in forested ecoregions that conform to the river continuum concept (Vannote 1980), rather than prairie streams that have somewhat different trophic dynamics, the authors also suggested that the metrics within the QHEI that are most important to fish assemblages may be masked in the total score due to redundancy and correlation. Sharing this concern, I evaluated individual metrics from the index and repeated the analyses. Although I found no strong relationships between individual metrics and pre-removal assemblage characteristics, the presence of pool habitat strongly encouraged recovery of fish abundance.

The positive relationship between the availability of pool habitat and fish assemblage recovery suggests that habitat influences the recovery process. Deeper, slow-moving pool habitat can serve as cover for stream fish (Harvey and Stewart 1991) and may have encouraged individuals to colonize the study reaches. This habitat preference suggests that pool habitat, which is typically lost when streams are channelized to facilitate drainage, should be preserved in streams where fish conservation is a priority. Further, multimetric approaches like the QHEI might mask the most important parameters for fish assemblages. This emphasizes the importance of combining biological sampling with physical indices such as the QHEI to assess the state of stream ecosystems, despite the additional effort required to obtain meaningful results (Stauffer and Goldstein 1997).

I was also interested in pre-removal assemblage influences on resilience. Although the individuals present during the removal were not part of the colonist source pool, I hypothesized that the pre-removal assemblage may indicate the structure of the source pool and the suitability of the stream habitat within the study reaches. Sampling of stream habitat upstream and downstream of the study reaches typically revealed fish assemblages similar to those found within the study reaches (unpublished data). My finding that pre-removal species richness was unrelated to the rate and extent of richness recovery is consistent with previous work (see Detenbeck et al. 1992 for a review); species-poor streams recovered richness as well as speciose systems. This supports my earlier suggestion that members of all species in this system, both those considered mobile, such as cyprinids, and more sedentary species, such as darters, regularly travel outside individual channel units. These movements encourage the colonization of newly available habitat (Larson et al. 2002).

The negative relationship between pre-removal fish abundance and abundance recovery in my study reaches is worthy of consideration. Study reaches with fewer than

100 individuals per 100 m generally recovered abundance rapidly and completely, while reaches with more than 175 individuals tended not to recover fully within the month of observation. This may have been related to the quality of habitat available in adjacent stream reaches which provided potential colonists for the empty habitat. Study reaches with initially small populations may have represented relatively poorer habitat than source reaches, and simple diffusive movement from higher-quality, more densely populated source reaches may have been adequate for assemblage recovery. Conversely, densely populated study reaches may have been slow to recover in numbers because those reaches may have represented the best available local habitat. The majority of local fish may have been concentrated at that site, and following my removal of those individuals, adjacent source areas did not support a sufficient number of potential colonists to permit complete abundance recovery. This is consistent with the view that streams are heterogeneous systems composed of differing patches of habitat due to local disturbances and colonization dynamics (Townsend 1989, Melo et al. 2003). This heterogeneity combined with the apparent mobility of stream fishes emphasizes the need for stream conservation over long reaches that can support a variety of habitat types to meet the needs of a diverse biota.

Finally, the quality of fish assemblages as measured by Procedure 51 (MDEQ 1997) was unrelated to the recovery of species richness or abundance after defaunation. The Procedure 51 score is derived from four taxonomic metrics, three trophic metrics, two tolerance metrics, and one reproductive metric. Due to the rapid recovery of assemblage structure, I can state that there were not great differences in colonization ability among taxa in the study streams at the temporal and spatial scale I observed. Further, Detenbeck et al. (1992) found that trophic guild was not a good predictor of resilience. Therefore, since seven of ten Procedure 51 metrics were unlikely to relate to resilience of my fish assemblages, the lack of relationship is not surprising.

While the rapid recovery I observed should not be used to justify disturbance to streams or stream fishes (Sheldon and Meffe 1995), it does have positive implications for stream fish management. For example, small-scale fish kills due to temporary pollutant inputs should recover quickly without aid as long as source populations are available nearby and habitat remains unimpaired. Likewise, high resilience suggests that restored stream reaches from which flow is temporarily diverted should be rapidly colonized if relatively short reaches are restored at a time and source fish populations are unimpeded.

We are left with the question of how well current assessment techniques evaluate the health of stream fish communities. Multimetric indices such as the QHEI, and Procedure 51 and other indices of biotic integrity, are widely used to assess the health of stream ecosystems (Karr 1987, Lyons 1992, Stauffer and Goldstein 1997). They are efficient in terms of cost and time, but may not tell the whole story. Ecosystem health has been equated with sustainability, the ability to maintain structure and function in the presence of disturbance (Meyer 1997, Costanza and Mageau 1999). This suggests, logically, that resilience is a primary component of stream health, although it is not a part of any stream assessment index of which I am aware. A review of the recovery of temperate stream fish communities from disturbance led Detenbeck et al. (1992) to conclude that currently we can not predict recovery times, because they are a function of disturbance-specific, site-specific, and species-specific factors. It is not clear that the resilience of a system can be predicted using any kind of universal metric or index. However, it does appear that there are a number of characteristics of organisms (e.g., life history, dispersal ability), assemblages (e.g., spatial heterogeneity, degree of isolation), and disturbances (e.g., temporal and spatial scale, residual effects) that we can identify and use to predict, in a relative sense, the ability of a system to recover from disturbance (Detenbeck et al. 1992, Peterson and Bayley 1993, Sheldon and Meffe 1995). For example, fish assemblage recovery from a temporary, or pulse, disturbance such as an experimental defaunation is typically rapid, while long-term, or press, disturbances such as channelization may permanently disrupt the system unless mitigation actions are taken (Detenbeck et al. 1992). The exceptionally rapid recovery I observed in these experiments is likely attributable to (1) undisturbed habitat, (2) a mobile colonist assemblage dominated by cyprinids and centrarchids, and (3) the relatively small spatial scale of the disturbance (Sheldon and Meffe 1995). Additional scales and types of disturbance should be investigated to expand our understanding of fish assemblage resilience and its relevance to stream health.

Further, my results suggest that the relationship between resilience and metrics typically used to assess stream health, such as assemblage structure and overall habitat quality, is not a simple one. Valuable insights into overall stream health could potentially be gained by combining physical and biological assessments with experimental determinations of the ability of these systems to recover from disturbance. With improved understanding, metrics may be developed to estimate recovery potential without the need to disturb the stream system.

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CHAPTER 2

The vigor-organization-resilience concept of ecological health: lessons from temperate warmwater stream fish communities

Abstract

An ecologically healthy system is able to maintain vigor, or function, and organization, or structure, in the presence of disturbance (resilience). Measures of ecological vigor, such as abundance, productivity, and biomass, are relatively simple to obtain in the field, as are measures of organization, such as species richness and diversity. However, determination of system resilience in the field is less than straightforward because of its dependence on the nature of the disturbance and on the choice of endpoints for system recovery. I investigated the vigor, organization, and resilience of temperate warmwater stream fish communities subject to controlled disturbance to determine what relationships, if any, existed among these variables and stream habitat quality. I measured community resilience in a number of ways, including level of and time to recovery of fish density, richness, diversity, and community structure. I found no significant relationship between habitat quality and vigor or organization of the study communities or their recovery, although some individual physical parameters were significant. Interestingly, there was no relationship between the pre-disturbance vigor or organization of the fish community and its resilience to disturbance. While I found that measuring post-disturbance changes in structure and abundance over time was useful in determining recovery, these resilience values are applicable only to one type of disturbance at one spatial and temporal scale. Although vigor and organization may

serve as partial indicators of community health, a measurement of resilience to various types of disturbance would be invaluable for stream fishery management and warrants further research.

Introduction

Ecosystem management is based on our ability to assess the state of an ecological system and, if necessary, take steps to maintain or improve the quality of the system. Rich debate over assessment methods exists in the literature (Costanza 1992). This debate is due, in part, to the difficulty in devising assessment methods that are straightforward, inexpensive, and easily understood by stakeholders, yet comprehensive and rigorous.

The concepts of ecosystem integrity and health were developed as frameworks for assessment. Karr (1995) defined ecosystem integrity as "the capacity to support and maintain a balanced, integrated, adaptive biologic system having the full range of elements and processes expected in the natural habitat of the region". Therefore, integrity is the maintenance of structure and function in the context of evolutionary and biogeographic forces (Meyer 1997). Costanza and Mageau (1999) define a healthy system as one that can maintain its function (vigor) and structure (organization) over time in the presence of external stress (resilience). They go on to explain this concept in another way: "A healthy ecosystem is one that can develop an efficient diversity of components and exchange pathways (high organization) while maintaining some redundancy or resilience as an insurance against stress, and substantial vigor to quickly recover or utilize stress in a positive manner". They also equate health with sustainability, noting that sustainability refers not to a system lasting forever, but achieving its maximum life span within natural successional processes.

Measures of ecological vigor, such as abundance, productivity, and biomass, are relatively simple to obtain in the field, as are measures of organization, such as species richness and diversity (Table 1). However, determination of system resilience in the field is less than straightforward. Resilience can be measured as the magnitude of disturbance from which a system can recover (Holling 1973) or as the time required for a system to recover from a disturbance (Pimm 1984). Comparisons among systems are difficult because they depend on the nature of the disturbance and on the choice of endpoints used to determine system recovery. These complications may explain why field measurement of resilience has not received much attention as a health assessment tool.

Table 1. Components of ecological health (adapted from Costanza and Mageau 1999).

	Variable Type	Measures	Methods
Vigor	Static	Abundance, Productivity, Biomass	Direct measurement
Organization	Static	Species richness, Diversity, IBI	Direct measurement
Resilience	Dynamic	Time, Path, or Level of Recovery	Measurement over time, Simulation modeling

Because resilience refers to the ability of a system to recover structure and function following disturbance, it serves as a dynamic stress test for assessing system health and complements static measures of structure and function. Inclusion of resilience as an indicator of system health is logically appealing because of its role in sustainability. While system structure and function may appear healthy at a particular point in time, if the system is not resilient to disturbance, it is not sustainable or healthy.

I feel that the concept of ecological health is a useful metaphor for communication among scientists and with the public, despite its potential flaws (Wicklum and Davies 1995). It is not my goal in this paper to enter into the debate over the ecosystem health concept; for an in-depth discussion of the benefits and potential pitfalls of the ecological health concept, see Constanza et al. (1992). Assessment of the component variables of ecosystem health – vigor (function), organization (structure), and resilience – is relevant on ecosystem, assemblage, and population scales, and the health concept provides an excellent framework for discussion.

I investigated the vigor, organization, and resilience of temperate warmwater stream fish assemblages subject to controlled disturbance, focusing on the recovery process. I had three goals in mind during our study. First, I investigated whether habitat assessment measures, commonly used to indirectly assess stream health, were good predictors of the vigor or organization of the fish assemblage. Second, I looked for relationships among vigor, organization, and resilience that might further our understanding of fish assemblage recovery from disturbance. Finally, I used the recovery patterns observed in our experiments to develop a hypothesis about the recovery path taken by stream fish assemblages based on the nature of the disturbances they might face.

Methods

I conducted a series of field experiments to investigate the resilience of stream fish assemblages to disturbance in the Red Cedar River watershed, Michigan, USA, a warmwater system characterized by agricultural and, secondarily, urban development. The experiments described here are reported in greater detail in Chapter 1. I assessed stream habitat using the Qualitative Habitat Evaluation Index (QHEI; Rankin 1989). I disturbed the systems by removing all fish from 100 m reaches at 14 sites in second- and third-order streams of varying habitat quality and fish assemblage structure. The composition of the pre-disturbance assemblage was recorded. I then returned to these sites several times within a month to monitor fish assemblage recovery via catch-and-release sampling. Throughout the study, fish abundance and species richness represented vigor and organization, respectively. Resilience was measured as the maximum percent recovery of vigor and organization during the study period and by calculating Morisita's (1959) index of similarity to compare pre-disturbance assemblage structure to that of recovery samples.

Results

Neither pre-disturbance fish assemblage vigor, measured as the number of individuals (range = 23-342), nor organization (species richness; range = 5-18) was related to habitat quality as assessed using the QHEI (range: 16-65; Figure 1). Following fish removal, assemblage organization was highly resilient, resulting in an average Morisita's similarity of 0.83 across the watershed within 2 days of fish removal (Figure

2a). This similarity was maintained through the course of the experiments. In comparison, total fish abundance recovered more slowly but was increasing toward complete recovery by the end of a month on average (Figure 2b). Pre-disturbance organization did not influence organization recovery (Figure 3a), but pre-disturbance vigor was negatively related to vigor recovery (Figure 3b).

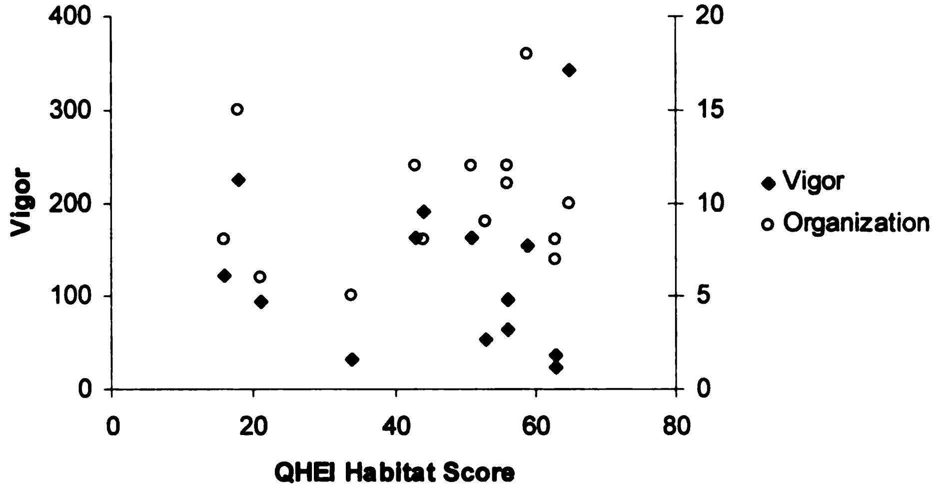

Figure 1. Neither fish assemblage vigor (abundance) nor organization (species richness) was related to habitat quality as measured by the Qualitative Habitat Evaluation Index (QHEI; Rankin 1989).

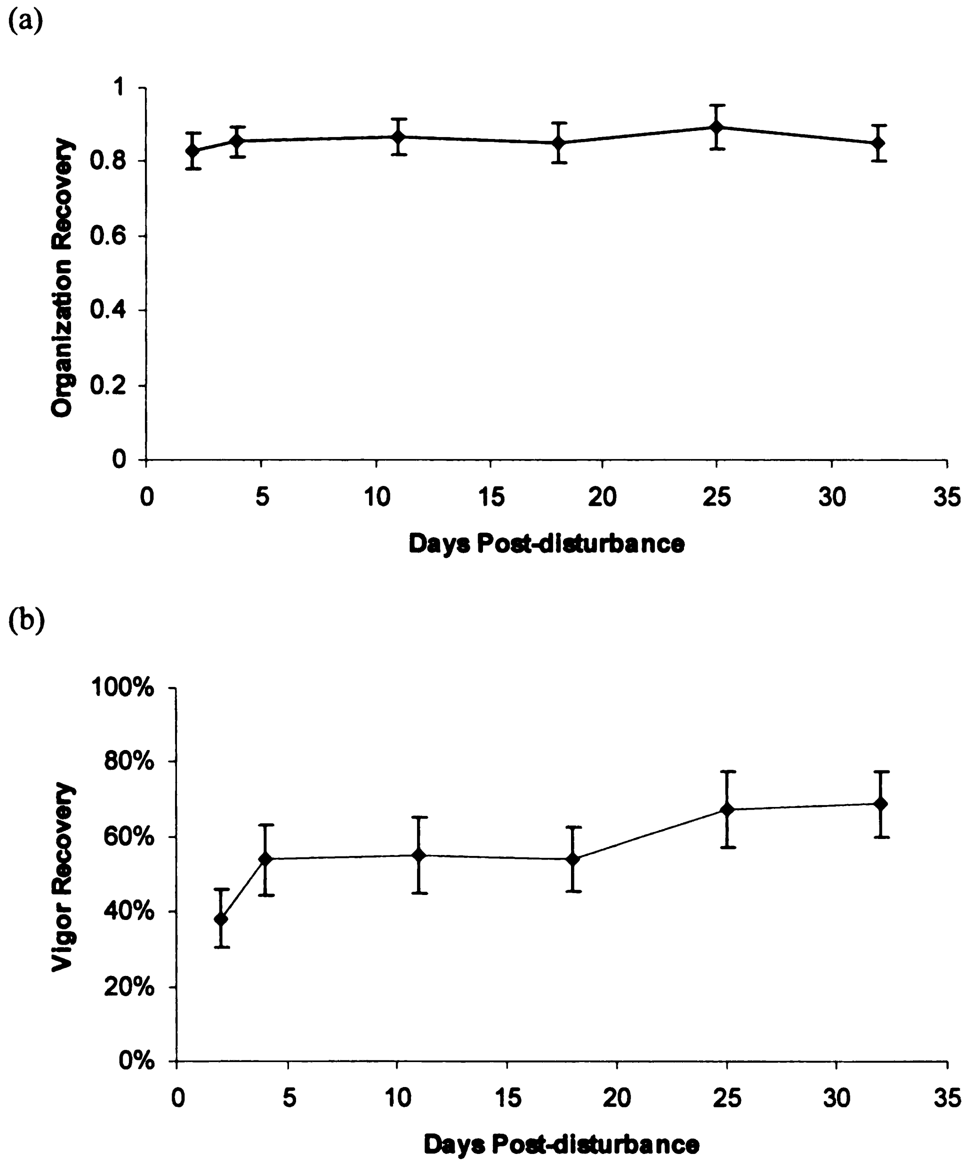

Figure 2. Fish assemblage organization (richness and proportional abundance) was highly resilient, showing strong similarity to pre-disturbance conditions throughout the recovery period. Morisita's (1959) similarity index ranges from 0 (completely dissimilar) to just above 1 (completely similar) (a). Assemblage vigor (fish abundance) recovered more slowly but increased over time (b).

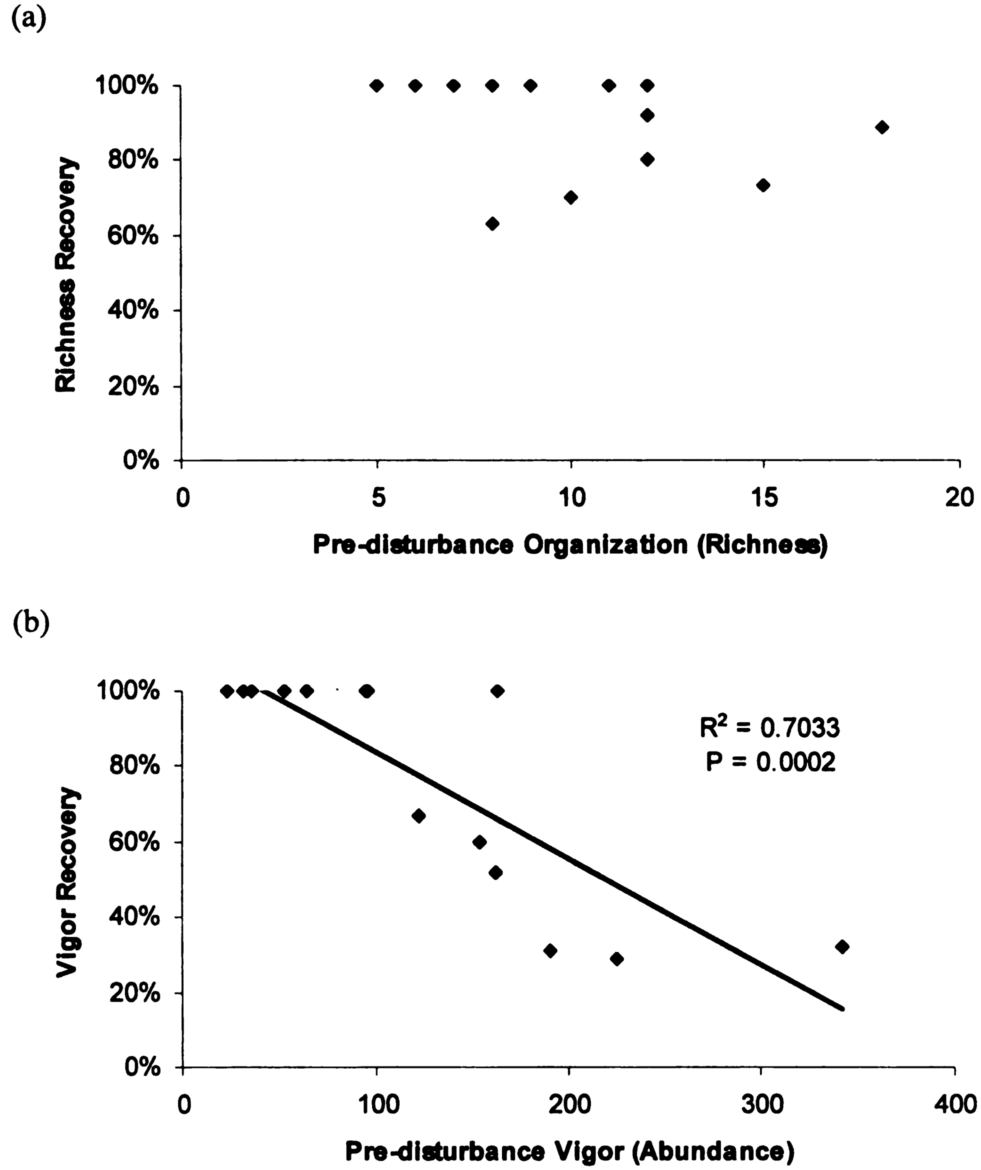

Figure 3. No clear relationship was found between pre-disturbance organization and organization recovery after one month (a). Pre-disturbance vigor was negatively related to its recovery after one month (b).

Discussion

Neither fish assemblage vigor nor organization was related to habitat quality as measured by the multimetric Qualitative Habitat Evaluation Index (QHEI). This index was designed to assess stream habitat quality for supporting fish, and is often used in place of biological sampling. The lack of relationship between QHEI score and the fish community metrics suggests that habitat evaluation alone, at least via this method, is not sufficient to assess the health of a stream system, and, in fact, may be misleading. Pre-disturbance assemblage organization, measured as species richness, was not a predictor of richness recovery. Fish abundance (vigor) was negatively related to recovery, suggesting that densely populated stream reaches may be more sensitive to disturbance. Further discussions of the implications of the above findings are available in Chapter 1.

A conceptual model linking the component variables of ecological health – vigor, organization, and resilience – can be developed to better understand and predict the path of recovery after disturbance. In our fish removal experiments, both the vigor and organization of the fish assemblage were decreased to zero. I predicted that, with habitat and colonist pools intact, organization would recover more quickly than vigor (abundance) as the stream reach was recolonized (Figure 4a). Our data support this hypothesis. The recovery of assemblage organization, as measured with Morisita's similarity index, was nearly complete within 2 days after fish removal. Vigor, measured as number of individuals, recovered more slowly and approached recovery within a month.

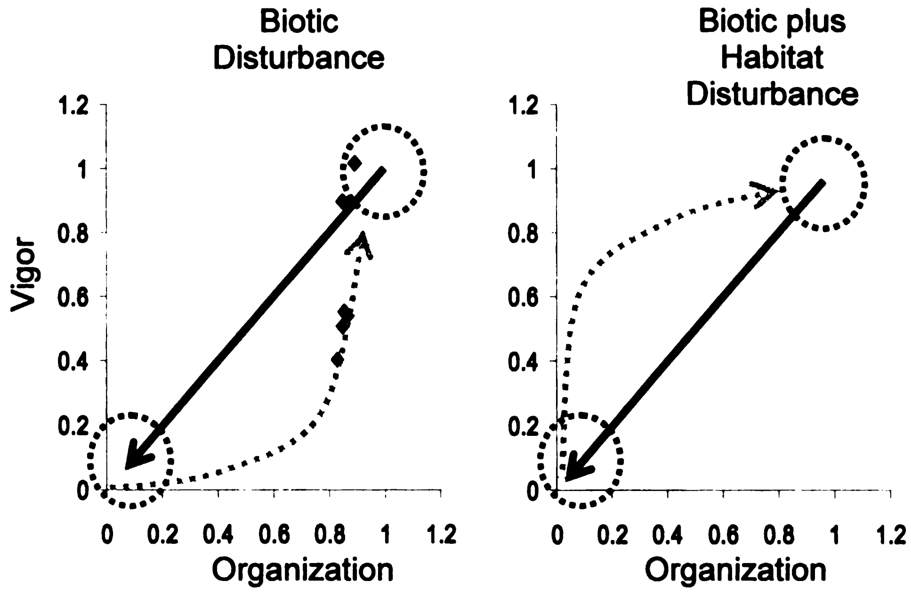

Figure 4. Paths of assemblage recovery (dotted arrow) following disturbance (bold arrow) of ***biota only***, as in our experimental fish removals. (a; ♦ represents the mean value across all sites for each time interval), and ***both biota and habitat*** (b).

I suggest that the path of recovery taken by the fish assemblage is influenced by the nature of the disturbance. The direction and extent of change due to disturbance would affect both the path and rate of recovery. For example, if I had not only removed fish from the experimental stream reaches, but also disturbed the habitat, I expect that assemblage vigor would recover more quickly than organization (Figure 4b). Degraded habitat would no longer be suitable for the full complement of fish species available in the adjacent colonist pools, so the experimental habitat would likely be rapidly colonized by generalist species, perhaps in substantial numbers, while less tolerant species would not recolonize until the habitat had recovered. As a result, the path of resilience would be different than in cases where habitat is undisturbed, and the time scale of biotic recovery would be greater as it would depend on habitat recovery.

This conceptual model of fish assemblage recovery has application in making comparisons between systems and for understanding the mechanisms behind the ecological recovery process. However, from a management standpoint, a complex system descriptor that requires measurement over time and is dependent on a number of extraneous variables, such as the type and scale of disturbance, is not particularly desirable in terms of cost and time. So, although system resilience is logically an important component of system health, it may not be feasible to measure in the field when a large number of systems are being considered. Because comparison depends on equivalent disturbances, it would be necessary to deliberately disturb the set of systems of interest, and then frequently resample these systems to determine progress along the path of recovery.

This large investment of effort led Costanza and Mageau (1999) to suggest simulation modeling as the best way to determine system resilience and make comparisons among systems. However, even this approach requires a large initial investment in gathering data to construct and validate the model. Further, prediction of system recovery would again be dependent on the nature of the disturbance and the choice of endpoints for determining recovery. Any framework using resilience as a relative measure of health in a set of systems, such as warmwater stream fish communities, would require the adoption of a particular disturbance type against which to measure recovery, and would have to be, at most, regional in scope, because variables such as mobility of potential colonists and habitat heterogeneity vary from region to region.

A review of the recovery of temperate stream fish communities from disturbance led Detenbeck et al. (1992) to conclude that currently we can not predict recovery times, because they are a function of disturbance-specific, site-specific, and species-specific factors. It is not clear that the resilience of a system can be predicted using any kind of universal metric or index. However, it does appear that there are a number of characteristics of organisms (e.g., life history, dispersal ability), communities/ ecosystems (e.g., spatial heterogeneity, degree of isolation), and disturbances (e.g., temporal and spatial scale, type of disturbance, residual effects) that we can identify and use to predict, in a relative sense, the ability of a system to recover from disturbance. I feel that further investigation of the features of ecological systems and the disturbances that affect them will allow us a better understanding of system resilience and health, and should be pursued. Although vigor and organization may serve as partial indicators of health, a clearer understanding of resilience dynamics would be invaluable for stream fishery management.

Acknowledgments

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CHAPTER 3

Habitat selection by creek chubs (*Semotilus atromaculatus* Mitchill) following experimental defaunation

Abstract

Ideal free distribution theory suggests that animals will occupy the most suitable habitats available. Suitability can be defined as the fitness that a particular habitat affords the individuals that occupy it. Therefore, an understanding of habitat selection under a range of conditions will yield information about the relative suitability of adjacent habitats and potentially reveal habitat characteristics for emphasis in species conservation. Traditional methods of assessing habitat suitability rely on correlating habitat characteristics with the number of individuals occupying the habitat under natural conditions. Distribution is a behavioral phenomenon, however, and the majority of these correlations do not consider movement or density-dependent interactions that may influence the suitability of a particular habitat. In this study, I considered both the influence of physical habitat and density of conspecifics on distribution during experimental defaunation of fishes from warmwater stream reaches. Habitats were left intact, and the distribution and movement of one species, the creek chub (*Semotilus atromaculatus* Mitchill), were tracked as densities increased via habitat recolonization. As observed in previous studies, chubs preferred pools over runs, and runs over riffles. Alternative methods of measuring selection, including selection indices and immigration rates, revealed similar insights. Density of creek chubs in the study reaches, which

ranged from zero immediately following defaunation to above pre-defaunation (natural) densities, had no apparent effect on habitat preferences.

Introduction

Habitat selection by animals results in distribution patterns that can be observed in the field and laboratory. These distribution patterns yield information about the suitability of different available habitats for the species of interest. Field observations of animals in their natural environments, and laboratory and field manipulations of animals and habitat, provide clues about the particular characteristics of a given habitat that make it more or less suitable for the species.

Habitat suitability can be defined as the fitness that a particular habitat affords the individuals that occupy it (Fretwell and Lucas 1970). Therefore, suitability is the product of birth, growth, and death rates and reproductive success for a species in a particular habitat. Traditional methods of calculating habitat suitability use the density of individuals at a site as a proxy for these more complicated variables, based on the assumption that animals will occupy the most suitable habitat available. This assumption is based on theories of species distribution, including the ideal free distribution described by Fretwell and Lucas (1970). Ideal free distribution theory suggests that if all individuals are free to move into any habitat, they will settle in the habitat most suitable to them (i.e., offering the highest fitness).

For example, the habitat suitability indices (HSIs) produced by the U.S. Fish and Wildlife Service primarily are based on literature reviews of distributions and correlations with physical habitat characteristics. These data are used to determine the best habitat for a species (e.g., McMahon 1982). HSIs do not consider density-dependent effects on habitat suitability, such as competition for resources, nor do they consider behavior or changes in distribution over time; however, these indices frequently form the basis of habitat management and species conservation efforts. Further, these models are largely untested and often refuted in experimental studies (Hubert and Rahel 1989).

Describing habitats by physical attributes alone may not be sufficient to explain distributions, and is possibly one of the biggest shortcomings of suitability indices like the HSI. Distribution is a behavioral phenomenon, the result of individual movement. Animal movement can be influenced not only by the physical environment but also by interactions with other animals, many of which are mediated by density (Fraser and Emmons 1984, Strange et al. 1993).

In a study of stream fishes, Belanger and Rodriguez (2002) suggested that measures of local movement, such as habitat-specific immigration and loss rates, provide useful indicators of habitat quality and provide a more reliable mechanistic basis for understanding than point observations of density. They argue that simple correlations of density to habitat type are weakened by transient fluctuations in abundance, seasonality, territorial interactions, and density dependence of habitat selection. Their movement-based model predicted lower turnover rates among fish occupying optimal habitat than among those in sub-optimal habitat. The authors reported that immigration rates were strongly correlated with species-specific habitat preferences observed in previous studies, and provided an integrated assessment of habitat quality as perceived by fish. They suggested that because immigration rate seems to reflect the attractiveness of a unit, habitat types that tend to show high immigration rates would be colonized most rapidly following transient declines in density, such as experimental defaunation.

In this study, I considered both the influence of physical habitat characteristics and density of conspecifics on distribution during recolonization following experimental defaunation of fishes from stream reaches. Habitats were left intact, and the distribution and movement of one species, the creek chub (*Semotilus atromaculatus* Mitchill), were tracked as densities increased via habitat recolonization. I sought to answer the following questions. What are the habitat preferences of creek chubs in our study streams? Do different methods of measuring suitability yield similar results? Finally, do habitat preferences change with the density of individuals in the stream reach?

Stream fishes are well suited for examining the behavioral mechanisms and habitat characteristics that lead to species distributions, because habitat units are arranged in a linear fashion, distinct habitat units are typically easily defined, and many species are abundant and easy to collect and identify. While early studies suggested that stream fishes exhibit only limited movement within streams (Gerking 1953), more recent work has documented extensive movement by at least a portion of the populations of many species (Smithson and Johnston 1999, Albanese 2001). Movement among habitat units by stream fishes allow them to sample available habitat and occupy the most suitable units available, making them more likely to conform to an ideal free distribution (Fretwell and Lucas 1970).

I chose to focus on creek chubs, the most abundant minnow in the eastern United States (Scott and Crossman 1973). They are widespread, are relatively long-lived, and adults are often the top predator in small streams, making life stages of creek chubs important on many levels of the trophic web (Copes 1978). Their ubiquity and abundance have made them a candidate "sentinel species" for assessing stream health (Fitzgerald et al. 1999), and make them an ideal species for examining distribution mechanisms in the field and laboratory. Further, the preference of adult creek chubs for pool habitat has been noted in an HSI (McMahon 1982) and other studies (Moshenko and Gee 1973, Copes 1978, Storck and Momot 1981, Hubert and Rahel 1989, Harvey and Stewart 1991) and forms a basis for comparison for the results of this study.

Methods

I conducted ten fish removal experiments in 100 m reaches of nine different streams in the Red Cedar River watershed, Michigan, during the summers of 2001 and 2002. These experiments are a subset of those described in Chapter 2; only sites that contained at least two of the three possible major channel unit types (pools, riffles, or runs; Dunne and Leopold 1978) were considered for this analysis.

The ten experimental stream sites averaged 103 m in length (range: 96.1-117.6 m) and 502 m^2 in surface area (range: 297.5-1090.12 m$^{2;}$ Table 1). Wetted width ranged from 0.9 – 13.8 m (median: 3.8 m). Five of the ten sites included pool, riffle, and run habitat. Three contained only riffles and runs, and two contained only pools and runs.

I removed all fish from the study sites via electrofishing. Species and pool, riffle, or run location within the study site were recorded for each individual collected. I relocated all fish collected during each removal to another stream site 2-10 km away from the study site to discourage their return to the study site; creek chubs generally move less than 1 km during spring and summer (Storck and Momot 1981). I then re-sampled each study site frequently during the following month to track fish assemblage recovery. See Chapter 2 for a detailed description of the methods used to characterize the stream habitat and conduct the fish removal experiments.

Table 1. Experimental fish removal sites in the Red Cedar River watershed.

Site		Mean Width	Length	Area (m^2)				Number			Mean Depth (m)		
#	Name	(m)	(m)	Total	% Pool	%Riffle	% Run	Pools	Riffles	Runs	Pool	Riffle	Run
1	Dobie Road Tributary	3.5	102	356	28	38	34	6	3	5	0.26	0.11	0.19
2	Corwin Road Tributary	2.8	109	318	47	16	37	5	2	4	0.44	0.25	0.30
3	Sloan Creek	4.2	118	539	0	54	46	0	3	3	-	0.16	0.21
6	Sycamore Creek	11.1	102	1090	0	10	90	0	1	2	-	0.19	0.20
9	Kalamink Creek, Van Orden Road	3.9	105	399	25	22	53	3	1	4	0.21	0.13	0.16
10	Doan Creek, Noble Road	6.4	96	627	25	32	43	2	2	2	0.28	0.16	0.25
11	Deer Creek	4.9	100	519	11	6	83	1	1	2	0.31	0.20	0.28
12	Doan Creek, Columbia Road	4.4	101	427	26	0	74	2	0	3	0.42	-	0.33
13	Wolf Creek	2.6	100	298	0	8	92	0	1	2	-	0.04	0.04
14	East Branch, Red Cedar River	4.7	101	446	14	0	86	1	0	2	0.51	-	0.29

I assessed habitat selection by creek chubs both with Strauss' linear selection index (Strauss 1979),

$$\mathrm{Li} = \mathrm{oi} - \hat{\pi}\mathrm{i}\,,$$

and Manly's standardized selection ratio (Manly et al. 2002),

$$\mathrm{Bi} = \hat{\mathrm{w}}\mathrm{i}/\left(\sum_{\mathrm{i}=1}^{\mathrm{I}} \hat{\mathrm{w}}\mathrm{i}\right),$$

Where o_i = sample proportion of used units in category i,

π_i = proportion of the available units in category i, and

$\hat{w}i = o_i/\ \pi_i$, the selection ratio.

Strauss' linear selection index simply shows the difference between the proportional availability of a habitat and its proportional use. A positive value indicates that a habitat was used in greater proportion than it was available, suggesting positive selection for that habitat. Manly's standardized selection ratio converts the same data into a ratio that is then standardized to represent the probability that an individual will use a particular habitat type (Manly et al. 2002). Both the linear selection index and the selection ratio are commonly used to quantify selection among habitats by individuals.

Immigration rate (individuals per day) was calculated as

$$I = \frac{(nt1 - nt0)}{t1 - t0}.$$

The linear correlation between the total number of creek chubs removed from each study site and the number collected in the first electrofishing pass during defaunation was very strong ($y = 0.819x - 11.931$, $R^2 = 0.95$). Because of this strong linear relationship, the number of creek chubs collected during the single electrofishing passes conducted during recovery sampling of the study sites was used as an estimator of the total density of creek chubs at each site.

I used a general linear model where site was a blocking factor and density was a continuous covariate to quantify the effects of these variables on creek chub habitat preferences. Interaction terms were evaluated to determine if the response of habitat selection to density varied across sites. Selection for pools, riffles, and runs were evaluated separately.

Results

The total number of creek chubs removed per site ranged from 10 to 198 individuals, resulting in a median density of 0.071 fish/m^2 (range: 0.021-0.62 fish/m^2). By comparing first-pass numbers from the removal to subsequent single-pass return catches, I determined that creek chubs recovered to or above removal densities at six out of ten sites during the month-long duration of the experiments (Table 2).

Table 2. Creek chub removal and recovery from experimental stream sites in the Red Cedar River watershed.

Site		Removal		First pass no. of fish		
#	Name	Total Removed	Density (fish/m^2)	Removal	Max. Recovery	% Recovery
1	Dobie Road Tributary	66	0.19	31	107	>100
2	Corwin Road Tributary	198	0.62	161	38	24
3	Sloan Creek	40	0.07	11	22	>100
6	Sycamore Creek	27	0.03	16	13	81
9	Kalamink Creek, Van Orden Rd	10	0.03	6	5	83
10	Doan Creek, Noble Road	13	0.02	6	7	>100
11	Deer Creek	63	0.12	20	37	>100
12	Doan Creek, Columbia Road	51	0.12	23	41	>100
13	Wolf Creek	20	0.07	12	7	58
14	East Branch, Red Cedar River	13	0.02	5	7	>100

Both Strauss' linear selection index and Manly's standardized selection ratio indicated that in stream reaches with pools, riffles, and runs available, creek chubs generally preferred pools over runs, and runs over riffles (Figure 1). If no distinct pool habitat existed, creek chubs continued to prefer runs over riffles (Figure 2). Interestingly, in the two sites with only runs and pools, runs were preferred over pools (Figure 3).

These preferences were not influenced by changes in creek chub density over the course of the experiments. Density in the study sites ranged from zero (immediately following defaunation) to 0.41 fish/m^2. When selectivity was plotted against density of creek chubs in the experimental reaches, it appears that selectivity is strongest at low densities, and the distribution becomes more even as densities increase (Figures 1-3). However, when the data are examined on a site-by-site basis, it becomes clear that stream site has a much stronger effect on selectivity than does density. For example, when Strauss's selection index is plotted against site density (Figure 4), sites with broad ranges of creek chub density during the experiment (i.e., sites 1 and 2) show a fairly constant strength of creek chub selection for pools. Sites where densities remained relatively low showed substantial fluctuations in selection strength. Similar site-clumped distributions were observed with runs and riffles (Figures 5 and 6).

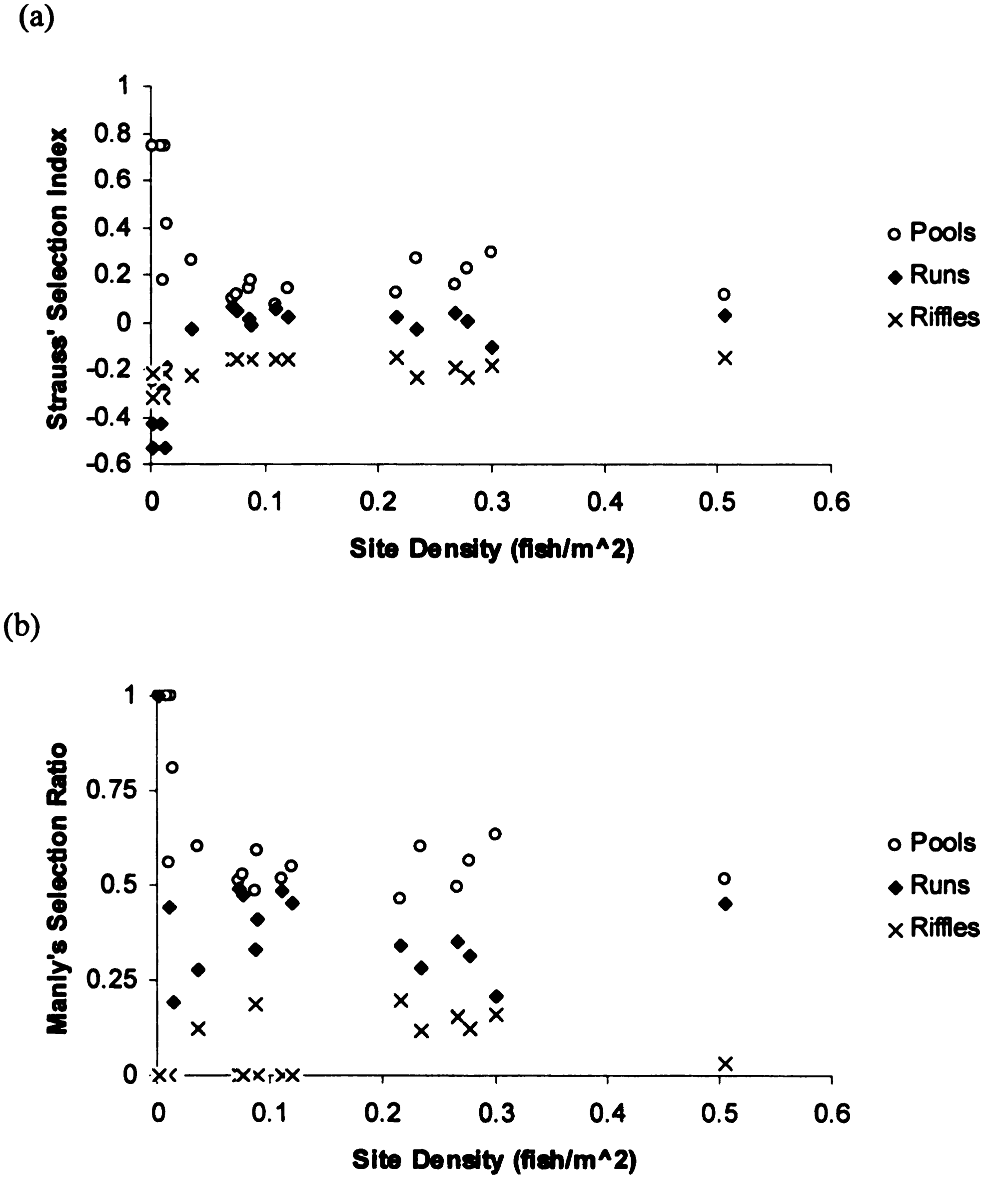

Figure 1. Creek chub habitat selection versus density of chubs in the experimental sites containing pools, riffles, and runs as assessed with (a) Strauss' (1979) linear selection index and (b) Manly's standardized selection ratio (Manly et al. 2002).

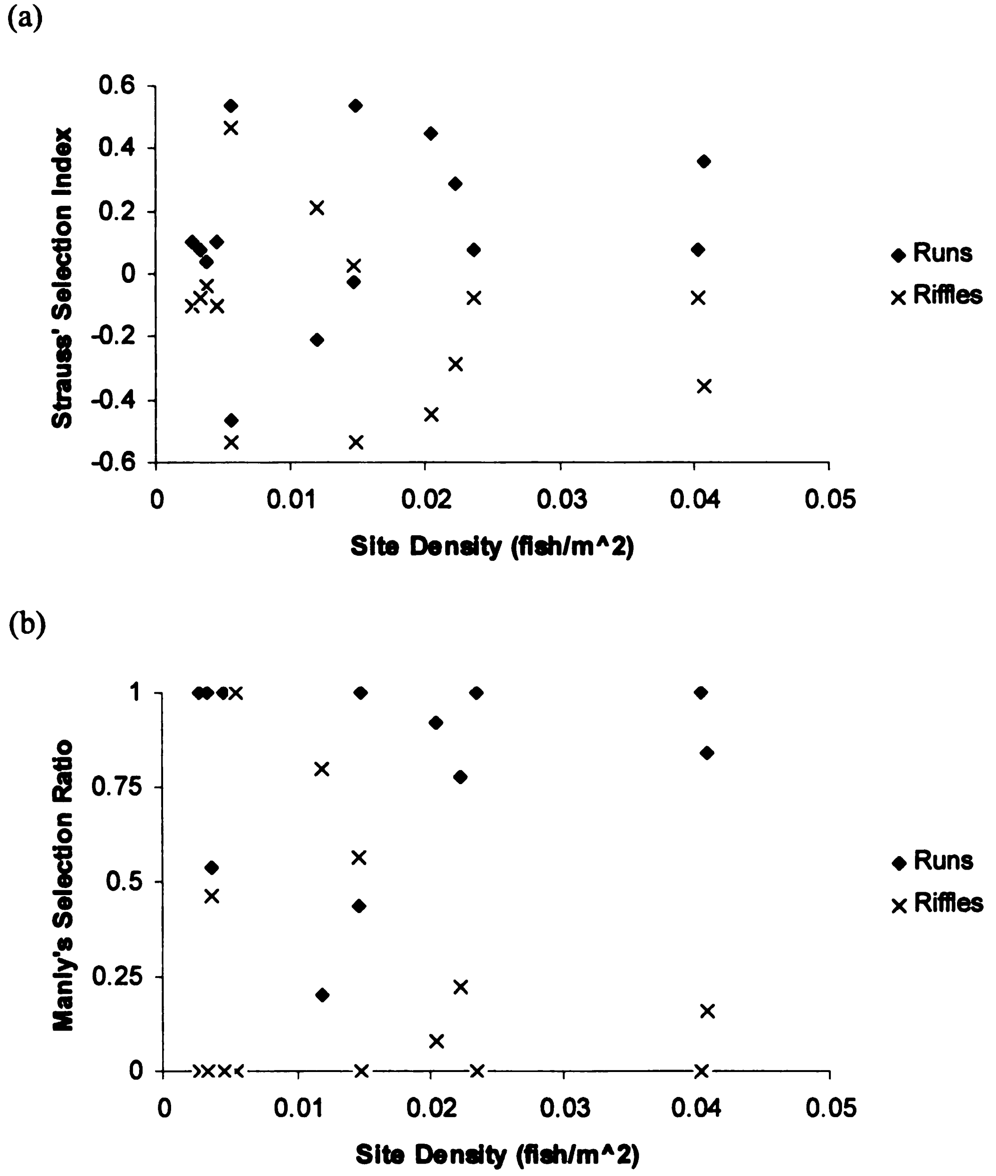

Figure 2. Creek chub habitat selection versus density of chubs in the experimental sites containing only riffles and runs as assessed with (a) Strauss' (1979) linear selection index and (b) Manly's standardized selection ratio (Manly et al. 2002).

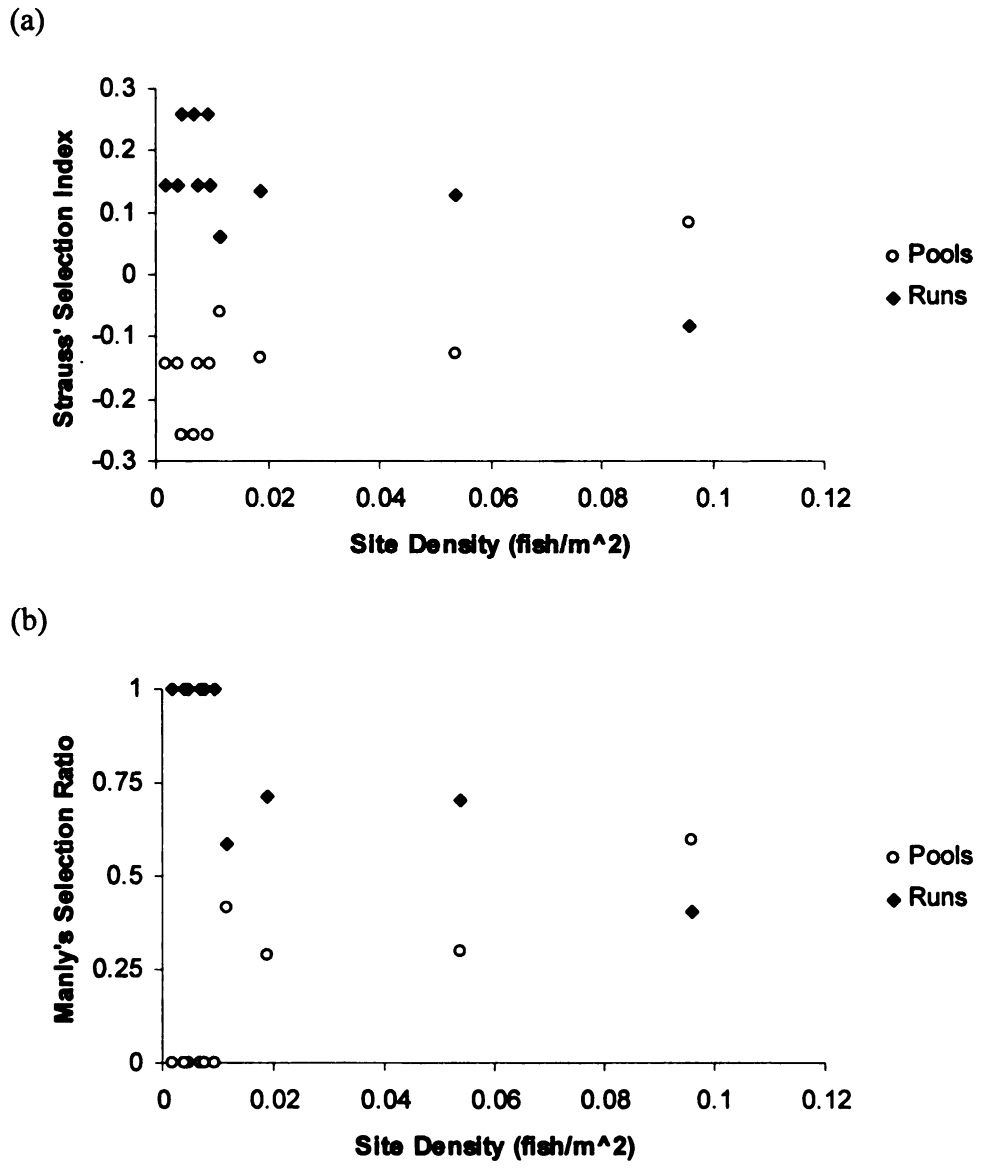

Figure 3. Creek chub habitat selection versus density of chubs in the experimental sites containing only pools and runs as assessed with (a) Strauss' (1979) linear selection index and (b) Manly's standardized selection ratio (Manly et al. 2002).

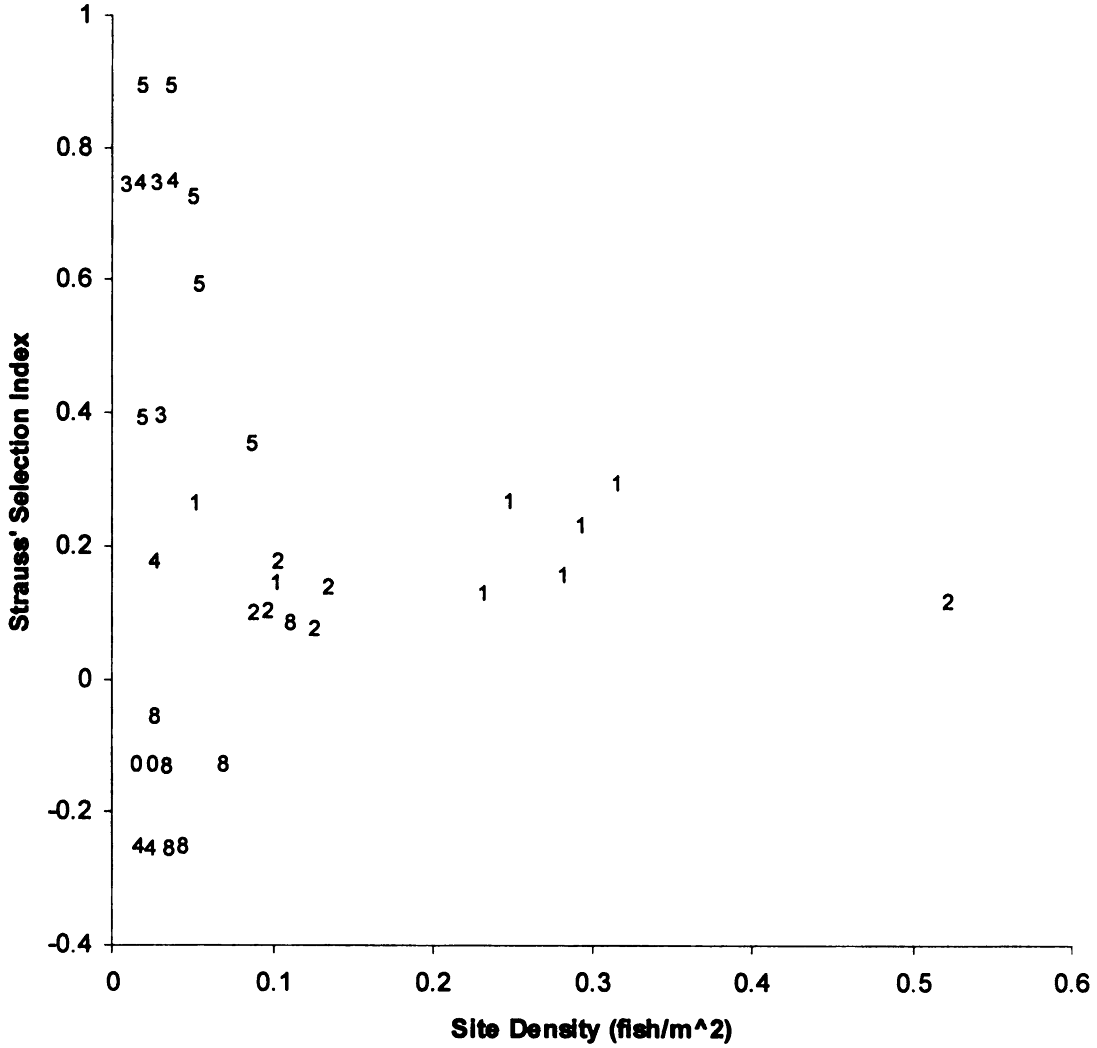

Figure 4. Strauss's linear selection index for pools plotted against site density for each observation. Numeric data markers represent individual sites.

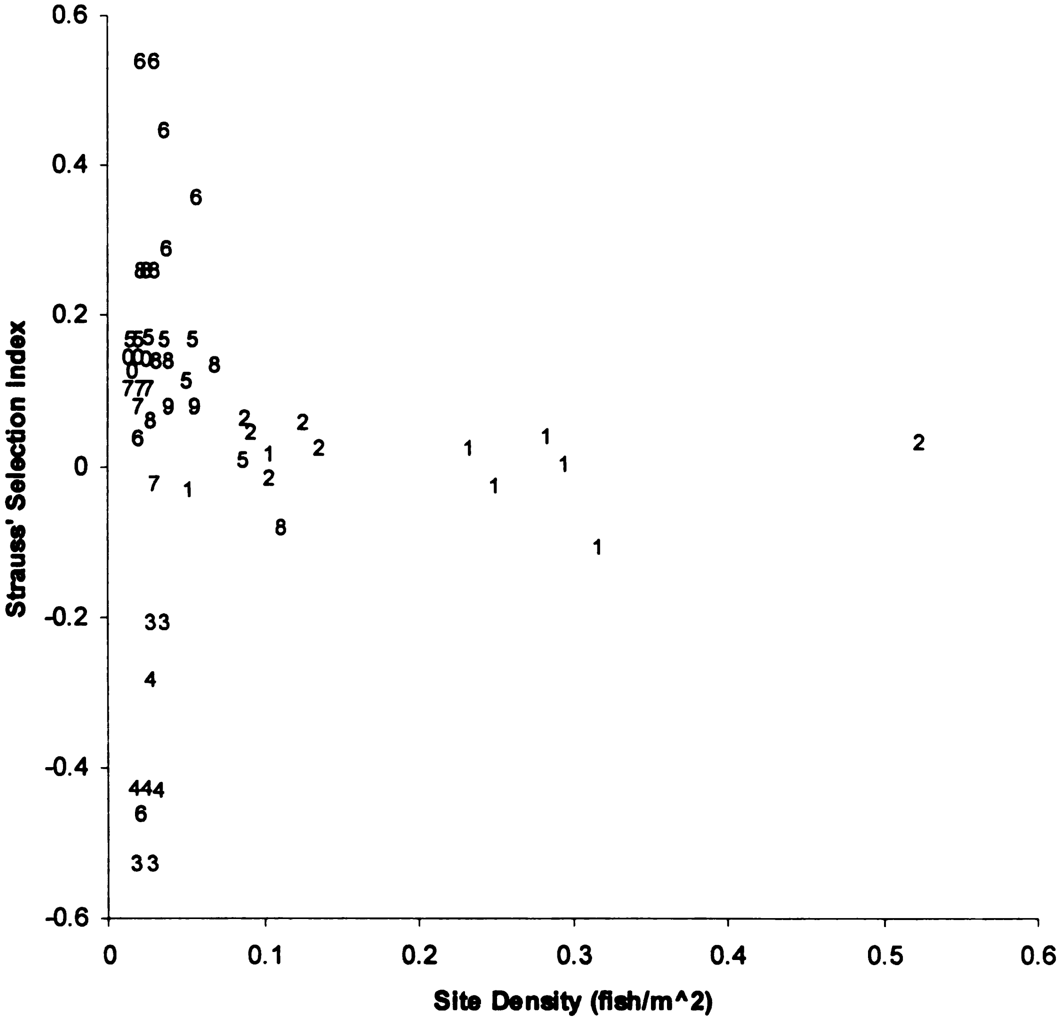

Figure 5. Strauss's (1979) linear selection index for runs plotted against site density for each observation. Numeric data markers represent individual sites.

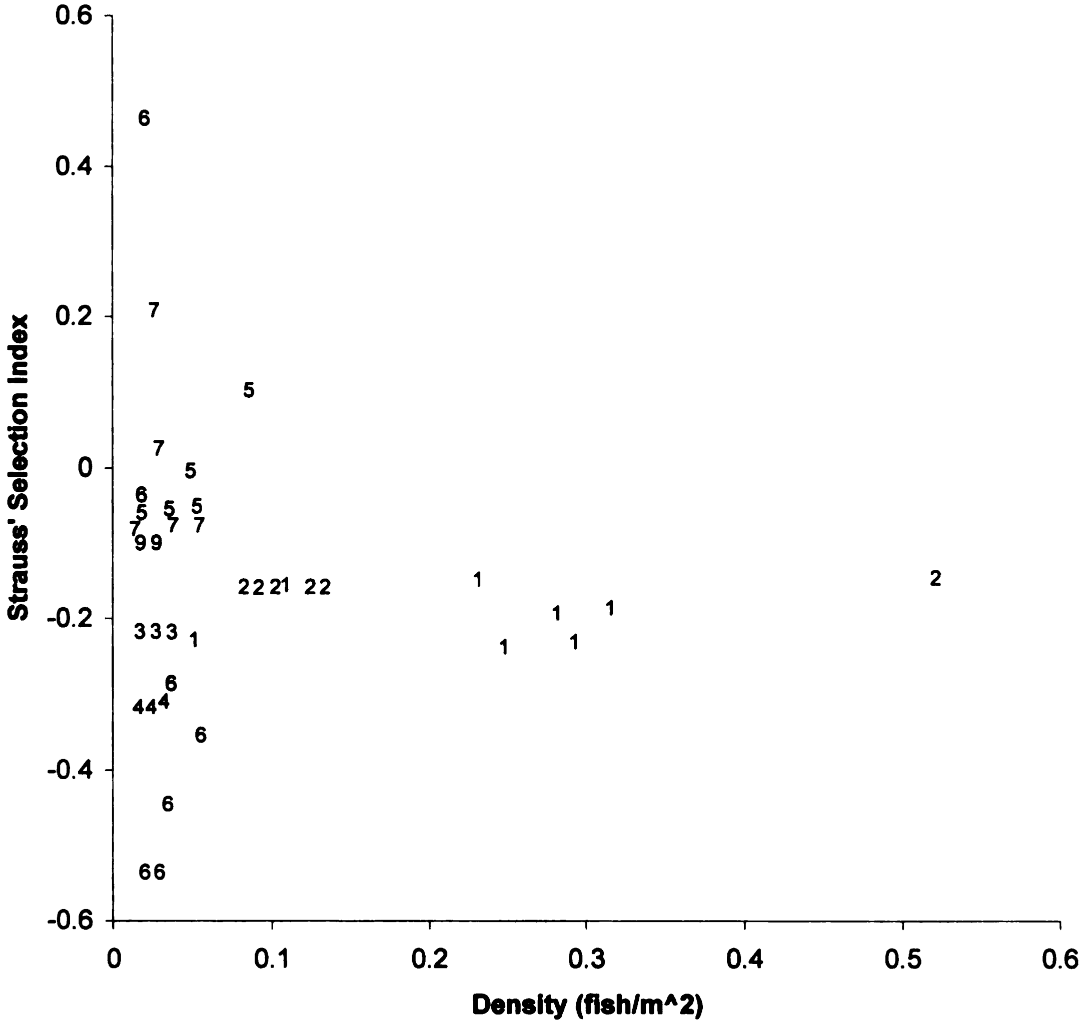

Figure 6. Strauss's (1979) linear selection index for riffles plotted against site density for each observation. Numeric data markers represent individual sites.

Analysis of variance further shows that the effect of site on habitat selection is significant, while there is no effect of density. Selection for pool habitat by creek chubs did not show any site by density interaction (df=6, F=0.55, P=0.7683), indicating that the response to density was similar across all sites. A reduced model, dropping the interaction term, showed that selection varied across sites (df=6, F=13.54, P<0.0001) but did not vary with density (df=1, F=0.15, P=0.7042). Selection for run habitat similarly did not show any site by density interaction (df=9, F=1.26, P=0.2919). The reduced model showed that selection again varied across sites (df=9, F=8.49, P<0.0001) but not with density (df=1, F=0.26, P=0.6155). Finally, no interaction of density with site was found in selection for riffles (df=7, F=0.86, P=0.5465). The reduced model indicated that selection did not vary with density (df=1, F=0.16, P=0.6936) or site (df=7, F=2.25, P=0.0551).

Immigration rates for pools, riffles and runs were calculated twice – once using collections from the first observation (typically 2, but as many as 6 days after defaunation), and using results from the last observation (after approximately a month). Both methods revealed the same patterns as Strauss' and Manly's selection indices. Pools had higher immigration rates than riffles, and riffles had higher rates than runs when all three were available (Figure 7). In sites with no pools, creek chubs immigrated into runs at a higher rate than riffles (Figure 8). Where only pools and runs existed, creek chubs moved into runs with much higher frequency than pools (Figure 9).

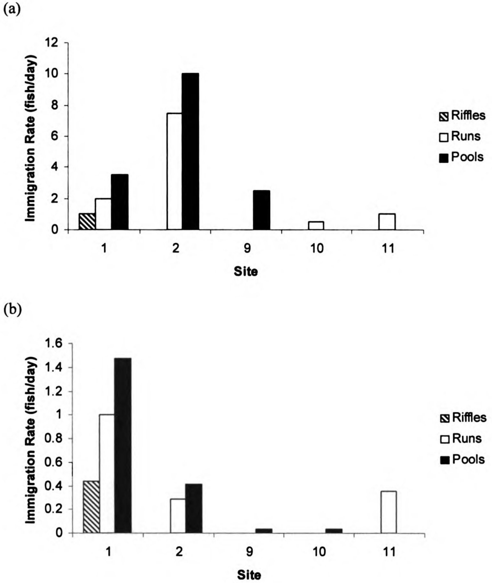

Figure 7. Immigration rates of creek chubs colonizing each habitat unit class in streams containing pools, riffles, and runs. Immigration was calculated for (a) the first return interval, 2 to 6 days after fish removal, and (b) an interval of one month, the length of the experiments.

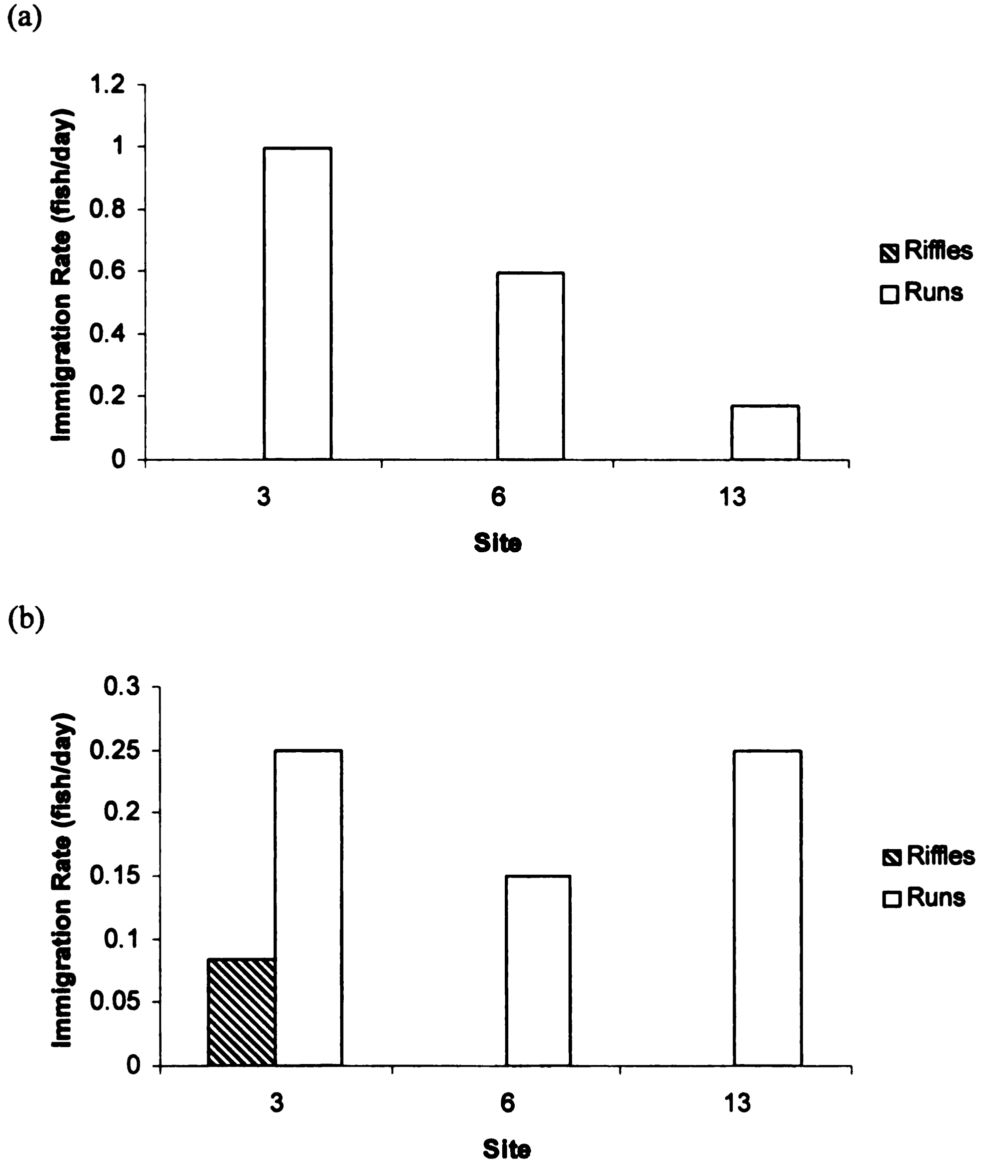

Figure 8. Immigration rates of creek chubs colonizing each habitat unit class in streams containing only riffles and runs. Immigration was calculated for (a) the first return interval, 2 to 6 days after fish removal, and (b) an interval of one month, the length of the experiments.

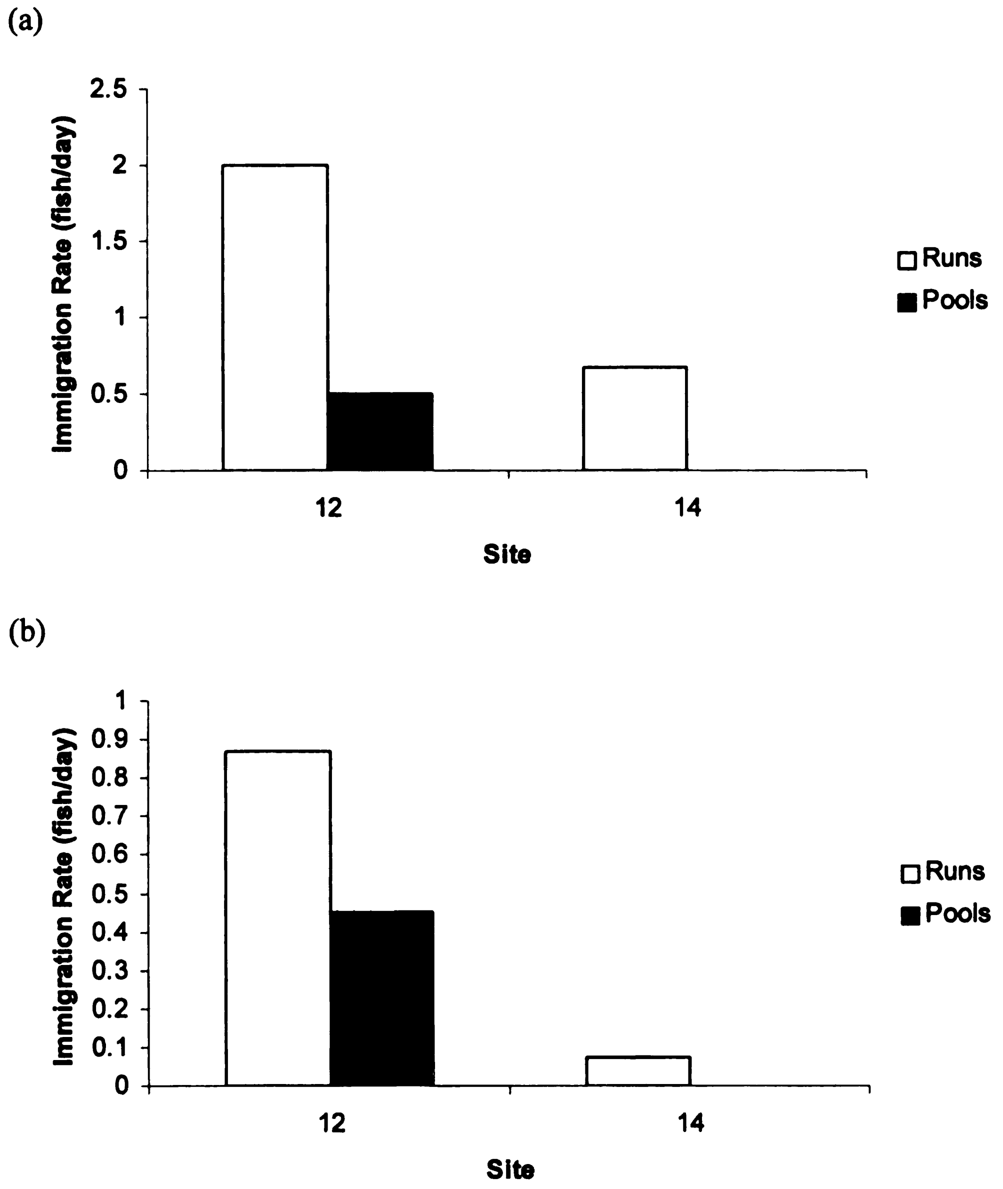

Figure 9. Immigration rates of creek chubs colonizing each habitat unit class in streams containing only pools and runs. Immigration was calculated for (a) the first return interval, 2 to 6 days after fish removal, and (b) an interval of one month, the length of the experiments.

Discussion

The habitat preferences of creek chubs (*Semotilus atromaculatus* Mitchill) have been documented by several investigators (Moshenko and Gee 1973, Copes 1978, Storck and Momot 1981, Hubert and Rahel 1989, Harvey and Stewart 1991). My observations agree with previous findings that adult creek chubs prefer deeper pool habitat to shallower runs and riffles. This preference is likely due to deeper water providing cover from terrestrial predators (Harvey and Stewart 1991).

All methods I used to quantify habitat suitability for creek chubs (Strauss's linear selection index, Manly's standardized selection ratio, and immigration rate) yielded similar insights. Close agreement of immigration trends with density-based habitat preferences from earlier studies also were discovered by Belanger and Rodriguez (2002) in their study of stream salmonids. The density of individuals in a habitat unit is the result of movement into and out of the unit, thus agreement between the two approaches could be expected. However, a focus on movement encourages observation of individuals over time, an approach that can integrate seasonality and behavioral responses to population density and community composition. Such an approach provides a much more mechanistic understanding than habitat suitabilities based on point counts and physical habitat attributes alone, which form the basis of most habitat suitability indices (HSIs).

The current HSI for creek chubs (McMahon 1982) lists the following variables as important for the species: percent pool, pool class, percent cover, winter cover, gradient, width, turbidity, pH, production, temperature, DO, flow, substrate, shade, percent stream bank vegetation, and depth. This list was based on literature review and author opinion. A cumulative HSI score for a particular site can be calculated from the above variables by following the procedure described in McMahon (1982). Hubert and Rahel (1989) found that neither HSI scores nor the majority of component HSI variables correlated with the biomass of creek chubs in their study sites. The availability of pools was the only variable included in the HSI that correlated with creek chub biomass. They also discovered that flow variability, the amount of submerged vegetation, and average velocity were significant, yet not included in the index. They suggest that the failure of the HSI may be due to non-additivity of the component variables and regional variation. These weaknesses further support the concept of a habitat suitability assessment that includes behavior and assemblage variables.

I found that creek chub habitat preference was site-specific and density-independent. Fretwell and Lucas (1970), when describing the theory of ideal free distribution, note that habitat suitability might decline with increasing density. They suggest that the most suitable habitat will decline with increasing density until it is equivalent to the next most suitable habitat. Animals will then move into both units equally, until those units decline to the level of the third most suitable habitat, and so on. The result is that with increasing density of individuals in an area, distribution among habitat types should become more even. This was not the case with creek chubs in the Red Cedar River watershed under the densities observed. Fraser and Sise (1980) similarly found that evenness did not significantly increase with density in adult creek chubs inhabiting pools varying in the amount of cover in a second order stream.

The design of this study allowed observation of creek chub habitat selection over a range of densities and across many stream sites, allowing separation of site and density effects. These data revealed trends in fish habitat selection that could not be observed if density was not manipulated, as is the case with most HSI data, or if a single site was used. There is a clear preference for pools over runs (except in the deepest streams, where no riffles existed), and for runs over riffles, and this did not vary with density. This is not to suggest that the tenets of the ideal free distribution do not hold, but only that suitability, in this case, is density-independent within the range of densities observed.

The site-specific variation in habitat preference suggests that the relative availability and characteristics of habitats at a particular site are the primary determinants of preference. For example, in this study, creek chubs showed stronger preference for runs than pools only in deeper streams where the average run was similar in depth to pools in other, shallower streams, and riffles were missing altogether. In these streams, the deepest areas may harbor larger, piscivorous fishes (including the occasional very large creek chub) that use the depths as cover from terrestrial predators (Harvey and Stewart 1991). The presence of predatory fishes reduces the suitability of pools for most creek chubs. Furthermore, time of day may influence the suitability of particular habitat types. Fraser and Emmons (1984) found that blacknose dace (*Rhinichthys atratulus*) would share pools with predatory fish during the day, but would move away from these occupied pools at night, when darkness reduced the risk posed by terrestrial predators. My study considered creek chub distribution only during daylight hours; however, it is likely that habitat suitability for chubs may shift over a 24-hour period. Proportional availability, and the habitat available adjacent to the study reaches may also play a role.

Why should we care about habitat selection? First, these observations provide information about the basic biology of the species. From a management standpoint, knowledge of how to determine the best habitat characteristics for a species, gleaned from observations in the field or laboratory, supports habitat conservation and restoration. Further, understanding habitat selection under a variety of conditions will help us anticipate responses to disturbance and a time frame for recovery, because distribution is a product of behavior. For these reasons, continued research into how best to interpret species movement and distribution to determine habitat suitability is warranted.

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