

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MOVEMENT BY THREE STREAM DWELLING CYPRINIDS
(NOTROPIS BOOPS, CAMPOSTOMA ANOMALUM, AND
CYPRINELLA VENUSTA)

A Dissertation

Submitted to The Graduate Faculty

in Partial Fulfillment of the Requirements for The

Degree of

Doctor of Philosophy

By

Jacob F. Schaefer
Norman, Oklahoma
1999

UMI Number: 9925602

UMI Microform 9925602
Copyright 1999, by UMI Company. All rights reserved.

**This microform edition is protected against unauthorized
copying under Title 17, United States Code.**

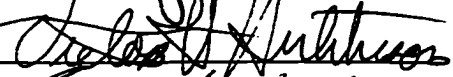
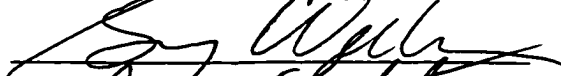
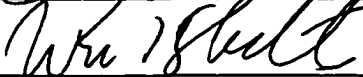
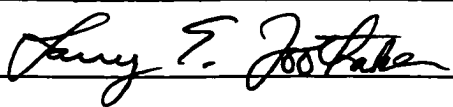
UMI
300 North Zeeb Road
Ann Arbor, MI 48103

**© Copyright by Jacob F. Schaefer 1999
All Rights Reserved.**

MOVEMENT BY THREE STREAM DWELLING CYPRINIDS
(NOTROPIS BOOPS, CAMPOSTOMA ANOMALUM, AND
CYPRINELLA VENUSTA)

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

Acknowledgments

I would like to thank all the members of my committee: Bill Matthews, Victor Hutchison, Bill Shelton, Larry Toothaker, and Gary Welborn for all of their help during my graduate work at the University of Oklahoma. I would also like to thank Keith Gido, Bill Lutterschmidt, David Lonzarich, Edie Marsh-Matthews, and Mel Warren for useful input into various aspects of this project. Some funding for this project was provided by the USDA Forest Service, University of Oklahoma Biological Station, University of Oklahoma Department of Zoology, and The University of Oklahoma Graduate Student. Finally, I would like to thank all the members of my family. Without their support I could not have completed graduate school.

Table of Contents

I. Riffles as Barriers to Inter-pool Movement by Three Cyprinids (Notropis boops, Campostoma anomalum, and Cyprinella venusta)

Summary	2
Introduction	3
Methods	6
Results	9
Discussion	13
Acknowledgments	18
Literature Cited	19
Figures	23
Appendix	32

II. Development and Testing of an Individual-based Model of Stream Fish Movement

Abstract	34
Introduction	35
Materials and Methods	38
Results	43
Discussion	46
Acknowledgments	50
Literature Cited	51
Tables	54
Figures	55

III. Modeling stream fish movement and dispersal: a mark-resight study in a small warmwater stream

Abstract	65
Introduction	66
Materials and Methods	69
Results	74
Discussion	76
Acknowledgments	80
Literature Cited	81
Tables	85
Figures	89

Preface

The first chapter of this dissertation has been formatted for the journal *Oecologia*, the last two chapters have been formatted for the journal *Oikos*.

Abstract

The effects of riffles as barriers to movement of stream fish were investigated in large, outdoor artificial streams. Rates of movement of three species of minnows (Cyprinidae) (Campostoma anomalum, Cyprinella venusta, and Notropis boops) among pools were measured at four riffle current velocities (0, 15, 30 and 45 cm/s), three thalweg depths (10, 50 and 100 mm), two riffle lengths (183 and 549 cm), and with and without the threat of predation. Overall, results suggest that biotic and abiotic factors in streams influence movement rates and assemblage structure in stream pools. An individual based model of fish movement was developed and tested by comparing predicted distributions to actual distributions of fish in a six pool, five riffle artificial stream. Trials were conducted under three sets of conditions: 1) all riffles had the same thalweg depth and current velocity; 2) when two of the riffles were shallower and faster; and 3) the fifth pool had a predator and the second pool had vegetative cover. Four different variations of the model were run, each with different parameters defining the movement of fish in simulated space. The best fit models suggest that it is important to take into account detailed information on species-specific behaviors, rather than accepting assumptions that species behaviors could be treated as redundant within a family or trophic guild. Movement of 100 Notropis boops and 100 Campostoma anomalum were tracked over a 28 day period in Brier Creek (Marshall Co., Oklahoma). An individual-based model was used to predict the location of tagged individuals over the course of the experiment. Three different models were used: 1) a model with actual

pool size and riffle permeability, 2) a model with all pools the same size and actual riffle permeability, and 3) a model with actual pool size, but all riffles 100% permeable. The model with actual pool size and riffle permeability was the most accurate, and the model with uniform pool size the least accurate.

Chapter I

Riffles as barriers to inter-pool movement by three Cyprinids (Notropis boops,
Campostoma anomalum, and Cyprinella venusta)

Summary

The effects of riffles as barriers to movement of stream fish were investigated in large, outdoor artificial streams. Pools were 183 cm in diameter, 45 cm deep; riffles were 183 cm long and 43 cm wide. Rates of movement of three species of minnows (Cyprinidae) (Campostoma anomalum, Cyprinella venusta, and Notropis boops) among pools were measured at four riffle current velocities (0, 15, 30 and 45 cm/s), three thalweg depths (10, 50 and 100 mm), two riffle lengths (183 and 549 cm), and with and without the threat of predation. Visual observation and video tape were used to quantify movement rate. Mean movement rate (proportion of fish crossing a riffle each 30 min.) was 18.1% at 0 cm/s and only 1.8 at 45 cm/s. Movement rate was 7.2% with no predators present and 20.2% with predators in pools. Notropis boops had a lower rate of movement than C. venusta or C. anomalum across all trials. The mean group size (number of individuals crossing a riffle together) was 1.2 fish overall, indicating most movement was by individuals, and not groups. Group size was significantly greater only with shallow riffles, or under the threat of predation. Overall, results suggest that biotic and abiotic factors in streams influence movement rates and assemblage structure in stream pools.

Introduction

Movement between habitats is essential in the life history of many stream fish (Schlosser 1992). In stream systems, species abundance can be influenced greatly by the boundaries between habitats, and the effect these boundaries have on dispersal (Dunning et al. 1992). Many stream fish mostly occur in pool habitats, and movement between pools may be regulated by barriers (riffles) between pools. As a result, stream pools and pool fish assemblages often are viewed as discrete units (Capone 1991; Matthews et al. 1994; Taylor 1997). The ability of species to move throughout a stream reach is important for populations in patchy environments (Sheldon and Meffe 1994). In highly disturbed habitats, species that can move quickly among patches will be able to recolonize faster, have access to new habitats, and may avoid predation more efficiently. Dispersal among patches also may be necessary to sustain populations in smaller patches that are prone to local extinction (Brown and Kordic-Brown 1977). Partial recolonization by Cyprinids (Cyprinidae) was observed from 30 min to 5.8 d after a disturbance (Peterson and Bailey 1983). Meffe and Sheldon (1990) removed fish from reaches of stream and demonstrated that pool assemblages returned to pre-disturbance states within one year, indicating rapid dispersal abilities. In a similar study, they tracked short term recolonization rates and found individuals of some species moving into defaunated pools within 2 days. Pools further from a source of colonizers were slower to return to pre-disturbed states, indicating that dispersal ability may be affected by the physical structure of the stream and other potential isolating factors (Meffe and

Sheldon 1994). Matthews (1987) showed rapid (weeks) recolonization of recently rewatered stream reaches in Brier Creek (Oklahoma). Other studies have also shown that exchange of individuals with source populations is slower in pools isolated by distance or restricted flow (Taylor 1997; Lonzarich 1998). Properties of riffles (road crossings) also affect rate of movement of fish between pools (Warren and Pardew 1998). Shallower, longer, and faster-flowing road crossings restricted dispersal of marked fish among pools. Bart (1989) reported that assemblage consistency did not significantly increase at most sites after extensive sampling, suggesting rapid recolonization.

The restricted movement paradigm (Gerking 1953; Gerking 1959; Gowan et al. 1994) states that many stream fishes are sedentary, and most adult individuals remain within a small home range. Movement by cyprinids has not been studied extensively (Goforth and Foltz 1998), with most work focused on larger temporal (weeks or months) or spatial (larger than individual pools) scales. Most studies on movement of fish in streams has focused on large game species (centrarchids and salmonids). For several species (Cottus bairdi, Rhinichthys cataractae, Clinostomus funduloides, Percina nigrofasciata and Lepomis auritus), most marked individuals were captured within 10-30 m of release points over 6-18 month periods (Hill and Grossman 1987; Freeman 1995), indicating limited movement rates within home ranges. Whereas most individuals may stay in one area, Freeman (1995) and Hill and Grossman (1987) found that a small portion of “wanderers” move long distances. Other studies have indicated

that movement rates of a few fish may be higher than previously thought (Warren and Pardew 1998; Gowan et al. 1994). Goforth and Foltz (1998) estimated larger and more variable home ranges for a cyprinid (Notropis lutipinnis), and hypothesized that reduced habitat availability and pool width might increase movement by individuals in their study. If prey species are highly mobile, presence of predators also can increase movement out of pools with predators, and effectively isolate groups of fish by lowering movement frequency (Fraser et al. 1995). Campostoma anomalum quickly move among pools or shift habitat use from pool centers to pool edges to avoid predators (Power and Matthews 1983; Power et al. 1985). Both abiotic (e.g., pool and riffle size) and biotic (e.g. predation pressure or density of competitors) factors may influence movement rate of fishes at the scale of individual pools and riffles. Thus, quantification of these effects may help explain some of the dynamic processes that regulate fish assemblage structure in streams.

The purpose of my study was to 1) quantify the rate of inter-pool movement by three common stream cyprinids, 2) examine how riffles act as barriers to inter-pool movement and 3) test what effects predation pressure has on movement rates of prey species. Specifically, I tested the hypotheses that increased riffle length, decreased riffle thalweg (maximum water depth) depth, and increased riffle current velocity reduce movement among pools by stream cyprinids, and that pools with predators should be less desirable to fish and therefore increase inter-pool movement.

Methods

I used eight artificial streams located at the University of Oklahoma Biological Station to measure movement rates of Camptostoma anomalum (central stoneroller), Cyprinella venusta (blackspot shiner) and Notropis boops (bigeye shiner) between pools. Each artificial stream unit consisted of two pools (183 cm in diameter, 45 cm deep) connected by a riffle (183 cm in length and 43 cm wide, Fig. 1). Submersable pumps circulated water from the downstream footbox to upstream pool headbox. Each pool had a small acrylic window in the side which allowed visual observations without disturbing fish. Substrate in streams consisted of cobble and gravel with a few large stones, and was sculpted to mimic natural pools and riffles. Macrophytes were removed regularly from streams to increase accuracy of visual counts. I seined fish for these trials from Brier Creek (C. anomalum and N. boops) (Marshall Co., Oklahoma), and Pennington Creek (C. venusta) (Johnson Co., Oklahoma). I used only adults >50mm SL, and removed (by seining) juveniles recruited into streams over the course of the experiment. All trials were conducted from March through September of 1996, 1997, and 1998.

I measured movement rates at four current velocities (0 cm/s, 15 cm/s, 30 cm/s, and 45 cm/s), three riffle thalweg depths (10 mm, 50 mm, and 100 mm), two riffle lengths (183 cm and 549 cm), and with a predator (200-250 mm SL largemouth bass, Micropterus salmoides) present in both pools. Normal riffle conditions were defined as 50 mm thalweg depth, 15 cm/s current velocity, and 183 cm length. For all trials, only

the variable being tested was altered, thus all other variables remained constant at normal conditions. For example, during thalweg depth trials current velocity remained at 15 cm/s and length at 183 cm while thalweg depth was manipulated (10, 50, and 100 mm). For riffle length trials, thalweg depth remained at 50 mm and velocity at 15 cm/s for the two riffle lengths. This approach did not allow testing of interaction effects between variables, but sample sizes necessary to test all combinations of all variables for all three species would have been prohibitive. I employed extra pumps (for deeper thalweg) or valves to constrict pump output (for shallower thalweg) to keep riffle current velocity constant while altering thalweg depth. To test the effects of predation pressure, I placed one predator in a cage (45 cm long, 40 cm wide, 40 cm high with 1 cm square wire mesh sides) in the center of both pools in a stream unit. Bass were left in cages 12-20 h before trials began. Three trials were run with each species: 1) without predators or cages, 2) with empty cages (a control), and 3) with one predator in each cage.

I used two methods to measure movement rate: visual counts and video trials (standard 8 mm video camera). For visual counts, 12-15 individuals of one species were placed in a stream, and the number of fish in the upstream and downstream pools was counted every 30 min for eight h. Treatments were rotated in a random order among days so that all streams were observed under all conditions an equal amount of time. From these data, the most parsimonious number of riffle crossings for each half hour was computed (minimum number of fish that had to move since the last observation to

allow the observed distribution). For analysis, the mean movement rate for each eight-hour period (16 observations) was used. For each species-treatment combination there were seven days of observations to give a sample size of seven for visual counts.

I used video trials when visual counts were not possible (e.g., higher current rates increased turbidity and did not allow accurate visual counts), and to confirm the accuracy of the visual count method described above. Video taping also allowed me to collect data on group size (number of fish that cross a riffle together), and turnaround rates (how often fish stop crossing and return to the pool of origin). Each species-treatment combination was video taped for eight 30 min periods (sample size of eight for each species-treatment combination), and the time, number of individuals crossing the riffle (group size), and direction of movement were recorded for each riffle crossing event observed. A riffle crossing event was defined as one or more fish crossing the riffle at the same time (within 10 sec of each other). A turnaround event occurred when a fish was observed passing through the field of view in one direction and then passing the opposite direction within 10 seconds, indicating that it had stopped crossing the riffle and turned back towards its original pool. Turnaround rate was then defined as the percentage of fish seen in a riffle that turned back in each 30 min. Video trials were used for the 45 cm/s velocity (fast riffle), 10 mm thalweg depth (shallow riffle), 549 cm riffle length (long riffle), and all predation trials. The fast, shallow, long, and one set of normal trials were also conducted with 12-15 individuals of each species combined. See Appendix 1 for a summary of method used for each treatment. Comparing movement

rate of each species alone with all species combined under normal conditions allowed me to test effects of density on movement.

For both methods, I calculated a final rate of movement (number of fish crossings per fish per 30 min) by dividing the number of riffle crossings by the number of fish in the artificial stream. A two way ANOVA (SPSS, GLM) with species and riffle condition as main effects was used with arc-sin transformed data to test for species and treatment effects of velocity, thalweg depth, and predation pressure. A one way ANOVA was used to test for a treatment effect of riffle length. Games-Howell multiple comparison procedure (SPSS) was used to test differences in movement rates among riffle conditions within each species, and differences between species within riffle conditions. Group size (using Dunnett multiple comparison procedure) and turnaround rate (using non-parametric Mann Whitney *U*) under normal conditions were compared to rates in trials with predators, shallow, long, and fast conditions. To test for directional bias (upstream vs downstream), I recorded the direction of the first movement event in each trial, and used Mann Whitney *U* analysis to test for differences among treatments.

Results

Comparison of Video and Visual Count Methods

Comparison of movement rates between trials with identical riffle conditions allowed testing for differences between the two observation methods as well as for possible density effects. The mean movement rate for all species combined did not

differ ($F=2.67$, $P=0.11$, $d.f.=1,64$) between the two methods (10.2 ± 1.0 SE for visual count; 7.2 ± 1.6 SE for video). Comparison of normal riffles with 15 of each species combined (45 fish per unit), and normal riffles with 15 of each species individually allowed me to test for an effect of density. Movement rate at high density (13.9 ± 4.4 SE) was not significantly different from that at low density (10.2 ± 1.0 SE).

Current Velocity

With riffle depth constant at 50 mm, greater current velocity significantly ($F = 31.07$, $P<0.001$, $d.f.=3,24$) reduced movement rate between pools for all species combined (Fig. 2). Mean movement rate for all species pooled dropped from $18.1(\pm 1.2$ SE) at 0 cm/s to $1.8 (\pm 1.2$ SE) in fast riffles. Movement rate at 15 cm/s (11.5 ± 1.1 SE) was significantly lower ($t=3.05$, $P=0.005$, $d.f.=13$) than at 0 cm/s (18.1 ± 1.9 SE), and higher ($t=7.34$, $P<0.001$, $d.f.=13$) than at 45 cm/s (1.9 ± 1.2 SE), but not significantly different ($t=1.26$, $P=0.75$, $d.f.=13$) from 30 cm/s (9.7 ± 1.2 SE). For 0, 15 and 30 cm/s trials combined, Notropis boops (7.44 ± 1.8 SE) moved significantly less ($t=3.46$, $P=0.001$, $d.f.=54$) than C. anomalum (17.2 ± 1.8 SE) and C. venusta ($t=3.44$, $P=0.001$, $d.f.=54$ mean= 17.0 ± 1.7 SE), and there was no significant difference in movement rate between C. anomalum and C. venusta (Fig. 2).

Thalweg Depth

With current velocity held constant, thalweg depth did not have a significant

effect ($F=1.73$, $P=0.20$, $d.f.=2,21$) on movement rate although there was a non-significant trend (decrease in rate from 10.0 to 6.0) for decreased movement across shallower riffles (Fig. 3). There were no significant differences between species at any given thalweg depth. Mean movement rate for N. boops (6.8 ± 1.6 SE), C. anomalum (9.1 ± 1.3 SE) and C. venusta (10.2 ± 1.2 SE) did not differ significantly at 50 or 100 mm thalweg depths (Fig. 3).

Riffle Length

Movement rate was significantly lower across the “long” (583 cm) riffles ($F=5.59$, $P=0.03$, $d.f.=1,14$). Movement rate across the long riffles (3.2 ± 1.1 SE) was less than one-fourth the rate across “normal” (183 cm) riffles (13.9 ± 4.4 SE). For riffle length trials, all species were combined in one treatment, so no species differences could be tested.

Predation Pressure

With current and thalweg depth held constant, movement rate with predators present (20.2 ± 3.1 SE) was significantly greater ($F=19.1$, $P<0.001$, $d.f.=2,63$) than movement without predators (7.2 ± 1.6 SE) (Fig. 4). There was no difference ($t=1.31$, $P=0.543$, $d.f.=47$) between trials with empty cages (5.0 ± 1.2 SE) and trials with no cages (7.2 ± 1.6 SE), indicating that the cages themselves did not cause increased movement. Two of the three species showed an increase in movement rate when

predators were present. Campostoma anomalum (increased from 12.3 to 28.4, $F=11.54$, $P<0.001$, $d.f.=2,21$) and C. venusta (increased from 5.9 to 23.4, $F=8.34$, $P=0.002$, $d.f.=2,21$) both significantly increased movement rate when predators were present. Notropis boops movement increased from 3.3 to 8.5 with predators present, but the difference was not significant ($F=1.37$, $P=0.287$, $d.f.=2,21$).

Group Size and Turnaround Rate.

Of the 320 crossing events observed on video tape, 97% consisted of one or two individual fish (Fig. 5). The largest groups seen were one group of six C. anomalum with predators in pools, and one group of nine N. boops during a shallow riffle trial. The mean group size for all video-taped treatments combined was $1.19 (\pm 0.07 \text{ SE})$. Group size was significantly larger for shallow ($t=1.99$, $P<0.01$, $d.f.=15$, $\text{mean} = 1.7 \pm 0.54 \text{ SE}$) and predation ($t=2.14$, $P=0.031$, $d.f.=18$, $\text{mean} = 1.32 \pm 0.13 \text{ SE}$) trials than for trials under normal ($1.1 \pm 0.04 \text{ SE}$) conditions (Fig. 6). None of the other treatments resulted in group sizes significantly different from those under “normal” conditions. Mean turnaround rate for all treatments combined was $13.8\% (\pm 3.6 \text{ SE})$, and only turnaround rate during predation trials ($26.6\% \pm 10.9 \text{ SE}$) was significantly ($U=9.0$, $P=0.005$, $d.f.=16$) greater than in normal trials ($3.0\% \pm 3.0 \text{ SE}$). Turnaround rates for fast riffles ($16.4\% \pm 11.8 \text{ SE}$), shallow riffles ($12.2\% \pm 5.0 \text{ SE}$), long riffles ($26.7\% \pm 19.5 \text{ SE}$), and trials with empty predator cages ($9.0\% \pm 5.8 \text{ SE}$) were not significantly greater than in normal trials (Fig. 7).

Directional Bias

Mann-Whitney analysis on the direction of movement showed no bias toward upstream or downstream movement in any trials. More fish moved upstream with no current (65% upstream) than with a current (29% upstream, current velocity = 30 cm/s and 45 cm/s combined), but these differences were not significant.

Discussion

The streams used in these experiments mimic natural streams in many ways, including structure, substrate, depth and current speed. Artificial streams have proved useful in testing theories in stream ecology (Gelwick and Matthews 1993; Gido et al. 1998). However, some trade-offs need to be addressed for systems like these. The artificial streams used can support densities greater than the largest density present in any one trial (15 of each species= 45 individuals). During the course of this experiment one of the artificial streams (used as a holding tank) supported > 50 fish year around, not including yearly juvenile recruitment. Movement rate at higher densities (15.3 ± 2.6 SE) was not different from movement at lower densities (11.5 ± 1.2 SE) under normal riffle conditions. Increasing density to above a theoretical “carrying capacity” for the artificial streams might increase movement rate if fish were searching for lower density patches, as in an ideal-free distribution. Tyler and Gilliam (1995) found that in a patchy habitat fish dispersed to areas with higher potential energetic gain due to lower densities of competitors. Because of the structure of the artificial streams used in this study, there

was no way to allow or detect long distance movement by individuals. Testing for a directional bias (upstream vs. downstream) also was difficult. For this analysis, only the first recorded movement in each trial was used. Any movement after the first would be dependant on the first (e.g. if all fish moved downstream then no more downstream movement could occur until fish moved upstream), and not a valid measure of directional movement. Ideally, a three-pool two-riffle system would be used with all fish starting in the middle pool and dispersal rates to the upstream and downstream pools measured.

The role of riffles as barriers to dispersal between pools is critical to regulating exchanges among patches in stream landscapes (Schlosser 1995). Current velocity, riffle length, and predation pressure all affected movement rate of these three cyprinids. Many authors have assumed that physical parameters such as current velocity, thalweg depth or riffle length should have direct effects on dispersal rates of fishes (Power et al. 1985; Cooper et al. 1990; Sih and Wooster 1994) (negative for increased velocity and length, positive for increased thalweg depth). Downstream dispersal of Gambusia affinis was related to current velocity, but movement on small spatial and temporal scales across individual barriers was not evaluated (Congdon 1994) . The results of my study indicate that increased current velocity decreases movement across riffles. With increasing current velocity, crossing a riffle against the current becomes more energetically expensive, and at extreme levels becomes impossible. Although movement rate at the three thalweg depths did not differ in this study, each species showed a tendency for

decreased movement at shallower depths. One would expect fish to enter extremely shallow riffles less often, as exposure to terrestrial predators (Power, 1987) and the chance of becoming stranded would increase. At extremely shallow depths, dispersal obviously becomes impossible.

Group size data indicated that fish often acted as individuals when crossing riffles. Overall, 97% of all fish observed crossing riffles were alone or with only one other individual. Even in trials in which all species were combined and density was higher (long and short riffle trials), mean group size was no different (mean at high density= 1.15, SE=0.12, mean at low density=1.10, SE=0.04). It was rare to see groups of more than two individuals cross riffles even though schooling behavior was commonly observed within pools. Small group size in riffle crossings supports the idea that most of a population of stream fish is sedentary, while a small number of floaters or wanderers move much greater distances (Gowan et al. 1994; Freeman 1995). Mean group size only increased significantly during “predation” and “shallow” riffle trials. Predators in pools represented a direct threat from an aquatic predator, whereas shallow thalweg depth might be perceived as increased exposure to terrestrial predators. Predation pressure influences distribution and dispersal rate of some fish. When predators were present in streams in Trinidad, Rivulus hartii were much more likely to disperse to adjacent predator-free tributaries, and areas with no predators were most likely to be colonized (Fraser et al. 1995). During my trials with predators, individual C. anomalum were observed holding position in riffles for long periods only when

predators were present, indicating a shift in habitat use similar to that observed by Power et al. (1985). Individuals were seen feeding, resting, and holding position for 20-30 min at a time in riffles. Although a habitat shift was not observed in N. boops or C. venusta, movement rate and group size did increase for these species in the presence of predators.

Turnaround events were rare for all treatments. Only 13.8% of fish seen within a riffle turned around, i.e., 86.2% of fish entering a riffle completed any attempted crossing. The lowest turnaround rate was observed during normal trials, and turnaround rates increased to some degree in all other conditions under which it was measured. However, significant differences in turnaround rate were not detected, possibly due to the rarity of such events. Turnaround rate in predation trials (mostly due to C. anomalum habitat shift) and long riffle trials were approximately equal but due to high variance, only the predation rate was significantly different from normal. Longer riffles and greater current velocity both require a greater energetic investment for crossing, and greater turnaround rates were observed under these conditions. The fact that fish are more likely to stop crossing a riffle part way through it indicates these energetic costs may play a role in determining actual movement rates among pools.

One would expect differences among species in movement rate. Centrarchids tend to stay more in home pools whereas cyprinids are more mobile species (Matthews et al. 1994). When a reach of stream was repeatedly sampled over a period of months, there was higher within-pool variance over time for numbers of cyprinids than for

centrarchids, indicating more inter-pool movement by the former (Matthews et al. 1994). Of the three species in these experiments, N. boops moved less than the other two species under most conditions. This could, in part, be due to some of the N. boops current velocity trials being conducted earlier in the year when water temperatures were lower. However, N. boops also moved less (not significantly) than the other two species during thalweg depth trials conducted in mid summer when temperatures were warmer and the same for all species. Campostoma anomalum also increased movement during predation trials more than did the other two species.

Biotic and abiotic factors influence stream assemblages on small spatial and temporal scales as many important processes in streams take place in pools. Studying individual pools may give the most information about the system being studied. Assemblages in pools that were connected by flow across riffles were strongly influenced by individual species' dispersal abilities, whereas isolated pool (no dispersal possible) assemblages were more strongly influenced by pool size, and therefore local extinction rate (Taylor 1997). The results of my study indicated that isolation can result not only from distance to a source, but from the morphology of riffles (thalweg depth), species composition (predation pressure), and current velocity. The results of this study also indicate that individual species may react to these parameters in different ways. Understanding the processes that control dispersal of species on small spatial and temporal scales provides a framework for understanding dispersal on larger scales. In the future, data on movement and dispersal rates can be extrapolated and used to

predict home range sizes, population mixing rates, or in metapopulation studies. A logical next step would be to see how accurately the results of this study can be used in predicting dispersal rates in real streams.

Acknowledgments

I thank all the members of my committee: Bill Matthews, Victor Hutchison, Bill Shelton, Larry Toothaker, and Gary Welborn. I thank Keith Gido, David Lonzarich, and Mel Warren for useful input into various aspects of this project. I thank the USDA Forest Service, University of Oklahoma Biological Station, University of Oklahoma Department of Zoology, and The University of Oklahoma Graduate Student Association for funding and supplying facilities. This paper is presented as partial fulfilment for a doctorate from the University of Oklahoma Department of Zoology.

Literature Cited

Bart HL (1989) Fish habitat association in an Ozark stream. *Env Biol Fish* 24(3):173-186.

Brown JH, Kordic-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.

Capone TA, Kushlan JA (1991) Fish community structure in dry-season stream pools. *Ecology* 72:983-992.

Congdon BC (1994) Characteristics of dispersal in the eastern mosquitofish Gambusia holbrooki. *J Fish Biol* 45:943-952.

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that effect populations in complex landscapes. *Oikos* 65:169-175.

Freeman MC (1995) Movements by two small fishes in a large stream. *Copeia* 1995: 361-367.

Fraser DF, Gilliam JF, Yip-Hoi T (1995) Predation as an agent of population fragmentation in a tropical watershed. *Ecology* 76:1461-1472.

Gelwick FP, Matthews WJ (1993) Artificial streams for studies of fish ecology. *J North Am Benth Soc* 12(4):343-347.

Gerking SD (1953) Evidence for the concepts of home range and territory in stream fishes. *Ecology* 34:347-365.

Gerking SD (1959) The restricted movement of fish populations. *Biological Review*. 34:221-242.

- Gido KB, Schaefer JF, Work KA, Lienesch PW Marsh-Matthews E, Matthews WJ (1999) Effects of red shiner (Cyprinella lutrensis) on Red River pupfish (Cyprinodon rubrofluviatilis). In Press. SW Assoc Nat.
- Goforth RR, Foltz JW (1998) Movements of the yellowfin shiner, Notropis lutipinnis. Ecol Fresh Fish 7:49-55.
- Gowan C, Young MK, Fausch KD, Riley SC (1994) Restricted movement in resident stream salmonids: A paradigm lost? Can. J Fish Aqu Sci 51:2626-2637.
- Hill JA, Grossman GD (1987) Home range estimators for three North American stream fishes. Copeia 1987:376-380.
- Lonzarich GD, Warren ML, Lonzarich MRE (1998) Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools. Can J Fish Aqu Sci 55:2141-2149.
- Matthews WJ, Stewart AJ, Power ME (1987) Grazing fishes as components of North American stream ecosystems: Effects of Campostoma anomalum. In: Matthews WJ, Heins DC (eds) Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, pp 128-135.
- Matthews WJ, Harvey BC, Power ME (1994) Spatial and temporal patterns in the fish assemblages of individual pools in a Midwestern stream (USA). Environ Biol Fish 39:381-397.
- Meffe GK, Sheldon AL (1990) The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. Am Mid Nat 120:225-240.

- Peterson JT, Bailey PB (1993) Colonization rates of fishes in experimentally defaunated warmwater streams. *Trans Am Fish Soc* 122:199-207.
- Power ME, Matthews WJ (1983) Algae-grazing minnows (Camostoma anomalum), piscivorous bass (Micropterus spp.), and the distribution of attached algae in a small prairie-margin stream. *Oecologia* 60:328-332.
- Power ME, Matthews WJ, Stewart AJ (1985) Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology* 66:1448-1456.
- Power ME (1987) Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. In: Kerfoot WC, Sih A (eds) *Predation*. University Press of New England, Hanoer, NH, pp. 333-351.
- Schlosser IJ (1995) Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* 76:908-925.
- Schlosser IJ (1995) Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* 303:71-81.
- Sheldon AL, Meffe GK (1995) Short-term recolonization by fishes of experimentally defaunated pools of a coastal plain stream. *Copeia* 1995:828-837.
- Sih A, Wooster DE (1994) Prey behavior, prey dispersal, and predator impacts on stream prey. *Ecology* 75:1199-1207.
- Taylor CM (1997) Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* 110:560-566.

- Tyler JA, Gilliam GJ (1995) Ideal free distributions of stream fish: a model and test with minnows, *Rhinichthys atratulus*. *Ecology* 76:580-592.
- Warren ML, Pardew MG (1998) Road crossings as barriers to small-stream fish movement. *Trans Am Fish Soc* 127:637-644.

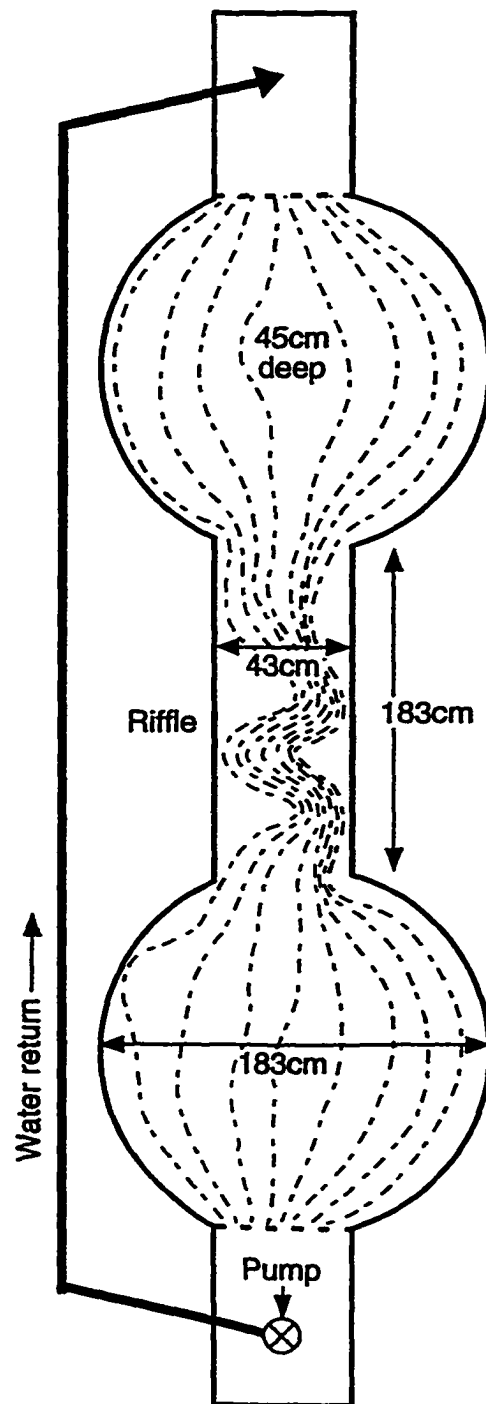
List of Figures

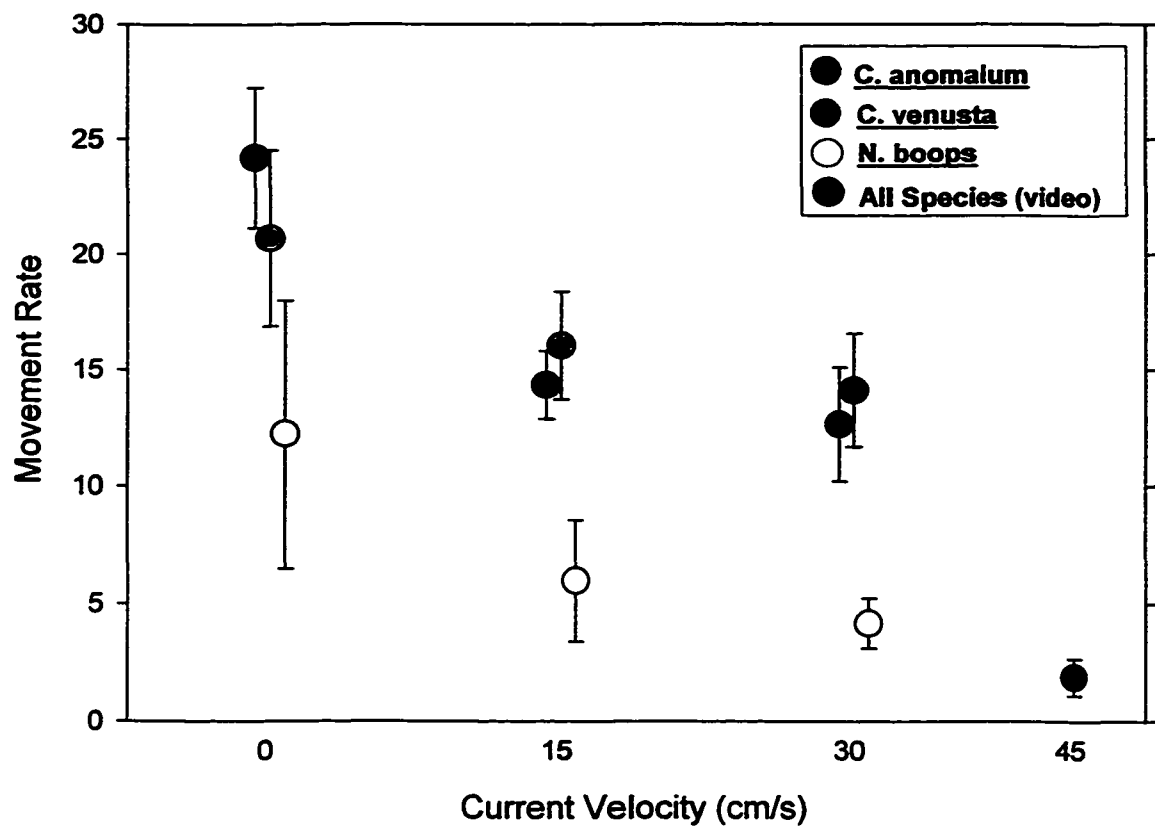
1. Diagram of one artificial stream unit used in these experiments. Eight identical units were used.
2. Rate of movement (percent of fish crossing riffle per 30 min.) for all three species at four current velocities. The first three velocities were tested for individual species by observation (n=7 for each species-treatment combination), “fast” trials were for all three species combined using video tape (n=8). Error bars represent ± 1 SE.
3. Rate of movement (percent of fish crossing riffle per 30 min.) for all three species at three thalweg depths. The first two depths were tested for individual species by observation (n=7 for each species-treatment combination), “shallow” trials were for all three species combined using video tape (n=8). Error bars represent ± 1 SE.
4. Rate of movement (percent of fish crossing riffle per 30 min.) for each species with and without predators present. Trials were with no predators or cages, empty cages, and with predators in cages (n=8 for each species-treatment combination). Error bars represent ± 1 SE.
5. Group size (number of individuals crossing a riffle at one time) for all video trials combined. For cases where large groups were observed, the treatment where it was

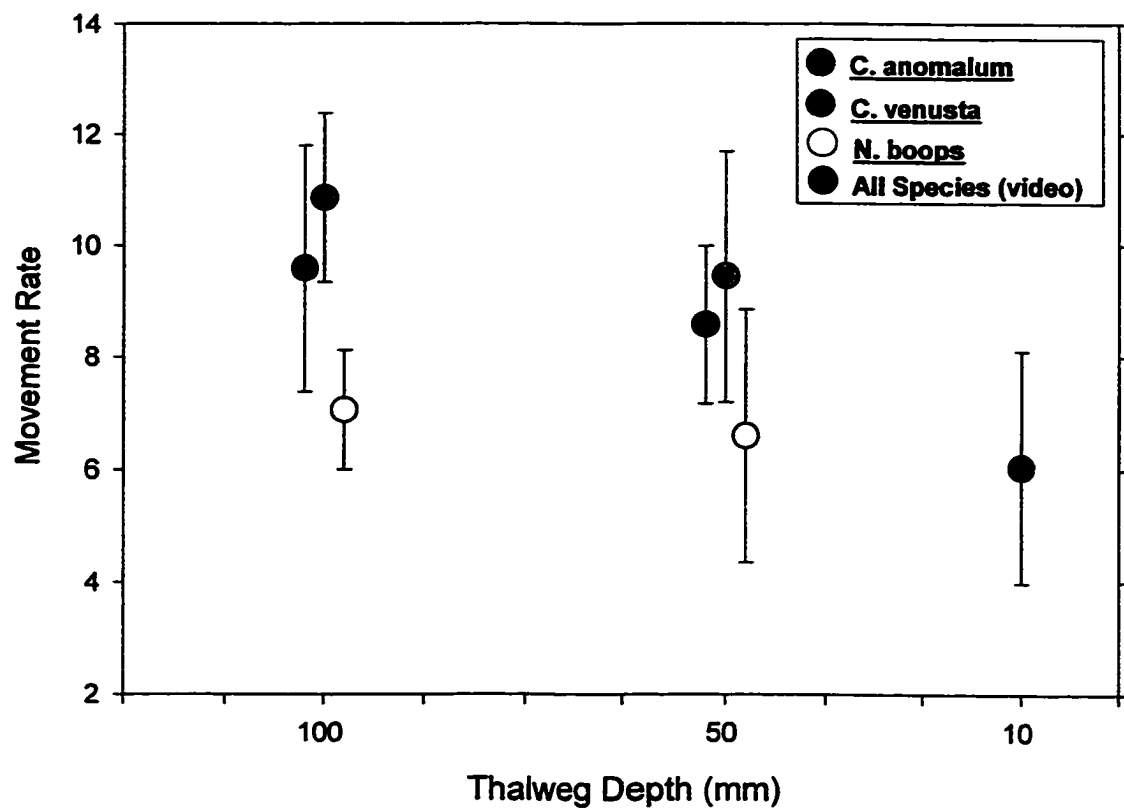
observed is shown.

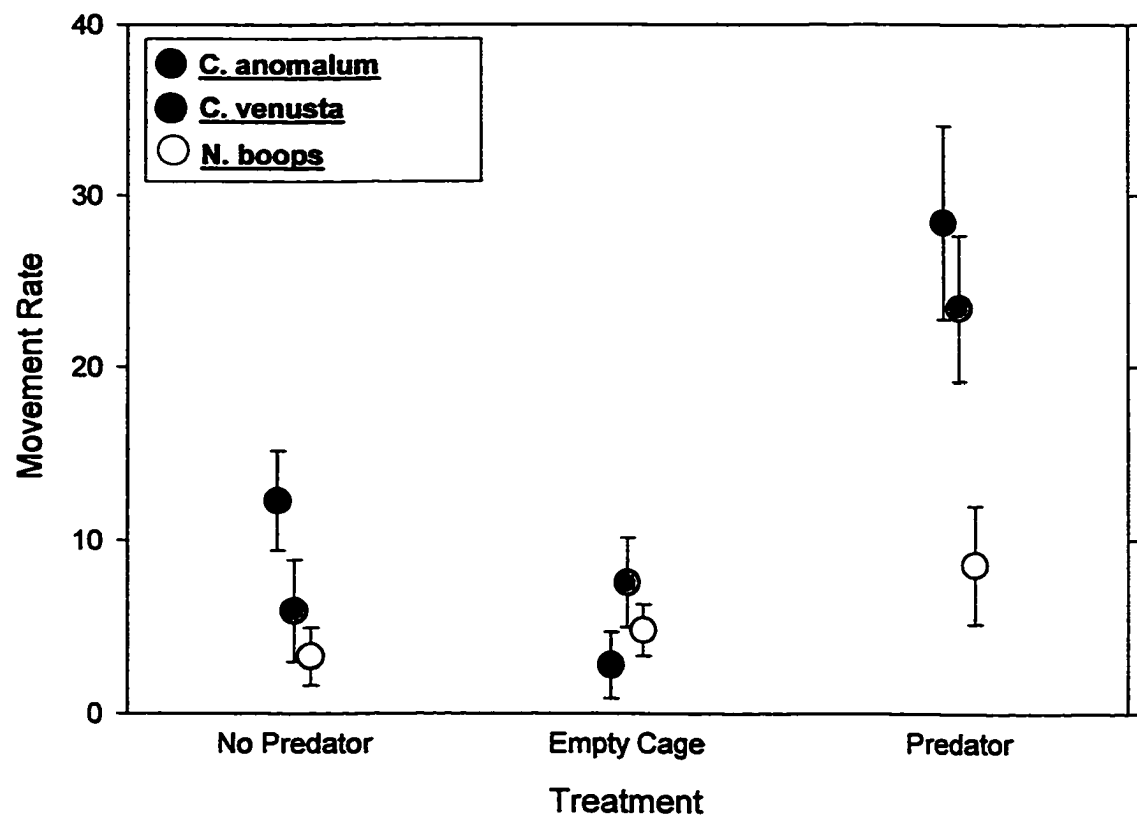
6. Mean group size (± 1 SE) for each of the treatments. * indicates group size was significantly different from group size under normal conditions.

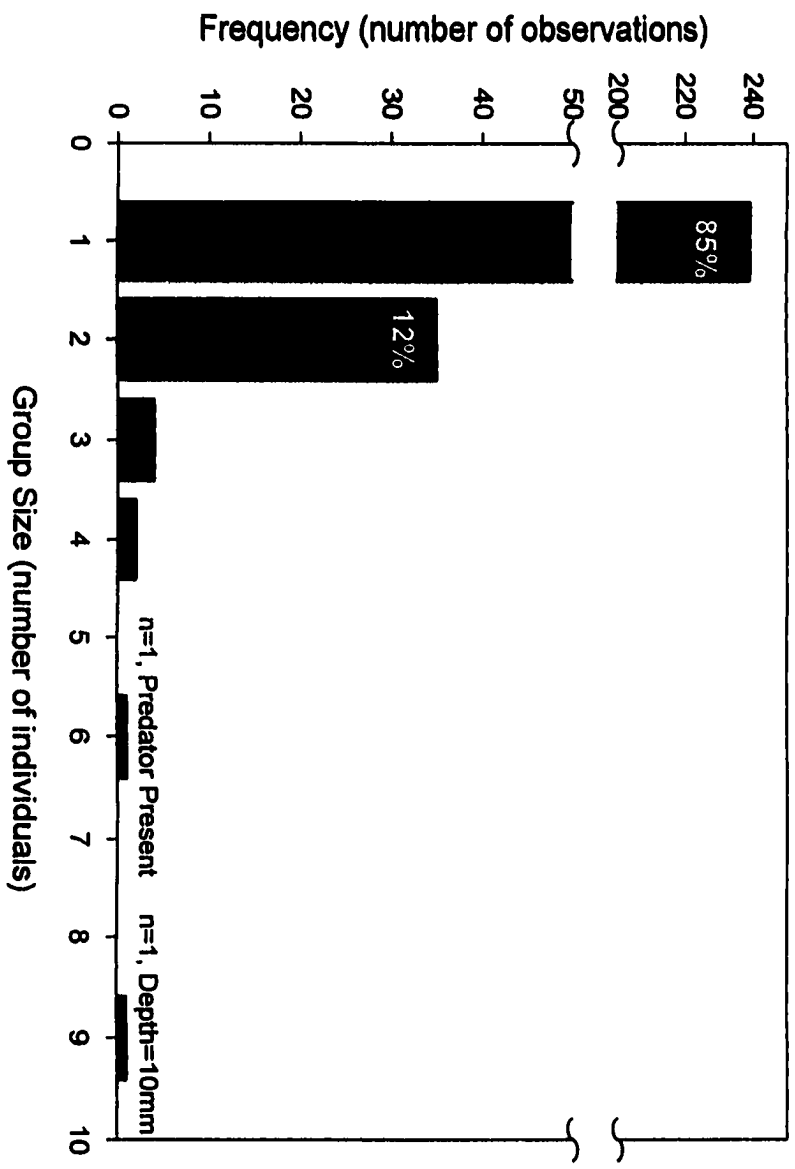
7. Turnaround rate (bars) and mean rate of movement for all species combined (closed circles, ± 1 SE) for each of the video-taped treatments.

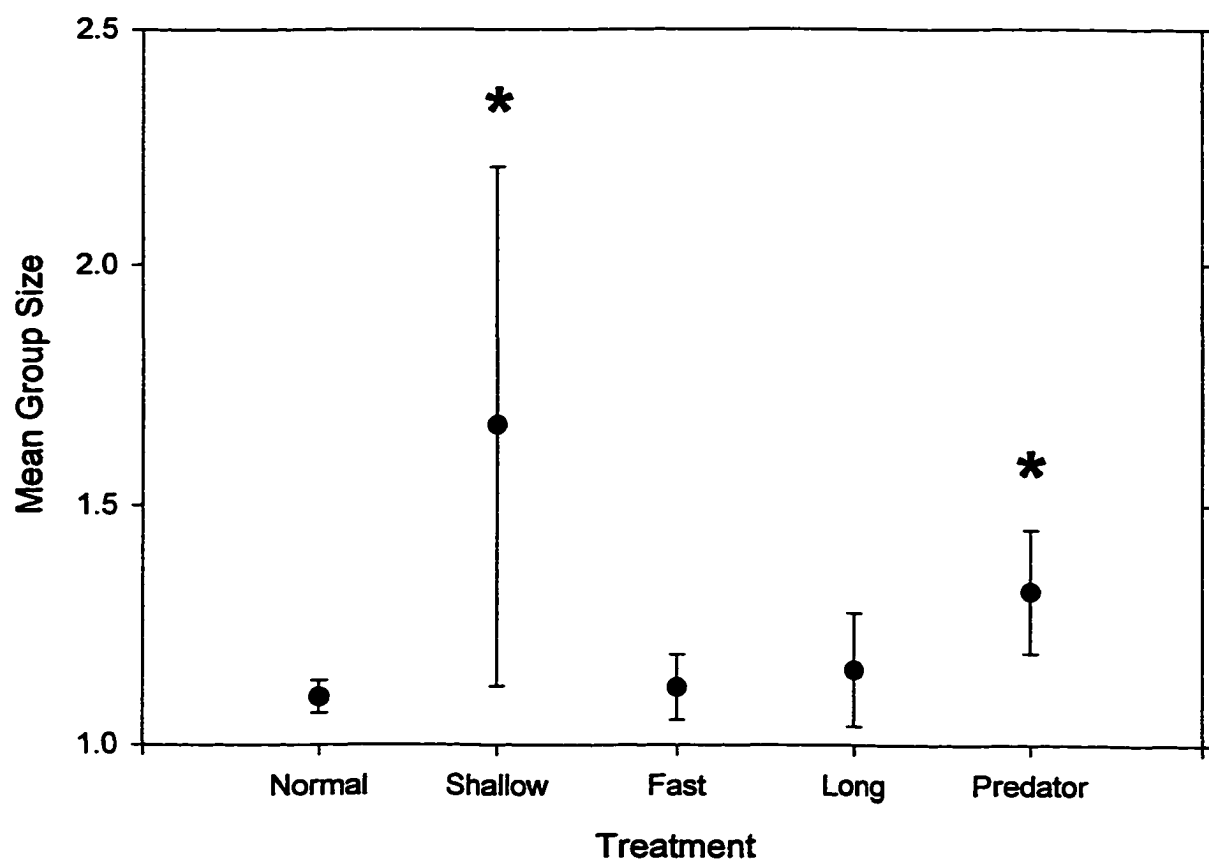


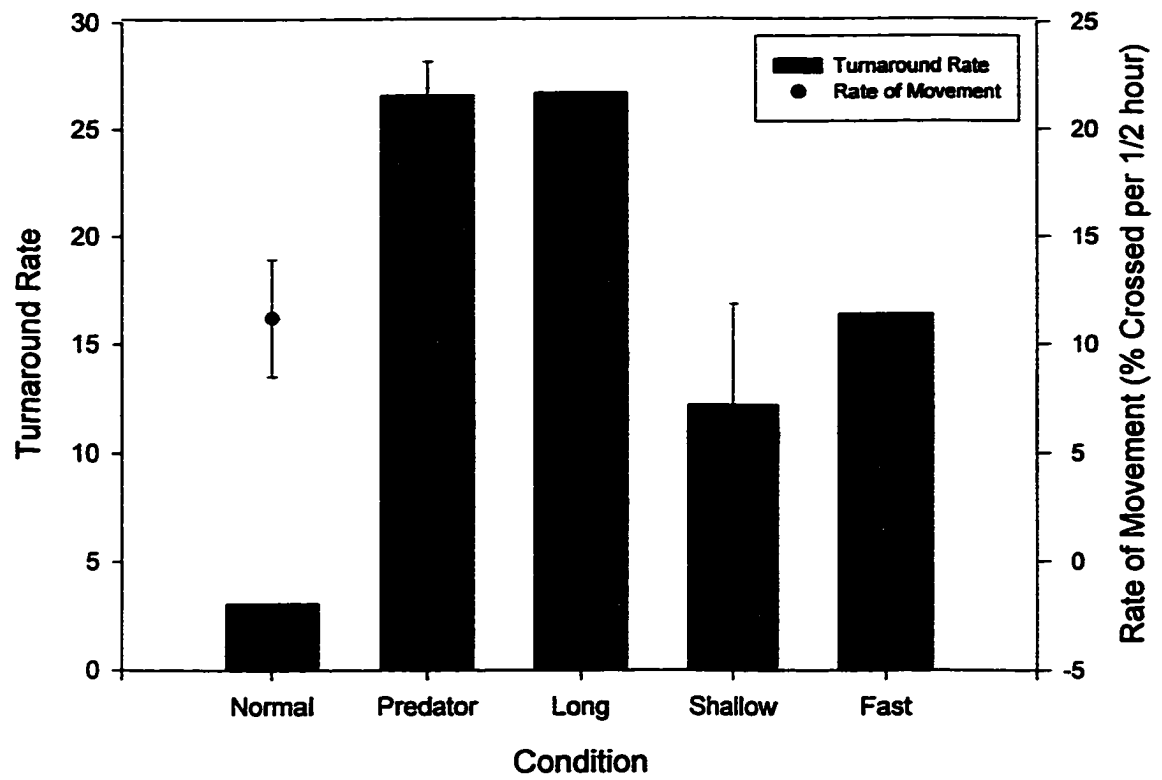












Appendix 1

Treatments and method of data collection used to determine movement rates of N.

boops, C. anomalum, and C. venusta. "Count" = visual count method, "Video" = video taping method.

	<u>N. boops</u>	<u>C. anomalum</u>	<u>C. venusta</u>
<u>Depth Trials</u>			
10 mm (shallow)	All species combined, video		
50 mm(normal)	Count +Video	Count+Video	Count+Video
100 mm	Count	Count	Count
<u>Velocity Trials</u>			
0 cm/s	Count	Count	Count
15 cm/s (normal)	Count+Video	Count+Video	Count+Video
30 cm/s	Count	Count	Count
45 cm/s (fast)	All species combined, video		
<u>Length Trials</u>			
183 cm (normal)	All species combined, video		
549 cm (long)	All species combined, video		
<u>Predation Trials</u>			
None (normal)	Count+Video	Count+Video	Count+Video
None (empty cage)	Video	Video	Video
1 per pool (caged)	Video	Video	Video

Chapter II

Developement and testing of an individual-based model of stream fish movement

Abstract

An individual based model of fish movement was developed and tested by comparing predicted distributions to actual distributions of fish in a six pool, five riffle artificial stream. Pools were 183 cm in diameter and riffles were 43 cm wide and 183 cm long. From 15 to 20 individuals of each minnow (cyprinid) species (Campostoma anomalum, Cyprinella venusta, and Notropis boops) were placed in the third and fourth pools of the stream and allowed to disperse. Numbers of each species in each pool were recorded hourly for nine hours. Trials were conducted under three sets of conditions: 1) all riffles had the same thalweg depth and current velocity; 2) when two of the riffles were shallower and faster; and 3) the fifth pool had a predator and the second pool had vegetative cover. Four different variations of the model were run, each with different parameters defining the movement of fish in simulated space. Two of the models included species-specific differences in movement rates (different probabilities of crossing riffles when encountered, Schaefer 1999), whereas the other two assumed the same movement rate for all species across all riffles. One of the models also included schooling behavior (individual fish moved toward their nearest neighbors), whereas the other three models were correlated random walks. Overall, the models that accounted for species-specific differences in movement rate were more accurate (70% vs. 61% accuracy) under all conditions for all observed times. The best fit models suggest that it is important to take into account detailed information on species-specific behaviors, rather than accepting assumptions that species behaviors could be treated as redundant within a family or trophic guild.

Introduction

Fish in streams move among pools to escape predation, avoid competition, find resources, or for a number of other reasons (Waser 1985, Fausch and Young 1995). The dynamics of a population therefore, is related closely to the movement of individuals (Pulliam 1988, Schlosser 1995), and understanding the rules that govern individual movements is crucial (Jones 1977, Jones et al. 1980, Root and Karieva 1984). Fish that move more can sample more patches and may find a greater number of suitable habitats. However, there are tradeoffs to increased movement, because moving in streams can be energetically demanding (especially upstream) and spending time in shallow riffles increases exposure to terrestrial predators. I measured movement and dispersal rate of three species of stream-dwelling cyprinids in an artificial stream and used those data to assess the accuracy of several potentially reasonable models of fish movement.

The restricted movement concept (Gerking 1959) proposed that most fish remain in one area. This theory has been supported by many studies (e.g. Bachman 1984). Hill and Grossman (1987) found that the majority of marked fish were recaptured near the site of release. Daily movements by brown trout were common, but fish homed back to specific cover structures by the next morning (Clap and Clark 1990). Radio tagged trout moved to stream margins during spates, but showed little overall longitudinal displacement (Gido and Larson unpublished data). Other studies have shown greater movement rates (Gowan et al. 1994), and fast recolonization rates into defaunated areas (Lindfield 1985, Meffe and Sheldon 1990). Recovery time in artificially defaunated pools varied widely among species, but that most cyprinids began to appear in pools

from 2-19 days after disturbance (Lonzarich et al. 1998) . Assemblages in stream reaches (ca. 200 m) returned to states similar to original within eight months after a major flood event (Matthews 1986). Physical factors (riffle lengths, or distance upstream or downstream from source) also influences recolonization rates, with more isolated pools being colonized more slowly (Detenbeck et al. 1992, Taylor 1996, Lonzarich et al. 1998). Studies that have tracked the assemblage structure of fish in pools over time have shown large variance within pools (Matthews et al. 1994), suggesting that movement and mixing among pools is rapid under relatively undisturbed conditions. Fausch and Bramblett (1991) showed that variance between pools over time was equal or greater than interpool variance at one time. Even though variance is large, species seem to show affinities for certain pools or patches. Species may vary within sites, but do not usually disappear from favorable patches, indicating that movement among patches is important on the population level for individual species (Finger 1982).

Studying movement by taking samples at regular intervals can give misleading results, as the observed pattern could be arrived at by a number of different means (Jones 1977). The problem with some studies of movement is that recapture rates are very low and it is impossible to determine if fish are moving out of the study area, dying due to handling stress, or evading capture (Fausch and Young 1995). Some of the more reliable techniques (radio telemetry) are not practical for cyprinids, or for large sample sizes. Other sampling techniques (weir traps) might prevent fish from moving out of study areas, and introduce a bias against long distance moves across multiple traps by individuals.

Individual based models (IBM) track a number of individuals in a population and allow the investigator to set and monitor variables (spatial position, for example) for individuals instead of whole populations (DeAngelis and Gross 1992, Turchin 1998). By comparing predictions from models to observed data, hypotheses can be tested concerning whole populations. Jones (1977) used IBM to explain how different movement behaviors in two populations of cabbage butterflies resulted in different egg distributions in a given habitat. These models are often more useful in situations where variation is important on the individual level (DeAngelis and Gross 1992, Dong and DeAngelis 1998). In studies of movement, individual fish may move separately from the group, or individuals may have different propensities for crossing barriers or moving long distances. An IBM simulates and tracks movement of individuals, something not possible with other modeling techniques.

Schaefer (1999) investigated the interpool movement rate of fish in artificial streams at small spatial (two pools and one riffle) and temporal (30 min) scales. These results suggested that riffles act as barriers to movement, and that shallower thalweg (maximum water depth) depth, greater current velocity and increased riffle length all decrease permeability of riffles. One would also expect that pool conditions (resource availability, habitat structure, or presence of competitors or predators) might affect the desirability of a pool, and therefor movement rate out of that pool.

In this study, I used the results from Schaefer (1999) to develop a general IBM of fish movement in streams. Model predictions were compared to observed movement to test the following hypotheses: I) are models that account for species-specific

differences in movement rate, as well as different riffle and pool conditions more accurate than ones that do not? 2) is a schooling model more accurate than a simpler correlated random walk model? In addition, the model was used to test how pool diameter and riffle width affect predicted dispersal rates of fish. Specifically, I examined movement rate and dispersal of three species of cyprinids in a large, outdoor artificial stream and compared the observed results to those predicted by an IBM of fish movement. My prediction was that models with species-specific and riffle-specific differences would be the most accurate, and that schooling models would be more accurate than those based on a simple correlated random walk.

Materials and Methods

Artificial Streams

I measured fish movement and dispersal over time in an outdoor artificial stream in the research park of the University of Oklahoma Biological Station consisting of 6 pools (183 cm in diameter) and 5 riffles (183 cm in length, 43 cm wide). Stream substrate consisted of cobble, gravel and some sand sculpted to mimic a natural stream bed. Macrophytes in pools were periodically removed (unless a treatment called for a vegetative cover in a pool), as they made accurate visual counts difficult. Water was pumped from a headbox on the most downstream pool to a headbox on the most upstream pool. I altered current velocity and thalweg depth of individual riffles by changing the amount of substrate in riffles. Pool and riffle size was fixed. The direction of flow in the stream was reversed after each trial so that the number of flow-days in

each direction was equal for each treatment. I placed 15-20 Campostoma anomalum (central stoneroller), Notropis boops (bigeye shiner), and Cyprinella venusta (blackspot shiner) in the artificial stream and allowed them to adjust to trial conditions for at least 48 h before trials began. Twelve h before a trial, I seined as many of the fish as possible and placed them in the two middle pools (3 and 4). Screens placed in riffles on either side of these pools prevented any dispersal out of the middle pools. A few individuals (especially C. anomalum) avoided capture by seine, and began trials in pools other than the middle two. At 0900 h the following day, I removed screens and recorded the number of each species in each pool at the beginning of the trial, and each hour thereafter (visual counts made through acrylic windows in pools sides) for eight h.

I conducted trials under three sets of stream conditions (treatments). The first (all same) treatment had all five riffles equal in thalweg depth (50 mm) and current velocity (15 cm/s). The second (two shallow) treatment had the first three riffles at the same thalweg depth (50 mm) and current velocity (15 cm/s), but the last two riffles were shallow (20 mm thalweg depth) and faster (30 cm/s). The third (predator/vegetation) treatment had all five riffles at 50 mm thalweg depth and 15 cm/s current velocity, with a caged predator in pool five and vegetative cover in pool two (predator/vegetation). I placed predators (150-250 mm Micropterus salmoides) in 45 X 40 X 40 cm cages in the center of pools. Cages were constructed of plexiglass on the sides, and 1 cm mesh screening on both ends, top and bottom. Plexiglass allowed direct visual contact, while screening allowed for water circulation through cages. Vegetative cover consisted of cattails and various macrophytes, and covered approximately 80% of the bottom of pool

2. For the all same and two shallow trials, I assumed all pools equal (no predators or macrophytes). The trials with all riffles the same lasted seven days, the other two trials were for six days. I conducted all trials between 0900 and 1700 h, May through August of 1997 and 1998.

Models

I used individual based models (written in the C programming language) to predict the location of individuals of all three species in the artificial stream for each trial. Fish movement was modeled as a series of straight line moves of a given length and direction (Jones 1977, Root and Karieva 1984, Karieva and Shigesada 1998). Pools in simulated space defined the area where fish were allowed to move. Riffles between pools acted as barriers to movement, and probabilities of crossing riffles when they were encountered (riffle permeability) depended on the specific model being run. At each time step in the simulation each fish moved one unit in simulated space along its vector. At the end of a vector, a new turning angle and distance was calculated for each fish (similar to method described by Root and Karieva 1984). Figure 1 shows a flow chart of one iteration for a fish. One unit of simulated space corresponded to 1 cm of real space. Each fish moved 1.5 cm at each iteration, and there were 3000 iterations in each simulated hour resulting in a cruising speed of 1.25 cm/s in simulated space (45 m/h). This cruising speed was arrived at through visual observations and a sensitivity analysis with movement rates measured in two pool systems (Schaefer 1999). Micropterus dolomieu move between 120 (at 4 °C) and 980 (at 27.5 °C) m/day Todd and Rabeni (1989). I assumed that swimming speeds and total daily movement of cyprinids would

be equal or greater than for centrarchids, on average.

Predictions from four models of fish movement were compared to observed values. Models differed in the way fish moved and in the probability of riffle crossing (Table 1). For the predictive model (PM), and the non-species specific (NSS20 and NSS40) models, turning angles were normally distributed around zero with a standard deviation of (0.3π) , and were therefore a correlated random walk (Root and Kerieva 1984, Karieva and Shigesada 1998). For the schooling model (SM) turning angles were normally distributed, but centered on the angle towards the center of its four nearest neighbors position (Fig. 2), following the method described by Huth and Wissel (1992). In all models, if a fish came within range of a riffle (a riffle was encountered when a fish was within $0.5 \times$ riffle width of the center of the end of the riffle), the probability of it crossing the riffle (riffle permeability, Schaefer 1999) was used to determine if it moved to the next pool. Riffle permeability for all species in all models is listed on Table 1. If a fish did not move to the next pool, it changed direction and moved away from the riffle. If a fish did cross a riffle, it was placed in the center of the next pool. If a simulated fish ran into the edge of a pool, a new turning angle was calculated that directed the fish away from the pool edge and towards the center of the pool. For all models, distance traveled (length of line) was drawn from a uniform distribution of 10-20. The PM and SM models included species specific probabilities of riffle crossing (Schaefer 1999) depending on riffle parameters (current velocity, thalweg depth), while the NSS20 and NSS40 models assumed equal probabilities of riffle crossing (20% and 40% respectively) for all species under all conditions. For PM and SM models of streams

with predators and vegetation, the probability of moving out of the pool was tripled when a predator was present and decreased by 50% when vegetation was present (Schaefer 1999).

Model Accuracy

Simulations generated predicted fish distributions for each pool at each observation time. Fish positions to start a simulation matched actual fish positions at the first hourly observation for the trial being simulated. Therefore, by definition each model had no error for the first observation. For each observation after the first, I calculated model error as:

$$\text{Model Error} = \frac{\sum_{p=1}^6 \sum_{s=1}^3 |\text{observed}_{ps} - \text{predicted}_{ps}|}{\text{Number of fish} * 2}$$

Where p is the number of pools, s is the number of species, and predicted values were the simulated mean abundance of each species in a pool at the specified time. Model error potentially ranged from 0.0 (perfect prediction) to 1.0. For each set of conditions, model error was calculated for the PM, SM, NSS20, and NSS40 models. Each model was run 20 times and the mean values for each species in each pool at each time was used as the predicted value for that model. For analysis, mean model error over the nine hour observation period was used. Paired t-tests (comparing paired mean model errors within one day) were used with a Bonferroni correction (6 comparisons, $\alpha=0.0083$) to test for differences in model accuracy across all treatments, and within each of the three

treatments.

Model Sensitivity

I ran simulations to test the sensitivity of the model to pool and riffle size. These were two factors that I assumed would influence movement rates, but that could not be manipulated in the artificial streams. Simulated pool width varied from 1 to 6 m in diameter (riffle width remained at 43 cm), simulated riffle width varied from 10 cm to 1 m (pool width remained at 183 cm). Simulated streams were six pools and five riffles long, and were simulated for 9 h with 200 fish starting in the first pool. NSS20 model parameters were used, and the number of fish in the last pool was recorded after each simulated hour.

Another set of simulations was run to test the efficacy of the schooling algorithms in the SM. Simulations were run with 200 fish placed at random positions in a 5 m diameter pool and allowed to move for 150 simulated minutes. At 10 min intervals, 20 fish were selected at random and their distance (Euclidian) to their four nearest neighbors was calculated. Three models were tested: a completely random walk, a correlated random walk, and a schooling model. Mean nearest neighbor distances for each ten min interval was used in a one-way ANOVA to test for overall model differences. I used Ryan's multiple comparison procedure (SPSS, REGWQ) to test individual model differences.

Results

For all treatments combined the SM(0.299 ± 0.014 SE) was more accurate than

the NSS20 (0.327 ± 0.016 SE, $t=5.21$, $p<0.001$, d.f.=18) and NSS40 (0.389 ± 0.021 SE, $t=6.59$, $p<0.001$, d.f.=18) models, but was not significantly different than the PM model (0.303 ± 0.013 SE, $t=1.08$, $p=0.269$, d.f.=18). The PM model was more accurate than the NSS20 ($t=3.51$, $p=0.003$, d.f.=18) and the NSS40 ($t=6.08$, $p<0.001$, d.f.=18, Fig 3), and the NSS20 was more accurate than the NSS40 ($t=5.08$, $p<0.001$, d.f.=18). For all trials the SM and PM models were very similar, and the different types of movement (schooling vs. correlated random walk) seemed to have little influence on overall distributions. For all treatments, differences among the four models were most obvious in the first 4–5 hours, after which the models began to converge (Fig. 4). For every observation in every trial, the NSS40 had the greatest error, and either the PM or the SM had the least error (Fig. 4).

During actual trials in experimental streams, fish dispersed from the middle two pools into outer pools during the course of each eight hr trial, and were close to an equal distribution across all six pools by the end of the day. For all trials combined, the mean number of fish in the two middle pools decreased from 42.7 to 20.9, and increased from 10.59 to 32.16 in all other pools. This same trend was true for each individual trial. Each of the models predicted the same pattern of movement out of the middle two pools. If allowed to run long enough, most models (with the exception of PM and SM models of predator/vegetation trials) would predict even distributions of fish across all six pools.

Trials With All Riffles the Same

The PM (0.34 ± 0.024 SE) and SM (0.35 ± 0.026 SE) models had the least error

in predicting distributions in these trials, but were not significantly different from NSS20 (0.38 ± 0.034 SE) or NSS40 (0.43 ± 0.045 SE) models (Fig. 5).

Trials With Two Shallow Riffles

Dispersal into pools 4 and 5 (isolated by shallower and faster riffles) was slower than into pools 1 and 2. Comparing total number of fish in pools for the first and last observation over all trials, showed a net loss of 167 fish out of pools 3 and 4. There was a net gain of 127 fish into pools 1 and 2, and a gain of only 40 fish into pools 5 and 6. The PM (0.26 ± 0.015 SE) and SM (0.25 ± 0.014 SE) models had the least error in predicting distributions in these trials, but were not significantly different from NSS20 (0.28 ± 0.013 SE) or NSS40 (0.33 ± 0.020 SE) models (Fig. 5).

Predator/vegetation trials

In predator/vegetation trials fish avoided the pool with a predator, and spent more time in the pool with vegetation. Camptostoma anomalum showed the most avoidance of predators and greatest affinity for vegetation. Out of 837 C. anomalum counted during these trials, only two were observed in the pool with the predator while 346 were counted in the pool with vegetation. Notropis boops also was most common in the vegetated pool and least common in the predator pool; C. venusta was least common in the predator pool, but was not most common in the vegetated pool (Fig. 6). In the PM and SM of this treatment, biases for moving out of the predator pool and against moving out of the vegetated pool meant that the PM and SM did not predict even distributions of fish in all six pools (NSS20 and NSS40 did not account for these differences). The PM and SM had the least error, and were much better than the null

models for these trials (Fig. 4, Fig. 5).

Model Sensitivity

Increased pool diameter and decreased riffle width both decreased the rate of dispersal in simulations (Fig. 7). These variables could not be altered in the artificial streams, but would obviously be factors when modeling dispersal in natural systems. Fish in the schooling model were much closer to their nearest neighbors. Mean nearest neighbor distance differed significantly among the three movement types ($F = 105.2$, $p < 0.001$, $d.f. = 2, 57$). The mean distance to the four nearest neighbors for random movement (30.2 ± 0.85 SE) was not significantly (REGWQ, $t = 0.269$, $p = 0.782$, $d.f. = 38$) different from a correlated random walk (29.8 ± 0.73 SE). Mean distance for the schooling model (16.4 ± 0.72 SE) was significantly lower than for random movement (REGWQ, $t = 12.4$, $p < 0.001$, $d.f. = 38$) or a correlated random walk (REGWQ, $t = 13.2$, $p < 0.001$, $d.f. = 38$).

Discussion

Differences in model accuracy were a result of different interpool movement rates (probabilities of crossing riffles). Models with species specific riffle crossing probabilities based on previous experiments (PM and SM) were more accurate than models with null values (non-species specific, NSS20 and NSS40). These results indicate that movement rate measured at small spatial and temporal scales (Schaefer 1999) can be useful in predicting movement and dispersal at larger scales. These results also show that individual species have different propensities to move, and information

on individual species is also necessary. Except for the difference in the probability of riffle crossing, parameters for the two non-species specific (NSS20 and NSS40) models were identical. The fact that the NSS20 model was more accurate than the NSS40 model at each observation indicated that riffle crossing probability (permeability of barriers) was a controlling factor in dispersal rates, and that a probability of 0.20 was closer to an actual probability than 0.40 for these three species in this particular system.

For individual treatments, significant differences in model accuracy were difficult to detect due to low sample size ($n=6$ or 7). Differences between models for all treatments combined ($n=19$) were significant ($p<0.001$, $\alpha=0.0083$), and the same pattern of PM and SM being more accurate than NSS20 and NSS40 was observed for each of the three treatments at all observation times.

Accuracy for the four models converged toward the end of the eight h trials. Most of the models predicted an even distribution of fish in all pools similar to the observed distributions. Once fish were evenly distributed, error would be similar for all models. However, in the predator/vegetation trials models did not converge as quickly. The PS and SM were noticeably more accurate than the NSS20 and NSS40 models, and would probably remain so indefinitely because they predict the observed avoidance of predators and affinity to vegetative cover. From these data one could conclude that pool properties and habitat heterogeneity are a more important factors in determining interpool movement than are riffle or other barrier properties. Some fish are able to cross seemingly impossible barriers. Clap and Clark (1990) recorded radio-tagged brown trout crossing rock dams that were thought unpassable. The three species also

had different avoidance of or affinity for pools. Campostoma anomalum showed the greatest avoidance of predators and affinity for vegetation. Other habitat parameters such as depth, substrate, or resource availability may be influential for these or other species, again emphasizing the need for species specific data to model movement and dispersal.

The addition of schooling behavior did not significantly change model accuracy. However, schooling behavior in a model may be more important when simulating larger systems. In the small pools of this system, no two fish in the same pool could ever be more than 183 cm apart in real or simulated space. Schooling behavior may be more influential when modeling larger systems where simulated fish would travel and encounter riffles as groups. In a correlated random walk model with 100 fish in a pool 20 m in diameter, fish would be very scattered and would encounter riffles alone and at a constant rate. If a schooling model was used, many of the fish would move as a cluster, and could encounter a riffle at the same time, a much more realistic simulation.

The artificial stream used in this study is a good representation of real midwestern streams. The setup described supported small populations of all three species for two years. Fish seemed to behave normally, and newly recruited juveniles often had to be removed from the stream to keep numbers constant. While there are many benefits to using artificial streams, some of the disadvantages need to be addressed. First, the artificial stream did not allow dispersal out of the study area. It is probable that some fish in real streams of the same size would have left the system in an eight hour period. In a few cases, individuals appeared in the most distant pools (1 or 6) just one

hour into a trial, indicating they had crossed two riffles and two pools in the first hour of the trial. Distinguishing characteristics of some fish allowed me to track a few individuals, and on one occasion a fish moved the entire length of the stream (crossed five riffles and five pools) in one hour. These were rare occurrences, but they indicated that a few individuals move much more than the rest, and that models of fish movement need to be tested on larger spatial and temporal scales in natural streams. Second, the artificial stream only allowed dispersal on a small scale. Dispersal rate in the artificial stream is probably greater than in a typically sized 6 pool - 5 riffle stretch of natural stream. Simulations suggest that dispersal in systems with larger pools will be much slower, and not in a linear fashion (Fig. 7). Model error in natural systems might therefore remain lower for the PM and SM over much longer periods. Small pool size in relation to that in a real stream may also have artificially increased the threat predators represented. Fish that moved into pools with the predator were in close proximity (≤ 1 m away) with little shelter available. This might have led to predator effects greater than would be expected in a regular stream.

In conclusion, the results of this study show that individual-based models can be used to predict and test hypotheses about movement and dispersal of fish in streams. These types of models should prove of interest to ecologists who are interested in the spatially explicit distribution of the populations they study. Future studies in this area should focus on testing the accuracy of these models in real streams.

Acknowledgments

This paper was presented as partial fulfilment for the requirements of a Ph.D. from the Department of Zoology at the University of Oklahoma. I thank the members of my committee: Bill Matthews, Victor H. Hutchison, Bill Shelton, Larry Toothaker, Gary Welborn. I thank Keith Gido, David Lonzarich, and Mel Warren for useful input into various aspects of this project. I thank the USDA Forest Service, University of Oklahoma Biological Station, University of Oklahoma Department of Zoology, and The University of Oklahoma Graduate Student Association for funding and supplying facilities.

Literature Cited

- Bachman. R.A. 1982. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Trans. Am. Fish. Soc.* 113:1-32.
- Clapp. D.F. and Clark. R.D. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. *Trans. Am. Fish. Soc.* 119:1022-1034.
- Dong. Q. and DeAngelis. D.L. 1998. Consequences of cannibalism and competition for food in a smallmouth bass population: An individual-based modeling study. *Trans. Am. Fish. Soc.* 127:174-191.
- DeAngelis. D.L. and Gross. L.J. (eds.). 1992. Individuals-based models and approaches in ecology: populations, communities and ecosystems. Chapman and Hall, New York..
- Detenbeck. N.E. Devore. P.W. Niemi. G.J. and Lima. A. 1992. Recovery of temperate stream fish communities from disturbance: a review of case studies and synthesis of theory. *Env. Manag.* 16:33-53.
- Fausch. K.D. and Bramblett. R.G. 1991. Disturbance and fish communities in intermittent tributaries of a western great plains river. *Copeia*.1991:659-674.
- Fausch. K.D. Young. M.K. 1995. Evolutionarily significant units and movement of resident stream fishes: a cautionary tale. *Am. Fish. Soc. Symp.* 17:360-370.
- Finger. T.R. 1982. Fish community-habitat relations in a central New York stream. *J. Fresh. Ecol.* 1:343-352.
- Gerking. S.D. 1959. The restricted movement of fish populations. *Biol. Rev.* 34:221-242.

- Gowan. C. Young M.K. Fausch. K.D. and Riley. S.C. 1994. Restricted movement in resident stream salmonids: A paradigm lost? *Can. J. Fish. Aq. Sci.* 51:2626-2637.
- Huth. A. and Wissel. C. 1992. The simulation of the movement of fish schools. *J. Theor. Biol.* 156:365-385.
- Hill. J.A. and Grossman. G.D. 1987. Home range estimators for three North American stream fishes. *Copeia* 1987:376-380.
- Jones. R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. *J. Anim. Ecol.* 46:195-212.
- Jones. R.E. Gilbert. N. Guppy M. and Nealis. V. 1980. Long-distance movement of Pieris rapae. *J. Anim. Ecol.* 49:629-642.
- Karieva. P.M. and Shigesada. N. 1998. Analyzing insect movement as a correlated random walk. *Oecologia.* 56:234-238.
- Lonzarich. G.D. Warren M.L. and Lonzarich. M.R.E. 1998. Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas. *Can. J. Fish. Aq. Sci.* 55:2141-2149.
- Linfield. R.S.J. 1985. An alternative concept to home range theory with respect to population of cyprinids in major river systems. *J. Fish Biol.* 27(Supplement A):187-196.
- Matthews. W.J. 1986. Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia.* 1986 :388-397.
- Matthews. W.J. Harvey. B.C. and Power. M.E. 1994. Spatial and temporal patterns in

- the fish assemblages of individual pools in a midwestern stream (USA). *Env. Biol. Fish.* 39:381-397.
- Pulliam. H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* (132):652-661.
- Root. R.B. and Karieva. P.M. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): Ecological consequences and adaptive significance of markovian movements in a patchy environment. *Ecology.* 65:147-165.
- Schaefer. J.F. 1999. The effects of riffles as barriers to movement of stream fish. Unpublished dissertation. University of Oklahoma, Department of Zoology.
- Schlosser. I.J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology.* 76:908-925.
- Taylor. C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Fresh. Biol.* 36:101-112.
- Todd. B.L. and Rabeni. C.F. 1989. Movement and habitat use by stream-dwelling smallmouth bass. *Trans. Am. Fish. Soc.* 118 (3):229-242.
- Turchin. P. (ed.). 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts.
- Waser. P.M. 1985. Does competition drive dispersal? *Ecology.* 66 (4):1170-1175.

Table 1

Types of models and the different parameters that defined movement in each. Uniform indicates a random number drawn from a uniform distribution from the specified range. Normal = normal distribution with the mean and standard deviation indicated. Max = maximum length of a move vector. Cur. Dir = current direction of movement. PM and SM probability of rifle crossing is for *N. boops*, *C. anomalum*, and *C. venusta* respectively. PM and SM probabilities changed with riffle or pool conditions.

Model	Parameters		
	Move Length	Move Direction	Prob. of riffle cross
Predictive (PM)	Uniform ($\frac{1}{2}$ Max-Max)	Normal (Cur.Dir.,0.3*PI)	0.06, 0.14, 0.16
Schooling (SM)	Uniform($\frac{1}{2}$ Max-Max)	Normal (Center of 4 nearest neighbors, 0.3*PI)	0.06, 0.14, 0.16
Non Species-Specific (NSS20)	Uniform ($\frac{1}{2}$ Max-Max)	Normal (Cur.Dir.,0.3*PI)	0.20
Non Species-Specific (NSS40)	Uniform ($\frac{1}{2}$ Max-Max)	Normal (Cur.Dir.,0.3*PI)	0.40

List of Figures

Figure 1

Flow diagram of one iteration for one simulated fish. Each fish completes 3000 iterations for 1 hour of simulated movement. One move in the model corresponds to 1.5 cm moved in simulated space. ① = new direction is from a normal distribution centered around the direction towards the pool center. ② = new direction is from a normal distribution centered around the fish's current direction (correlated random walk). ③ = new direction is from a normal distribution centered around the direction towards the centroid of the fish's four visible nearest neighbors.

Figure 2

Diagram of how a typical new direction is selected in the schooling model (following method of Huth and Wissel 1992). The shaded area represents space visible to the fish where it looks for its nearest neighbors. Numbers 1-4 show the four nearest visible neighbors. Fish outside of shaded area are not visible. Line A represents the distance a fish can see (defined as 100 cm in simulated space).

Figure 3

Model error for all treatments combined. Error bars represent 1 SE. Models with different letters are significantly different (paired t-tests, Bonferroni correction).

Figure 4

Mean model error for all four models vs. time in each treatment.

Figure 5

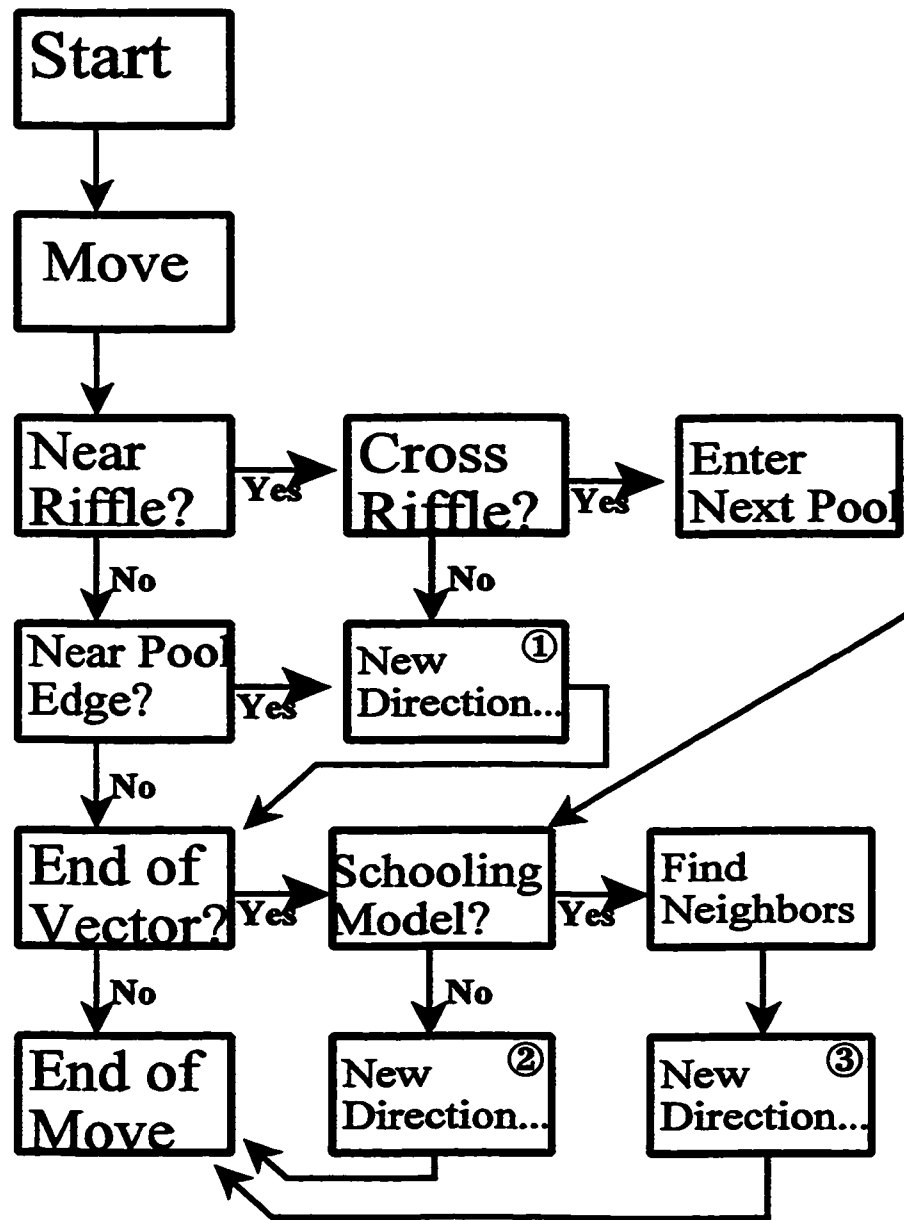
Mean model accuracy summed over time (± 1 SE) for each model in each treatment.

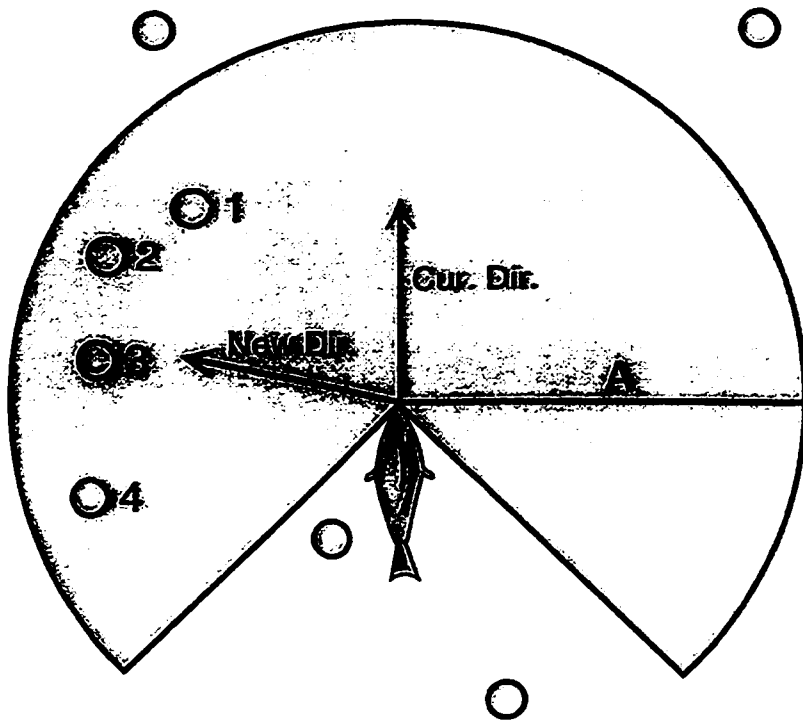
Figure 6

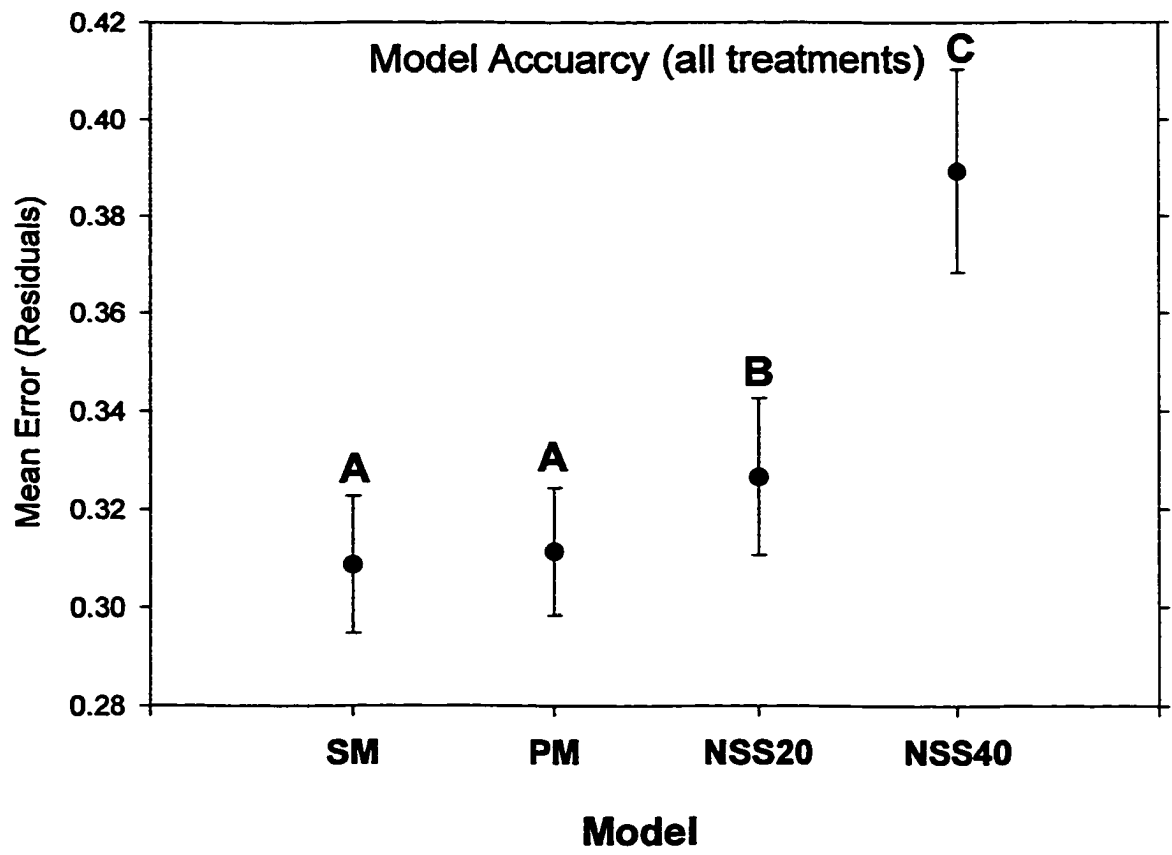
Total numbers of each species counted in each pool during predator/vegetation trials.

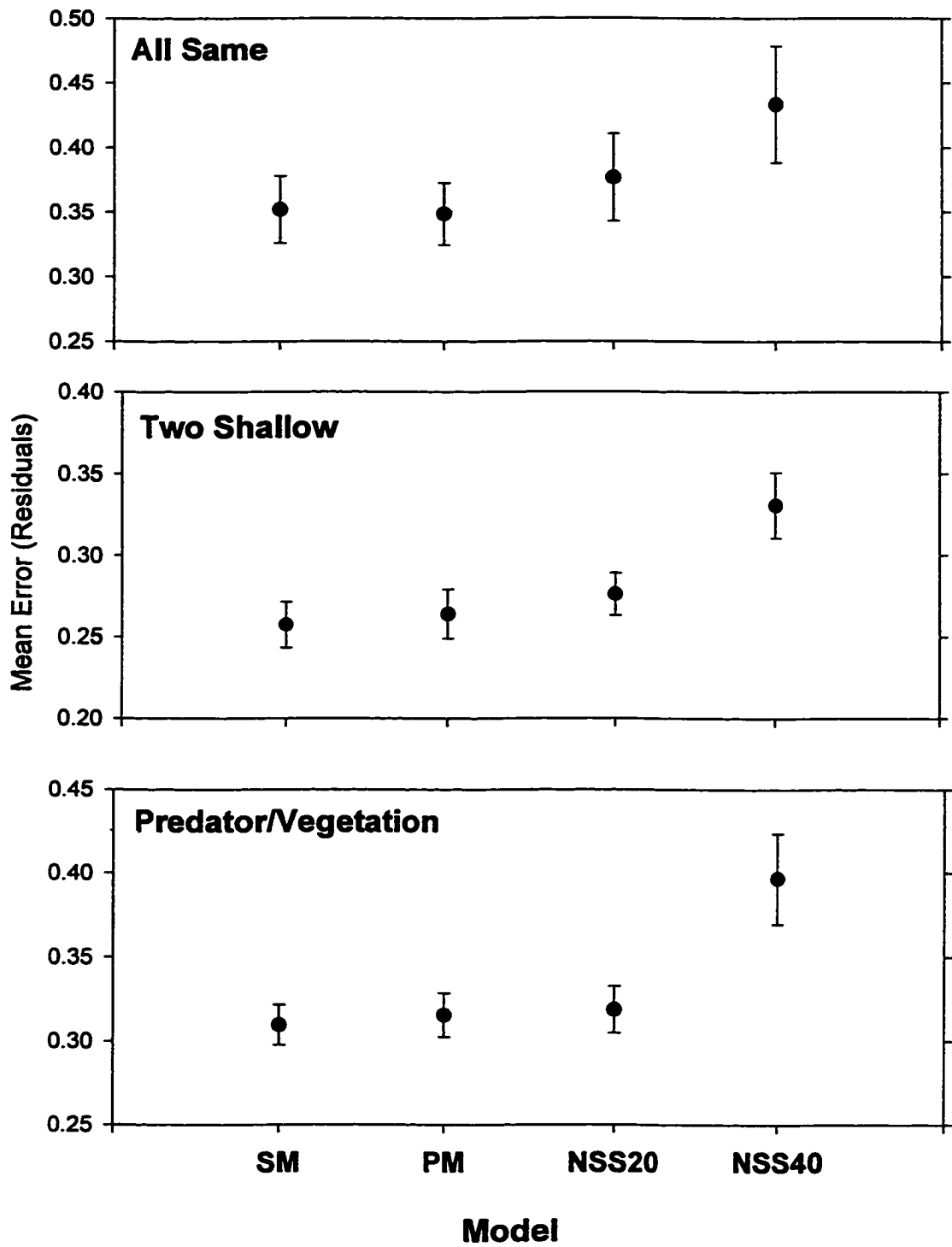
Figure 7

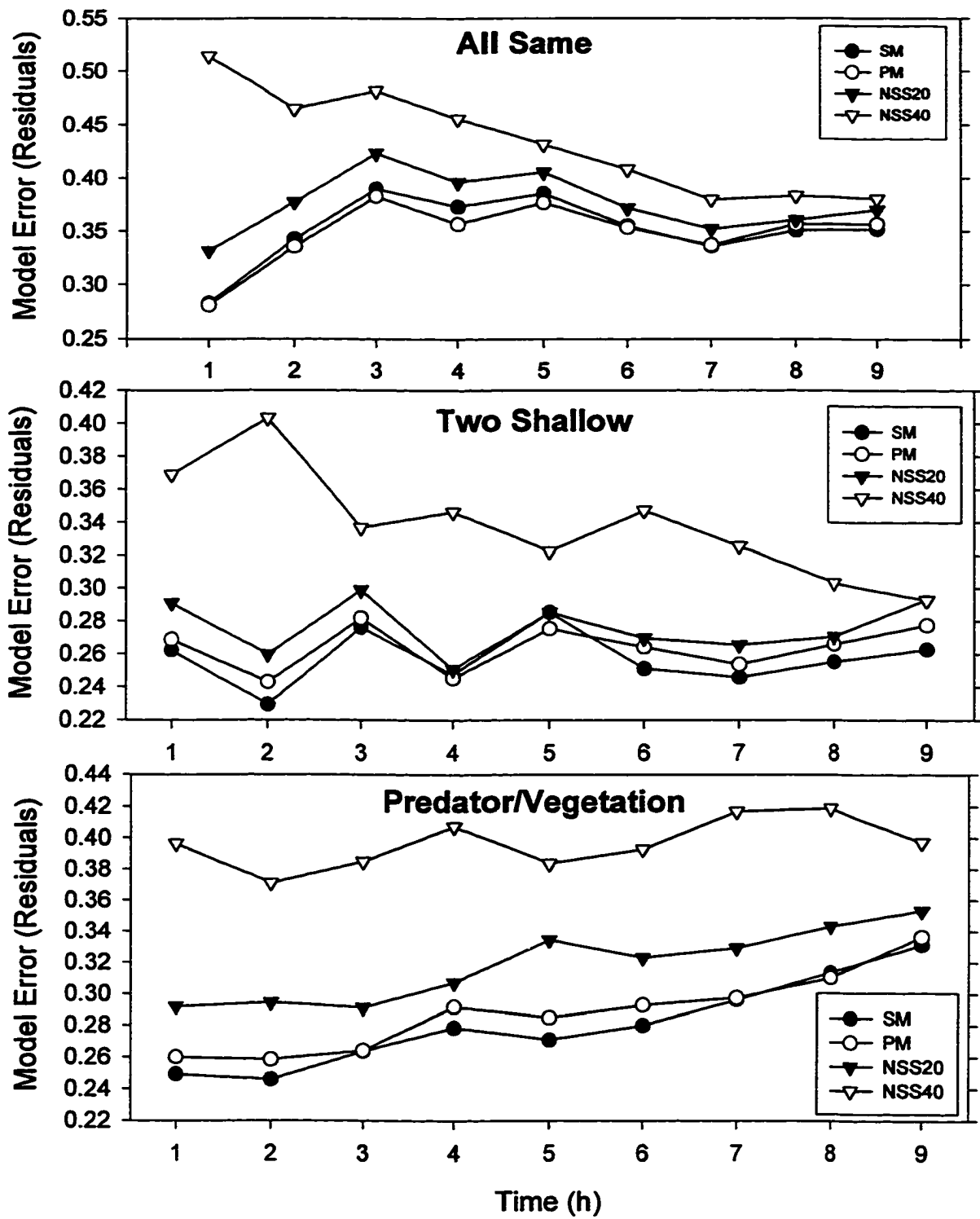
Effects of pool diameter (A) and riffle width (B) on simulated dispersal rate of fish using the NSS20 model movement parameters. See text for complete model parameters.

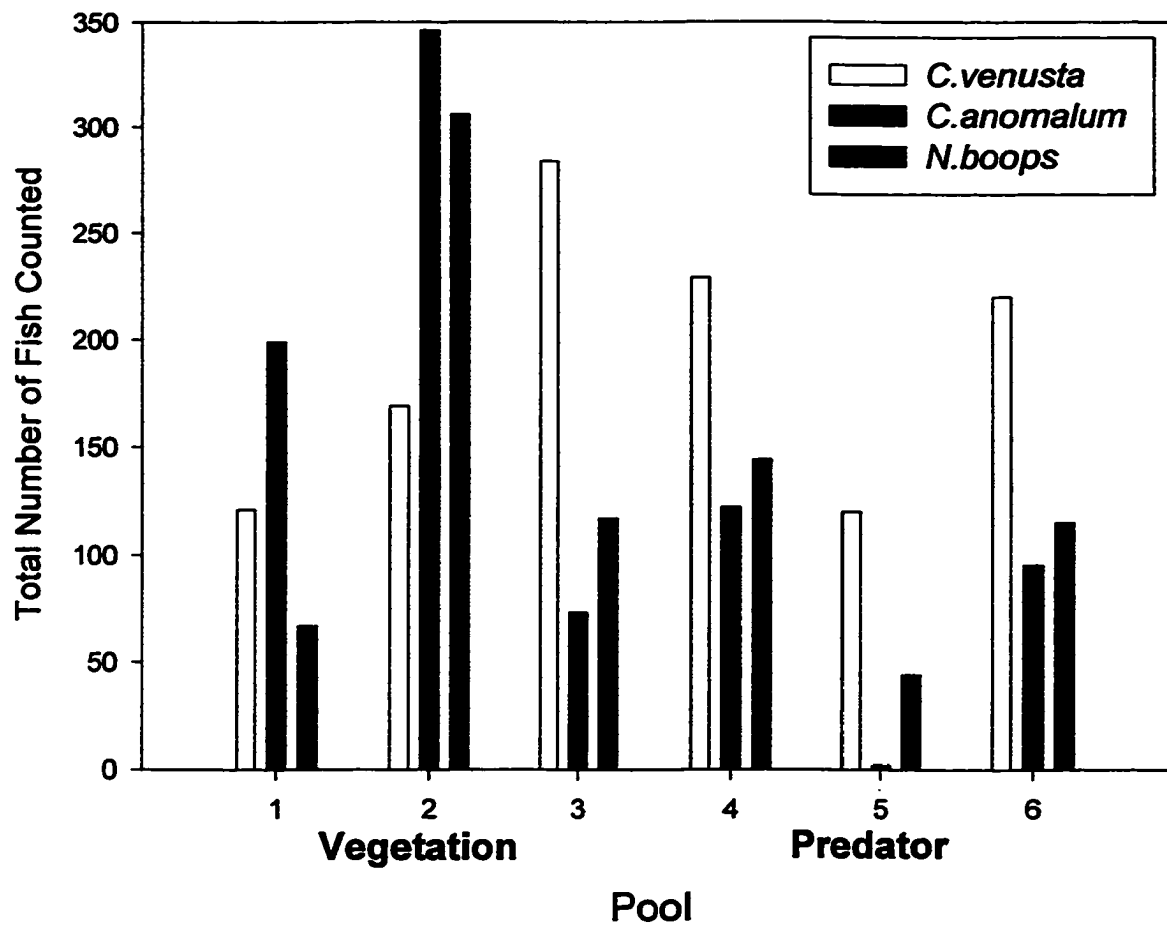


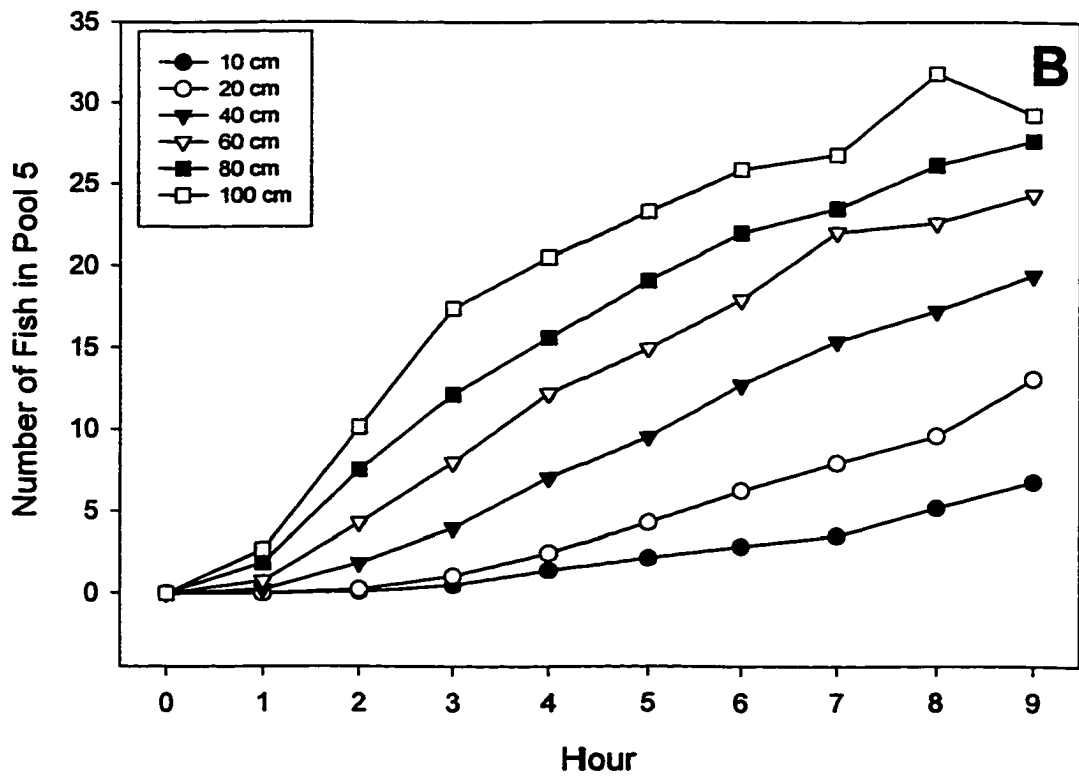
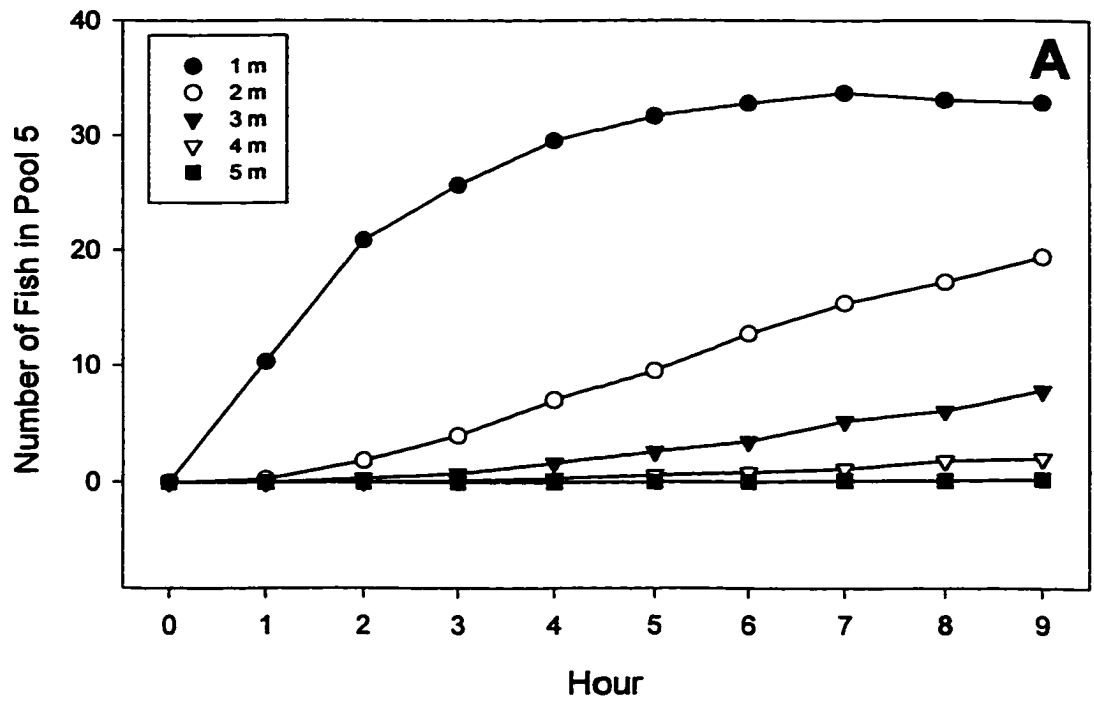












Chapter III

Modeling stream fish movement and dispersal: a mark-resight study in a small warmwater stream

Abstract

Movement of two cyprinids (Notropis boops and Camptostoma anomalum) were tracked over a 28 day period in Brier Creek (Marshall Co., Oklahoma). One hundred N. boops (on 26 May 1998) and 100 C. anomalum (on 16 June 1998) were marked by injecting a small amount of acrylic paint subcutaneously. An individual-based model was developed using movement data collected in outdoor artificial streams, and used to predict the location of tagged individuals over the course of the experiment. A nine pool, eight riffle stretch of stream (737.5 m in total length) was sampled by snorkeling on 13 of the 28 days following the mark and release of N. boops. During surveys, the total number of each species was recorded for each pool, including any marked individuals seen. A total of 45,881 observations (including 553 marked) of fish were made during the 13 surveys. A principle components analysis of species data by pools showed some species were consistently more common in certain pools. Comparing different model predictions to observed distributions allowed me to test hypotheses about the importance of pool area and riffle permeability to dispersal. Three different models were used: 1) a model with actual pool size and riffle permeability, 2) a model with all pools the same size and actual riffle permeability, and 3) a model with actual pool size, but all riffles 100% permeable. The model with actual pool size and riffle permeability was the most accurate, and the model with uniform pool size the least accurate.

Introduction

Fish in streams may move on a local (among individual pools) scale for many reasons including resource availability, competition, shelter or predator avoidance. Movement of fish among patches may influence stream food webs and productivity by controlling distribution and levels of primary productivity among patches (Power 1990, Schlosser 1995b, Winemiller and Jepsen 1998). Threat of predation has been shown to restrict movement of algivores (Power et al. 1985, Gelwick et al. 1997), which caused an increase in algal growth in predator rich areas, and reduced algal stocks in predator-free areas. These and other factors controlling movement of fishes among patches in streams are important to community dynamics on many levels (Winemiller and Jepsen 1998). Little is known about daily movement rates of fish in small streams and the role barriers play in regulating the exchange rate of individuals among landscape units (Bart 1989, Hillborn 1990, Schlosser 1995a). This study investigated daily movement of fish among pools in a natural stream.

Many small midwestern streams are divided into pool and riffle habitats with many species showing distinct habitat preferences (Finger 1982, Gelwick 1990, but see Bart 1989). In these streams, riffles act as barriers to movement among pools (Matthews et al. 1994, Warren and Pardew 1998). Schaefer (1999a) measured inter-pool movement rate of three cyprinids (Notropis boops, Camptostoma anomalum and Cyprinella venusta) in artificial streams under four riffle current velocities, three riffle thalweg depths, and two riffle lengths. Movement rate decreased with increasing current and riffle length, and there was a trend toward decreased movement at lower thalweg depths.

The presence of predators also caused increased movement by all species and a habitat shift (from pools to riffles) by some individual C. anomalum. In a follow up study, Schaefer (1999b) used these results to develop an individual-based model (IBM) to predict fish movement in larger artificial streams (six pools, five riffles) over longer periods of time (eight hours). One goal of this study was to determine how well that same model might predict fish movement in a natural stream, and use the model to quantify the role of pool size and riffle permeability to dispersal.

Most mass mark-recapture (MMR) studies mark individuals, release them in one area, and sample surrounding areas at a later date to determine the density of marked individuals at various distances from the release area. Standard mark and recapture studies can be problematic for many reasons (Gowan et al. 1994). Often they rely on commercial capture and therefore do not allow for multiple captures (Hilborn 1990). Mark and recapture studies also can suffer from low recapture rates (see Freeman 1995, Hill and Grossman 1987) because they require sampling that is time consuming and disturbing to fish. Low recapture results also leave questions about mortality, individuals leaving the study area, or insufficient sampling techniques. In most instances, samples cannot be collected at short intervals and many sites. Because of the time scale of these studies (months to years), it is often difficult to come to any conclusions about movement rates. It cannot be determined if individuals are moving quickly and returning to home areas, or if movement is slower and more direct (Gowan and Fausch 1996). Other techniques address these problems by using traps or radio telemetry to measure fish movement (Baade and Fredrich 1998, Schlosser 1995a,

Gowan and Fausch 1996). Wier traps capture fish that are attempting to move either up or down stream, however fish can only be trapped once and are not allowed to continually move and possibly return to home pools. Radiotelemetry is an ideal method for a small number of larger fish. However, the use of radio telemetry for small stream dwelling fish is not practical with current technology.

Another technique of analyzing animal movement is to collect data on, and model movement of individuals, as in path analysis. Path analysis tracks a few individuals continuously and the distance and direction of each move is recorded (Jones 1977, Turchin 1998). Jones (1977) used path analysis and an IBM to explain egg distribution patterns in cabbage butterflies. This technique provides the most detailed information about individual movement, but statistical analysis is difficult due to autocorrelation of moves, and a limited number of animals can be followed for only a short period (Turchin 1997). In this study, I attempted to monitor movement of many small stream fish from day to day. The goal was to record short term movement data with high recapture (resight) rates without using standard trapping or seining that may disturb fish or habitat.

The purpose of this study was to: 1) track the daily movement of Notropis boops (bigeye shiner) and Campostoma anomalum (central stoneroller) by marking and then resighting individuals on snorkeling surveys, 2) test the accuracy of an IBM of fish movement (Schaefer 1999b), and 3) use the model to test the role of stream physical structure (pool area and riffle permeability) on fish movement.

Materials and Methods

Study Area

Brier creek is a small prairie-margin stream located in Marshall County, Oklahoma. The fish fauna consists of 30 known species (Smith and Powell 1971). This study focuses on two of the most common species in the stream, Campostoma anomalum (central stoneroller) and Notropis boops (bigeye shiner). The headwaters of the stream drain pastures while reaches further downstream are lined by forests and fed by subsurface springs (Power and Matthews 1983). In the stretch of stream studied, pools range from 6-15 m wide, 20-135 m long, and up to 2.0 m deep (2.0 m depth is atypical and found only in pool 1 under a bridge). Stream substrate consists of cobble, gravel, sand and sandstone bedrock. Riffles vary from 2-40 m in length, 0.5-3 m wide, and 1-18 cm thalweg depth. Throughout the duration of this study (26 May - 24 June 1998) water flowed through all pools and riffles and no large flood events occurred (1 day of rainfall, < 2.5 cm).

The study site consisted of a nine pool, eight riffle stretch starting at highway 32 and extending upstream 737.5 m (Table 1). This is the same stretch described by Power and Matthews (1983) with a few exceptions. The area used in this study began one pool further downstream so that pool 1 described here is downstream from pool 1 in Power and Matthews. From that point, pools 2, 3, and 4 correspond to Power and Matthews pools 1, 2, and 3 respectively. Pools 4 and 5 from Power and Matthews are no longer distinct pools and were combined into pool 5 for this study. Pools 6-9 correspond to

Power and Matthews pools 6-9. A natural waterfall (20 cm high) at the top of pool 9 was considered unpassable during the experiment (but certainly not unpassable under higher water conditions), and pools upstream were not surveyed. The pool below pool 1 was surveyed twice but not modeled or included in analysis as no marked fish were seen there.

Mark and Snorkel Method

On 26 May 1998 I seined 100 N. boops from pool 5, marked, and returned them to pool 5 within a 6 h period. On 16 June 1998, I seined 100 C. anomalum from pool 7 and marked them same way. For marking, I sedated fish (MS-222) and injected non-toxic acrylic paint (liquitex, red) subcutaneously using a disposable hypodermic needle (following the method of Lotrich and Meredith 1974). I made marks on both sides of the body. After marking, I allowed fish 1 h recovery, and observed them for any obvious adverse effects from marking. This method has been established as an effective method of marking small fishes (Thresher and Gronell 1978, Hill and Grossman 1987, Freeman 1995, Goforth and Foltz 1998). A pilot study was conducted to test the efficacy of the marking technique on 50 N. boops and C. anomalum. There were no mortalities, and most marks were still visible one month later. Lotrich and Meredith (1974) found that 90% of fish marked retained marks (depending on pigment used) after two months and only C. anomalum showed any signs of stress (fin rot, body fungus). These effects were not observed in the pilot study, however there were two mortalities (both C. anomalum) during marking for trials.

I conducted snorkeling surveys on thirteen individual days (6 following N. boops

marking: 27- 29 May, 1-3 June and 7 following C. anomalum marking: 17- 19, 22- 25 June). I began surveys in pool 1 and progressed upstream through pool 9. One pass was made up the middle of each pool and numbers of each species was recorded. On most days, visibility was high enough to allow bank to bank observation from the middle of the pool. On one occasion water clarity was much lower (due to local gravel digging) and counts were considerably lower in all pools. On two other occasions livestock blocked access to the three most upstream pools and only pools 1-6 were surveyed. Riffles in the study area were shallow with high current and could not be effectively sampled by snorkeling, so estimates of riffle dwelling species (darters) were not accurate and eliminated from analysis. Individual C. anomalum or N. boops were never observed maintaining position in any riffles in this stretch of stream. Some species were also divided into size or age classes: Lepomis were divided into juvenile (<25 cm, all species combined), and adult groups (>25, species differentiated), Micropterus sp. were divided into juvenile (<25 mm), small (25-75 mm) and adult groups (>75 mm), cyprinids and all other species were divided into juvenile (<25 mm if present) and adult (>25 mm). A principal component analysis (PCA) was used to examine pool assemblage similarities across all surveys.

Environmental data Collected

I collected environmental data on individual pools and riffles to quantify parameters for movement models (pool length and width, riffle length, width, current velocity, and thalweg depth, Table 1). I collected other environmental data (below) to quantify habitat differences among pools. Three transects were selected that represented

the range of pool or riffle morphology. Depth, current velocity (only in riffles), and substrate were measured at five points along each transect. Estimates of percent substrate cover, percent aquatic vegetative cover, type of aquatic vegetative cover, and percent canopy cover were made for each pool and riffle.

Movement Model

An individual-based model of fish dispersal (described by Schaefer 1999b) was used to predict movement and dispersal of the 200 marked fish. The model was originally developed and tested using movement data on C. anomalum, N. boops and Cyprinella venusta (blackspot shiner) in two pool outdoor artificial streams (University of Oklahoma Biological Station) built to mimic Brier Creek. The model was spatially explicit, so pool and riffle lengths and widths were incorporated into the model (1 cm of real stream = one unit in simulated space). Fish moved one unit for each time step (one second of real time), resulting in a cruising speed of 1.5 cm/s. When a fish in the model encountered a riffle, a probability (= riffle permeability) determined if it crossed the riffle or “bounced” off and remained in the original pool. Riffle permeability data were from Schaefer (1999a), and modified according to measured conditions in Brier Creek (riffle length, mean thalweg depth, and mean current velocity, Table 1). All other model parameters used were the same as the correlated random walk model described in Schaefer (1999b) with one exception. In the model for this study, 1% of the fish (chosen at random each simulated hour) were designated wanderers (“strayers”, Freeman 1995). I added wanderers based on work by many authors (Stefanich 1951, Funk 1955, Gerking 1959, Freeman 1995, but see Hill and Grossman 1987) and personal

observations made in artificial streams (Schaefer 1999a, 1999b) where individual fish were seen moving large distances over short time periods. Wanderers in the model differed in that they had a bias to move toward the nearest riffle in the model, resulting in greater net distance moved (obviously, manhattan distance would be no different). Three different models were run. The first model (predictive) included actual pool sizes and riffle permeability data from Schaefer (1999a, Table 1). The second model (pools equal) was the same except that all pools were made the same size (the mean length and width of all pools). The third model (no barrier) had actual pool sizes but riffle permeabilities were set at 1.0 (100%), so that riffles did not act as barriers to movement. Each model was run 20 times, and the mean number of predicted fish for each pool at each time was used for analysis.

Model Accuracy

The model predicted the number of marked fish in each pool for each survey. These predictions were compared to observed number of marked fish in pools during surveys to obtain measures of model error. Model error was the percent of fish locations incorrectly predicted by a model, and was defined (for one species, one model, on one survey) as:

$$\text{Model Error} = \frac{\sum_{p=1}^9 |\text{observed}_p - \text{predicted}_p|}{\text{Number of fish} * 2}$$

Where p is the number of pools (n=9), observed values are the percent of marked fish

seen in each pool, predicted values are the mean number of fish in each pool from simulations, number of fish was the number of marked individuals (100). Model error potentially ranged from 0.0 (perfect prediction) to 1.0 (Schaefer 1999b). Model accuracy was assessed for both species on the survey seven days following release and the last survey made.

Results

PCA Analysis of Species Data

The first two axes of the PCA accounted for 34.1% of the variation in species abundance among pools (Fig. 1, Table 2). Notropis boops abundance was positively ($r = 0.423$) and C. anomalum abundance negatively ($r = -0.147$) correlated with axis I. Thus, pools that consistently had many N. boops (e.g. pool 5) were toward the right side of Figure 2 while pools with more C. anomalum (e.g. pool 7) were on the left.

I counted a total of 45,881 fish, including 553 marked individuals. Numbers of marked individuals sighted decreased as the experiment progressed. Forty-seven and 69% of marked N. boops were seen on the first two surveys respectively, whereas only 18 and 10% were seen the last two surveys (Fig. 3). Campostoma anomalum were only surveyed seven out of nine days after release, and percent of resightings remained 25-35% except on one day with reduced visibility.

One group of 120-150 N. boops (the same group used for marking) was seen in pool 5 just above the downstream riffle in every survey. This area was shallow (30-40 cm) with a cobble substrate and complete canopy cover. No N. boops were seen in any

other part of pool 5 (typically deeper with gravel or bedrock substrate and incomplete canopy cover, Table 1). For all surveys, the majority of marked N. boops were always seen in pool 5 at the release point. Two days after release, two marked N. boops were seen in pool 6, while 67 were seen in pool 5. In the last two surveys marked N. boops were seen as far downstream as pool 2 ($n = 2$) and as far upstream as pool 8 ($n = 2$) and in pools 4 ($n=2$), 5 ($n=21$), and 6 ($n=1$, Fig. 5).

Campostoma anomalum were abundant in all pools except 1 and 5 (no individuals seen in pool 1, one individual seen in pool 5, Fig. 2), and accounted for 66.9 % of all fish counted (Table 2). Over all surveys, the majority of marked C. anomalum were seen in pool 7 (release point). Over the nine days following release, marked C. anomalum were seen as far downstream as pool 6 ($n=1$) and as far upstream as pool 9 ($n=1$), however no marked individuals were seen in pool 8 (Fig. 4). High variance for total C. anomalum in pool 7 was due to low counts on 28 and 29 May (5 and 220 individuals, respectively) caused by low visibility. Numbers of C. anomalum for pool 9 were typically low (<30 , none marked) until 24 June when 350 were seen in the pool (one of them marked), accompanied by a decrease in the numbers in pools 7 and 8. The following day, many left the pool and numbers dropped back down to 170 (one marked, Fig. 5). This accounts for the high variance in number of C. anomalum for pools 8 (mean = 65.4, SE = 29.3) and 9 (mean = 43.9, SE = 38.9) compared other species in other pools. Variance in C. anomalum counts for other pools was much lower.

Model Results and Accuracy

The “predictive” model was more accurate in predicting fish movement than the

other two models (pools equal and no barrier). After seven days, the predictive model had 7.2 and 46.8% error for N. boops and C. anomalum respectively. The no barrier model was more accurate (10.6% vs 46.5%) than the pools equal model for N. boops, but the opposite was true (50.3% vs 52.4%) for C. anomalum (Fig. 6).

After 28 days, the predictive model for N. boops was more accurate (26.3 % error) than the other two models (54.3 % for pools equal, 28.6 % for no barrier, Fig. 6). After nine days, the predictive model for C. anomalum was more accurate (46.6 % error) than the other two models (55.6 % for pools equal, 48.8 % for no barrier, Fig. 6).

Discussion

While resight numbers dropped off quickly, it is not likely that marked fish left the study area. The top of pool 9 was impassable due to a small waterfall, so fish could only leave the study area by moving downstream out of pool 1. Marked N. boops were only seen as far downstream as pool 2, 26 days after release in pool 5. Two surveys of the pool downstream from pool 1 failed to reveal any marked fish. Most likely, low resight numbers were due to low visibility and fading marks. Within a week of release, some individuals were seen with fading marks on one side of the body. Some fish were later seen with visible marks on only one side. It is possible fading marks would have been visible if fish were seined and closely inspected, but the combination of low visibility on some days and fading marks caused decreasing resight numbers. Even with fading marks, there were 2.7 resights for each marked fish over all surveys combined (higher relative to other mark and recapture studies).

Most of the inter-pool movement events observed in this study were by one or

two individuals. The majority of marked fish remained in the pool where they were released. When marked fish were seen outside of these pools, they were always with other members of their species, but usually not with other marked fish. However, observations of unmarked fish do indicate that movement of groups did occur on occasion. Large groups (100-300) of C. anomalum had to have moved among pools 7, 8 and 9 to account for changes in numbers in those pools on 24-26 June. The only evidence for movement of groups of N. boops was the occasional disappearance of a group (30-45) usually seen in pool 1. However, they may have escaped detection as there was no corresponding increase in adjoining pools during the same surveys. This area of pool 1 is especially wide and shallow with large boulders which made it the most difficult area to survey. There was also evidence of movement by groups of Moxostoma erythrurum (golden redhorse). Groups (25-50) of juvenile M. erythrurum were seen in shallow areas of pools just below riffles. These groups were often seen in the same location (pool 3 and 7) for two or three days before disappearing. It is possible these fish were moving large distances as a group, or that they moved into riffles and avoided detection. A group of 20 adult M. erythrurum was seen on two consecutive surveys in pool 7, but were not seen again. These observations indicate this species might make a good subject for future research on fish movement.

Notropis boops and C. anomalum differed in their movement within pools. Marked C. anomalum were all released in one location, but were seen scattered throughout pool 7 the following day. There were many separate groups of C. anomalum in the pool, and marked fish were seen in each of these. Notropis boops were also

released together, however this same group remained at the release point for the duration of the study. I assumed this was the same group of N. boops because no other group of N. boops that large was seen in any other pool, and marked individuals were seen in this group in every survey. One explanation for the differences is in the feeding behavior of the two species. Campostoma anomalum is a herbivore and would be expected to cover more area (either within of among pools) to graze than N. boops which is an insectivore that feeds on aquatic invertebrates at riffle-pool interfaces.

Pools with unfavorable conditions may act as barriers to movement just as riffles do. Unfavorable pools could be physically difficult to cross (abiotic factors), or expose individuals to predators (biotic factors). Goforth and Foltz (1998) hypothesized that reduced habitat availability in pools increased movement out of those pools by individual Notropis lutipinis. Pools 1 and 5 clearly were not favorable to C. anomalum, as only one individual was ever seen in either pool. Other authors have hypothesized that areas with high concentrations of predators could be barriers to C. anomalum (Power and Matthews 1983; Power et al. 1985) or other species in general (Cooper et al. 1990, Sih and Wooster 1994, Winemiller and Jepsen 1998). Pools 1 and 5 both had numerous predators (Micropterus sp. and large Lepomis sp.), but not unusually high densities for this reach of stream (Fig 2). Schaefer (1999b) showed that C. anomalum and N. boops had an affinity for pools (in outdoor artificial streams) with vegetative cover and avoided pools with predators (Micropterus salmoides). This indicates that inter-pool fish movement was dependant on habitat structure and quality. One would expect individuals in a low quality habitat more likely to move out of that habitat, and

individuals in high quality habitat less likely.

The model that accounted for riffle permeability and pool size (predicted) was the most accurate, indicating that both play a role in regulating dispersal. Riffle permeability seemed to have less effect on model accuracy than did pool size (Fig. 6). Models that had actual pool size (predicted, no barrier) predicted little movement by N. boops because pool 5 was the largest in the study by far (this pool was actually two separate pools in Power and Matthews 1983). Due to pool size, the rate at which fish encountered riffles in pool 5 of these models was very low, making riffle permeability less a factor. However, models that did not account for pool size (therefore making pool 5 much smaller) were by far the least accurate, and predicted an almost even distribution of N. boops among all pools after 28 days (Fig. 5). In reality, only a small area of the downstream portion of pool 5 was ever occupied by N. boops. It is not clear if the lack of movement by marked fish was due to large pool size, low riffle permeability, or simply low inherent movement rate by N. boops.

Few studies have successfully evaluated the daily movement rate of fishes between areas in streams, and tested the effects of biotic and abiotic factors. The results of my study and others suggest that some fish occupy relatively small ranges (Gerking 1959, Berra and Gunnig 1972) and only a few individuals ever move substantial distances (Schlosser, 1982, Herbold, 1984, but see Linfield 1985). Over 18 months, Freeman (1995) recaptured the majority of the tagged Percina nigrofasciata within 33 m of their original location. A few individuals however, were recorded traveling more than 100 m in just one day. It is not clear if individuals were moving daily and returning to

their “home pools”, or if there was simply very little movement. Studies of recolonization into empty areas after disturbances has shown that large numbers of individuals may recolonize patches in as little as half an hour (Peterson and Bailey, 1993), or larger reaches in weeks (Larimore et al. 1959, Matthews et al. 1987). In addition, most movement seems to be by individuals, with movement by large groups occurring less often. Displacement studies similar to this one (capturing fish from one pool, marking them, and releasing them in a different pool) would address questions about increased movement rates out of unfavorable pools and home pool affinity. Mark-resight methods could also be used to test the effects of natural disturbance on fish movement and distribution.

Acknowledgments

This paper was presented as partial fulfillment for the requirements of a Ph.D. from the Department of Zoology at the University of Oklahoma. I thank the members of my committee: Bill Matthews, Victor H. Hutchison, Bill Shelton, Larry Toothaker, Gary Welborn. I thank Keith Gido, David Lonzarich, and Mel Warren for useful input into various aspects of this project. I also thank the USDA Forest Service, University of Oklahoma Biological Station, University of Oklahoma Department of Zoology, and The University of Oklahoma Graduate Student Association for funding and supplying facilities.

Literature Cited

- Baade, U. and Fredrich, F. 1998. Movement and pattern of activity of the roach in the River Spree, Germany. *J. Fish Biol.* 52:1165-1174.
- Bart H.L. 1989. Fish habitat association in an Ozark stream. *Env. Biol. Fish.* 24 (3):173-186.
- Berra, T.M., and Gunning, G.E. 1972. Seasonal movement and home range of the longear sunfish, Lepomis megalotis (Rafinesque) in Louisiana. *Am. Midl. Nat.* 88:368-375.
- Cooper, S.D. Walde, S.J. and Peckarsky, B.L. 1990. Prey exchange rates and the impact of predators on prey populations in streams. *Ecology* 71(4):1503-1514.
- Finger, T.R. 1982. Fish community-habitat relations in a central New York stream. *J. Fresh. Ecol.* 1 4:343-352.
- Freeman, M.C. 1995. Movements by two small fishes in a large stream. *Copeia* 1995:361-367.
- Funk, J.L. 1955. Movement of stream fishes in Missouri. *Trans. Am. Fish. Soc.* 85: 39-57.
- Gelwick, F.P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. *Copeia* 1990:1072-1082.
- Gelwick, F.P. Stock, M.P. and Matthews, W.J. 1997. Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river ecosystem. *Oikos* 80:1-17.
- Gerking, S.D. 1959. The restricted movement of fish populations. *Biol. Rev.* 34:221-

- Goforth, R.R. and Foltz, J.W. 1998. Movements of the yellowfin shiner, Notropis lutipinnis. Ecol. Fw. Fish 7:49-55.
- Gowan, C. Young, M.K. Fausch, K.D. and Riley. S.C. 1994. Restricted movement in resident stream salmonids: A paradigm lost? Can. J. Fish. Aq. Sci. 51:2626-2637.
- Gowan, C. and Fausch, K.D. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Can. J. Fish. Aq. Sci. 53:1370-1381.
- Herbold, B. 1984. Structure of an Indiana stream fish association: choosing an appropriate model. Am. Nat. 124:561-572.
- Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aq. Sci. 47:635-643.
- Hill, J.A. and Grossman, G.D. 1987. Home range estimators for three North American stream fishes. Copeia 1987:376-380.
- Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 46:195-212.
- Larimore, R.W. Childers, W.F. and Heckrotte, C. 1959. Destruction and reestablishment of stream fish and invertebrates affected by drought. Trans. Am. Fish. Soc. 88:261-285.
- Linfield, R.S.J. 1985. An alternative concept to home range theory with respect to population of cyprinids in major river systems. J. Fish Biol. 27(Supplement

A):187-196.

Lotrich, V.A. and Meredith, W.H. 1974. A technique and the effectiveness of various acrylic colors for subcutaneous marking of fish. Trans. Am. Fish. Soc. 103:140-142.

Matthews, W.J. Harvey, B.C. and Power, M.E. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (USA). Env. Biol. Fish. 390:381-397.

Matthews, W.J. Stewart, A.J. and Power, M.E. 1987. Grazing fishes as components of North American stream ecosystems: Effects of Campostoma anomalum. -pg. 128-35 In: Matthews, W.J. and Heins, D.C. (eds.). Community and Evolutionary Ecology of North American Stream Fishes University of Oklahoma Press, Norman.

Power, M.E. and Matthews, W.J. 1983. Algae-grazing minnows (Camostoma anomalum), piscivorous bass (Micropterus spp.), and the distribution of attached algae in a small prairie-margin stream. Oecologia 60: 328-332.

Power, M.E. Matthews, W.J. and Stewart, A.J. 1985. Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. Ecology 66:1448-1456.

Power, M.E. 1990. Effects of fish in river food webs. Science 250:811-814.

Schaefer, J.F. 1999a. Riffles as barriers to inter-pool movement by three cyprinids (Notropis boops, Campostoma anomalum, and Cyprinella venusta). Ch. 1.

Unpublished dissertation, University of Oklahoma, Department of Zoology.

Schaefer, J.F. 1999b. Development and testing of an individual-based model of stream

- fish movement. Ch. 2. Unpublished dissertation, University of Oklahoma, Department of Zoology.
- Schlosser, I.J. 1982. Fish community structure and function along tow habitat gradients in a headwater stream. *Ecol. Mono.* 52:395-414.
- Schlosser, I.J. 1995a. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* 76:908-925.
- Schlosser, I.J. 1995b. Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* 303:71-81.
- Sih, A. and Wooster, D.E. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. *Ecology* 75:1199-1207.
- Smith, C.L. and Powell, C.R. 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. *Am. Museum Novitates.* 258:1-30.
- Thresher, R.E. and Gronell, A.M. 1978. Subcutaneous tagging of small reef fishes. *Copeia* 1978: 352-353.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts. 396 pp.
- Warren, M.L. and Pardew, M.G. 1998. Road crossings as barriers to small-stream fish movement. *Trans. Am. Fish. Soc.* 127:637-644.
- Winemiller, K.O. and Jepsen, D.B. 1998. Effects of seasonality and fish movement on tropical river food webs. *J. Fish Biol.* 53(Supplement A):267-296.

Table 1

Pool and riffle measurements that effected model parameters. For substrate types, Snd=sand, Gr=gravel, Cb=cobble, Bdr=sandstone bedrock, Bld=boulder. For vegetation, Fa = filamentous algae, Dia = diatoms. Both substrate and vegetation are listed in order of bottom coverage, and only if it covered more than an estimated 20%. Standard riffle permeabilities were 0.12 for N. boops and 0.15 for C. anomalum (Schaefer 1999a). Permeability decreased by 50% for riffle length > 10 m, Max thalweg < 8.0, and average current velocity > 10 cm/s.

Pool	Length	Max.Width	Max.Depth	SubStrate	Vegetation	Can.Cvr.
P 1	62.7 m	12.9 m	2.2 m	Gr,Cb,Bdr	Fa	65%
P 2	76.9	11.8	0.82	Cb,Bdr,Snd	Fa	40
P 3	56.6	6.2	0.39	Bdr	Dia	100
P 4	19.7	7.5	0.84	Bdr,Gr	-	10
P 5	135.0	12.1	1.40	Cb,Gr,Bdr	Fa	60
P 6	86.8	8.4	0.98	Bdr,Cb,Bld	Fa	10
P 7	79.8	10.7	0.83	Cb,Bdr	-	15
P 8	81.0	11.2	0.77	Cb,Bdr,Gr	Fa	40
P 9	22.0	13.2	0.87	Bdr,Bld,Cb	-	100

Riffles	Length Max	Width	Min - Max Thalweg	Avg Current	Permeability (<u>N. boops</u> , <u>C. anomalum</u>)
R 1-2	5.9 m	4.2 m	1.0 - 5.5* cm	11.7* cm/s	0.03, 0.038
R 2-3	24.6*	3.5	2.0 - 14.0	7.7	0.06, 0.075
R 3-4	34.0*	4.8	3.0 - 18.0	13.4*	0.03, 0.038
R 4-5	34.3*	2.3	1.5 - 12.0	9.5	0.06, 0.075
R 5-6	6.8	2.4	2.0 - 7.5*	18.0*	0.03, 0.038
R 6-7	3.8	4.6	1.5 - 4.0*	12.4*	0.03, 0.038
R 7-8	3.6	2.4	2.0 - 7.5*	17.6*	0.03, 0.038
R 8-9	4.0	4.6	1.6 - 9.5	12.3*	0.06, 0.075

* - factor reduced riffle permeability by 50%.

Table 2

Species observed, total number of individuals counted, and loadings
(=correlations with) the first two axis of the PCA. Marked N. boops and C. anomalum
were included with adults for analysis.

Species	Total Count	Axis I	Axis II
<u>Notropis boops</u>	3359	0.423	0.068
<u>Notropis boops</u> <2 cm	6545	0.234	-0.048
<u>Notropis boops</u> (marked)	362	-	-
<u>Campostoma anomalum</u>	14310	-0.147	0.172
<u>Campostoma anomalum</u> <2 cm	16210	-0.190	-0.278
<u>Campostoma anomalum</u> (marked)	191	-	-
<u>Notemigonus chrysoceph</u>	172	0.049	-0.405
<u>Lepomis megalotis</u>	1860	0.453	-0.085
<u>Lepomis macrochirus</u>	125	0.286	-0.099
<u>Lepomis humilus</u>	42	0.309	-0.180
<u>Lepomis cyanellus</u>	187	0.289	0.179
<u>Lepomis sp.</u> <2 cm	660	0.202	-0.297
<u>Micropterus salmoides</u> large	206	0.021	-0.197
<u>Micropterus salmoides</u> sm	315	-0.016	-0.204
<u>Micropterus salmoides</u> Juv	143	0.348	-0.218
<u>Moxostoma erythrurum</u> juv	519	-0.149	-0.254
<u>Moxostoma erythrurum</u> adult 230		0.172	0.250

<u>Fundulus notatus</u>	309	-0.049	-0.358
<u>Ameurus mealas</u>	67	0.148	0.374
<u>Etheostoma spectabile</u>	111	0.051	-0.173
Total	45,881		

List of Figures

Figure 1. Scatter plot of individual pools from all surveys projected onto the first two axes of the PCA.

Figure 2. Mean abundance (± 1 SE) of N. boops, C. anomalum, Lepomis sp. (age classes and species combined), and Micropterus sp. (age classes combined) for each pools over all surveys.

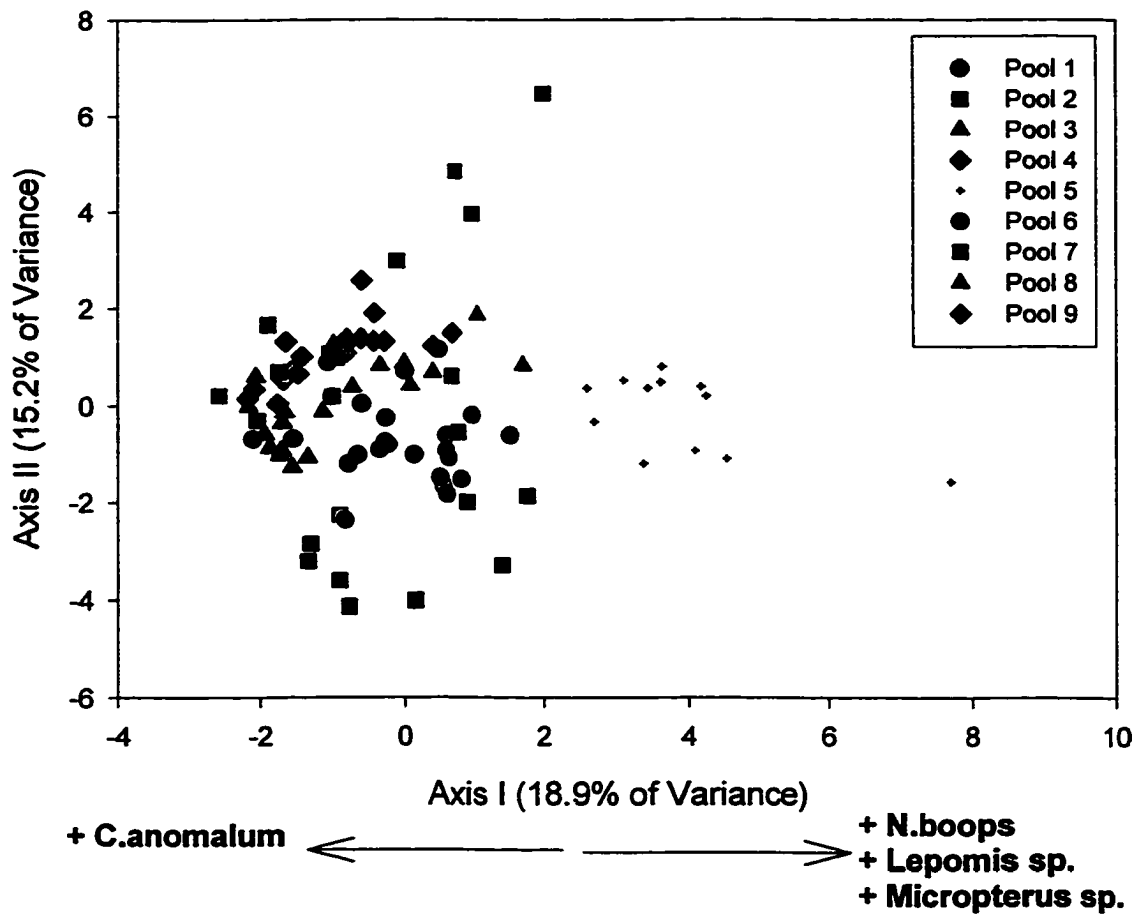
Figure 3. Percent of marked C. anomalum and N. boops fish resighted over the course of the experiment.

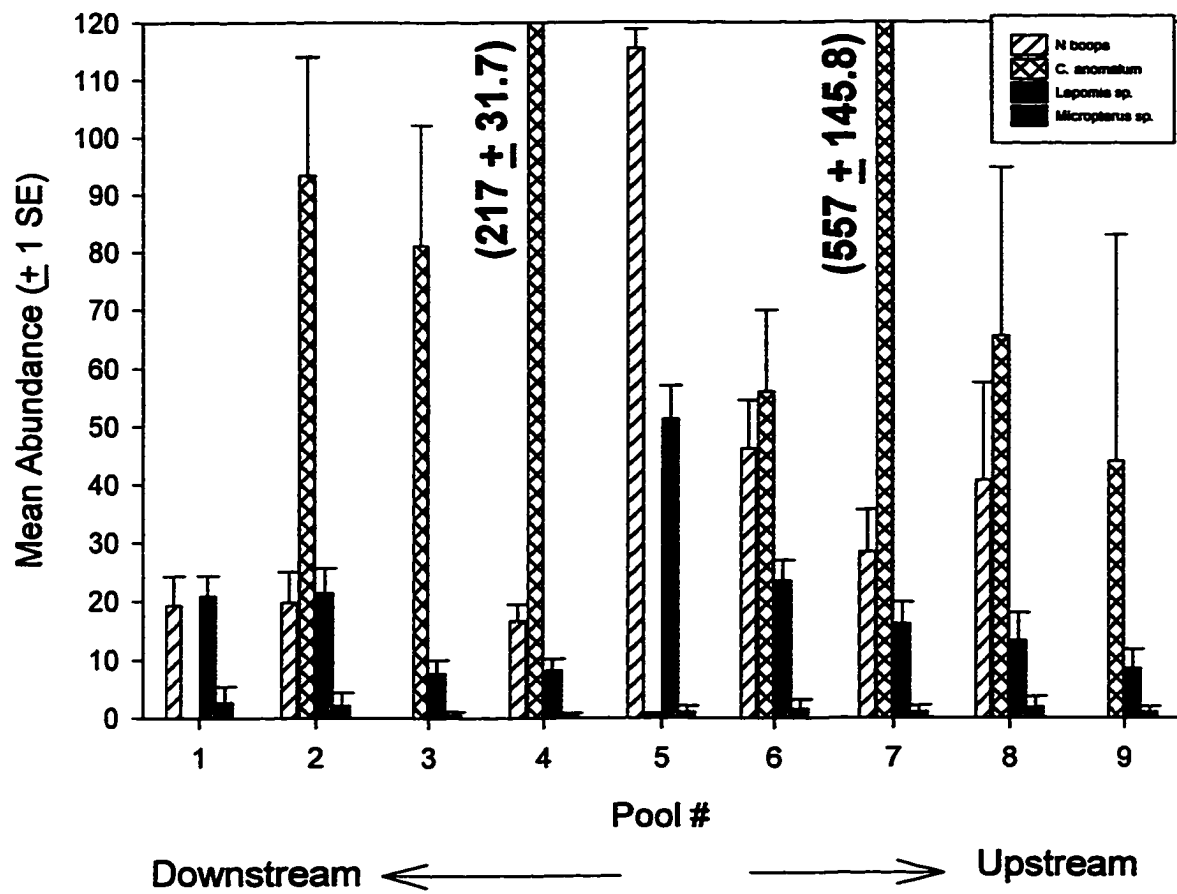
Figure 4. Percent of marked fish observed (from surveys) and expected (from predictive model, ± 1 SE) in each pool seven days after mark and release. Top pane is N. boops (2 May survey), bottom pane is C. anomalum (23 June survey).

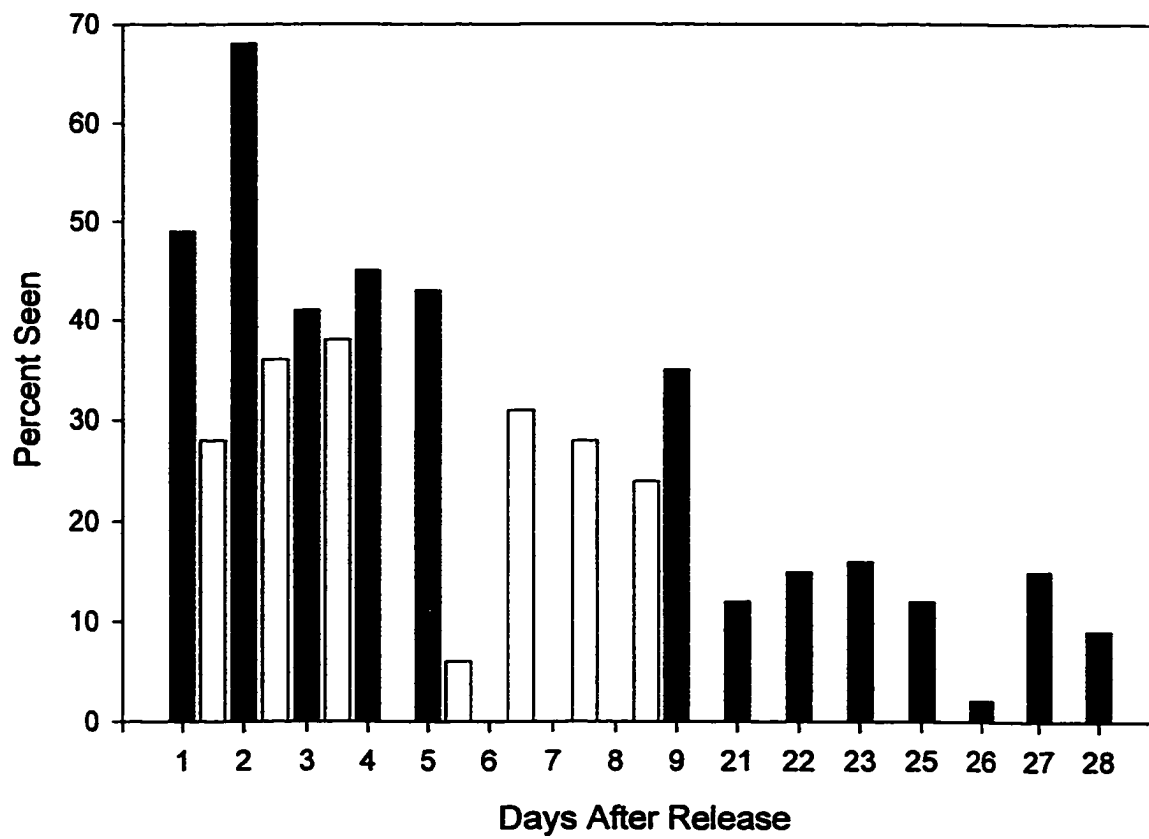
Figure 5. Percent of fish observed (from survey) and predicted from the three models (± 1 SE) on the last survey (24 June). See text and Table 3 for detailed model description. Top pane is N. boops (28 days after mark and release), bottom pane is C. anomalum (9 days after mark and release).

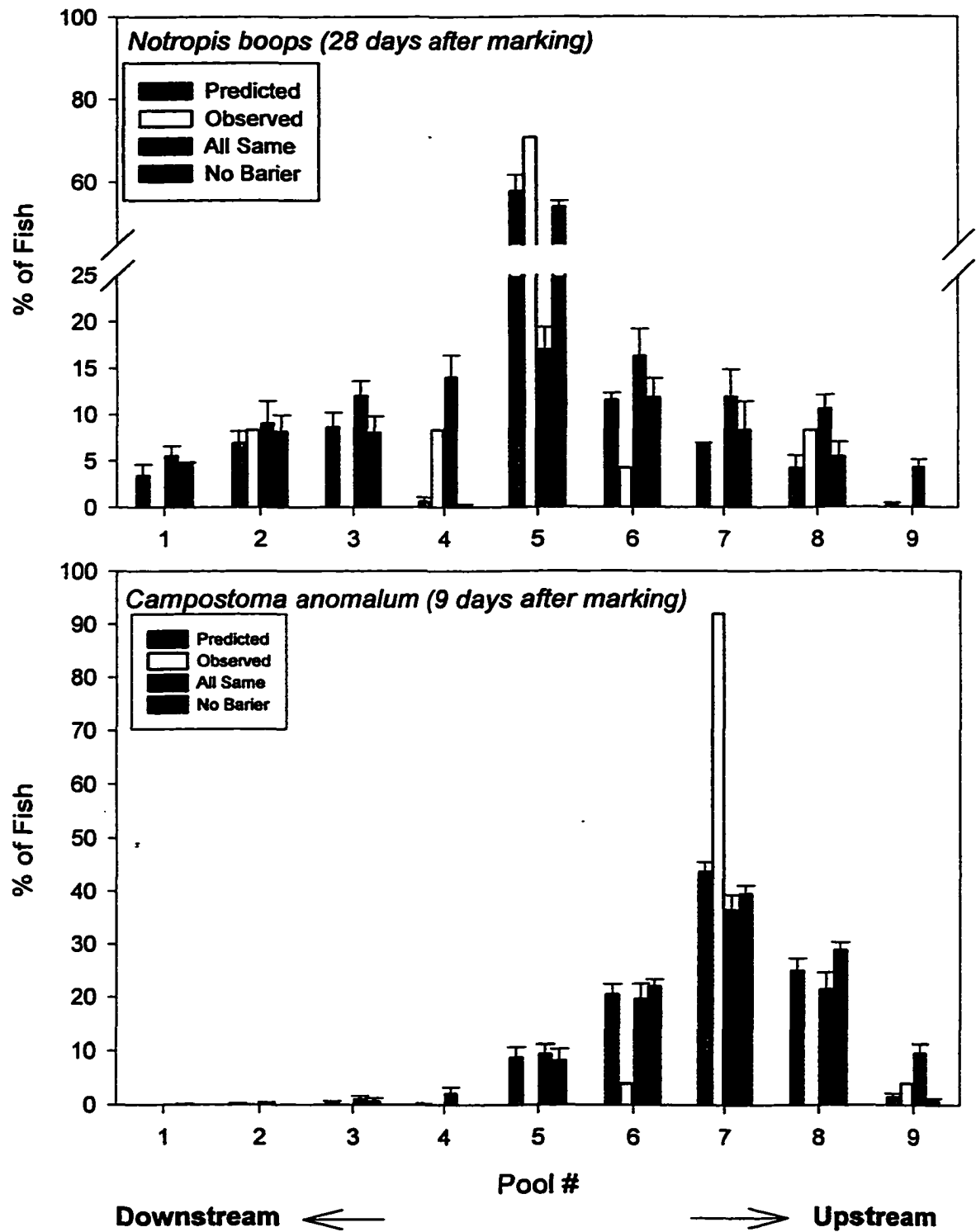
Figure 6. Model accuracy for both species 7 days after mark and release (N. boops 7,

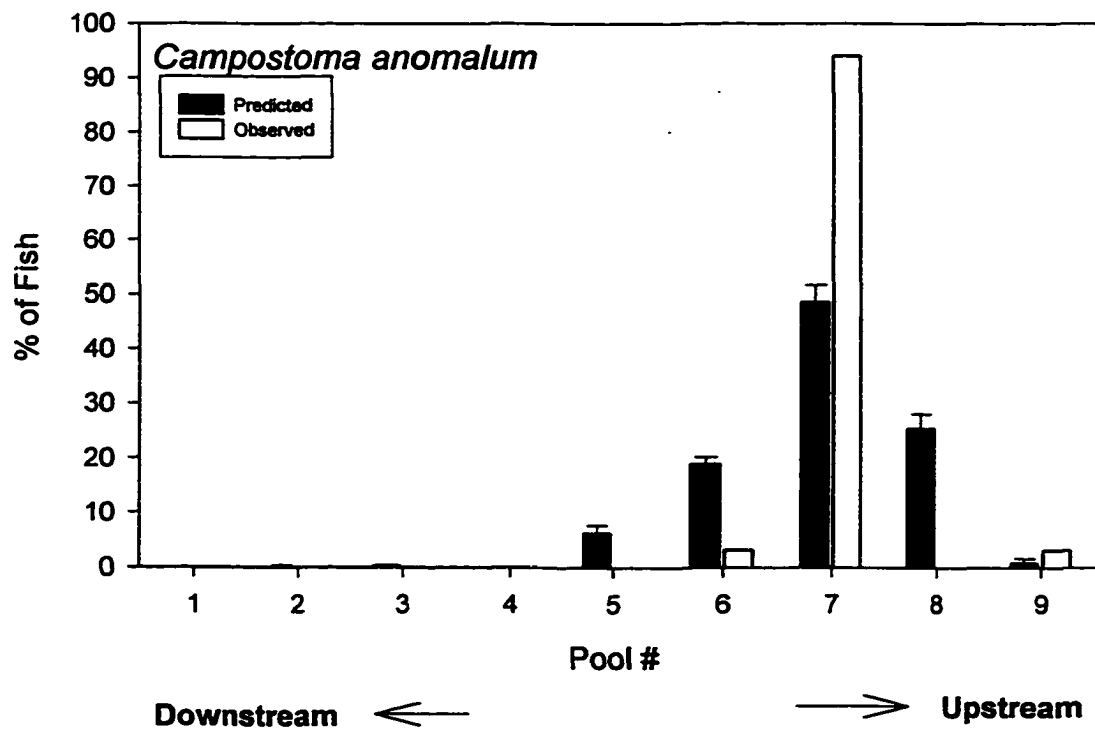
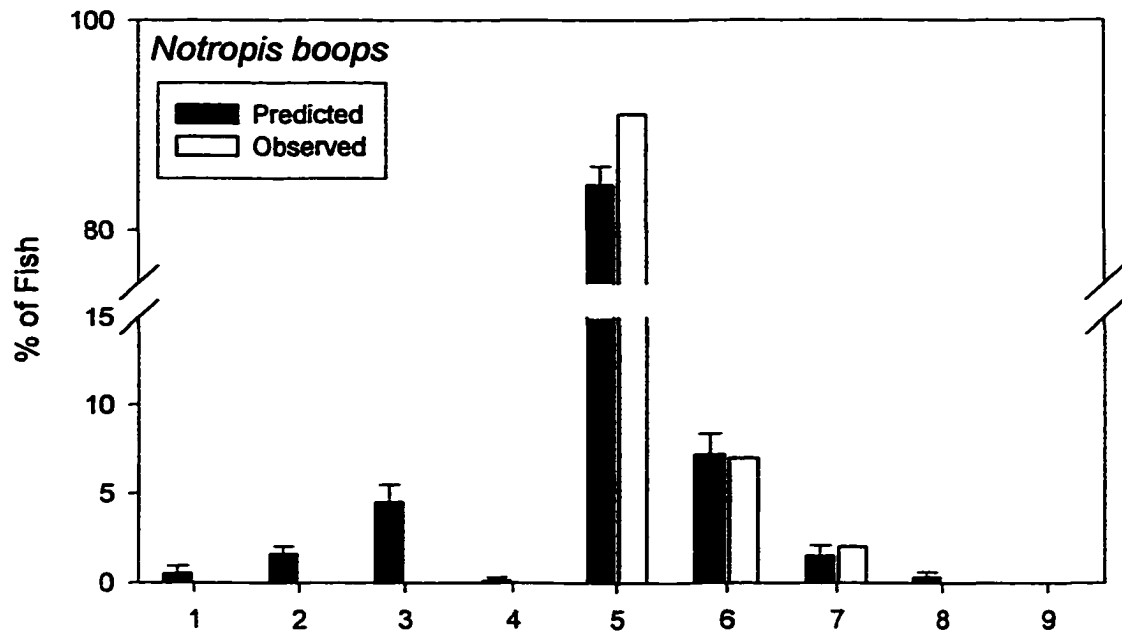
and C. anomalum 7) and on the last survey date (N. boops 7, C. anomalum 9). Model error is expressed as the percent of fish incorrectly located by a model. See text for full model descriptions.











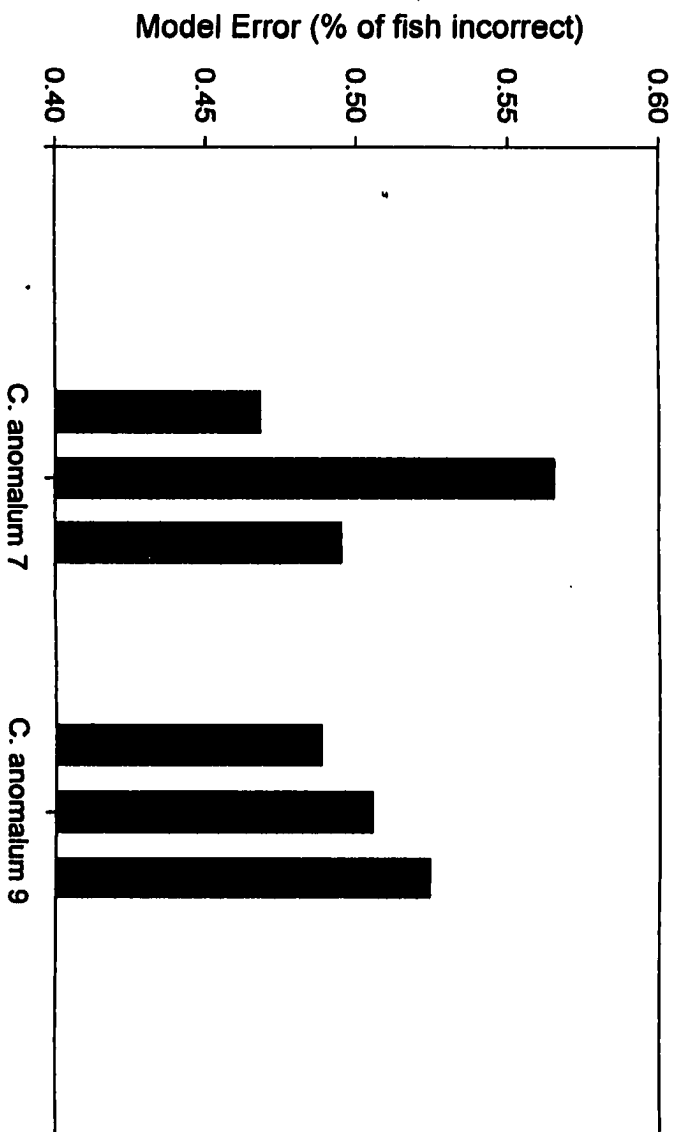
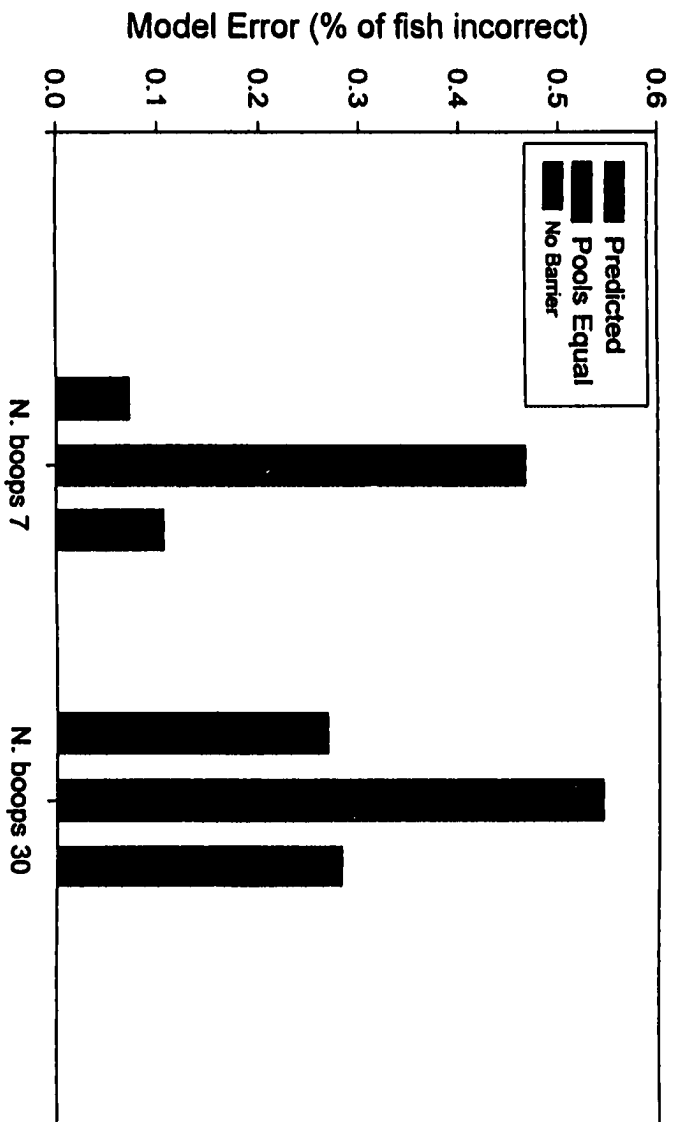
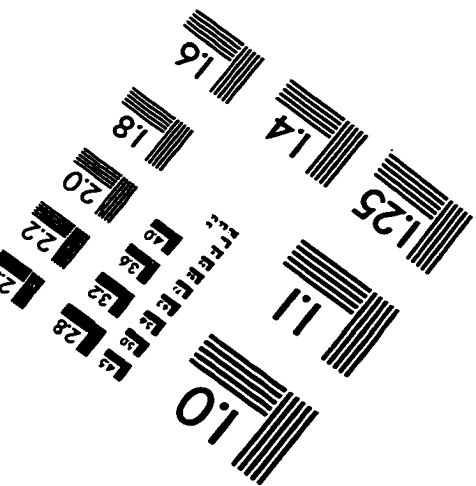
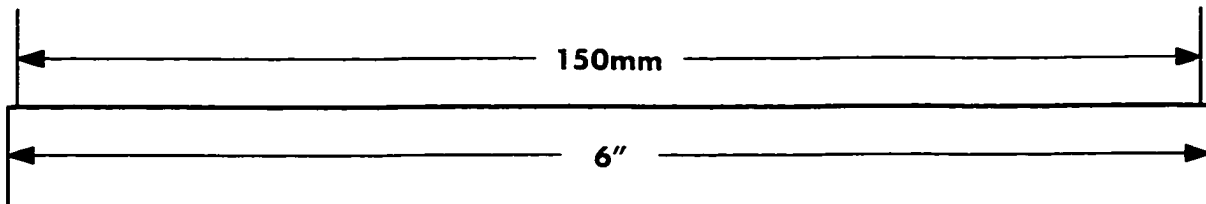
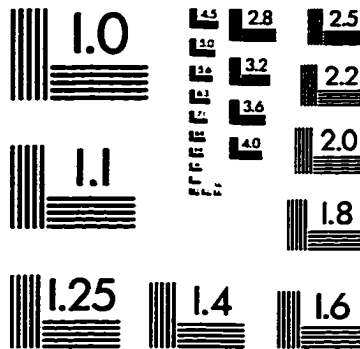
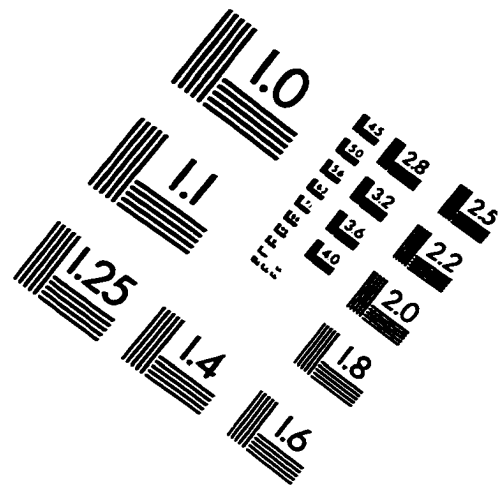
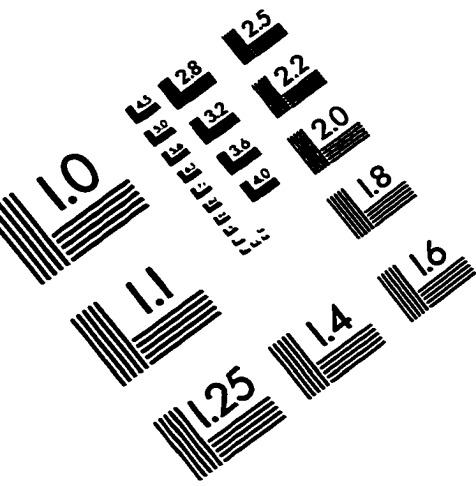


IMAGE EVALUATION TEST TARGET (QA-3)



APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved

