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DR. WILLIAM J. MATTHEWS, PRINCIPAL INVESTIGATOR

JACOB SCHAEFER, GRADUATE STUDENT

University of Oklahoma Biological Station

HC 71 Box 205

Kingston, OK 73439

# Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum* and *Cyprinella venusta*)

JACOB SCHAEFER

Department of Zoology, University of Oklahoma, Oklahoma 73019, Norman, U.S.A.

## SUMMARY

1. The effects of riffles as barriers to movement of stream fish was investigated in a set of eight large, outdoor artificial streams. Pools were 183 cm in diameter and 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<sup>-1</sup>), 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 cameras were used to quantify movement rate.

2. Mean movement rate (percentage of fish crossing a riffle each 30 min) was 18.1% at 0 cm s<sup>-1</sup> and only 1.8 at 45 cm s<sup>-1</sup>. Movement rate was 7.2% with no predators present and 20.2% with caged 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.

3. Overall biotic and abiotic factors in these artificial streams do influence movement rates and may affect movement among pools in natural streams.

*Keywords:* barrier, Cyprinidae, dispersal, fish movement, stream

## Introduction

Movement between habitats is essential in the life history of many stream fish (Schlosser, 1995a). In stream systems, species abundance can be influenced greatly by the boundaries between habitats and the effect these boundaries have on dispersal (Dunning, Danielson & Pulliam, 1992). Many stream fish mostly occur in pool habitats and movement between pools may be restricted by barriers (riffles) between pools. As a result, some stream (e.g. small intermittent streams) pools and pool fish assemblages are viewed

as discrete units (Capone & Kushlan, 1991; Matthews, Harvey & Power, 1994; Taylor, 1997, 2000). The ability of species to move throughout a stream reach is important for populations in patchy environments (Sheldon & Meffe, 1994; Garrick & Gilliam, 2000). 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 & Kordic-Brown, 1977).

Peterson & Bailey (1993) observed partial recolonization in streams by cyprinids (Cyprinidae) from 30 min to 5.8 days after a disturbance. Meffe & Sheldon (1990) eliminated fish from the reaches of a stream and found pool assemblages returned to

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Correspondence: Jacob Schaefer, Department of Biology, Southern Illinois University at Edwardsville, Edwardsville, IL 62026, U.S.A.

E-mail: jschaefer@ou.edu

predisturbance states within 1 year, however, short-term dispersal rates were not assessed. In a similar study (Sheldon & Meffe, 1994) 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 predisturbed states, indicating that dispersal ability may be affected by the physical structure of the stream and other potential isolating factors (Meffe & Sheldon, 1990). Matthews *et al.* (1987) showed rapid (within weeks) recolonization of recently rewatered stream reaches in Brier Creek (Oklahoma). Exchange of individuals with source populations was slower in pools isolated by distance or restricted flow (Taylor, 1997; Lonzarich *et al.*, 1998). Physical properties of riffles also affect rate of movement of fish between pools with shallower, longer and faster-flowing riffles restricting dispersal of fish among pools (Warren & Pardew, 1998).

The restricted movement paradigm (Gerking, 1953, 1959; Gowan *et al.*, 1994; Smithson & Johnston, 1999) 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 (Grossman *et al.*, 1985; Hill & Grossman, 1987; Goforth & Foltz, 1998); most work has focused on large game species (centrarchids and salmonids) and larger temporal (weeks or months) or spatial (larger than individual pools) scales. For several species (*Cottus bairdi*, *Rhinichthys cataractae*, *Clinostomus funduloides*, *Percina nigrofasciata* and *Lepomis auritus*), most of the recovered marked individuals were captured within 10–30 m of release points over 6–18-month periods (Hill & Grossman, 1987; Freeman, 1995), indicating limited movement rates within home ranges. Whereas most individuals may stay in one area, there is evidence that a small portion of individuals move long distances (Freeman, 1995; Smithson & Johnston, 1999; Garrick & Gilliam, 2000). Other studies have indicated that movement rates of some fish may be higher than previously thought (Gowan *et al.*, 1994; Warren & Pardew, 1998). Goforth & 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. 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 through

areas with predators (Fraser, Gilliam & Yip-Hoi, 1995). *Camptostoma anomalum* quickly move among pools or shift habitat use from pool centres to pool edges to avoid predators (Power & Matthews, 1983; Power, Matthews & Stewart, 1985). Both abiotic (e.g. pool and riffle size) and biotic (e.g. predation pressure or density of competitors) factors may influence the movement rate of fishes at the scale of individual pools. Thus, quantification of these effects may help explain some of the dynamic processes (e.g. predator–prey interactions, coexistence of competitors) that regulate fish assemblage structure in streams (Garrick & Gilliam, 2000).

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

## Methods

### Experimental streams

Experimental streams were located at the University of Oklahoma Biological Station. These streams have been used in previous experiments with various cyprinids that were observed to behave and reproduce normally (Gelwick & Matthews, 1993; Gido *et al.*, 1999). All three species used in these trials behaved normally and reproduced in the streams. All juveniles recruited into the streams were removed by seining. 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). One to three (depending on treatment) 0.25 hp pumps circulated water from the downstream footbox to upstream pool headbox. Plastic mesh (0.5 cm) prevented movement of adult fish into headbox or footbox. 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 some large stones (taken from a local stream), and was sculpted to form concave pool bottoms and riffles to

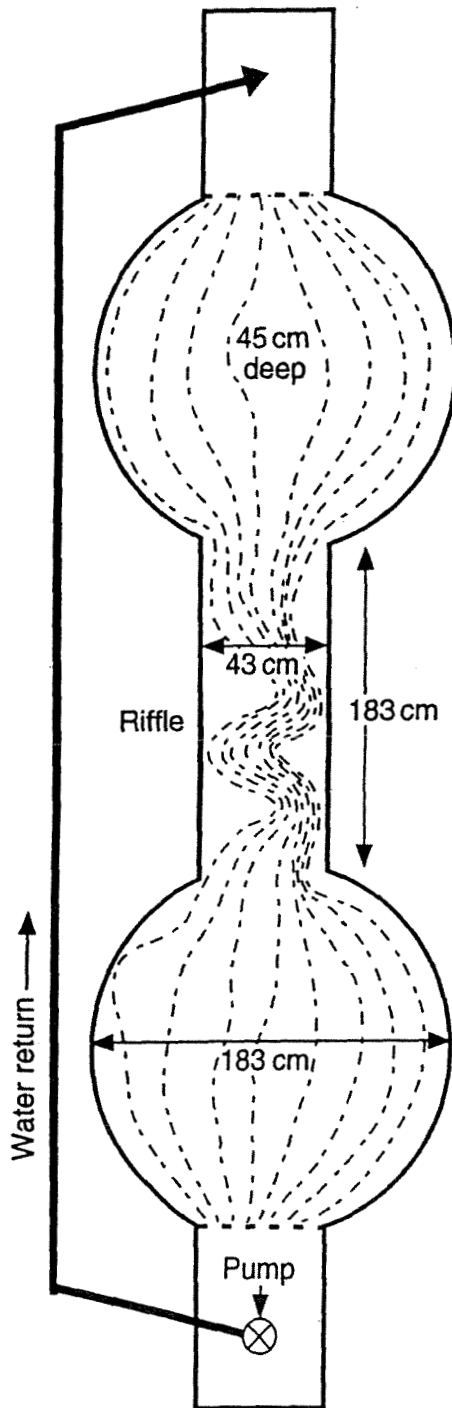


Fig. 1 Diagram of one artificial stream unit used in these experiments. Eight identical units were used.

mimic natural streams. Because streams were outdoors and uncovered they were subjected to ambient light, temperature and colonization by winged insects and their larvae (mostly dipterans). Other allochtho-

nous material (mostly insects and leaves) commonly entered the streams. Macrophytes colonized the streams and were reduced regularly to increase accuracy of visual counts. Invertebrate and plant communities in these streams are similar in both density and diversity to those found in local streams (Matthews and Gido, personal com.). I seined adult fish (>50 mm SL) for these trials from Brier Creek (*C. anomalum* Rafinesque and *Notropis boops* Gilbert) (Marshall Co., Oklahoma), and Pennington Creek (*Cyprinella venusta* Girard) (Johnson Co., Oklahoma). All trials were conducted from March to September of 1996, 1997 and 1998.

#### Measuring movement rate

I measured movement rates of *C. anomalum* (central stoneroller), *C. venusta* (blackspot shiner) and *N. boops* (bigeye shiner) at four current velocities (0, 15, 30 and 45 cm s<sup>-1</sup>), three riffle thalweg depths (10, 50 and 100 mm), two riffle lengths (183 and 549 cm), and with a predator (200–250 mm SL largemouth bass, *Micropterus salmoides* Lacepede) present in both pools. The thalweg depths, riffle lengths and current velocities used are within the range of values seen in local streams. In a 1K stretch of Brier Creek (Marshall Co., OK) nine riffles ranged in thalweg depth from 10 to 180 mm, mean current velocity from 7.7 to 18 cm s<sup>-1</sup> and riffle length from 3.6 to 34.3 m. Normal riffle conditions were defined as: 15 cm s<sup>-1</sup> current velocity, 50 mm thalweg depth 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<sup>-1</sup> 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<sup>-1</sup> 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 centre of both pools in a stream unit.

Predators 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) (3) with one predator in each cage.

I used two methods to measure movement rate: visual counts and video trials using a standard video camera. For visual counts, 12–15 individuals of one species were placed in an experimental stream unit and the number of fish in the upstream and downstream pools were counted every 30 min from 8:00 to 16:00 hours. These fish densities were supported by the system with no additional feeding, allowed accurate visual counts in pools (too many fish would complicate counts), and were within the range of densities seen in natural streams. On average, 95% of fish in an artificial stream were seen during a visual count. Treatments were assigned randomly among days so that all stream units were observed under all conditions for 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). Movement rate was defined as the percentage of fish that crossed a riffle every 30 min. For analysis, the mean movement rate for each 8-h period (16 observations) was used. For each species-treatment combination there were 7 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 velocities increased turbidity and did not allow accurate visual counts through windows in the pools), when stream alterations for a treatment (long riffles and shallow riffles) could only be made to one artificial stream unit and to confirm the accuracy (normal riffles) of the visual count method described above. For video trials, a video camera was mounted above the riffle so that it recorded any movement in the riffle. For each trial, 30 min of video was recorded in real time. 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 a riffle and returned to the original pool) that could not be gathered by visual counts. Each species-treatment combination was video taped for eight randomly selected 30-min periods between 8:00 and 16:00 hours over a 4-day period (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 s of each other). A turnaround event occurred when a fish was observed passing through the field of view (approximately 40 cm stretch of riffle) in one direction and then passing the opposite direction within 10 s, 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 each 30 min. Video trials were used for the 45 cm s<sup>-1</sup> 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 of the three sets of normal trials were also conducted with 12–15 individuals of all three species combined (Table 1). See Table 1 for a summary of all observation methods and riffle conditions 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 example, comparing 183 cm riffle length trials (12–15 fish of one species) to 50 mm thalweg depth trials (12–15 of each species) tested for density effects of movement.

#### *Statistical analysis*

For both methods, I calculated a final rate of movement (percentage of fish crossing 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. The Games–Howell multiple comparison procedure is designed to control error rate when sample sizes are <15 (Toothaker, 1993). Group size (using Dunnett multiple comparison procedure) and turnaround rate (using non-parametric Mann–Whitney *U*) under normal conditions were compared with rates in trials

**Table 1** Treatments and method of data collection used to determine movement rates. Count = visual count method, Video = video taping method. Count + video = both techniques used in independent trials. If alone, 12–15 individuals of a species were used, if combined there were 12–15 individuals of each species

	<i>Notropis boops</i>	<i>Camptostoma anomalum</i>	<i>Cyprinella venusta</i>
Thalweg depth trials (mm)			
10 (shallow)	All species combined, video		
50 (normal)	Count + video	Count + video	Count + video
100	Count	Count	Count
Riffle velocity trials ( $\text{cm s}^{-1}$ )			
0	Count	Count	Count
15 (normal)	Count + video	Count + video	Count + video
30	Count	Count	Count
45 (fast)	All species combined, video		
Riffle length trials (cm)			
183 (normal)	All species combined, video		
549 (long)	All species combined, video		
Predation trials			
None (normal)	Count + video	Count + video	Count + video
None (empty cage)	Video	Video	Video
1 per pool (caged)	Video	Video	Video

with predators, shallow, long and fast conditions. The Dunnnett multiple comparison procedure designed to control error rates when comparing all treatments to one control (Toothaker, 1993). To test for directional bias (upstream versus 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. Only the first movement of a trial was used for this analysis as these are closed systems and any subsequent movement would not be independent of the first movement.

## 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 methods (video versus count for 50 mm thalweg, 15  $\text{cm s}^{-1}$  velocity and no predator or cage; Table 1) as well as for possible density effects (183 cm long versus 50 mm thalweg depth). 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 ( $10.2 \pm 1.0$  SE for visual count;  $7.2 \pm 1.6$  SE for video). Comparison of movement rate across normal riffles with 15 of each species combined and normal riffles with 15 of each species individually allowed me to test for an effect of density. Movement

rate at high density ( $15.3 \pm 3.2$  SE) was not significantly ( $t = 1.02$ ,  $P = 0.31$ , d.f. = 34) different from that at low density ( $11.9 \pm 1.6$  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. 2A). Mean movement rate for all species pooled dropped from 18.1 ( $\pm 1.2$  SE) at 0  $\text{cm s}^{-1}$  to 1.8 ( $\pm 1.2$  SE) in fast riffles. Movement rate at 15  $\text{cm s}^{-1}$  ( $11.5 \pm 1.1$  SE) was significantly lower ( $t = 3.05$ ,  $P = 0.005$ , d.f. = 13) than at 0  $\text{cm s}^{-1}$  ( $18.1 \pm 1.9$  SE), and higher ( $t = 7.34$ ,  $P < 0.001$ , d.f. = 13) than at 45  $\text{cm s}^{-1}$  ( $1.9 \pm 1.2$  SE), but not significantly different ( $t = 1.26$ ,  $P = 0.75$ , d.f. = 13) from 30  $\text{cm s}^{-1}$  ( $9.7 \pm 1.2$  SE). For 0, 15 and 30  $\text{cm s}^{-1}$  trials combined, *N. boops* ( $7.44 \pm 1.8$  SE) moved significantly less ( $t = 3.46$ ,  $P = 0.001$ , d.f. = 54) than *C. anomalum* ( $17.2 \pm 1.8$  SE) and *C. venusta* ( $t = 3.44$ ,  $P = 0.001$ , d.f. = 54, mean =  $17.0 \pm 1.7$  SE), and there was no significant difference in movement rate between *C. anomalum* and *C. venusta* (Fig. 2A).

### *Thalweg depth*

With current velocity held constant, thalweg depth did not have a significant effect ( $F = 1.73$ ,  $P = 0.20$ ,

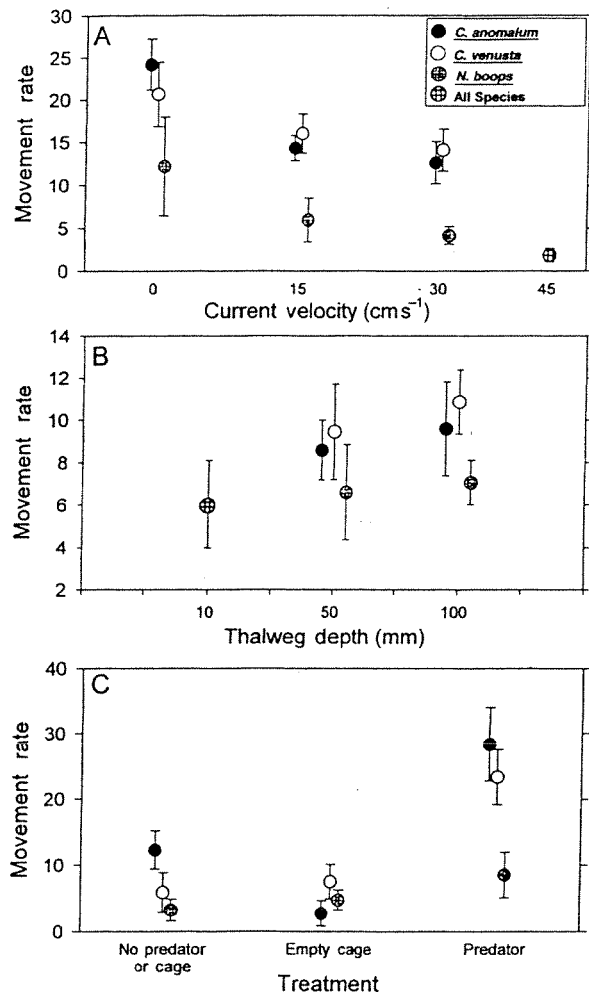


Fig. 2 Rate of movement (percentage of fish crossing riffle in 30 min) for all three species at four current velocities (A), three thalweg depths (B) and under the threat of predation (C). The first three velocities were tested for individual species by visual observation ( $n = 7$  for each species-treatment combination), 'fast' trials were for all three species combined using video tape ( $n = 8$ ). The last two thalweg depths were tested for individual species by visual observation ( $n = 7$  for each species-treatment combination), shallow trials were for all three species combined using video tape ( $n = 8$ ). Threat of predation trials were with no predators or cages, empty cages, and with predators in cages ( $n = 8$  for each species-treatment combination). Error bars represent  $\pm 1$  SE.

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. 2B). There were no significant differences in movement rates between species at any given thalweg depth (Fig. 2B).

### 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 ( $3.2 \pm 1.1$  SE) was less than one-fourth the rate across normal (183 cm) riffles ( $13.9 \pm 4.4$  SE). For riffle length trials, all species were combined in one treatment, so species differences could not be tested.

### Predation pressure

With current velocity and thalweg depth held constant, movement rate with predators present ( $20.2 \pm 3.1$  SE) was significantly greater ( $F = 19.1$ ,  $P < 0.001$ , d.f. = 2,63) than movement without predators ( $7.2 \pm 1.6$  SE) (Fig. 2C). There was no difference ( $t = 1.31$ ,  $P = 0.543$ , d.f. = 4.7) between trials with empty cages ( $5.0 \pm 1.2$  SE) and trials without cages ( $7.2 \pm 1.6$  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. *Camptostoma 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). *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 282 crossing events observed on video tape, 84.8% were single fish, 12.4% were two fish and 1.4% were groups of three. There were two occasions when a group of four was observed and the largest groups seen were one group of six *C. anomalum* with caged 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 1.2 ( $\pm 0.1$  SE). Group size was significantly larger ( $t = 2.14$ ,  $P = 0.03$ , d.f. = 18, mean =  $1.32 \pm 0.13$  SE) for predation trials than for trials under normal ( $1.1 \pm 0.04$  SE) conditions (Fig. 3). 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% ( $\pm 3.6$  SE), and only turnaround rate during predation trials ( $26.6\% \pm 10.9$  SE) was significantly

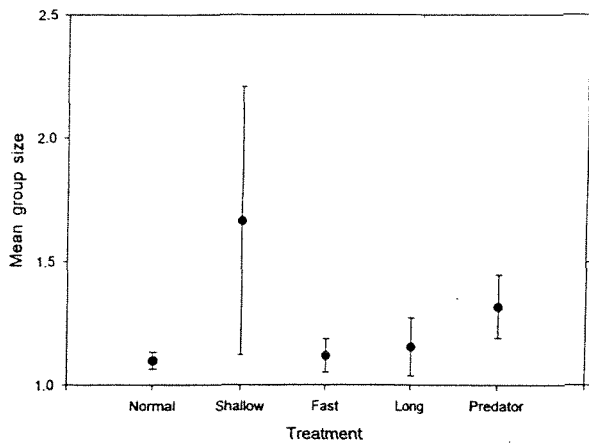


Fig. 3 Mean group size ( $\pm$  SE) for each of the treatments for all species pooled.

( $U = 9.0$ ,  $P = 0.03$ , d.f. = 16) greater than in normal trials ( $3.0\% \pm 3.0$  SE). Turnaround rates for fast riffles ( $16.4\% \pm 11.8$  SE), shallow riffles ( $12.2\% \pm 5.0$  SE), long riffles ( $26.7\% \pm 19.5$  SE), and trials with empty predator cages ( $9.0\% \pm 5.8$  SE) were not significantly greater than in normal trials (Fig. 4).

#### 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 and 45  $\text{cm s}^{-1}$  combined), but these differences were not significant.

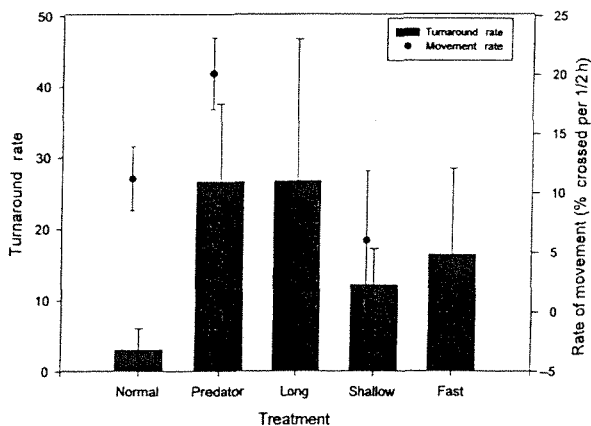


Fig. 4 Turnaround rate (bars) and rate of movement (closed circles,  $\pm$  SE) for each of the video-taped treatments for all species pooled.

## Discussion

The streams used in these experiments mimic natural streams in many ways, with realistic structure, substrate, depth and current speed. These same artificial streams (Gelwick & Matthews, 1993; Gido *et al.*, 1999) and artificial streams in general (e.g. Fraser & Cerri, 1982; Schlosser, 1989) have proved useful in testing theories in stream ecology. The use of artificial streams allowed me to measure accurately movement rate across riffles while controlling many extraneous variables. 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 more than 50 fish year around, not including yearly juvenile recruitment. Movement rate at higher densities ( $15.3 \pm 2.6$  SE) was not different from movement at lower densities ( $11.5 \pm 1.2$  SE) under normal riffle conditions. Increasing density 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 & Gilliam (1995) found that in a patchy habitat fish dispersed to areas with higher potential energetic gain because of 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 versus downstream) was also difficult. For this analysis, only the first recorded movement in each trial was used. Any movement after the first would be dependent 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, 1995b). Current velocity, riffle length and predation threat 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, Walde, & Peckarsky, 1990; Sih & 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 rates 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 although schooling behaviour was commonly observed within pools. Small group size in riffle crossings supports the idea that most of the 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. Bass 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.

One might 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, Matthews *et al.* (1994) found higher within-pool variance over time for numbers of cyprinids than for centrarchids, indicating more interpool movement by the former. 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 midsummer 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. Taylor (1997) found that 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. The results of my study indicated that dispersal rates are affected not only by distance to a source, but also 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. Using modelling techniques, this type of movement data 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.

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