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dissertation entitled

SIZE RELATED HABITAT USE IN A RIFFLE DWELLING FISH:
THE LONGNOSE DACE (RHINICHTHYS CATARACTAE)

presented by

DENNIS MICHAEL MULLEN

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in ZOOLOGY

Thomas M. Burton
Major professor

Date 5/10/91

SIZE RELATED HABITAT USE IN A RIFFLE DWELLING FISH: THE LONGNOSE DACE (RHINICHTHYS CATARACTAE)

By

Dennis Michael Mullen

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Zoology

1991

ABSTRACT

SIZE RELATED HABITAT USE IN A RIFFLE DWELLING FISH: THE LONGNOSE DACE (*RHINICHTHYS CATARACTAE*)

By

Dennis Michael Mullen

Most fish in mid-order streams exhibit across-habitat size specific habitat segregation. Usually, smaller fish are found in shallow areas, while larger fish are found in pools. While several studies have examined the factors that cause this pattern, little attention has been paid to the patterns of size specific habitat use of fish within one habitat type. The purpose of this study was to examine the extent and cause(s) of size specific habitat use (within one habitat type) in a common riffle dwelling fish: the longnose dace (*Rhinichthys cataractae*).

A survey of the habitat use patterns of juvenile and adult dace (in the Ford river system in Dickinson County, Michigan), using kick seining and electrofishing, indicated that adult dace use faster, deeper areas of riffles and larger substrates than juveniles (< 67 mm Tl). Habitat choice experiments conducted in a multiple habitat maze indicated that dace > 55 mm Tl prefer faster areas in the absence of other fish, and dace < 55 mm Tl prefer slower areas. A laboratory flow chamber, used to determine maximum swimming velocities of dace, indicated that dace < 55 mm Tl were unable to swim faster than 40 cm/sec and were, therefore, excluded from faster areas of riffles. Instream

cages, with only one shelter, were used to examine the effect of adult dace on the shelter use of juveniles (> 55 mm Tl). With adults present, juveniles used the shelter significantly less than they did when the adults were absent.

Manipulations of adult densities in enclosed riffles were used to examine the effect of adults on the habitat use of juveniles, over the first two years of their life. Juvenile habitat use was not affected by adults densities until they reached a size of 60 mm Tl. After that size, the juveniles responded to reductions in adult densities by moving into the faster areas. Adult density manipulations had no effect on the depth or substrate use of the juveniles.

The pattern of size specific velocity segregation exhibited by longnose dace appears to result from a combination of physical constraints and intra-specific competition, acting sequentially as longnose dace grow.

To Susan; my inspiration when I needed it most

ACKNOWLEDGMENTS

My appreciation is extended to the members of my advisory committee; Dr. Thomas Burton, Dr. William Cooper, Dr. Donald Hall and Dr. William Taylor, for their, patience and advice over the course of this study. Dr. Thomas Burton, Sue Eggert and Steve Mero deserve special thanks for their advice, invaluable assistance and patience during the field portions of this study. I would also like to thank the following for their field assistance and advice; Dr. Jean Stout, Deborah Repert, Bob Stelzer, Mike O'Malley, Steve Marod and Natalie Briethaupt.

My parents; Mike and Shirley Mullen, have been my major source of support and motivation throughout my career. Without their love, none of this would be possible.

This rersearch was funded by; An American Museum of Natural History: Theodore Roosevelt Grant and a Michigan Polar-Equator Club Research Grant. Logistical support was provided by a U.S. Navy grant to Dr. Thomas Burton.

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INTRODUCTION

All animals exhibit some degree of habitat selection over the course of their lives. Many motile animals exhibit specific patterns of habitat selection that occur on both small scales (daily or seasonal patterns) and large scales (ontogenetic patterns). Daily patterns of habitat selection involve movements between feeding and resting/shelter habitats (eg. diel offshore movements for foraging by the golden shiner (Notomigonus crysoleucas) (Hall et. al. 1979)), while seasonal patterns are usually associated with reproduction (eg. seasonal waterfowl migrations). Ontogenetic patterns are innate patterns of habitat selection that are usually associated with age/size or developmental stage (eg. aquatic and terrestrial phases in the life cycles of many species of amphibians) (see Werner and Gilliam (1984) for a review of ontogenetic niche shifts).

The choice of a habitat and the timing of habitat shifts can be affected by many factors, including; foraging returns, predation risk, inter-specific competition, intra-specific competition and physical constraints and/or requirements. Foraging returns have been shown to affect the habitat choice, and behavior within a habitat, of many organisms. In the absence of predators, bluegill sunfish (Lepomis macrochirus) of all sizes foraged according to the predictions of the optimal foraging model, switching habitats when one habitat became more profitable than the other habitats (Werner et. al. 1983a). When predators (largemouth bass: Micropterus salmoides) were added to the system, however, small bluegills tended to restrict their habitat use to the protected, vegetated areas near the shores of the experimental pond (Werner et. al. 1983b). Juvenile aquatic insects (Notonecta hoffmanni) altered their pattern of habitat use in the presence of predatory adults of the same species (Sih 1982). When predatory adults were present, the small juveniles used the food rich habitat (pool center) less than they did when the adults were absent. Larger juveniles remained in the center of the pools with the adults present, but altered their behavior by reducing the amount of movement and, therefore, the amount of prey captured, while foraging.

Habitat choice may also be a function of the physical requirements of the individual or species. Many species of fish are stenothermal and only exist in areas that fall within the range of thermal tolerance exhibited by that species. This may be one of the factors behind non-reproductive seasonal migrations in stream fishes. Brook trout (Salvelinus fontinalis) in two Ontario streams moved upstream as the temperatures in the downstream areas reached 24° C (near the lethal temperature of the species) (Meisner 1990).

Inter-specific and intra-specific competition may also affect habitat use. In the face of competition with riffle sculpin (Cottus gulosus), speckled dace (Rhinichthys osculus) forages in stream margins, but, when sculpin are not present, due to high temperatures, the dace utilize the riffle habitats (Baltz et. al. 1982). Territorial juvenile coho salmon (Oncorhynchus kisutch) actively chase other juveniles of the same species out of their feeding territories in stream riffles (Puckett and Dill 1985). When territories are limiting, the juveniles that are not able to hold a territory adopt alternate strategies. These fish either move into pools to forage, or exist in the riffles by moving between the territories of the dominant juveniles. In either case, intra-specific competition is forcing some members of the population to utilize a different habitat or to alter their behavior within a habitat.

A common result of predation risk, inter-specific and intra-specific competition is size related habitat segregation. Many species of stream fishes segregate the local habitat according to size, with smaller fish occurring in areas not occupied by larger individuals of the same species (Mahon and Portt 1985, Power 1984, 1987 and Schlosser 1987). In most cases, the larger species, or individuals, occur in the pools, while the smaller species or individuals occur in the shallow areas or riffles. Smaller fish either, are not able to compete with the larger fish for space in the pools or, use the shallow areas as a refuge from the predators found in the pools. In some cases, the smaller fish will use the pools when the larger fish are absent (Power and Mathews 1983). Larger fish, on the other hand, may avoid the shallow areas due to a high predation risk from avian or terrestrial predators (Power 1987).

Size related habitat segregation may also be produced by size related energetics. Smaller fish may not be able to cope with the rigors of the adult habitat (especially in the case of riffle dwelling fishes). As the profitability of a habitat is measured in terms of energy gained per energy expended while foraging, the profitability of a habitat is as much a function of the physical nature of the habitat as it is a function of prey quality and availability. The ability of an organism to utilize a habitat may be strongly influenced by physical factors such as temperature and current.

Many species of stream fishes exhibit morphological adaptations to the riffle habitat (Hynes 1970). Bottom dwelling riffle fish tend to be dorsal-ventrally flattened with subterminal mouths for picking food off of the bottom. The swimbladders of riffle dwelling fish may be reduced in size (Gee 1968). Most species of riffle dwelling fish start life in the stream margins and undergo an ontogenetic shift into the riffle habitat as they grow. These fish may also undergo a morphometric (shape) change that adapts them to the riffle habitat as they grow. If so, the timing and rate of shape change may affect the ability of these fish to use the riffle habitat.

Size related habitat segregation by stream fishes is a fairly ubiquitous phenomenon in mid-sized streams throughout North America (Mahon and Portt 1985), and has been well studied (Power 1984, 1987, Power et. al. 1985, Schlosser 1987, 1988a and 1988b). Little attention, however has been paid to the patterns of size related habitat use within a specific habitat type, especially within the riffle habitat. Since the riffles serve as a refuge for the smaller individuals of pool dwelling species, as well as the permanent habitat of all sizes of riffle dwelling species, there is a potential for strong inter and intra-specific interactions within the riffle habitat. The purpose of the studies reported here was to examine the nature, degree and cause(s) of size related habitat segregation within the riffle habitat. Specifically, this study examined the pattern of size related habitat use by the longnose dace (Cyprinidae: Rhinichthys cataractae Valenciennes).

The longnose dace is a ubiquitous stream minnow that utilizes quiet stream margins for the first few weeks of life and moves into stream riffles as it grows. Adult longnose dace spawn in riffles during early summer when the daily maximum temperature exceeds 15° C (Bartnik 1970). The fry emerge during mid-summer and recruit into the stream margins. They remain there for several weeks and move into the riffles in mid to late August. There is some evidence to suggest that the timing of the habitat shift into the riffles is affected by competition with blacknose dace (Rhinichthys atratulus) fry (Gibbons and Gee 1972, Gee 1972). After moving into the riffle habitat, the longnose dace tend to move into areas of faster water as they grow (Gibbons and Gee 1972). The result is size related partitioning of the riffle habitat by current velocity.

As longnose dace grow, the relative size of their swimbladder decreases as does their ability to adjust the swimbladder size to alter buoyancy (Gee 1972). The ability to adjust their swimbladder size may allow the fry and juvenile longnose dace some plasticity in habitat use that is not experienced by the adults. Adult longnose dace may be more morphologically adapted to the riffle habitat than are the fry and juvenile longnose dace. Although size related morphometric differences (other than swimbladder volume) in longnose dace have not been demonstrated, different populations of longnose dace in Nebraska streams vary significantly in; caudal peduncle depth, pre-dorsal length and snout length (Woodman 1986), all of which may affect the ability of a longnose dace to utilize the riffle habitat. Morphometric differences between the size classes of longnose dace may contribute to size related habitat segregation.

Longnose dace feed primarily on benthic insects of the orders; Diptera (Chironomidae and Simuliidae), Ephemeroptera (Baetidae and Heptageniidae) and Tricoptera (Hydropsychidae) (Reed 1959, Gerald 1966, Pappantoniou and Dale 1982). The proportions of these food items in the guts of longnose dace change as the longnose dace grow. Chironomidae make up the major portion of the diets of small longnose dace while Simulidae and Hydropsychidae are more important in the diets of larger longnose dace (Gerald 1966). Although longnose dace were observed foraging in the early morning hours in this study, longnose dace studied in Canadian rivers foraged exclusively at night (Culp 1989, Beers and Culp 1989) (even though most species of stream minnows are more active during the crepuscular periods (Helfman 1986)). However, the longnose dace that they studied rested behind shelters during the daytime in the same areas that they use for foraging (Culp 1989).

The objectives of this study were: to determine the nature and degree of size related habitat use by longnose dace (chapter one), to conduct behavioral studies that investigate possible causes of size related habitat use (intra-specific competition and physical constraints) (chapter two), to conduct whole riffle manipulations of longnose dace densities to verify the results of the behaviotal studies (Chapter three), and to examine the possibility that size related shape differences contribute to size specific habitat segregation.

Study site:

This study was conducted in the Ford River system in Michigan's upper Peninsula. All study riffles were located on the Ford River and Twomile Creek (the major tributary to the Ford) in Dickinson County, Michigan at T43N, R30W (46°08' north latitude and 87°54' west longitude), between the towns of Channing and Ralph (Figure 1). The Ford and Twomile are third order streams above their confluence, and the Ford is a fourth order stream below the confluence. Studies were conducted in riffles located in three areas of the Ford and Twomile (Figure 1). These riffles were all cobble/boulder riffles and ranged in depth (during normal summer flows) from 5 cm to 35 cm. Widths varied from 8 to 13 m in the Ford River, and from 5 to 10 m in Twomile Creek. Velocities reached a maximum of 120 cm/sec in the study riffles. The Ford River is considered a marginal trout river with maximum summer temperatures exceeding 24° C, while Twomile Creek remains a few degrees cooler than the Ford. The surrounding watershed is primarily glacial till with granite bedrock and a few shale outcroppings. The

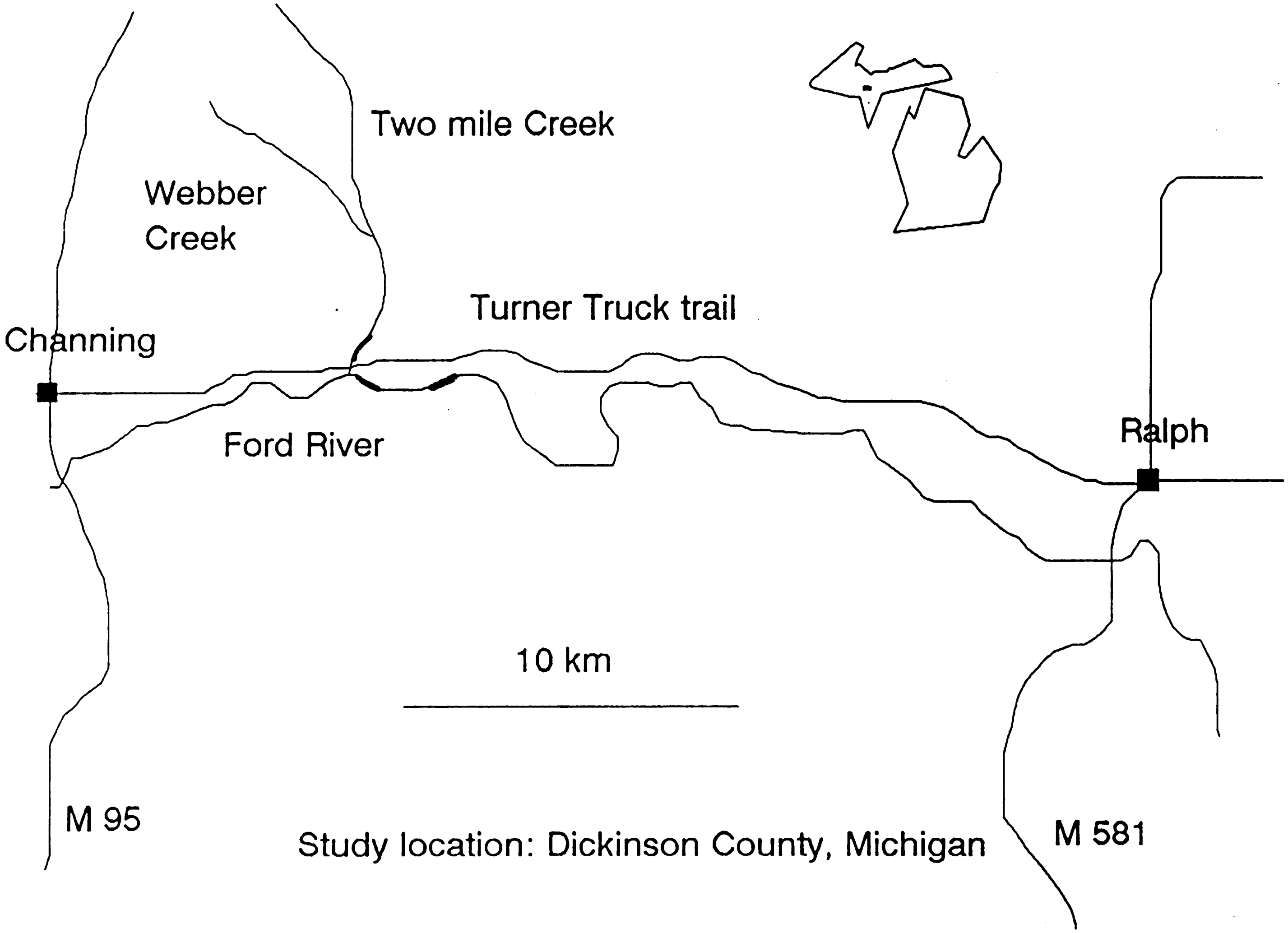

Figure 1: Study site on the Ford River system in Dickinson County, Michigan USA. The darkened stretches indicate the specific locations of the riffles used in this study.

bank vegetation is dominated by; speckled tag alder (*Alnus rugosa*), balsam popular (*Populus balsamifera*), northern white cedar (*Thuja occidentalis*) and white pine (*Pinus strobus*).

CHAPTER ONE

HABITAT USE SURVEY

INTRODUCTION

To date, most research on size specific habitat segregation by stream fishes has focused on pool dwelling species (Power 1984, Schlosser 1987, 1988a, 1988b). Thus, little is known about the pattern of size specific habitat use of riffle dwelling fishes. The purpose of this study was to examine the pattern of size specific habitat use and diet in a common riffle dwelling fish, the longnose dace (Rhinichthys cataractae). Longnose dace fry move out into the riffles around late July or early August, shortly after emerging and, as they grow, they move into the faster areas of the riffle (Gibbons and Gee 1972). They are a highly adapted riffle fish with subterminal mouths, for feeding on benthic invertebrates, and neutral or negative buoyancy, achieved by the ability to decrease the size of their swimbladder (Gee 1968).

A two year survey of habitat use patterns of both juveniles (age 1 - 2 years) and adults (> 2 years) was used to document the degree of size specific habitat segregation in longnose dace. Comparisons were made between the depth, water velocity, and substrate use, and the diets of both size classes of dace and between the densities of the major prey items in the slower and faster areas of the riffles.

METHODS

Habitat Segregation:

During the summer of 1987, the size distribution of longnose dace in two habitat types (defined by water velocity; medium velocity = 25 - 45 cm/sec and fast velocity = > 45 cm/sec) was sampled twice, once during late spring and once during mid summer. These velocities were chosen to match the velocity categories of Gibbons and Gee (1972). Areas to be sampled were selected the day before sampling by locating sections of riffles with the desired velocity range and recording the length, width and velocity range of each section. Sampling of an area consisted of kick seining into a 3.2 mm mesh hand held seine (2 m wide and 1.5 m deep). The seine was held by two people while two other people vigorously kicked the area 2 m immediately upstream of the seine. All the captured fish were held in a bucket until the entire area was sampled. The sampling crew started at the downstream end of the sampling area and worked upstream 2 m at a time until the entire area was sampled. All captured fish were identified, measured to total length (Tl) and released.

On June 12 (shortly after the longnose dace spawning season), four medium velocity and three fast velocity areas (2 - 3 m wide and 10 -15 m long) were sampled, and on August 12, five medium and five fast velocity areas were sampled.

A students' t-test was used to compare the mean size of longnose dace captured in the medium velocity areas with the mean size of longnose dace captured in the fast velocity areas.

A more detailed approach was used in 1988 to document the pattern of size specific habitat use in longnose dace. The habitat use of juvenile and adult longnose dace in nine individual riffle sections (25 - 30 m in length) was sampled every three weeks for twelve weeks. The riffles were grouped into sets of three and each set was sampled every three weeks with a different set being sampled every week. Sampling consisted of slowly electrofishing upstream with a boat electroshocker (1 - 2 amps, 240 volts) and capturing every dace encountered in the riffle. The location of encounter for each dace was marked with a colored flag (to identify size class) and three habitat variables were measured at each of these locations. The depth, predominant substrate type (using Cummin's (1962) classification) and mean water column velocity were recorded for each dace captured. Velocities were measured using a Pygmy-Gurley current meter, and the mean water column velocity was measured at 0.6 depth. Predominant substrate type was visually estimated. Mean water column velocity was used because it is more characteristic of the immediate area than focal point velocity, which, for a benthic fish, can be 0 cm/sec in the fastest and slowest areas of the riffle. The mean water column velocity is more characteristic of imvertebrate densities (orth and Maughan 1983) and of the velocities that may be encountered in the area while foraging. All dace were measured (Tl) and released back into the riffle. The size frequency distribution of the population was monitored weekly. These data were used to track the growth of the juveniles and facilitate proper identification of the size class of a captured dace.

On three occasions (independent of normal sampling), a three pass removal method (Zippin 1958) was used to determine the efficiency of the sampling method. The population estimate for each size class from the removal method was divided into the number of each size class caught on the first pass to produce an efficiency estimate.

The sampling technique used in 1988 was slightly more efficient for the adults (efficiency = 60 ± 4.8%) than for the juveniles (efficiency = 50 ± 5.0%). Given the structural complexity of a stream riffle and the difficulty of netting shocked fish in a fast current, these efficiencies are fairly high. The time it took to sample a riffle depended on the water level and the density of dace in the riffle and ranged from one to two hours. Since the capture efficiencies were different for the two size classes, the capture data for each size class was corrected for its respective capture efficiency before statistical analysis was conducted.

A four dimensional contingency table and chi squared goodness of fit was used to test for independence of the four variables; velocity, depth, substrate and dace size. The velocity, depth, substrate type, and size of each dace captured was fit into one of two categories for each variable: velocity categories were; slow (<40 cm/sec) and fast (> 40 cm/sec), depth categories were; shallow (<15 cm) and deep (>15 cm), and substrate categories were; boulder and others (over 95% of the others were cobble). The dividing line between categories for a variable was chosen to be the median of the range used by about 95% of the dace captured. For instance, for the variable velocity, approximately 90% of the dace were captured at velocities less than 70 cm/sec and 98% were captured at velocities less than 80 cm/sec. As 80 cm/sec falls close to the 95% mark, 0 - 80 cm/sec was chosen as the commonly used range and 40 cm/sec as the dividing line between slow and fast. In order to test for specific interactions between size and each of the habitat variables, the original four dimensional table was broken down into three two dimensional tables, all involving size as one of the variables.

Contingency table analysis was also used to examine the possibility that either size class utilized a specific combination of the habitat variables. Tests for associations were conducted for the variable pairs; depth - velocity, depth - substrate and velocity - substrate, using data from all the dace captured in each size class and using data generated from the riffle at large (see Habitat Selection).

In this analysis, segregation was defined as a significant chi-square value in the contingency tables involving size and a habitat variable. Positive results from these analyses would indicate that the distributions of the adults and juveniles along a given habitat variable were different than would have been expected if size were not important, and therefore, segregation occurred by that variable. Positive results would not indicate habitat preferences for either size class, nor would they indicate any effect of one size class on the habitat use of the other.

All of the measurements of the habitat use of longnose dace in this study were made between the hours of 0700 and 1100 hr. Even though most species of stream minnows are most active during the crepuscular periods (Helfman 1986), snorkling observations in the Ford River indictated that longnose dace were active during this period. However, longnose dace studied in Canadian rivers foraged exclusively at night (Culp 1989, Beers and Culp 1989). In these studies, the longnose dace spent the daylight period behind or under shelters in the same areas that they used for foraging. It is not clear why the longnose dace in this study were more active in the morning hours than the longnose dace studied by Beers and Culp, however, since longnose dace rest in the same areas they forage in, the results from this study should also apply to the longnose dace populations studied by Beers and Culp.

Habitat Selection:

On seven of the twelve sampling days during the summer of 1988, the availability of each of the three habitat variables was measured using ten evenly spaced measurements on each of 5 evenly spaced transects along the entire length of each of the three riffles sampled that day (150 measurements total). On five of the twelve sampling dates in 1988, a combination of equipment failure and afternoon thundershowers prevented habitat availability measurements. Habitat availability measurements were taken at least twice at each set of three riffles and three times in one set of riffles.

These data were pooled and used to test the hypothesis that all adult and juvenile longnose dace caught on these seven days used the habitat (defined by the three habitat variables) at random. Velocity was divided into six 10 cm/sec cells, depth into four 10 cm cells and substrate type into two cells and the availability data were used to calculate the expected catches of adults and juveniles in each cell assuming random habitat use. The chi-square values were used to determine the range of a habitat variable that each size class avoided (utilized in a proportion that was less than the proportion of that range in the environment) and the range of each habitat variable that each size class selected (utilized in a proportion that was greater than the proportion of that range in the environment).

Diet Analysis:

On the last sampling date in the summer of 1988, all the longnose dace were kept for diet analysis. Thirty five juveniles and 45 adults were preserved in 70% ETOH and transported to the laboratory. At the laboratory the anterior loop of the gut was removed from each dace and the contents were identified to the lowest taxonomic level practical (at least to family) and enumerated. The dietary overlap (Schoener 1970) was computed using the proportions of the most prominent items in the diets of both size groups.

Two days prior to the last sampling date three replicate invertebrate samples were taken from fast and three from medium velocity areas of a riffle in order to compare the densities between habitats for the major prey items of both size classes. Samples were taken with a 0.11 m^2 modified Hess sampler, and sample locations were chosen with the aid of a current meter to identify areas with mean velocities between 50 and 60 cm/sec (fast) and between 30 and 40 cm/sec (medium). All samples were preserved in 70% ETOH and sorted at the laboratory. All the invertebrates were identified (at least to family) and counted from these samples and statistical comparisons of densities were made on the major prey items.

RESULTS

Habitat Segregation:

In both June and August of 1987 (Figures 2 and 3), the fast velocity areas contained larger longnose dace than did the medium velocity areas. In June, 16 dace (mean Tl = 62.1 mm) were captured in the medium velocity areas and 25 dace (mean Tl = 75.1 mm) were captured in the fast velocity areas. The null hypothesis: The mean size of longnose dace captured in medium velocity areas was not different than the mean size of longnose dace captured in fast velocity areas, was rejected ($t = 2.74$, $p < 0.01$). In August, 46 dace (mean Tl = 60.2 mm - including 18 fry that recruited to the riffles in late July) were captured in the medium velocity areas and 32 dace (mean Tl = 81.1 mm - including two fry) were captured in fast velocity areas. Once again, the null hypothesis of no size difference between the areas was rejected ($t = 5.21$, $p < 0.001$). As this result may have been due to the recruitment of longnose dace fry into the medium velocity areas, and the purpose of this study was to

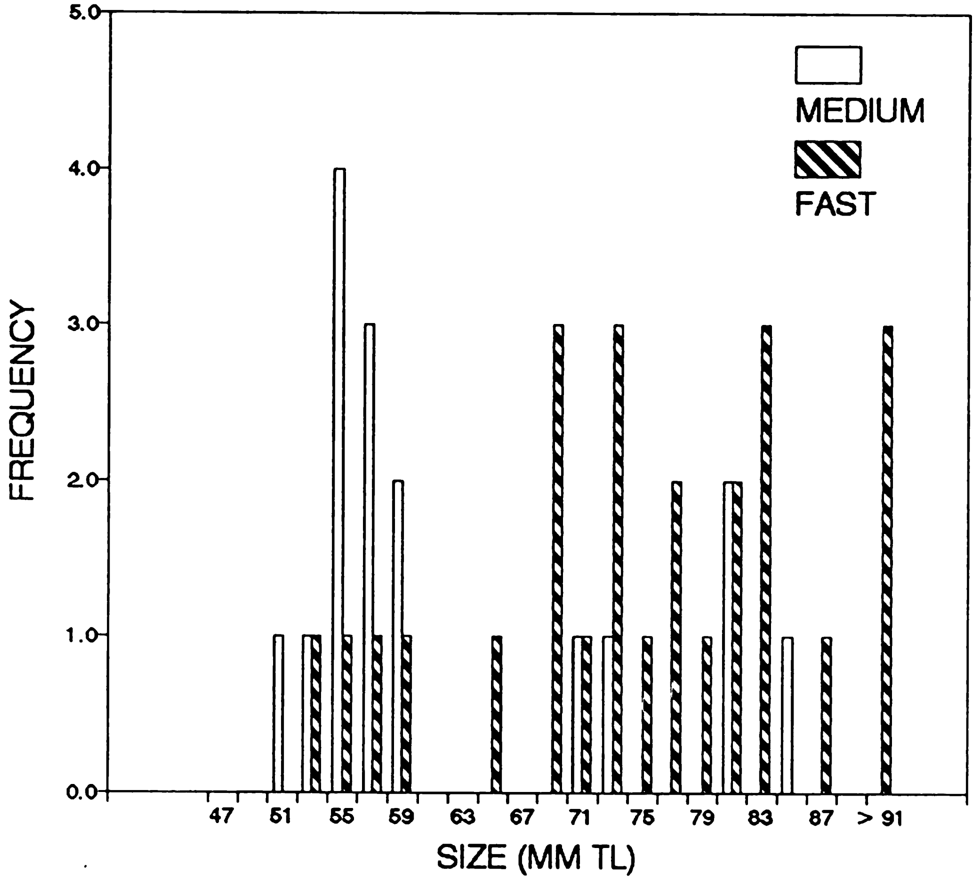

Figure 2: Size frequency distributions of longnose dace captured in fast (N = 25) and medium (N = 16) velocity areas in June 1987.

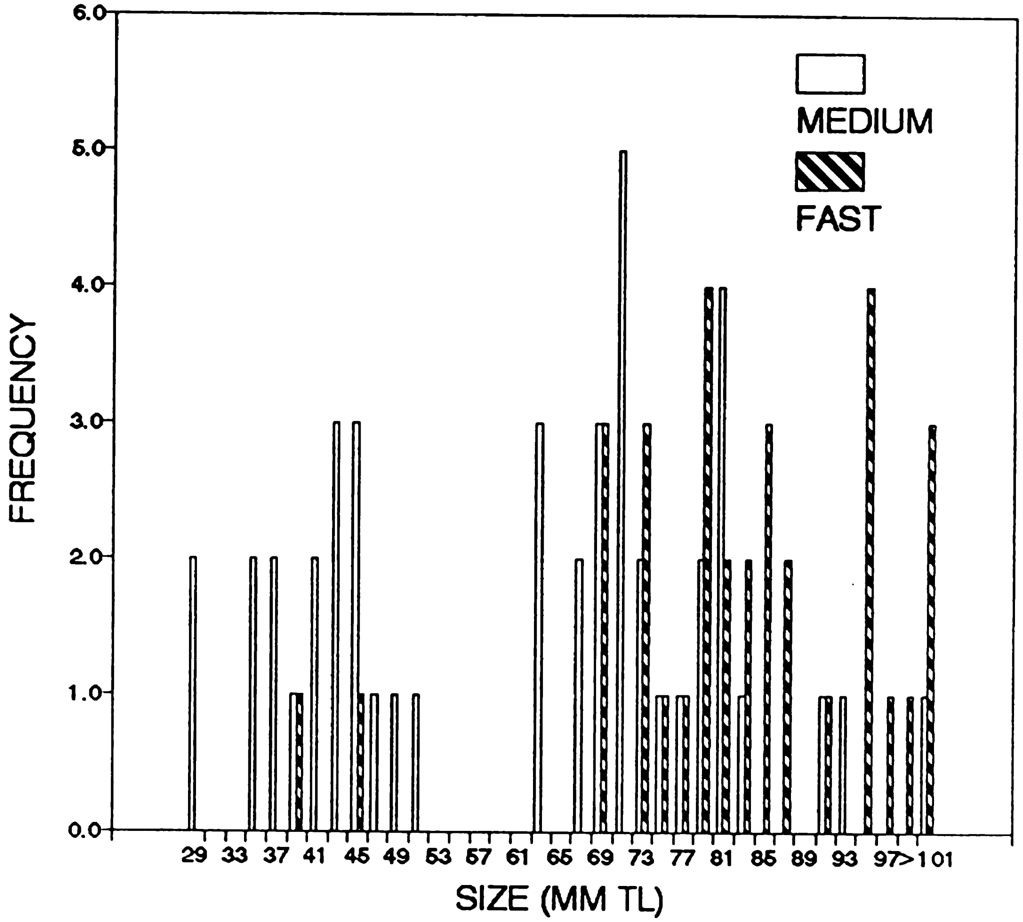

Figure 3: Size frequency distributions of longnose dace captured in fast (N = 32) and medium (N = 46) velocity areas in August 1987.

examine the habitat use of only the juveniles and adults, the fry were removed from the dataset and the t-test was conducted with just the juvenile and adult data. Even without the fry in the medium velocity areas, there was a significant difference between the size distributions of longnose dace in the medium and fast areas ($t = 3.42$, $p < 0.001$).

In 1988, data on the depth, velocity and substrate use of 1,640 longnose dace were collected over the summer. The four dimensional contingency table indicated that size, depth, velocity and substrate type were highly dependent on each other (chi-square = 87.85, $p < 0.001$). The two dimensional contingency table analysis of size versus each habitat variable indicated that size segregation occured by depth, velocity and substrate type (Table 1 - a significant chi-square value indicates that the two variables [i.e. size and velocity] were not independent). Juveniles were found more frequently in shallow, slow non-boulder areas and adults were found more frequently in deep, fast boulder areas than would be expected if size were not important.

Tests for associations between habitat variables for juveniles, adults and the riffle at large (Table 2) indicated that substrate type was not associated with depth or velocity but that depth was associated with velocity for each size class. Therefore, the depth at which both juvenile and adult longnose dace were captured was a

Table 1: Chi-square contingency table analysis of the first order interactions involving size from the 1988 riffle survey. Data are the actual numbers captured in each cell with the chi-square values for each cell and the sign of the difference (observed - expected). N = 2994 longnose dace.

Size	Depth		Velocity		Substrate type	
	Shallow	Deep	Slow	Fast	Boulder	Other
Juveniles						
Observed	800	766	1178	388	254	1312
chi-square	1.26+	1.21-	4.80+	11.50-	8.34-	2.01+
Adults						
Observed	670	758	935	493	328	1100
chi-square	1.38-	1.34+	5.26-	12.61+	9.15+	2.21-
Significance	$p < 0.05$		$p < 0.001$		$p < 0.001$	

Table 2: Chi-square contingency table analysis for associations among habitat variables for Juveniles (N = 783), adults (N = 857) and a random sample of the available habitat (N = 450) for 1988. Data are the actual numbers captured in each cell with the chi-square values for each cell and the sign of the difference (observed - expected).

	JUVENILES		ADULTS		AVAILABLE	
			DEPTH X SUBSTRATE			
	Shallow	Deep	Shallow	Deep	Shallow	Deep
Boulders						
Observed	58	69	81	116	33	37
chi-square	0.73-	1.02+	1.41-	1.24+	0.47	0.54+
Others						
Observed	342	314	321	339	206	174
chi-square	0.14	0.15	0.42	0.37	0.09	0.10
Significance	NS		NS		NS	
			DEPTH X VELOCITY			
	Shallow	Deep	Shallow	Deep	Shallow	Deep
Slow						
Observed	332	257	288	273	210	166
chi-square	3.21+	3.36-	2.34+	2.07-	0.53+	0.60-
Fast						
Observed	68	126	114	182	29	45
chi-square	9.76-	10.19+	4.43-	3.91+	2.70-	3.06+
Significance	p < 0.00 1		p < 0.001		p < 0.01	
			VELOCITY X SUBSTRATE			
	Slow	Fast	Slow	Fast	Slow	Fast
Boulders						
Observed	100	27	133	64	55	15
chi-square	0.21	0.64-	0.12	0.24	0.21	1.07-
Others						
Observed	489	167	428	232	321	59
chi-square	0.04	0.12	0.04	0.07	0.04	0.20
Significance	NS		NS		NS	

function of the velocity at each capture location, perhaps indicating that the juveniles and adults were utilizing a specific combination of depth and velocity. However, the pattern of the association (+'s and -'s in Table 2) between depth and velocity was similar for both size classes, and this pattern was similar to the pattern of association of these two variables in the riffle at large ("available" in Table 2). Therefore, the observed association in the depth and velocity use of both size classes probably resulted from the correlation of these two variables in the environment.

Habitat Selection:

Data on habitat selection was collected on 485 juveniles and 539 adults. Longnose dace of both size classes selected depths between 10 and 19 cm (Figure 4). Juveniles avoided depths over 20 cm and used depths less than 10 cm in proportion to their availability while the adults avoided depths less than 10 cm and deeper than 30 cm. In both cases, the overall chi-square value was significant ($p < 0.001$) indicating that neither size class utilized the habitat (defined by depth) at random. Both size classes showed a similar pattern of velocity selection (Figure 5), avoidance of slow velocities (less than 10 cm/sec) and selection of faster velocities (greater than 40 cm/sec). Although selectivity was much stronger (the magnitude of the chi-square values indicates the degree to which each size

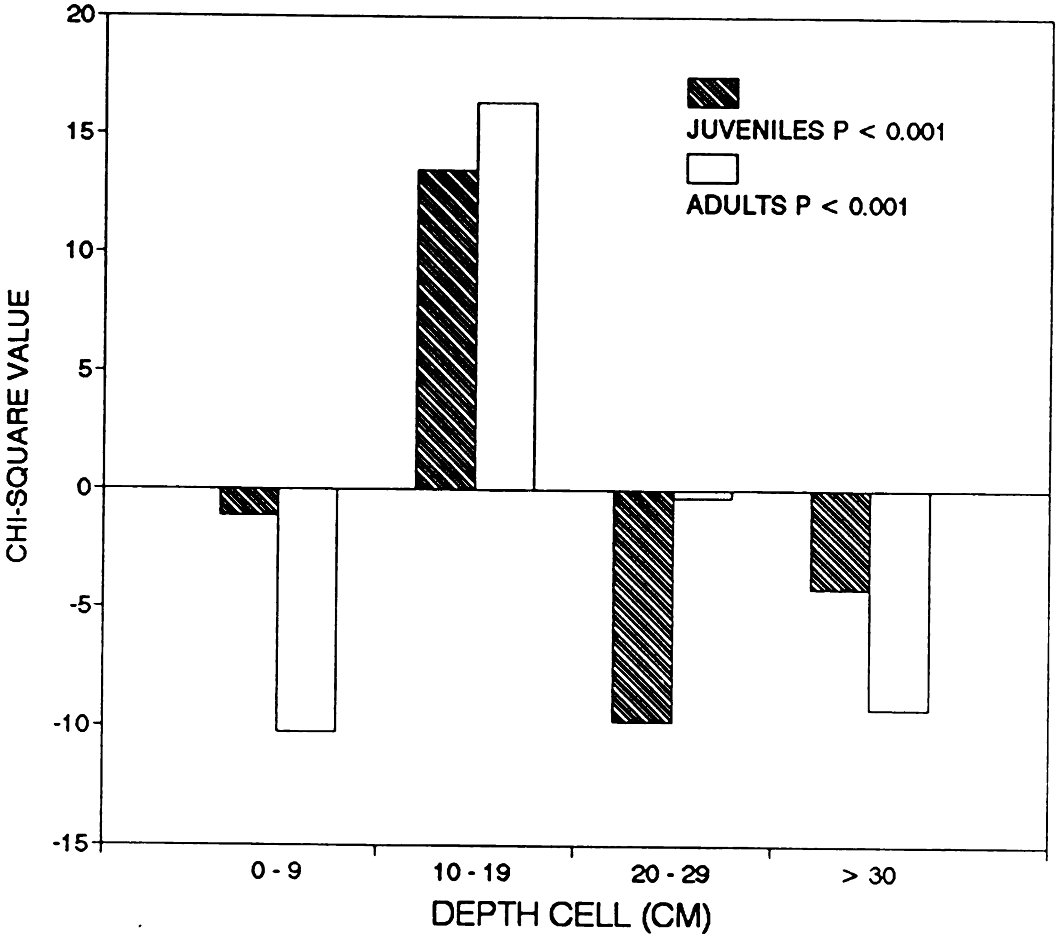

Figure 4: Chi-square analysis of the depth distribution of juvenile (N = 485) and adult (N = 539) longnose dace captured in 1988. Positive values signify selection of that depth cell while negative values signify avoidance of that depth cell.

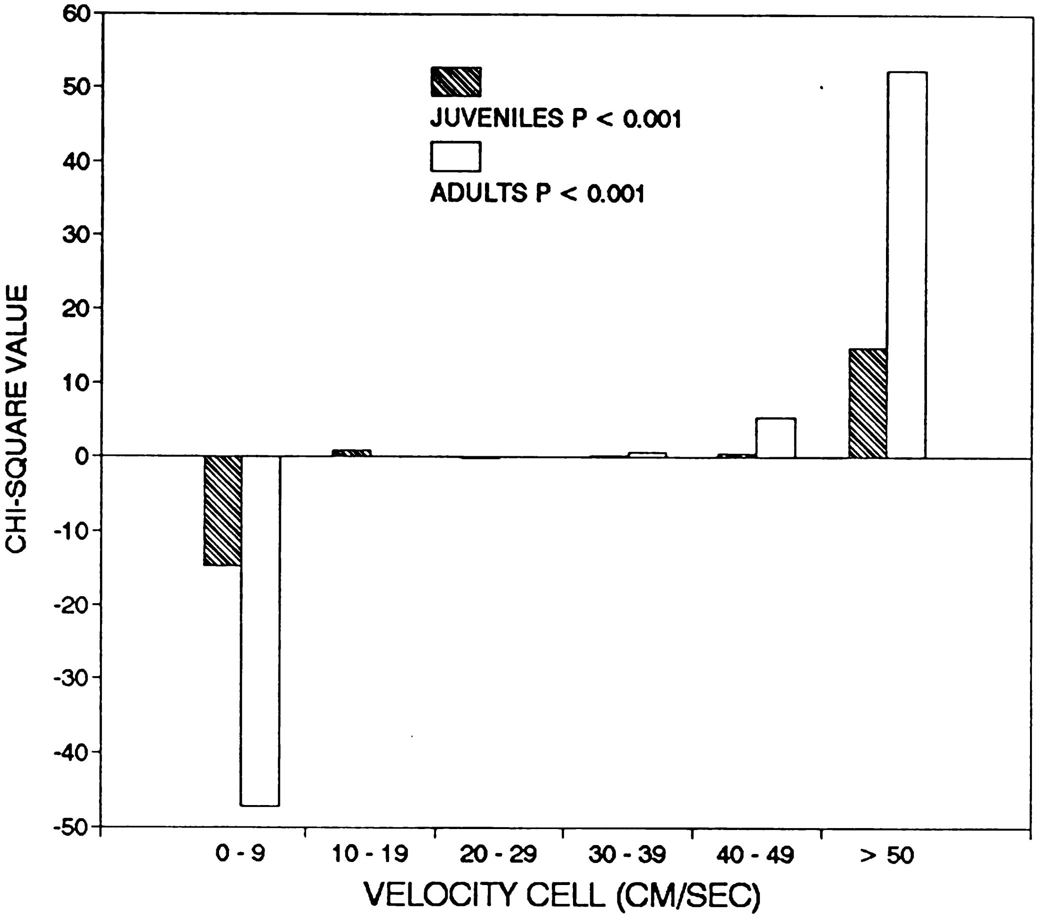

Figure 5: Chi-square analysis of velocity distributions of juvenile (N = 485) and adult (N = 539) longnose dace captured in 1988.

class used or avoided each velocity cell) for adults, the overall chi-square value for both size classes was significant ($p < 0.001$). The pattern of substrate selection was also similar (Figure 6). Both size classes selected boulders and avoided other substrates. Again, the overall chi-square value for both size classes was significant ($p < 0.05$ for juveniles and $p < 0.001$ for adults), but the adults showed a stronger degree of selectivity.

Diet analysis:

The diets of the 35 juvenile and 45 adult longnose dace sampled in early September 1988 were similar (overlap = 83%), with slight differences occurring in the proportion of Chironomidae, Baetidae, Simuliidae and Hydropsychidae in the diet (Table 3). The juvenile diet consisted primarily of Chironomidae, while the adult diet was slightly broader, including more Baetidae, Simuliidae and Hydropsychidae. These results are similar to those of Gerald (1966) who studied the diets of 439 longnose dace from the Yellowstone River, Montana, but differ markedly from those of Pappantoniou and Dale (1982) who found that hydropsychids dominated the diets of 52 longnose dace collected from the Waccabuc River, New York. In general, these prey items occured at higher densities in the fast areas than in the medium velocity areas of the Ford River (Table 4).

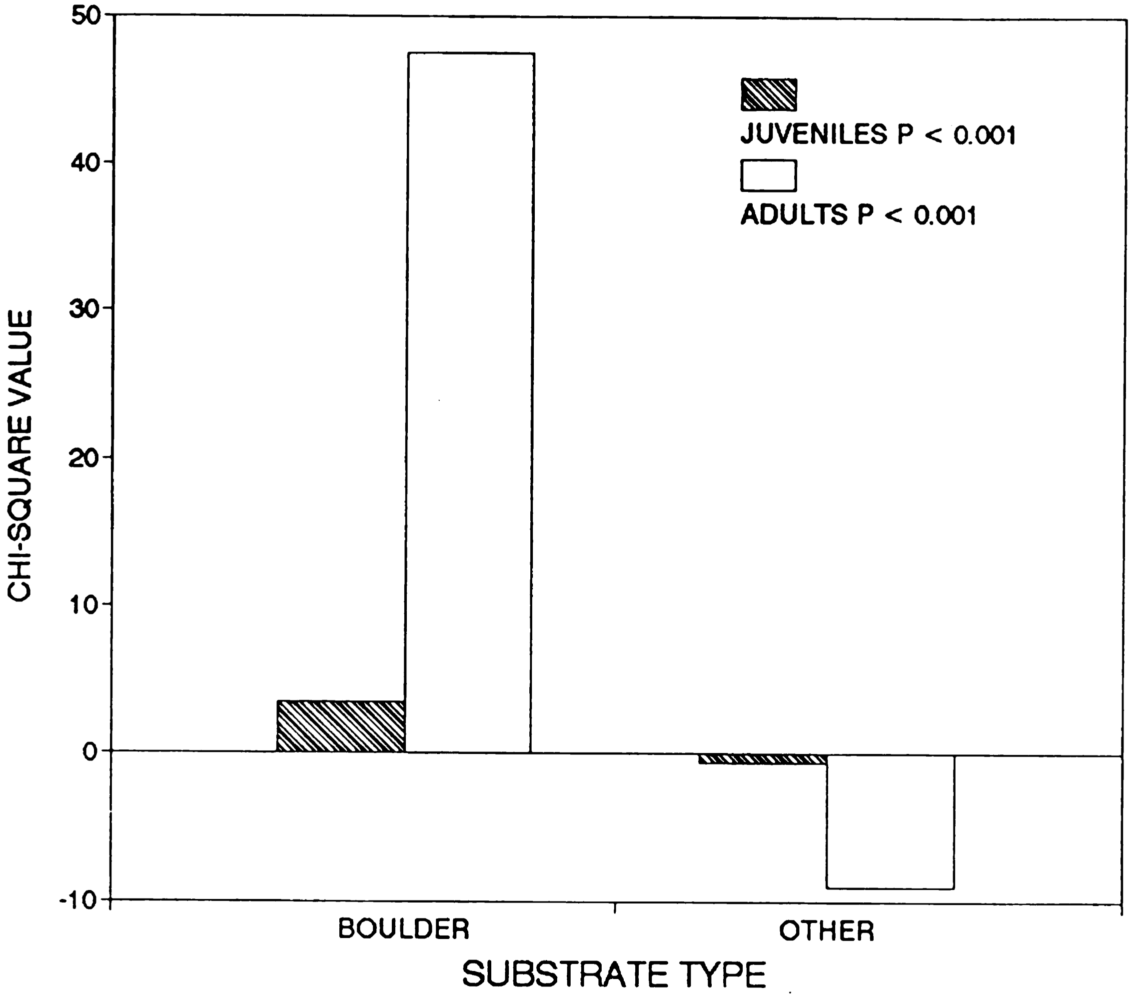

Figure 6: Chi-square analysis of substrate use patterns of juvenile (N = 485) and adult (N = 539) longnose dace captured in 1988.

Table 3: Dietary overlap between juvenile (n = 35) and adult (n = 45) longnose dace captured in the first week of September 1988. Overlap is calculated according to Schoener (1970).

Item	Proportion		
	Juveniles	Adults	$\lvert P_j - P_a \rvert$
Chironomidae	0.86	0.75	0.11
Baetidae	0.02	0.08	0.06
Simuliidae	0.01	0.06	0.05
Hydropsychidae	0.02	0.06	0.04
Psychomyiidae	0.04	0.03	0.01
Others	0.07	0.00	0.07
Total $\lvert P_j - P_a \rvert$			0.34
Overlap			83%

Table 4: Habitat specific densities of selected insect families in the Ford river on September 10 1988. Student t-tests were used to test for significant differences between the habitats.

Item	Density (#/m^2) ± S.E.		Significance	
	Medium	Fast	t	P
Chironomidae	2775 ± 55	4968 ± 1168	-1.70	0.165
Baetidae	121 ± 64	394 ± 67	-2.93	0.043
Hydropsychidae	1358 ± 531	5077 ± 623	-4.54	0.011
Psychomyiidae	27 ± 5	3 ± 3	1.19	0.39
Simuliidae	15 ± 10	163 ± 63	-2.32	0.081

DISCUSSION

Some degree of habitat segregation between adult and juvenile longnose dace occurred by all three habitat variables. Segregation by velocity was strongest (chi-square = 34.17) with adults occurring in fast water in a much higher proportion than expected while the juveniles occured in the fast water in a much lower proportion than did the adults (Table 1). Similarly, the adults utilized boulders much more than expected and the juveniles utilized the boulders in a lower proportion than the adults (chi-square = 21.71). Segregation by depth was the weakest (chi-square = 5.19) and probably resulted from the positive association between depth and velocity in the riffle at large (Table 2). Since deeper waters were associated with faster velocities, and the adults used the faster velocities in a much higher proportion than did the juveniles, they would also have used deeper waters in a higher proportion.

Despite the strong degree of habitat segregation, both size classes selected similar velocity and depth ranges and substrate types. In all cases the adults showed the stronger selectivity, indicating that segregation resulted from a higher proportion of the adults utilizing the fast areas and boulders than the proportion of juveniles in those areas, even though both size classes utilized those areas in higher proportions than they occurred in the environment.

The actual cause of segregation is unknown, but, several possible explanations exist. Adults may utilize the faster areas of riffles and larger substrates as a refuge from predators. Potential aquatic predators in the Ford River include adult brook trout (Salvelinus fontinalis) and burbot (Lota lota), both of which forage in riffles and pools (personal observation). Differential predation rates on the two size classes may be forcing the adults into the refuge areas, resulting in the observed size segregation. However, juvenile dace would also be susceptible to predation by these predators. The mean length of the juvenile size class exceeded 60 mm Tl by the end of June (at least as large as the minnows used as bait by many trout anglers). Segregation may arise from intraspecific competition for the shelter provided by the faster areas (where the cost of foraging should be high for a large piscivore) and around boulders. By this scenario, the juveniles and adults should show selection for faster areas and larger substrates (assuming that these areas are not completely limited). Alternatively, juveniles may lack the physical ability to escape predation by moving into the faster areas of the stream due to the strength of the current. Under this scenario, the juveniles should show avoidance of the faster areas but still show selection for boulders as a refuge from predation.

Segregation may have also resulted from predation pressure on adult longnose dace from terrestrial or avian predators. Kingfishers, herons, mink and raccoons are all potential longnose dace predators in the Ford River. In general, these types of predators prey on larger fish (Power 1987 and Schlosser 1988a, 1988b) often confining these fish to the deeper areas of the stream. Adult longnose dace may be using the faster areas of the riffle because they are positively associated with depth (although this is only within a riffle and the depths are usually less than 25 cm and may not offer much refuge) or more likely, because the faster areas are areas of high turbulence which would inhibit non-aquatic predators. Larger substrates may also increase the turbulence and offer more hiding places from these predators. Juvenile longnose dace, due to their small size, should not be as susceptible to non-aquatic predators and therefore should show less selectivity of velocity or substrate types barring any other factors that might affect juvenile habitat use.

Alternatively, adults may be utilizing the faster areas of the riffles because they have higher invertebrate prey densities. With the exception of Chironomidae, the major prey items of longnose dace (Baetidae, Hydropsychidae and Simuliidae) are more dense in the faster areas of the riffles (Table 4, Orth and Maughan 1983 and Brown and Brown 1984). By this scenario, segregation should occur by velocity but not by substrate size (invertebrate densities are highest in areas dominated more by cobbles rather than by boulders (Brown and Brown 1984). Juveniles should show selection for faster velocities if competition for foraging space in the fast areas explains segregation, or they should show avoidance of faster velocities if physical constraints on the juveniles explain segregation. There should be selection for smaller substrates by both size classes.

Five explanations for habitat segregation have been proposed and can be separated on the basis of the predictions that each makes about segregation between the size classes and selection by the juvenile size class (Table 5). According to these predictions, the results from this study (segregation by velocity, depth and substrate type and juvenile selection for faster velocities and larger substrates) are consistant with the hypothesis that segregation resulted from predation pressure on the dace by aquatic piscivores and size class competition for the shelter from predation that was offered by fast velocities and large substrates. However, some other possible cause of segregation may be acting on the habitat use of the dace. For instance, this study used data collected over an entire growing season and physical constraints on the juvenile dace may be important early in the summer and not later in the summer. Also, higher invertebrate prey densities may combine with lowered predation risk to make the faster areas

Table 5: Predictions of 5 possible explanations for size specific habitat segregation in longnose dace. See text for more details.

	Predictions				
	Segregation by;			Juveniles select;	
Explanation	Velocity	Depth	Substrate	Velocity	Substrate
Predation					
Aquatic					
Physical constraints	yes	yes	no	slow	boulder
Competition	yes	yes	yes	fast	boulder
Non aquatic	yes	yes	yes	neither	neither
Invertebrate density					
Physical constraints	yes	yes	no	slow	others
Competition	yes	yes	no	fast	others

more desirable to both size classes.

Most species of fish exhibit an optimal temperature for growth. Young sockeye salmon (Oncorhynchus nerka) grow fastest at about 15°C, but as the food ration is decreased the optimal temperature for growth decreases (Brett 1971). When surplus food is available, young sockeye reach their highest growth rate at high temperatures (Biette and Geen 1980). The thermal preferences for brook trout (Salvelinus fontinalis) increases from 8 - 11.5°C as fry to 17.5°C as fingerlings (Peterson et. al. 1979). Longnose dace may move into the faster areas of the riffle as they grow in response to changing temperature optima, however the optimal temperatures for growth of longnose dace of various sizes are unknown. There is probably only a little variation in temperature across a riffle and thermal preferences are probably not the cause of size specific habitat use of longnose dace. In addition, when food is abundant (as it is in riffles), fish growth rates tend to be higher at higher temperatures, which would occur in the slower, shallower areas of the riffle and not in the deeper, faster areas preferred by adult longnose dace.

This study relied on observational data and, although it documents habitat segregation between the size classes, it can only suggest possible causes for that segregation. Experiments have been conducted to specifically test for the effects of adult longnose dace on the habitat use and diet of juvenile longnose dace, and to examine the ability of the juveniles to physically utilize the faster areas. In addition, an analysis of shape changes with growth was conducted to examine the possibility that segregation results from shape differences between the size classes. These will be the subjects of the following chapters.

CHAPTER TWO

BEHAVIORAL STUDIES

INTRODUCTION

The pattern of velocity segregation between juvenile and adult longnose dace detected in the habitat use survey (chapter one) may result from size specific habitat preferences. Juveniles may prefer slower habitats for energetic reasons. The higher food densities in the faster areas may not be enough to offset the energetic costs of foraging in those areas. Since the ratio of surface area to volume is higher for smaller fishes of the same shape as their larger conspecifics, those costs should be proportionally higher for smaller fish (Vogel 1988). For practical purposes, the volume of a fish determines the amount of muscle mass available and the surface area represents the area that has to be moved against the current. As the fish grow, they develop a larger muscle mass for moving a proportionally smaller surface area against the current. Smaller dace, therefore, may be physically unable to utilize the faster areas of the riffle.

Interactive segregation may also be responsible for the habitat segregation observed in the habitat use survey. Adult and juvenile longnose dace may compete for shelters from the current (or from predation) in the faster areas of the riffle. If shelter space is not completely limited there should be some overlap in habitat use with the subordinate group using proportionally less of the preferred habitat. This pattern was observed in the riffle survey (Figures 5 and 6).

The purpose of the studies reported here was to examine the size specific habitat preferences (in the absence of other longnose dace) of various size classes of longnose dace, to examine the effect of adults on the shelter use of juvenile longnose dace, and to determine the maximum swimming velocities of various sizes of longnose dace.

METHODS

Habitat Choice Experiments:

The habitat preferences of 18 fry (0+ years old; 37 - 51 mm Tl), 18 juvenile (1+ years old; 55 - 64 mm Tl) and 18 adult (2+ years old; 67 - 88 mm Tl) longnose dace were tested one at a time in a maze designed to give fish a choice of three habitats: slow (0 - 10 cm/sec), medium (25 - 35 cm/sec) and fast (40 - 50 cm/sec) current velocities (Figure 7). The maze was constructed in a 1 m^2, 50 centimeter deep cage built from treated plywood and ¼ inch hardware cloth and was situated in a riffle in the Ford River in about 15 centimeters of water. Each habitat contained substrates from the equivalent habitat in the river. Longnose dace for testing were captured the day

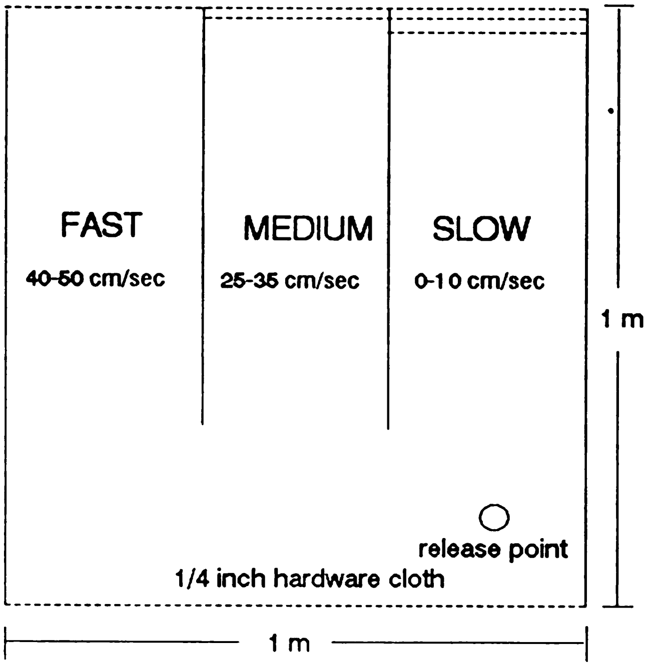

Figure 7: Maze design for the habitat choice experiments. The maze was 0.5 m deep and situated in a riffle so that the desired velocities were achieved in each channel.

before testing by kick seining in a nearby riffle and held in small flow-through holding cages in a medium velocity riffle (the holding cages contained rocks to provide cover for the dace). Testing consisted of choosing a dace of the appropriate size class (predetermined before each test) from the holding cage, rubbing a small amount of fluorescent powder (Cabela's Magic Powder) (the powder remained on the fish for 15 - 20 min and facilitated observation in the faster channel where turbulence was high) onto the dorsum of the fish and placing the dace into the maze at the downstream end of the slow channel. This location was chosen because the dace quickly moved out of this spot, usually exploring the slow channel before moving into the medium or fast channels. Dace released in the medium or fast channels usually found the nearest cover and remained there for the duration of the test. The dace were allowed 5 minutes to adjust and then were observed from a spot behind the cage for 15 minutes. The amount of time a dace spent in a predetermined habitat was recorded. This gave the amount of time spent in each habitat by longnose dace of each size class. A dace was timed in only one habitat in order to provide independence between habitats for statistical analysis. All observations were made between 07:00 h and 10:00 h, and all the adults and juveniles were tested between June 25 and July 5, 1987. The fry were tested between August 20 and August 29, 1987. This was done in order to provide data on as wide a range of longnose dace sizes as possible (the fry had not recruited into the riffle areas at the time of the June/July testing).

A Kruskal-Wallis (non-parametric analysis of variance) test was used for each size class to test the null hypothesis that there was no difference in the amount of time spent in each habitat for that size class. When the null hypothesis was rejected, a Tukey-type multiple comparison of means (Zar 1984) was used to determine which habitats were used differently.

Shelter Competition Study:

The effect of adults on the shelter use of fifteen juvenile longnose dace was examined using ½ m^2 (1 m long x 0.5 m wide) cages situated in a riffle in the Ford River. Five cages were constructed of ½ inch treated plywood sides with ¼ inch hardware cloth screens at the front and back. The bottom of the cages were filled with gravel and pebbles from the river and the cages were situated so that a current of 15 - 20 cm/sec was flowing through each cage. The cages were placed in the river three weeks prior to use to allow invertebrate colonization. One shelter was provided in each cage. The shelter was a piece of clay tile, about 10 m wide and 15 m long, that, when viewed from the side, was shaped like an "L". The tile was laid in the middle of the cage so that the short leg of the "L" was vertical to the substrate and the long leg of the "L" was nearly horizontal to, and suspended above, the substrate at the forward end. Preliminary observations demonstrated that both sizes of dace readily used the shelters and could easily move in and out from under the shelter. A slow current was used in this study because it was nearly impossible to observe the dace in the cages when faster currents were used (the fluorescent powder that was used for the observations of habitat preference did not stay attached to the fish long enough to be useful in this study). The forward screen produced turbulence in the cages at higher velocities. Also, the cages were left undisturbed for 24 h before each observation, and over that time enough debris accumulated on the forward screen to lower the velocities in the cages to 15 - 20 cm/sec. This debris was not removed until after observations were made (removal of the debris disturbed the cages and may have affected the results if this were done before the observations were made).

Observations were made between 08:00 and 10:00 h over three, three day periods between June 29 and August 11, 1990. The experiments were conducted as follows: 1) Juvenile longnose dace (61 - 69 mm Tl) were captured by kick seining and placed in the cages (one to a cage) one day prior to the initial observation, 2) The shelter use of each juvenile was recorded during the initial observation and one adult (75 - 90 mm Tl) was placed in each cage immediately after the observations were made, 3) The shelter use of the juveniles in the presence of adults was recorded 24 hours later and the adults were removed from the cages immediately after the observations were made, 4) The shelter use of the juveniles (without the adults) was recorded 24 hours later and then all fish were released. This design was used to control for the possibility that differences in shelter use observed after the adults were added occurred because the juveniles were becoming acclimated to the cages, and therefore more active, instead of being due to the presence of adults.

Prior to observation, each cage was approached slowly from the downstream direction and the observer sat in a chair behind the cage at a distance that allowed the interior of the cage to be seen. The observer carefully searched the cage for the dace and if the dace was not found it was assumed to be under the shelter (this assumption was verified at the end of the observation period). This was the case for 42 of the 45 observations, in the other three observations the dace was located outside the shelter. Once the location of the dace was determined, the observer recorded the total amount of time that the dace used the shelter over a 15 minute period, and the number of times the dace used the shelter. These values were used to determine the average time/use for each juvenile longnose dace without an adult present, with an adult present and again without an adult present. In all cases, the adult, when present, spent the entire observation period under the shelter. In nearly all cases, when a juvenile exited the shelter it quickly re-entered the shelter.

Kruskal-Wallis (nonparametric analysis of variance by ranks) was used to test for an adult effect on the time/shelter use of the juveniles. A Dunnett's-type test for comparing a control group (initial observation) to each of the other groups (with an adult present and the second observation without adults) was used to examine the possibility that a significant Kruskal-Wallis result was due to an adult affect (control versus adults present) or due to an acclimation affect (control versus the second adult free observation) (Zar 1984, pg. 204 -205).

Maximum swimming velocity:

In order to examine the possibility that juvenile longnose dace were excluded from faster habitats by virtue of an inability to swim against the currents encountered in the fast habitats, the maximum burst velocities of dace of several sizes were measured. Measurements were made on 41 dace ranging in size from 41 to 103 mm Tl. Measurements were made in a clear plastic tube with a 4.9 cm inner diameter that was screened off and attached at both ends to flexible tubing (an input hose and an output hose). The input hose was attached to a Teal model 2P390 pump capable of pumping up to 2520 gph. A hand valve was placed on the input hose to regulate the flow rate through the tube. The whole apparatus (except the pump and valve) was submerged in a Frigid Unit living stream.

The longnose dace were collected from the Ford River in early May (1987) and transported to East Lansing in an aerated ice chest. The dace were kept in a living stream set at 10 °C (the temperature at which the dace were collected), provided with shelter and fed four cubes of tubifex worms every other day (the dace were observed eating and appeared healthy throughout their captivity). Dace were held for at least ten days before testing, and testing was completed in four days. All dace were returned to the Ford River after the completion of the study.

A dace was placed in the tube by removing the screen at the outlet and replacing it after the dace was in the apparatus. A strip of black electrical tape was wrapped around the tube in the middle to give the dace something to orient to (without the tape the dace tended to cower near the outlet, with the tape the dace showed a strong tendency to keep their heads within the area covered by the tape). To start each trial the pump was turned on with the valve closed and then the valve was opened slowly at a constant rate (one complete turn per ten seconds). The dace immediately oriented to the current and came to a resting position on the bottom of the tube, normally with their heads in the area covered by the tape. The valve was opened at the constant rate until the dace was swept backwards in the tube. At this point the velocity was held constant until the fish made an effort to advance against the current. This usually happened immediately after the dace was swept out of position but in some cases the fish did not attempt to swim until it contacted the outlet screen. If the dace was not able to swim forward the trial was stopped there. If the dace was able to advance and hold a position the velocity was increased and the trial continued until the dace could no longer advance (no trial lasted longer than 1.5 min.). At the end of the trial, the pump was turned off (the valve was left at the setting at which the trial ended) and the dace was removed from the apparatus. In order to determine the final velocity, the apparatus was reassembled and the pump turned on. The output from the apparatus was collected in a bucket for 10 seconds and the volume was measured. The volume was used to calculate discharge (cm^3/sec) which was divided by the cross sectional area of the tube to determine velocity in cm/sec. This procedure was repeated three times for each trial and the average velocity was used. The standard errors from the three velocity measurements ranged from 0.21 to 0.81 cm/sec with an average of 0.43 cm/sec. The upper limit of the apparatus was 60 cm/sec.

RESULTS

Habitat Choice Experiments:

In the habitat choice experiment, adult and juvenile longnose dace used the fast habitat more than the other habitats while the fry used the slow habitat more than the others (Figure 8). Kruskal-Wallis (nonparametric analysis of variance) tests for all size classes reject the null hypothesis that the mean time spent in each habitat was the same (fry; $H_c = 6.73$ $P < 0.05$, juveniles; $H_c = 12.19$ $P < 0.005$, adults; $H_c = 6.23$ $P < 0.05$). Tukey-type multiple comparisons showed that the difference was due to the fast versus slow comparisons for all size classes (for the large size class, the fast versus slow comparison was not significant at the 0.05 confidence level but was significant at the 0.07 confidence level). Although the juveniles and adults did not use the fast channel significantly more than the medium channel, neither size class was limited by the velocities in the fast channel.

Shelter Competition Study:

The fifteen juvenile longnose dace in this study spent nearly the entire observation period under the shelter in the absence of adults (in only one case did the juvenile leave the shelter during the observation period). After adults were added, however, the average time per shelter use

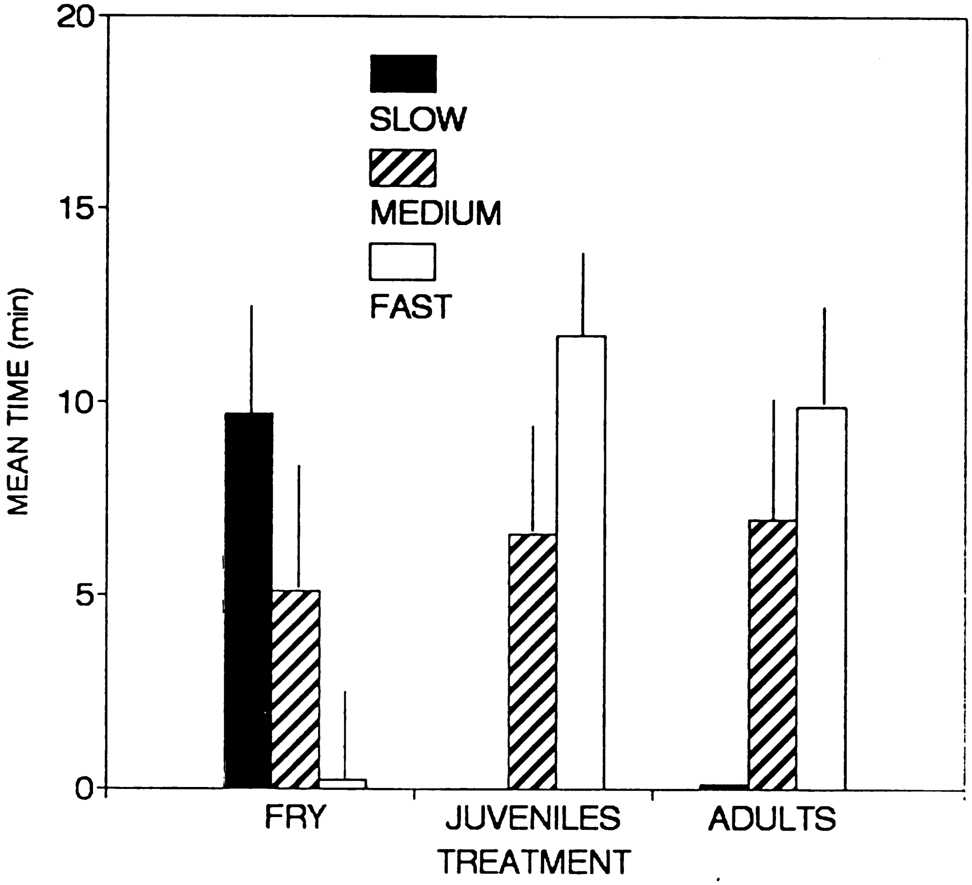

Figure 8: Mean time spent by all size classes in each of the three habitats of the maze. Bars indicate standard errors. The Kruskal-Wallis (non-parametric analysis of variance) results were significant for all size classes and the Tukey-type multiple comparison indicate that use of the fast habitat was significantly different than use of the slow habitat for all size classes.

dropped significantly (Figure 9). In seven cases the juvenile shelter use was not affected by the presence of the adults, but in three cases, the juveniles did not use the shelter when the adults were present and in five cases the juveniles exited and re-entered the shelter a number of times (1 - 6 exits). In all cases the adults spent the entire observation period under the shelters. After the adults were removed, the juvenile shelter use returned to the level observed before the adults were added (Figure 9), thirteen of the juveniles did not leave the shelter during the observation period while two exited and re-entered the shelter once. The Kruskal-Wallis results were significant ($H_c = 11.14$, $P < 0.005$). The Dunnett's-type test contrasting the initial observations with the adult present observations and with the second adult free observations indicated that the difference detected in the Kruskal-Wallis test was due to an adult affect ($q = 2.27$, $P < 0.01$) and not due to an acclimation affect.

Maximum Swimming velocity:

Of the forty one longnose dace tested, twenty four, ranging in size from 68 to 107 mm Tl were able to swim faster than the 60 cm/sec limit of the apparatus. As a result, burst velocity measurements were made on 17 longnose dace ranging in size from 41 to 74 mm Tl (Figure 10). Maximum burst velocity increased with size, with dace less

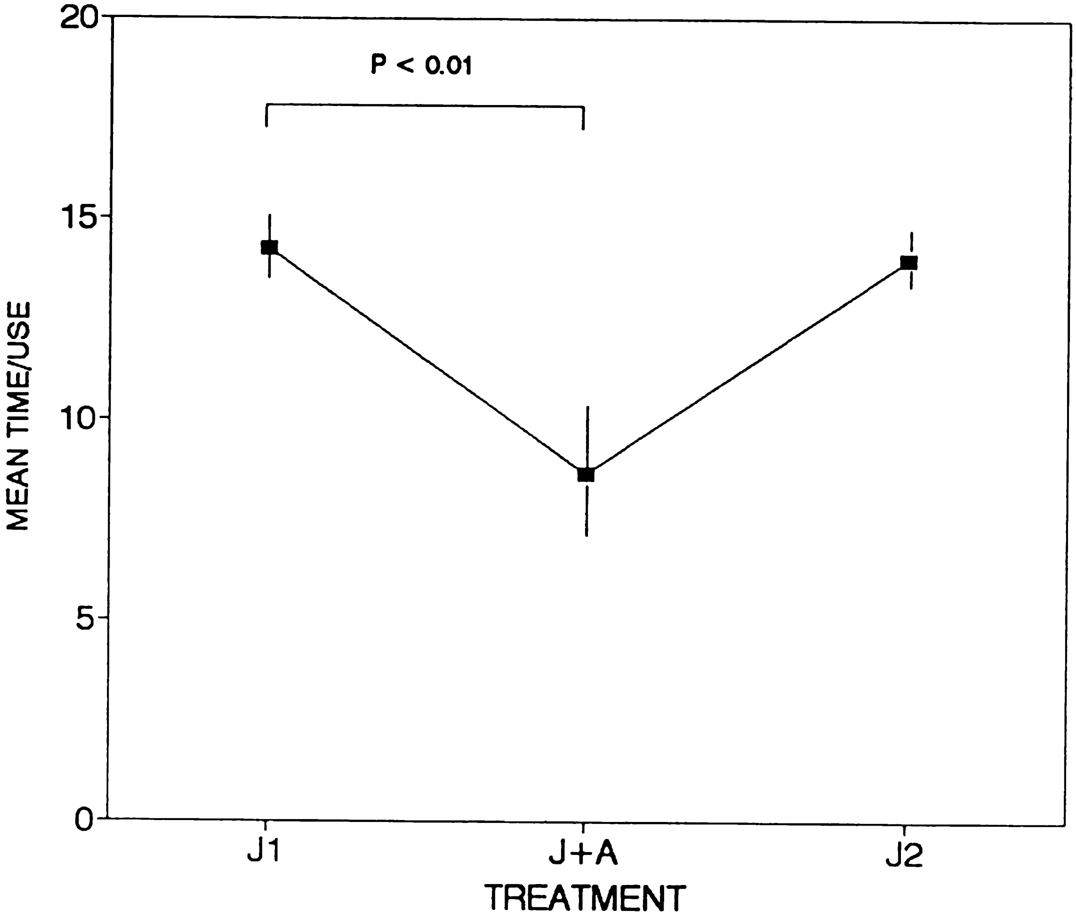

Figure 9: Mean time/use of shelters by juvenile longnose dace; before adults were added (J1), after adults were added (J+A) and after adults were removed (J2) from the experimental cages. Bars indicate standard errors. The Kruskal-Wallis (non-parametric analysis of variance) results were significant and the Dunnetts-type test indicates that the shelter use of the juveniles after the adults were added was different was different than the shelter use before the adults were added.

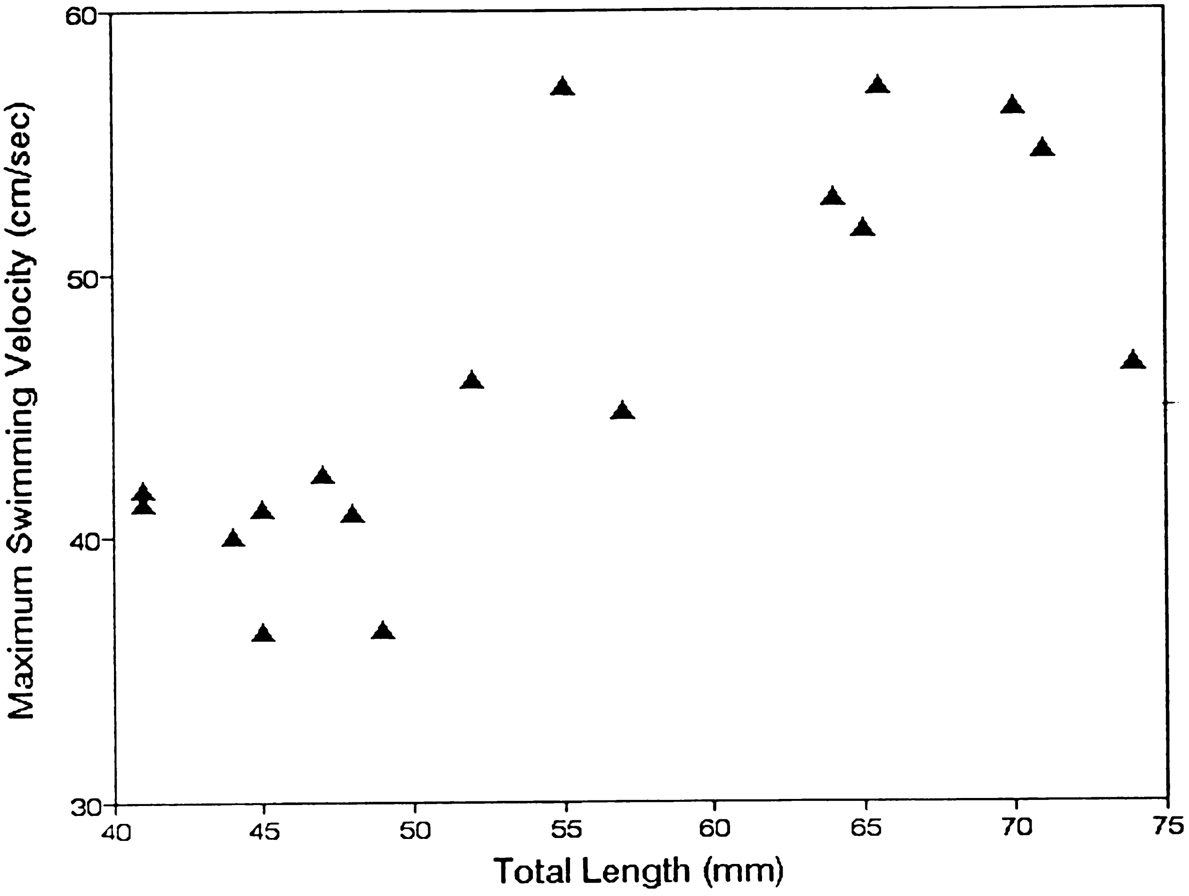

Figure 10: Maximum swimming velocities of 17 longnose dace.

than 60 mm Tl generally unable to burst faster than 50 cm/sec while dace greater than 60 mm Tl were able to burst faster than 50 cm/sec.

DISCUSSION

Both adult and juvenile longnose dace were able to utilize the fast channel in the habitat choice experiment. The dace moved around in the fast channel by staying close to the substrate surface and darting from rock to rock (frequently pausing behind a rock before moving on). The 40 - 50 cm/sec currents in the fast channel were not prohibitive to the juveniles of this size range, although, by staying close to the substrate surface, the juvenile dace may have been able to avoid prohibitive velocities. These results confirm the observation made from the habitat use survey (chapter one) that both the adults and juveniles prefer the faster areas of the riffle (Figure 5). However, the velocities in the fast channel were at the low end of the range of velocities that make up the fast habitat (higher velocities were not used because they inhibited observations in the fast channel) and higher velocities limit juvenile longnose dace in this size range (55 - 64 mm Tl).

Even though the fry in this experiment were collected from a nearby riffle, they preferred the slow channel over the medium and fast channels. This supports the hypothesis of Gibbons and Gee (1972) that longnose dace fry move out of the quiet stream margins and into the riffles in response to competition with blacknose dace fry in the stream margins. The longnose dace fry may have also been inhibited by the velocities in the faster channel, but, some fry did use the fast channel (as evidenced by the error bar in figure 8).

The effect of adults on the shelter use of the juveniles was to decrease the average time/use of the shelter. In this experiment, the juveniles were more likely to exit the shelter when the adults were present than when they were absent. However, the results obtained here were probably partly a function of the experimental design. Only one shelter was available in the cages, whereas many shelters are available in a normal riffle. The repeated exit and re-entry observed by the juveniles when adults were present would probably occur less frequently in a normal riffle where the juvenile has a choice of shelters to use. However, this study does demonstrate the significant point that adult longnose dace can and will displace a juvenile longnose dace from a shelter. This fact implies two costs to juveniles coexisting with adults in the faster areas of a riffle. First, every time a juvenile exits a shelter it increases its risk of predation (there are few predators in the faster areas of riffles, but, brook trout (<u>Salvelinus</u>

fontinalis) do forage in stream riffles and, historically, were probably more abundant than at present). Second, every time a juvenile exits a shelter it encounters the current. Even if it is physically able to swim against the current, it would still incur an energetic cost while looking for another shelter.

If adult densities are high in a riffle, and, as has been demonstrated, adults prefer the faster areas of a riffle, a juvenile using the faster areas of the riffle runs a high risk of being displaced from its shelter. There is also a fair probability that the juvenile will encounter a larger dace in the next shelter it finds, thereby increasing the cost (both energetic and predation costs) to the juvenile while it searches for an uninhabited shelter. Thus, even though the resource (shelter) is not completely limited in the faster areas of riffles, the probability of being displaced from a shelter may be high enough, for smaller longnose dace, that the gains of foraging in this high food density area are more than offset by the energetic costs of existing in the faster areas. In conclusion, even though longnose dace develop a preference for the faster areas of the riffle by the end of their first year of life, they remain segregated from the adult longnose dace in those faster areas. This segregation is probably maintained until the juveniles grow to a size where the probability of being displaced from a shelter in the faster areas by a larger dace is low enough that the energetic costs of existing in the faster areas no longer offset the gains of foraging in these high food density areas.

CHAPTER THREE

RIFFLE MANIPULATIONS

INTRODUCTION

The results from the behavioral studies indicate that the size related habitat segregation observed in the habitat use survey may be the result of both intra-specific competition for space in the faster areas of the riffle and physical limitations on hte swimming ability of smaller longnose dace. At smaller sizes (< 60 mm Tl) the longnose dace are not physically able to use the faster areas of the riffle.

The purpose of this study was to examine the roles that physical constraints on the juveniles and intra-specific competition with the adults play in determining the habitat use of juvenile longnose dace. A series of whole riffle manipulations of adult densities over a two year period was conducted in order to assess the effects of adult densities on the habitat use and diet of a single cohort of juveniles as it grew through it's first two full summers.

METHODS

Study site:

This study was conducted during the summers of 1989 and 1990 on Twomile Creek, a third order stream in Michigan's upper peninsula. The study site was located in Dickinson County, T43N, R30W, about 500 m upstream of the confluence of Twomile Creek and the Ford River. Three sequential riffles were selected for the riffle manipulation study, and a fourth was used for a study of the distribution of invertebrates on rock surfaces within a riffle.

Riffle manipulations:

During the 1989 field season, adult and juvenile dace densities were manipulated in three enclosed riffles in order to examine the effects of adult density on the habitat use of juvenile longnose dace. Three adjacent riffles in Twomile creek were enclosed with ¼ inch hardware cloth fences (Figure 11), which were cleaned daily in order to reduce their effect on the flow within the riffle. The fences were placed in pools or runs between the riffles. These fences were installed in mid-June after the late spring floods had subsided. Fish traps (weir boxes) were placed at the upstream and downstream ends of the study area to capture all fish moving upstream and downstream through the area. These traps were checked daily and all fish were hand carried around the enclosed study area and released in the direction of travel when captured.

Three treatments were used; 1) a control with no adults or juveniles removed or added, 2) a low adult treatment with all adults captured during a sample run removed, and 3) a

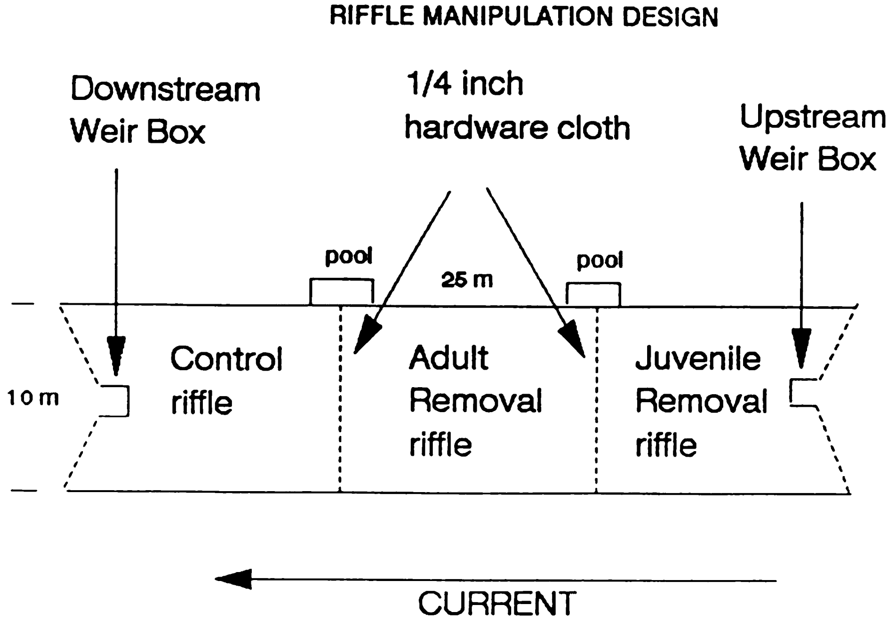

Figure 11: Design of riffle manipulations used in 1989 on Twomile Creek

low juvenile treatment with all captured juveniles removed. The riffles were 25 to 30 m long and each riffle varied in width from 5 to 10 m. Each riffle was sampled with electrofishing gear (using the procedure described in chapter one) once a week for five weeks during early summer. Data from the first sampling date (June 16) were on longnose dace in the riffles before manipulation. After sampling on that date, the juvenile and adult manipulations were executed and maintained for the next four weeks. After sampling on each date, the availability of three habitat variables; depth, mean water column velocity and substrate type was estimated using ten points on each of five evenly spaced transects in each riffle (as described in chapter one). On July 23, the fences were removed and normal fish movements were allowed for 8 days. During this period, the adult and juvenile longnose dace re-colonized the experimental riffles (see table 6 for pre-manipulation densities of adults and juveniles in each riffle). The riffles were again enclosed on August 2, and the three riffles were sampled before manipulation. Manipulations of adult and juvenile densities were then conducted and maintained for the next three weeks while the habitat use of the longnose dace in each treatment was sampled weekly.

In 1990, this design was altered to eliminate the potential confounding effects of inter-riffle differences. Only one riffle (the juvenile removal riffle in 1989) was used and manipulations of adult densities were conducted sequentially within the riffle. The riffle was isolated in the manner already described and manipulations were conducted as follows; control (sample prior to manipulation, the adults were removed immediatly after this sample) - low adult (sample of juvenile habitat use in experimental riffle one week after the adults were removed. Adults were planted in the riffle immediatly after the low adult sample was taken) - control (sample of adult and juvenile habitat use taken one week after the adults were returned to the riffle, the adults were removed immediatly after this sample was taken) - low adult. Sampling occurred once each week for four weeks in early summer and late summer. After sampling the habitat use patterns of the adults and juveniles on a control day, as many adults as possible were removed from the riffle by making multiple passes through the riffle with electrofishing gear. After sampling on a low adult density day, adults (as many as were removed the previous week) were captured from nearby riffles and placed within the enclosed riffle in order to provide normal adult densities for the following week. The first experiment lasted from June 20, 1990 to July 11. The second experiment lasted from August 1, 1990 to August 22. The enclosure was removed between experiments.

Comparisons of the velocity, depth and substrate use were made between all of the adults and juveniles captured at the start of each manipulation experiment, and between the juveniles captured in each treatment after manipulation. Two dimensional contingency table analysis using chi-square goodness of fit was used for tests of independence between each of the habitat variables and size, and between each of the habitat variables and treatments (for the juveniles). Also, as described in chapter one, chi-square goodness of fit was used to test for selectivity of each of the habitat variables by the adults and juveniles in each treatment.

Diet analysis:

During the course of the 1989 riffle manipulation studies, several longnose dace were collected for diet comparisons between the juveniles and adults. At the start of each experiment (June 21 and August 2), ten juveniles were taken from both the control and adult removal riffles and ten adults were taken from both the control and juvenile removal riffles and preserved in 70% ETOH. These fish were replaced with dace of the appropriate size class from the river at large. At the end of each experiment, ten juveniles and ten adult were taken from the control riffle and ten juveniles were taken from the adult removal riffle and ten adults were taken from the juvenile removal riffle. All invertebrates in the guts were identified to family. Invertebrates that occurred frequently (> 10%) in the guts were divided into size groups based on head capsule lengths (small = $\mathrm{HCL} < 0.5$ mm., medium = $0.5 < \mathrm{HCL} < 1.0$ mm. and large = $\mathrm{HCL} > 1.0$ mm.). Schoener's (Schoener 1970) index of dietary overlap was used to make comparisons between all adults and juveniles collected prior to manipulation. Comparisons were also made between juveniles from the control and adult removal treatments.

During the 1990 riffle manipulation studies, twenty adult and twenty juvenile longnose dace were collected on the first day of sampling (control) for both experiments (June 20 and August 1). The twenty juveniles were replaced by twenty juveniles from a nearby riffle. Also, twenty juveniles were collected for diet analysis on the first low adult sampling day of each experiment. These were also replaced by twenty juveniles from a nearby riffle. Comparisons were made between adults and juveniles in the high adult treatment, and between juveniles in the low adult treatment and juveniles in the high adult treatment.

Invertebrate distribution on rock substrates:

The distribution of stream invertebrates on substrates was examined at the end of each of the riffle manipulation studies in 1989. On June 22 and on September 8, five replicate samples of invertebrates on each of three velocity exposures (substrate surfaces) were taken from rocks (cobbles) in the fastest flowing areas of a riffle (velocities ranged from 50 to 70 cm/sec). Substrate surfaces were classified by their exposure to the current; F = fully exposed (usually the front and/or top surface of the rock), P = partially exposed (usually the sides of the rock) and N = not exposed (usually the back of the rock). A different rock was used for each exposure replicate (15 rocks were sampled on each date). Sampling of an exposure surface consisted of selecting a rock surface of the desired classification in the riffle (the riffle from which these samples were taken is mostly composed of boulders and cobble ranging in size from 15 to 30 cm maximum length and all surfaces chosen were within that range of greatest dimension), quickly picking the rock up out of the river and holding the selected surface over a bucket while vigorously brushing the invertebrates on that surface into the bucket. Care was taken to prevent invertebrates from the other surfaces of the rock from dropping into the bucket. The invertebrates were preserved in 70% ETOH and later identified to family or genus and common items were divided into size classes using the system described above for diet comparisons. For comparative purposes, the surface that was sampled was covered with foil which was trimmed to match the surface as closely as possible. This foil piece was then marked to identify the sample with which it corresponded. A leaf area meter was used to determine the surface area of the foil, and therefore, the area of the surface sampled. Comparisons of the invertebrate densities on each surface were based on numbers/m^2.

Kruskal-Wallis single factor analysis of variance by ranks was used to compare the densities of each invertebrate group on all three exposure surfaces (F, P and N). When appropriate, a nonparametric Tukey-type multiple comparison (Zar 1984) was used to determine which substrate surfaces differed from each other.

RESULTS

Riffle Manipulations:

The juvenile removals conducted in the June and August 1989 riffle manipulations were unsuccessful. In June: 20, 26, 30, 31 and 38 juveniles were captured on successive sampling dates, and in August 31, 35, 28 and 22 juveniles were captured on successive sampling dates in the juvenile removal riffle. The slight increase over time in June and the slight decrease over time in August were also observed in the other riffles indicating that the juveniles were able to move through the hardware cloth fences unimpeded (more adults than juveniles were captured in the wier boxes while the studies were taking place, however due to gear selectivity for larger fish, little can be said about differential movement patterns between the two size groups). As a result, the low juvenile treatment will be considered to be a second control (control 2) riffle in this study. Adult removal, on the other hand, significantly reduced adult densities in the low adult treatment for three of the four riffle manipulation studies (August 1989, and June and August 1990) (Table 6). In the June 1989 study, the adult manipulation was ineffective in the low adult treatment. This riffle contained a low density of adults prior to manipulation.

Comparisons of the three riffles used in the 1989 studies indicated that these three riffles were different (Table 7). The control 2 riffle had more deep water, fast water and boulders than the other two, while the other two were well matched by depth and velocity but not by substrate. In addition, the three riffles differed in their habitat associations; in the control 1 riffle, substrate size was associated with depth (boulders were found in deeper water) and velocity (boulders were found in slower water), in the control 2 riffle, substrate size was associated with depth (boulders in deeper water) but velocity was not associated with substrate size or depth, in the low adult riffle, velocity and depth were positively associated (faster velocities in deeper areas) but substrate size was not associated with depth or velocity. Due to these inter-riffle differences, the results of the 1989 riffle manipulations are difficult to interpret. The protocol of the 1990 riffle manipulations was altered (as

Table 6: Juvenile and adult densities (numbers/m^2) in each treatment during each of the riffle manipulation studies in 1989 and 1990. The densities are corrected for estimated capture efficiencies of 50 % for juveniles and 60 % for adults (see chapter 1 for details on the determination of capture efficiencies). The values in parentheses with the 1989 data indicate the pre-manipulation densities for each treatment. Pre-manipulation densities for the 1990 studies are the control densities.

Date	Density (#/m2)	
Treatment	Juveniles	Adults
June 1989		
Control 1	0.652 (0.420)	0.180 (0.203)
Control 2	0.376 (0.238)	0.265 (0.085)
Low adult	0.706 (0.268)	0.118 (0.100)
August 1989		
Control 1	0.490 (0.498)	0.125 (0.168)
Control 2	0.406 (0.438)	0.225 (0.353)
Low adult	0.456 (0.448)	0.068 (0.192)
June 1990		
Control	0.182	0.188
Low adult	0.214	0.053
August 1990		
Control	0.268	0.187
Low adult	0.182	0.118

Table 7: Comparison of the habitat availabilities of each habitat variable in each of the three riffles used in the 1989 riffle manipulation studies. The data are the proportions of each habitat variable in each riffle.

	Riffle		
Habitat variable	Control 1	Low adult	Control 2
Shallow (< 15 cm)	0.51	0.48	0.42
Deep (> 15 cm)	0.49	0.52	0.58
Slow (< 40 cm/sec)	0.86	0.88	0.69
Fast (> 40 cm/sec)	0.14	0.12	0.31
Boulder	0.19	0.30	0.40
Other	0.81	0.70	0.60

discussed in methods) to eliminate inter-riffle effects.

In the June 1989 manipulation, the adults and juveniles were not segregated by depth in the three riffles before manipulation or in the control 1 riffle after manipulation (Table 8). However, the adults and juveniles were segregated by depth in the control 2 riffle, and in the low adult riffle. In the control 2 riffle, the juveniles selected shallow water (Figure 12), while in the control 1 riffle the juveniles were not selective of depth, and before manipulation, the juveniles selected mid range depths In the low adult riffle, the juveniles did not select a particular depth range but did avoid deep areas. There is no apparent pattern to suggest an adult affect on the depth selection of the juveniles. Contingency table analysis of the depth use of the juveniles in the low adult riffle versus the depth use of the juveniles in the control 1 riffle (Table 9) and versus the depth use of the juveniles in the control 2 riffle (Table 10) indicated that the depth use was similar across treatments and was not affected by adult densities. The different selection patterns illustrated in Figure 11 may reflect inter-riffle differences in availability. For instance, about 42% of the control 2 riffle was shallow, compared to 51% for the control 1 riffle and 48% for the low adult riffle. Since the juveniles in each treatment used the shallow areas in similar proportions (Tables 9 and 10), they showed stronger selection for shallow areas in the

Table 8: Contingency table analysis (using chi-square goodness of fit) of first order interactions between size and each of the habitat variables in unmanipulated (Initial) and manipulated riffles in the June 1989 riffle manipulation study. The sign next to chi-square values greater than 0.5 indicates the direction of the difference (observed - expected).

Size	Depth		Velocity		Substrate Type	
	Shallow	Deep	Slow	Fast	Boulder	Other
			Before			
Juveniles						
Observed	16	186	160	42	58	144
chi-square	0.04	0.00	1.69+	3.33-	1.36-	0.69+
Adults						
Observed	8	78	48	37	38	47
chi-square	0.09	0.01	3.00-	7.90+	3.25+	1.63-
Significance	NS		$p < 0.001$		$p < 0.025$	
			Control 1			
Juveniles						
Observed	238	304	430	112	96	446
chi-square	0.00	0.00	0.29	0.82-	5.62-	1.64+
Adults						
Observed	65	83	105	45	60	90
chi-square	0.00	0.00	1.04-	3.56+	20.31+	5.91-
Significance	NS		$p < 0.025$		$p < 0.001$	
			Low Adult			
Juveniles						
Observed	252	330	474	108	216	366
chi-square	2.33+	1.51-	0.94+	3.30-	0.96-	0.63+
Adults						
Observed	15	82	55	42	53	43
chi-square	14.01-	9.06+	5.61-	19.83+	5.83+	3.83-
Significance	$p < 0.001$		$p < 0.001$		$p < 0.001$	
			Control 2			
Juveniles						
Observed	118	132	202	48	110	140
chi-square	5.46+	3.36-	3.29+	8.11-	3.05-	3.30-
Adults						
Observed	48	138	108	78	117	70
chi-square	7.34-	4.51+	4.43-	10.89+	4.08+	4.41-
Significance	$p < 0.001$		$p < 0.001$		$p < 0.001$	

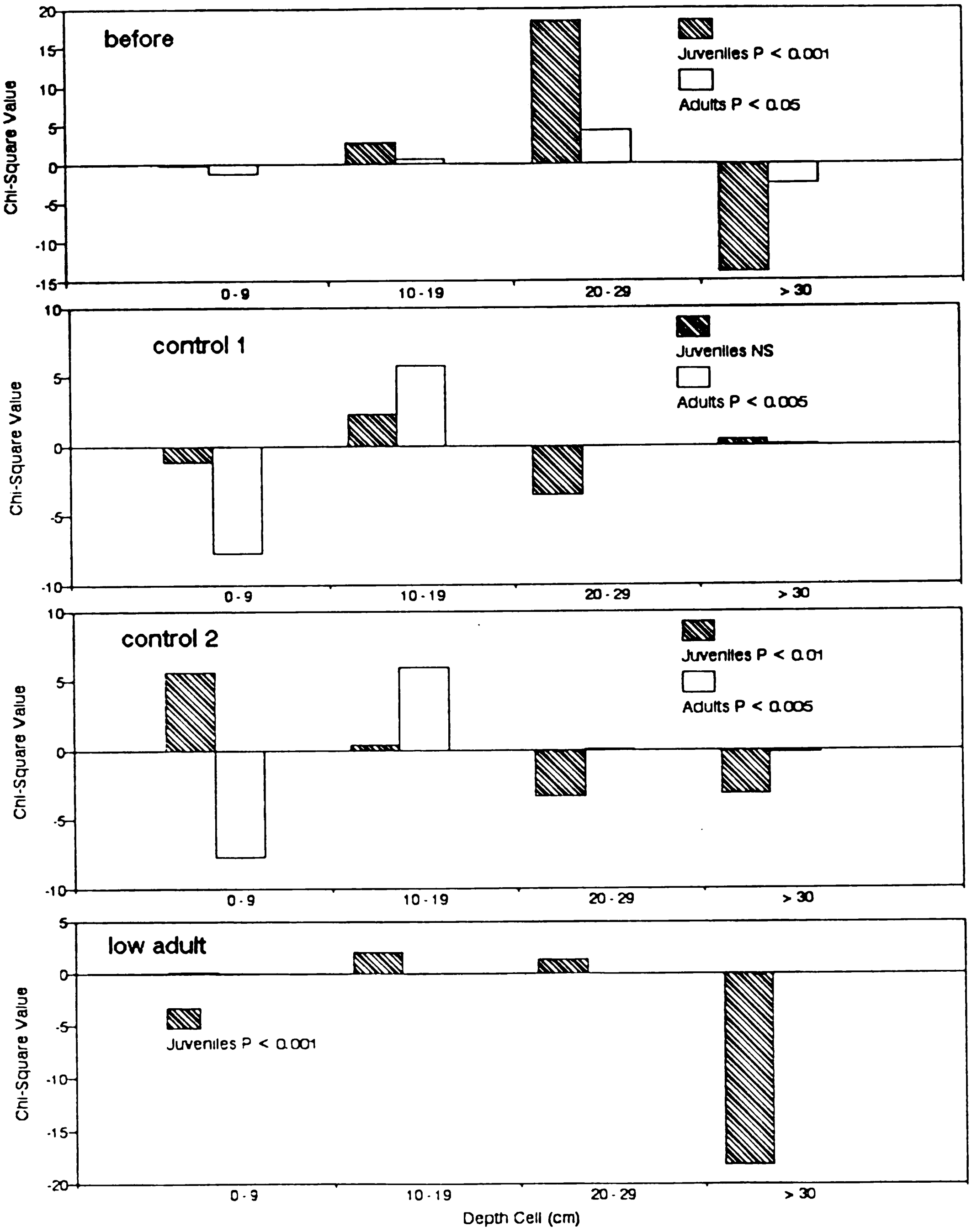

Figure 12: Chi-square analysis of the depth distribution of juvenile and adult longnose dace captured in each treatment during the June 1989 riffle manipulation study.

Table 9: Contingency table analysis (using chi-square goodness of fit) of first order interactions between the control 1 and low adult treatments and the use of each of the habitat variables by the juveniles in each treatment for each riffle manipulation study in 1989. The sign next to chi-square values greater than 0.5 indicates the direction of the difference (observed - expected).

Size	Depth		Velocity		Substrate type	
	Shallow	Deep	Slow	Fast	Boulder	Other
			June 1989			
Low Adult						
Observed	252	330	474	108	216	366
chi-square	0.01	0.00	0.07	0.31	18.31+	7.04-
Control 1						
Observed	238	304	430	112	96	446
chi-square	0.01	0.00	0.08	0.33	19.67-	7.56+
Significance	NS		NS		p < 0.001	
			August 1989			
Low Adult						
Observed	126	144	224	46	88	182
chi-square	4.29-	5.49+	3.03+	8.57-	12.84+	3.68-
Control 1						
Observed	196	108	200	104	40	264
chi-square	3.81+	4.87-	2.69-	7.62+	11.39-	3.27+
Significance	p < 0.001		p < 0.001		p < 0.001	

Table 10: Contingency table analysis (using chi-square goodness of fit) of first order interactions between treatments and the use of each of the habitat variables by the juveniles in each treatment for each riffle manipulation study in 1989 and 1990. The sign next to chi-square values greater than 0.5 indicates the direction of the difference (observed - expected).

Size	Depth		Velocity		Substrate type	
	Shallow	Deep	Slow	Fast	Boulder	Other
			June 1989			
Low Adult						
Observed	252	330	474	108	216	366
chi-square	0.17	0.14	0.00	0.00	0.64-	0.40
Control 2						
Observed	118	132	202	48	110	140
chi-square	0.42	0.33	0.00	0.04	1.46+	0.94-
Significance	NS		NS		NS	
			August 1989			
Low Adult						
Observed	126	144	224	46	88	182
chi-square	0.12	0.12	0.30	1.18-	0.08	0.06
Control 2						
Observed	86	84	128	42	60	110
chi-square	0.20	0.18	0.48	1.88+	0.14	0.06
Significance	NS		$p = 0.05$		NS	
			June 1990			
Low Adult						
Observed	30	24	28	26	22	32
chi-square	0.56	0.52	2.36-	5.32+	0.10	0.06
Control						
Observed	36	46	66	16	30	52
chi-square	0.36	0.34	1.56+	2.36-	0.06	0.04
Significance	NS		$p < 0.001$		NS	
			August 1990			
Low Adult						
Observed	14	58	30	42	36	36
chi-square	0.16	0.04	2.16-	2.58+	0.08	0.06
Control						
Observed	26	86	70	42	52	60
chi-square	0.10	0.02	1.40+	1.66-	0.04	0.04
Significance	NS		$p < 0.01$		NS	

control 2 riffle where the shallow areas were less abundant.

In the August 1989 riffle manipulation study, the adults and juveniles were not segregated by depth in the three riffles before manipulation but they were segregated by depth in each of the riffles after manipulation (Table 11). In all cases except the control 2 riffle, the juveniles selected mid range depths, in the control 2 riffle, the juveniles did not select any specific depth range (Figure 13). A comparison of the depth use of the juveniles in the low adult riffle versus the depth use of the juveniles in the control 1 riffle indicated that the distributions were different (Table 9), however, there was no difference in the depth use of the juveniles in the low adult treatment and the juveniles in the control 2 treatment (Table 10). The juveniles in the control 1 riffle used the shallow areas in a higher proportion than the juveniles in the low adult riffle (Table 9), but the selection patterns for these two riffles were similar (Figure 13). This also appears to be due to inter-riffle differences in availability. About 41% of the control 1 riffle was between 10 and 19 cm deep, while only 27% of the low adult riffle fell within that range. Even though a lower proportion of the juveniles in the low adult riffle used this depth range (51%) than did the juveniles in the control 1 riffle (60%), the lower proportion of the available habitat that fell

Table 11: Contingency table analysis (using chi-square goodness of fit) of first order interactions between size and each of the habitat variables in unmanipulated (Initial) and manipulated riffles in the August 1989 riffle manipulation study. The sign next to chi-square values greater than 0.5 indicates the direction of the difference (observed - expected).

Size	Depth		Velocity		Substrate type	
	Shallow	Deep	Slow	Fast	Boulder	Other
			Before			
Juveniles						
Observed	118	150	210	58	96	172
chi-square	0.60+	0.42	0.68+	1.93-	0.44	0.27
Adults						
Observed	42	80	78	43	53	68
chi-square	1.31-	0.91+	1.50-	4.29+	0.97+	0.60-
Significance	NS		$p < 0.005$		NS	
			Control 1			
Juveniles						
Observed	196	108	200	104	40	264
chi-square	0.94+	1.42-	0.00	0.00	0.60-	0.10
Adults						
Observed	35	45	53	27	17	62
chi-square	3.57-	5.38+	0.00	0.00	2.29+	0.40
Significance	$p < 0.001$		NS		NS	
			Low Adult			
Juveniles						
Observed	126	144	224	46	88	182
chi-square	0.90+	0.67-	0.37	1.44-	0.20	0.10
Adults						
Observed	7	33	23	17	18	22
chi-square	6.05-	4.56+	2.48-	9.78+	1.35+	0.70-
Significance	$p < 0.001$		$p < 0.001$		NS	
			Control 2			
Juveniles						
Observed	86	84	128	42	60	110
chi-square	5.99+	3.81-	4.66+	7.68-	3.26-	2.61-
Adults						
Observed	17	78	37	58	58	37
chi-square	10.73-	6.82+	8.33-	13.77+	5.83+	4.68-
Significance	$p < 0.001$		$p < 0.001$		$p < 0.001$	

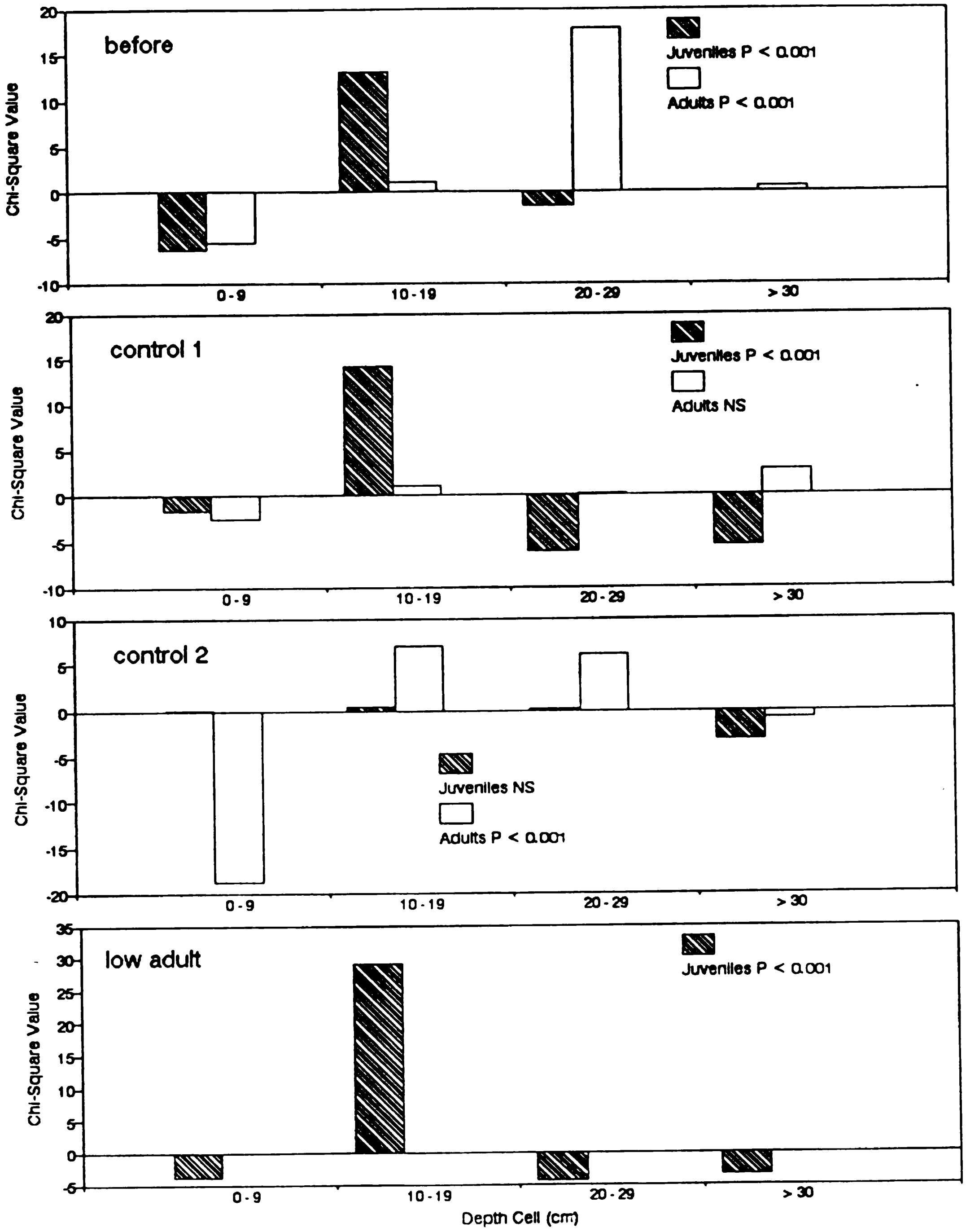

Figure 13: Chi-square analysis of the depth distribution of juvenile and adult longnose dace captured in each treatment during the August 1989 riffle manipulation study.

within that range combined with the lowered proportion of juvenile use of that range to produce a selection pattern that was similar to the pattern exhibited in the control 1 riffle. The difference in the depth use of the juveniles in the low adult riffle and the control 1 riffle may be related to adult densities, however, there was no difference in the depth use of the juveniles in the low adult riffle and the control 2 riffle (Table 10), indicating that adult densities had no affect on the depth use of the juveniles.

In the 1990 riffle manipulations, the adults and juveniles were segregated by depth in the control treatments in June but not in August (Table 12). Two days prior to the last sampling day of the June manipulation (a low adult sample), a storm event raised the water levels and washed out a portion of the weirs allowing the adults into the experimental riffle. The data from this date were not used due to the high adult densities and the high water velocities. In June, the juveniles were found in shallow waters in a higher proportion than the adults (Table 12). In the control treatment, the juveniles were not selective of depth (Figure 14), but they selected shallower areas (< 10 cm deep) in the low adult treatment. However, this selection was weak and contingency table analysis of the depth use of the juveniles in the low adult treatment versus the depth use of the juveniles in the control treatment indicated that there was no difference in the depth use of

Table 12: Contingency table analysis (using chi-square goodness of fit) of first order interactions between size and each of the habitat variables in unmanipulated riffles at the start of each riffle manipulation study in 1990. The sign next to chi-square values greater than 0.5 indicates the direction of the difference (observed - expected).

Size	Depth		Velocity		Substrate type	
	Shallow	Deep	Slow	Fast	Boulder	Other
			June 1990			
Juveniles						
Observed	36	46	66	16	30	52
chi-square	6.00+	2.48-	7.78+	10.39-	1.32-	1.09+
Adults						
Observed	15	77	33	58	48	43
chi-square	5.33-	2.22+	7.00-	9.38+	1.20+	0.98-
Significance	$p < 0.001$		$p < 0.001$		$p < 0.05$	
			August 1990			
Juveniles						
Observed	26	86	70	42	52	60
chi-square	0.34	0.09	1.53+	1.79-	3.60-	5.48+
Adults						
Observed	13	63	32	45	62	15
chi-square	0.50-	0.13	2.22-	2.60+	5.24+	7.95-
Significance	NS		$p < 0.005$		$p < 0.001$	

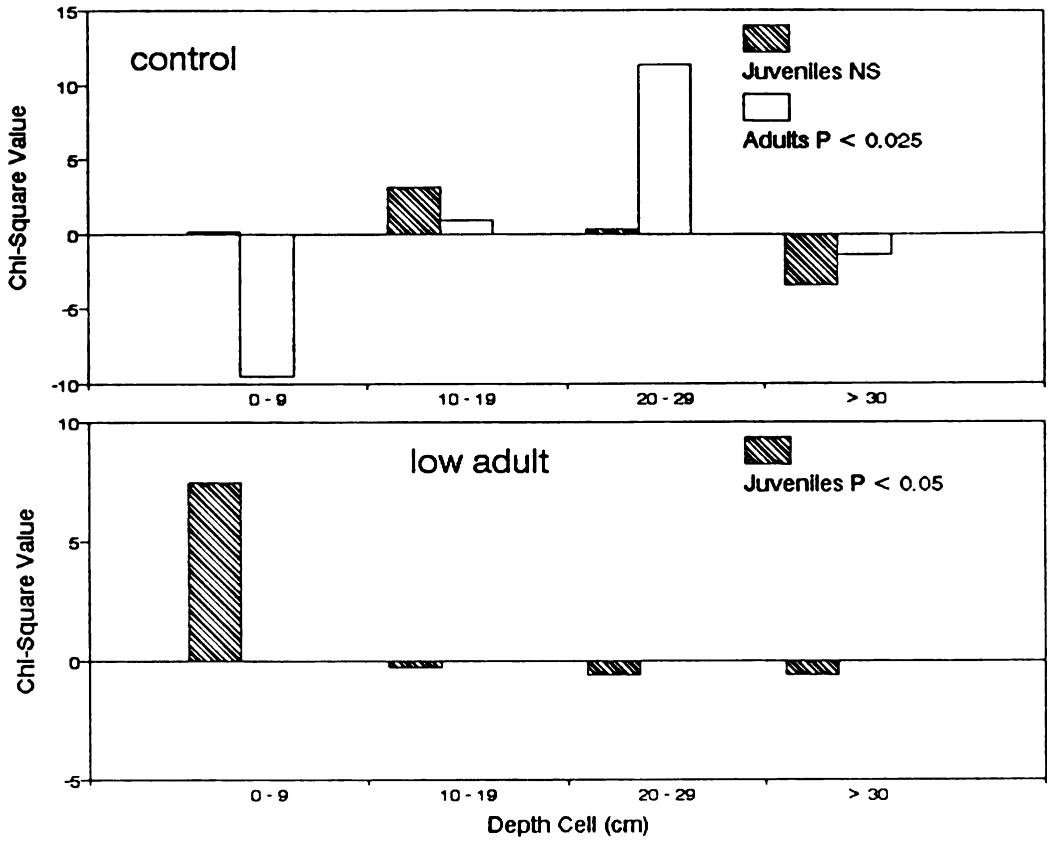

Figure 14: Chi-square analysis of the depth distribution of juvenile and adult longnose dace captured in each treatment during the June 1990 riffle manipulation study.

the two groups of juveniles (Table 10). In August of 1990, the juveniles in both treatments avoided shallow areas (< 10 cm deep) although not significantly so in the control treatment (Figure 15). Contingency table analysis of the depth use of the juveniles in each treatment indicated that adult removal had no effect on the depth use of the juveniles (Table 10).

The juveniles and adults were segregated by substrate size in all treatments in the June 1989 riffle manipulation (Table 8). In all cases, the adults selected boulders (Figure 16) while the juveniles were either non-selective of substrate size (before manipulation and control 2), avoided large substrates (control 1) or selected large substrates (low adult). The substrate use of the juveniles in the low adult riffle was not significantly different than that of the juveniles in the control 2 riffle (Table 10) but was different than the substrate use of the juveniles in the control 1 riffle (Table 9). In the August 1989 riffle manipulation, the juveniles and adults were segregated by substrate type in the control 2 riffle (Table 11) but not in the other riffles. In all cases, the juveniles were not selective of either substrate type (Figure 17), although there was a trend toward avoidance of boulders by the juveniles in the control 1 riffle. The substrate use of the juveniles in the low adult riffle was similar to that of the juveniles in the control 2 riffle (Table 10) but different

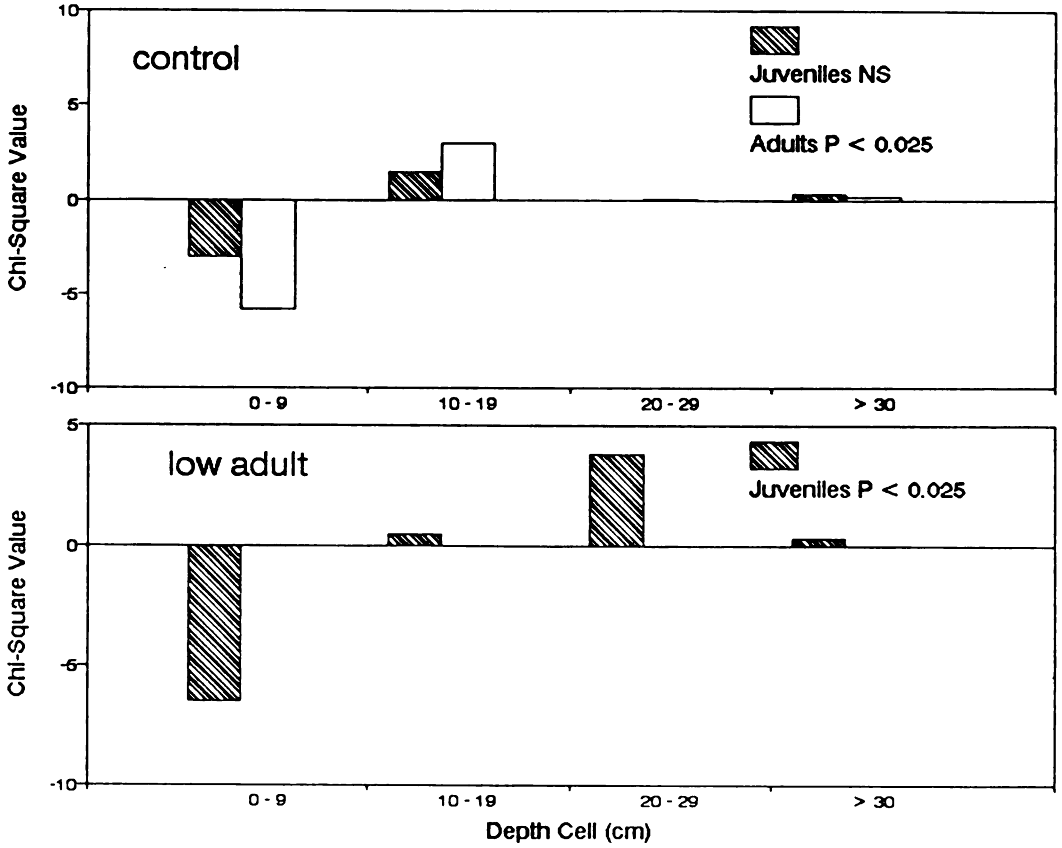

Figure 15: Chi-square analysis of the depth distribution of juvenile and adult longnose dace captured in each treatment during the August 1990 riffle manipulation study.

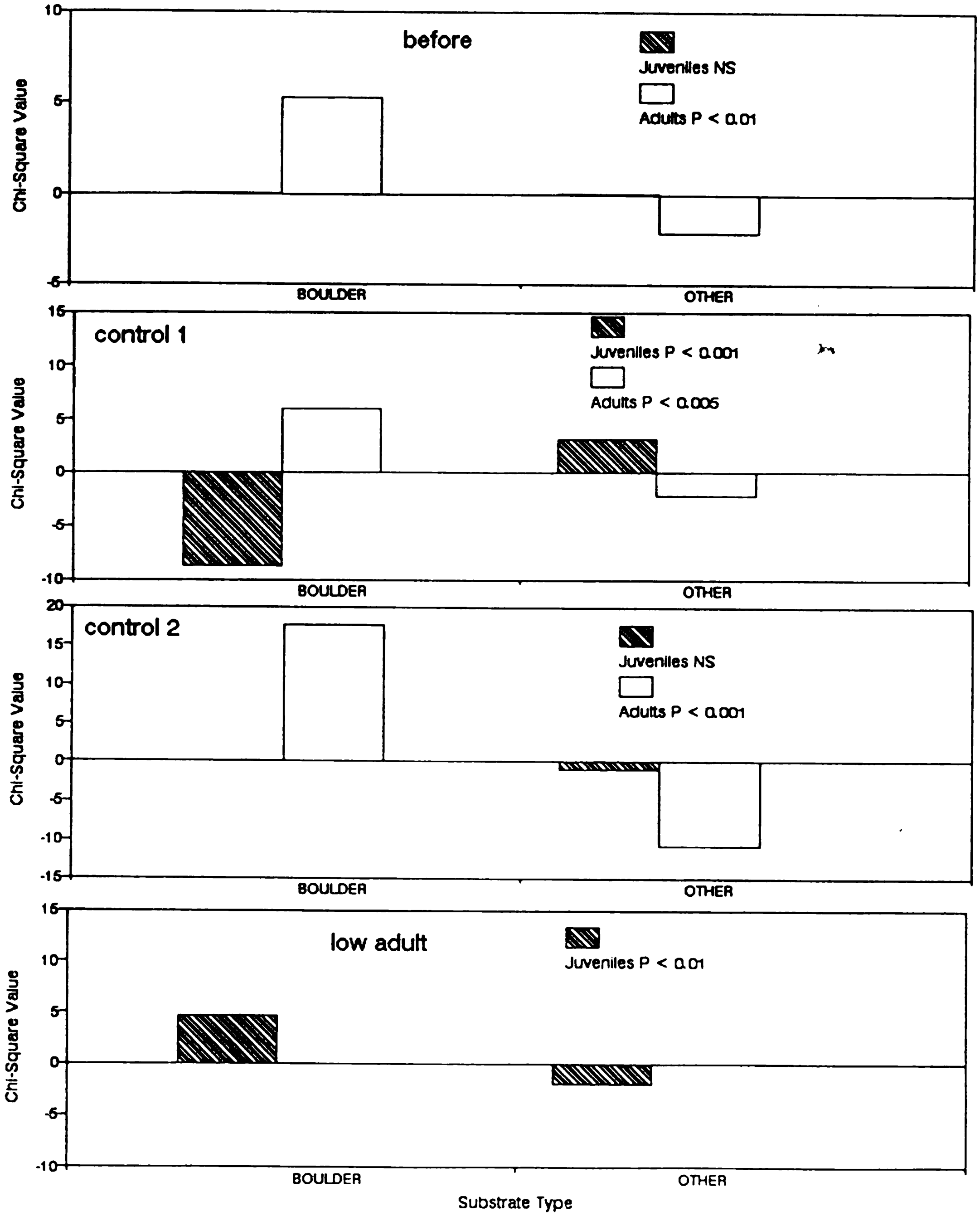

Figure 16 Chi-square analysis of substrate use patterns of juvenile and adult longnose dace captured in each treatment during the June 1989 riffle manipulation study.

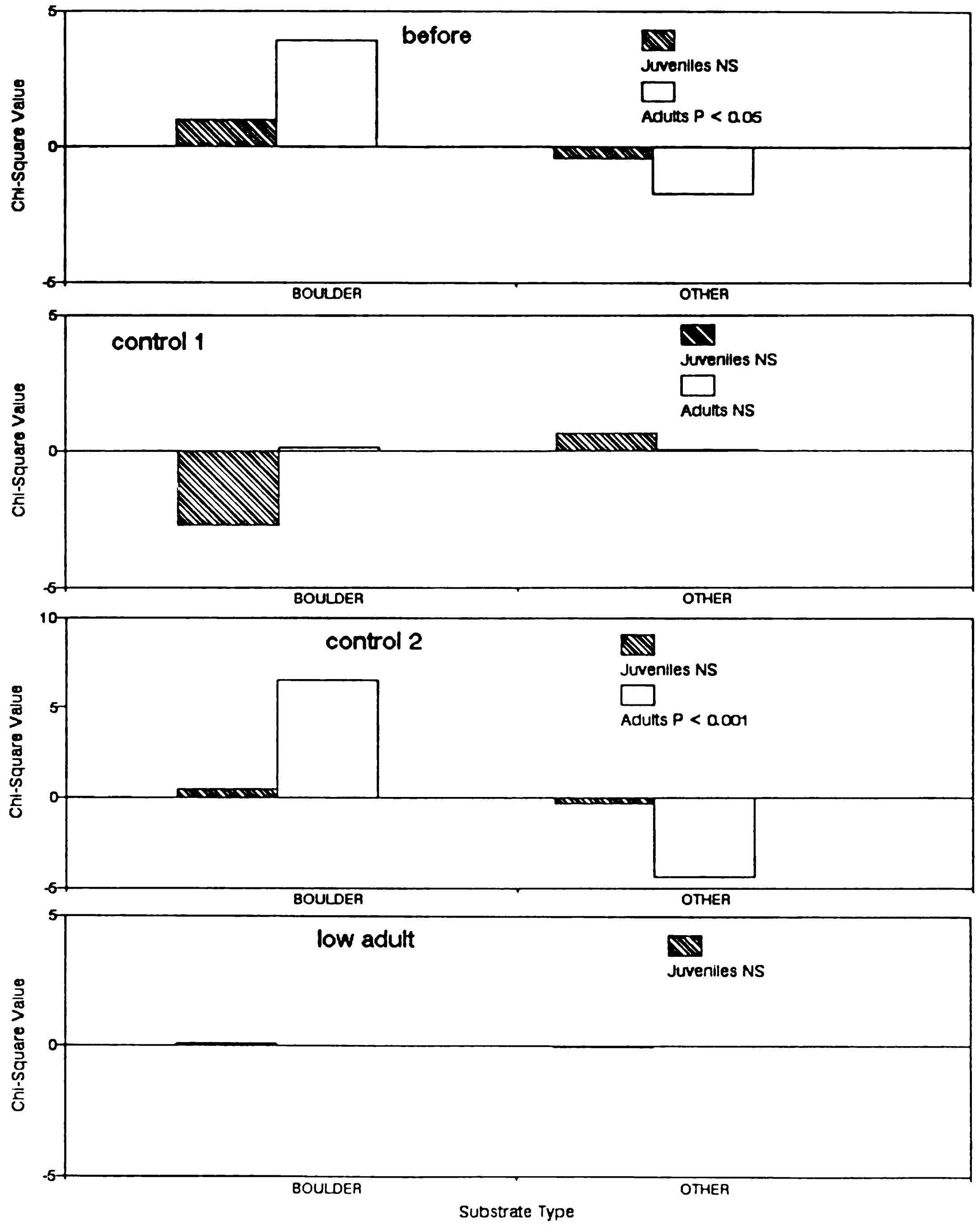

Figure 17: Chi-square analysis of substrate use patterns of juvenile and adult longnose dace captured in each treatment during the August 1989 riffle manipulation study.

to that of the juveniles in the control 1 riffle (Table 9). In both the June and August riffle manipulation studies, the juveniles in the control 1 riffle displayed some degree of avoidance of boulders (Figures 16 and 17). This may be related to inter-riffle differences in habitat variable associations. In the control 1 riffle (and not in the other two riffles), boulders were associated with slow velocities and (as discussed below) the juveniles in this riffle used faster velocities than did the juveniles in the control 2 and low adult riffles.

The adults and juveniles were segregated by substrate type in the control treatments of both the June and August 1990 studies (Table 12). In both cases, the adults selected boulders and the juveniles were not selective of substrate type (Figures 18 and 19). Contingency table results from the analysis of the substrate use of the juveniles in the low adult treatments versus that of the juveniles in the control treatments for both studies were non-significant, indicating that the adult removal had no effect on the substrate use of the juveniles (Table 10).

During the June 1989 riffle manipulation study, the adult and juvenile longnose dace were segregated by velocity before manipulation and in all treatments after manipulation (Table 8). Before manipulation and in the control 1 riffle, the adults did not select a particular velocity range, but they selected faster velocities in the control 2 riffle

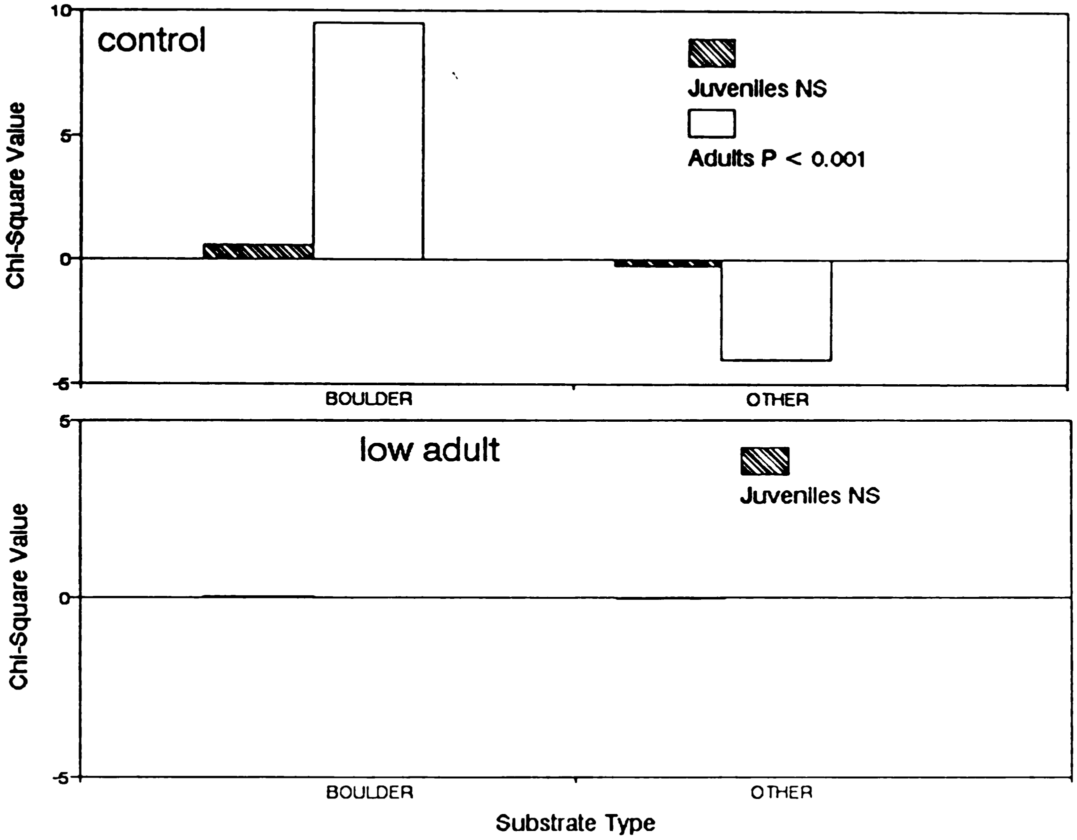

Figure 18: Chi-square analysis of substrate use patterns of juvenile and adult longnose dace captured in each treatment during the June 1990 riffle manipulation study.

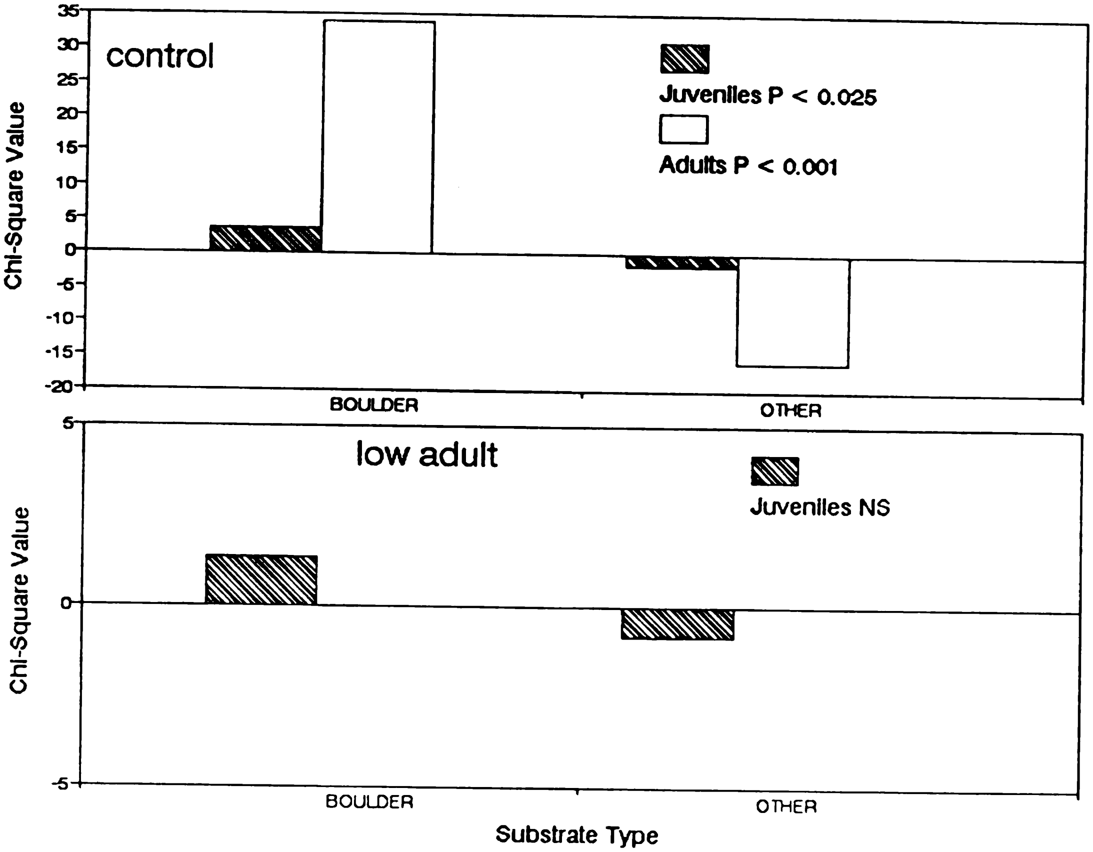

Figure 19: Chi-square analysis of substrate use patterns of juvenile and adult longnose dace captured in each treatment during the August 1990 riffle manipulation study.

(Figure 20). In all cases, the juveniles selected mid-range velocities and avoided high velocities. Contingency table analysis of the velocity use of the juveniles in the low adult riffle versus the velocity use of the juveniles in the control 1 riffle (Table 9) and versus the velocity use of the juveniles in the control 2 riffle (Table 10) indicated that adult densities had no effect on the velocity use of the juveniles. In August of 1989, the adults and juveniles were segregated by velocity before manipulation and in the low adult and control 2 riffles after manipulation (Table 11). In the control 1 riffle, however, there was no size related segregation by velocity. Contingency table analysis of the velocity use of the juveniles in the low adult riffle versus the velocity use of the juveniles in the control 1 riffle (Table 9) and the velocity use of the juveniles in the control 2 riffle (Table 10) indicated that the juveniles in the low adult riffle used velocity differently than the juveniles in the control riffles. In both cases, the juveniles in the low adult riffle used slower velocities than the juveniles in the control riffles. The juveniles in the low adult riffle selected velocities between 30 and 49 cm/sec, while in the control 1 riffle they strongly selected velocities between 40 and 49 cm/sec and in the control 2 riffle they were not selective of velocity (Figure 21). However, velocities > 40 cm/sec in the control 2 riffle were much more abundant (31%) than they were in the low adult

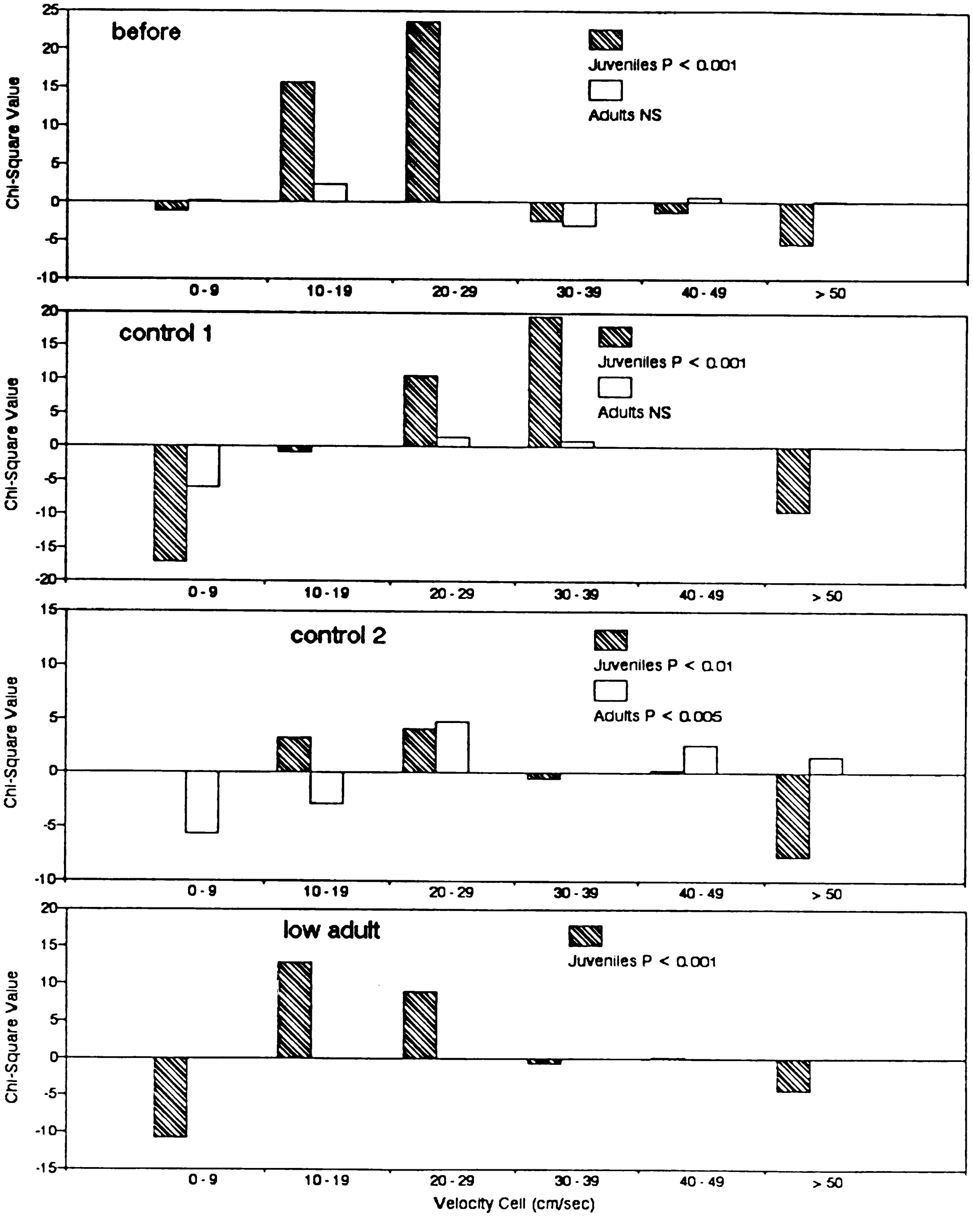

Figure 20: Chi-square analysis of velocity distributions of juvenile and adult longnose dace captured in each treatment during the June 1989 riffle manipulation study.

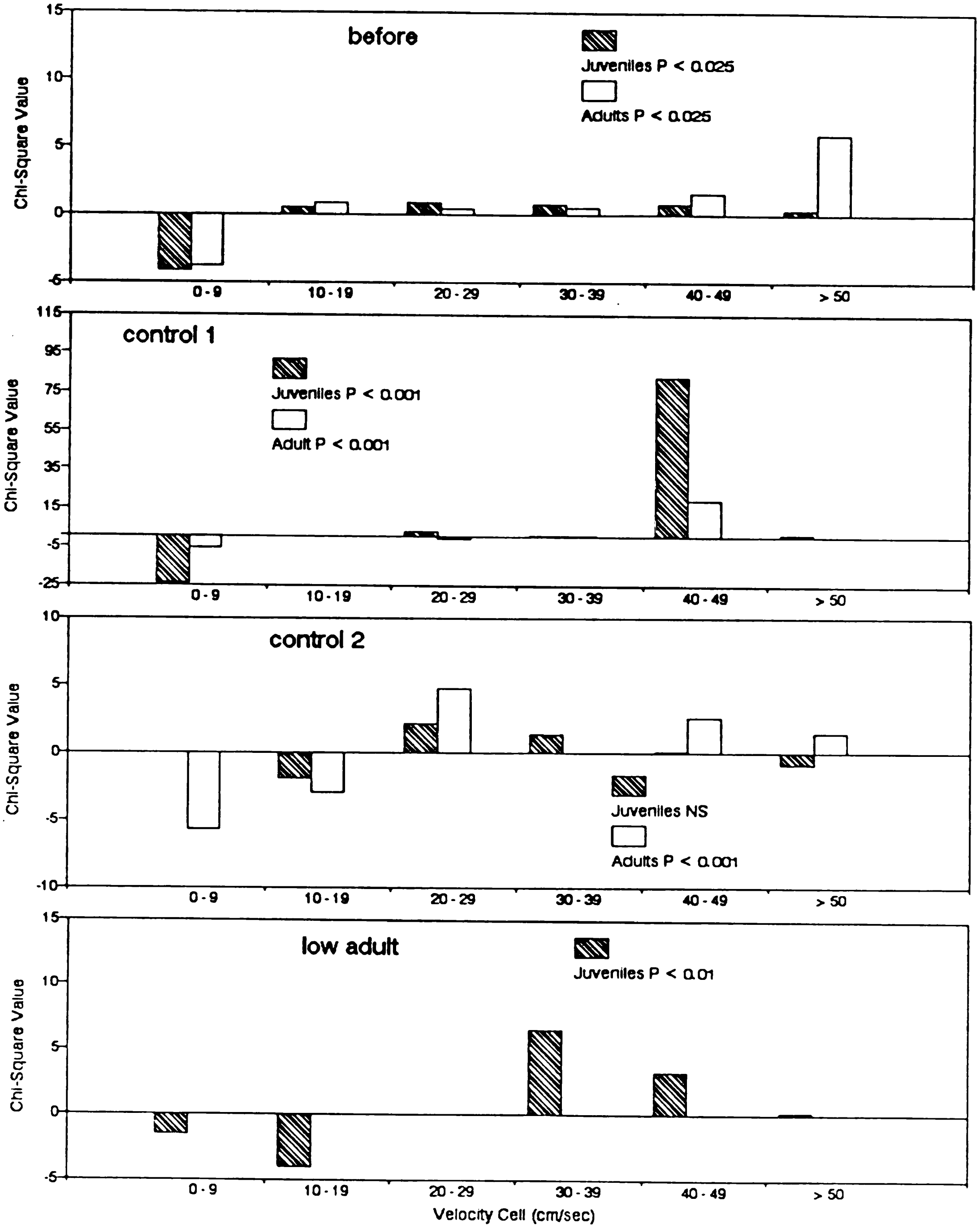

Figure 21: Chi-square analysis of velocity distributions of juvenile and adult longnose dace captured in each treatment during the August 1989 riffle manipulation study.

riffle (12%), accounting for the different selection patterns seen between these riffles. The juveniles in the control 2 riffle used these faster velocities in a higher proportion than the juveniles in the low adult riffle (Table 10), but since the faster velocities were more scarce in the low adult riffle, the juveniles in the low adult riffle showed stronger selection for faster velocities (Figure 21). Since the juveniles used slower velocities in the low adult riffle than in the other riffles, and adults generally use higher velocities than the juveniles, the difference in the juvenile velocity use observed between the low adult riffle and the two control riffles was not related to adult removal.

The adults and juveniles were segregated by velocity in control treatments during both of the 1990 riffle manipulations (Table 12). Contingency table analysis of the velocity use of the juveniles in the low adult treatments versus that of the juveniles in the control treatments for both studies indicated that the juveniles responded to adult removal by moving into faster water (Table 10). In June 1990, this move involved a change in selection from 20 - 39 cm/sec with adults present to non-selective in the absence of adults (but with a trend towards selecting velocities between 40 and 49 cm/sec) (Figure 22). In August 1990, for the first time in this study, the juveniles responded to adult removal by moving into the fastest areas of the riffle

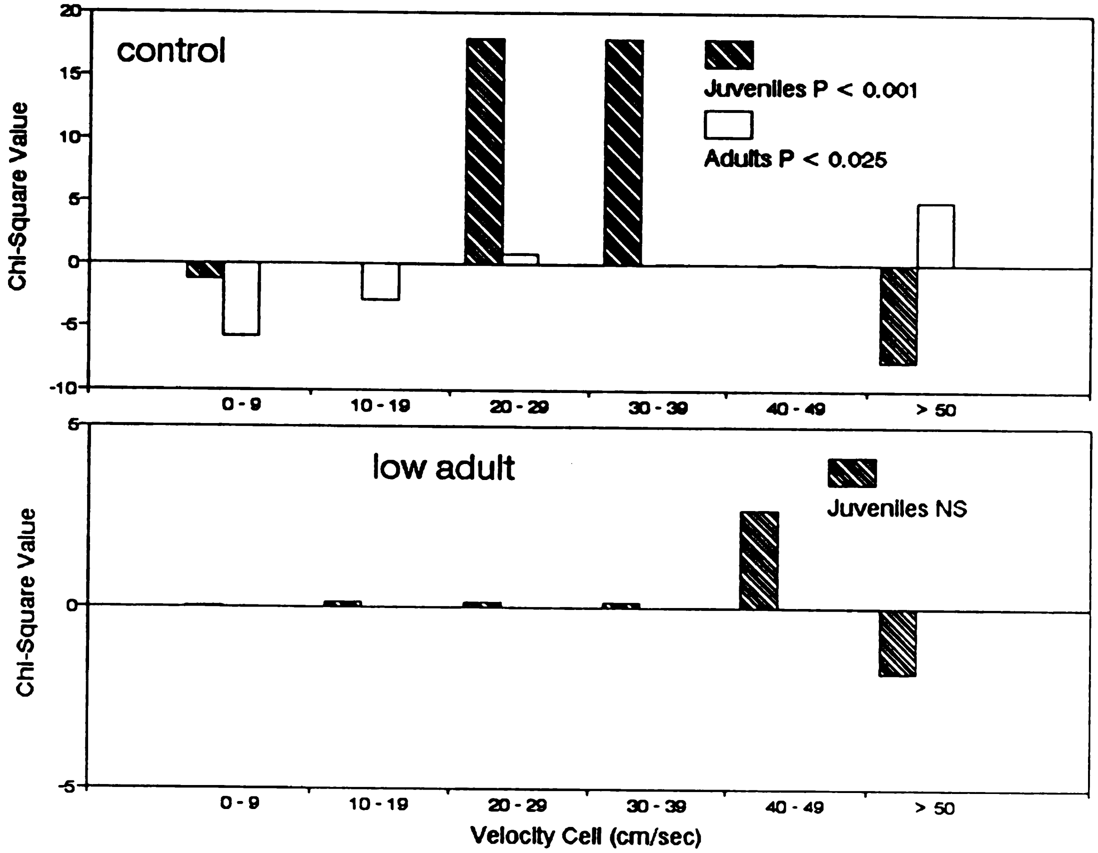

Figure 22: Chi-square analysis of velocity distributions of juvenile and adult longnose dace captured in each treatment during the June 1990 riffle manipulation study.

(Figure 23).

The design of the riffle manipulation studies in 1989 was plagued by inter-riffle differences in habitat availability (Table 7) and by ineffective manipulations of adult densities in the June study (Table 6). As a result, few conclusions can be made from this data. However, by comparing the habitat use of the juveniles in the low adult riffle after manipulation with the habitat use of the juveniles in that riffle before manipulation for the August 1989 study (adult density manipulations were ineffective for the June study but reduced the adult densities by about 65% in the August study), it is possible to assess the effects of the adults on the habitat use of the juveniles for that period. There was no change in the depth use and the substrate use of the juveniles in this riffle after manipulation (Table 13), however, there was a change in the velocity use. The juveniles used faster velocities before the adults were removed than they did after the adults were removed. Since velocity segregation between the size classes involved the adults using higher velocities than the juveniles, adult removal does not explain this shift into slower water by the juveniles after the adults were removed. Adult longnose dace had no apparent effect on the habitat use of the juveniles in the August 1989 riffle manipulation study.

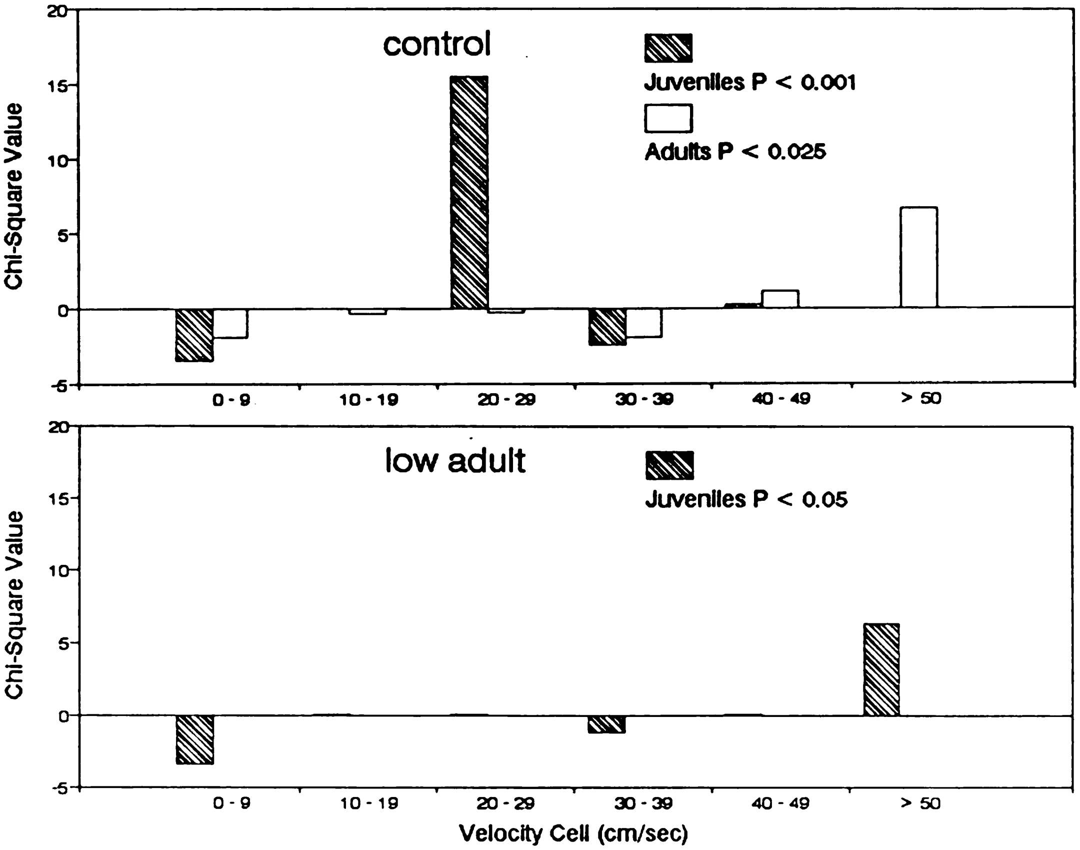

Figure 23: Chi-square analysis of velocity distributions of juvenile and adult longnose dace captured in each treatment during the August 1990 riffle manipulation study.

Table 13: Contingency table analysis (using chi-square goodness of fit) of first order interactions between juvenile habitat use in the low adult riffle before to manipulation of adult densities in August 1989 and juvenile habitat use in that riffle after adult removal. The sign next to chi-square values greater than 0.5 indicates the direction of the difference (observed - expected).

Size	Depth		Velocity		Substrate type	
	Shallow	Deep	Slow	Fast	Boulder	Other
Before						
Observed	48	50	72	26	38	60
chi-square	0.06	0.06	0.59-	2.41+	0.58+	0.30
After						
Observed	126	144	224	46	88	182
chi-square	0.02	0.02	0.21	0.88-	0.21	0.11
Significance	NS		$p < 0.05$		NS	

Diet analysis:

The dietary overlaps between the juveniles and adults captured at the start of each riffle manipulation study were relatively low (Table 14). In some cases, the adult diets were broader, but in general the differences arose from varying proportions of the major diet items of juveniles and adults. For instance, in all cases, Chironomidae made up the major component of the juveniles diet (from 57 to 74%), while Chironomidae made up a much smaller proportion of the adults diet (from 6 to 39%). In addition, although Simulidae occurred in the diets of both the adults and the juveniles on two dates, Simulidae constituted a larger portion of the adults diet than of the juveniles diet (Table 14).

Under the original study design in 1989, the juveniles for between treatment diet comparisons of juveniles in the low adult treatment versus juveniles in the control treatment were taken from the control 1 riffle. As a result, there is no data available for comparing the diets of the juveniles in the low adult treatment with the diets of the juveniles in the control 2 treatment. The guts of the juveniles collected after manipulation in the June 1989 study were nearly all empty. Therefore, inter-treatment comparisons of the diets of the juveniles cannot be made for the June 1989 study. The diets of the juveniles in the low adult treatment in the August 1989 study were fairly

Table 14: Dietary overlaps (Schoener 1970) between adult and juvenile longnose dace captured in unmanipulated riffles at the start of each riffle manipulation study in 1989 and 1990. B = Baetis, C = Chironomidae, G = Glossosoma, H = Hydropsychidae, Hp = Heptageniidae, L = Leucotrichia, P = Psychomyia, R = Rhyacophilidae and S = Simuliidae. Subscripts refer to size class based on head capsule lengths where; S = 0 - 0.5 mm, M = 0.5 - 1.0 mm and L = > 1.0 mm. Values in parantheses indicate the percentage of the food items in the diets of the juvenile and adult dace.

				Major Diet Items	
Date	N_J	N_A	Overlap	Juveniles	Adults
June 1989	22	19	55%	C (61) P (11) B (17)	C (39) P (7) $H_{M,L}$ (5,15) Hp (13) $S_{S,M}$ (6,6)
August 1989	20	17	48.5%	C (64) S_S(8) L (10)	C (19) $S_{S,M}$ (37,9) G (8)
June 1990	11	10	30%	C (74) $S_{S,M}$ (9,12)	C (6) $S_{S,M}$ (51,38)
August 1990	17	18	40%	C (57) B (11) P (17)	C (11) B (15) R (13) $S_{S,M}$ (22,7) $H_{S,M}$ (6,6)

different (overlap = 61.5%) (Table 15) from the diets of the juveniles in the control 1 riffle. The juveniles in the control 1 riffle had a broader diet than the juveniles in the low adult riffle, including more Simuliidae. This difference is probably due to the fact that the juveniles in the control 1 riffle used faster areas than the juveniles in the low adult riffle (Table 9). The diets of the juveniles in the control treatment in June 1990 were similar to the diets of the juveniles in the low adult treatment (Table 15), while the diets of the juveniles in the control treatment in August 1990 were substantially different than the diets of the juveniles in the low adult treatment. The main difference in the August diets was the inclusion of Simulidae into the diets of the juveniles in the low adult treatment (Table 12).

Invertebrate distribution on rock substrates:

Total invertebrate densities on the three exposure surfaces were not different on either of the sampling dates. There were, however, differences for some of the invertebrate groups (Table 16). Simulidae and Hydropsychidae were more abundant on the exposed surfaces in the early summer and only small Hydropsychidae were more abundant on exposed surfaces in late summer.

Table 15: Dietary overlaps (Schoener 1970) between juvenile longnose dace captured in low adult density and control treatments during the riffle manipulation studies in 1989 and 1990. B = <u>Baetis</u>, C = Chironomidae, H = Hydropsychidae, L = <u>Leucotrichia</u>, P = <u>Psychomyia</u> and S = Simuliidae. Subscripts refer to size classes based on head capsule lengths where S = 0 - 0.5 mm and M = 0.5 - 1.0 mm. Values in parentheses indicate the percentage of the food items in the diets of the juvenile dace in each treatment.

				Major Diet Items	
Date	N_{LA}	N_C	Overlap	Low Adult	Control
June 1989	too many empty guts to permit comparison				
August 1989	10	9	62%	C (69) L (9)	C (38) $S_{S,M}$ (14, 6) $H_{S,M}$ (5,6)
June 1990	12	11	72%	C (50) $S_{S,M}$ (9,8) B (28)	C (74) $S_{S,M}$ (9,12)
August 1990	12	17	56%	C (23) B (17) P (6) S_S(24,6)	C (57) B (11) P (17)

Table 16: Results of Kruskall-Wallis comparisons of invertebrate densities on each of three exposure surfaces (N = not exposed, P = partially exposed and F = fully exposed).

	SIGNIFICANT COMPARISONS [*]	
N vs P	N vs F	P vs F
	7/22/89	
small Hydropsychidae	medium Hydropsychidae	none
total Hydropsychidae	large Hydropsyhchidae	
	total Simuliidae	
	9/8/89	
small Hydropsychidae	none	none

[*] all significance levels are $P < 0.05$ and in all cases N was less than either P or F.

DISCUSSION

Due to the inter-riffle differences in the 1989 riffle manipulations, only a few conclusions can be made from these studies. Specifically: 1) There was no evidence to suggest an adult effect on the depth use of the juveniles. Juvenile depth use was consistent across treatments in June and varied between treatments in August, but did not change in the low adult riffle after the adults were removed in August (Table 13). 2) There was no evidence to suggest an adult effect on the substrate use of the juvenile longnose dace. There was a difference in the boulder use of the juveniles in the low adult riffle and the boulder use of the juveniles in the control 1 riffle, but this appeared to be related to inter-riffle differences in boulder availability and habitat associations. The boulder use of the juveniles in the low adult riffle did not change after the adults were removed (Table 13). 3) There was no evidence to suggest an adult effect on the velocity use of the juveniles. The juveniles in the low adult riffle reduced their velocity use after the adults were removed (Table 13), but, since the adults use higher velocities than the juveniles, this does not appear to be a response to adult removal. 4) Regardless of adult densities, the juveniles avoided faster velocities (> 50 cm/sec) in June and did not select faster velocities in

August (Figures 20 and 21).

The study design used in 1990 eliminated the problem of inter-riffle differences and demonstrated that the adults had no effect on the depth and substrate use of the juveniles, but did affect the velocity use of the juveniles (Figures 22 and 23, Table 10).

There was no consistent pattern of depth segregation exhibited in this study, but there was a fairly consistent pattern of substrate segregation. With the exception of the August 1989 study, the adults were always associated with larger substrates than the juveniles (Tables 1, 8, and 12). In the August 1989 study (Table 11), segregation did not occur before manipulation or in two of the riffles after manipulation. However, the pattern of the + and -'s in the contingency tables for these riffles indicated that there was a tendency for the adults to use larger substrates. Adult removal had no effect on the substrate use of the juveniles indicating that substrate segregation resulted from some factor(s) other than intra-specific competition. Larger substrates may harbor predators (brook trout, <u>Salvelinus</u> <u>fontinalis</u> and/or burbot, <u>Lota</u> <u>lota</u>) of small longnose dace. However, in most cases the juveniles displayed some degree of selection for larger substrates, indicating that predation risk on the juveniles probably does not explain segregation. Alternatively, larger substrates may provide shelter for larger longnose dace from avian or terrestrial predators and longnose dace may develop a preference for larger substrates as they grow.

There was a consistent pattern of velocity segregation between the adults and juveniles throughout the course of this study. The effect of adult longnose dace on the velocity use of juvenile longnose dace appeared to be a function of juvenile size. Throughout the period of this study, the adults and juveniles in control or un-manipulated riffles were segregated by mean water column velocity (with the exception of the control 1 riffle in August 1989) (Tables 8, 11 and 12). Low adult densities in June 1989 (mean size of the juveniles was 51.7 mm Tl) had no effect on the velocity use of the juveniles (Table 8, Figure 20). In August 1989, the juveniles (mean size = 56.7 mm Tl) showed a slight shift towards slower water when the adults were removed (Figure 21 and Table 13). In June 1990 (mean juvenile size = 62.6 mm Tl.), the juveniles showed a significant shift into faster water in response to adult removal (Figure 22 and Table 10). The juveniles moved into the 40 - 50 cm/sec velocity range but still avoided velocities greater than 50 cm/sec. In August 1990 (mean juvenile size = 66.5 mm Tl.), the juveniles responded to adult removal by moving into the fastest velocity range (Table 10 and Figure 23).

The juvenile habitat shift observed in the August 1990 riffle manipulation study was apparent in the diets of the juveniles in the low adult treatment in that study (Table 15). These juveniles incorporated Simulidae in a fairly high proportion into their diets (similar to the adults in the high adult treatment) compared to the juveniles in the high adult treatment. A similar change in diet was not detected in the June 1990 study, even though there was a significant habitat shift by the juveniles after adult removal. This may be due to the fact that the juveniles still avoided the fastest velocities in the absence of the adults (Figure 22).

The faster areas within a riffle generally contain higher invertebrate densities, especially of key longnose dace diet items such as Simuliidae, Baetidae and Hydropsychidae (Table 4, Brown and Brown 1984, Orth and Maughan 1983). This higher food availability coupled with the fact that the slower areas in a riffle are more likely to contain the juveniles of many species of stream fishes (Schlosser 1987, Schlosser 1988a, 1988b, Power 1987) including; mottled sculpin (Cottus bairdi) and blacknose dace (Rhinicthys atratulatus) in addition to adult and juvenile burbot (Lota lota) (personal observation) may make the faster areas of the riffle an energetically optimal habitat for those fish that are able to use it. In order to effectively utilize the faster areas, a fish must be able to swim against the currents encountered there and maintain its position behind or under a shelter. Even in the face of possible competition for that shelter from other riffle dwelling fish. Juvenile longnose dace are not able to swim against the faster currents at small sizes (Figure 10). In this study, the juveniles did not show a significant response to adult removal until June 1990 when their mean size was 62.6 mm Tl. Even then, they avoided velocities greater than 50 cm/sec (against which they were not able to swim (Figure 10)). By August of 1990, the juveniles had reached a size (66.5 mm Tl) where they were able to utilize the faster currents (Figure 10) and responded to adult removal by moving into the fastest areas of the riffle (Figure 23). However, in the presence of adults, in June and August 1990, the juveniles used the slower velocities (Table 10) suggesting that they were not able to compete with the larger adults for space within the faster areas of the riffles.

Throughout the course of this study, however, juvenile longnose dace were captured in fast velocity areas (sometimes in mean water column velocities exceeding 90 cm/sec). This velocity overlap with the adults indicates that segregation between the adults and juveniles is only partial. Partial segregation is likely to occur if the faster habitat is the optimal habitat for both size classes and shelter in that habitat is abundant enough to not be completely limiting. Shelter from the current in fast areas dominated by boulder and cobble substrates should be abundant and, unless adult densities are very high, should not be completely unavailable to the juveniles. In addition, the velocity at the substrate surface is generally lower than the mean water column velocity (Hynes 1970), and although it may be prohibitively high in many areas, it should be possible for juveniles to enter and utilize some portion of the faster areas without actually encountering prohibitive velocities. Juveniles in the faster areas, would be able to take advantage of the higher invertebrate densities in the faster areas because, with the exception of Hydropsychidae, and the Simuliidae in early summer, most invertebrates were as dense on the non-exposed surfaces of rocks in the fast areas of riffles as they were on the exposed surfaces (Table 16). However, a juvenile in a faster area would be at risk of being displaced from its shelter by a larger conspecific foraging in the area.

Ideally, evidence for competition includes some measure of the effect of one group on the fitness of another (Connell 1980). For fish, because of the strong relationship between fecundity and size (Bagenal 1978), growth may be used as one indicator of fitness (Werner et al. 1983a). Several attempts were made to measure the growth rates of juvenile longnose dace confined to slow and fast areas within a riffle. However, due to the necessity of using cages to confine the fish and the length of time required to be able to determine growth rates, all attempts were unsuccessful. Even with daily cleaning, the cages affected the flow and invertebrate drift into the caged area. In all cases, longnose dace confined to cages (½ m^2 in area) lost weight. In the absence of direct evidence of a fitness effect, documented resource overlap between the two groups and a reduction in the realized niche of one group in the presence of the other is used as evidence for competition (Colwell and Futuyma 1971, Diamond 1978, Gatz et al. 1987). By the start of their second full summer of life (June 1990), the juvenile longnose dace in this study showed a high resource overlap with the adults (they both occurred within riffles and their velocity ranges overlapped), and they showed a reduction in their realized niche in the presence of adults (as evidenced by the niche shift into faster areas in the absence of adults) indicating that the adults and juveniles competed for space in the faster areas of the riffles.

In addition to providing higher invertebrate prey densities for both juvenile and adult longnose dace, the faster areas may also be important as a refuge from predation. Adult longnose dace may reach the size were they are vulnerable to avian predators such as kingfishers and herons (both were seen frequently in the study area) and terrestrial predators such as mink and raccoons (several mink were seen in the study area). The faster areas within a riffle are also the areas with the highest turbulence and should, therefore, offer refuge from non-aquatic predators. Also, the slower areas of a riffle are generally the shallower areas of a riffle (Chapter one, Table 2) where predation risk from avian and terrestrial predators is high for larger fish (Power 1984, 1987, Schlosser 1988a). This may explain the avoidance of shallow areas by adults observed throughout this study. Smaller fish like juvenile longnose dace are not as vulnerable to avian and terrestrial predators (Power 1987, Schlosser 1988a) and, therefore, would not need the refuge offered by the faster areas. This lack of vulnerability, rather than physical constraints, may explain the lack of a habitat shift into faster areas by the juveniles after adult removal in June and August of 1989. However, this study was not designed to examine habitat specific predation risks, and this possibility is mentioned only as a viable alternative to physical constraints as an explanation of the juveniles habitat use in the 1989 studies.

Several studies document the effects of predation risk on the habitat choice of fishes (Mittlebach 1981, 1984, Werner et al. 1983b, Power 1984, Power et al. 1985, Schlosser 1987, 1988a, Gotceitas and Colgan 1990). In all these studies, small fish reduced their use of high risk areas in the presence of predators, in some cases at the cost of lowered foraging returns. To demonstrate that predation risk in the slower shallower areas of a riffle causes adult longnose dace to utilize the faster areas of the riffle, it would be necessary to show that the adults shifted their habitat use to the slower areas of the riffle in the absence of predators. However, it may not be possible to demonstrate a habitat shift in the absence of predators. Habitat preferences produced by avian or terrestrial predators may be innate. Predation risk has been shown to cause innate behavior patterns in at least two species of fish. Guppies (Poecilia reticulata) from areas with high predation risk formed tighter schools and reacted at a greater distance to risk when piscivorous fish were present than did guppies from areas of low predation risk (Seghers 1974). As these differences were maintained through several generations of laboratory stocks, they are most likely due to genetic differences between the two groups. Three-spined sticklebacks (Gasterosteus aculeatus) from areas with high predation risk develop an escape response to heron attacks without prior experience to a predator (Giles 1984). Members of this species taken from an area with predators and an area without predators soon after hatching were tested for their response to simulated predators. Sticklebacks from the high predator area showed a greater tendency to respond to the predator by either; rapid jumping, freezing or taking cover in the weeds (when available), than did the sticklebacks from the area without predators (Tulley and Huntingford 1987). These responses did not occur until the fish were at a size that is vulnerable to predation (about 30 mm Tl). Innate predator defense behaviors are likely to develop in situations where the cost of learning (injury or mortality) to avoid predators is fairly high. Innate behaviors probably develop in stream fishes that are susceptable to avian and/or terrestrial predators. Avian and terrestrial predators may be difficult to detect for stream fishes, in which case, anti-predator behaviors in response to predator detection would be of little value, while avoidance of areas of possible high predation risk (regardless of predator presence or absence) would be a highly adaptive behavior. This avoidance may be the case with large armored catfish (Loricariidae) (Power 1984), bigmouth chub (_Nocomis platyrhynchus_) (Lobb and Orth 1988), mottled sculpin (_Cottus bairdi_) (Freeman and Stouder 1989) (see Mahon and Portt, 1985 for a summary of the size distribution of many species of fishes occurring in riffles, raceways and pools) and the larger longnose dace in this study.

Regardless of whether the faster areas of the riffle are selected for their higher invertebrate densities or for their value as a predation refuge (or both), there was a consistent pattern of habitat segregation by velocity between juvenile and adult longnose dace for at least the first two full summers of the dace's life. This study demonstrated that the cause of this pattern changed as the juvenile longnose dace grew. At smaller sizes, even at low adult densities, the juveniles did not use the faster areas of the riffles. This avoidance of faster areas may be due to physical constraints (as evidenced by the burst velocity measurements) or due to a lack of predation risk to the juveniles in the slower areas of the riffle. As the juveniles grew, the pattern of velocity segregation was maintained by intra-specific competition with the larger longnose dace for space in the faster areas of the riffles.

This study was designed to assess the roles of physical constraints and intra-specific competition in determining the habitat use of the juvenile longnose dace. However, the results from the 1989 studies and the fact that adult densities do not explain the consistent pattern of substrate segregation suggest longnose dace habitat use may be affected by other factors in addition to physical constraints and intra-specific competition.

CHAPTER FOUR

MORPHOMETRIC ANALYSIS

INTRODUCTION

As discussed above, the inability of juvenile longnose dace less than 60 mm Tl to swim faster than 50 cm/sec may be the initial cause of velocity segregation between the adults and juveniles. Maximum swimming velocity is a function of both body size and body shape (Moyle and Cech 1982). Fish with elongate bodies, flattened heads, large forked caudal fins and posteriorly placed dorsal and anal fins are highly adapted for rapid swimming. Longnose dace may not develop morphometric adaptations for faster burst swimming until later in life, thus accounting for velocity segregation between the size classes.

The purpose of this study was to examine the degree of morphometric variation between, and within, the juvenile and adult size groups.

METHODS

Data on the shapes of 87 longnose dace ranging in size from 36 to 121 mm Tl were gathered according to the methods provided by Bookstein et. al. (1985) for quantifying shape change between groups of varying sizes. Longnose dace were captured from the Ford river by kick seining and photographed in late September 1987. Each dace was anesthetized with MS 222 (Finquil), wiped dry and photographed against a white background using a 28 - 80 mm macro-zoom lens attached to a 35 mm camera mounted on a tripod. Each photograph contained: the fish, an identifying tag and a section of a ruler. The photographs were enlarged and shape measurements were made by hand to the nearest 0.5 mm. The ruler in each photograph was used to convert all measurements to actual size.

Six landmarks were chosen on the fishes profile and a "box truss" (Bookstein et. al. 1985) was drawn connecting all six landmarks (Figure 24). This allowed eleven shape measurements on which principal component analysis (using S.A.S. on the MSU IBM mainframe computer) was conducted to examine the pattern of variation between three size groups (36 - 56 mm Tl, 65 - 80 mm Tl, and 81 - 121 mm Tl) and within each size group. The division into size groups was based on the length frequency distribution of the 87 longnose dace used in this study. Originally, the analysis of shape variation within and between size groups was to be conducted using the "shear" method of size free shape discrimination (Bookstein et. al. 1985). However, "shearing" does not necessarily remove size variation from the shape analysis (Rohlf and Bookstein 1987). Hence, principal component analysis was chosen as the more effective means of examining the patterns of shape variation in longnose dace.

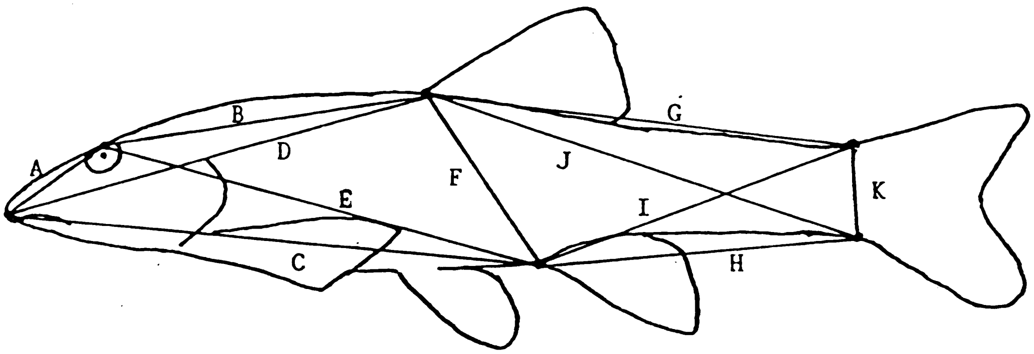

Figure 24: Outline of an adult longnose dace showing the landmarks and measurements used for the analysis of shape change with growth.

RESULTS

Overall, over 97% of the variation in measurements can be attributed to size variation within the data set (all variables (factors) load significantly onto the first principal component) (Table 17). An examination of the individual size groups separately indicates that there is some shape variation within each size groups. Within the fry size group, over 84% of the variation is due to size and 7.4% of the shape variation (PC2) is related to the insertion of the dorsal fin. In the juvenile size class, 70.4% of the variation is due to size, 14.6% (PC2) is related to the insertion of the anal fin and 7.5% is due to PC3 which is difficult to interpret but may be related to the insertion of the dorsal fin. Most (84.1%) of the variation within the adult size class is due to size, and PC2 and PC3 (accounting for 11.9% of the variation) seem to both relate to the placement of the dorsal and anal fins.

DISCUSSION

Principal component analysis of the eleven shape variables for the 87 longnose dace in this study failed to detect any significant variation in shape within the entire data set. This may be because the large variation in size

Table 17: Results of principal component analysis on eleven shape measurements from 87 longnose dace. Factors with loadings greater than 0.2 (on a scale of 0 - 1) were considered major factors for a component. Factors are listed in order of decreasing loadings. The shape variables designated by each letter are illustrated in figure 24.

Group	Component	% Variation	Major Factors
ALL	PC1	97.8	ALL (size)
FRY	PC1	84.3	ALL (size)
N = 26	PC2	7.4	B,F,J,G,E
JUVENILES	PC1	70.4	ALL (size)
N = 31	PC2	14.6	H,F,I,D,C
	PC3	7.5	B,J,E,K,G,F
ADULTS	PC1	84.1	ALL (size)
N = 30	PC2	6.8	F,H,B,I,E,G,J
	PC3	5.1	H,I,G,J,E,B,C

(PC1) of the dace used swamped any variation in shape. Indeed, when the size groups were considered separately, more of the variation within each group appeared to be related to shape, or, more specifically, to the placement of the dorsal and anal fins.

This shape variation is relatively small and may not be ecologically important to the fish. However, posterior placement of the dorsal and anal fins is an adaptive trait for fish that are lie in wait predators (Moyle and Cech 1982). Lie in wait predators must be capable of bursting forward at rapid speeds in order to capture prey. Posterior placement of the dorsal and anal fins places the trailing edge (the part of the fin that delivers the propulsive thrust) of those fins far back on the body where the greatest amount of movement occurs during the tail beat, thereby increasing the thrust derived from those fins. Although longnose dace are not classic lie in wait predators, their mode of existence in stream riffles may require the same morphometric adaptations that are useful to lie in wait predators. Longnose dace spend most of their time under or behind shelters in the riffles. When foraging, they will exit the shelter and burst forward into the current to grab a prey item off of the substrate surface and then drift back to the same or another shelter (personal observation). Posterior placement of the dorsal and anal fins would aid in their ability to burst forward and would be adaptive to this mode of existence.

Because of the small amount of variation detected between groups, however, there is insufficient evidence to support speculation that size related velocity segregation in longnose dace is a function of morphometric differences between the adults and juveniles.

SYNOPSIS

Longnose dace undergo a gradual niche shift into faster, deeper areas of riffles and larger substrates as they grow. Or, more precisely, the niche of the longnose dace gradually expands to include faster velocities, deeper areas and larger substrates as it grows. As a result, the juvenile niche is encompassed within the niche of the adult, and partial habitat segregation within a riffle occurs between the juvenile and adult longnose dace.

Adult and juvenile longnose dace were consistently segregated by current velocity throughout this study. The faster areas of a riffle have higher invertebrate densities and probably offer shelter from predation for those dace that are physically able to cope with the current velocities found there. When they reach 55 - 65 mm Tl, in the absence of other fish, juvenile longnose dace show a preference for the faster areas. At this size, their maximum burst velocities are fast enough to allow them to use some portion of the faster areas. Prior to that size, the juveniles show a preference for the slower areas of the riffle, possibly due to a physical inability to cope with the faster currents. This preference for slower velocities results in size specific velocity segregation within the riffle area. Velocity segregation between the juveniles and adults, however, occurs consistently, at least until the juveniles reach an average size of 67 mm Tl (the average size of the juveniles at the end of the riffle manipulation studies).

Once the juveniles become large enough to utilize the faster areas of the riffle, velocity segregation is maintained by intra-specific competition for space in the faster areas of the riffle. Adult longnose dace are superior competitors and displace juveniles from behind or under shelters, exposing them to the current, and possibly to predation. When adult densities were high, partial velocity segregation occurs between the adults and juveniles, but when the adult densities were lowered, the juveniles (> 60 mm Tl) moved into the faster areas of the riffle.

Adult and juvenile longnose dace exhibited partial depth segregation during this study. However, depth segregation was inconsistent, occurring in only five of the ten cases where size specific depth use was examined. Depth segregation was not related to the size of the juveniles, and juvenile depth use was not affected by adult density manipulations. In all cases where depth segregation occurred, the adults used deeper areas than did the juveniles. Adult longnose dace may use the deeper areas of the riffle as a shelter from terrestrial or avian predators, or adults may use the deeper areas of the riffle because, in some cases, the deeper areas are also the faster areas.

Partial substrate segregation occurred fairly consistently throughout this study. In all cases, the adults used larger substrates than did the juveniles. However, manipulations of adult densities had no effect on the substrate use of the juveniles. Boulders generally are associated with lower invertebrate densities than cobble substrates (Orth and Maughan 1983), indicating that factors other than foraging returns are responsible for the adult preference for larger substrates. Adult longnose dace may use the larger substrates as a shelter from avian or terrestrial predators, or, conversely, juvenile longnose dace may avoid larger substrates because they might harbor aquatic piscivores, to which they are vulnerable.

Several factors appear to be important in determining the habitat use of longnose dace. Those factors differ according to the size of the dace. The habitat choice of larger dace appears to be a function of foraging returns and predation risk, while the habitat choice of smaller longnose dace appears to be a function of physical constraints, intra-specific competition and, possibly, predation risk. These factors all interact to produce a temporally consistent pattern of size related habitat segregation within a stream riffle.

Niche separation by stream fishes occurs through a variety of mechanisms (Ross 1986). Inter-specific competition is responsible for the spatial separation of; riffle sculpin (Cottus guloses) and speckled dace (Rhinichthys osculus) (Baltz et. al. 1982), rainbow trout (Salmo gairdneri) and brown trout (Salmo trutta) (Gatz et. al. 1987), and redline darters (Etheostoma rufilineatum) and tennessee snubnose darters (*Etheostoma simoterum*) (Greenburg 1988). In all three examples, removal of the dominant species results in a niche shift by the subordinate species. Intra-specific competition between juvenile and adult mottled sculpins (*Cottus bairdi*) results in size related depth segregation (Freeman and Stouder 1989). Temporal differences in feeding patterns results in niche separation between juvenile and adult creek chub (*Semotilus atromaculatus*) (Magnan and FitzGerald 1984), and between torrentfish (*Cheimarrichthys fostrei*) and bluegilled bullies (*Gobiomorphus hubbsi*) (Scrimgeour and Winterbourn 1987). Size specific predation risk results in separation between juvenile and adult loracariid catfish (Power 1984). All these mechanisms, in addition to physical constraints, can act singly, simultaneously, or sequentially to reduce inter-specific and intra-specific niche overlap in stream fishes. More research into the interactions of these mechanisms is essential to a better understanding of the patterns of habitat use by stream fishes.

There are still several questions to be answered concerning the factors affecting the habitat choice of longnose dace. For instance, in one control riffle, the adults and juveniles were segregated by velocity and substrate type in June 1989, while in August 1989, they were segregated by depth but not by substrate type or velocity. The availability of each of these habitat variables in this riffle differed from that of the other two riffles used in the riffle manipulation studies. This riffle was also shallower and slower during the August study than it was during the June study. It is unclear how spatial and temporal habitat variability affect the habitat choice and size specific interactions of longnose dace.

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