DOES A PREDATOR TRANSITION DETERMINE THE DISTRIBUTION OF CRAYFISH IN THE NEW RIVER, NC?

A Thesis

by

KENNETH FORTINO

Submitted to the Graduate School

Appalachian State University

in partial fulfillment of the requirements for the degree of

MASTERS OF SCIENCE

May, 2000

Major Department: Biology

DOES A PREDATOR TRANSITION DETERMINE THE DISTRIBUTION OF CRAYFISH IN THE NEW RIVER, NC?
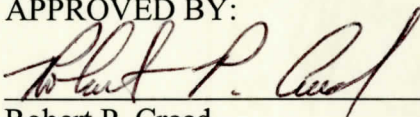
A Thesis

by

KENNETH FORTINO

May 2000

APPROVED BY:

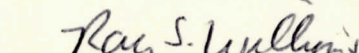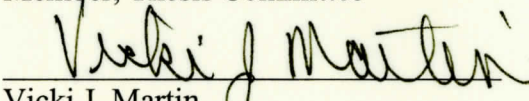Robert P. Creed
Chairperson, Thesis Committee
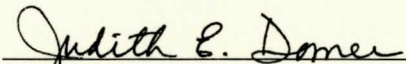
Matthew P. Rowe
Member, Thesis Committee

Ray S. Williams
Member, Thesis Committee

Vicki J. Martin
Chairperson, Department of Biology

Judith E. Domer
Dean of Graduate Studies and Research

ABSTRACT

DOES A PREDATOR TRANSITION DETERMINE THE DISTRIBUTION OF

CRAYFISH SPECIES IN THE NEW RIVER, NC? (May 2000)

Kenneth Fortino, B.A., Greensboro College

M.S., Appalachian State University

Thesis Chairperson: Robert P. Creed Jr.

The stream-dwelling crayfish fauna of the New River in western NC, consists of

three common species (*Orconectes cristavarius, Cambarus chasmodactylus,* and

Cambarus bartonii) and a rare species (*Cambarus aspermanus*). Both *C. bartonii* and *C.*

aspermanus occur almost exclusively in the first and second order tributaries of the New

River. *C. chasmodactylus* is found primarily in the third order tributaries as adults and

young-of-the-year (YOY) but only as adults in the fourth order New River. *O.*

cristavarius is found in the New River as both adults and YOY and is virtually absent

from the tributaries. Thus, the adults of *C. chasmodactylus* and *O. cristavarius* coexist in

the New River but the YOY do not. In this study I evaluated the factors that may be

responsible for the virtual absence of *C. chasmodactylus* YOY from the New River,

despite the presence of the adults. I hypothesized that the exclusion of the *C.*

chasmodactylus YOY could be the result of either intolerance of the abiotic conditions

found in the New River, competition with *O. cristavarius* YOY, or predation by rock

bass. The importance of abiotic factors and competition was tested using a target -

neighbor design field experiment where a uniform density of *C. chasmodactylus* YOY

was enclosed in the New River with *O. cristavarius* YOY at densities ranging from none

iv

to approximately two times ambient density. Neither the growth nor the survival of *C. chasmodactylus* was affected by increased competitor density. Thus, these species do not appear to compete as YOY. Furthermore, 100% of the *C. chasmodactylus* YOY were recovered from three of the four enclosures containing no *O. cristavarius* indicating that the *C. chasmodactylus* is tolerant of the abiotic environment of the New River. Since predators have been shown to have important effects on the distribution of aquatic organisms, a laboratory experiment was used to determine the vulnerability of the YOY of each species when exposed simultaneously to rock bass. The vulnerability of each species was estimated using Manly's selectivity index. *C. chasmodactylus* YOY were significantly more vulnerable than *O. cristavarius* YOY to rock bass predation. The virtual exclusion of *C. chasmodactylus* YOY from the New River appears to be the result of intense predation pressure exerted by the abundant rock bass population in the New River. Field observations suggested that the two crayfish species differed in their anti-predator behavior. These differences were tested using a laboratory experiment. *C. chasmodactylus* never swam when initially disturbed and swam shorter distances than *O. cristavarius*. These differences in escape behavior may contribute to the differences in the vulnerability of the two species to rock bass predation. In temperate streams the predatory fish fauna shifts from cold-water species (e.g., trout) to warm-water species (e.g., bass and rock bass) as one moves down through the watershed. In the New River watershed rock bass are common in the South Fork of the New River and are rare in the tributaries. The results of this study suggest that this shift in predatory fish type may be important in determining the distribution of crayfish species in the New River.

ACKNOWLEDGEMENTS

My decision to attend Appalachian State University could be said to have been based on chance, or perhaps more appropriately, proximity. I chose to apply to ASU because it was close to where I was living at the time. Since I did not actively research the school, I knew little of the program or the professors and therefore, I entered ASU without an advisor. During my first semester of my attendance I set out to find a major professor and a thesis project. I wanted to work in plant ecology so I spent much of the beginning of that first semester in the offices of the people who studied plant ecology. None of them, however, were accepting students at the time. During my interview with the school the summer before, I had spoken with Dr. Robert Creed, the resident aquatic ecologist. At the time he had told me that he would not be accepting students in the fall either (also he was not working with plants) so I had not considered him a potential advisor. However, as chance would have it I wound up in his Freshwater Ecology class, which I enjoyed sufficiently to decide to approach him regarding a thesis project, just on the chance that he would have room. To make a medium-length story very short, he did have room. The fact that I began working with Dr. Creed was due to chance, the success of the undertaking was not due to chance, however, but rather his patience, friendship, expertise, and inspiring passion for science. I cannot thank him enough for so thoroughly preparing me for success.

Well, chance brought me to ASU and introduced me to Dr. Creed, and chance also acquainted me with three people, who have had more than an ancillary effect on my success at ASU. The first of whom is Nate Bickford. Nate is tireless and cheerful despite the fact that his jobs usually involve the lifting and carrying of heavy objects. He is among the most loyal friends that a person could be lucky enough to have. Being a person with transient but strongly held opinions, a loyal friend is a rare and much coveted fortune. Additionally, I must thank Nate for his industrious creativity in the construction of all things (essential and recreational) as well as for finding opportunities for summer employment. I owe Nate for all the burgers I did not flip during my time at ASU.

Another person to whom I owe thanks is Bryan Brown. Bryan, while he did assist me in the field, was more instrumental in the development of my ideas. No matter how carefully formulated and researched any of my ideas were, Bryan was always available to assert that they were groundless and without merit. Furthermore, Bryan was steadfast in his commitment arguing the above points. My ideas and my humility are much better developed for his efforts as well as his friendship.

Another person that I would like to thank, but for whom all thanks falls short, is Brian Helms. Much of the work presented in this thesis could not have been completed without Brian's involvement in terms of both technical assistance and, more importantly, companionship. He aided considerably in the execution of virtually every aspect of this study and his friendship and companionship enriched and deepened the experience. Despite highly divergent backgrounds, Brian and I seem to share a common understanding of the world that cannot be (nor rarely is) expressed in words.

DEDICATION

To Bailey, who is my greatest inspiration and truest companion.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

xi

Introduction

Both abiotic factors and biotic interactions can influence the distribution and abundance of species. Furthermore, the magnitude of biotic interactions is often dependent on environmental context. This context dependence results in spatial and temporal variation in the strength of the biotic interactions. As a result of this environmental heterogeneity, species are presented with a landscape comprised of hospitable and inhospitable habitats (McPeek 1990a). Furthermore, whole assemblages of species may change across the landscape as a result of their adaptation to a specific subset of abiotic factors and biotic interactions (McPeek 1990a, Wellborn et al. 1996). The best demonstration of this type of change in community structure has been the variation of lentic communities across a gradient of habitat permanence.

A major abiotic factor affecting lentic community structure is habitat permanence. Lentic systems range from small ephemeral pools to large permanent lakes (Wellborn et al. 1996). This gradient in pond permanence has been demonstrated to play an important role in determining the distribution of a number of taxa (McPeek 1990a, Skelly 1995, Wellborn et al. 1996). The primary factors that influence the distribution of taxa change across this gradient. In temporary habitats the principal factor determining community structure is the duration of the pond's wet period. In permanent habitats both abiotic factors (e.g., wintertime anoxia) and predator assemblage determine community structure. Differences in the environmental conditions of small and large permanent

1

ponds result in a shift in the dominant predator taxa in these habitats. Smaller permanent ponds are typically dominated by invertebrate predators and larger permanent habitats are dominated by fish (McPeek 1990a, Wellborn et al. 1996). The absence of fish from smaller ponds may be due to the inaccessibility of these ponds to fish or from fish kills that result from wintertime anoxia. As a result of the differences in abiotic factors and biotic interactions, the communities in these three habitat types (temporary, permanent fishless, and permanent fish-containing) contain different species of both vertebrates (Woodward 1983, Wellborn et al. 1996, Skelly 1995, 1996) and invertebrates (McPeek 1990a, Jeffries 1994, Wellborn et al. 1996).

The shift in the importance of abiotic factors in ephemeral habitats to predation in permanent ponds is clearly illustrated by certain amphibian communities. Skelly (1995) found that the larvae of chorus frogs (*Pseudacris triseriata*) tended to be more abundant in ephemeral ponds, whereas the larvae of spring peepers (*P. crucifer*) were more abundant in more permanent habitats. The spring peeper larvae were largely excluded from ephemeral habitats because the longer duration of their larval period made them more susceptible to pond drying (Skelly 1995). The shorter development time of chorus frogs allowed them to occupy ephemeral ponds. However, chorus frog larvae were more vulnerable than spring peepers to the predators found in permanent ponds (Skelly 1995). The variation in the magnitude of the effect of predation and pond drying across the gradient of habitat permanence delimited a shift in the primary force limiting community

membership. Thus, both pond permanence and predators influenced the distribution of the larvae of these similar frog species (Skelly 1995).

In permanent ponds, the impact of the shift from a system dominated by invertebrate predators to one dominated by fish predators on community structure can be seen in the distribution of certain species of damselflies in the genus Enallagma. McPeek (1990a) observed that the larvae of some Enallagma damselfly species tended to inhabit only ponds containing fish, while other species inhabited only fishless ponds. Both pond types had well-developed predator assemblages which differed only in the type of dominant predator. Predatory fish were the dominant predator in fish-containing ponds, whereas the principal predators in fishless ponds were the larvae of large dragonflies (McPeek 1990a). McPeek (1990a) found that Enallagma larvae were less vulnerable to the predator species that they coexisted with (fish or dragonfly larvae) than to the predators with which they did not coexist. This difference in prey vulnerability combined with the distribution of predator taxa resulted in the exclusion of some Enallagma species from otherwise suitable habitats (McPeek 1990a). Thus, a change in the type of dominant predator determined which prey species could occupy a given pond (McPeek 1990a). Wellborn et al. (1996) refer to this as the predator transition in lentic communities.

The idea that lotic systems also exist along a gradient of environmental conditions is well established (Vannote et al. 1980, Poff and Ward 1989, Allan 1995). Despite the clearly delimited habitats characteristic of lentic systems, there is still evidence to support distinct shifts in the factors affecting lotic community organization. Lotic systems can,

like lentic systems, be visualized along a gradient of permanence (Peckarsky 1983, Poff and Ward 1989, Creed, (in preparation)). For example, the headwaters of a watershed often contain small, ephemeral streams where abiotic factors play the largest role in determining community composition (Bovbjerg 1970, Peckarsky 1983, Poff and Ward 1989, Storfer and Sih 1998). In permanent streams there is a reduction in the severity of abiotic conditions and an increase in trophic complexity (i.e., the introduction of predators) (Peckarsky 1983, Creed, (in preparation)). Fish are usually absent from these small headwater streams (Storfer and Sih 1998, Englund 1999); thus, the dominant predators are probably invertebrates (crayfish, predatory insects) and amphibians. Therefore, in small permanent headwater streams invertebrate predators may play a larger role in determining community composition, whereas in larger fish-containing streams with relatively benign environmental conditions, fish predation may be the principal factor influencing community structure (Peckarsky 1983, Reice and Edwards 1986, Poff and Ward 1989, Sih et al. 1992, Storfer and Sih 1998, Englund 1999, Creed, in preparation). Thus, lotic systems appear to contain transitions similar to the permanence transition and predator transition described by Wellborn et al. (1996) for lentic habitats.

Creed (in preparation) has suggested that an additional predator transition may exist in lotic systems. Many temperate fish are classified as belonging to one of two groups, i.e., cold-water and warm-water, based on their thermal preference (Moyle and Cech 1996). In general, the cold-water predatory fish fauna of North America is dominated by trout (Salmonidae) and sculpins (Cottidae), whereas the warm-water predatory fish fauna consists primarily bass and other sunfish (Centrarchidae), and catfish

(Ictaluridae) (Moyle and Cech 1996). Since stream order is highly correlated with stream temperature, substrate, size, and gradient, smaller headwater streams tend to have a steeper gradient and colder temperatures (Allan 1995) and thus are dominated by a cold-water fish fauna (Moyle and Cech 1996). Accordingly, larger streams tend to have warmer temperatures and a lower gradient and thus are dominated by a warm-water fish fauna (Moyle and Cech 1996). This shift in predatory fish from cold-water species to warm-water species can, therefore, be inserted into the generalized gradient of factors that may affect lotic community membership (Creed, in preparation). Since cold-water and warm-water fish are known to be ecologically different (e.g., differences in diet and foraging behavior), it is possible that these differences may have impacts on community structure in the habitats containing the different fish assemblages.

In summary, in small ephemeral headwater streams the dominant force regulating community membership is the harsh environmental conditions that species must endure. In small permanent streams, the development of an invertebrate predator fauna is possible and community membership may be limited to those species that can coexist with the dominant predators. The continued increase in stream size allows for the establishment of a predatory fish fauna. In North American temperate streams the upstream fish community is frequently dominated by cold-water species while further downstream the predatory fish fauna switches to primarily warm-water fish. The prey organisms that live in each of these stream sections may be limited to only those species that can coexist with the resident fish species (Creed, in preparation).

In this study I investigated the impact that the transition from a cold-water to a warm-water fish fauna might have on the distribution of the young-of-the-year (YOY) crayfish in a portion of the New River watershed. The South Fork of the New River, a fourth-order stream, contains two common crayfish species, *Orconectes cristavarius* and Cambarus chasmodactylus. The adults of both species coexist in the New River while only the adults of *C. chasmodactylus* are common in third-order tributaries. The YOY of these two species have a parapatric distribution. The YOY of *O. cristavarius* essentially occur only in the New River while the YOY of *C. chasmodactylus* occur almost exclusively in the third-order tributaries. In this study I evaluated the factors that could be responsible for the virtual exclusion of *C. chasmodactylus* YOY from the mainstem of the New River, despite the presence of *C. chasmodactylus* adults. I hypothesized that the rarity of *C. chasmodactylus* YOY in the mainstem could be due to at least one of the following three factors: 1) *C. chasmodactylus* YOY may be intolerant of the abiotic conditions found in the New River and therefore unable to survive there, 2) *C. chasmodactylus* YOY may be excluded from the New River through competition with the more abundant *O. cristavarius* YOY, 3) *C. chasmodactylus* may be excluded from the New River by a predator found in the New River, such as a warm-water fish that is not present in the tributaries. I tested the possible role of abiotic factors and competition using a field experiment and the role of predation using laboratory preference trials. The effect of possible differences in the anti-predator behavior of the two species was also evaluated.

Study Animals

The stream - dwelling crayfish fauna of the New River watershed in NC consists of three common species (*O. cristavarius*, *C. chasmodactylus*, C. bartonii) and a rare species (C. aspermanus). Both the YOY and adults of all four species are readily identifiable in the field. Cooper and Braswell (1995) report that both *C. chasmodactylus* and *O. cristavarius* are endemic to the New River drainage and both can be found in the South Fork of the New River. C. bartonii, on the other hand, is a broadly distributed species ranging from the southern tip of the Appalachians into Canada (Crocker and Barr 1968, Hobbes 1981). In the South Fork of the New River watershed C. bartonii occurs almost exclusively in the smaller tributaries (Fortino and Creed, unpublished data). To date, the few C. aspermanus that have been collected were found only in first and second order streams.

This study focuses on *C. chasmodactylus* and *O. cristavarius* which, like most crayfish, are omnivorous (Helms 2000). The life histories of these crayfish are virtually unstudied. Therefore our knowledge of the timing of their life cycle is based exclusively on field observations. *O. cristavarius* appears to be a synchronous breeder with the females coming into berry in the late spring (Brown 1999, Fortino, personal observation). Berried females of *C. chasmodactylus*, on the other hand, have been collected in every month of the year (Brown 1999), suggesting *C. chasmodactylus* breed asynchronously. Although species with asynchronous breeding can release offspring throughout the year, other species of Cambarus still release most YOY during the summer (Hamr and Berrill 1985).

Study Site

This study was conducted in the headwaters of the New River drainage (Watauga County, NC.) The primary study sites utilized in this study were Winkler's Creek (downstream of the bridge on Winkler's Creek Road), Howard's Creek (immediately downstream of the Appalachian State University dam on Howard's Creek Road), and the South Fork of the New River (where it passes through the Greenway Park in Boone, NC). Winkler's Creek is a third-order tributary of the South Fork of the New River. The Winkler's Creek study site was located approximately 1.06 km from the confluence of Winkler's Creek with the New River in a run with a sand/cobble substrate. Howard's Creek is also a third-order tributary of the South Fork of the New River. The Howard's Creek study site was located approximately 5.8 km from the confluence of Howard's Creek with the New River and consisted of a pool and riffle. The substrate ranged from cobble to boulder to a sand/cobble mixture. The mainstem of the South Fork is a fourth-order stream consisting mostly of runs with a sand/gravel substrate. Interspersed between the runs are riffles with cobble and boulder substrate that are frequently covered with river weed (*Podostemum ceratophyllum*) and pools of moderate (< 1 m) depth with cobble/gravel substrate.

Methods

Field Surveys

Quadrat Sampling. Quadrat samples were used to estimate the density of each crayfish species in various habitats within the New River. Samples were taken during July and August, 1998 and 1999, using a 1 m^2 quadrat, a 4 m^2 quadrat, and a standard Surber

sampler (240 μm mesh). The two larger quadrats were square and constructed of 12 mm PVC pipe with a 1 cm mesh minnow seine stretched around the downstream half of the quadrat. The location of each sample was determined randomly and crayfish were collected first by visual inspection of the quadrat and then by disturbing the substrate to drive the crayfish into the net. Density estimates were limited to adult crayfish, since YOY crayfish were not reliably retained by the minnow seine. The Surber sampler was used to sample YOY in the New River, Winkler's Creek and Howard's Creek, since the mesh size was sufficient to retain the smallest free-living YOY. Surber samples were collected in the New River during June and August 1999 and in Howard's Creek and Winkler's Creek during August 1999. The samples were taken on gravel substrate in June and on cobble substrate in August because the YOY appeared to shift from gravel to cobble substrate as they increased in size (K. Fortino, personal observation). The crayfish were collected by disturbing the substrate within the sampler. Species, carapace length (CL, the distance from the tip of the rostrum to the posterior margin of the cephalothorax), and sex (when possible) were recorded for all of the crayfish collected from each quadrat and Surber sample. After the sampling was completed the mean water depth and current velocity (using a Scientific Instruments® Model 1205 current meter) were determined within each quadrat with the exception of the Surber sampler. The substrate type was then visually estimated to be either simple (e.g., sand, gravel) or complex (e.g., cobble, boulder, or vegetation).

The density of each crayfish species along the river edge habitats was estimated using a randomly placed 2m X 0.5m quadrat. Crayfish were collected initially by

visually inspecting the quadrat area with a hand net and then by sweeping a dip net repeatedly upstream through the quadrat to capture any remaining crayfish. The species, CL, and sex were recorded for all of the crayfish collected from the quadrat. After the sampling was completed the average depth of the water was determined from three locations within the quadrat. The substrate type was estimated visually to be either simple (e.g., sand, gravel) or complex (e.g., cobble, boulder, or vegetation).

Experiments

Competition Experiment. To determine if the rarity of *C. chasmodactylus* YOY in the mainstem of the New River was the result of competitive interactions with the more abundant YOY of *O. cristavarius*, I performed a field experiment. The experiment was designed to test the effect of interspecific competition between *O. cristavarius* and *C. chasmodactylus* YOY, as well as intraspecific competition among *O. cristavarius*. I used a target-neighbor experimental design (Goldberg and Werner 1983, Mittlebach 1988) in which all cages contained 2 *C. chasmodactylus*, the target species, and either 0, 2, 4, or 6 *O. cristavarius*. This design held intraspecific competition constant for *C. chasmodactylus* YOY while varying the magnitude of interspecific competition with *O. cristavarius* YOY. All crayfish were collected within two days of the beginning of the experiment. *O. cristavarius* YOY were collected from the New River and *C. chasmodactylus* YOY were collected from Howard's Creek.

The experimental unit consisted of a 50 X 50 X 15cm cage with a removable lid constructed of 12 mm mesh hardware cloth. The floor of the cage was covered with cobbles and the entire cage was enclosed within a 1 mm mesh fiberglass window screen

envelope. The 1 mm mesh size prevented the immigration or emigration of YOY crayfish. To prevent the cages from being dislodged they were anchored to landscaping spikes driven into the riverbottom.

The experimental design was a randomized complete block design with four treatments (0, 2, 4, or 6 *O. cristavarius* per cage) and four replicates per treatment. The location of the treatments within the rows, as well as the assignment of the crayfish to treatments, was randomized. The species, blotted wet mass, carapace length, sex, and cage assignment of each crayfish was noted. Due to a shortage of similarly-sized crayfish, row 2 was randomly assigned smaller crayfish than rows 1, 3, and 4. Crayfish were introduced into the cage via a small opening in the top of the cage that was sealed once the crayfish were inside. The cages were cleaned of debris and inspected for tears in the mesh envelope twice each day for the duration of the experiment. Any tears in the mesh were repaired immediately.

The experiment was terminated after 42 days. Each cage was carefully lifted into a large plastic container and carried to shore. The cage was opened while still in the plastic container and all crayfish were removed. The species, blotted wet mass, carapace length, sex, and condition (e.g., dead, missing chelae, etc.) was noted for each crayfish recovered. The data were analyzed using regression analysis and analysis of variance (ANOVA). The mean change in mass of each species was regressed against the number of crayfish remaining at the end of the experiment. The final number of crayfish YOY was used since this number did not always equal the initial density due to some crayfish escapes and mortality. Additionally, the change in mass of each species was analyzed

using a two-way ANOVA. The effect of the treatment on the survival of *C. chasmodactylus* was tested using a two-way ANOVA comparing the percent *C. chasmodactylus* recovered across treatments.

Predation Experiment. Since rock bass occur at higher densities in the mainstem of the New River and prey heavily on crayfish (Probst et al. 1984, Rabeni 1985, Roell and Orth 1993), the rarity of *C. chasmodactylus* YOY may be the result of rock bass predation. In order to determine the vulnerability of each species to rock bass, a laboratory experiment was conducted that simultaneously exposed both species to rock bass. The experiment was conducted in a 189.3 L aquarium containing aged tap water and was replicated six times. The water was filtered and aerated for the duration of each experiment. The aquarium also contained five 5 cm long sections of 2.54 cm diameter PVC pipe, each glued to a piece of gravel with aquarium cement to provide shelter for the crayfish. For the first three replicates the aquarium also contained a small stack of senescent maple leaves (*Acer* sp.) under a medium-sized cobble. These leaves were intended to serve as food for the crayfish but were omitted from subsequent replicates because the crayfish were not consuming them and it was difficult to see crayfish hiding within the leaves.

The *O. cristavarius* YOY used in the experiment were collected from the New River and Winkler's Creek and the *C. chasmodactylus* YOY used in the experiment were collected from Winkler's Creek and Howard's Creek. The two species were housed separately in 75.7 L aquaria filled with aged tap water. The crayfish were fed a combination of beef liver, senescent maple leaves, dead goldfish, nightcrawlers, and commercial fish food ad lib prior to their use in the experiment. The rock bass used in

the experiment were collected from the New River and housed in aquaria filled with aged tap water. The rock bass were fed crayfish, goldfish, and night crawlers ad lib prior to their use in the experiment.

A replicate of the experiment consisted of five crayfish of each species being placed in the aquarium for a 24-hour acclimation period. The crayfish were haphazardly selected from the holding tank and the sex and size of each individual was noted. All crayfish used in the experiment were of similar size (*C. chasmodactylus* mean mass ± SE = 1.01 ± 0.03 g, mean CL ± SE = 15.9 ± 0.19 mm and *O. cristavarius* mean mass ± SE = 1.03 ± 0.03 g, mean CL ± SE = 17.14 ± 0.20 mm). After the 24-hour acclimation period, a single rock bass (15 – 18 cm standard length) that had been starved for 48 hours was added to the aquarium. The total number of crayfish remaining in the aquarium was counted approximately every 1 - 2 hours and a trial was terminated when five total crayfish remained in the aquarium. The species, size, and sex of all surviving crayfish were noted.

Manly's Selectivity test (Manly 1974, Chesson 1983, McPeek 1990a) was used to ascertain rock bass feeding biases. An α value for each species, which is the probability that the predator will consume that species. The value α_i is defined as:

$$\ln[(n_i - c_i)/ n_i] / \ln[(n_i - c_i)/ n_i] + [(n_j - c_j)/ n_j]$$

where i = species 1, j = species 2, n = the initial number of a species, and c = the number consumed of a species (McPeek 1990a). The mean α was determined for each species and then compared using a two sample t-test.

The mean mass (g) of the initial group of crayfish was compared to the mean mass (g) of the surviving group of crayfish using a Wilcox rank sum test, to evaluate any effect of crayfish size on predator preference.

Escape Behavior Trial – Wading Pool. Field observations of the two crayfish species suggested that they differed in their escape behaviors. Since these differences may influence the vulnerability of each species to rock bass predation, I quantified the escape behavior of the two species. Crayfish were collected from Winkler's Creek (*C. chasmodactylus* and *O. cristavarius*) and the New River (*O. cristavarius*) no more than one day prior to the experiment. The two species were held separately in 11.4 L buckets containing aerated river water. The trials were conducted simultaneously in two 1.83 m diameter wading pools each filled to a depth of approximately 20 cm with aged tap water that had been aerated prior to the beginning of the experiment. Four 7.63 cm diameter terra cotta flowerpots were placed on their sides around the perimeter of the pool 90°, from each other. A fifth pot was placed upside down in the center of the pool to serve as a crayfish holding area (fig. 1). The crayfish species to be tested was randomly selected using a coin flip. A crayfish was then haphazardly selected from the appropriate bucket and the species, carapace length, and sex were noted. The crayfish was placed under the pot in the center of the pool and allowed to acclimate for 10 minutes to prevent any influence of the prior handling on initial escape behavior. After the acclimation period, the pot was gently lifted and I noted whether the crayfish walked away, swam away, or remained in place. The distance of either a walk or swim was measured by dropping a
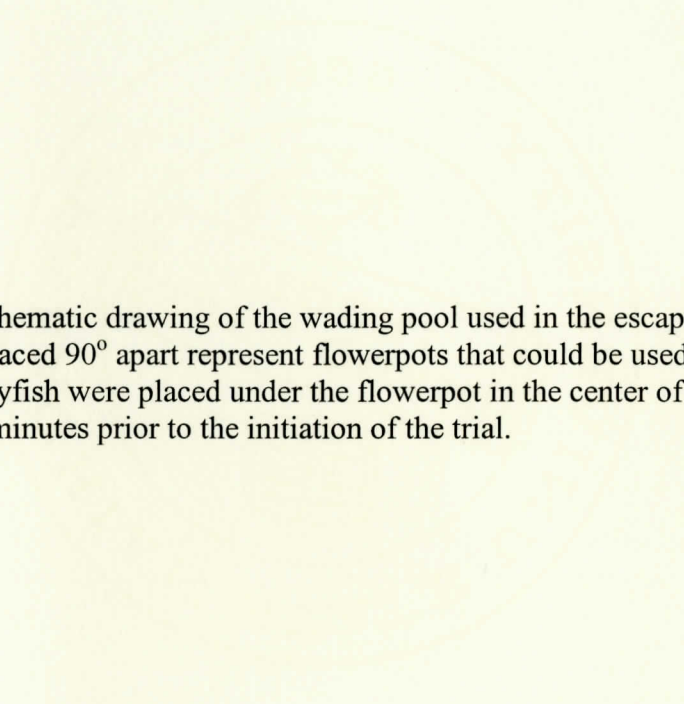
Figure 1.   Schematic drawing of the wading pool used in the escape behavior trials. The trapezoids spaced 90° apart represent flowerpots that could be used as shelter by the crayfish. The crayfish were placed under the flowerpot in the center of the pool to acclimate for 10 minutes prior to the initiation of the trial.

flowerpot
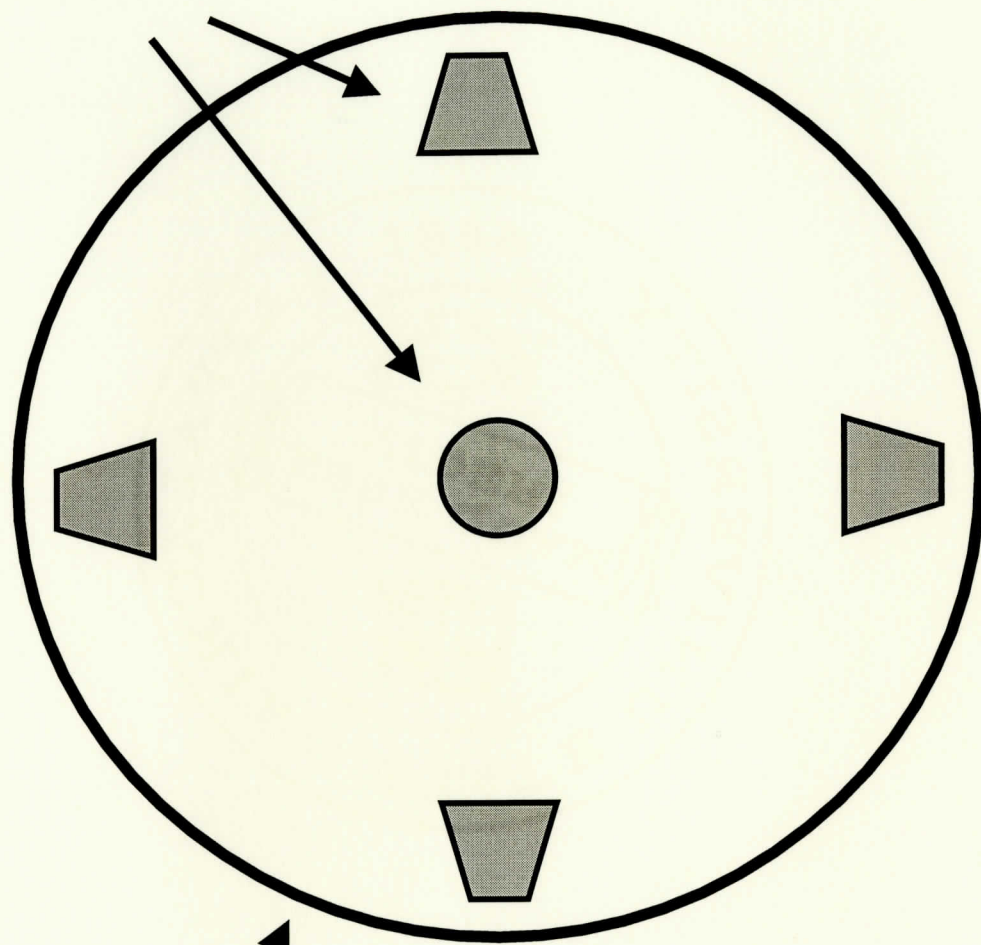
pool

small pebble where the crayfish began moving, stopped moving, and changed direction. The distance between the pebbles was then measured. Lifting the pot was considered the initial disturbance. After the initial disturbance the crayfish was disturbed three more times with a grabbing motion to simulate a predator attack. The distance of any swims or walks was recorded for each disturbance. Disturbance number will hereafter refer to the different times that the crayfish was disturbed (e.g., the initial lifting of the pot and the three simulated predator attacks). The experiment was conducted on two different dates and pool temperature differed between the two days. The pool temperature on September 7 1999 was 20 °C and the pool temperature on September 18 1999 was 15 °C. These differences in temperature were included in the analysis.

The effect of disturbance number, temperature, and species on the swim distance of the YOY crayfish was tested using a three-way ANOVA. The effect of temperature and species on the distance swum by a YOY crayfish as a result of the initial disturbance was tested using Wilcox Rank Sum tests.

Escape Behavior Trial – New River. The swim distance of the two crayfish species in response to a simulated predator attack was quantified to assess the escape behavior of the two species in the field. The experiment was conducted in the New River on June 22, 1999, and the water temperature was 20 °C. Crayfish were located by carefully lifting cobbles. The crayfish was then gently poked with a meter stick to simulate an attack. The path of the swimming crayfish was noted and the swim distance measured. Each crayfish was collected at the end of the swim for positive identification of the species and determination of the CL.

Results

Field Surveys

Quadrat Samples. *O. cristavarius* adults and YOY occurred at consistently higher densities than either the adults or YOY of *C. chasmodactylus* in all of the habitats sampled in the New River between July and August 1998. Since both species of crayfish were uncommon on simple substrate, only the data from complex substrate are used to compare their distributions. In deep water (> 25 cm), adult *O. cristavarius* had a mean (± 1 SE) density of 1.9 (± 0.48) crayfish / m^2 (range: 0 – 7 / m^2). In shallow water (< 25 cm) the mean (± 1 SE) of adult *O. cristavarius* was 1.1 (± 0.37) crayfish / m^2 (range: 0 – 4 / m^2) (fig. 2). The mean density (± 1 SE) of adult *C. chasmodactylus* was 0.27 (± 0.1) crayfish / m^2 in deep water (range: 0 – 1 / m^2) and 0.52 (± 0.29) crayfish / m^2 (range: 0 – 3 / m^2) in shallow water (fig. 2).

The mean density (± 1 SE) of *O. cristavarius* YOY in the New River during June was 30.1 (± 11.5) crayfish / m^2 (range: 0 - 64 / m^2) (fig. 3). The mean density (± 1 SE) of *O. cristavarius* YOY in the New River during August was 14 (± 5.0) crayfish / m^2 (range:0 – 32 / m^2) (fig. 4). No YOY of *C. chasmodactylus* were found in the New River in either the June or August samples (figs. 3 & 4). The mean density (± 1 SE) of *O. cristavarius* YOY in Winkler's Creek during August was 15.1 (± 2.2) crayfish per m^2 (range: 0 – 32 / m^2) while that of *C. chasmodactylus* YOY was 8.6 (± 2.2) crayfish per m^2 (range: 0 -22 / m^2) (fig. 4). The mean density (± 1 SE) of *C. chasmodactylus* YOY in

Figure 2.   The density of *O. cristavarius* adults (shaded bars) and *C. chasmodactylus* adults (open bars) in shallow and deep habitats with complex substrate (cobble, boulder, or vegetation) in the New River. Bars represent the mean (+1 SE) density from 1 and 4 m^2 quadrat samples collected during July and August 1999.
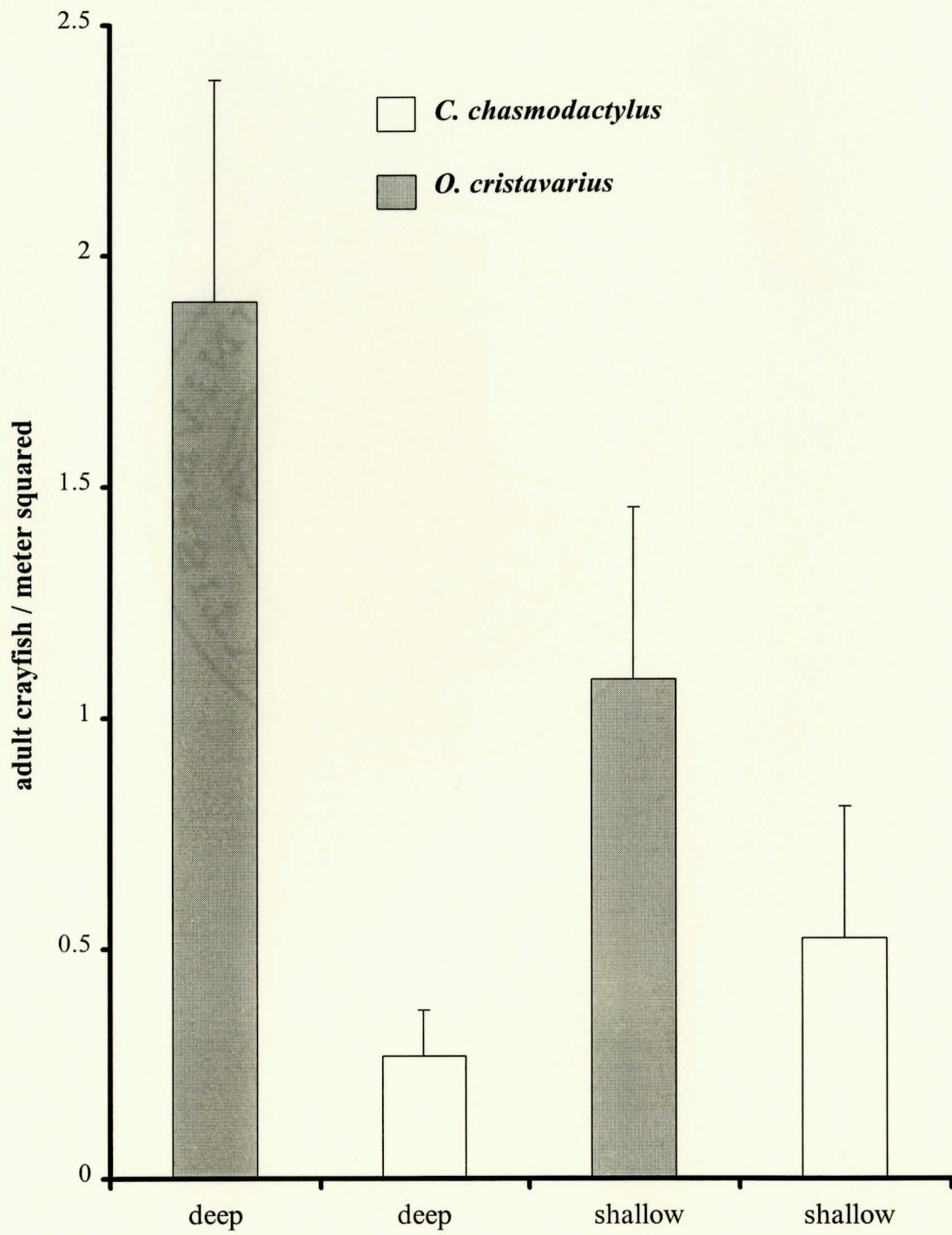
Figure 3.   The density of *O. cristavarius* YOY in the New River during June 1999. Bars represent the mean (+ 1 SE) density from Surber samples in shallow water on gravel substrate. No *C. chasmodactylus* were collected in these samples
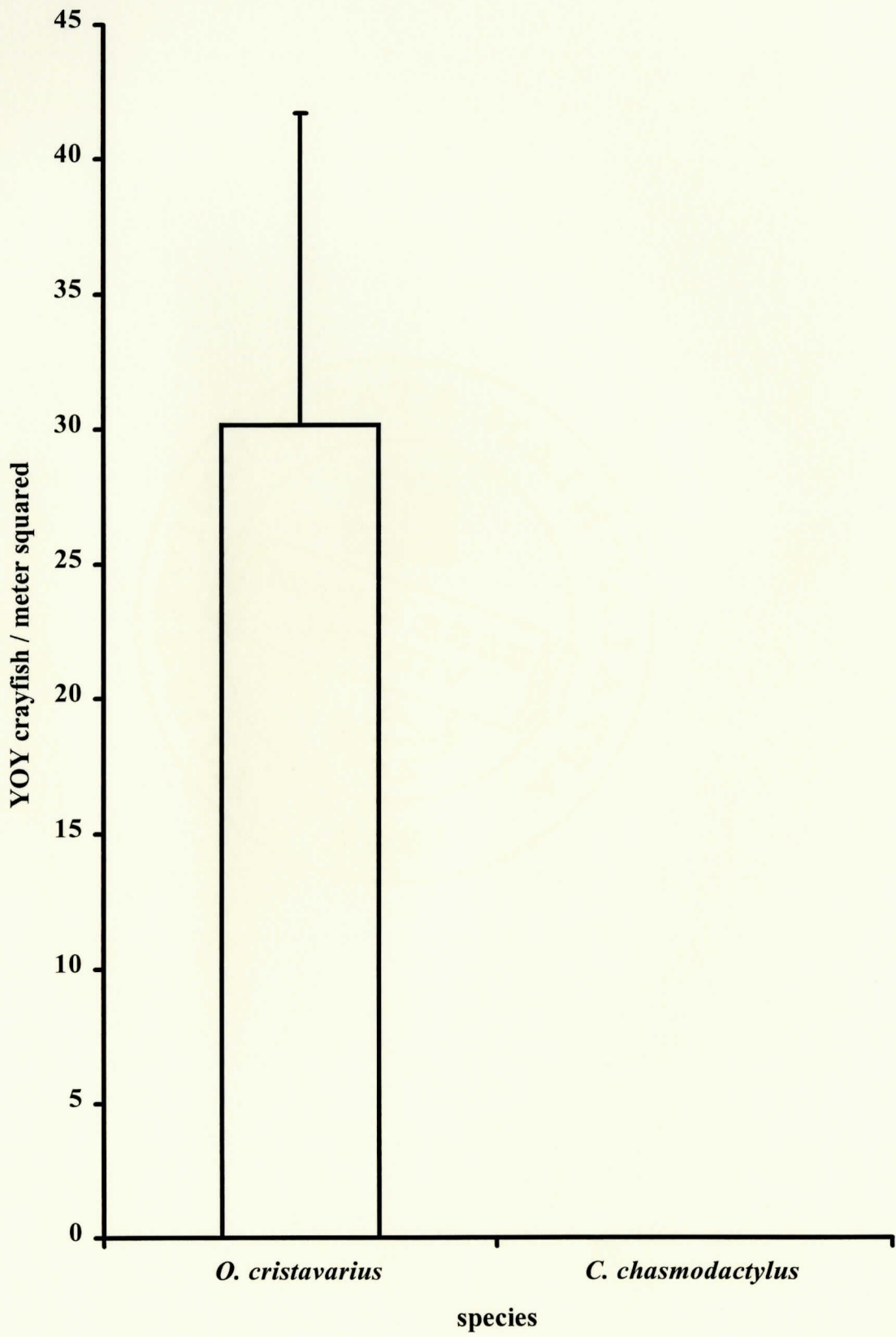
Figure 4.   The density of *O. cristavarius* (open bars) YOY and *C. chasmodactylus* (shaded bars) YOY in the New River, Winkler's Creek, and Howard's Creek during August 1999. Bars represent mean (+ 1 SE) density from Surber samples on cobble substrate.
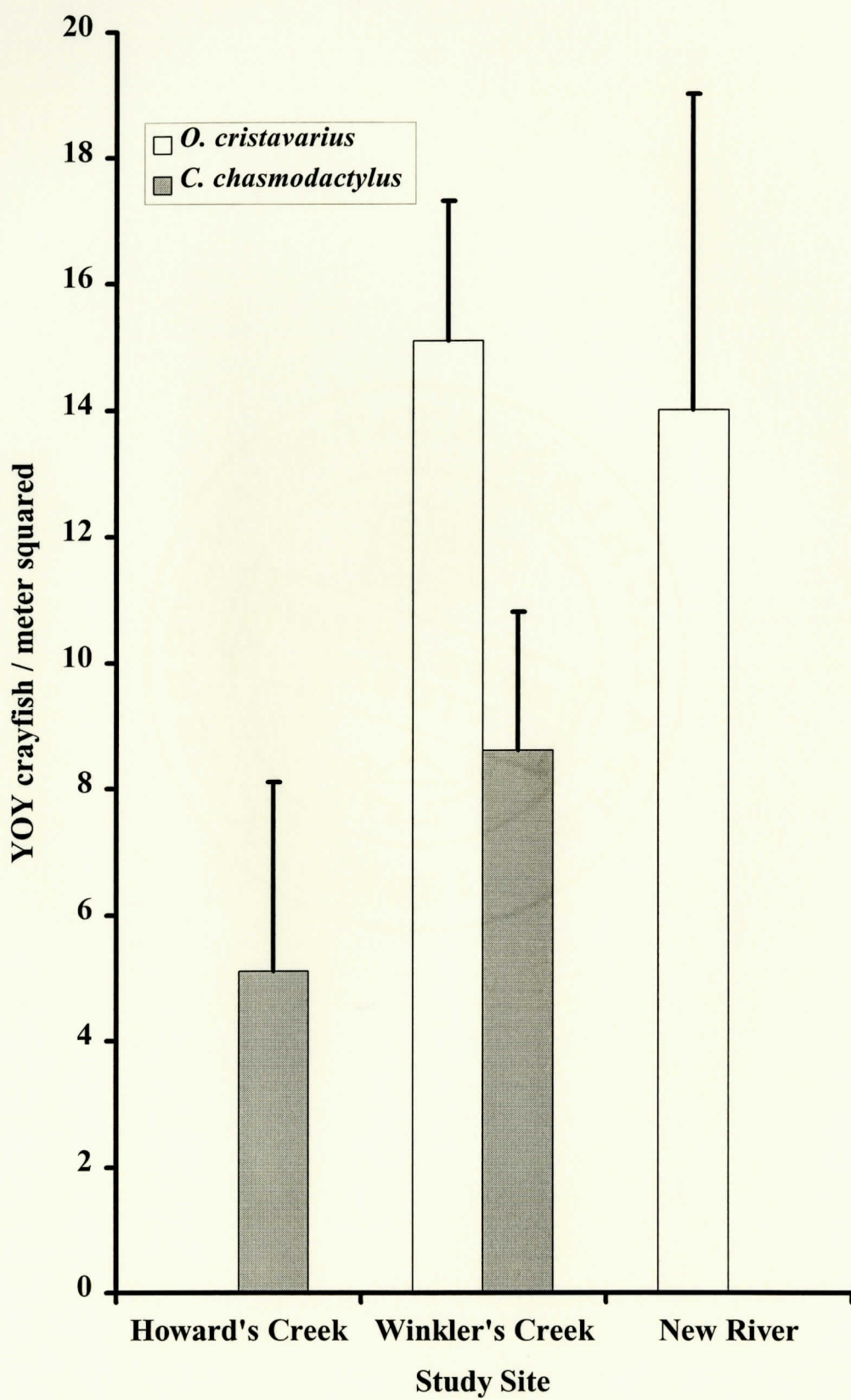
Howard's Creek during August was 5.1 (± 3.0) crayfish / m^2 (range 0 - 11 / m^2) (fig. 4).

No *O. cristavarius* YOY were collected from Howard's Creek (fig. 4).

Experiments

Competition Experiment. There was no significant effect of *O. cristavarius* YOY density on the change in mass of either *C. chasmodactylus* YOY (F = 0.889, p = 0.498, df = 3) or *O. cristavarius* YOY (F = 0.02, p = 0.977, df = 2) (Table 1, fig. 5). The regression analysis also failed to demonstrate any significant relationship between the final number of crayfish in the cage at the end of the experiment and the change in mass of *O. cristavarius* (r^2 = 0.006, p = 0.95) or *C. chasmodactylus* (r^2 = 0.02, p = 0.483) (fig 6). The mean (± 1 sd) gain in mass of *O. cristavarius* YOY was 1.35g (± 0.282) over the 42-day duration of the experiment, whereas the *C. chasmodactylus* YOY gained an average of 0.439g (± 0.147) (fig. 7). The change in mass of *O. cristavarius* was approximately three times greater than the change in mass of *C. chasmodactylus* (F = 105.29, p < 0.001, df = 1).

All of the *C. chasmodactylus* YOY were recovered from 3 the 4 treatments containing no *O. cristavarius* YOY (fig. 8). The crayfish not recovered from the remaining replicate were believed to have escaped from a large hole in the mesh surrounding this cage. There were no significant differences between the percent of *C. chasmodactylus* YOY recovered from each treatment at the end of the experiment, whether the missing YOY were assumed to be dead (F = 0.631, p = 0.631, df = 3) (fig. 8) or to have escaped (i.e. assuming 100% survival in the no *O. cristavarius* treatment) (F =

Table 1 Results of the ANOVA in which the change in mass of each species resulting from treatment in the competition experiment was examined

O. cristavarius

Source	df	SS	MS	F	p
row	3	0.39984	0.13328	1.69	0.267
treatment	2	0.00373	0.00373	0.02	0.977
error	6	0.47301	0.47301		
total	11				

C. chasmodactylus

Source	df	SS	MS	F	p
row	3	0.10669	0.03556	2	0.215
treatment	3	0.04744	0.01975	0.8896	0.498
error	6	0.10665	0.01777		
total	12				

The reduction in the df error for the analysis of *C. chasmodactylus* is due to three cages that were not included in the analysis. The three cages were not used because no *C. chasmodactylus* YOY were recovered from them.

Figure 5.   The mean (± 1 sd) change in mass (g) of *O. cristavarius* (circles) and *C. chasmodactylus* YOY (diamonds) at the end of the 42-day competition experiment as a function of the number of *O. cristavarius* YOY originally placed in the cage.
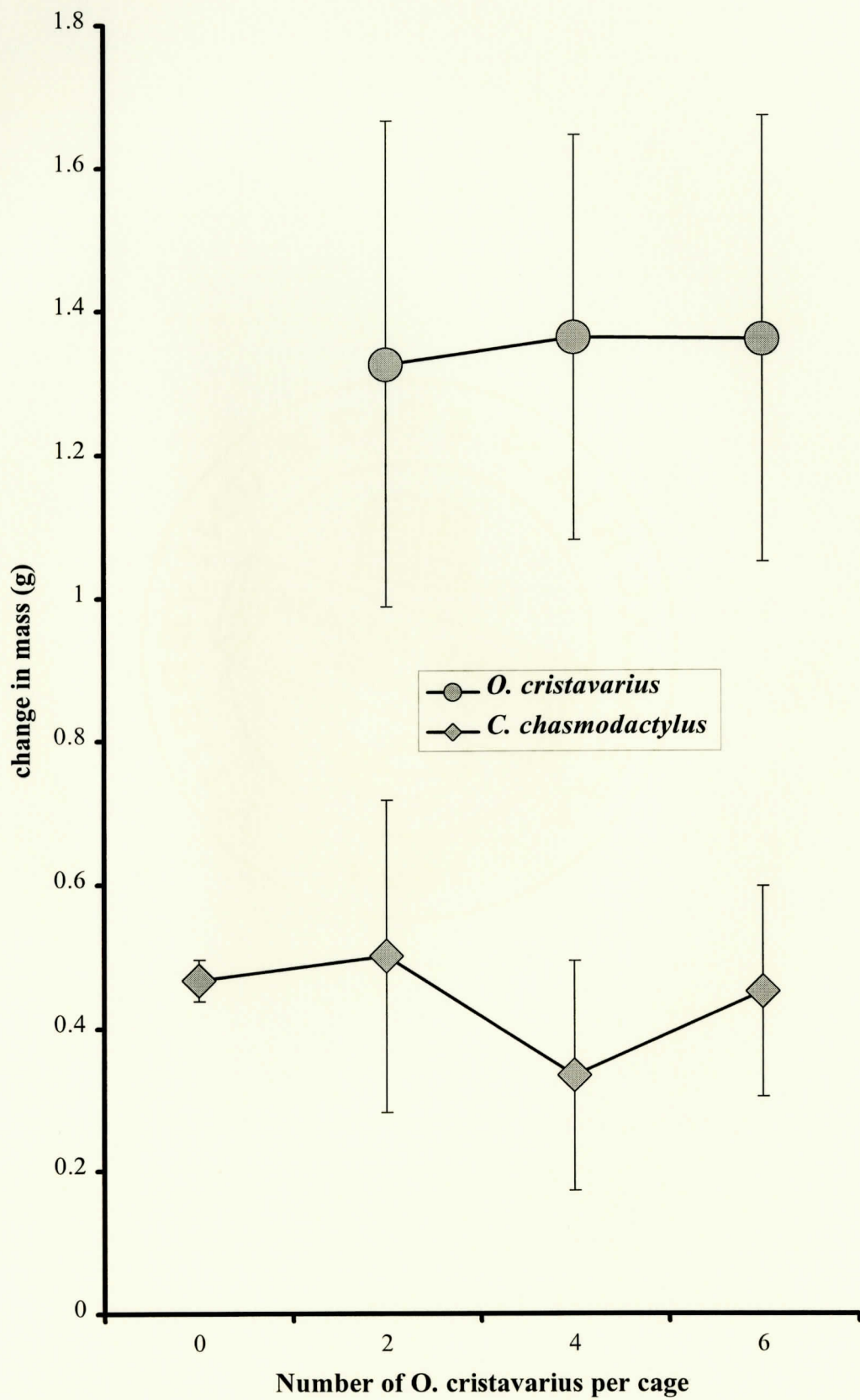
Figure 6.   Regression analysis of the change in mass of *C. chasmodactylus* YOY (diamonds) and *O. cristavarius* YOY (circles) against the final number of crayfish recovered from the cage. Each point represents the mean change in mass of the crayfish in a single cage and the line is a best fit linear regression. *C. chasmodactylus* has an $r^2 =$ 0.02 and a p = 0.48. *O. cristavarius* has an $r^2 = 0.006$ and a p = 0.95.
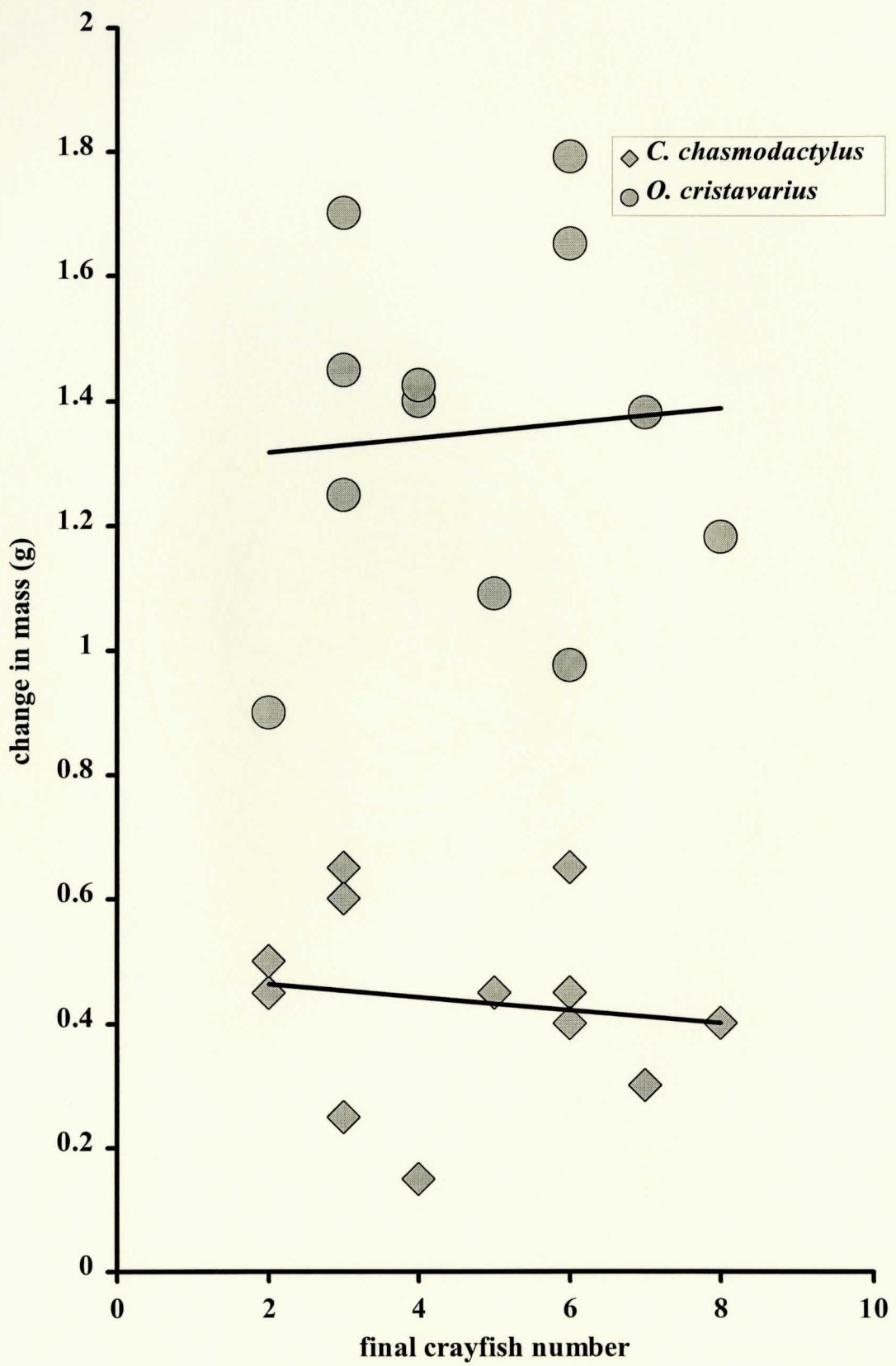
Figure 7.   The initial and final mass (g) of all *O. cristavarius* (circles) and *C. chasmodactylus* (diamonds) YOY used in the competition experiment. Points represent the mean mass of a single cage and the lines are best fit linear regression for *O. cristavarius* YOY (solid) and *C. chasmodactylus* YOY (dashed).
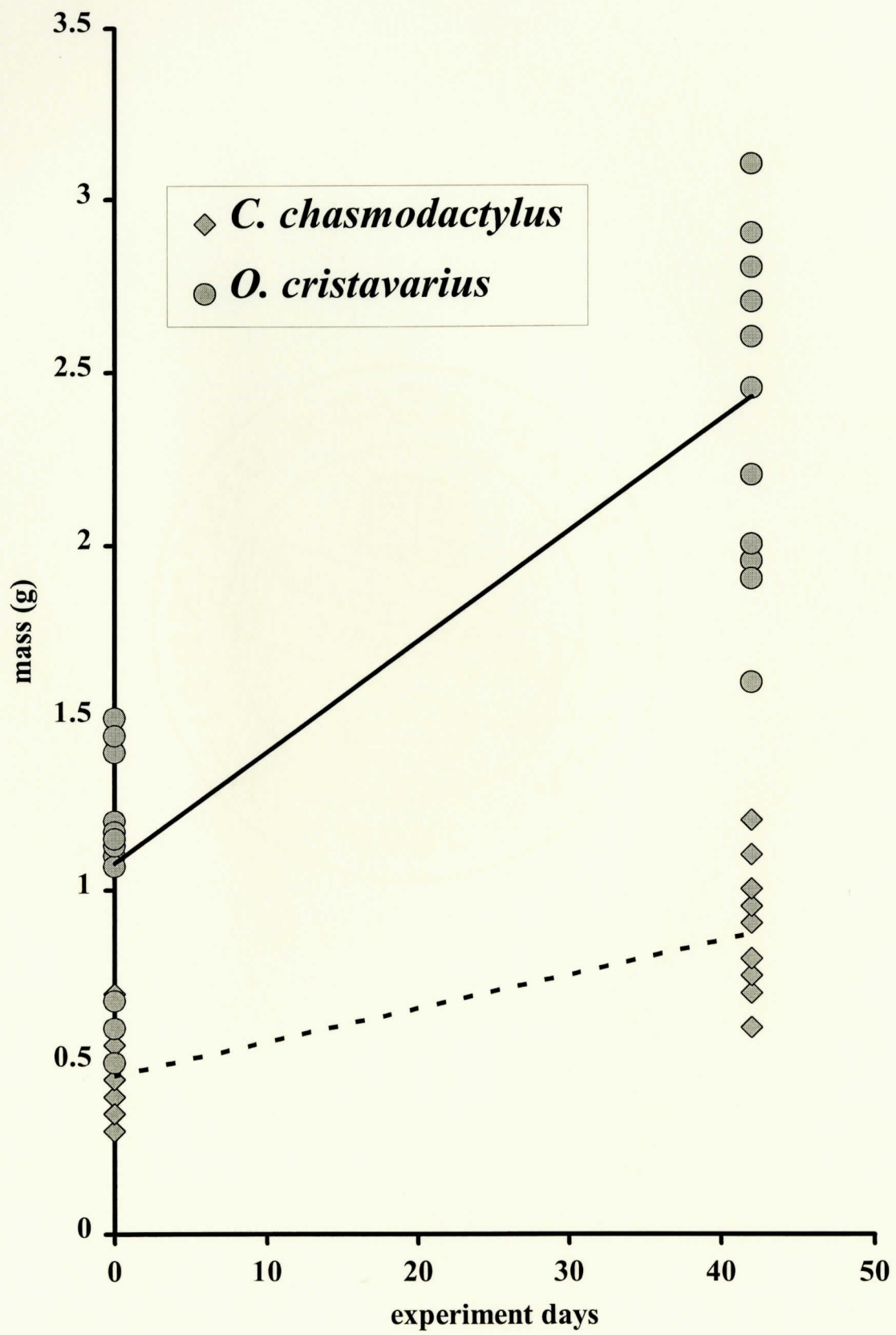
Figure 8.   The percent *C. chasmodactylus* YOY recovered (this includes both dead and escaped crayfish) from each treatment. Bars represent the mean percent recovered plus 1 standard deviation. There was no significant difference between the treatments.
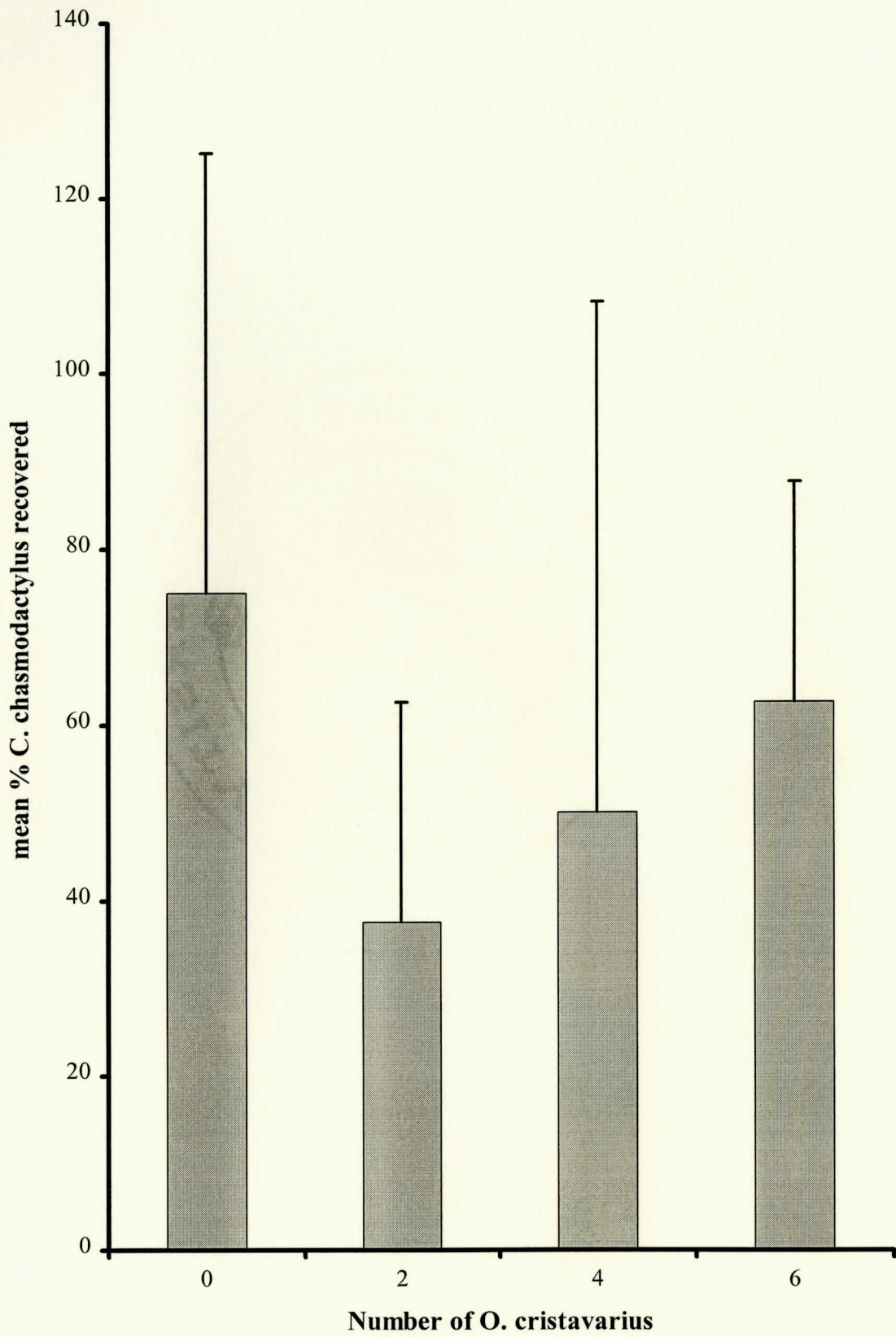
3.50, p = 0.063, df = 3). This indicates that increased *O. cristavarius* density did not result in greater *C. chasmodactylus* mortality.

Predation Experiment. The mean α value of 0.705 (± 0.197) for *C. chasmodactylus* YOY was significantly greater than the mean α value of 0.295 (± 0.197) for *O. cristavarius* (t = 3.61, p = 0.005, df = 10) (Table 2). Since the α value represents the probability that a species will be consumed, the significantly greater α value of *C. chasmodactylus* indicates that this species has a greater chance of being consumed by rock bass.

There was no evidence that the rock bass were exhibiting any size-biased consumption as there was no significant difference between the initial and final masses of the crayfish in the tank (W = 773.5, p = 0.63) (fig. 9). Additionally, the masses of the two crayfish species were not significantly different (W = 858, p =1), indicating that the predator feeding bias toward *C. chasmodactylus* was not based on any difference in size between the two species (fig. 9).

Escape Behavior Trial – Wading Pool. There was a significant effect of disturbance number on the distance swum by YOY crayfish. The greatest variation occurred in the response of the YOY to the initial disturbance (F = 9.026, p < 0.0001, df = 3) (Table 3) (fig. 10). The mean (± 1 SE) swim distance of *O. cristavarius* YOY when initially disturbed was 7.6 (± 7.6) cm in 20 °C water and 48.7 (± 13.9) cm in 15 °C water. *C. chasmodactylus* YOY never swam when initially disturbed in either water temperature.

Table 2. Mean alpha values and standard deviation (sd) for each crayfish species used in the predation experiment. Values are based on 6 trials.

Species	mean alpha value	sd
C. chasmodactylus	0.705	0.197
O. cristavarius	0.295	0.197

Figure 9.   The mean (+ 1 SE) mass (g) of the initial and surviving populations of *O. cristavarius* YOY (shaded bars) and *C. chasmodactylus* YOY (solid bars) used in the fish predation experiment. There was no significant difference between the mean mass of the initial and surviving populations of the YOY combined (p = 0.927) or for each species (p = 1), indicating that the predator was not displaying size-biased consumption.
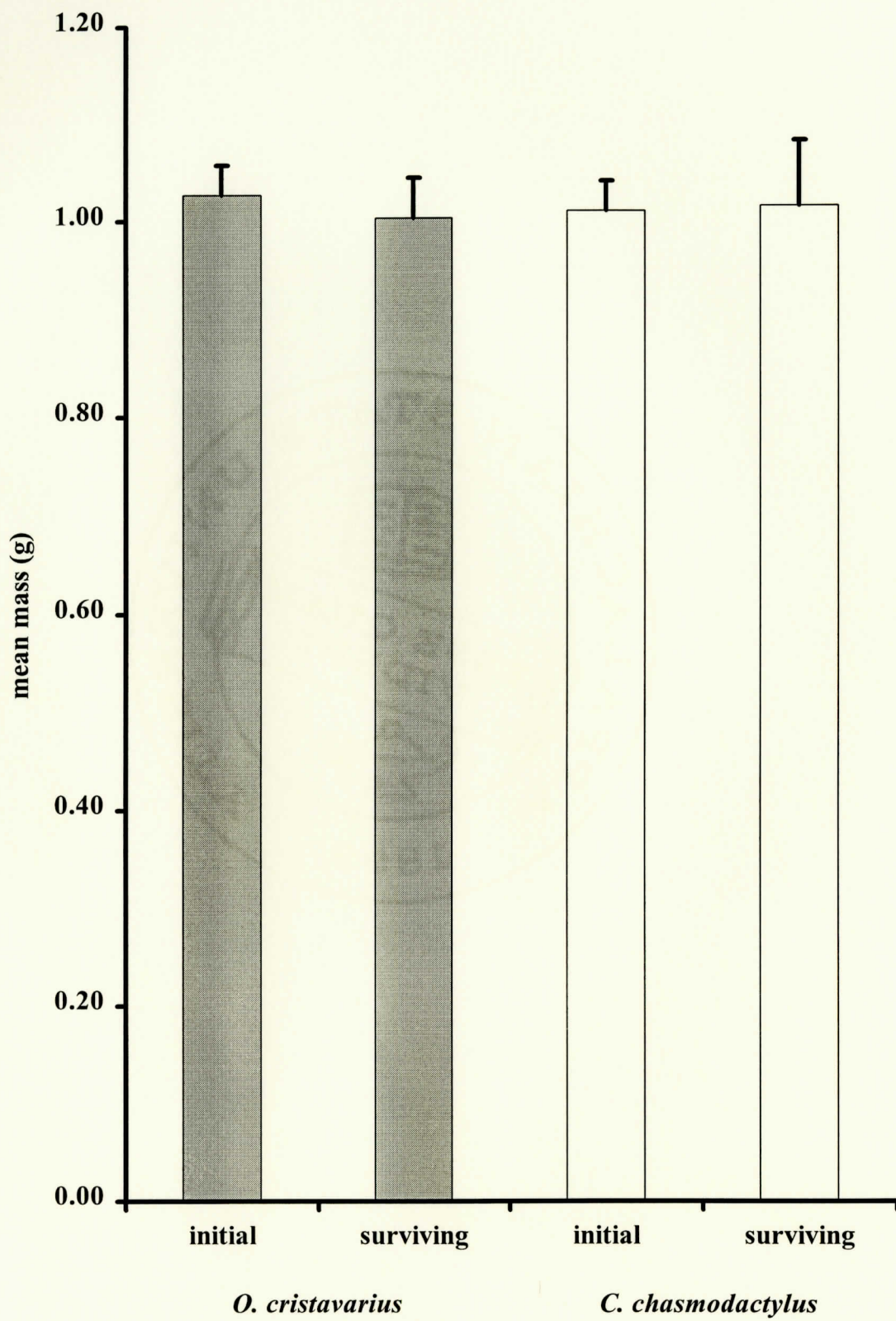
Table 3. ANOVA table for three-way analysis of disturbance number, species, and temperature.

Source	df	SS	MS	F	p
temperature	1	1.42	1.42	0.228	0.633
disturbance	3	168.16	56.05	9.026	<0.001
species	1	0.28	0.28	0.045	0.831
temperature * disturbance	3	122.05	40.68	6.551	<0.001
temperature * species	1	4.49	4.49	0.724	0.396
disturbance * species	3	167.69	55.9	9	<0.001
disturbance * temperature * species	3	120.79	40.26	6.483	<0.001
error	188	1167.56	6.21		

Figure 10.   The mean (±1 SE) swim distance of *C. chasmodactylus* YOY (diamonds) and *O. cristavarius* YOY (circles) as a function of disturbance number. The dashed lines represent trials in 20 °C water and the solid lines represent trials in 15 °C water.
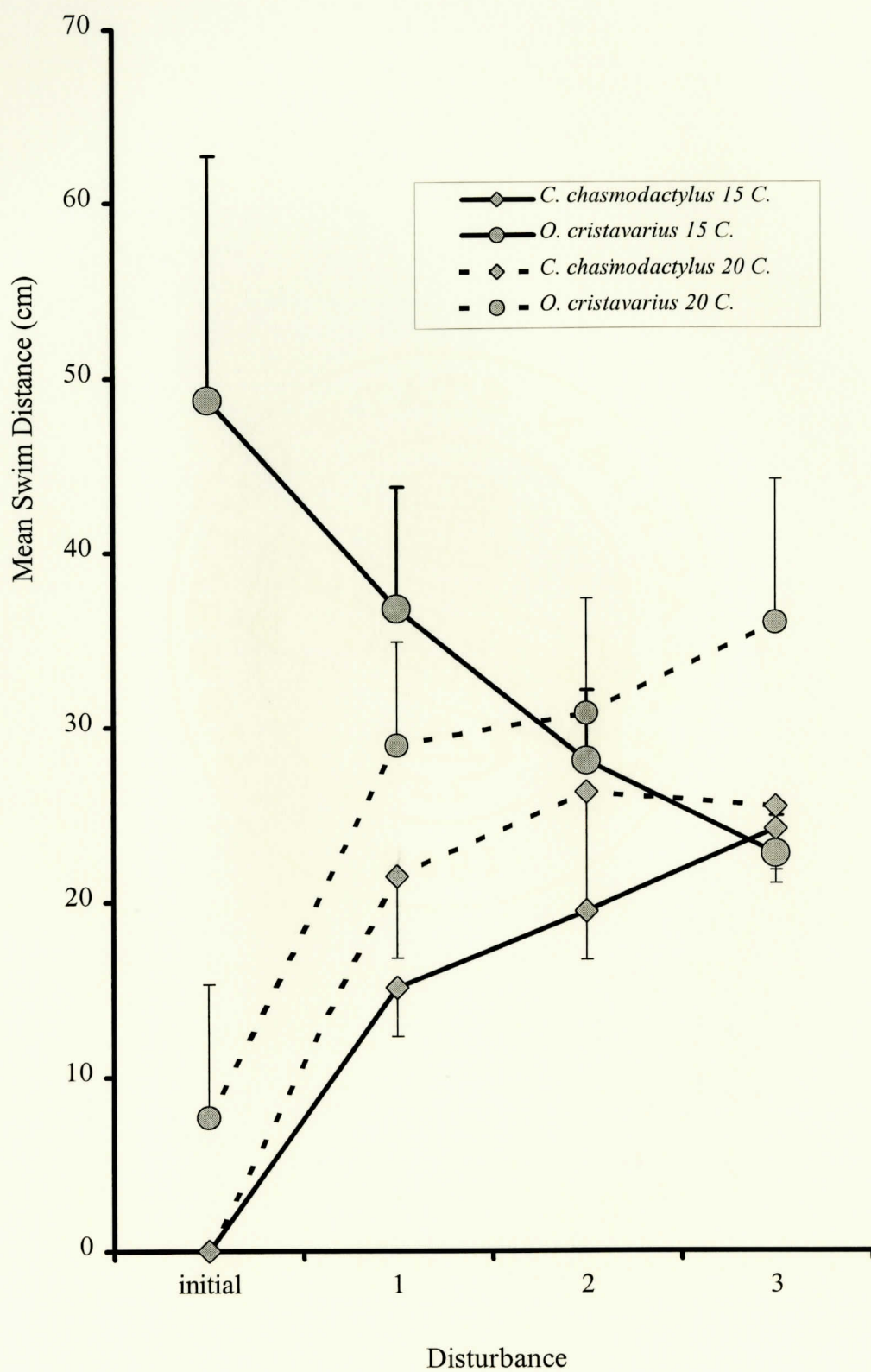
The interaction between disturbance number and temperature ($F = 6.551$, $p < 0.001$, $df = 3$), disturbance number and species ($F = 9$, $p < 0.001$, $df = 3$), and the three way interaction between disturbance number, temperature, and species ($F = 6.483$, $p < 0.001$, $df = 3$) were significant (Table 3) (fig. 10). Neither the effects of temperature nor species alone, nor the interaction between temperature and species, were significant when all disturbance numbers were analyzed (Table 3). Since the largest differences occurred during the initial disturbance, the individual effects of species and temperature on the swim distance of the crayfish YOY when initially disturbed were analyzed using Wilcox Rank Sum tests. Both species ($W = 212.5$, $p = 0.001$) and temperature ($W = 234.5$, $p = 0.01$) had a significant effect on the swim distance of YOY crayfish during the initial disturbance (fig. 10).

The maximum swim distance of an individual crayfish of each species during the first disturbance (the first simulated predator attack after the initial disturbance) was similar in 20 °C water (*C. chasmodactylus* = 60 cm, *O. cristavarius* = 60 cm) (fig. 11). However, in 15 °C water, *C. chasmodactylus* showed a reduction in maximum swim distance (42 cm) while *O. cristavarius* showed a slight increase (65 cm) (fig. 12). Despite the similarity in maximum swim distance between the species, *O. cristavarius* had a greater frequency of longer swims (> 20% maximum swim distance) during the first disturbance in both high and low temperatures (figs. 11 & 12). *O. cristavarius* swam greater than 15 cm 64 % of the time in 20 °C water and 88 % of the time in 15 °C water.

Figure 11. Frequency histogram of swim distances of *O. cristavarius* (open bars) and *C. chasmodactylus* (shaded bars) in 15 °C water in the escape behavior experiment conducted in the wading pools.
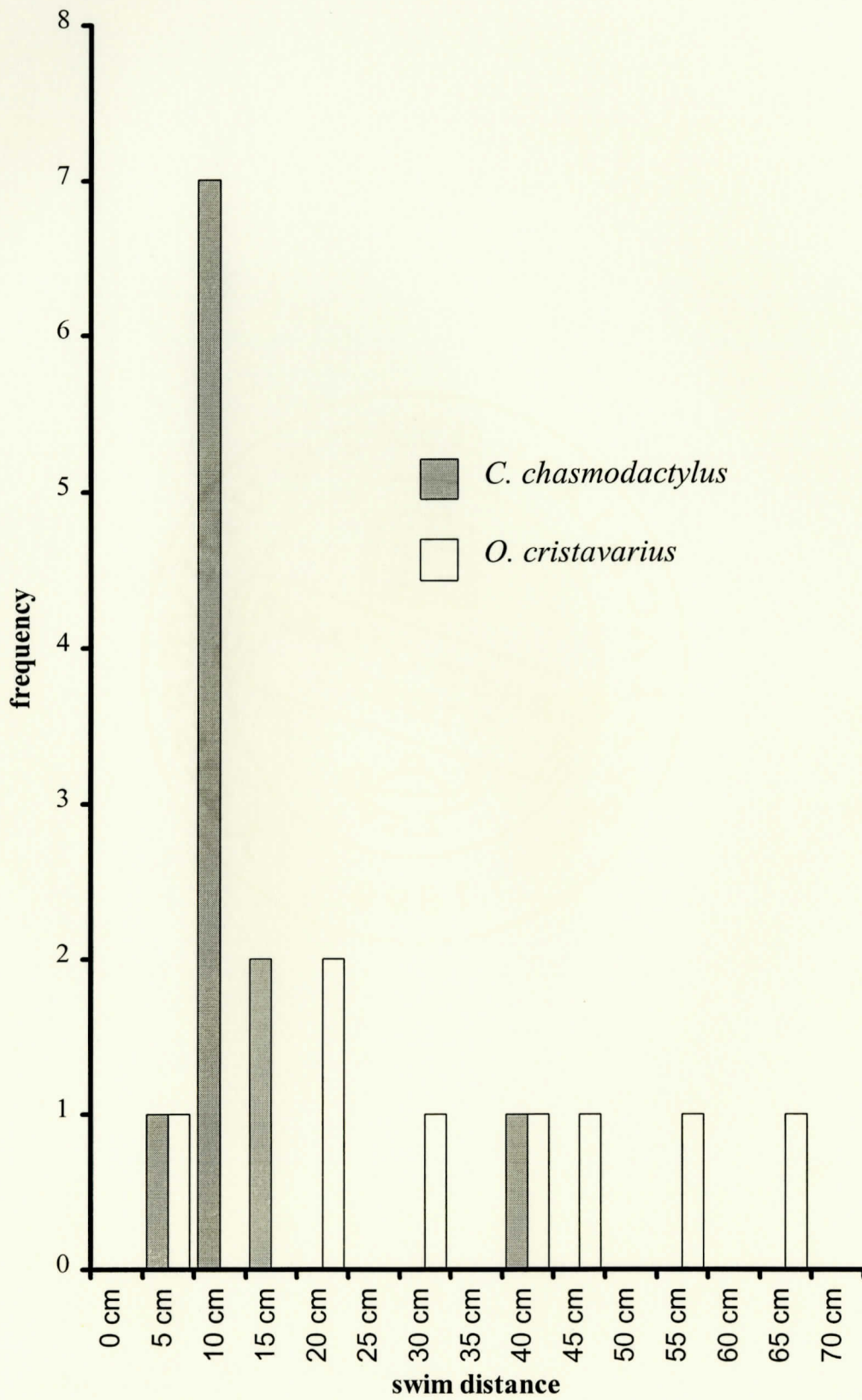
Figure 12.   Frequency histogram of swim distances of *O. cristavarius* (open bars) and *C. chasmodactylus* (shaded bars) in 20 °C water in the escape behavior experiment conducted in the wading pools.
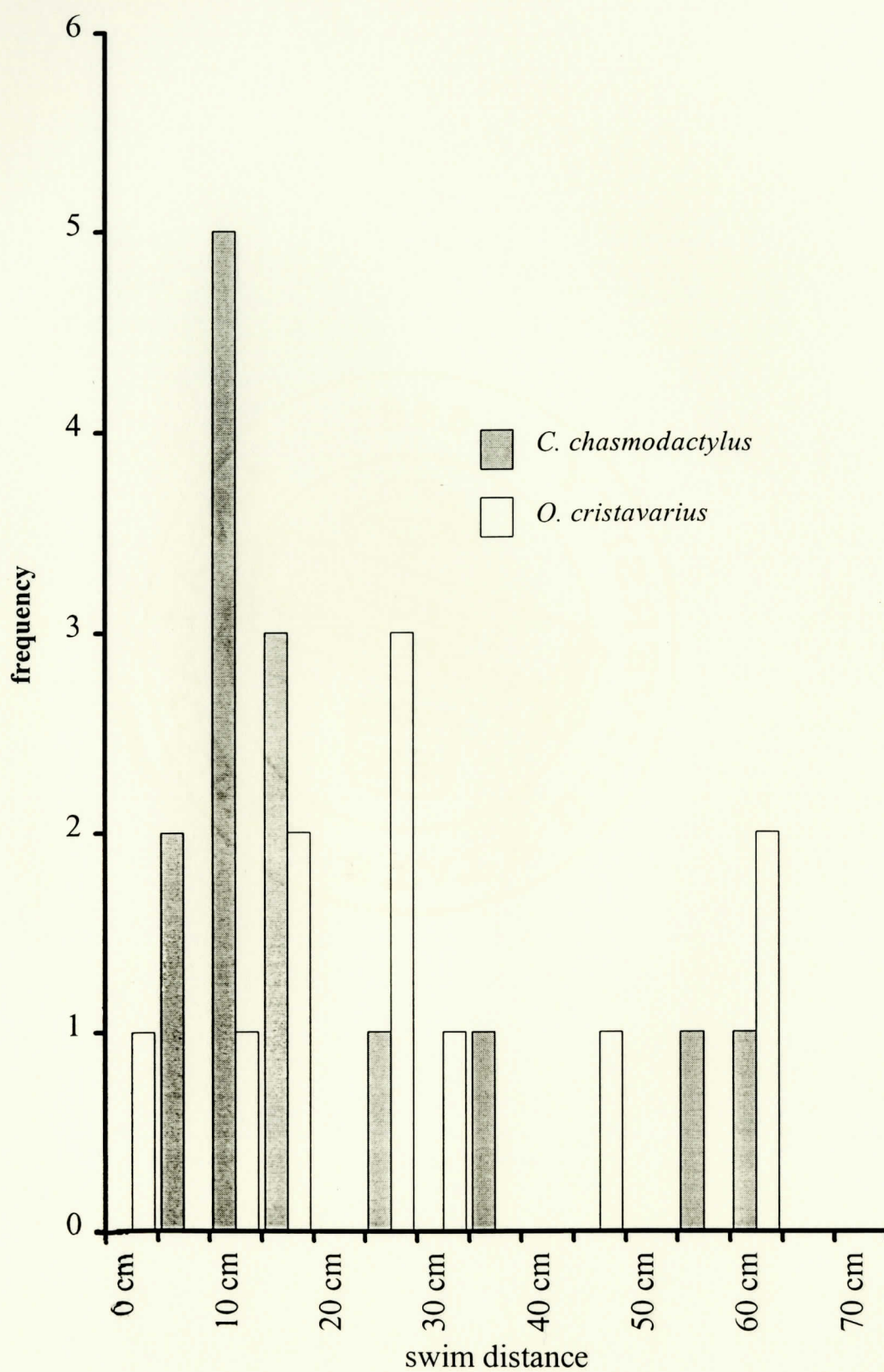
Escape Behavior Trial – New River. Overall the swim distances observed in the field were greater than in the pool experiment. The maximum swim distance observed for *O. cristavarius* was 260 cm, whereas the maximum swim distance observed for *C. chasmodactylus* was 110 cm . *O. cristavarius* had a greater frequency of longer swims (> 20% maximum distance swum by either species) than *C. chasmodactylus* (figs. 13 & 14). *O. cristavarius* swam greater than 52 cm 72 % of the time, while *C. chasmodactylus* swam greater than 52 cm only 60 % of the time.

Discussion

The rarity of *C. chasmodactylus* YOY in the mainstem of the New River was unexpected given the density of adults. Female *C. chasmodactylus* have been found both with attached eggs and young (Brown 1999, Fortino, personal observation), demonstrating that the species is capable of producing viable eggs in the New River. The virtual disappearance of the YOY subsequent to their release from the female indicates that their rarity is not a consequence of reproductive failure but likely the result of extraordinarily high mortality of the free-living YOY.

Intense predation pressure from rock bass appears to be responsible for this high mortality of *C. chasmodactylus* YOY in the New River. Rock bass are common in the New River and a large portion of their diet consists of crayfish (Probst et al. 1984, Rabeni

Figure 13.   Frequency histogram of swim distances of *O. cristavarius* in the escape behavior experiment conducted in the New River.
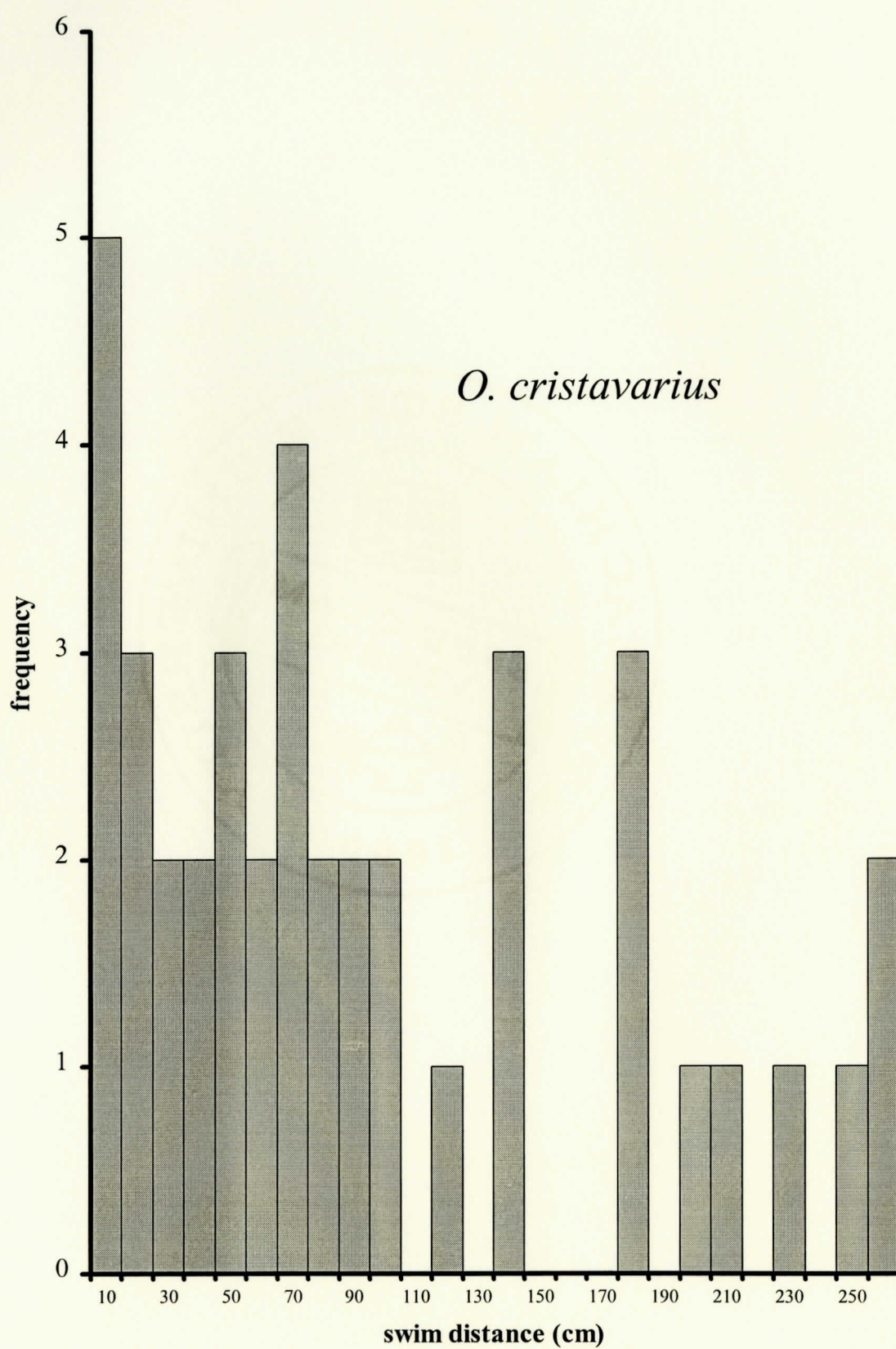
Figure 14.   Frequency histogram of swim distances of *C. chasmodactylus* in the escape behavior experiment conducted in the New River.
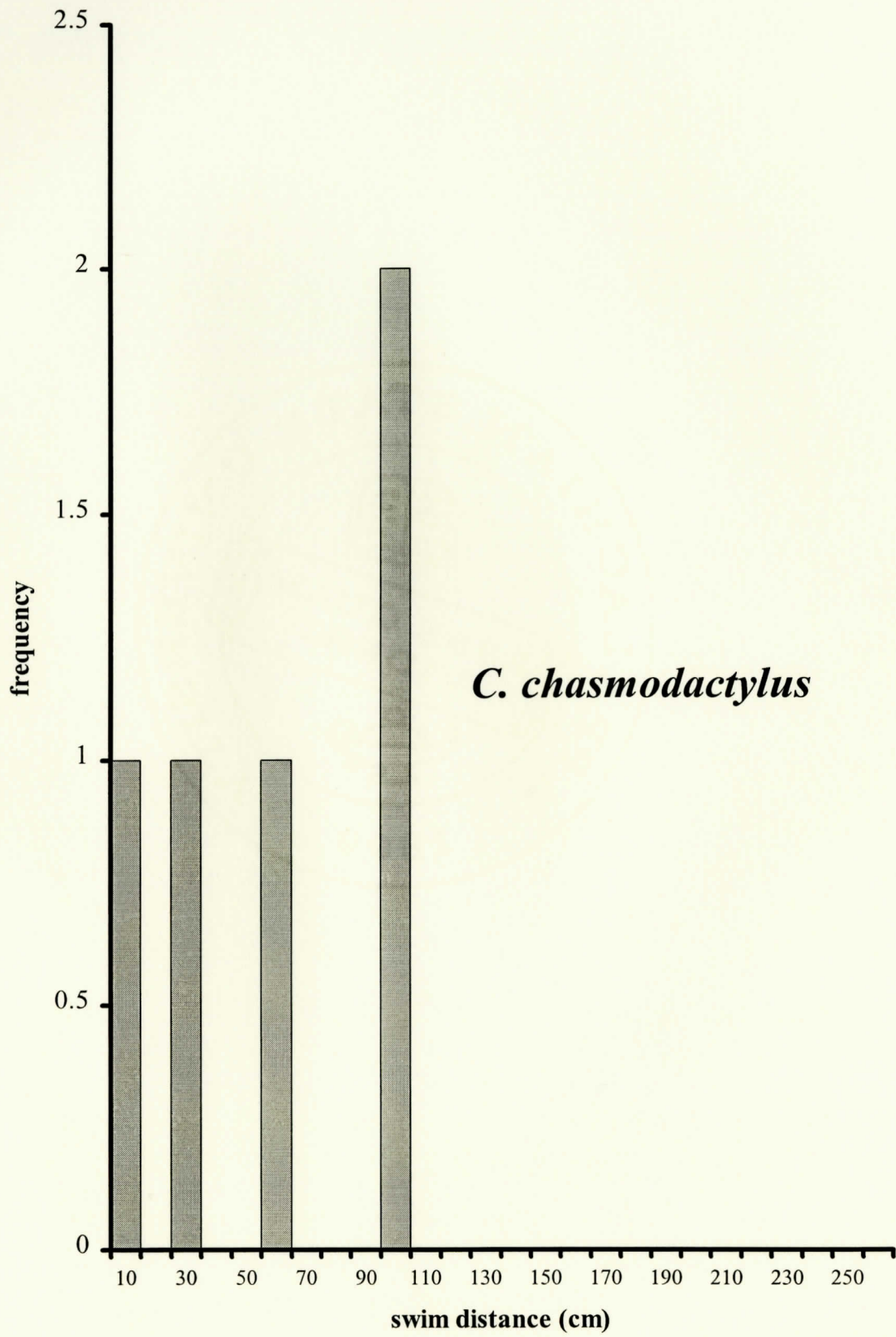
1985, Roel and Orth 1993). Additionally, rock bass are rare in the tributaries of the
South Fork of the New River (Neil Medlin, North Carolina Division of Water Quality,
personal communication, K. Fortino, personal observation), thus the tributaries appear to
represent a significant refuge from rock bass predation. It is expected that prey which are
highly susceptible to rock bass predation would be excluded from the New River and
would be found in higher densities in the tributaries, whereas prey that are less vulnerable
to rock bass predation would coexist with the predator (e.g., McPeek 1990a). *C.
chasmodactylus* YOY were much more vulnerable to rock bass predation than *O.
cristavarius* YOY in the laboratory experiment, indicating that *C. chasmodactylus* YOY
may experience significantly greater predation pressure from rock bass and would
therefore be excluded from the New River. The lower level of predation experienced by
O. cristavarius in the laboratory experiment is consistent with their coexistence with rock
bass in the New River. Furthermore, the importance of predation in excluding *C.
chasmodactylus* YOY from the New River is further supported by the persistence of adult
C. chasmodactylus in this habitat. Roel and Orth (1993) and Probst et al. (1985) both
reported a low frequency of larger crayfish in the gut contents of rock bass. Therefore,
adult crayfish that enter the New River from the tributaries would no longer be
susceptible to the predation pressure that excluded the YOY.

Competition between *O. cristavarius* and *C. chasmodactylus* YOY does not
appear to be responsible for the virtual exclusion of *C. chasmodactylus* YOY from the
New River. There was no evidence of competition between the two species, even at the
highest densities used in the experiment. Increasing the density of *O. cristavarius* YOY

resulted in neither a reduction in *C. chasmodactylus* growth nor an increase in *C. chasmodactylus* mortality. Furthermore, *C. chasmodactylus* YOY coexist with *O. cristavarius* YOY at densities similar to those found in the New River at the Winkler's Creek study site. If competition was a significant factor regulating the distribution of *C. chasmodactylus* YOY in the New River, then we would expect significant competition between the YOY of the two species in Winkler's Creek as well and the exclusion of *C. chasmodactylus* YOY from the Winkler's Creek site.

Although shelter competition has been demonstrated to be important in structuring other crayfish communities (Bovbjerg 1970, Rabeni 1985, Garvey et al. 1994, Blank and Figler 1996), there was no evidence that shelter competition plays a large role in this system. The greater vulnerability of *C. chasmodactylus* YOY in the laboratory predation experiment was not the result of limited shelter. The 5 PVC pipe shelters included in the experimental aquarium each provided multiple refuge locations as did the corners of the tank. The combination of the pipe shelters and the tank corners provided sufficient shelter for all of the crayfish in the tank. Thus, the predator feeding biases observed in the predation trials do not appear to be the result of competition for limited shelter. Additionally, *C. chasmodactylus* YOY are absent from the New River as early as June when the primary shelter utilized by the YOY is gravel and vegetation. Samples taken in these habitats revealed a highly patchy distribution of the *O. cristavarius* YOY, suggesting that shelter is not limited at the time when the YOY are excluded from the New River.

There was no evidence that abiotic factors had an impact on the survival of *C. chasmodactylus* YOY in the New River. All of the YOY of *C. chasmodactylus* were recovered from 3 of the 4 treatments containing no *O. cristavarius* YOY in the competition experiment. The mesh surrounding the one cage from which the YOY were not recovered was damaged in a flood just prior to the termination of the experiment. Since no crayfish remains were found in the cage, it is probable that the crayfish escaped from this cage. The definite survival of all of the *C. chasmodactylus* YOY in 3 of the remaining cages containing no *O. cristavarius* indicates that the *C. chasmodactylus* YOY are capable of surviving in the New River. Thus, the absence of evidence for competition or intolerance to abiotic conditions lends additional support to the hypothesis that rock bass predation is limiting the distribution of *C. chasmodactylus* YOY.

The difference in vulnerability of the YOY of the two species to rock bass may be related to differences in their predator escape behaviors. The escape behaviors of the two species differed both in the field and in the laboratory. *O. cristavarius* YOY have a greater tendency to swim when initially disturbed and have a greater frequency of longer swims. This greater tendency of *O. cristavarius* to begin swimming sooner, as well as to swim longer distances when threatened, may increase its chances of successfully eluding rock bass. The escape behavior of *O. cristavarius* and its persistence in the presence of rock bass predation is inconsistent with much of the literature concerning the interactions between fish and their prey in lentic communities. A number of studies have shown for a variety of prey taxa, that reducing activity in the presence of fish predators increased the prey's chance of surviving (Stein and Magnuson 1976, Woodward 1983, McPeek 1990b,

Angermeier 1992, Skelly 1995, Storfer and Sih 1998). Swimming is not a successful

strategy for most invertebrates and some vertebrates in the presence of fish predators,

because the swimming ability of the fish far exceeds that of the prey. Yet, it may be

possible that, in certain situations, prey individuals that actively flee fish predators may

increase their chance of eluding the predator. *O. cristavarius* are large relative to the

rock bass and are strong swimmers; thus they may be able to remain outside of the range

of the bass by fleeing approaching fish. *O. cristavarius* also appear to have a longer

reactive distance than *C. chasmodactylus* in response to the approaching predator

(Fortino, personal observation). The tendency of *O. cristavarius* YOY to enter the water

column further from the predator combined with their tendency to swim longer distances

may increase their ability to coexist with rock bass. If *O. cristavarius*, when approached

by rock bass, begin swimming sooner and swim long distances, they may quickly swim

beyond the range that rock bass are likely to strike and may even swim beyond the range

that they can be detected by the fish. Conversely, the proclivity of *C. chasmodactylus* for

shorter swims may actually increase its vulnerability to rock bass, since the short swim

may attract the fish.

Despite the successful production of offspring, the YOY of *C. chasmodactylus*

remained exceedingly rare in the New River, suggesting that there is insufficient

recruitment for the maintenance of the adult population in the New River. The New

River adult population is likely the result of downstream dispersal from the tributaries.

Since the scarcity of *C. chasmodactylus* YOY is a feature unique to the New River

population, recruitment from populations in the tributaries probably maintains not only

the adult populations in the tributaries but also the adult population in the New River. The densities of *C. chasmodactylus* YOY in the tributaries seasonally exceed adult population densities and are typical of other lotic crayfish populations (e.g., Rabeni 1985, Creed 1994).

My results suggest that it is rock bass predation that excludes the YOY of *C. chasmodactylus* from the New River. However, it is not clear what results in the lack of *O. cristavarius* YOY in the tributaries. It is possible that the escape behavior of *O. cristavarius* makes it more vulnerable to the predators commonly found in the tributaries (e. g. trout and sculpin) and the species is therefore excluded from the tributaries by mechanisms similar to those excluding *C. chasmodactylus* YOY from the New River. Since *O. cristavarius* swam greater distances in the cooler temperatures, then the species may be more likely to swim longer distances in the tributaries where water temperatures are cooler. The tendency of *O. cristavarius* to swim more often and long distances may prove to be an ineffective strategy against the predators in the tributaries. Since trout tend to feed by maintaining a feeding station and allowing food items to drift to them, then the frequent long swims of *O. cristavarius* YOY may increase its likelihood of being swept into a trout feeding station. If *O. cristavarius* is more vulnerable to trout predation then the high predation levels combined with the reduced likelihood of upstream dispersal would result in the exclusion of both the adults and YOY from the tributaries. Other possible explanations for the absence of *O. cristavarius* in the tributaries include intolerance to the abiotic environment of the tributaries (i.e. cooler temperatures, lack of suitable substrate). Helms (2000) reports differences in the diets of adult *C.*

chasmodactylus and *O. cristavarius*. His analysis of the gut contents of adult crayfish of both species show that *O. cristavarius* consumes significantly more sediment than *C. chasmodactylus* (Helms 2000). It is possible that the reduced abundance of fine sediment substrate in the tributaries limits the colonization of these habitats by YOY and adult *O. cristavarius*.

Predator Transitions in Lotic Communities

Predators have been shown to have important effects on the distributions of certain taxa in both lentic and lotic systems. Significant reductions in the abundance of certain taxa have been observed on both sides of the transition between fishless and fish-containing habitats (McPeek 1990a, Storfer and Sih 1998, Englund 1999).

Wellborn et al. (1996) proposed a model of the principal forces limiting community membership in lentic habitats. They placed lentic habitats on a habitat permanence gradient. The principal force limiting community membership in temporary habitats is abiotic factors (i.e. desiccation) and the principal factor limiting community membership in permanent habitats is predation (Wellborn et al. 1996). Their model also suggests that within permanent habitats there exists an important transition between habitats dominated by fish predators and habitats dominated by invertebrate predators (Wellborn et al. 1996). The model predicts a shift in community structure as you move from habitats dominated by invertebrate predators to habitats dominated by vertebrate predators, since prey adapted to coexisting with invertebrate predators would be eliminated by fish and vice versa (Wellborn et al. 1996). Creed, (in preparation) proposes a similar model for lotic habitats. His model predicts that there are similar

transitions between the forces limiting community membership in permanent and temporary streams. He hypothesizes that the principal forces limiting community membership in ephemeral streams are abiotic factors (e.g., desiccation) and that the principal force limiting community membership in permanent streams with more benign environments is predation. Permanent streams that do not contain fish should be dominated by invertebrate and amphibian predators. In many temperate streams there is a transition from fishless streams to cooler headwater streams dominated by cold-water fish predators (e.g., trout sculpin). This transition is similar to the predator transition proposed by Wellborn et al. (1996) for lentic communities. Furthermore, Creed (in preparation) proposes that there may exist an additional important predator transition between permanent habitats dominated by cold-water fish assemblages and those dominated by warm-water fish assemblages.

The data presented in this study support the importance of this second predator transition (the shift from cold-water to warm-water fish predators) in limiting the downstream dispersal of *C. chasmodactylus* YOY. The YOY of *C. chasmodactylus* appear to be prevented from inhabiting the mainstem of the New River by the predation pressure exerted by rock bass. The virtual absence of rock bass in the tributaries provides *C. chasmodactylus* YOY with a refuge from rock bass predation. Thus, the downstream distribution of *C. chasmodactylus* YOY is determined by the shift in predators from taxa with which the YOY can coexist (cold-water fish) to taxa with which the YOY cannot coexist (warm-water fish). It is possible that this predator transition may be important in limiting the distribution of other prey taxa as well. Additional research is needed to

determine if the transition from cold-water to warm-water fish is important in

determining the distribution of other lotic taxa.

LITERATURE CITED

Allan J. D. 1995. Stream Ecology. Structure and Function of Running Water. Chapman and Hall, London, UK.

Angermeier, P. L. 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. Environmental Biology of Fishes 34: 171 – 180.

Blank G. S., and M. H. Figler. 1996. Interspecific shelter competition between the sympatric crayfish *Procambarus clarkii* (Girard) and *Procambarus zonangulus* (Hobbes and Hobbs). Journal of Crustacean Biology 16: 300 – 309.

Bovbjerg, R. V. 1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). Ecology 51: 225 – 236.

Brown, B. L. 1999. Ecological Interactions of the Branchiobdellid *Cambarincola* with the Host Crayfish *Cambarus chasmodactylus* and *Orconectes cristavarius*. Masters Thesis. Appalachian State University, Boone North Carolina.

Chesson, J. 1983. The estimation and analysis of preference and its relation to foraging models. Ecology 64: 1297 – 1304.

Cooper, J. E., and A. L. Braswell. 1995. Observations on North Carolina crayfishes (Decopoda: Cambaridae). Brimleyana 22: 87 – 132.

Creed, R. P., Jr. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75: 2091 – 2103.

Creed, R. P., Jr. Predator transitions in lotic communities: a simple model. (in preparation for JNABS).

Crocker, D. W., and D. W. Barr. 1968. Handbook of the Crayfishes of Ontario. University of Toronto Press. Toronto, Ontario.

Englund, G. 1999. Effects of fish on the local abundance of crayfish in stream pools. Oikos 87: 48 – 56.

Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75: 532 – 547.

Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities. A null hypothesis and field experimental approach. American Journal of Botany. 70: 1098 – 1104.

Hamr, P., and M. Berrill. 1985. The life histories of north-temperate populations of the crayfish *Cambarus robustus* and *Cambarus bartoni*. Canadian Journal of Zoology 63: 2313 – 2322.

Helms, B. S. 2000. The Effects if Two Coexisting Crayfish (*Orconectes cristavarius* and *Cambarus chasmodactylus*) on Sediment Accumulation and Macroinvertebrates in the South Fork of the New River. Masters Thesis. Appalachian State University, Boone North Carolina.

Hobbs H. H. III. 1991. Decopoda. *in* Thorp J. H., and A. P. Covich (editors). Ecology and Classification of North American Freshwater Invertebrates. Academic Press. San Diego, CA.

Jeffries, M. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology 32: 603 – 612.

Manly, B. F. J. 1974. A model for certain types of selection experiments. Biometrics 30: 281 – 294.

McPeek, M. A. 1990a. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71: 83 – 98.

McPeek, M. A. 1990b. Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. Ecology 71: 1714 – 1726.

Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69: 614 – 623.

Moyle, P. B., and J. J. Cech. 1996. Fishes. An Introduction to Ichthyology. Prentice – Hall, NJ, USA.

Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure . Pages 303 – 323 *in* Fontaine T. D. III and S. M. Bartell, (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers , Ann Arbor, Michigan, USA.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Science. 46: 1805 – 1817.

Probst, W. E., C. F. Rabeni, W. G. Covington, and R. E. Marteney. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. Transactions of the American Fisheries Society 113: 283 – 294.

Rabeni, C. F. 1985. Resource partitioning by stream-dwelling crayfish: the influence of body size. American Midland Naturalist 113: 20 – 29.

Reice, S. R., and R. L. Edwards. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Quebec, Canada. Canadian Journal of Zoology 64: 1930 – 1936.

Roel and Orth 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Transactions of the American Fisheries Society. 122: 46 – 62.

Skelly, D. K. 1995. A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. Ecology 76: 150 – 164.

Skelly, D. K. 1996. Pond drying, predators, and the distribution of *Psuadacris* tadpoles. Copeia: 599 – 605.

Sih, A., L. B. Kats, and R. D. Moore. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. Ecology 73: 1418 – 1430.

Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of a crayfish to a fish predator. Ecology 57: 751 – 761.

Storfer, A., and A. Sih. 1998. Gene flow and ineffective antipredator behavior in a stream-breeding salamander. Evolution 52: 558 – 565.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics. 27: 337 – 63.

Woodward, B. D. 1983. Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. Ecology 64: 1549 – 1555.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science. 37:

APPENDIX A

Carapace Length by Mass Regression

Carapace Length – Mass Regressions for Young-of-the-Year Crayfish

Introduction. Measurement of the carapace length of crayfish in the field is practical and easy, whereas, measurement of crayfish mass is not. This study was undertaken to generate a mass by carapace length regression that would permit the estimation of the mass of young-of-the-year crayfish collected in the field.

Methods. A total of 91 crayfish YOY (*C. chasmodactylus* n = 45, *O. cristavarius* n = 46) were collected from Winkler's Creek and the New River. The carapace length (mm) and blotted wet mass (g) of each crayfish was measured. The mass of each species was then regressed against the CL of that species using a best fit quadratic linear model.

Results. *C. chasmodactylus* ranged in CL from 13mm to 18mm and in mass from 0.7g to 1.4g. *O. cristavarius* ranged in CL from 13mm to 20mm and in mass from 0.6g to 1.5g. The r^2 for *C. chasmodactylus* was 0.636 and the r^2 for *O. cristavarius* was 0.873 (fig 1). The regression equations are included in Figure 1. This analysis indicates that *C. chasmodactylus* YOY have more mass than *O. cristavarius* YOY at equivalent carapace length.

Figure 1.   Mass by carapace length regression of 45 *C. chasmodactylus* YOY (diamonds) and 46 *O. cristavarius* YOY (circles). The dashed line represents the best fit quadratic equation for *C. chasmodactylus* and the solid line the best fit quadratic equation for *O. cristavarius*.
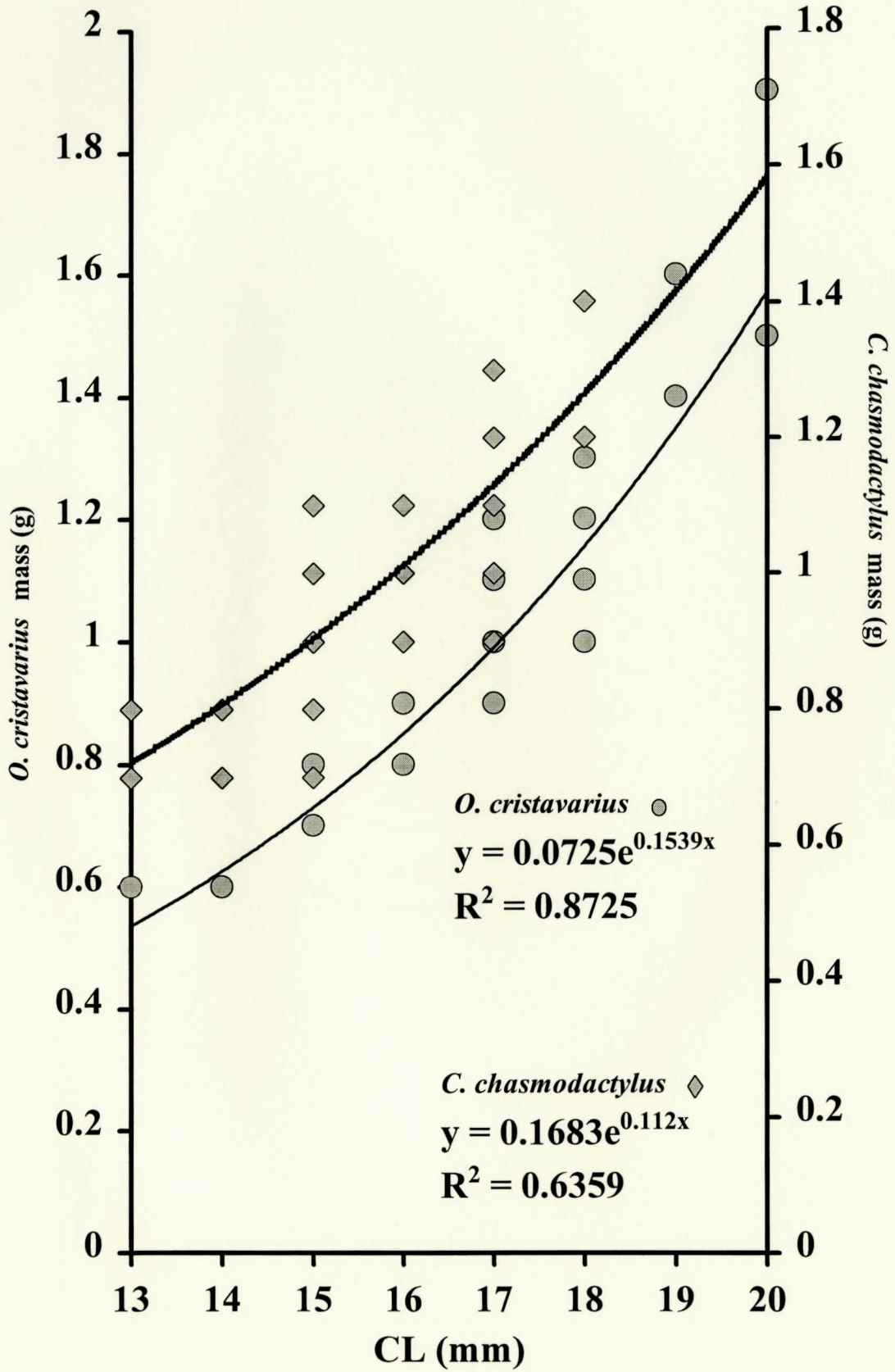
VITA

Kenneth Fortino was born in Paterson, New Jersey, on November 17, 1972. He lived and attended school in Hawthorne, New Jersey until he was 13 years old, at which time he moved to Midlothian, Virginia where he completed his pre-baccalaureate education. He graduated from Midlothian High School in June 1990 and entered Greensboro College in Greensboro, North Carolina the following August. In May 1994, he received a Bachelors of Science degree in Biology from Greensboro College. After working in the toxicology department of Laboratory Corporation of America from 1995 to 1997, he entered Appalachian State University in the fall of 1997 and began study toward a Master's degree in biology. He received this degree in May of 2000.

Kenneth Fortino is a member of the Ecological Society of America, the North American Benthological Society, the Association of Southeastern Biologists, and Tri Beta. His parents are Mr. Roger and Mrs. Beverly Fortino of Jamison, Pennsylvania.