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THE EFFECTS OF TWO COEXISTING CRAYFISH (*ORCONECTES CRISTAVARIUS* AND *CAMBARUS CHASMODACTYLUS*) ON SEDIMENT ACCUMULATION AND MACROINVERTEBRATES IN THE SOUTH FORK OF THE NEW RIVER.

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A Thesis

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Brian Scott Helms

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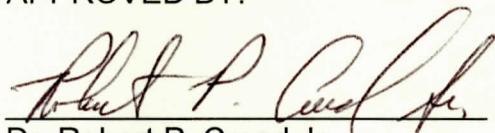
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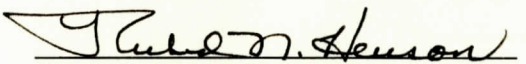
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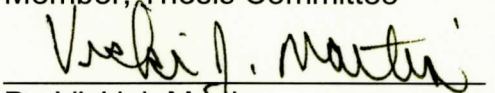
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ABSTRACT

THE EFFECTS OF TWO COEXISTING CRAYFISH (*ORCONECTES CRISTAVARIUS* AND *CAMBARUS CHASMODACTYLUS*) ON SEDIMENT ACCUMULATION AND MACROINVERTEBRATES IN THE SOUTH FORK OF THE NEW RIVER. (May 2000)

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Crayfish are considered to be strong interactors in some freshwater systems. They can have direct effects on animals, plants, and sediment accumulation. They can also have a variety of indirect effects on coexisting taxa. Two species of crayfish, *Orconectes cristavarius* and *Cambarus chasmodactylus*, coexist in the South Fork of the New River in western North Carolina. The influence of these crayfish on sediment accumulation and benthic macroinvertebrates was investigated using gut-content analyses and an enclosure-exclosure experiment. Crayfish guts contained mostly sediment, vegetative detritus, and a small fraction of animal material. Overall, there were differences in the gut contents of the two species, with *C. chasmodactylus* containing more detritus and *O. cristavarius* containing more sediment. Both species, especially *O. cristavarius*, contained surprisingly high amounts of sediment in their guts. For the cage experiment, five rows of cages (0.25 m²)

were placed in the river with each row consisting of five treatments (*O. cristavarius* enclosure, *C. chasmodactylus* enclosure, crayfish enclosure, cage control, open treatment). Both the cage control and the open treatment were exposed to all stream organisms, including benthic-feeding fish. There was significantly more sediment in the exclosures, an intermediate amount in the crayfish enclosures, and very little in the open treatments and cage controls. Chironomid abundance was positively associated with sediment volume. There were significantly more *Calopteryx* [Zygoptera] in both crayfish enclosures than the open treatments and cage controls, and more cyclopoid copepods with *O. cristavarius* than *C. chasmodactylus*. Hydropsychid caddisflies and hydracarina water mites exhibited significant cage effects. Although there were significant differences in crayfish diet, this did not result in significant differences in community-level impacts. These results suggest that there is a high degree of functional redundancy in the New River and that these crayfish along with the benthic-feeding fish, are a suite of taxa that influence sediment abundance and community structure in the South Fork of the New River.

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Introduction

A major theme in community ecology is the examination of feeding relationships with an attempt to determine their impact on community structure. However, the strength of trophic interactions cannot be assumed equivalent for all members of a food web (Paine 1980, Laska and Wootton 1998). Interaction strength is considered to be the magnitude of the effect of a consumer on a prey species' population growth or density (Navarette and Menge 1996, Laska and Wootton 1998) and may be a function of the consumer's density, size, or food preference (Paine 1966, 1969, 1976). Assessments of interaction strength are useful in determining functional redundancy, community stability, indirect effects, and food web arrangement (Ruesink 1998).

Organisms considered to be strong interactors (*sensu* Paine 1980) play a disproportionately important role in determining community structure (Paine 1980). Strong interactors affect resource availability to other organisms (Jones et al. 1994), either directly or indirectly, and pronounced community changes often result upon their removal (Paine 1980). This idea is exemplified by the seastar *Pisaster ochraceus* and its influence on rocky intertidal communities resulting from direct predation on mussels (*Mytilus californianus*). These mussels can outcompete other benthic organisms for space on exposed

coastlines. They are also the preferred prey of *P. ochraceus* (Paine 1976). By reducing *M. californianus* abundance, *P. ochraceus* promotes an increase in the diversity of seaweeds and invertebrates otherwise removed or outcompeted by *M. californianus* (Paine 1966, 1976). This type of strong interactor is referred to as a 'keystone predator', as its predatory actions are the "keystone of the community's structure" (Paine 1969).

The effects of a strong interactor do not always have to be the result of trophic interactions. An organism can also affect the availability of resources to other organisms by physically changing certain biotic or abiotic aspects of the environment. For example, the beaver (*Castor canadensis*) has substantial impacts on its community through the physical alteration of its environment (Naiman et al. 1988). Beavers change stream morphology and hydrology through the construction of dams. This not only changes sediment and organic matter retention in the stream channel, but also changes the surrounding area into a wetland (Naiman et al. 1988). This alters decomposition dynamics and nutrient cycling which ultimately modifies plant and animal community structure (Naiman et al. 1988). Strong interactors of this sort are considered to be 'ecosystem engineers' in that they influence resource availability and/or modify, maintain, or create habitats (Jones et al. 1994). The effects of a strong interactor may be a result of that organisms' functional uniqueness in a particular setting. For example, there are no other organisms functionally

similar to beavers in their habitats. However, there are many functionally similar species of insectivorous warblers in a wooded community that differ on a much finer scale (MacArthur 1958). These types of similar organisms are much more common and have weaker, but not necessarily less important, interactions (McCann et al. 1998, Polis 1998). Organisms that are not functionally unique may have only minor community effects and might be considered 'redundant species' (Navarrete and Menge 1996, Ehrlich and Walker 1998, Covich et al. 1999).

Recent research has demonstrated that fish and large crustaceans are keystone species and ecosystem engineers in some lotic communities (Power et al. 1985, Gilliam et al. 1989, Creed 1994, Lodge et al. 1994, Flecker 1996,1997). Strong effects of fish have been demonstrated in some systems (Power et al. 1985, Power 1992, Flecker 1997). Power et al. (1985) demonstrated that the distributions of the grazing fish *Campostoma anomalum* and attached algae within pools were influenced by the presence of predatory bass (*Micropterus salmoides* and *M. punctulatus*). *C. anomalum* significantly reduce algal abundance by grazing. However, the presence of bass reduces *Campostoma* grazing (through predator avoidance and predation) which causes an increase in algae (Power et al. 1985). Both bass and *Campostoma* are strong interactors in this community. Roach (*Hesperoleucas symmetricus*) and steelhead (*Oncorhynchus mykiss*) are also strong interactors in a northern

California river, but their effects are habitat specific. By suppressing invertebrate predator densities in cobble habitats, algivorous chironomids are released from predation, which in turn leads to an increase in algal standing crops (Power 1992). This cascading effect however is not seen on gravel substrates (Power 1992). Flecker (1996,1997) demonstrated that fish can also function as ecosystem engineers in lotic communities. Flannel-mouthed characin (*Prochilodus mariae*) affected strongly sedimentation in pools of tropical Andean streams (Flecker 1996,1997). The removal of these fish resulted in increased sedimentation and changes in algal and invertebrate assemblages. *Prochilodus* is a detritivorous fish that generates and maintains habitat heterogeneity for sediment dwelling organisms through its processing and bioturbation of sediment (Flecker 1996,1997).

Although the roles of vertebrates, especially fish, have been extensively studied in stream communities, the impacts of invertebrate consumers have received less attention until recently. Recent studies have demonstrated that invertebrates, primarily large crustaceans, may function as keystone species (Hart 1992, Creed 1994) and ecosystem engineers (Pringle et al. 1993, Creed 1994, Zantell and Peckarsky 1996, Reed 1997). Most of the studies have focused on the impact of crayfish and freshwater shrimp.

Crayfish, which are relatively large omnivorous invertebrates, can dominate the benthic biomass of lakes and streams and are often important

trophic components in these communities (Momot et al. 1978, Momot 1995, Huryn and Wallace 1987, Feminella and Resh 1989, Lodge et al. 1994, Creed 1994, Charlebois and Lamberti 1996, Nystrom et al. 1999). Crayfish are strong interactors in many freshwater systems and have a major influence on the distribution and abundance of macroinvertebrates (e.g. Creed 1994, Lodge et al. 1994, Charlebois and Lamberti 1996, Nystrom et al. 1999). Crayfish also influence the distribution and abundance of algae (Hart 1992, Creed 1994) and can affect detrital processing rates (Huryn and Wallace 1987, Parkyn et al. 1997, Reed 1997). Certain crayfish have been classified as keystone consumers (Creed 1994). Direct grazing by the crayfish *Orconectes propinquus* reduced the abundance of the filamentous alga *Cladophora glomerata* in deep-water habitats in a Michigan stream. Diatom abundance on substrates was higher in the absence of *C. glomerata* and this increase in microalgal resources indirectly facilitated grazing macroinvertebrates (Creed 1994).

Crayfish have also been recognized as ecosystem engineers (Creed 1994, Momot 1995, Parkyn et al. 1997, Reed 1997). An ecosystem engineer “directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials” (Lawton, 1999). For example, Creed (1994) postulated that the *Cladophora* mats could deter epilithic diatom accrual by acting as sediment traps. Significantly more

microalgae were present on experimental substrata that did not have a *Cladophora* mat (Creed 1994). By indirectly influencing sediment accumulation, these crayfish were acting as ecosystem engineers. In an Appalachian headwater stream, Reed (1997) found that fine particulate matter (FPM) decreased with the presence of *Cambarus bartonii*. In addition, numbers of chironomids and harpacticoid copepods were positively correlated with FPM abundance. Crayfish can be considered to be allogenic ecosystem engineers in these cases in that they transform living or non-living materials from one physical state to another (Jones et al. 1994, Lawton 1999).

We have learned much about the interactions of keystone consumers and ecosystem engineers in lotic communities in the last decade. In particular, researchers have demonstrated important roles for large crustaceans in these systems. Interestingly, we know more about the impacts of large crustaceans on tropical communities than on temperate ones. In a tropical headwater stream in Puerto Rico, pool food webs are dominated by several shrimp species, including two detritivorous species, *Atya lanipes* and *Xiphocaris elongata* (Covich et al. 1999). These atyid shrimp strongly influence the physical character of stream habitats through the processing of sediment and detritus (Pringle et al. 1993). The physical removal of sediment by these shrimp can enhance indirectly certain algae, which may facilitate algal exploitation by the Ephemeropteran grazer *Cloedes maculipes* (Pringle et al.

1993). Also, chironomids were negatively affected by the physical removal of these resources, which were needed to construct retreats (Pringle et al. 1993). Further, *X. elongata* shreds leaf litter and ingests larger leaf fragments than *A. lanipes*. As a result of these differences, the relative spatial location of these two species can affect the overall efficacy of detrital processing (Covich et al. 1999).

In temperate systems, most work has focused on impacts of crayfish in small streams (e.g. Hart 1992, Creed 1994, Charlebois and Lamberti 1996, Reed 1997). Little research has been conducted in larger rivers. In addition, all of these studies have focused on the effects of single species. In this study, I evaluated the impact of crayfish on community structure in a larger river, the South Fork of the New River in western North Carolina. In addition, I compared the impact of two coexisting species of crayfish on this community. The two species are *Orconectes cristavarius* and *Cambarus chasmodactylus*, both of which are endemic to the New River (Cooper and Braswell 1995, C. Taylor, pers. comm.)

Objectives and Hypotheses

The objectives of this study were two-fold. The first objective was to determine the effect crayfish might have on the community structure of the South Fork of the New River through sediment processing and predation. The second objective was to compare the impact of *O. cristavarius* and *C.*

chasmodactylus on this community. A field experiment was used to quantify the effects of the crayfish on the river community and to compare the effects of the two crayfish species. The specific questions addressed in the field experiment were:

Question #1: Do crayfish have an effect on macroinvertebrate abundance and sediment accumulation in the New River?

Question #2: Do the two crayfish species differ in their effects?

Question #3: Are the combined crayfish effects different than the effects of all of the large benthic-feeding organisms in the community?

Gut content analyses were used to determine if there were differences in the diet of the two species. Specific hypotheses were:

Question #4: Is there a difference between the gut contents of the two crayfish species?

Question #5: Is there a difference in gut contents between the two crayfish at different times of day?

Question #6: Is there a difference in gut fullness between the two crayfish at different times of day?

This experiment and gut-content analysis allowed me to 1) assess the effect of crayfish in general on the river community, 2) compare the diet and community-level effects of the two species of crayfish, 3) compare the crayfish effects to the effects of those of other taxa, primarily benthic-feeding fish.

Study Animals

The crayfishes *Orconectes cristavarius* and *Cambarus chasmodactylus* are endemic to the New-Kanawha river system and are found in close association with one another in the South Fork of the New River (Cooper and Braswell 1995). In the main stem of the South Fork, *O. cristavarius* is more abundant (see results). However, in some habitats (e.g., pools), *C. chasmodactylus* densities can equal those of *O. cristavarius* and both can often be found under the same cobble (B. Helms, *personal observation*). In both species, larger individuals are generally found in deeper water and smaller individuals in shallow water, a pattern similar to that documented by Creed (1994) for *O. propinquus* in a Michigan stream.

No extensive study on the natural history of these crayfish has been performed, so most information is observational and/or based on studies of similar crayfish. Like other members of the genus *Orconectes*, *O. cristavarius* seems to be a synchronous breeder. Mating occurs in late summer through the fall with females in berry typically occurring in early spring and the release of young-of-the-year (YOY) in late spring (Brown 1999, B. Helms, *personal observation*). *C. chasmodactylus*, like other members of the genus *Cambarus*, appears to be an asynchronous breeder, with no well-defined mating season (Hamr and Berrill 1985). Female *C. chasmodactylus* have been found with attached eggs or young in the South Fork in every season (Brown 1999).

However, YOY *C. chasmodactylus* tend to be more common during the summer, which suggests that most young are released during the summer.

Both species can reach carapace lengths (CL) of 40 mm or more. However, *C. chasmodactylus* tends to be very robust with a broad cephalothorax and fairly large chelae while *O. cristavarius* tends to be more slender with smaller chelae. Although *C. chasmodactylus* generally reach a larger adult mass (Brown 1999), *O. cristavarius* has a faster growth rate as juveniles (Fortino, 2000). The behavior of the two crayfishes is also different. *C. chasmodactylus* appears much less active than *O. cristavarius* (B. Helms *personal observation*). When disturbed, *C. chasmodactylus* tend to swim very short distances, if at all, whereas *O. cristavarius* tend to swim longer distances to escape (Fortino, 2000).

Study Site

The study was conducted in the South Fork of the New River in Watauga County, North Carolina (4,007,200 m N, 441,600 m E). The South Fork is a meandering fourth-order stream and the study section is in the Boone Greenway. This portion of the river is ~10 m wide and comprised of riffles (depth 0-10 cm, current velocities ~30-50 cm/s) and pools (depth 40+ cm, current velocities 0-10 cm/s), often with expanses of medium flow between the riffles and pools (depth ~30 cm, current velocities 15-25 cm/s). The substrate in the South Fork ranges from expanses of sand and gravel to cobbles (often covered with riverweed *Podostemum ceratophyllum*) to bedrock comprised of biotite granitic gneiss. The field experiment was conducted in a pool that was ~20 m long. The substrate was cobble/gravel with fairly uniform depth and current throughout (~30 cm and ~16 cm/s, respectively).

Methods

Crayfish surveys

In order to determine the density and distribution of the two crayfish species in the Greenway portion of the South Fork, surveys were conducted in the summer of 1998. A stratified sampling design was used to estimate crayfish densities in different habitats. Habitats were classified on the basis of depth (>25 cm, <25 cm), substrate (simple, complex), and current (>20 cm/s, <20 cm/s). For every sample, crayfish species, size (carapace length) and sex were determined along with current velocity, depth, and substrate type.

Qualitative surveys were also conducted day and night by flipping rocks and capturing crayfish with aquarium nets. Crayfish species, size, and sex, as well as depth and substrate, were recorded with each capture.

Gut Content Analysis

Adult crayfish were collected from the South Fork of the New River where the two crayfish species co-occur. A total of sixty-seven *O. cristavarius* and fifty-four *C. chasmodactylus* were collected from June 1, 1999 to August 30, 1999. Collections were made at dawn (6:00-7:00 AM), in the afternoon (3:00-5:00 PM), and at dusk (7:00-9:00 PM). Once a crayfish was captured, it

was immediately put on ice to slow digestion. The animals were then transported to the lab, placed in freezer bags, and immediately frozen.

Crayfish guts were removed by cutting along the sides of the carapace and then making one incision at the base of the rostrum. The carapace was then gently lifted as underlying mesentery was disconnected with a blunt probe. Once the carapace was removed, the foregut (or cardiac stomach) was removed. Only items from the foregut were examined. Percent fullness of the foregut was estimated as empty (0%), 25%, 50%, or full (100%). Contents of the foregut were then flushed into a Petri dish, distributed as evenly as possible, and viewed under a dissecting scope. Percent composition of the flushed gut material was then estimated with the aid of a grid that was on the underside of the Petri dish. Food items were assigned to one of the following categories: sediment, detritus, green vegetation, and animals.

Gut content data were analyzed with one-way analysis of variance (ANOVA) for each category. Using the categorical data, Schoener's index of diet overlap (Schoener 1970) was determined for both crayfish at each of the three times of day. Schoener's index (α) is determined using the following formula:

$$\alpha = 1 - 0.5 (\sum |p_{xi} - p_{yi}|)$$

where p_{xi} represents the proportion of food category i in the diet of species x , p_{yi} represents the proportion of food category i in the diet of species

y, summed across all food categories. If $\alpha = 0$, there is no overlap in the diets of the two species. If $\alpha = 1$ there is complete overlap. Further, if $\alpha > 0.6$, interspecific competition may be occurring assuming resources are limiting and, if $\alpha < 0.4$, the two species are using significantly different resources and should not be competing (Scott and Angermeier 1998). This index is preferable when resource-availability data are absent (Wallace 1981).

Field Experiment

To assess the impacts of the two crayfish species on sediment accumulation and benthic macroinvertebrates, an enclosure-exclosure experiment was conducted. The experiment ran for 6 weeks in the late summer of 1998.

Cages were constructed of 12 mm mesh hardware cloth and were 0.5 m X 0.5 m X 15 cm. Baskets, which served as the experimental unit, were constructed with 6 mm mesh hardware cloth and were 30 cm X 30 cm X 5 cm. Each basket was lined with 1 mm mesh fiberglass window screen and contained 5-7 scrubbed, fist-sized cobbles. An unglazed ceramic tile was placed in the center of each basket to serve as a standard substrate for sediment accumulation. Cobbles were also placed in the spaces between the edges of the baskets and cage walls to minimize edge effects.

Five replicates of five treatments were placed in the river in a randomized block design. Treatments consisted of two crayfish enclosures

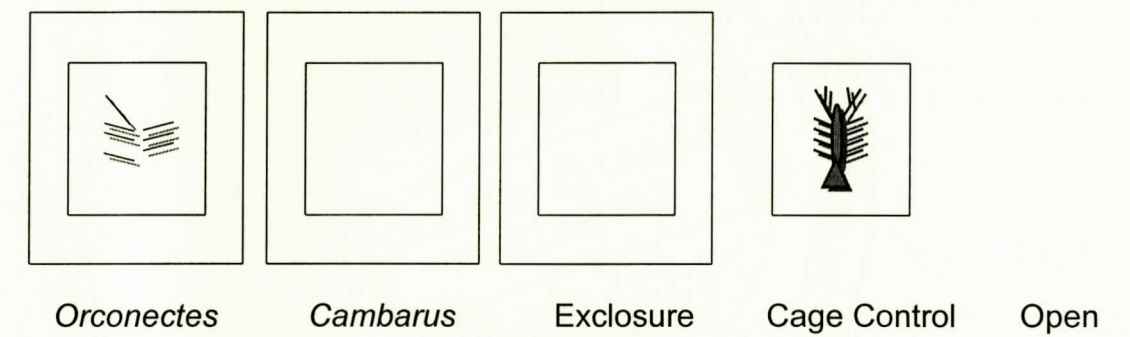
(one for each species), crayfish enclosure, cage control and an open basket (Figure 1). The cage control was open on the downstream end to allow access by all stream inhabitants. Each crayfish enclosure contained one adult crayfish, which created a crayfish density of 4/m² inside the cages, which is slightly higher than the observed mean densities of adults of both species (see Results). Each block was placed in the river at approximately equal depths (~32 cm) and current velocities (~16 cm/s), creating 5 rows (blocks) spaced two to three meters apart.

Crayfish used in the field experiment were all caught in the pool where the experiment was conducted. Crayfish were sexed and measured (carapace length). To minimize variation between crayfish, all crayfish used were female with ~30 mm carapace length. One *C. chasmodactylus* and one *O. cristavarius* were randomly assigned to appropriate cages in each row.

Cages were cleaned of debris twice daily. Water temperature was recorded daily. Current velocity and depth were recorded weekly at each cage and basket using a hand-held Scientific Instruments® Model 1205 Price Type "Mini" current meter.

After six weeks, the baskets and tiles were retrieved from the river. For basket retrieval, a retrieval apparatus lined with a 250 µm Nitex® catch-net was employed. The retrieval apparatus was placed behind a cage or open basket and the basket was carefully lifted into the apparatus and carried to shore. Any

Figure 1. Diagram of one block from the field experiment. Treatments (from left to right) are *Orconectes cristavarius* enclosure, *Cambarus chasmodactylus* enclosure, crayfish exclosure, cage control, and open basket. Schematics represent accessibility of each treatment to large crayfish and fish. The experimental unit for each treatment was the sampling basket (shaded).



organisms that might have been dislodged during this procedure were caught in the Nitex® mesh. Each tile was carefully removed from each basket (without disturbing material on the tile) and placed in its own plastic container filled with water filtered through a 250 µm sieve. Cobbles in each basket were scrubbed in filtered stream water and this water, as well as the contents of the basket and retriever catch net, was poured through a 250 µm sieve. The filtered material was then preserved in 70% ethanol. The crayfish in the enclosures were removed and put on ice in the field and later frozen for gut content analysis.

In the laboratory, the material on each tile was removed with a toothbrush and preserved in 70% ethanol. Volume of fine particulate matter (FPM— a mix of organic and inorganic sediment) for each tile and basket was then estimated volumetrically to the nearest 20 ml. Rose Bengal dye was then added to the contents and to the material removed from the remaining cobbles in order to stain macroinvertebrates. The contents of each tile and each basket were poured through a sieve stack (top sieve -1 mm mesh, bottom sieve - 250 µm mesh). This resulted in a coarse and fine fraction for each tile and for the material from the corresponding basket. All macroinvertebrates in the coarse fractions (1mm mesh sieve) were sorted from the coarse particulate matter (CPM) under a dissecting scope and identified to the lowest taxonomic level possible (generally genus or species). Since fine particulate matter (FPM)

associated organisms are often dependent on the amount of FPM, and the tiles were a consistent surface area for FPM accrual across treatments, only the macroinvertebrates associated with FPM on the tiles were enumerated and identified. Tile FPM was subsampled and the number of invertebrates per ml FPM was determined and multiplied by the total FPM volume on the tile to estimate the total number of invertebrates on the tile when the entire sample could not be sorted.

All data for the field experiment were log transformed because of obvious correlations between means and variances (Sokal and Rohlf 1981). Multivariate analysis of variance (MANOVA) was used to test for a general treatment effect in the field experiment at three levels, 1) total basket, 2) coarse fraction of the basket and 3) total tile. Differences among treatments were determined using orthogonal contrasts. There were four *a priori* contrasts: 1) the exclosure was compared to all other treatments, 2) the two crayfish enclosures were compared with the cage control and the open basket, 3) the two crayfish enclosures were compared, 4) the cage control was compared to the open basket. The first comparison (exclosure vs. all others) tested for a general large consumer effect (e.g., crayfish and benthic-feeding fish). No large consumers had access to the exclosures. The second comparison (both crayfish enclosures vs. cage control and open) compared the effects of crayfish to those of crayfish *and* fish since fish also had access to substrates in the cage

control and open baskets. The third comparison (comparison of the two crayfish enclosures) compared the effects of the two crayfish species. The comparison of the cage control and the open basket determined if there was a cage effect on sediment accumulation or macroinvertebrate abundance.

In a previous study, Reed (1997) had determined that there was a significant relationship between the abundance of small taxa (small chironomids and Harpacticoid copepods) and FPM volume on substrates. Therefore, regression analyses were used to determine any relationships between chironomid and harpacticoid copepod abundance and FPM volume. All data were log transformed for these regression analyses.

When the experiment was terminated, all crayfish were alive and accounted for except the row 2 *Cambarus* treatment, where the crayfish was missing, and the row 3 *Cambarus* treatment, where the crayfish was dead. However, all crayfish were alive 5 days prior to the termination of the experiment.

Results

Crayfish surveys

O. cristavarius and *C. chasmodactylus* were the two numerically dominant adult crayfish encountered in the surveys. There were essentially no adults in simple substrates (sand and gravel). From the quadrat samples, *O. cristavarius* densities in deep complex habitats (>25 cm) averaged 2.1/m² with a range of 0 – 6/m². *C. chasmodactylus* densities in deep complex habitats were 0.5/m² with a range of 0 – 1/m². In shallow complex habitats (<25), *Orconectes* averaged 1.1/m² and ranged from 0 - 3/m². *C. chasmodactylus* densities in shallow complex habitats averaged 0.4/m² and ranged from 0 - 2/m².

Qualitative sample results were similar to the quantitative sample results in that 70-75% of the crayfish encountered were *O. cristavarius* and 25-30% were *C. chasmodactylus*. However, the qualitative samples revealed that crayfish distributions were patchy, with some sections of river with higher crayfish densities than in other seemingly similar stretches. This was especially true for *C. chasmodactylus*. Densities were ~3/m² for both species in the study site.

Gut Content Analysis

Total gut fullness did not differ between times of capture for *C. chasmodactylus* ($F_{2, 51} = 1.08$, $p = 0.346$) and only marginally so for *O.*

cristavarius ($F_{2,64} = 2.76$, $p = 0.071$). *C. chasmodactylus* had greater gut contents than *O. cristavarius* in the morning ($F_{2,64} = 2.76$, $p = 0.071$), and in the evening ($F_{1,27} = 17.5$, $p < 0.001$) but they were not different in the afternoon ($F_{1,31} = 1.43$, $p = 0.242$, Figure 2). *C. chasmodactylus* had overall greater gut fullness values than *O. cristavarius* ($F_{1,119} = 13.01$, $p < 0.001$, Figure 2). Crayfish guts contained mostly sediment and/or vegetative detritus plus a small fraction of animal material (Figure 3). In the morning surveys, *O. cristavarius* contained more sediment ($F_{1,53} = 11.12$, $p = 0.002$) and *C. chasmodactylus* contained more detritus ($F_{1,53} = 51.33$, $p < 0.001$, Figure 3). In the afternoon surveys, *O. cristavarius* again contained more sediment ($F_{1,31} = 19.90$, $p < 0.001$, Figure 4) and *C. chasmodactylus* contained more detritus ($F_{1,31} = 14.43$, $p = 0.001$, Figure 4). The same trend held for the evening samples, with a marginally significant effect on sediment ($F_{1,27} = 2.84$, $p = 0.103$) and a strongly significant effect on detritus ($F_{1,27} = 27.92$, $p < 0.001$, Figure 5). Overall, there were differences in the gut contents between the two species, with *C. chasmodactylus* guts containing significantly more detritus ($F_{1,119} = 39.89$, $p < 0.001$) and *O. cristavarius* guts containing significantly more sediment ($F_{1,119} = 65.87$, $p < 0.001$, Figure 6). Also, *C. chasmodactylus* contained more animal remains than *Orconectes* ($F_{1,119} = 3.40$, $p = 0.068$, Figure 6). *C. chasmodactylus* had a higher percentage of detritus in their guts at all times

(Figure 7) and *O. cristavarius* had a higher percentage of sediment in their gut at all times (Figure 8).

The Schoener index of diet overlap suggested that there was a partial overlap in the diet of adults (Table 1). There was a 61.4% overlap in the morning, 51.6% overlap in the afternoon, and a 50.2% overlap in the evening. For all samples combined, there was a 57.5% diet overlap between the two species.

Table 1: Mean gut contents and Schoener's index of diet overlap for *C. chasmodactylus* (CAM) and *O. cristavarius* (ORC). Gut content means are percentages. Overlap values (α) range from 0-1 where 0 = no overlap, 1 = total overlap, > 0.6 = resource partitioning (given limited resources), < 0.4 = different resource use. Gut content categories are sediment (SED), detritus (DET), green plant material (GRN), crayfish remains (CRAY), hydropsychid remains (HYD), unknown insect remains (INS), and unknown animal remains (ANI).

TIME	SPECIES	GUT CONTENT CATEGORIES							OVERLAP VALUE
		SED	DET	GRN	CRAY	HYD	INS	ANI	α
6AM	CAM	25.4	59	2.2	1.8	1.8	4.4	5.4	0.61
	ORC	63.1	30	0.5	2.1	0.5	1.3	2.6	
5PM	CAM	27.9	55	2.4	0	1.5	12.4	0.9	0.52
	ORC	75.6	15.6	2.3	0.3	0.6	5.9	0.6	
9PM	CAM	34.6	56.8	0	0.5	2.7	1.8	3.6	0.51
	ORC	68.9	15.8	7.3	7.3	0	0.4	0.4	
TOTAL	CAM	28.1	57.3	1.8	0.9	1.9	6.4	3.6	0.58
	ORC	67.7	23.1	2.2	2.8	0.4	2.3	1.6	

Figure 2. Mean gut fullness for *C. chasmodactylus* and *O. cristavarius*. Times of capture were dawn (6:00 – 7:00 am), afternoon (3:00 -5:00 pm), and dusk (7:00 – 8:00 pm). The last pair of bars labeled "Total" is the sum of all times of capture. Bars with different letters above them are significantly different from one another (within and across times).

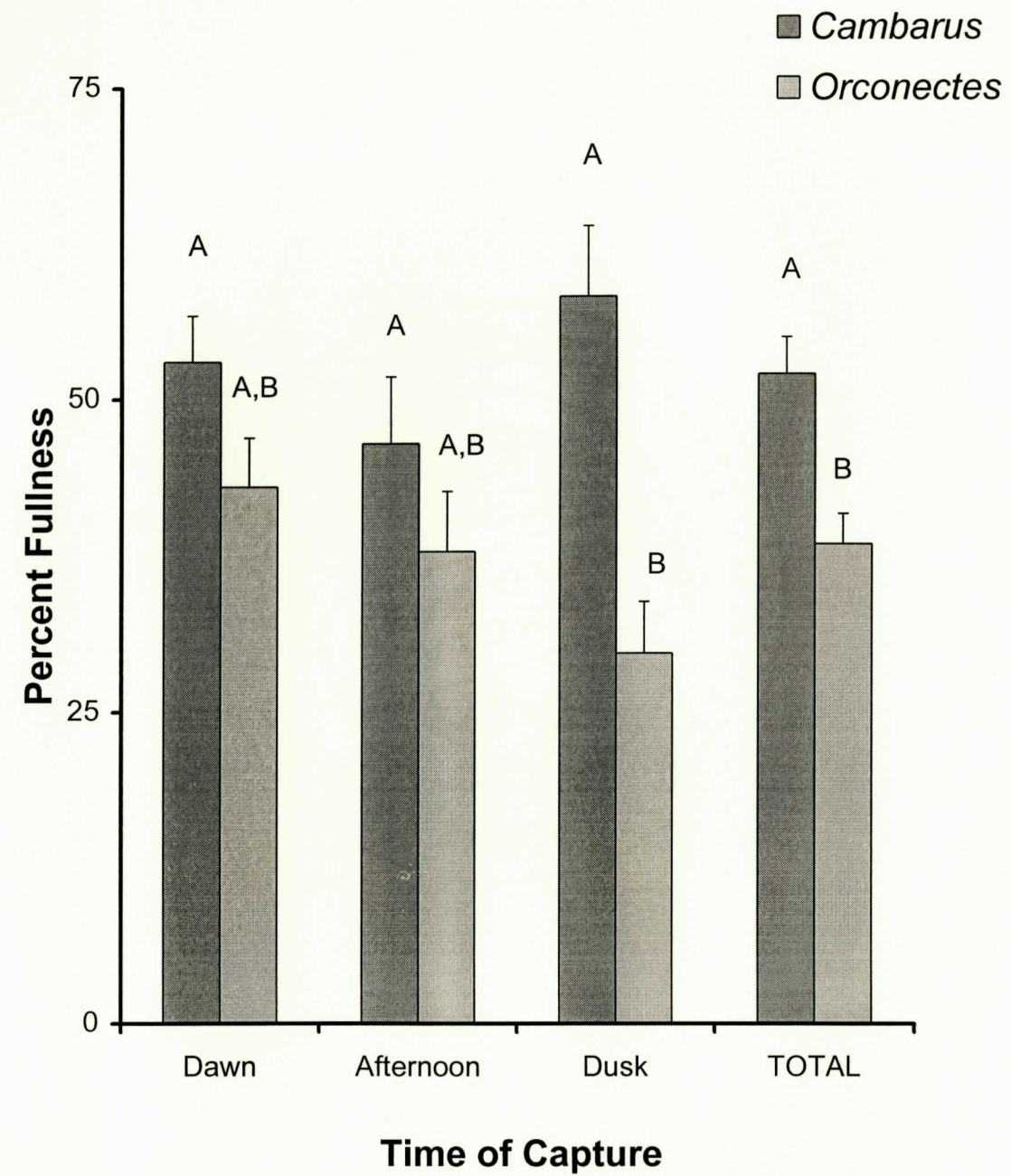


Figure 3. Mean morning (6:00 – 7:00 am) gut contents for *C. chasmodactylus* and *O. cristavarius*. Values are percentage of total gut contents. Asterisks represent significant differences within a particular category.

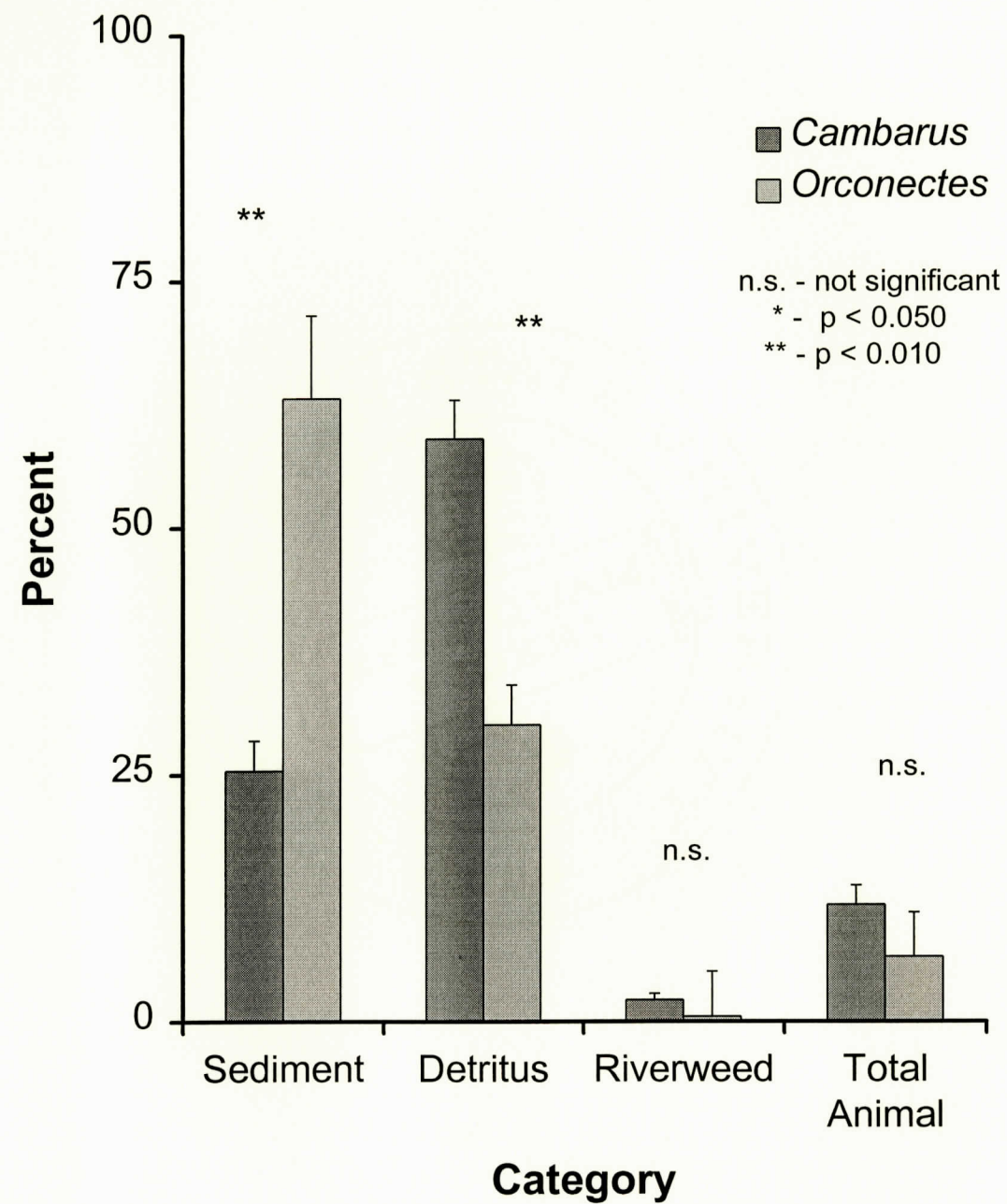


Figure 4. Mean afternoon (3:00 – 5:00 pm) gut contents for *C. chasmodactylus* and *O. cristavarius*. Values are percentage of total gut contents. Asterisks represent significant differences within a particular category.

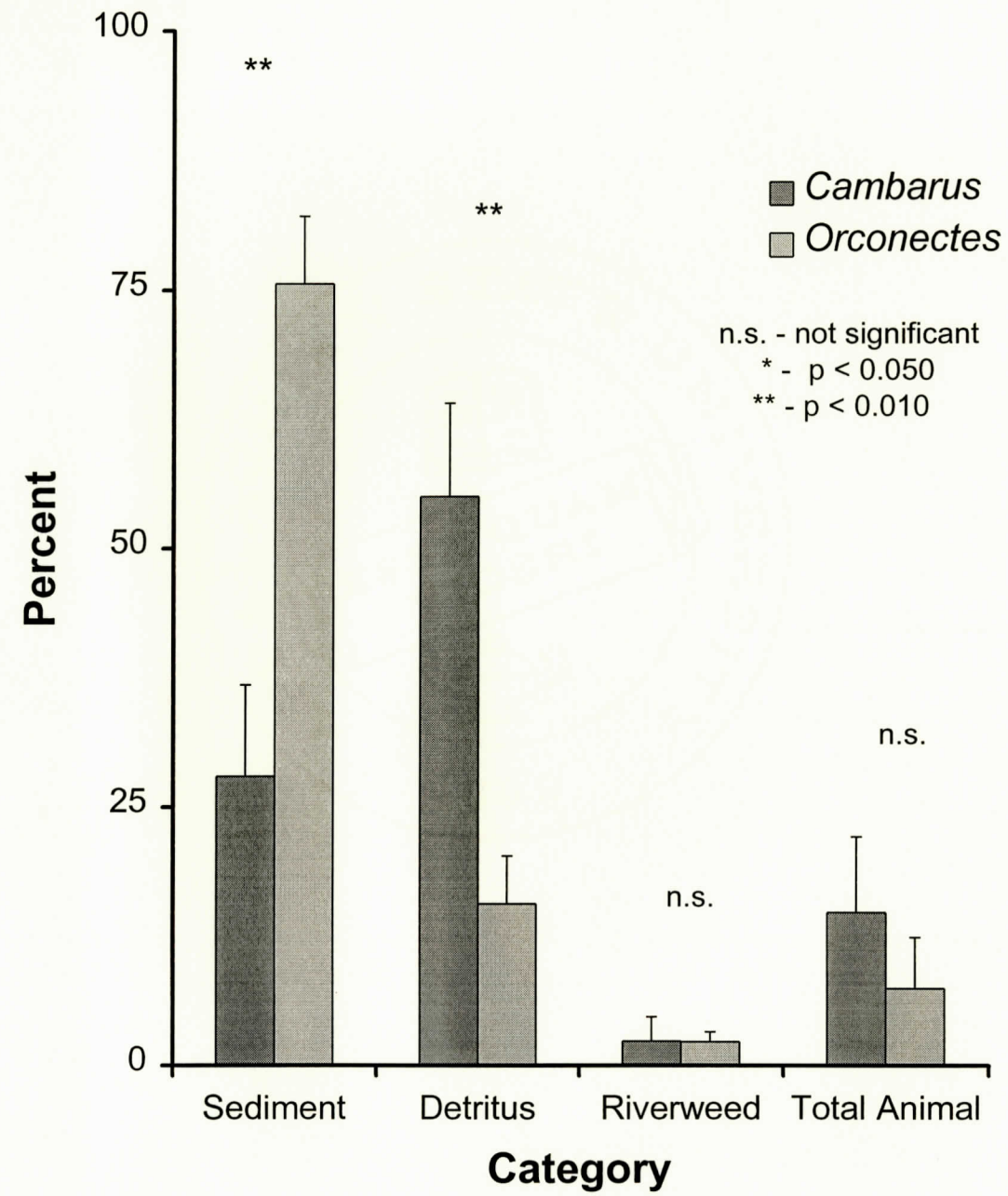


Figure 5. Mean evening (7:00 – 8:00 pm) gut contents for *C. chasmodactylus* and *O. cristavarius*. Values are percentage of total gut contents. Asterisks represent significant differences within a particular category.

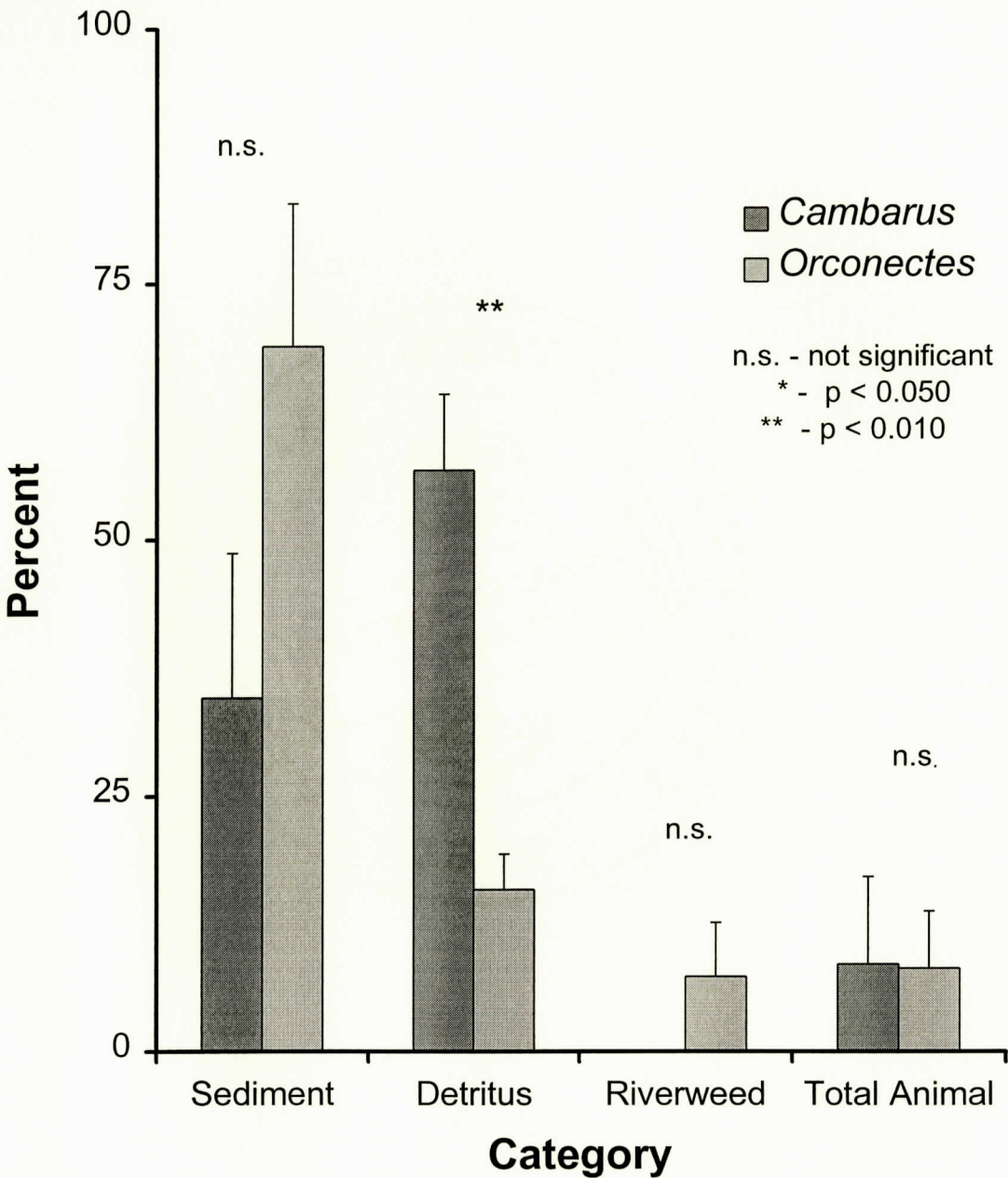


Figure 6. Mean total gut contents for *C. chasmodactylus* and *O. cristavarius*. Values are average percentage for all capture times. Asterisks represent significant differences within a particular category.

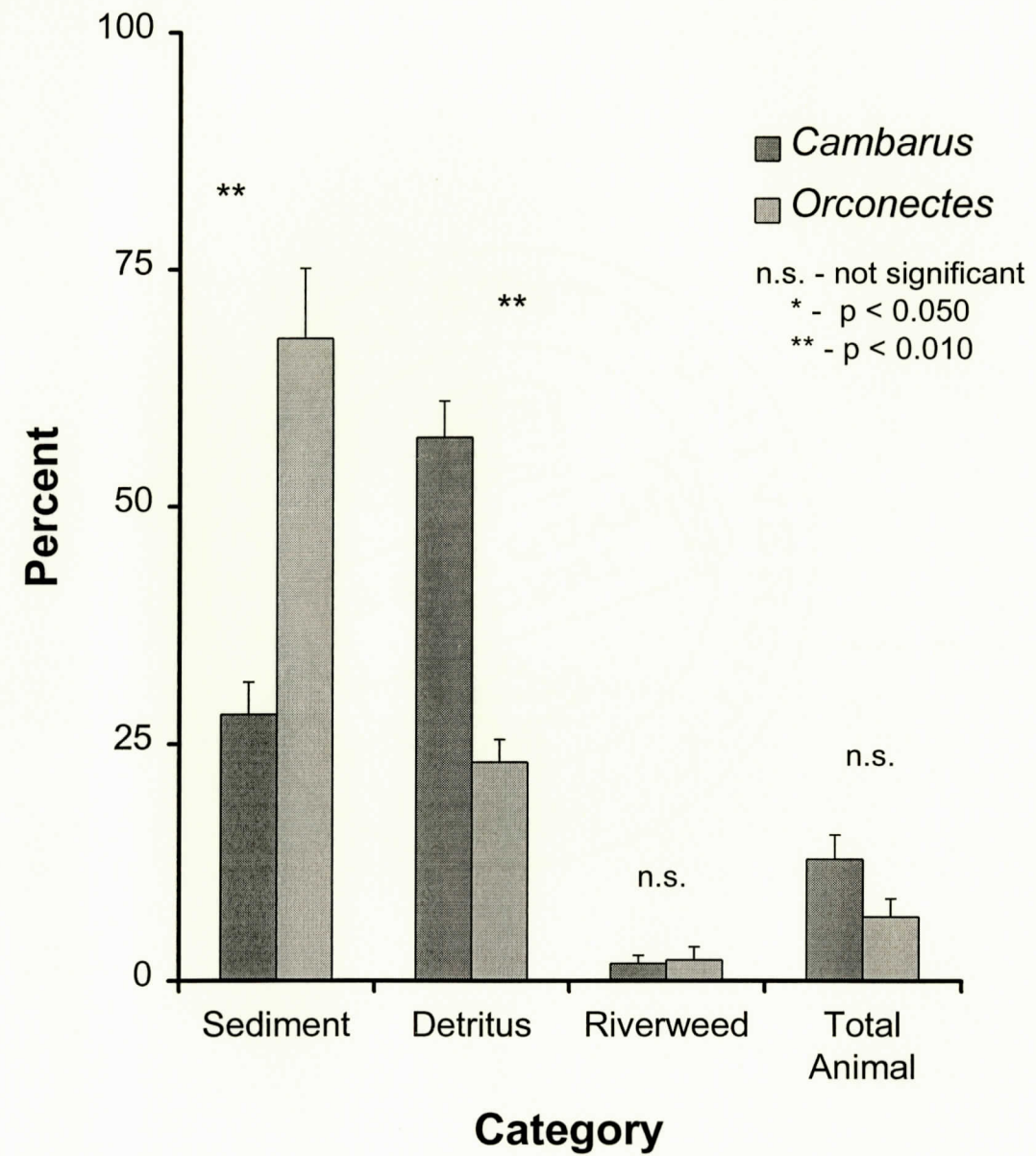


Figure 7. Mean percent detritus for *C. chasmodactylus* and *O. cristavarius* at different times of capture. Values are percentage of total gut contents. Asterisks represent significant differences within a particular time.

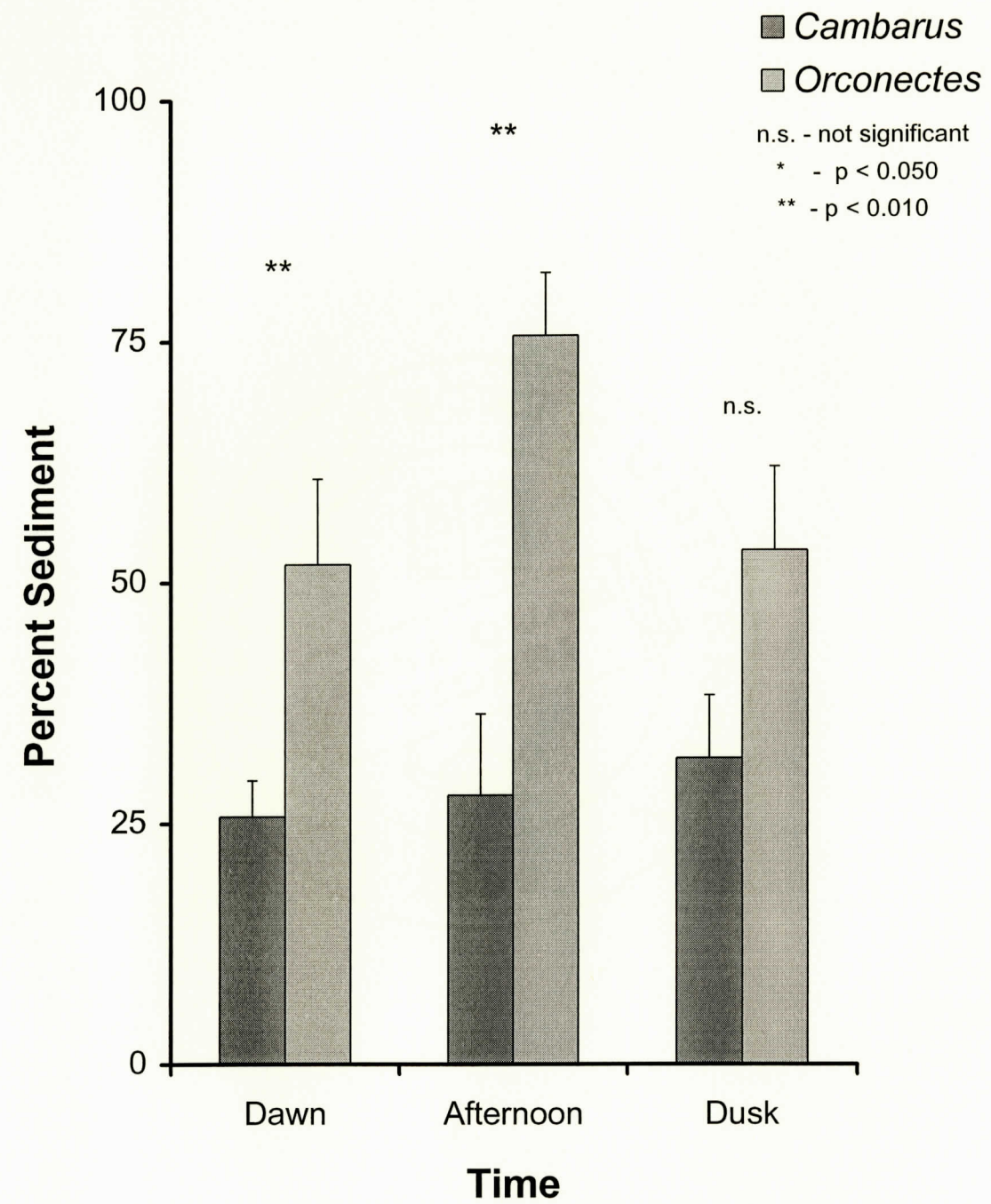
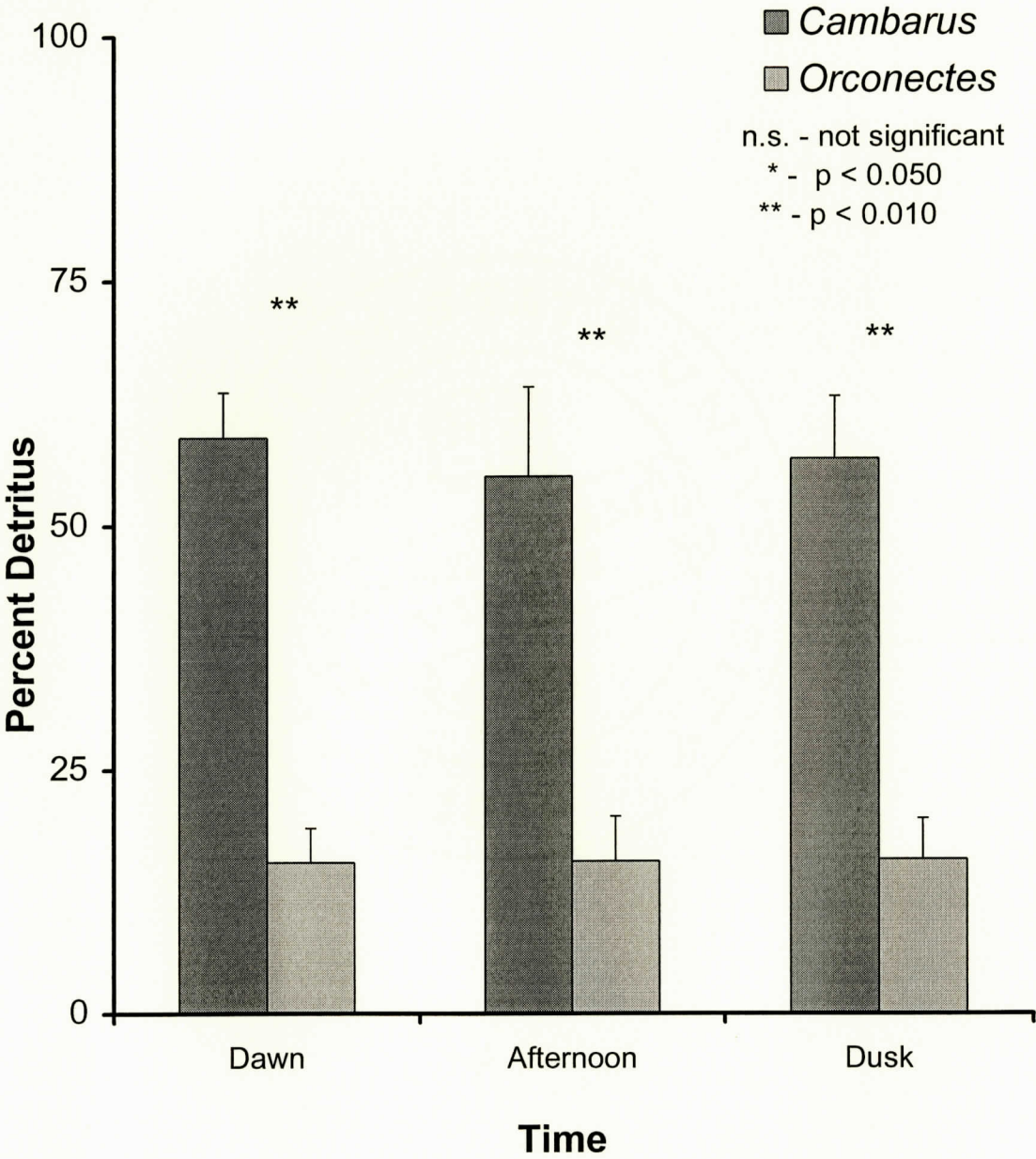


Figure 8. Mean percent sediment for *C. chasmodactylus* and *O. cristavarius* at different times of capture. Values are percentage of total gut contents. Asterisks represent significant differences within a particular time.



Field experiment

General Observations

The cages effectively excluded large crayfish and fish, but not smaller organisms. Young-of-the year crayfish of both species and small fish, including many unidentified minnows (Cyprinidae), fan-tailed darters (*Etheostoma flabellare*), and mottled sculpins (*Cottus bairdi*), were often observed in and around all treatments. Large crayfish of both species and larger fish, including northern hogsuckers (*Hypentelium nigricans*), central stonerollers (*Campostoma anomalum*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), and cyprinids (primarily silver shiners (*Notropis photogenus*)) were often observed between rows and in cage controls and open baskets.

Temperature and Current Velocity

Water temperature ranged from 12.2 °C to 22.8 °C over the course of the experiment with a mean of 18.9 °C (Table 2).

TABLE 2: Mean (+ 1 standard error) weekly water temperature (° C) for the six-week field experiment.

WEEK	WATER TEMPERATURE (°C)	±	SEM
1	21.1	±	*
2	*	±	*
3	16.1	±	3.9
4	19.3	±	2.7
5	20.1	±	2.2
6	18.4	±	2.5

* missing data

The lower water temperatures coincided with colder air temperatures from 9-4-98 to 9-14-98. Crayfish activity decreased with decreasing water temperature. Weekly current velocity measurements ranged from 7.3 cm/s to 24.3 cm/s. Mean current velocity for the treatments and the rows are shown in Table 3.

TABLE 3: Mean current velocity measurements (n = 6) for each treatment and row. Treatments are *O. cristavarius* enclosure (ORC), *C. chasmodactylus* enclosure (CAM), open basket (OPEN), cage control (CAGE), and exclosure (EXC).

TREATMENT	CURRENT VELOCITY (cm/s)	±	SEM	ROW	CURRENT VELOCITY (cm/s)	±	SEM
ORC	14.8	±	7.7	1	12.9	±	3.9
CAM	15.2	±	5.5	2	11.1	±	4.1
OPEN	16.7	±	8.1	3	12.3	±	4.1
CONT	13.5	±	5.3	4	14.6	±	4.4
EXC	13.5	±	5.4	5	22.9	±	6.3

Although row 5 had significantly higher current velocities ($p < 0.001$) than all other rows, there were no significant differences in current velocity among treatments.

FPM accumulation and macroinvertebrates

There was an overall significant treatment effect in the field experiment (for Wilks' Lambda, $F_{40,28} = 2.7721$, $p = 0.0033$). The exclosure contained significantly more sediment ($F_{1,16} = 19.37$, $p = 0.004$) and there was significantly more sediment ($F_{1,16} = 12.26$, $p = 0.003$) associated with the combined crayfish treatments than the cage control and open basket (Figure 9).

FPM volume followed the same trend with exclosures containing significantly more FPM volume ($F_{1,16} = 21.41$, $p = 0.0003$), and there was significantly more FPM ($F_{1,16} = 4.6$, $p = 0.0486$) associated with the combined crayfish treatments than the cage control and open basket (Figure 10). There was a marginally significant positive relationship between FPM and current velocity ($r^2 = 0.148$, $p = 0.06$).

The baskets contained 11% hydropsychid caddisfly larvae (*Hydropsyche scalaris*), 2% calopterygiid damselfly larvae (*Calopteryx maculata*), 66% chironomid larvae, 3% cyclopoid copepods, and 3% aquatic mites (hydracarina). All other macroinvertebrates found in the baskets were left out of the analyses because they were not present in sufficient numbers for the analysis.

There was a marginally significant treatment effect on chironomid abundance ($F_{4,16} = 2.11$, $p = 0.0973$), with more chironomids associated with the exclosure than all other treatments ($F_{1,16} = 3.72$, $p = 0.0718$), and a marginally significant difference between crayfish, with more chironomids found in the *Orconectes* treatment ($F_{1,16} = 3.79$, $p = 0.0692$, Figure 11). Chironomid abundance also showed a marginally significant cage effect, with more in the open basket than cage control ($F_{1,16} = 4.31$, $p = 0.0544$). Chironomid densities increased with FPM volume ($r^2 = 0.429$, $p = 0.002$, Figure 12).

There was a significant effect of treatment on hydropsychid abundance ($F_{4,16} = 6.02$, $p = 0.0037$). Specifically, there was a significant cage effect on *H. scalaris* abundance ($F_{1,16} = 17.5$, $p = 0.0007$, Figure 13). There was also a marginally significant treatment effect on damselfly larvae ($F_{4,16} = 2.65$, $p = 0.0716$). There were more *C. maculata* associated with the crayfish treatments than the cage control and open basket ($F_{1,16} = 7.55$, $p = 0.0143$, Figure 14).

There was a marginally significant treatment effect on cyclopoid copepods ($F_{4,16} = 2.34$, $p = 0.0996$), with more in the *Orconectes* treatments than the *Cambarus* treatments ($F_{1,16} = 4.87$, $p = 0.0423$, Figure 15). Hydracarina water mites showed a significant treatment effect ($F_{4,16} = 3.06$, $p = 0.0474$). This was a cage effect, with more hydracarina in the open baskets than the cage controls ($F_{1,16} = 9.02$, $p = 0.0084$, Figure 16).

Figure 9. Log volume (ml) of sediment from the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values.

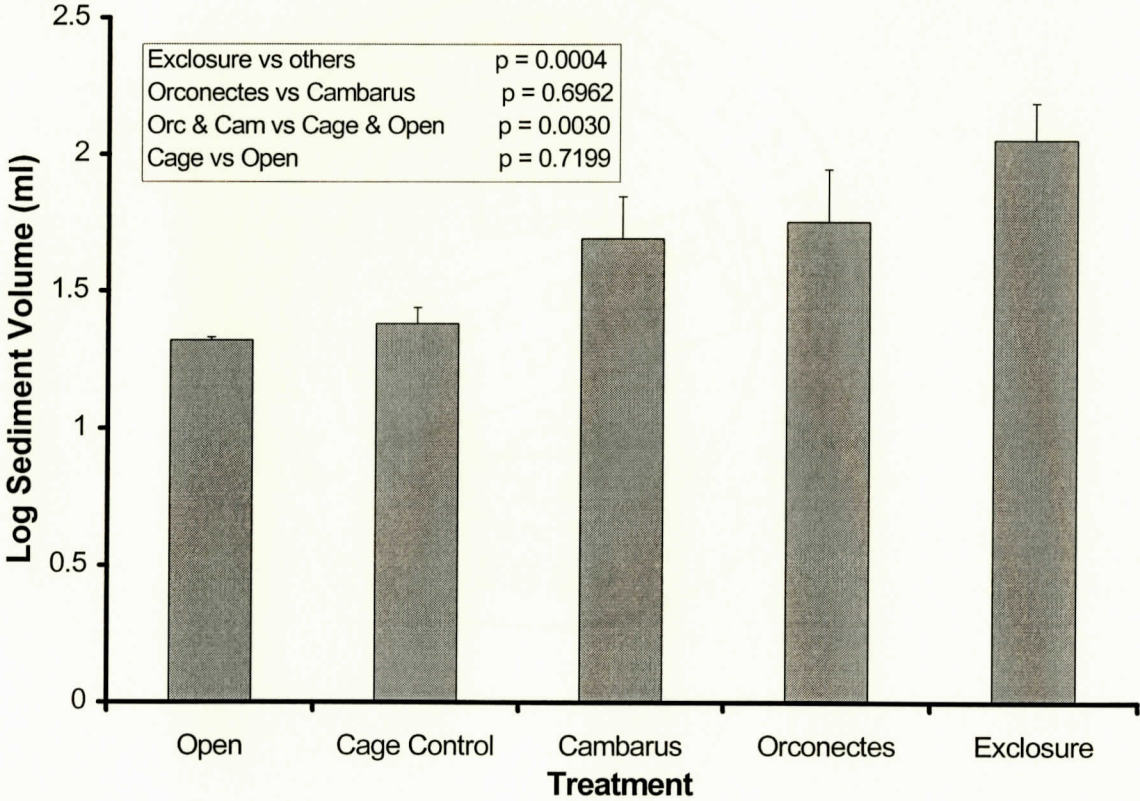


Figure 10. Log volume (ml) of fine particulate matter (FPM) from the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values.

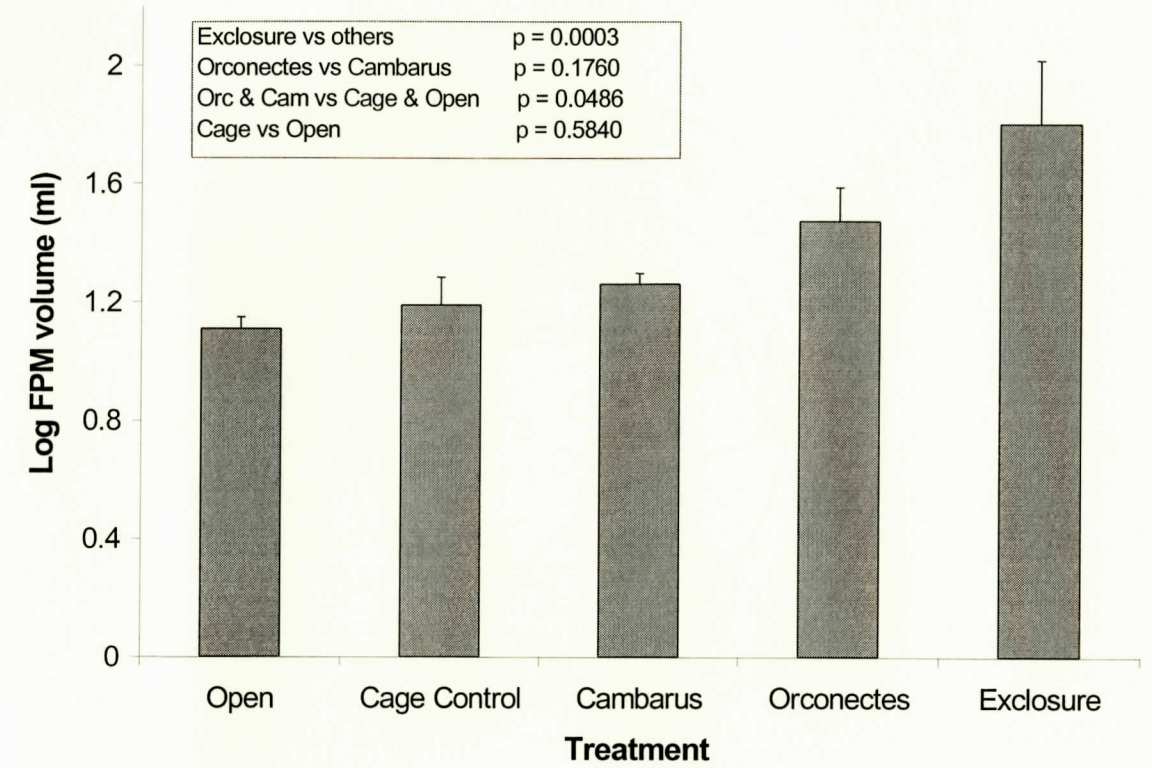


Figure 11. Log chironomidae abundance from tiles in the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values. All logs are base 10.

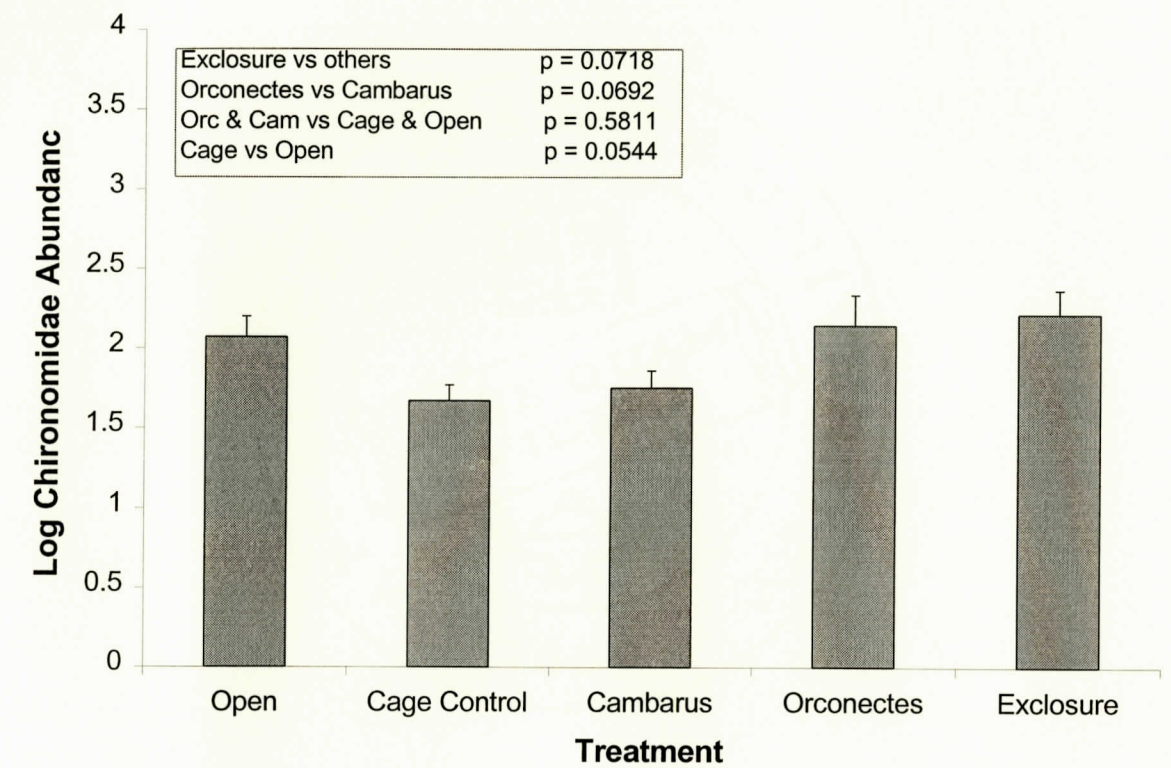


Figure 12. Log chironomidae abundance from tiles in the field experiment as a function of log FPM volume (ml). All logs are base 10.

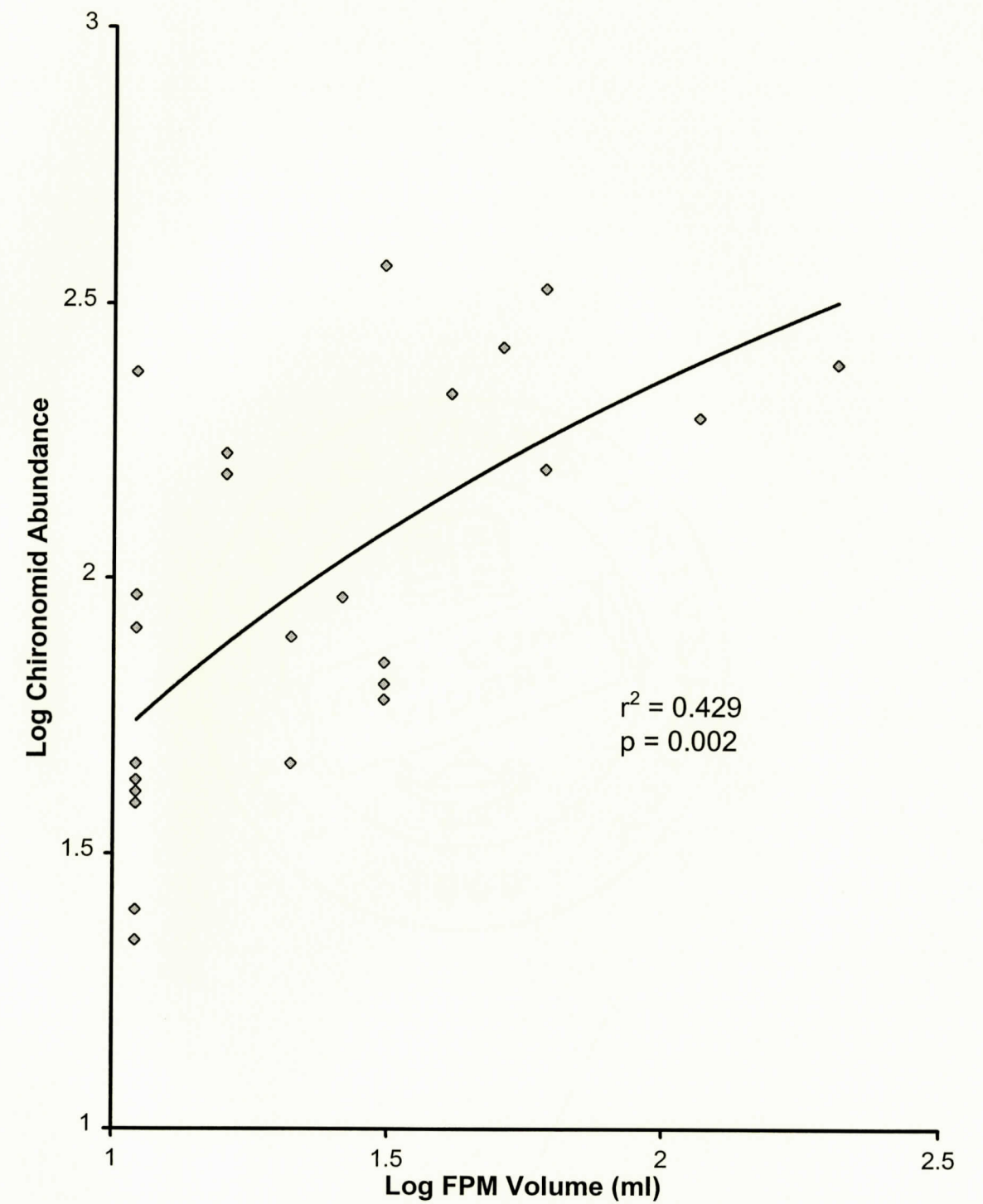


Figure 13. Log *Hydropsyche* abundance from tiles in the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values. All logs are base 10.

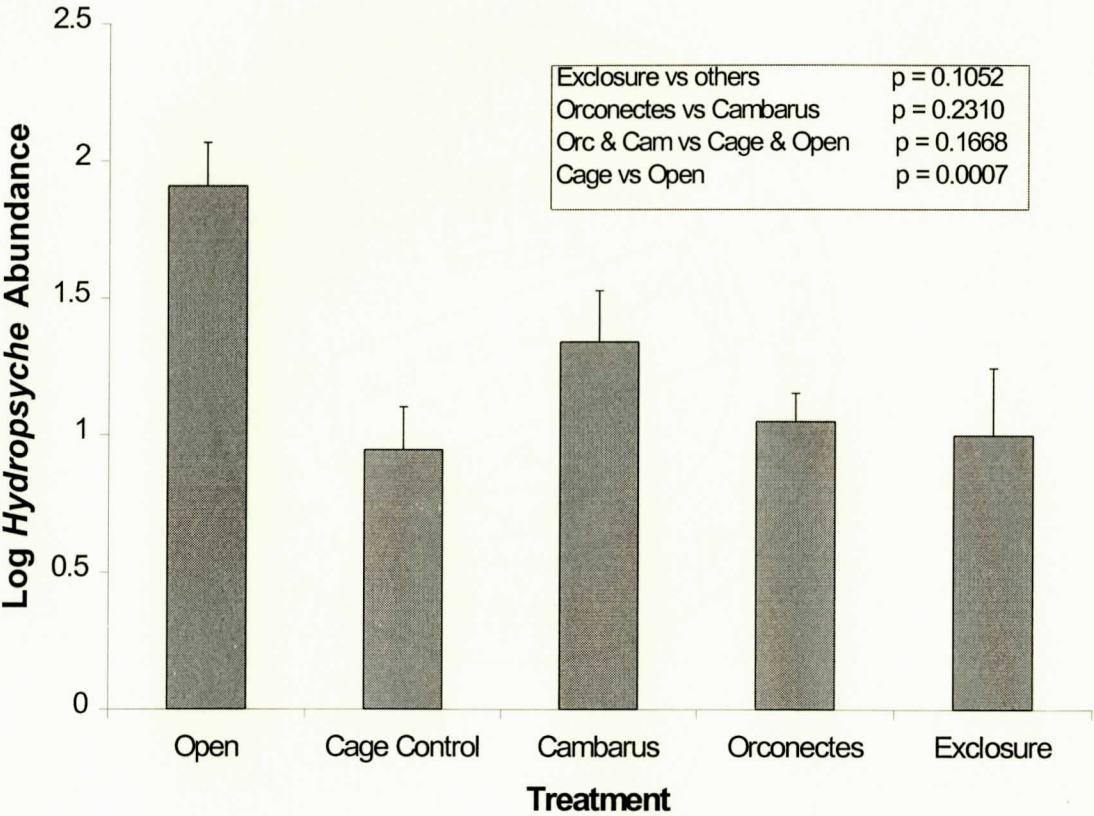


Figure 14. Log *Calopteryx* abundance from tiles in the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values. All logs are base 10.

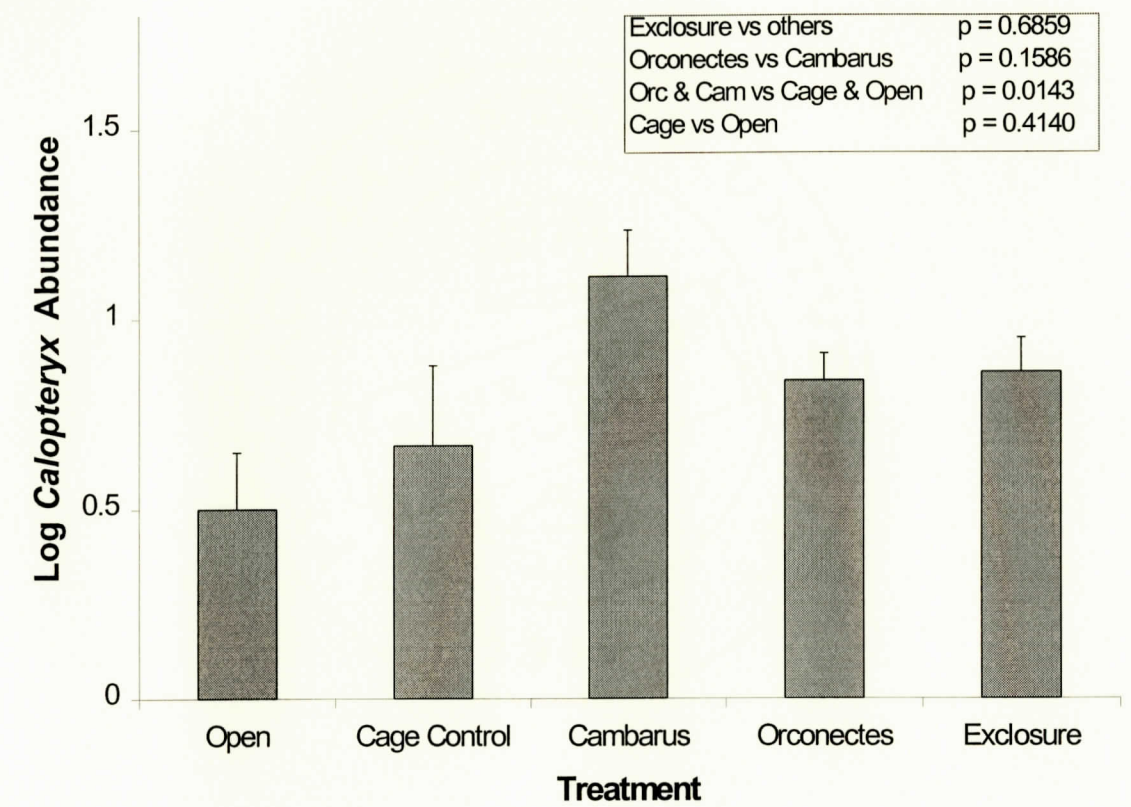


Figure 15. Log cyclopoid copepod abundance from tiles in the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values. All logs are base 10.

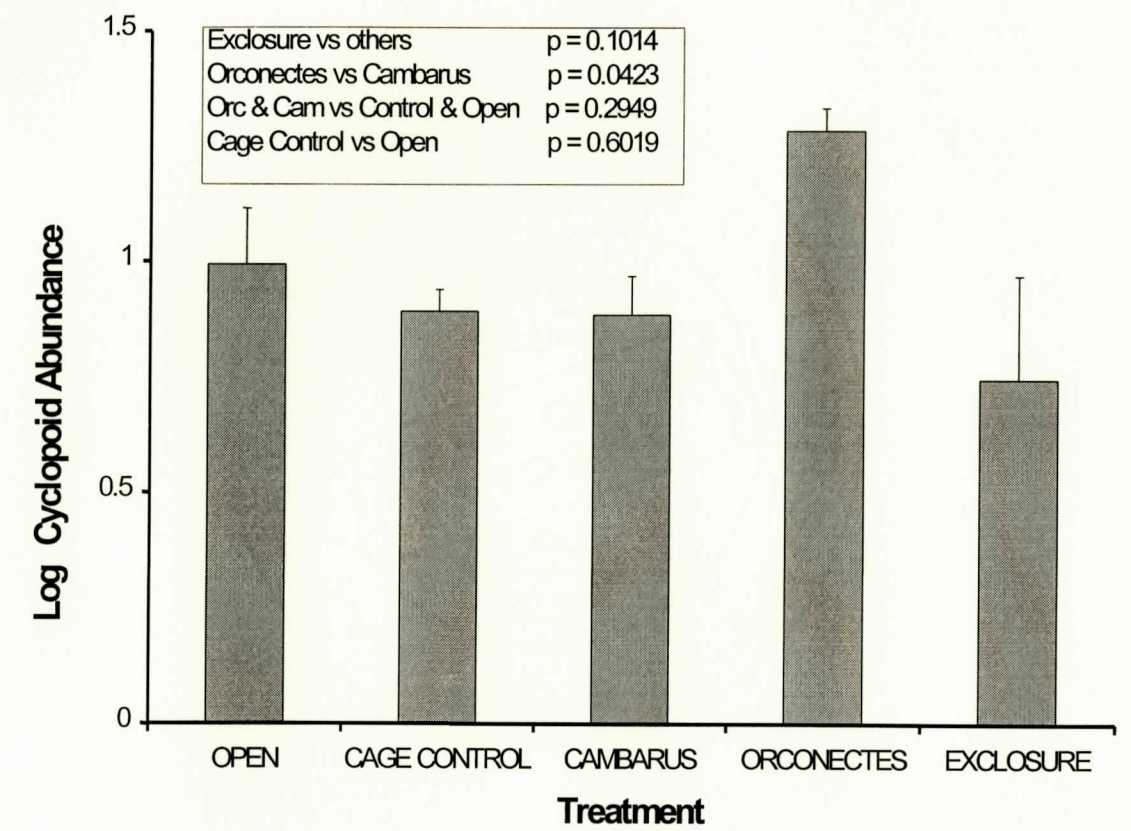
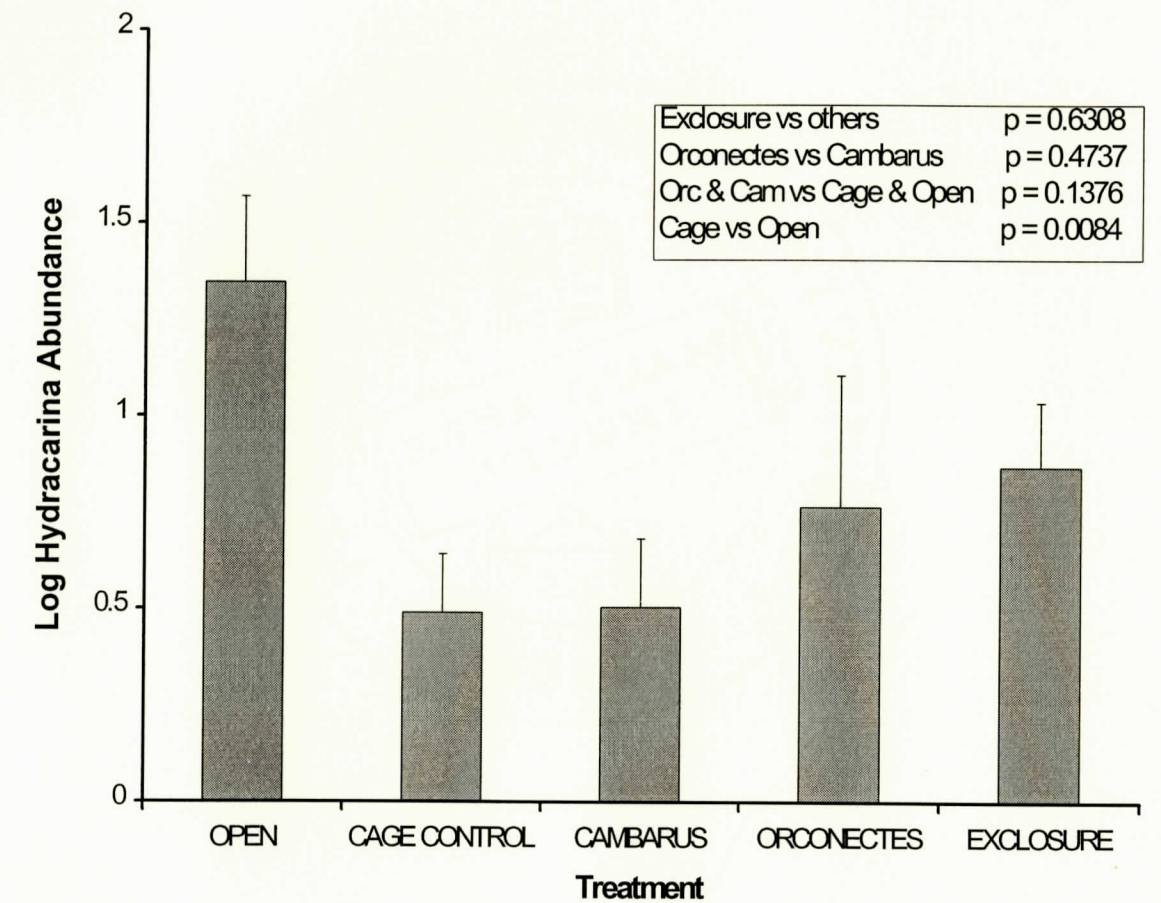


Figure 16. Log Hydracarina water mite abundance from tiles in the field experiment. Treatments are *O. cristavarius* enclosure ('Orconectes'), *C. chasmodactylus* enclosure ('Cambarus'), crayfish enclosure ('Exclosure'), Cage Control, and open basket ('Open'). Inset includes orthogonal contrasts and associated p values. All logs are base 10.



Discussion

Gut Content Analyses

While these two species of crayfish consumed a range of food items, sediment and detritus made up the majority of the gut contents for both species. Only a small fraction of the gut contents consisted of invertebrates and pieces of green vegetation (algae, riverweed, etc.). There was a significant difference between the two crayfish species with regards to the amounts of sediment and detritus in their guts. *C. chasmodactylus* contained more detritus and *O. cristavarius* contained more sediment. This difference in their diets was evident at all times of the day. Although the two species differed with regard to the amounts of sediment and detritus they consumed, there was nevertheless considerable overlap in diet. The calculated values of Schoener's index of overlap ranged from 50-61%, which suggests that this difference in diet may not be that dramatic. According to the index, these values suggest that some resource partitioning may be occurring.

The diet of *C. chasmodactylus* is similar to those of other crayfish (Bovbjerg 1952, Capelli 1980, Creed 1990, Whitledge and Rabeni 1997, Gutierrez-Yurrita et al. 1998). These studies have demonstrated that crayfish consume large proportions of detritus, plant and algal material, and animal

remains. Sediment was not a major component of the diet of the crayfish examined in these previous studies. In the present study, however, both species had large proportions of sediment in their guts. In fact, sediment constituted the majority of the gut contents of *O. cristavarius*. Previous studies have suggested that crayfish ingest sediment incidentally while consuming food (e.g. Capelli 1980, Gutierrez-Yurrita et al. 1998). However, gut sediment amounts of 50-100% suggest more than incidental consumption. *O. cristavarius* seems to intentionally consume sediment. It is probable that these crayfish are gaining some nutritive value from microinvertebrates and fecal material in the sediment as well as the biofilm, a gelatinous polysaccharide matrix containing diatoms, fungi, detrital and fecal particles, and bacteria and bacterial exudates associated with sediments (Allan 1995). Bacteria and algae produce large quantities of exopolymers, polysaccharides that extend from bacterial cell surfaces and encompass the capsule and slime layer (Prescott et al. 1993, Hall and Meyer 1998). Various species of invertebrates can consume these exopolymers (Hall and Meyer 1998). Hall and Meyer (1998) concluded that invertebrates could derive anywhere from 10 to 100% of their carbon from bacterial exopolymers. Both crayfish, but especially *O. cristavarius*, may be deriving substantial nutrition from these exopolymers. Future investigations need to determine the importance of these exopolymers to these two species of crayfish, especially *O. cristavarius*.

FPM and Macroinvertebrates

Both crayfish species seem to function as ecosystem engineers in the South Fork of the New River. Both species sift through and consume sediment when foraging and excavate under cobbles. These activities, along with disturbances from locomotion, suspend sediments in the water column, which are then transported downstream. This affects resource and habitat availability for many other organisms. Many species of chironomid depend upon benthic sediments as a food resource and as habitat, and are positively correlated with sediment abundance (Flecker 1996, Reed 1997). Therefore, reduction of sediment and FPM would have a negative impact on these taxa. Chironomids were positively associated with FPM abundance in this study, with the highest chironomid abundance in the exclosures. It is unclear exactly how these crayfish affect chironomid abundances and in fact, the crayfish may differ from one another in their effects on chironomids. In the field experiment fewer chironomids were associated with *C. chasmodactylus* than *O. cristavarius*. Also, there was more animal material in *C. chasmodactylus* guts and significantly more sediment in *O. cristavarius* guts. It is possible that these crayfish are processing sediment for different reasons. *C. chasmodactylus* may be sifting through sediment for invertebrates while *O. cristavarius* may be directly consuming sediment. Both of these activities would reduce sediment and FPM abundance and could result in reduced chironomid abundance.

However, the effect of crayfish on chironomids was not as dramatic as in other studies. Reed (1997) conducted an enclosure-exclosure experiment with *C. bartonii* in a second-order Appalachian stream. He found that FPM was lowest in crayfish enclosures and that chironomid and harpacticoid copepod abundances were highest in exclosures, where FPM abundance was significantly higher. The removal of FPM by crayfish also may have increased available substrate for algae growth. This could partially explain why significantly more grazing heptageniid mayflies were associated with the crayfish in Reed's study. Although the crayfish in the South Fork of the New River behaved similarly, their impacts on FPM and macroinvertebrates were not as profound. It is likely that the crayfish in the tributaries of the New River behave similarly to the crayfish in Reed's study, having greater per-capita sediment impact than the crayfish in the main stem. One possible reason for this difference is that the sedimentation rates of the New River may be greater than in a headwater stream. The fourth-order New River has longer stretches of stream with relatively low flow compared to lower order tributaries. It may also have a much heavier sediment load than the tributaries. The ability of crayfish to remove sediment from substrates seems constant, regardless of species and location. Thus, in habitats where sedimentation rates are higher, crayfish may have a less pronounced effect on sediment accumulation. The

sediment removal rate of crayfish may be much less than the actual sedimentation rate of the river.

The increased sedimentation rate encountered with increasing stream order may be offset by the addition of other organisms. In my experiment, the greatest reduction in sediment occurred when all macroconsumers had access to the baskets. Four species of macroconsumers in the South Fork of the New River probably have the greatest impact on sediment accumulation. These include the two crayfish species and two species of benthic-feeding fish, the central stoneroller (*Campostoma anomalum*) and northern hogsucker (*Hypentelium nigricans*). The central stoneroller scrapes sediment, algae and detritus off hard substrates (Power et al. 1985, Rohde et al. 1994). The northern hogsucker also scrapes benthic material and sucks up sediment and associated organisms as well as overturns rocks (Rohde et al. 1994). Benthic feeding fish also fan the substrate with their fins when foraging (Helms, personal observation). These actions, along with those of the crayfish, further act to suspend sediments for downstream transport.

The fact that the crayfish effects observed in Reed's (1997) experiment were stronger than the effects in this experiment may also be explained by the absence of benthic-feeding fish in the stream where he conducted his study. Large benthic-feeding fish, although abundant in the fourth order New River, are not common in its smaller tributaries (Helms, personal observation). In

these tributaries, crayfish are frequently the only large organisms that affect sediments. Therefore, they may have more dramatic effects in the smaller streams. In the New River, on the other hand, there does not seem to be one, but a host of benthic organisms that can influence sediment abundance. Therefore, the role of bioturbator (an organism that re-suspends sediment) is shared by several taxa. Thus, increasing sedimentation rates and the presence of additional taxa that perform similar functions may result in the impacts of crayfish decreasing in larger order streams. In the more complex downstream communities a variety of taxa may perform similar roles. I use the term "role diffusion" to describe a situation where a process performed by one group of taxa in one system is performed by several in another system.

Similar role diffusion has been demonstrated in tropical Costa Rican streams that contain Atyid shrimp. In the first order streams, the benthic community is dominated by three genera of Atyid shrimp (Pringle et al. 1993). One algivorous fish (*Sicyium plumieri*) is present, although at very low densities (Pringle et al. 1993). The shrimp in these streams can significantly reduce the amount of sediment on substrates, which leads to a reduction in the abundance of sediment-dwelling insects (Pringle et al. 1993). Third- and fourth-order streams, on the other hand, contain several species of omnivorous fish as well as several species of shrimp (Pringle and Hamazaki 1998). In these larger streams, although shrimp and fish each have negative effects on

chironomids and sediments, the greatest reductions occurred in the presence of both omnivorous fish and shrimp (Pringle and Hamazaki 1998). The role that shrimp play in the first-order streams is shared by many organisms in the larger rivers. The results of these studies are strikingly similar to the findings in Reed (1997) and the present study. Crayfish may have more pronounced effects in small streams but in more complex downstream communities their effect is not as great as that of an entire group of taxa (crayfish and benthic-feeding feeding fish) that reduce sediment.

There seemed to be few strong crayfish effects on other macroinvertebrate taxa in this study. There were more cyclopoid copepods associated with *O. cristavarius* than *C. chasmodactylus*, which is consistent with the gut content analyses. Most stream-dwelling copepods live in the interstices of sediment (Thorp and Covich 1991). It is possible that *C. chasmodactylus* may seek out these organisms while processing sediment, which could possibly account for the higher amount of animal material found in their guts. *O. cristavarius*, on the other hand, may not actively search for invertebrates in the sediment.

The densities of the damselfly *Calopteryx maculata* were similar in the exclosures and the crayfish enclosures. *C. maculata* abundance was significantly lower in the open baskets and cage controls, which were exposed to fish. The cages may have served as refuge from fish predators.

Alternatively, *C. maculata* may have avoided habitats where there was additional disturbance of the substrate by benthic-feeding fish.

Crayfish and Community Structure

C. chasmodactylus and *O. cristavarius* had similar effects on community structure in the New River, but their effects were weaker than those reported for other crayfish species (e.g., Creed 1994, Charlebois and Lamberti 1996). Thus, these crayfish are not strong interactors in this system. They are important in affecting resource availability to other organisms, but pronounced changes in community structure did not occur upon their exclusion. There are several possible explanations for their weaker effects on invertebrates in this study. First of all, the exclosures could be considered 'islands of refuge' in a 'sea of hostility' for most small invertebrates and the chances of finding this refuge were small. Further, coexisting organisms are not expected to interact strongly (McPeck 1990). Crayfish may exclude certain unknown taxa that would otherwise be abundant in the absence of crayfish. Therefore, the observed patterns may be the outcome of undetected interactions. Such a small-scale manipulation like this experiment may not reveal these types of interactions. These may only be determined by transplanting crayfish or potential prey species throughout the watershed.

It is possible that the observed crayfish interactions are no stronger than they appear and these crayfish are indeed weak interactors. Further, since the

two species were so similar, they may be considered “redundant species”. The redundancy hypothesis suggests that not all organisms within a functional group are equally necessary at one time for the maintenance of community structure and ecosystem processes (Ehrlich and Walker 1998, Covich et al. 1999). If an organism is redundant in its functional role, its removal should not have a pronounced effect on energy flow (Ehrlich and Walker 1998). This could possibly be argued for any given large benthic-feeding organism in the New River. Crayfish effects were very similar for most of the measured variables and their exclusion did not have profound effects. Although not examined directly, crayfish and fish effects in this system seem to be additive, especially in terms of sediment processing. Individually, none of these organisms may be dominant ecosystem engineers, but collectively, they have a strong effect on sediment and taxa associated with FPM.

It should be stressed that organisms under one set of environmental conditions may play a different role in other circumstances (Mills et al. 1993, Power 1992, Creed 1994, Menge et al. 1994, Flecker 1997). Organisms often respond to variation in environmental factors with the result that their effects are not consistent from one habitat to the next. Creed (1994) demonstrated that the crayfish *O. propinquus* was a keystone consumer in deep-water habitats but its effects did not extend to shallow-water habitats. The effects of the

crayfish in the New River and their association with other organisms may be different in other habitats such as riffles.

Based on the results from the gut content analyses and field experiment as well as data from Fortino (2000), a simplified, hypothesized food web for the South Fork of the New River was constructed (Figure 16). Detritus and sediment were important resources for both species of crayfish and probably for benthic feeding fish, as well as other invertebrates (mainly chironomids). Since *Orconectes* is the more abundant crayfish, it is assumed that the diet of rock bass (*Ambloplites rupestris*), a crayfish specialist (Rohde et al. 1994), contains mostly *O. cristavarius*. Also, central stonerollers and northern hogsuckers are known to consume large amounts of sediment as well as associated invertebrates (Rohde et al. 1994). There is a high level of connectedness in this hypothesized food web. This connectivity dampens the effects of any given organism. This is consistent with Strong's (1992) idea that trophic architecture in diverse systems is often comprised of a high level of omnivory, food-web looping and connectivity, and these type of systems are rarely controlled by just a few species (Strong 1992).

Relevance for Crayfish Invasions

A large body of literature has focused on the invasions of exotic crayfish and their effects on native crayfish and aquatic communities. The reductions of native crayfish by exotic crayfish have been documented in the United States,

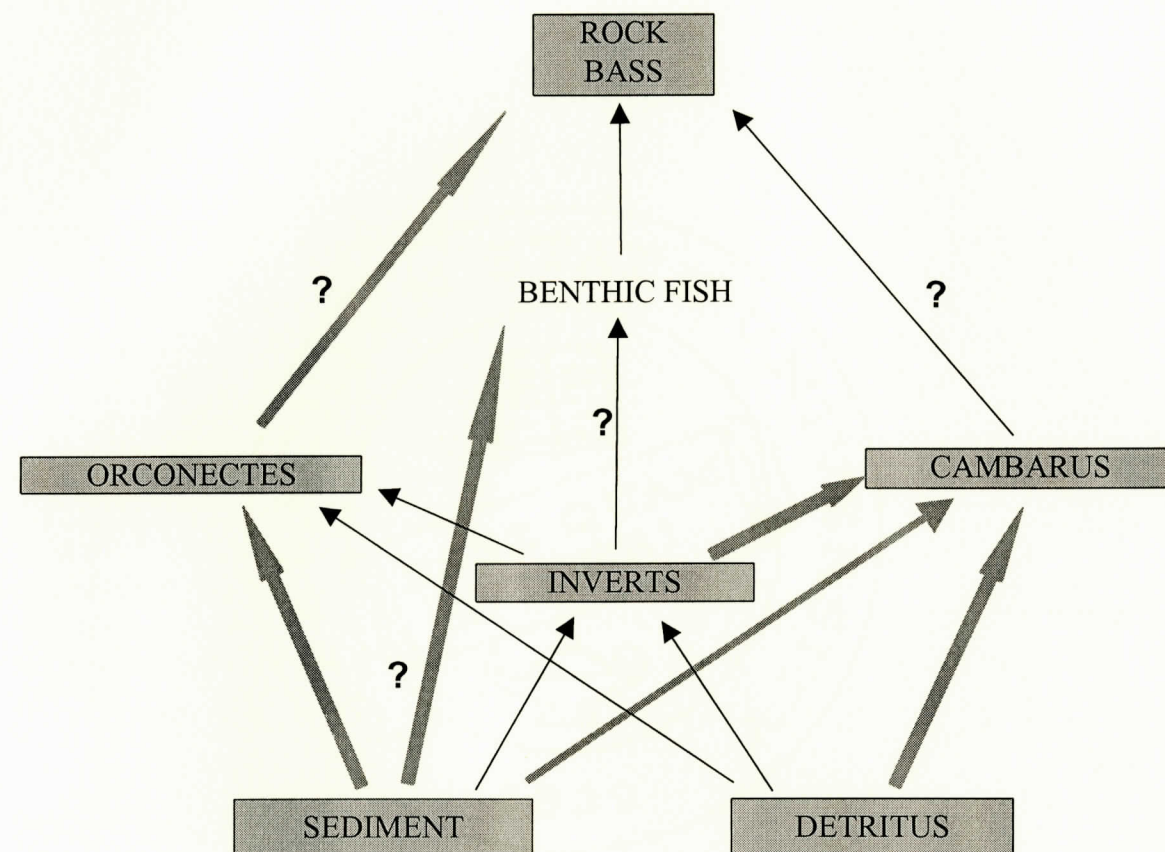
Canada, Britain, and Sweden (Olsen et al 1991, Lodge et al. 1994, Guan and Wiles 1997). In Europe, *Pacifasticus leniusculus* has been introduced and has a greater impact on macrophytes than the native crayfish, *Astacus astacus* (Nystrom and Strand 1996). In North America, *Orconectes rusticus*, a crayfish which is native to the Ohio drainage of the United States, has been introduced into many freshwater systems of the upper Midwest and Northeast as well as into Ontario (Berrill 1978, Olsen et al 1991). This crayfish is replacing two congeners, *O. propinquus* (a previous invader) and *O. virilis* (the native crayfish), in northern Wisconsin lakes (Olsen et al. 1991, Lodge et al. 1994). In central Ohio streams, *O. rusticus* is replacing another native congener, *O. sanborni* (Mather and Stein 1993). This invading crayfish may have a greater impact on the abundance of benthic flora and fauna than its congeners, thus having strong effects in these systems (Olsen et al. 1991, Lodge et al. 1994). However, there have been no field experiments that simultaneously compare the effects of *O. rusticus* to *O. propinquus* or *O. virilis*. Resource utilization determines a crayfish species' influence on community structure (Momot 1995). There may be differences in the ways invading and native crayfish utilize resources, thus differences in their effects on communities. It is therefore vital to understand the dynamics of all the crayfish species involved so as to be able to better predict the community response to a change in the dominant crayfish species. Direct, in-field comparisons instead of speculation based on

monospecific experiments and diet analysis are needed when trying to determine the community dynamics of such a disturbed system. The two *endemic* crayfish species in the New River differed somewhat in their diets, but overall they did not have dramatically different effects on the community. Describing diet alone would not have been sufficient to determine if the two organisms had different effects on the community. Based on the gut content analysis, I would have predicted more dramatic differences in their effects on community structure. Further, taxonomic differences are also not a good indicator of differences in community effect. The crayfish in this study were of different genera and their effects were very similar. Therefore, we cannot always assume that invading crayfish will have a different impact than the native species. Direct experimental comparisons of the impacts of invaders and natives are needed to determine if the replacement of the native species by the invader will have any impact on the rest of the community.

In conclusion, the two crayfish species that inhabit the New River function as ecosystem engineers through sediment processing. While they have some impact on benthic invertebrates, these effects are not as strong as those reported for crayfish in smaller streams. Further, although these two crayfish are in different genera and have somewhat different diets, they seem to be functionally redundant species in the New River. Two species of benthic-feeding fish appear to play a somewhat similar role as the two crayfish species.

Crayfish and benthic-feeding fish all affect sediment accumulation and are a suite of taxa that affect community structure in the South Fork of the New River. These organisms appear to be increasing habitat heterogeneity through bioturbation, thus affecting resource availability to other organisms, and collectively they have a strong influence on community structure.

Figure 17. Simplified food web for the South Fork of the New River based on results from gut content analyses and the field experiment. Bold lines denote strong feeding interactions, fine lines denote weaker interactions. Lines with question marks have not been specifically tested in the New River. "Rock Bass" refers to *Ambloplites rupestris*, "Benthic Fish" refer to *Campostoma anomalum* and *Hypentelium nigricans*, "Cambarus" refers to *Cambarus chasmodactylus*, and "Orconectes" refers to *Orconectes cristavarius*. "Inverts" are primarily represented by chironomids and *Hydropsyche scalaris*. "Sediment" refers to sediment and fine particulate matter and "Detritus" refers to nongreen vegetative detritus.



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Appendix 1

All macroinvertebrate taxa encountered in the field experiment.

- Insecta
 - Ephemeroptera
 - Oligoneuridae
 - Ephemerellidae (*Danella* sp.)
 - Heptageniidae (*Stenonema* sp)
 - Leptophlebiidae
 - Baetisidae
 - Leptoceridae (*Leptocerus americanus*)
 - Plecoptera
 - Perlidae
 - Taeniopterygidae
 - Trichoptera
 - Hydropsychidae (*Hydropsyche scalaris*)
 - Odonata
 - Gomphidae
 - Calopterygidae (*Calopteryx maculata*)
 - Megaloptera
 - Sialidae
 - Diptera
 - Tipulidae
 - Empididae
 - Chironomidae
 - Coleoptera
 - Elmidae
 - Psephenidae
- Ostracoda
- Copepoda
 - Harpacticoida
- Arachnida
 - Acari
 - Hydracarina
- Tardigrada

Appendix 1

All macroinvertebrate taxa encountered in the field experiment

VITA

Brian Helms was born in Gastonia, North Carolina, on February 27, 1973. He attended elementary and high school there and graduated from Ashbrook High School in June 1991. The following August he entered North Carolina State University in Raleigh, North Carolina. In December 1995, he received Bachelor of Science degrees in Biology and in Zoology. He spent the next year and a half employed by N.C. State working at Fort Bragg on avian ecology as well as working in Raleigh on air quality research. In the fall of 1997, he accepted a teaching assistantship at Appalachian State University and began study toward a Master's Degree. This degree was awarded in May 2000.

Brian is a member of the Association of Southeastern Biologists and the North American Benthological Society. His parents are Mr. and Mrs. R. Gary Helms of Buford, Georgia. He is married to the former Kristen T. Lehman of Chapel Hill, North Carolina.