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THE CENTRAL STONEROLLER, *CAMPOSTOMA ANOMALUM* (FAMILY:
CYPRINIDAE): ECOSYSTEM ENGINEERS IN THE NEW RIVER?

A Thesis

By

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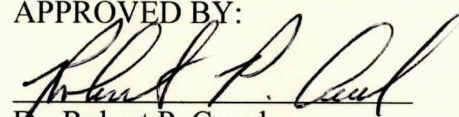
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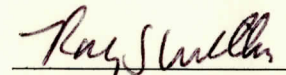
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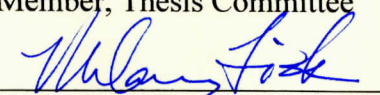
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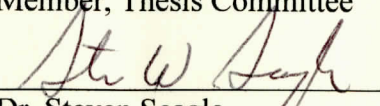
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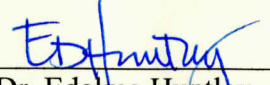
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ABSTRACT

THE CENTRAL STONEROLLER, *CAMPOSTOMA ANOMALUM* (FAMILY:
CYPRINIDAE): ECOSYSTEM ENGINEERS IN THE NEW RIVER

(May 2005)

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An ecosystem engineer is an organism that creates, modifies, and maintains habitats. They can also modulate the availability of resources. This can be via a physical action, or where an organism supplies habitat passively. A variety of species function as ecosystem engineers in streams, including beavers, crayfish, insects, frogs, snails, and benthic-feeding fish. Each of these organisms alters characteristics of the habitat. While there have been formal investigations of benthic-feeding fish acting as ecosystem engineers in tropical streams, there has been almost no investigation of their impact in temperate streams. The central stoneroller (*Campostoma anomalum*) is found throughout the Midwest and in the Tennessee drainages of the southern Appalachians. I hypothesized that the central stoneroller is engineering habitats by reducing sediment accumulation while feeding. This activity could indirectly affect macroinvertebrate assemblages by altering sediment amounts on substrate in the South Fork of the New River, NC.

Fine particulate matter (FPM, a mix of inorganic sediment and organic matter) accrual and macroinvertebrate community structure were compared among four experimental treatments in a field experiment: central stoneroller enclosure, central stoneroller exclusion, a cage control, and an open basket treatment exposed to the natural fish assemblage and crayfish. Selective exclusion of the central stoneroller resulted in differences in FPM and change in macroinvertebrate community structure after 14 days. Central stoneroller exclusion resulted in a significant increase in FPM accumulation. Principal components analysis indicated an overall treatment effect on macroinvertebrate abundances. Individual ANOVAs indicated significant treatment effects for chironomids, hydroptychid caddisflies, and harpacticoid copepods. Tipulids, and heptageniid mayflies exhibited marginally significant responses to treatments. Stonerollers had a negative effect on heptageniid mayflies and harpacticoid copepods. They had a mixed effect on hydroptychid caddisflies, chironomids, and tipulids. These mixed effects may be the result of a positive effect from sediment removal and a negative effect from predation. The potential for stoneroller predation on macroinvertebrates was evaluated by examining gut contents and with stable isotope analysis. Gut contents suggests that stonerollers consume mainly sediments. However, stable isotope analysis data shows the central stoneroller may be carnivorous. Thus, the mechanism by which the central stoneroller affects macroinvertebrate assemblages may be a combination of habitat modification and predation.

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Academic pressure requires external stimulation to keep everything balanced. The Hellbenders softball team and the Mudpuppies basketball squad was exactly what I needed. These two teams, made up of fellow biology graduate students and faculty, allowed for fun and play outside of the scientific world. We all became great friends and I will never forget the days on the court or the field. Go Benders!

I never could have done this without my beautiful wife, Nancy Wood. She has supported me in every way one can imagine. She is my motivation to achieve all of my goals in life. We have a baby on the way and soon the two of us will be experiencing a new chapter in our lives. She supports all of my passions and helps me maintain a great outlook on every new day. I love her with all of my heart and couldn't imagine life without her. Thank you, Nancy, for all of your help and support throughout this degree. It will all be worth it.

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INTRODUCTION

The mechanisms that organize communities have been a long-standing research interest to ecologists. Historically, arguments centered on the extent to which communities were regulated by abiotic vs. biotic interactions, and the importance of competition vs. predation (Hairston et al. 1960, Peckarsky 1983, Menge and Sutherland 1987, Hart 1992). Many community ecologists believed there was little direct evidence demonstrating that species assemblages were determined by biological interactions, since other factors (e.g. environmental tolerances, dispersal, disturbances) kept populations below the point at which serious competitive pressure was developed. Others viewed interspecific competition for limited, depletable resources as the prime factor in organizing communities and influencing evolution (Hutchinson 1959, Connell 1983, Schoener 1983). Recently, more pluralistic approaches have been proposed linking abiotic and biotic factors that may affect patterns of distribution and abundances of organisms between and within ecosystems (Connell 1978).

Many ecologists noted that biotic interactions are limited by abiotic factors (Connell 1978, Peckarsky 1983, Menge and Sutherland 1987, Poff and Ward 1989). Biological interactions may be unimportant to community structure in harsh environments. In these systems, life history and tolerances to environmental variables are potentially more important in structuring communities (Menge and Sutherland 1987, Poff and Ward 1989, Helms and Creed 2005).

However, in less harsh environments, i.e., benign environments, biological interactions become more important as organisms are released from physical limitations on their distributions and abundance (Peckarsky 1983, Menge and Sutherland 1987, Poff and Ward, 1989, Wellborn et al. 1996, Helms and Creed 2005).

Initially, the prevailing view in stream ecology was that biological interactions were insignificant with respect to structuring stream communities compared with abiotic factors (Barnes and Minshall 1981). Abiotic factors (i.e. temperature, flow regimes, flooding frequency, substrate) were thought of as the most important mechanisms for controlling species assemblages in stream ecosystems (Barnes and Minshall 1981). Environmental gradients in freshwater systems have also been recognized as a critical axis along which stream communities are organized (Vannote et al. 1980). However, stream ecosystems vary with respect to many abiotic variables, including flow regimes and disturbance frequency; thus, there is potential for many streams to have environmental conditions where biological interactions may outweigh abiotic factors in determining community structure (Peckarsky 1983, Poff and Ward 1989, Helms and Creed 2005). Most recent research which looks at the ability of biological interactions to structure stream communities focuses on competition and the trophic effects of consumers. The effects of competition have been demonstrated in some streams (Hemphill and Cooper 1983, McAuliffe 1983, Hill 1992, Feminella and Resh 1991, Kohler 1992). Consumers have also been shown to affect stream community structure (Powers et al. 1985, Lamberti et al. 1987, Gilliam et al. 1989, Schlosser and Ebel 1989, Cooper et. al 1990, Gilliam et al 1993, Creed 1994). Not all organisms affect communities equally. Certain organisms may facilitate communities that would be

transformed in their absence. Consumers can affect communities through trophic level interactions (e.g., keystone species and strong interactors) or by modifying the habitat (e.g., ecosystem engineer).

An ecosystem engineer as defined by Jones et al. (1994) is an organism that creates, modifies, and maintains habitats. This can be via a physical action, or where an organism supplies a habitat passively (e.g., a tree supplying habitat for associated epiphytes). A variety of species function as ecosystem engineers in streams including beavers (Naiman et al. 1986), crayfish (Creed 1994, Statzner et al. 2000, Creed and Reed 2004, Helms and Creed 2005), insects (Hill and Knight 1987, Statzner et al. 1996, Zanetell and Peckarsky 1996), frogs (Flecker et al. 1999), snails (Harvey and Hill 1991), shrimp (Pringle et al. 1993) and benthic-feeding fish (Power 1990, Flecker 1996, 1997). Each of these organisms alters characteristics of the habitat. Beavers are the best example of an ecosystem engineer, as they can dramatically alter stream chemistry, thermal regimes, and flow of a stream by blocking it with a dam (Naiman et al. 1986).

Crustaceans have also received much attention for being ecological engineers. Creed (1994) showed that the crayfish, *Orconectes propinquus*, could benefit diatoms and certain grazing insects by reducing the density of a filamentous alga (a trophic effect) and reducing sediments on substrate (an engineering effect). Creed and Reed (2004) showed that the crayfish, *Cambarus bartonii*, could reduce sediment accrual in a headwater stream. This resulted in reduced numbers of chironomid larvae and harpacticoid copepods. However, heptageniid mayflies benefited from the sediment reductions. Ewing (2002) described similar effects in a North Carolina stream. Statzner et al. (2000) showed that crayfish can affect stream sediment. They found that the

crayfish, *Orconectes limosus*, could facilitate erosion. Another study showed that two crayfish coexisting in the same stream can both affect sediment accrual (Helms and Creed 2005). Helms and Creed (2005) noted that in the presence of fish and crayfish sediment abundance was even lower. Freshwater shrimp in Puerto Rican tropical streams have been shown to dramatically influence communities (Pringle et al. 1993). These shrimp are capable of reducing sediment accumulation on cobble substrate. Chironomids were negatively affected while some grazing mayflies were positively affected. The positive effect shown by the grazing mayflies may have resulted from an increase in algae biomass (Pringle et al. 1993).

Several studies show that insects and snails have ecosystem engineering capabilities. Hill and Knight (1987) demonstrated how the grazing mayfly, *Ameletus validus*, has the ability to reduce sediment loads on substrate in an artificial stream. Three species of diatoms were negatively affected by the reduction of sediment abundance by the mayfly. Statzner et al. (1996) and Zanetell and Peckarsky (1996) both showed that predacious stoneflies have the ability to act as ecosystem engineers. Populations of the stonefly, *Dinocras cephalotes*, were able to erode up to 400 kg of sand under favorable flow conditions (Statzner et al. 1996). Zanetell and Peckarsky (1996) demonstrated that another stonefly, *Megarcys singata*, affects sedimentation by reducing sediment in interstitial spaces while feeding. Thus, these macroinvertebrates also can influence community structure indirectly via habitat modification.

Flecker et al. (1999) demonstrated the ability of a frog species, *Rana palmipes*, to influence sediment loads and, potentially, community structure in neotropical streams by reducing sediment. As tadpoles, this species feeds on algae and sediment and in high

densities has the ability to clear sediment from substrate. High densities of the tadpoles are commonly seen in their native streams and the potential exists for communities to respond to sediment alterations.

Fish can also act as ecosystem engineers. Power et al. (1990) showed that armored catfish in a Panamanian stream acted as an ecosystem engineer. It removes silt from the substrate, thus aiding in the growth of algae that prefer substrate with little sediment. Flecker (1996, 1997) also observed dramatic impacts of benthic-feeding fish on sediment accrual in a tropical stream. *Prochilodus mariae* reduced sediment loads in Andean streams during the dry season. This fish removes sediment on substrate by ingesting large amounts of sediment and detritus. Sediment reduction resulted in an increase in cyanobacteria and a decrease in some invertebrates but increases in others.

While there have been formal investigations of ecological engineering by benthic-feeding fish in tropical streams (Power et al. 1990, Flecker 1996, 1997), Creed and Reed (2004) noted that there has been almost no investigation of their impact in temperate streams (but see Ewing 2002). Several species of temperate, benthic-feeding fish including suckers, (Catostomidae), and the central stoneroller (Cyprinidae: *Campostoma anomalum*) should be capable of influencing sediment abundance on rocks. As these taxa are widely distributed across North America they may be important players in many streams on this continent. In this study I will focus on the impact of the central stoneroller. The central stoneroller is found throughout the Midwest, in the Tennessee drainages of the southern Appalachians, and a few Atlantic drainages (Mathews et al. 1987, Menhinick). It is a common species, shown to influence standing crops of filamentous green algae (Power and Mathews 1983, Power et al. 1985). Evans-White et

al. (2001) described the feeding ecology of the central stoneroller in Midwestern streams and suggested that the traditional notion that this fish is only herbivorous was false. They found that stonerollers consumed a variety of foods, including macroinvertebrates. Thus, stonerollers have the potential to influence macroinvertebrate community structure by reducing sediment levels on substrate as well as through direct predation. However, Evans-White et al. (2001) did not test this experimentally.

I hypothesized that the central stoneroller affects sedimentation, and that it could indirectly affect macroinvertebrate assemblages in the South Fork of the New River between high flow events and during droughts. This fish often comprises a large portion of the biomass in mountain streams. In the South Fork of the New River, this benthic-feeding fish is 30% of the total fish density (approximately $.5-1.0/m^2$) (Creed, unpublished data). However, the potential exists for stonerollers to directly affect macroinvertebrates through consumption. It was my goal to evaluate the impact of stonerollers on the macroinvertebrate community via sediment alteration and/or predation in the South Fork of the New River using a field experiment, gut content analysis, and stable isotope analysis.

The following hypotheses were addressed in this study:

- H_{1NULL}: *Campostoma anomalum* has no effect on sedimentation in the South Fork of the New River.
- H_{1A}: *Campostoma anomalum* affects sedimentation in the South Fork of the New River.
- H_{2NULL}: *Campostoma anomalum* has no effect on macroinvertebrate assemblages in the South Fork of the New River.
- H_{2A}: *Campostoma anomalum* affects macroinvertebrate assemblages in the South Fork of the New River.

MATERIALS AND METHODS

Field Experiment

The experiment was conducted in the South Fork of the New River, Boone, NC in the section adjacent to the Boone Greenway Trail at latitude 36.2114 N, longitude 81.6529 W. The section of river where the experiment was conducted was 10-15 m wide and spanned a 100 m segment. Substrate was variable with areas of sand and gravel, cobble that may be covered in the vascular riverweed, *Podostemum ceratophyllum*, and small sections of exposed bedrock. Treatments were placed in fairly homogenous sections composed of shallow runs (mean depth = 32 cm) and equal flow (mean current velocities = 21 cm/s). Selective inclusion and exclusion of *C. anomalum* was necessary to determine the influence of *C. anomalum* compared to other benthic fish and crayfish on sediment accrual and macroinvertebrate community structure. *Campostoma anomalum* is a fairly large benthic-feeding fish (up to 250 mm TL) (Mundahl and Ingersoll 1989). This attribute allowed me to selectively exclude or enclose larger stonerollers. Large individuals of other species (e.g., hogsuckers, white suckers, rockbass, crayfish etc.) were excluded by the cages. However, small individuals of some of those species and small species (e.g., New River shiners, darters etc.) could move in and out of cages.

There were four treatments in the experiment: (1) *C. anomalum* exclusion, (2) *C. anomalum* enclosure, containing 8 large stonerollers, (3) a cage control to account for any

cage effect, and (4) no cage. Cages were approximately 3.2 m² and 1 m high. Cages were built as hydrodynamically as possible (i.e., bullet shaped) to minimize the amount of debris collected on the front and to reduce the impact of high flow events on the cages. They were constructed of 12 mm hardware cloth to exclude large *C. anomalum*. The wire mesh was supported by 1.2 m x 12 mm diameter rebar stakes. The cages did not have bottoms. Instead, the mesh was buried approximately 15 cm in the substrate. The four treatments were replicated in three randomized complete blocks. Three baskets made of 12 mm mesh (30 cm x 30 cm x 2 cm) lined with 1 mm window screed filled with cobble substrate were placed slightly upstream of center of each cage or open treatment. Baskets contained 6-7 cobbles and a 9 cm x 9 cm ceramic tile. The tile served as a standardized substrate that was used for quantification of sediment accumulation.

The experiment began on September 7, 2003. Twice a day during the experiment the cages were cleaned of any debris and any crayfish that entered the cage were removed. The initial plan was to sample the experiment after 7, 14, and 28 days. However, a high flow event on day 15 resulted in samples being collected on just days 7 and 14.

On days 7 and 14 a basket and tile were collected from each treatment to determine invertebrate abundance and sediment mass, respectively. Baskets were placed in a retrieval apparatus lined with 243-micrometer mesh to catch any dislodged invertebrates. The tile was removed and placed in a separate container filled with filtered stream water. The cobbles were removed and scrubbed in a dishpan to remove any macroinvertebrates. The baskets were also cleaned to remove any macroinvertebrates.

Contents of the dishpan were preserved in 70% ethanol. The invertebrates were separated from the associated debris and identified in the lab. Macroinvertebrates were identified to the lowest possible taxon and enumerated. Sediment from tiles was measured volumetrically.

Principal Components Analysis (PCA) was used to test for overall treatment effects on sedimentation and density of invertebrate taxa. Subsequent analysis of variance (ANOVA) was used to determine which variables contributed to any significant response in the PCA. There were three *a priori* orthogonal contrasts for both the PCA and ANOVAs: 1) the exclusion compared to all other treatments, 2) the stoneroller enclosure treatment compared to the cage control and the open treatment, and 3) the cage control compared to the open treatment. The first comparison tests for a large consumer effect (e.g., the effect of excluding all large benthic-feeding fish and crayfish). The second comparison compares the effects of stonerollers to those of all benthic-feeding fish and crayfish, i.e., it tests for a stoneroller effect. The third comparison determines if there is any cage effect on sediment accumulation and macroinvertebrate abundance.

Gut Content and Stable Isotope Analysis

Collections of stonerollers for gut contents were conducted in the summer and fall of both 2003 and 2004 in the same section of river as the field experiment. Several other fish species were also collected for gut contents. These included the blue-head chub (*Nocomis leptoccephalus* n= 18), northern hogsucker (*Hypentellium nigricans* n= 5), rockbass (*Ambloplites rupestris* n= 5), molted sculpin (*Cottus bairdi* n= 2), and blacknose

dace (*Rhinichthys atratulus* n=2). Fish were collected using a backpack electro-shocker. Stonerollers from the wild and from experimental treatments (n=59 in 2003, n=30 in 2004) were preserved for gut content analysis and stable isotope analysis. Stonerollers foreguts were removed and examined for food items. Contents of the foregut were flushed into a Petri dish, distributed as evenly as possible, and viewed under a dissecting microscope. Food items were assigned to one of the following categories: sediment, detritus, green vegetation, and animals. A grid was placed over the petri dish and percent composition was estimated based on how much of the contents covered the grid. I determined the area of each of the potential food items and divided that by the total area covered by all the food items. The gut contents of the other fish species were only enumerated.

Stonerollers and the aforementioned fish taxa were also used in stable isotope analysis. Non-stoneroller taxa were included to provide a context for interpreting the stable isotope signatures of stonerollers, especially the ^{15}N signatures. Rockbass, sculpin, and blacknose dace are known carnivores that feed on macroinvertebrates. Rockbass also consume crayfish and fish. These known dietary components will allow for us to interpret the isotopic signatures of the stonerollers and aid in estimating trophic position.

Chironomids, hydropsychid caddisflies, and ephemereid mayflies were collected for stable isotope analysis using a 240 μm sieve kick-net, identified and sorted in the field, then placed in H_2O and immediately brought to the lab. Algal samples were collected in September 2004 by placing three 9cm x 9cm tiles in the South Fork and allowing the periphyton layer to grow. Tiles were collected after two weeks and

scrubbed with a toothbrush and periphyton was collected in a clean dishpan. Water in the dishpan was filtered and then the periphyton carefully removed and placed into a ceramic dish for drying. Sediment was collected using a 9cm x 9 cm tile positioned in a pool directly above the study site. After 1 week the tile was gently placed in a container with stream water. The water and sediment was poured through a 240-micrometer sieve and the leftover sediment was dried at 60 °C for three days.

Muscle samples for stable isotope analysis from all fish taxa were taken from the caudal peduncle region dorsal to the lateral line. The caudal peduncle region was chosen because this region contains white muscle that is less variable in isotopic concentrations (Pinnegar and Polunin 1999). All samples (insects, algae, sediment, detritus, and fish) were dried at 60 °C for 72 hours then pulverized to a fine powder using a mortar and pestle. The powder was weighed to 1.0 mg and placed in 4 x 6 mm pressed tin capsules. Samples were then sent to Colorado Plateau Stable Isotope Laboratory, Northern Arizona University, Flagstaff, Arizona for analysis. Analyses were performed by gas isotope-ratio mass spectroscopy. The lab uses a Finnigan Delta Plus Advantage with a Carlo Erba NC 2100 Elemental Analyzer. Stable isotope abundances are expressed as the ratio of the amount of isotope in the sample compared to the same ratio in an international standard. Because the differences in ratios between the sample and standard are very small, they are expressed as parts per thousand (‰) deviation from the standard :

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$$

where $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. A positive isotopic signature is said to be isotopically enriched. The standard material is Pee Dee belemnite limestone for $\delta^{13}\text{C}$ (Craig 1957),

and atmospheric nitrogen for $\delta^{15}\text{N}$. Recently, the use of stable isotope analysis in studying food webs has increased dramatically. Isotopic C tends to stay approximately the same through trophic levels and can be a good indicator of initial sources of energy (Petersen and Fry 1987). It is conserved up the food chain but can vary at the bottom of the food chain depending on the primary producers (Vander Zanden and Rasmussen 1999). Isotopic N tends to become enriched in tissues by 3-5 ppt with each trophic level. This can serve as a time-integrated indicator of trophic position, based on the pathways of energy flow (Vander Zanden and Rasmussen 1999). Thus, we can estimate food choices by this enrichment and can also get an idea of the potential for omnivory. The use of both gut contents and stable isotope analysis together provides a more robust analysis, allowing us to describe both direct consumption and a time-integrated indication of energy sources.

RESULTS

Field Experiment

Day 7 samples

The numerically dominant macroinvertebrate taxa found in the day 7 basket samples were chironomidae, harpacticoid copepods, and heptageniid mayflies. These taxa were used in the PCA and the univariate ANOVAs. The first three PCs accounted for 99% of the variance in the dependent variables. Neither the PCA nor the individual univariate ANOVAs showed significant treatment effects for any taxa or FPM volumes (Table 1 and Figure 1). However, both FPM volume and harpacticoid copepods showed a pattern of decreasing as large consumers were added (Figure 1 and Figure 2).

Day 14 samples

The numerically dominant macroinvertebrates found in the day 14 basket samples were dipteran larvae (chironomidae and tipulidae), caddisfly larvae (hydropsychidae), mayfly larvae (baetidae, heptageniidae, and ephemereidae), harpacticoid copepods, beetle larvae (elmidae), and mollusks (planorbidae, and pleurobrachia). These taxa were used as dependent variables in the PCA and individual univariate ANOVAs. The first three PCs accounted for 74% of the variance in the dependent variables. Chironomids, hydropsychids, harpacticoids, planorbids, ephemereids, and FPM volume had the strongest loadings on the first PC (Table 2), the only PC for which a significant treatment

Table 1. ANOVA results showing effects of treatment for the dominant macroinvertebrate taxa and FPM volume in day 7 basket samples.

Dependent Variable	df	Sum of Squares	Mean Square	F	p
Chironomidae	3	.0700	.0233	.97	.4667
Harpacticoids	3	.6727	.2242	1.72	.2619
Heptageniidae	3	.1565	.0522	3.82	.0763
Total Macros	3	.0408	.0136	.88	.5024
FPM Volume	3	.2755	.0918	2.61	.1462

Figure 1. Comparison of day 7 mean (\pm 1 SE) FPM volumes on unglazed ceramic tiles per treatment. Mean \pm 1SE. Horizontal lines show results of orthogonal contrasts. The uppermost horizontal line represents contrast 1. The middle horizontal line represents contrast 2. The lower horizontal line represents contrast 3. Contrast 1 tested for a large consumer effect by comparing the exclusion treatment with the other three treatments. Contrast 2 tested for a stoneroller effect by comparing the enclosure to the cage control and open baskets. Contrast 3 tested for a cage effect by comparing the cage control to the open baskets. NS= not significant.

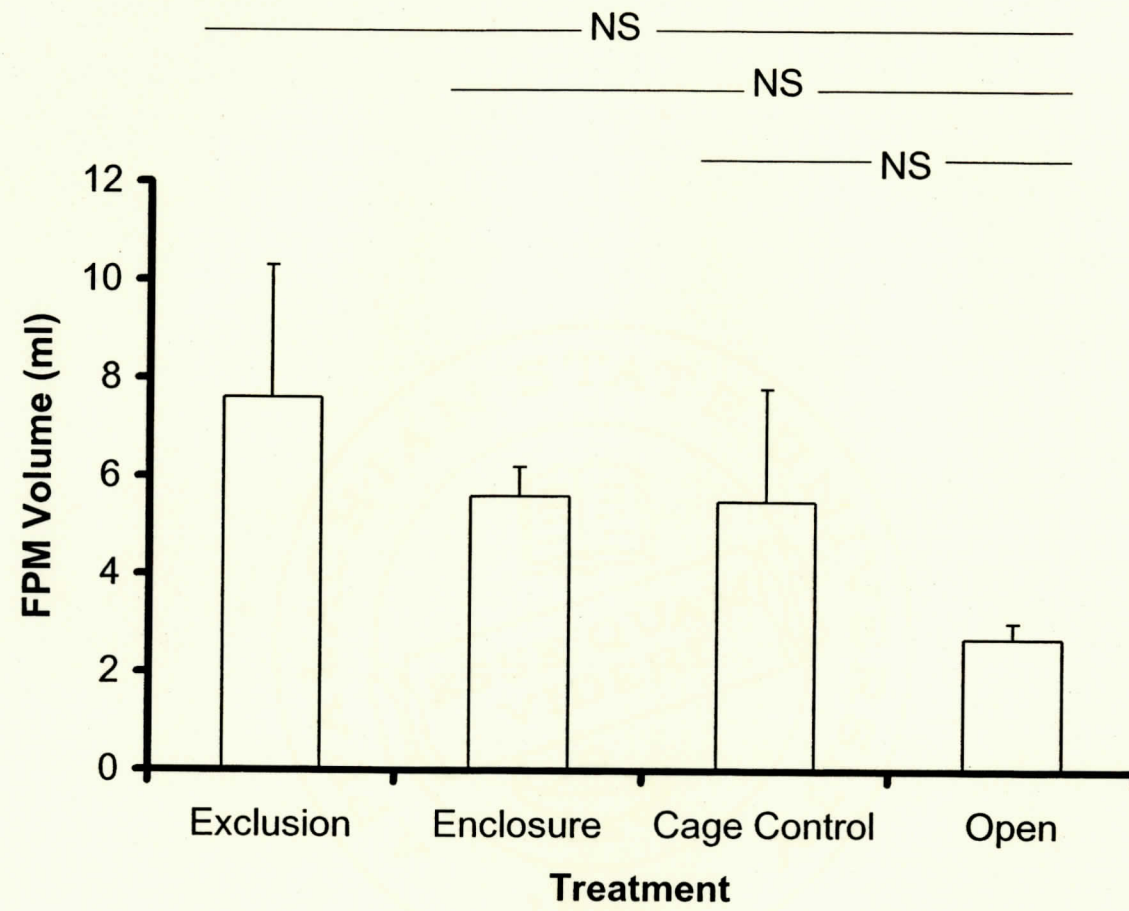


Figure 2. Comparison of day 7 mean (± 1 SE) numbers of harpacticoid copepods per treatment in cobble contained in baskets. Horizontal lines show results of the orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.

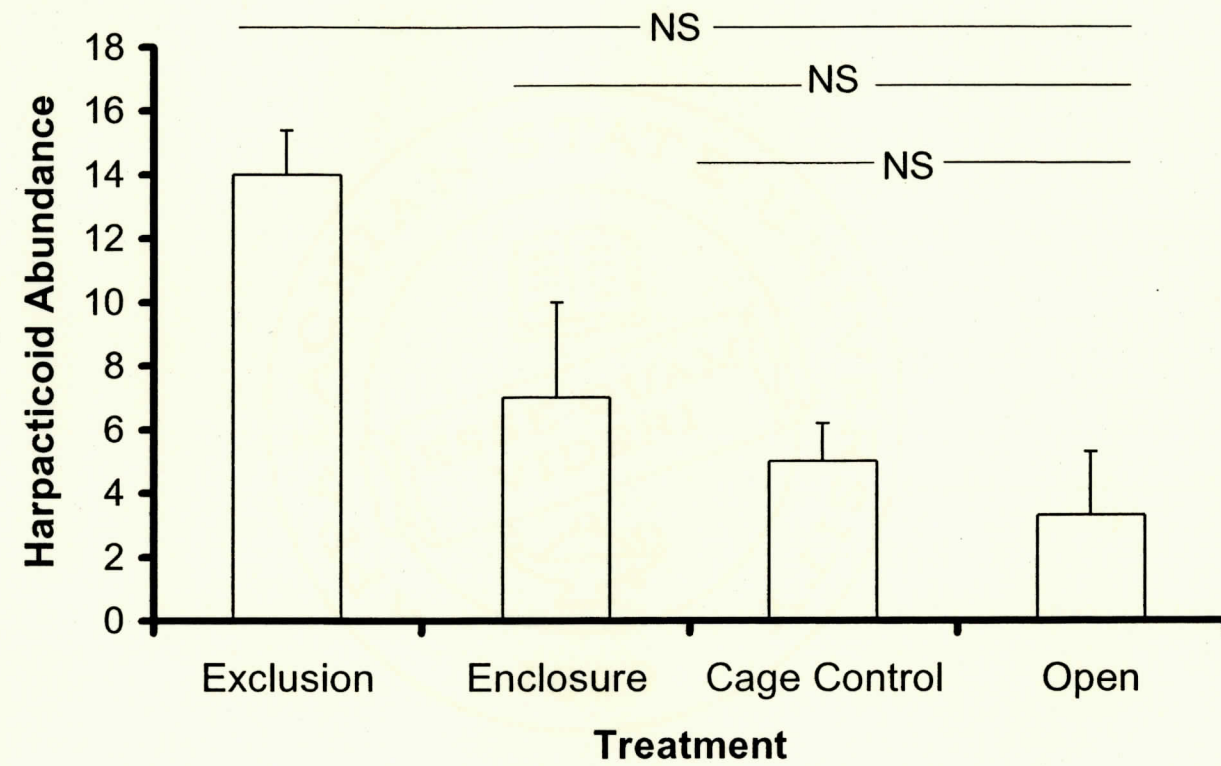


Table 2. Eigenvectors for the dominant macroinvertebrate taxa and FPM volume from the day 14 basket samples for the first 3 principle components (PC).

Variable	PC1	PC2	PC3
Chironomidae	.3264	.3277	-.1399
Hydropsychidae	.3406	.1008	-.3554
Tipulidae	.1036	.6843	-.3554
Harpacticoid	-.3151	-.0743	.4148
Baetidae	.2508	.3857	.0721
Elmidae	.3052	-.0965	.3514
Planorbidae	.3786	.0870	.1098
Heptageniidae	-.2813	.3369	-.0629
Ephemerellidae	.3619	-.1483	.2250
Pleurobanchia	.3018	-.1553	.4672
FPM Volume	-.2585	.2887	.4904

effect was found ($F= 7.71, p= 0.0176$) (Table 3). All three orthogonal contrasts were significant for the data from PC1.

Individual univariate ANOVAs indicated significant treatment effects for chironomids, hydropsychid caddisflies, harpacticoid copepods, FPM volume, and total macroinvertebrates. Tipulids, and heptageniid mayflies exhibited marginally significant responses to treatments. ANOVA results for numbers of baetid mayflies, elmids beetles, limpets, aquatic mites (acaria), leptophlebiid mayflies, and pleurobranchs were all nonsignificant (Table 4).

Day 14 samples of FPM volume amounts were significantly higher in the exclusion treatment compared to the other three treatments ($F=19.89, p= 0.0043$) (Figure 3). The enclosure had approximately 3X the FPM as the enclosure. There were significantly fewer macroinvertebrates in the exclusion treatment compared with the other three treatments ($F= 12.65, p= 0.0117$). The enclosure treatment contained significantly fewer macroinvertebrates compared to the cage control and open basket treatments ($F= 22.25, p= 0.0033$). There was also a significant cage effect; the cage control contained significantly fewer macroinvertebrates than the open basket treatment ($F= 9.62, p= 0.0211$) (Figure 4). There was no significant treatment effect on taxon richness.

There were several taxa that showed significant responses to treatments in the day 14 samples. Chironomids were approximately 3.5X more abundant in the open baskets than in the exclusion and enclosure treatments, and 2X more abundant in the open basket treatment than in the cage control. All three contrasts were significant (Figure 5).

Table 3. Results from the ANOVA on PC 1. Data were from the day 14 basket samples. Contrast 1 tested for a large consumer effect by comparing the exclusion treatment with the other three treatments. Contrast 2 tested for a stoneroller effect by comparing the enclosure to the cage control and open baskets. Contrast 3 tested for a cage effect by comparing the cage control to the open baskets.

Source	df	Sum of Squares	Mean Square	F	p
Block	2	2.1759	1.0879	.59	.5817
Treatment	3	53.0259	17.6753	9.65	.0103
Contrast 1	1	18.7116	18.7116	10.21	.0187
Contrast 2	1	12.2234	12.2234	6.67	.0416
Contrast 3	1	22.0908	22.0908	12.06	.0133
Error	6	10.9919	1.8319		

Table 4. ANOVA results showing the effects of treatment for the 14 most dominant macroinvertebrate taxa, total macroinvertebrates, and FPM volume in the day 14 basket samples.

Dependent Variable	df	Sum of Squares	Mean Square	F	p
Chironomidae	3	.7217	.2406	15.07	.0034
Hydropsychidae	3	5.5234	1.8410	12.78	.0051
Tipulidae	3	.4245	.1415	4.41	.0581
Harpacticoid	3	1.2273	.4091	8.99	.0123
Baetidae	3	.8645	.2882	1.01	.4511
Elmidae	3	.5986	.1995	1.14	.4064
Planorbidae	3	.7919	.2639	5.01	.0451
Heptageniidae	3	.3464	.1155	3.22	.1037
Ephermerellidae	3	1.0789	.3597	3.53	.0882
Limpet	3	.3369	.1123	.32	.8110
Mite	3	.2329	.0777	.31	.8195
Leptaphlebiidae	3	.2039	.0679	1.29	.3617
Cyclopoid	3	1.4413	.4804	6.43	.0265
Pleurobanchia	3	.5367	.1789	1.18	.3936
FPM Volume	3	.4062	.1354	7.48	.0188
Total Macroinvertebrates	3	.5739	.1913	15.0	.0034

Figure 3. Comparison of day 14 mean (± 1 SE) FPM volumes on unglazed ceramic tiles per treatment. Mean ± 1 SE. Horizontal lines show results of orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.

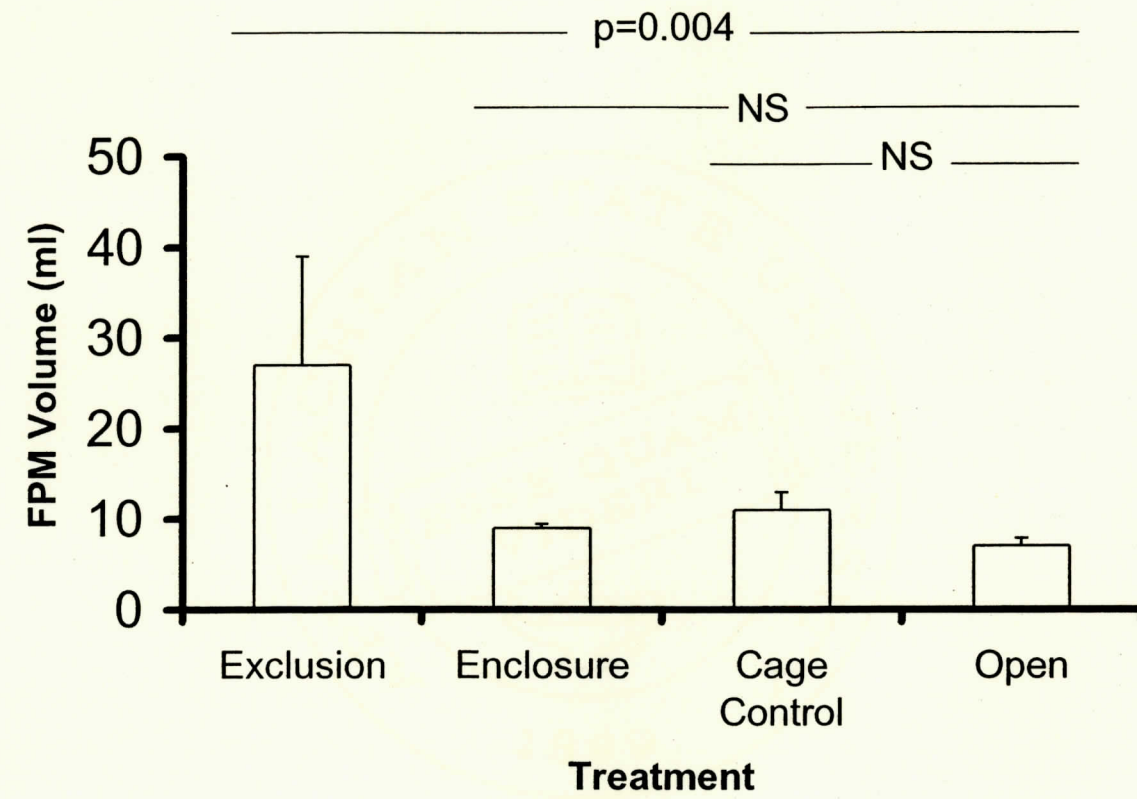


Figure 4. Comparison of day 14 mean (\pm 1SE) number of total macroinvertebrates per treatments in the baskets. Horizontal lines show results of the orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.

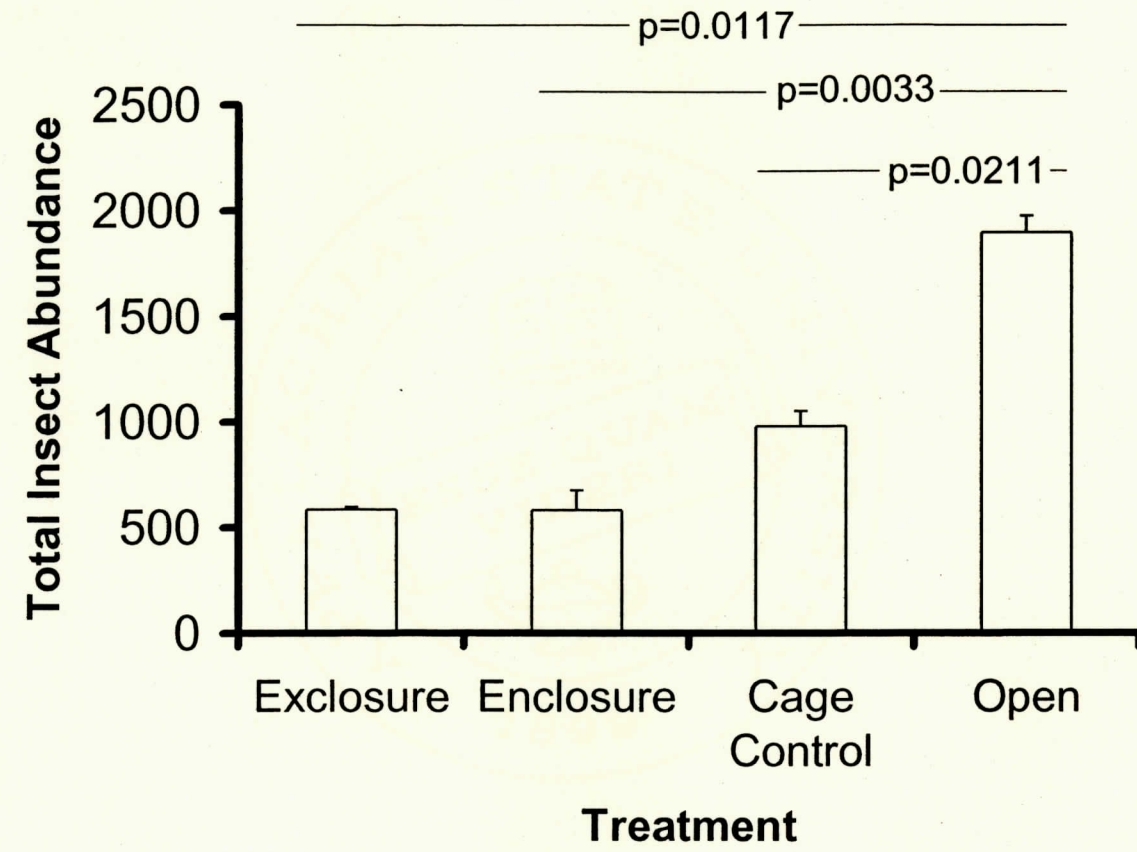
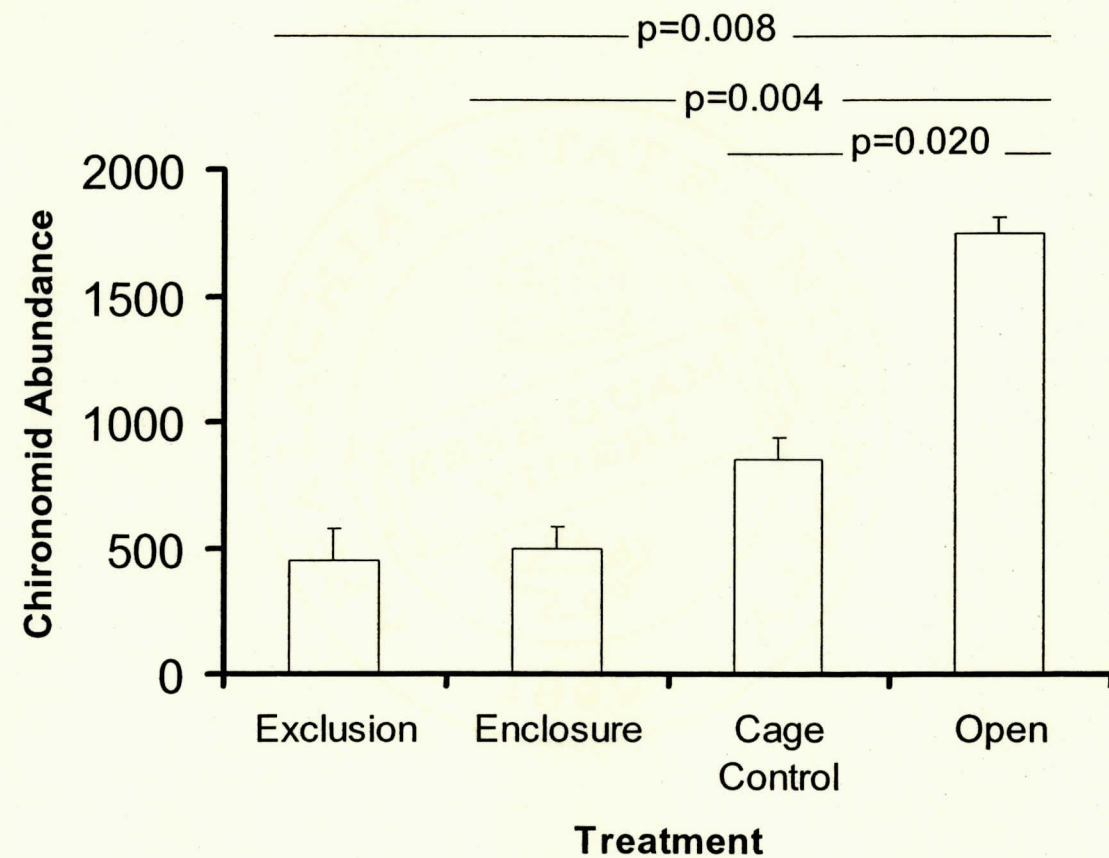


Figure 5. Comparison of day 14 mean (± 1 SE) numbers of chironomids per treatment in cobble contained in baskets. Horizontal lines show results of the orthogonal contrasts. See legend of Figure 1 for explanation of contrasts. NS= not significant.



Hydropsychid caddis flies were almost completely absent when all large consumers were excluded. Very few were observed in the stoneroller enclosure and cage control treatments. However, they were abundant in the open basket treatments. All three contrasts were significant in the 14-day samples (Figure 6).

Harpacticoid copepods were more abundant in the day 14 samples when all large consumers were excluded (Figure 7). There was a significant difference between the exclusion treatment and the other three treatments ($F= 8.96$, $p= 0.0072$), and the cage control compared to the open basket treatment ($F= 15.88$, $p= 0.0072$). There was no significant difference between the enclosure and the cage control and open basket treatments (Figure 7).

There were marginally significant overall treatment effects for both tipulids and heptageniids in the day 14 samples. There was a significant difference in tipulid numbers between the enclosure treatment and the cage control and open basket treatments ($F= 13.00$, $p= 0.0113$) (Figure 8). There were significantly less tipulids in the enclosure treatment than the other three treatments. No other contrasts were significant for tipulids (Figure 8). Heptageniids were most abundant when all large consumers were excluded. There was a significant difference between the enclosure treatments and the other three treatments ($F= 9.24$, $p= 0.0228$) (Figure 9). No other contrasts were significant for heptageniids.

Figure 6. Comparison of day 14 mean (± 1 SE) numbers of hydropsychid caddis flies per treatment in cobble contained in baskets. Horizontal lines show results of the orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.

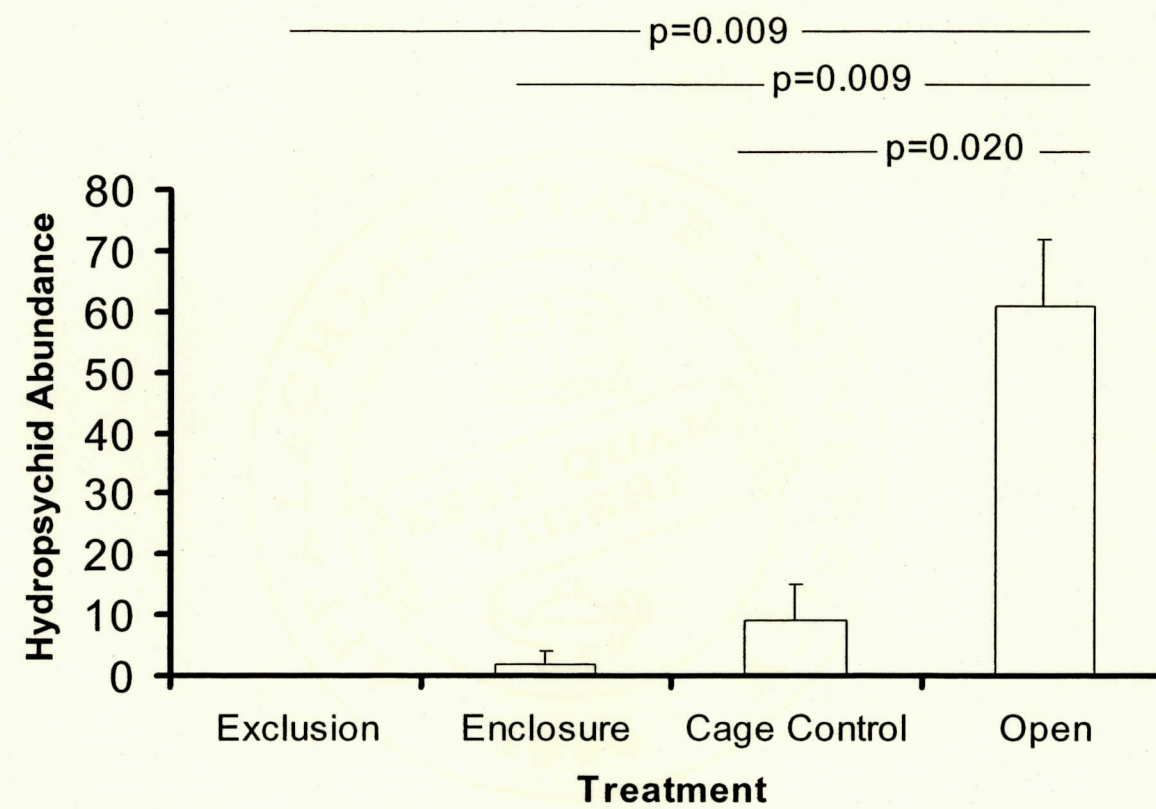


Figure 7. Comparison of day 14 mean (± 1 SE) numbers of harpacticoid copepods per treatment in cobble contained in baskets. Horizontal lines show results of the orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.

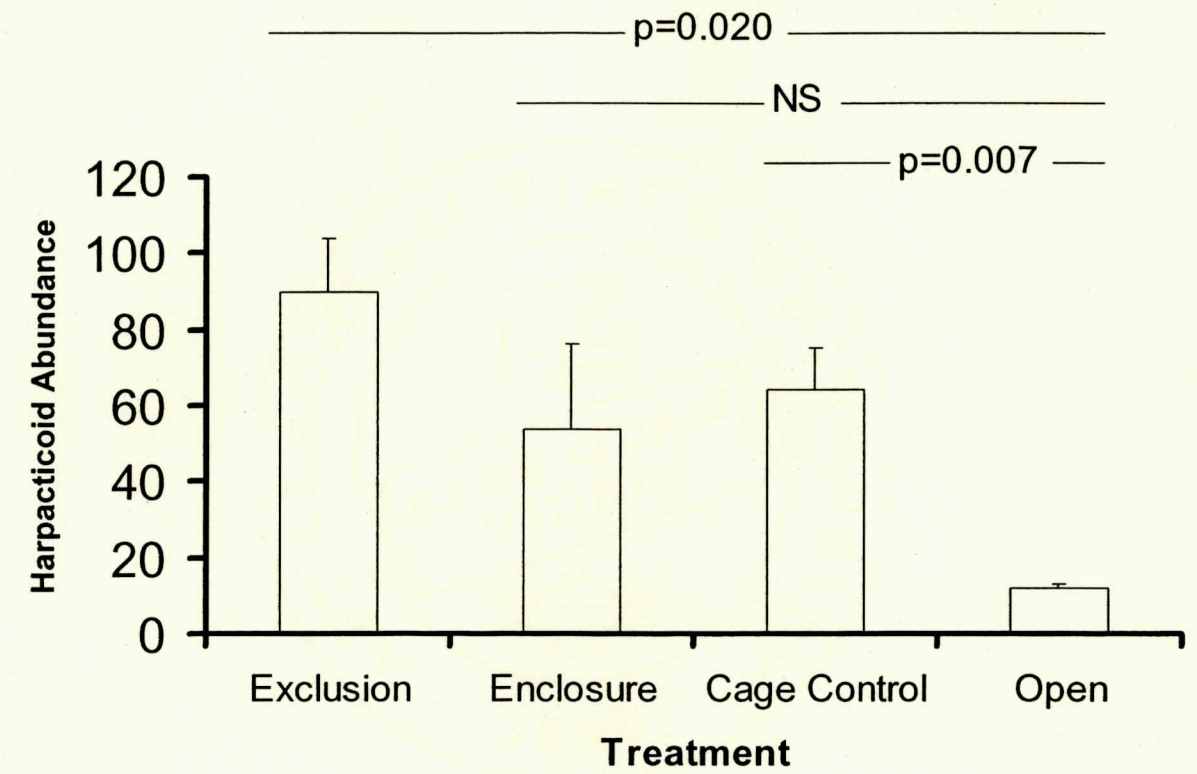


Figure 8. Comparison of day 14 mean (± 1 SE) numbers of tipulids per treatment in cobble contained in baskets. Horizontal lines show results of the orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.

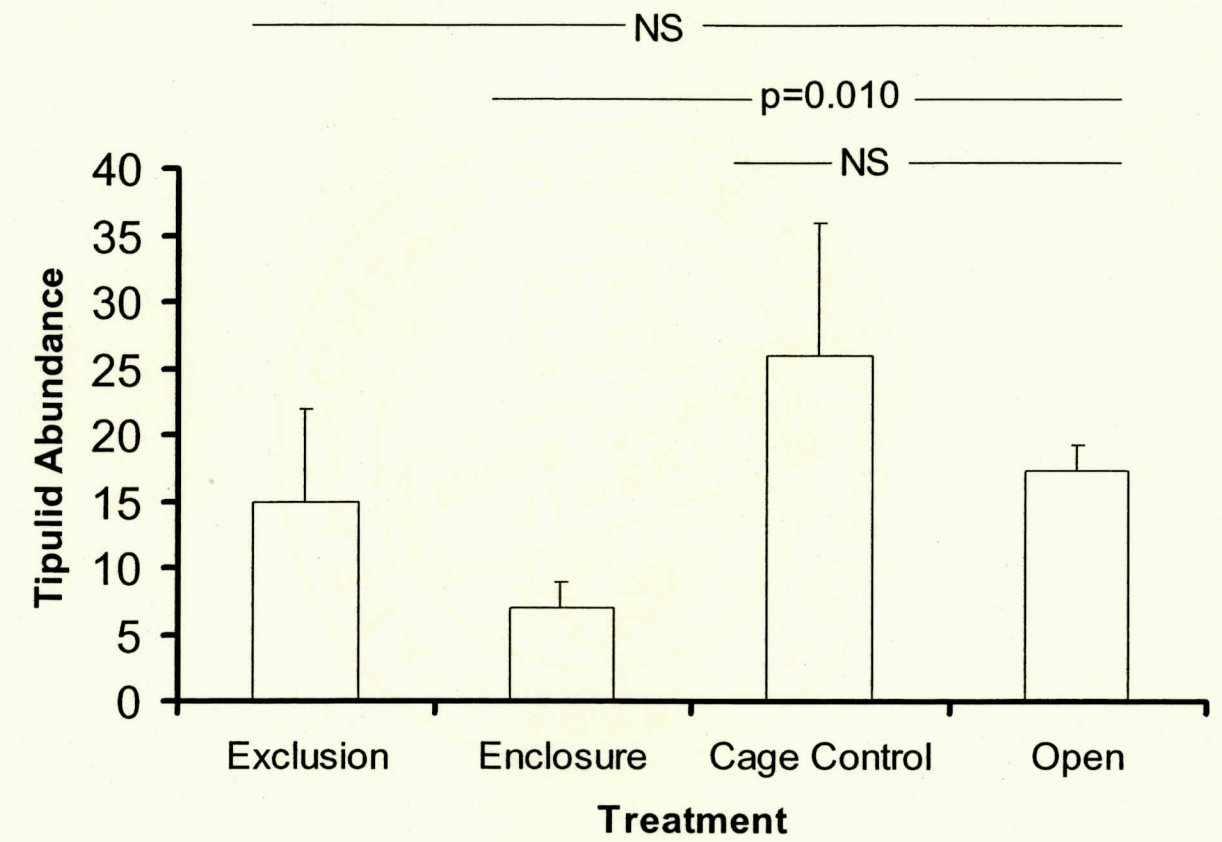
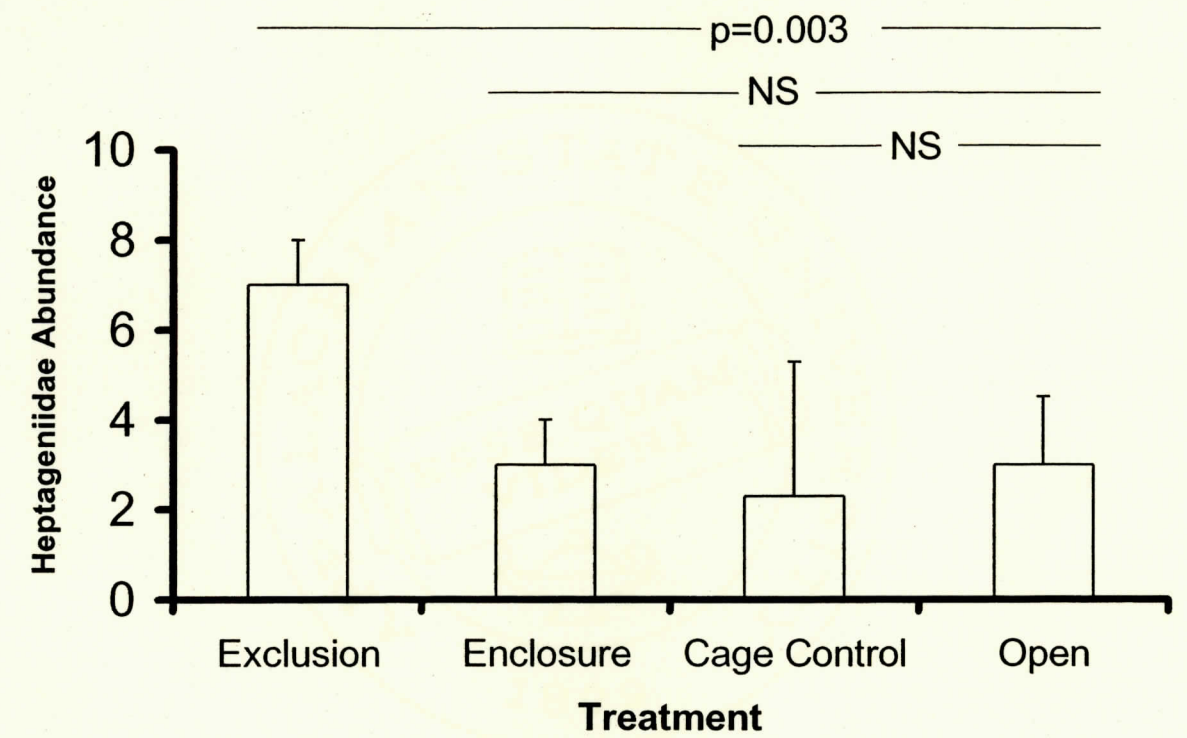


Figure 9. Comparison of day 14 mean (± 1 SE) numbers of heptageniid mayflies per treatment in cobble contained in baskets. Horizontal lines show results of the orthogonal contrasts. See legend for Figure 1 for explanation of contrasts. NS= not significant.



Gut Contents

Stonerollers collected in 2003 contained essentially only sediments in their guts. There were a few hydropsychid thoracic segments and one chironomid head capsule observed in one fish. No vegetation or detritus were present in the guts. The percent composition of the gut contents showed an overwhelming dominance of sediments (mean= 99.9%, sd=0.71, n= 51). All of the stonerollers collected contained sediment in their stomachs. Less than 2% contained insect material (Figure 10).

Stonerollers collected in 2004 showed more variation in their gut contents, although, as in the 2003 sample, essentially all of the stomach contents consisted of sediment (97.9%, sd= 4.6, n=28). One hundred percent of the stonerollers contained sediment in their guts. Eighteen percent of the stonerollers contained insect material. Chironomid head capsules were the main insect components observed. Almost 15% of the stonerollers had identifiable detritus in their guts, while only 3.7% contained green vegetation (Figure 11).

Bluehead chubs consumed detritus, riverweed, and a variety of macroinvertebrates including elmids, tipulids, and copepods. The northern hogsucker consumed mainly insects. Hydropsychids, ephemereids, and copepods were the dominant prey items of northern hogsuckers. Rockbass consumed insects, crayfish, and fish. Sculpins guts contained mainly insects, and, in one case, a fish.

Figure 10. Mean (\pm 1SD) gut contents for *C. anomalum* in 2003. Values are percentages of total gut contents.

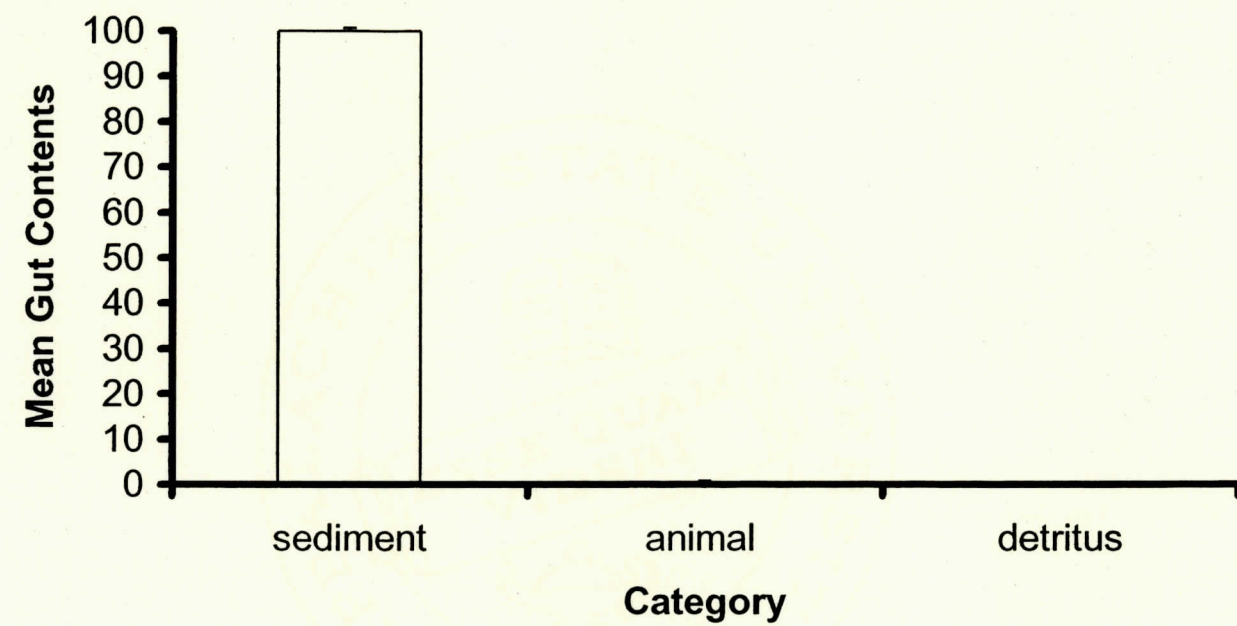
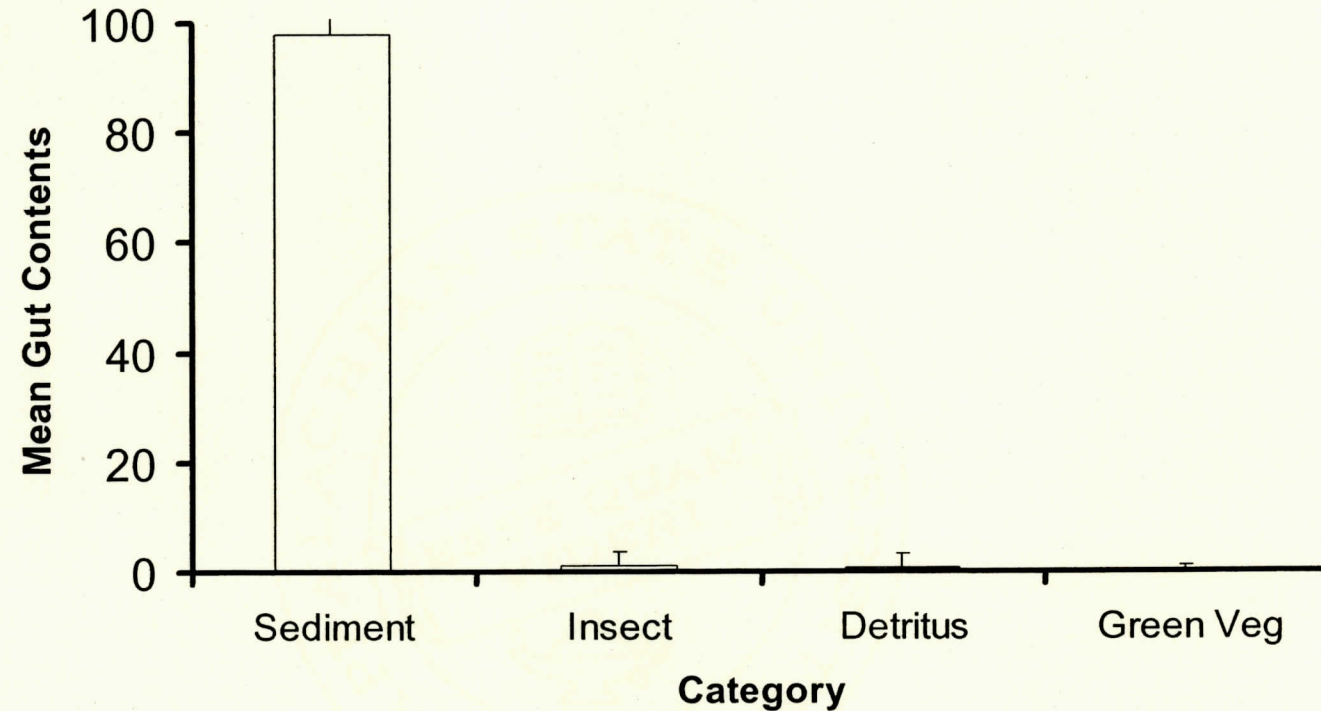


Figure 11. Mean (\pm 1SD) gut contents for *C. anomalum* in 2004. Values are percentages of total gut contents.



Stable Isotopes

Stonerollers collected in 2003 had a higher $\delta^{15}\text{N}$ signature (mean= 10.77, sd=0.39) than hydroptychids (mean =7.64, sd= 0.12) and chironomids (mean= 5.58, sd=0.15). The difference in $\delta^{15}\text{N}$ signatures between stonerollers and hydroptychids is slightly over 3 ppt. Stonerollers also had an enriched $\delta^{13}\text{C}$ signature (mean= -19.54, sd= 1.31) compared to both hydroptychids (mean= -23.79, sd= 0.1) and chironomids (mean= -22.04, sd= .19) (Figure 12).

In 2004, the $\delta^{15}\text{N}$ ratio of the stonerollers was comparable to 2003 (mean= 10.25, sd= 0.30). Hydroptychid caddisflies were also comparable to 2003 (mean= 7.90, sd= 0.12). Algae had the lowest $\delta^{15}\text{N}$ ratio out of all samples (mean=0.50, s.d.= 0.1). Sediment had a $\delta^{15}\text{N}$ ratio in between algae and insects (mean= 4.99). Rockbass had the highest $\delta^{15}\text{N}$ signature (mean= 12, sd= 0.92). The $\delta^{15}\text{N}$ signature of stonerollers was comparable to those of with northern hogsuckers (mean=10.97, sd= 0.18), bluehead chubs (mean=10.41, sd=0.64), and sculpins (mean= 10.85, sd= 0.45) (Figure 13). However, stonerollers had the highest $\delta^{13}\text{C}$ signature (mean= -19.38, sd= 1.56).

Figure 12. Mean (± 1 SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for stonerollers and potential food items in 2004. Mean. Values are the amount of the isotope in the sample compared to a standard. See text for an explanation of how this ratio is derived.

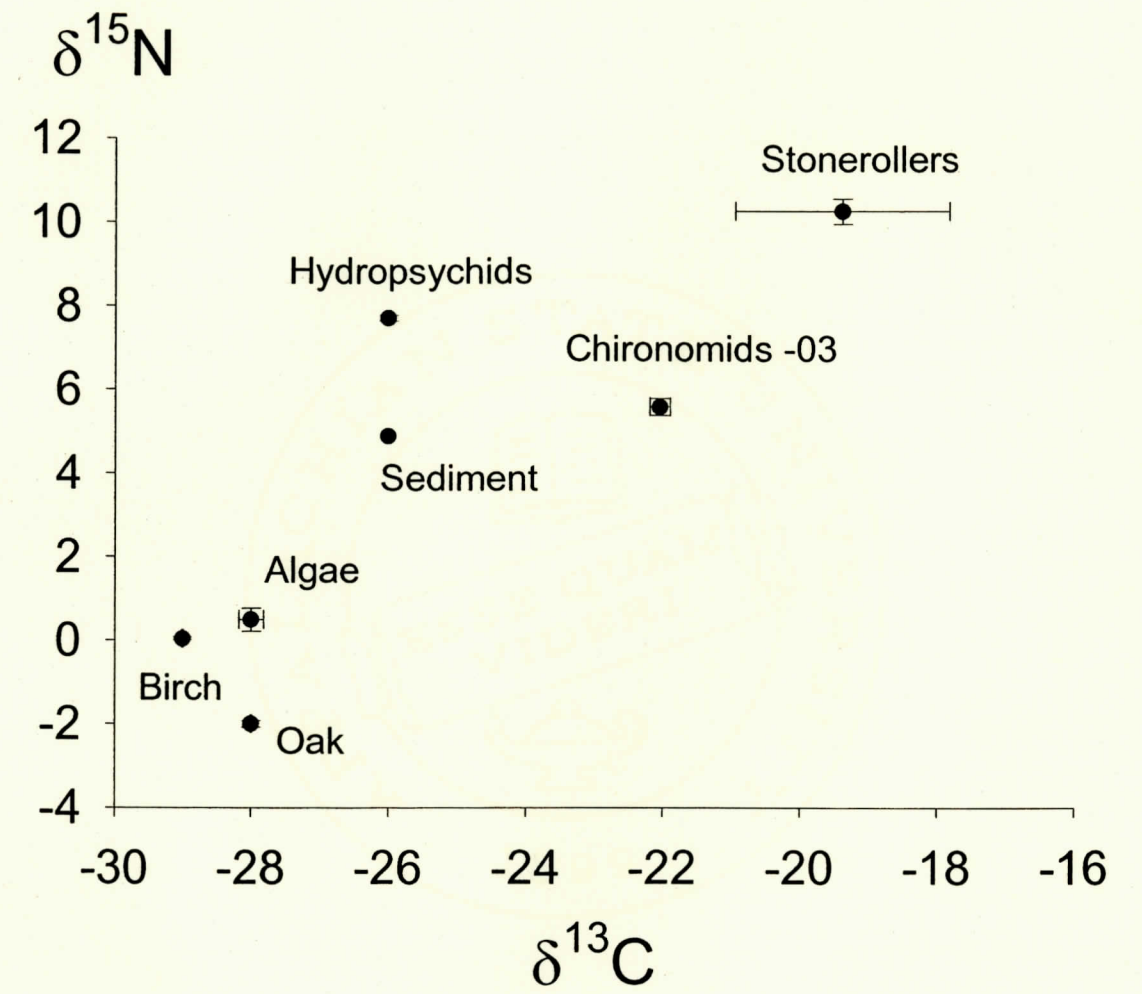
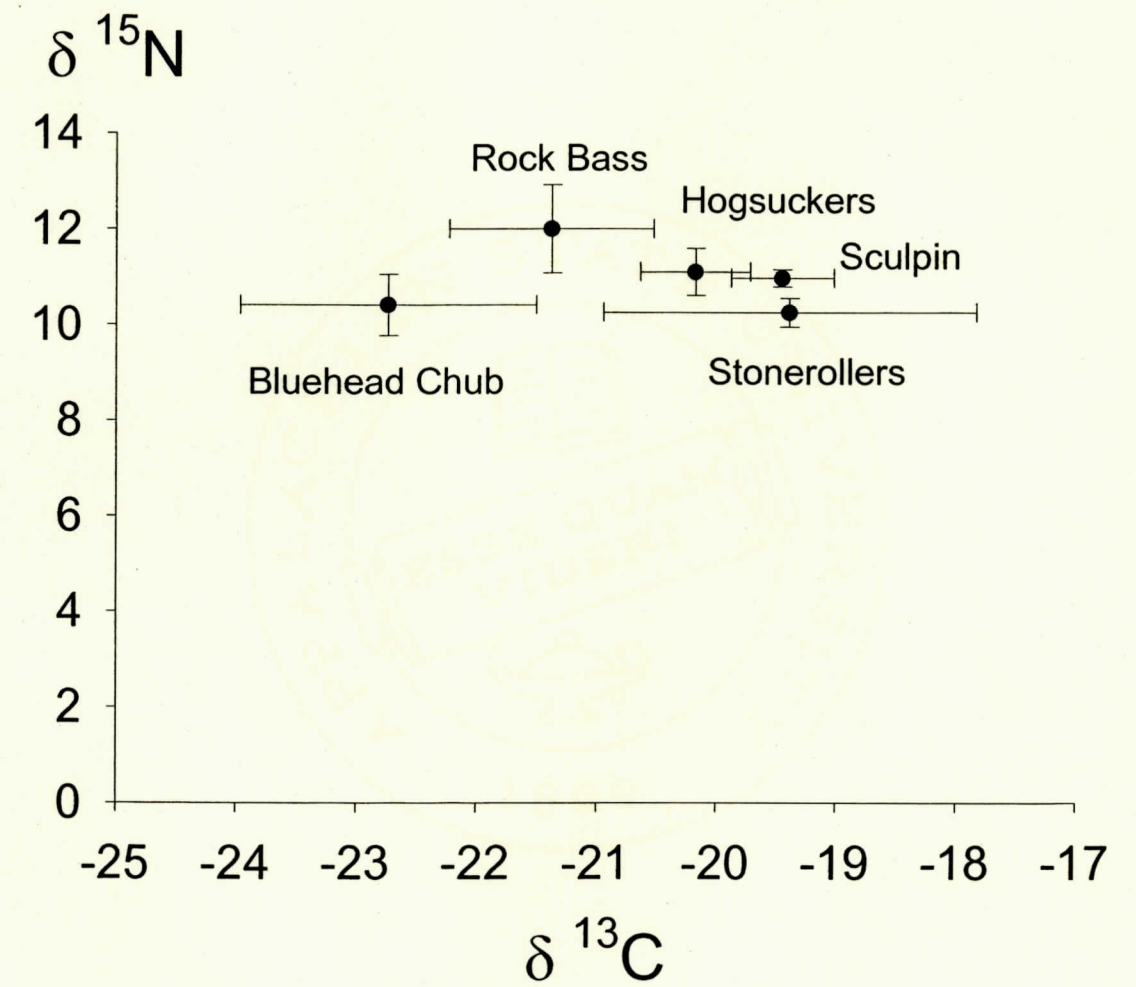


Figure 13. Mean (± 1 SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for stonerollers, northern hogsuckers, sculpin, bluehead chub, and rockbass in 2004. Values are the amount of the isotope in the sample compared to a standard. See text for an explanation of how this ratio is derived.



DISCUSSION

Effects of Central Stonerollers on Sediment Accumulation

The central stoneroller significantly reduced sediment accumulation on substrata during the two-week field experiment. Baskets in treatments with no large benthic consumers were completely covered in sediments. When central stonerollers were enclosed in cages the baskets were significantly cleaner. In the cage control and open baskets there was a similar amount of sediment compared to the stoneroller enclosure treatments. This suggests that central stonerollers were driving the decrease in sediment observed when all large benthic consumers were allowed to access the baskets. Therefore, they act as allogenic ecosystem engineers in the South Fork of New River during low flow and in between droughts. The South Fork of the New River had low discharge during the two-week experiment. During periods such as low flow and in between droughts, stonerollers seem to impact sedimentation accrual and macroinvertebrates most. Ewing (2002) also showed a dramatic decrease in sediment on substrata when central stonerollers were present. Gelwick et al. (1997) noted that substrate in the presence of stonerollers was silt free, and that in their absence silt accumulated. Other than Ewing (2002), this is the only study that has quantified the ability for temperate benthic fish to reduce sediment on substrata. My results are similar to those of studies that documented that tropical fish act as ecosystem engineers via

bioturbation (Power 1990, Flecker 1996). These studies showed that tropical benthic-feeding fish can keep substrata free of sediment. Flecker (1996) conducted his experiment on anadromous fish during the drought season in tropical streams. This is comparable to the central stonerollers effect between high flow events in a temperate stream described in my study.

Central stonerollers may be less dramatic and subtler in their ability to alter ecosystems compared to other described ecosystem engineers (e.g., beavers). However, the potential exists for system wide effects as opposed to localized effect due to the widespread distribution and high densities of central stonerollers. Central stonerollers are also schooling fish, which may increase the ability for localized sediment removal. Past research has shown that predators can alter central stoneroller behavior, which may influence the spatial distribution and patterns of sediment removal. Power et al. (1985) showed that these fish tend to aggregate in shallow stretches of river to avoid predators. In streams with bass, central stonerollers will leave deeper pools and congregate in shallow stretches ≤ 20 cm in depth (Harvey et al. 1988). Central stonerollers also tend to stay out of areas ≤ 10 cm deep, probably to avoid terrestrial predators (Power et al. 1985). Therefore, the impacts of stonerollers on sediment may be less in deeper stretches of river inhabited by predatory fish. Ewing (2002) noted that the crayfish are active at night and enter the deeper pools. Crayfish also act as ecosystem engineers in the South Fork of the New River via bioturbation (Helms and Creed 2005). They may re-suspend sediment in the deeper pools that central stonerollers avoid, resulting in similar effects in deep stretches to the central stoneroller in shallow stretches of river. Thus, crayfish may act as

a functional analog to the central stoneroller in deeper water at night when predators are present.

Strong (1992) states that systems with high diversity (e.g., tropical and temperate streams) should remain stable and not be affected by an individual species. The central stoneroller was shown to have a strong effect on sediment accumulation. No other taxa removed amounts of sediment comparable to the central stoneroller. In temperate headwater streams where species richness is low, crayfish may be the main bioturbators (Creed and Reed 2004, Helms and Creed 2005). As stream order increases, species richness increases allowing for more redundancy in function (Helms and Creed 2005). Crayfish, large aquatic insects, and benthic feeding fish may all have similar roles in engineering ecosystems in higher order streams via bioturbation (Helms and Creed 2005). This increase in functional redundancy along an environmental gradient has been termed "role diffusion" (Helms 2000). This diffusion of roles as stream order increases makes isolating the effects of an individual taxon difficult. If an organism has no functional equivalent and the organism's density is manipulated, change should occur (Ehrlich and Walker 1998). The central stoneroller was shown to have significant effects on sediment in shallow stretches of river between spates. Helms and Creed (2005) showed that crayfish and stonerollers both affect sediment accumulation. My experiment suggests that stonerollers have the dominant effect on sediment accumulation in the South Fork of the New River among taxa. I should point out that the central stoneroller densities in the enclosures were approximately 2.5-5x greater than natural densities in the stream. Thus, the strong stoneroller effect on sediment observed in the enclosures may be due in part to the higher densities in this treatment.

The synergistic effects of stonerollers and crayfish mentioned in Ewing (2002) were not seen in this experiment. The similar amounts of sediment observed in the stoneroller enclosure treatment compared to the cage control and open basket treatments suggest the stoneroller is the main bioturbator in this experiment. If crayfish and other benthic-feeding fish were acting synergistically with stonerollers then the cage control and open baskets would have contained significantly less sediment compared to the enclosure. However, this does not suggest that crayfish are not engineering habitats via bioturbation in this stream. They may in fact be functionally redundant but separated spatially and temporally or may simply have a weaker effect.

Effects of Central Stonerollers on Macroinvertebrates

Ecosystem engineers can have both positive and negative effects on other organisms in their communities (Jones et al. 1994, 1997). Central stonerollers had a mixture of effects on several macroinvertebrates in this experiment. Harpacticoid copepods were negatively affected by stonerollers. This is most likely a result of reductions in sediments. Harpacticoids live in interstitial spaces within fine sediment (Thorpe and Covich 1991). Sediment removal by the central stonerollers decreased preferred habitat and negatively affected harpacticoids. This was similar to the results of Creed and Reed (2004) and their investigation of crayfish as bioturbators.

Heptageniid mayflies were also negatively affected by stonerollers. Results from another experiment showed an increase in Heptageniid mayflies with decreased sediment (Creed and Reed 2004). Heptageniids are mainly scrapers that obtain the majority of their food from the periphyton layer on cobble substrate (Cummins and Klug 1979).

Covering substrata with sediment may decrease the periphyton layer and has been suggested to discourage Heptageniid colonization (Creed and Reed 2004). In my study, these insects were more abundant in the absence of stonerollers, which means they were more abundant in habitats with more sediment. These results suggest a potential for predation by the central stoneroller. Thus, even though stonerollers are reducing sediment and creating a habitat that heptageniids appear to prefer they may also be preying on these mayflies and reducing their abundance.

Several organisms showed a mixture of effects; a positive sediment effect and a negative stoneroller effect. Chironomids were more abundant in the open baskets. Past studies showed a positive correlation between chironomid abundance and FPM volume (Creed and Reed 2004, Helms and Creed 2005). In my study, chironomids were more abundant in the treatments with less FPM. The short duration of my experiment may explain this result. Previous studies reported results from field experiments that ran from 6 to 8 weeks (Creed and Reed 2004, Helms and Creed 2005). In these studies, there may have been sufficient time for sediments to accumulate and be colonized by chironomids that prefer sediment. Chironomids normally found on cobbles in the New River may not like lots of sediment, which would explain why their numbers were greater on cobbles in the open basket.

Hydropsychid caddisflies were uncommon in exclusion treatments and central stoneroller enclosure treatments. They were very common in the open baskets. These insects are filter feeders and increased sediment accumulation on substrata may prevent them from successful filter feeding. However, when enclosed with central stonerollers they were uncommon although FPM levels were significantly reduced. When all large

consumers were allowed access hydropsychids were very common. The lower density of central stonerollers feeding in the cage control and open basket treatments may have influenced this distribution. This suggests a mixed result. Hydropsychids may prefer substrate with less sediment, but their numbers may be reduced when stoneroller densities are high. There also seems to be a cage effect with hydropsychids. This is probably due to reduced current velocities, which also results in greater sediment accumulation.

The mixture of results observed with macroinvertebrates may be explained in part by the trophic analysis of the central stoneroller. Traditionally, central stonerollers were thought of as algivores (Evans-White et al. 2001). Evans-White et al. (2001) demonstrated that they may be insectivores using stable isotope analysis. However, no experimental data were obtained to describe effects on macroinvertebrate communities. My investigation of gut contents showed an overwhelming preference for sediment. Sediment contains fine particulate organic matter, diatoms, and bacteria, all of which could be potential energy sources for the stoneroller. Insects and insect parts were rare in stoneroller gut, as were detritus and green vegetation. However, analyzing the natural abundances of ^{13}C and ^{15}N of the central stoneroller, their potential prey items, as well as associated fish taxa that are known to be piscivores and insectivores, in addition to gut contents, gives a more robust estimate of food preferences and trophic dynamics. Traditionally, trophic analyses were based on just gut content analysis. The disadvantage of gut content analysis is that it simply provides a snapshot of dietary choices and does not integrate temporal diet information. Stable isotope analysis can give an estimation of

preferred food items over time and provides information on which food items are actually assimilated by an organism and not incidentally consumed (Pinnegar and Polunin 1999).

Stable isotope analysis suggests stonerollers are consuming macroinvertebrates. Stonerollers are enriched in ^{15}N within the range suggestive of consuming hydropsychids and chironomids. Isotopic N signatures were also similar to known insectivorous fish (e.g., hogsuckers, sculpins). Thus, the mixed effects that were observed in the field experiment may indeed be a combination of a positive effect due to sediment removal and a negative effect due to predation.

Sediment, Central Stonerollers, and Community Structure

Data from this study suggest that stonerollers are influencing their community by acting as ecosystem engineers. Stonerollers act as ecosystem engineers by keeping sediment levels low on substrata. Lenat et al. (1981) showed that increased sediment loads can decrease species richness in North Carolina streams. Sediment is a non-point pollutant that has the ability to dramatically alter habitat and productivity (Parkhill and Gulliver 2002). Sediment occurs naturally in streams but increased destruction of riparian habitat can greatly increase sediment loads in freshwater systems (Lenat et al. 1981).

Minshall (1984) showed that macroinvertebrate abundance was positively correlated with substrate size heterogeneity. This suggests that the more heterogeneous a stream bottom is with respect to substrate, the greater the abundance and diversity of aquatic macroinvertebrates. Large amounts of sediment decrease stream substrate

heterogeneity, which is a form of habitat degradation for benthic macroinvertebrates.

Many benthic macroinvertebrates forage on the surface of stones and utilize interstitial spaces between larger stones as a refuge from predation and/or high flow events (Minshall 1984). Lemly (1982) showed a dramatic decrease in aquatic macroinvertebrates in Cullowhee Creek, NC, as sedimentation increases due to logging. Inorganic sediment was shown to reduce heterogeneity of substrate and reduce interstitial living space. In another study conducted in a laboratory, artificial streambeds were treated with varying amounts of sediment. McClelland and Brusven 1986 showed a negative correlation between aquatic insect survival and the degree of embeddedness of cobble substrate. They also showed that when macroinvertebrates could not access the bottom of cobble substrate their likelihood of survival decreased. Rutherford and Mackay (1986) showed a decrease in successful pupation in a caddisfly species with increased sedimentation due to sediment clogging up the pupal case and decreasing respiration. Many caddis species pupate on the underside of rocks. Increased embeddedness of cobble substrate due to excess sedimentation may smother pupating caddis preventing successful pupation.

Lenat et al. (1979, 1981, 1988) have extensively investigated the effects of sedimentation on stream macroinvertebrates in North Carolina. Lenat et al. (1979) summarized the effects of sedimentation on macroinvertebrates; First, with small amounts of sediment the density of benthic organisms will decrease due to loss of habitat, but the species composition of the community may not change. Second, greater sedimentation that results in a dramatic reduction in substrate heterogeneity (i.e., from a

cobble-gravel substrate with patches of silt and sand to a sand and silt substrate) will alter the species composition of the community.

Various stream taxa have the ability to keep sediment levels low on large substrata (e.g. crayfish, insects, frogs, benthic-feeding fish) (Hill and Knight 1987, Power et al. 1990, Flecker 1996, 1997, 1999, Zanetell and Peckarsky 1996, Creed and Reed 2004, Helms and Creed 2005). An increase in sedimentation rates due to anthropogenic activities may decrease the effectiveness of these taxa to remove sediment from substrate. Increased destruction of riparian habitats through urban development on the South Fork of the New River may have dramatic effects on the amount of sediment entering the system. As riparian habitats become less of a buffer against incoming sediments, sedimentation rates are going to increase in the stream. It is possible that at some point sediment inputs into a stream will overwhelm the ability of bioturbators to reduce it. Future research needs to be focused on this issue.

A decrease in riparian habitats due to extensive urban development may also alter the frequency and intensity of high flow events. A combination of greater sediment loadings and increased high flow events may outweigh the ability for stonerollers to influence communities. Frequency and intensity of disturbances can influence community structure (Connell 1978). Historically, the South Fork of the New River was considered a mesic groundwater system (Poff and Ward 1989). Biotic processes should play a dominant role in structuring the community in these systems (Poff and Ward 1989). My research and those of others (e.g. Helms and Creed 2005) suggests that this is the case currently. However, this system appears to be in the process of becoming flashier due to anthropogenic activities, particularly increased urbanization in the

watershed. Poff and Ward (1989) hypothesized that in a flashy system a community is mostly structured by abiotic factors, especially frequent disturbances. This suggests that the South Fork of New River could be shifting from a system in from a system in which biotic interactions are important in determining community structure to one with primarily abiotic control of community structure.

Increased sedimentation and high flow events may have a negative impact on stoneroller populations. These disturbances may decrease stoneroller densities in the South Fork of the New River affecting their ability to decrease sediment accrual and consume macroinvertebrates on a system wide scale. In natural conditions, this fish may be a key component structuring macroinvertebrate communities in temperate streams by acting as an ecosystem engineer and through predation in between high flow events. Anthropogenic disturbances may reduce the impact stonerollers have in temperate stream ecosystems. Preservation of riparian habitat and maintaining populations of ecologically important species like stonerollers will maintain species diversity and promote stream function.

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BIOGRAPHICAL SKETCH

Chris Wood was born in Wilmington, NC on February 6, 1976. His family moved to Charlotte, NC while he was an infant. He then attended grade school at St. Anne Catholic School. He graduated in 1994 from South Mecklenburg High School. The following August he began his freshman year at Montreat College in Montreat, NC on a baseball scholarship. An injury abruptly ended his baseball season in the spring of 1995 and then he decided to transfer to Appalachian State University where he obtained a B.S. in May 2000. He spent the following summer employed by NC State University as a field technician. The following fall he was hired by the NC State Museum of Natural Sciences where he stayed for one year. In August of 2002 he began his Master's Degree at Appalachian State University. He was awarded his degree in May, 2005.

Chris is a member of the NC American Fisheries Society and the North American Benthological Society. His parents, Mr. and Mrs. Richard T. Wood live in Wilmington, NC. He is married to Mrs. Nancy Wood and they live in Foscoe, NC.