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presented by

Robert Payson Creed Jr.

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of the requirements for

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THE DIRECT AND INDIRECT EFFECTS OF OMNIVOROUS CRAYFISH ON STREAM BENTHIC COMMUNITIES

By

Robert Payson Creed Jr.

A DISSERTATION

Submitted to
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ABSTRACT

THE DIRECT AND INDIRECT EFFECTS OF OMNIVOROUS CRAYFISH ON STREAM BENTHIC COMMUNITIES

By

Robert Payson Creed Jr.

Species associations in communities may best be understood if interactions between constituent taxa and rare or excluded species are evaluated. In this dissertation I demonstrate that the positive association between large crayfish, several micrograzer taxa and microalgae in a Michigan stream is the result of crayfish excluding the dominant alga (Cladophora) from deep water habitats.

In Augusta Cr., Cladophora was very abundant in shallow water but rare in water deeper than 20 cm. Two different invertebrate communities were found in these two habitats. Shallow, Cladophora-covered rocks were dominated by filter-feeders, mobile micrograzers and deposit-feeders. The deep, Cladophora-free rocks were dominated by various mobile and sessile micrograzer taxa.

Field experiments demonstrated that large crayfish, which were more abundant in deeper water, were excluding Cladophora and many invertebrate taxa associated with the alga from the deep water habitat. Laboratory predation trials found that invertebrates which were associated with large crayfish were largely invulnerable to crayfish predation. Cladophora was also found to inhibit the colonization of substrata by microalgae (primarily diatoms) which are a major food item for many micrograzer taxa. Together, these data demonstrate that large crayfish are indirectly facilitating several micrograzer taxa by excluding Cladophora from deep substrata. This is

a selective, indirect facilitation, however, as only those micrograzers that are invulnerable to crayfish can benefit from the increase in microalgal resources. Crayfish have negative direct and indirect effects on sessile filter-feeders and deposit-feeders. Thus, crayfish can influence both the taxonomic and functional structure of benthic communities.

Preliminary experiments in a nearby stream, Sevenmile Cr., suggest that the interaction between crayfish and Cladophora may not be as strong in cooler water. This may result in a breakdown in the indirect facilitation between many micrograzers, particularly sessile taxa, and crayfish.

Dedication

This dissertation is dedicated to my family for encouraging and supporting the interests of a young naturalist, even when it meant cleaning fish,

and to

the late Dr. Charles Jenner (UNC-Chapel Hill)
who introduced me to the invertebrate world
and taught me to "admire and appreciate" its wonders.

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Many land owners granted me access to sections of streams during this research. I am particularly grateful to Mrs. H. Nagel (and later Mr. Tim Earl), Mr. Frank Snyder, and Mr. G. Hendricks. The Departments of Zoology and Entomology provided the microscopes. Steve

Kohler kindly allowed me to use his water temperature data from Sevenmile Creek.

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Chapter One

INTRODUCTION

"When we try to pick out anything by itself, we find it hitched to everything else in the universe." John Muir

One of the fundamental issues in community ecology concerns the processes by which communities are organized. Two opposing points of view exist which can be traced to the works of Gleason (1926) and Elton (1933) from the early part of this century (McIntosh 1960, 1985, Roughgarden 1989). Gleason (1926) believed that the structure of communities was simply the result of the vagaries of dispersal in conjunction with environmental variability, i.e., that a community is a random association of populations whose presence is the result of dispersal into a patchy environment. Interactions between resident and newly arriving species were not thought to influence the establishment of the latter. Gleason referred to this as the individualistic view of community organization. While Gleason developed his ideas in response to Clements' organismic conceptualization of communities (McIntosh 1960, 1985) they also contrast with those of Elton (Roughgarden 1989). Elton (1933) contended that only a subset of the species that can possibly disperse to a site are represented in the community, the idea of "limited membership." The concept of limited membership implies that members of a community have properties that allow them to coexist with one another. Species unable to coexist with one or more of the established species will be excluded from the community or at least

not be very abundant. Limited membership also implies that non-random associations between species may develop since the properties of a species that allow for coexistence may be effective with some taxa but not all. Gleason accounted for non-random associations but attributed them to the non-random locations of source pools of immigrants. The major difference between these two conceptualizations of community structure is that one invokes interspecific interactions as the primary mechanism that structures communities and produces interspecific associations (Elton 1933) while the other does not (Gleason 1926).

There is a problem with the above dichotomy, however, and that is that these two processes are largely indistinguishable at the within community level. Properties that allow species to coexist, for example, the development of anti-predator behaviors by prey species (Sih 1987), may result in weak or even no interactions between co-occurring species. The absence of strong interactions among constituent species does not allow us to distinguish which process is involved in producing these interspecific associations. Consequently, simply looking at the species present <u>in</u> a community, particularly abundant species, and their interactions may provide little insight into how communities are structured with respect to these alternative processes (Roughgarden 1989).

A more fruitful approach would be to examine the species that do not occur in a community (or at least are not very abundant) as their absence may be indicative of very strong interactions with established members of the community. In other words, it is the species <u>not</u> in the community or those confined to a refuge that may hold the key to understanding a community's structure. The absence of these species

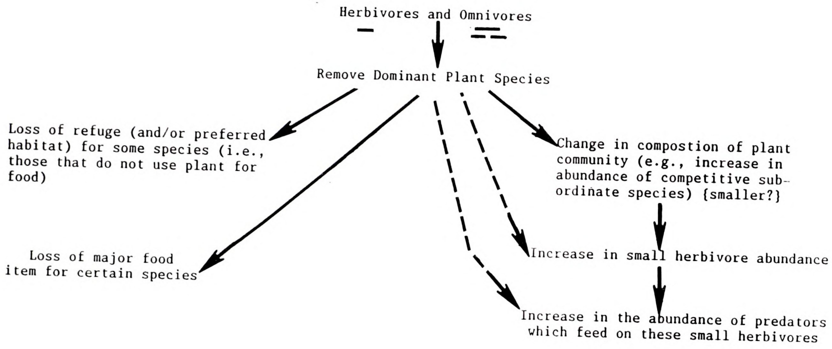
may point to strong interactions with established constituent species in the community. The indirect effects that emanate from these strong interactions may then illuminate previously unseen connections between species (or groups of species) that otherwise do not appear to interact and explain these species associations.

This idea can be illustrated as follows. Sampling a number of habitats may result in finding that species A and C are commonly associated as are B and D. Neither pair of species appear to be competing or engaged in a predator-prey relationship. If species pairs A and B, and B and C interact directly, with A having a strong negative effect on B, and B in turn having a strong negative effect on C, then the exclusion of B from the habitat by A results in a net positive effect for C and a positive association between A and C. Similar interactions could account for the association between B and D if they both interact with either A or C. Thus, it is possible to have positive, non-random associations between species that do not interact directly but are indirectly linked through intermediate, but excluded, species. If little or no response is observed in species C to either an increase in B when A is removed, or increases in A, then the conclusion that the community is not structured by interspecific interactions may indeed be valid. An important key to addressing the question of how communities are structured, then, lies in assessing whether the indirect effects generated by rare or excluded species are important.

Strong plant-herbivore interactions are one type of key interaction that has the potential to influence community structure through a variety of indirect effects, especially if the herbivore selectively excludes the competitively dominant plant species (Figure 1). As

Figure 1. Potential indirect consequences of the removal of the dominant plant species by a large herbivore (solid lines) or a large omnivore (both solid and dashed lines).

Figure 1.


Herbivores and Omnivores
Remove Dominant Plant Species
Loss of refuge (and/or preferred habitat) for some species (i.e., those that do not use plant for food)
Loss of major food item for certain species
Change in compostion of plant community (e.g., increase in abundance of competitive subordinate species) {smaller?}
Increase in small herbivore abundance
Increase in the abundance of predators which feed on these small herbivores

competitive dominance in plants is often a function of size, removal of significant amounts of dominant plant biomass may only occur when the herbivore is also large. This can be the consequence of the increased functional response of a larger herbivore and/or the fact that small herbivores may not be physically capable of removing or ingesting the tissue of a large plant. This is not to say that small herbivores are always unimportant (e.g., outbreaks of insect pests, immature plants may be vulnerable to smaller herbivores etc). For the following discussion, though, I wish to explore a situation where small herbivores are having an inconsequential effect on the dominant plant species.

First, removal of the competitive dominant(s) can result in an increase in the amount of space and/or nutrients available for colonization by less competitive plant species, with the large herbivore functioning as a keystone species (Paine 1966, 1980). Subsequent to this change in the species composition of the primary producer trophic level, one would anticipate increases in the abundance of herbivores which feed on these less competitive plant species. Thus, the grazing of the large herbivore can result in an indirect facilitation of coexisting herbivores (e.g., McNaughton 1976), i.e, a positive association between species that do not interact directly. A second consequence of the removal of the competitively dominant plant is a change in the physical structure of the community. The structure created by the dominant plant may be utilized as a refuge by various organisms (Crowder and Cooper 1982) or as a preferred habitat for foraging or reproduction. This effect would be more important if there are pronounced differences in plant size and/or architecture (Connell and Slatyer 1977, Futuyma 1983 and

references therein). Finally, large herbivores will be engaged in exploitative competition with those herbivores that also feed on the dominant plant species and these taxa would be anticipated to decline in abundance with the removal of the competitive dominant. Note the strong similarity in this series of interactions to the effects of predators on sessile invertebrates (Paine 1966, 1974, Connell and Slatyer 1977). Herbivory and predation on sessile animals should be viewed as similar sorts of interactions despite the differences in trophic levels involved.

The above interactions will be modified to some extent if the large herbivore is actually an omnivore (Figure 1). In addition to the effects described so far, omnivores will further modify the community by excluding certain species that might otherwise benefit from the changes in community structure resulting from herbivory (dashed lines in Figure 1). The implication is that taxa invulnerable to predation by the large omnivore, or at least invulnerable life stages of these taxa, would be positively associated with a large omnivore.

While the influence of large herbivores on the abundance and species diversity of plants has received considerable attention over the last half century from terrestrial plant ecologists (e.g. Tansley and Adamson 1925, Gillham 1955, Thomas 1960, Buechner and Dawkins 1961, Thomas 1963, Laws 1970, Lock 1972, Harper 1977 and references therein, McNaughton 1976, Davidson et al. 1984, Brown et al. 1986), and more recently by marine and freshwater ecologists (Lubchenco 1978, Wharton and Mann 1981, Power and Mathews 1983, Power et al. 1985, Lodge and Lorman 1987, Feminella and Resh 1989, Feminella et al. 1989, Power et al 1989), few studies of large herbivore - plant interactions

have evaluated the consequences of this interaction for the remainder of the community. In some cases, the effect on other plant species was investigated (e.g., Tansley and Adamson 1925, Lubchenco 1978) but rarely were the responses of other trophic levels evaluated (but see McNaughton 1976, Davidson et al. 1984, Brown et al. 1986). The results of the above studies, when considered within the context of the interaction network described in Figure 1, suggest that interactions between plants and large herbivores are the potential focus of widespread indirect interactions in many communities.

STRONG PLANT-HERBIVORE INTERACTIONS IN STREAMS

Historically, ecologists have viewed stream communities as being structured primarily by abiotic factors such as floods and droughts (Barnes and Minshall 1983). However, four features of stream communities suggest that strong plant-herbivore interactions could play an important role in structuring these communities. (1) First, these systems are strongly substrate oriented, with many organisms living and feeding in and around the surface of the substrate (Hynes 1970, Minshall 1984). Consequently, any factor that influences the nature of the substrate with respect to food availability, physical structure of the habitat etc. should have a strong effect on the distribution and abundance of the many benthic organisms associated with the substrate. (2) Second, considerable differences exist in the size and morphology of the dominant plant taxa, the attached algae, especially on larger substrates (e.g., gravel, cobble, boulder). They range in size from small, unicellular diatoms to large, filamentous forms which may exceed a meter in length. Different suites of animals

are found associated with these different algal growth forms (Pentelow 1937 cited in Whitton 1970, Blum 1957, Neel 1968, Whitton 1970). Filamentous algae are often inhabited by filter-feeders and fine particulate feeders (Blum 1957, Dudley et al. 1986, Creed pers. obs.). Animals capable of browsing on the epiphytes attached to the algal filaments may also be present (Creed, pers. obs.). Substrates free of filamentous algae are often covered with a layer of diatoms and fine particles of detritus, which serves as a food for a suite of small insect and gastropod grazers (Hynes 1970, Gregory 1983, Bott 1983, Lamberti and Moore 1984). (3) Third, the herbivores vary considerably in size, from small insect larvae and limpets to large fish and crayfish. (4) Finally, there appear to be positive correlations between both the size of the plant eaten and herbivore size (see Gregory 1983, Bott 1983), and plant size and competitive ability (e.g., Blum 1957).

Together, these four features of streams suggest that large, stream-dwelling herbivores would strongly influence community structure. Specifically, removal of the dominant macroalga should 1) lead to an increase in the abundance of epilithic microalgae, increasing resources for micrograzers, 2) change the physical structure of the substrate, removing an important habitat for many macroinvertebrates, and 3) remove an important food resource (the macroalga) for certain taxa (compare with Figure 1). Thus, changes in the structure and taxonomic composition of the substrate algae resulting from the activities of a large herbivore could have a pronounced effect on much of a stream's benthic community and might account for many of the observed patterns of species distributions and interspecific associations.

DISSERTATION OUTLINE

This dissertation addresses the consequences of a strong plant - herbivore interaction for stream communities. Specifically, I explore the direct and indirect effects of omnivorous crayfish on the distribution and abundance of benthic algae and macroinvertebrates in two, small, Michigan streams. In the next chapter, I describe the patterns of distribution and abundance of a crayfish (*Orconectes propinquus* Girard), other abundant macroinvertebrates, both by taxon and functional group, and *Cladophora glomerata* (L). Kütz, a large, filamentous green alga in Augusta Creek. In chapter three, I present the results of experiments that demonstrate that crayfish grazing determines *Cladophora* abundance in Augusta Cr. and that *Cladophora* effects the abundance of smaller algae, primarily epilithic diatoms. Chapter four examines the indirect effects of crayfish grazing on other benthic macroinvertebrates. Also, I demonstrate how crayfish predation can further influence habitat utilization by vulnerable invertebrate taxa. The potential influence of stream temperature on this set of interactions is explored in chapter five where I present the results of a study in Seven Mile Creek, a watershed adjacent to the Augusta Creek drainage.

Chapter Two

PATTERNS OF DISTRIBUTION AND ABUNDANCE OF THE CRAYFISH *Orconectes propinquus*, THE ALGA *Cladophora glomerata*, AND BENTHIC MACROINVERTEBRATES IN AUGUSTA CREEK.

INTRODUCTION

Large herbivores and omnivores are a common component of many tropical and temperate streams (Crocker and Barr 1968, Hynes 1970, Lippson 1975, Power 1983, 1984, 1987, Power and Mathews 1983, Power et al. 1985). They can be herbivorous (or omnivorous) crustacea such as crayfish and crabs (Crocker and Barr 1968, Hynes 1970, Lippson 1975) or fish from various families, e.g., Cyprinidae, Loricariidae (Hynes 1970, Power 1983, 1984, 1987, Power and Mathews 1983, Power et al. 1985). Crayfish appear to be the most common and most abundant large herbivore/omnivore in Michigan streams (Lagler and Lagler 1944, Lippson 1975). Herbivorous fishes, e.g., stonerollers (*Campostoma anomalum*), are uncommon. This was confirmed by a search through the fish collection records of the Michigan Department of Natural Resources for several drainages in southern Michigan. Stonerollers were found primarily in river systems in the extreme southern portion of the state (e.g., Towns 1984, 1985) and rarely were they ever very abundant. Thus the large herbivore/omnivore on which I focused my attention was the crayfish *Orconectes propinquus*, the most common crayfish in Michigan (Lagler and Lagler 1944, Lippson 1975) and a common inhabitant of streams throughout the state (Lagler and Lagler

1944, Lippson 1975, Creed, pers. obs.).

While certain species of aquatic macrophytes (e.g., *Valisneria*, *Potomageton*) are occasionally found in the stony-bottomed streams of Michigan, the most common, large aquatic plant found in this habitat is the filamentous alga *Cladophora glomerata* (Blum 1957, Creed pers. obs.). The aquatic macrophytes are more common in areas of slower current velocity and finer particle size. Whereas swifter currents will uproot macrophytes, *Cladophora* appears to thrive under such conditions, often tolerating currents in excess of one meter a second (Creed, pers. obs.). The genus *Cladphora* has a world-wide distribution and representatives are found in both lotic and lentic habitats where this species is capable of covering most, if not all, of the available substrate (Blum 1957, Whitton 1970, Wong and Clark 1976, Biggs and Price 1987). *Cladophora* is common in the streams and lakes of the Great Lake drainage basin (Blum 1957, Bellis and McLarty 1967, Wong and Clark 1976, Wolfe and Sweeney 1982, Creed, pers. obs.).

These two common species, *Orconectes propinquus* and *Cladophora glomerata*, would thus appear to be the most likely candidates for the players in a strong plant-herbivore interaction in the small streams of Michigan. However, do they show patterns of distribution and abundance that would suggest that they strongly interact? And do other stream organisms show complementary patterns of distribution and abundance that suggest that they are responding to this interaction? I will first describe the natural history of both species and the major study sites in the Augusta Creek drainage where I conducted my surveys and experiments. I then describe the patterns of distribution and abundance of *O. propinquus*, *Cladophora* and the invertebrates associated with *Cladophora*-covered and *Cladophora*-free substrates in

Augusta Creek.

NATURAL HISTORY OF ORCONECTES AND CLADOPHORA

Natural History of *Orconectes propinquus*

Orconectes propinquus (Girard) is a small to medium-sized crayfish (maximum carapace length of 35 - 40 mm, Crocker and Barr 1968, Lippson 1975) found throughout the Great Lakes region (Crocker and Barr 1968). It is also the most common crayfish in Michigan (Lagler and Lagler 1944, Lippson 1975). *O. propinquus* is commonly found in clear, rocky-bottomed streams or on rocky bottoms of lakes (Crocker and Barr 1968). While at least two other species of crayfish are found in the Augusta Creek watershed (Lippson 1975), *O. propinquus* is the only species found in the stream itself. *Orconectes propinquus* rarely constructs a burrow, a characteristic behavior of many other crayfish taxa. Instead, this species will excavate a small cavity beneath a rock for shelter. As with many crayfish species, *O. propinquus* becomes fairly inactive as water temperatures drop with the onset of winter (Van Deventer 1935). It burrows into the bottom and remains inactive until the water warms up again the following spring. Mating occurs primarily in the late summer/early fall although some matings do occur in the spring (Lippson 1975, Creed, pers. obs.). Shortly after the crayfish start to become active in the spring, the females extrude their eggs onto their pleopods. The female carries the young through the egg stage and their first couple of molts before releasing them (Crocker and Barr 1968). In Augusta Creek, free-living, young-of-the-year (YOY) *O. propinquus* are first present in late

May/early June and are 4.5 mm long (CL = carapace length) (Creed, pers. obs). By the end of the first growing season YOY are between 15 - 20 mm CL and have increased 40 to 60 times in weight (see Appendix D). *Orconectes propinquus* is an omnivore, consuming filamentous algae, detritus, invertebrates, carrion, fish eggs and other crayfish (Capelli 1980, Creed pers. obs).

The Natural History of *Cladophora glomerata*

Cladophora glomerata (L.) Kütz is a large, filamentous, green alga that is commonly found attached to hard substrata in lakes and streams throughout the Great Lakes region (Blum 1957, Bellis and McLarty 1967, Wong and Clarke 1976, Wolfe and Sweeney 1982, Creed, pers. obs.). As the generic name implies, *Cladophora* is a branched alga, and often forms thalli in excess of 1 m in length (Blum 1957, Bellis and McLarty 1967, Wong and Clark 1976, Creed pers. obs.). I have observed thalli that exceed 5 m in length. The filaments are quite tough, with several layers in the cell wall, including a chitinous layer (Wurdack 1923, Whitton 1970). The size of the filaments and the toughness of the cell walls probably reduces grazing on *Cladophora* by most aquatic invertebrates. Furthermore, the large size of the alga probably contributes to its competitive dominance over many co-occurring algal taxa (Kishler and Taft 1970, Whitton 1970 and references therein), as this species can overgrow other taxa and either shade them or inhibit their colonization. However, the surface of *Cladophora* provides substrate for epiphytes and it is often colonized by a number of algal taxa (Whitton 1970). Whitton and other researchers have noticed a uniformity in the floristic composition of the epiphytic community of

Cladophora from site to site (see Whitton 1970). *Cladophora* also provides a habitat for various aquatic animals (Blum 1957, Neel 1968, Dudley et al. 1986) and some researchers have noticed a difference in the fauna associated with *Cladophora*-covered vs. *Cladophora*-free substrates (Pentelow 1937 cited in Whitton 1970, Blum 1957, Neel 1968). *Cladophora* mats are present in Augusta Cr. from April to November. The alga dies back in the winter with only the holdfast remaining. For a comprehensive review of the influence of water chemistry and physical factors such as light, temperature and current velocity on the growth of *Cladophora*, the reader is directed to Whitton's extensive review (1970).

STUDY SITES

The Augusta Creek catchment is located in Kalamazoo and Barry counties in Michigan's lower peninsula. Augusta Creek is a third order stream at its confluence with the Kalamazoo River. The creek is characterized as having a low gradient (1-2%), a fairly stable discharge (USDA 1977), a high pH (8.2), and a high alkalinity (230 mg/l $CaCO_3$) (Mahan and Cummins 1978, see Appendix B). Nitrate-nitrogen levels are fairly high (2-5 mg/l); nitrate enters the stream primarily through groundwater inputs (USDA 1977, Mahan and Cummins 1978). Phosphate phosphorus levels range from 10 - 72 ug/l (USDA 1977, Mahan and Cummins 1978).

While I have qualitatively evaluated the distribution and abundance of *Cladophora* and *O. propinquus* throughout much of the Augusta Creek catchment, I focused most of my sampling efforts at three sites, Nagel's Site (NS), Snyder Site (SS) and Hickory Road Site

(HRS). All of the field experiments were conducted at Nagel's Site. Augusta Creek is a third order stream at both NS and SS. The creek is 7-8 m wide and has an open canopy at both sites. At NS the stream channel has a long run (35 - 45 cm deep) with steep sides and a cobble/gravel bottom for approximately 50 m above the bridge. Below the bridge the stream again is a run but with alternating shallow (15 - 25 cm deep) and deep (25 - 45 cm deep) sections. The substrate is almost entirely cobble/gravel although some areas of sand/gravel bottom are present. Scattered beds of macrophytes (Valisneria sp. and Potamogeton sp.) are also present.

Snyder Site has a more complicated channel morphology with two channels above the bridge and two channels below as well. The main channel above the bridge has a cobble/gravel/sand bottom which becomes cobble/gravel from 20 m upstream of the bridge to the bridge. Midchannel water depths in this region range from 30 - 40 cm. Immediately beneath and below the bridge is a deep section (40+ cm) after which the stream splits into two shallow (10 cm) riffles. The substrate below the bridge to the bottom of the riffles is cobble/gravel. There is a macrophyte bed off the main channel above the bridge. There is considerably more rock substrate in shallow water (<20 cm) at SS than at NS.

At Hickory Road Site Augusta Creek is a second order stream about 6 m wide with an open canopy. Above the bridge is a shallow run (5 - 25 cm) followed by a small pool (45 cm deep). Below the bridge the stream is a single shallow riffle (<10 cm deep) before it enters a large, deep (100+ cm) pool. Substrate above the pool consists of cobbles on gravel with some macrophytes growing in the openings between the cobbles. Cobbles and larger rocks (>15 cm diam) are

present in the small pool above the bridge. The riffle below the bridge also has a substrate of cobble underlain by gravel.

MATERIALS AND METHODS

Cladophora glomerata

Cladophora was sampled at NS on 3 August and at SS on 6 and 8 September, 1987. While no standardized sampling scheme was employed in 1987, an attempt was made to sample *Cladophora* across a range of depths and current velocities, and at different distances from shore. Percent cover of *Cladophora* on individual rocks was estimated in the stream using a small grid of quarter inch mesh hardware cloth. Small substrates were placed into separate buckets and returned to the lab where *Cladophora* was removed from the upper surface of the rock (entire surface for NS samples, subsample for SS samples) for ashing. The surface area of NS rocks was determined using foil impressions. For immovable substrates *Cladophora* was scraped from a known area and placed into a labeled container. All samples were preserved in 2% Lugols. For each sample, depth, current velocity (at substrate level) and distance to shore were noted. Current velocities were measured using a Scientific Instruments pygmy meter.

Cladophora was sampled at HRS on 28 July 1988 along three transects, two of which were located in the riffle below the bridge and the third was upstream of the bridge. One of the downstream transects was located in midchannel and the other near shore. The upstream transect was located in midchannel and spanned the range of depths in the run and the pool. Transect lines consisted of nylon

ropes that were marked every half meter and were staked down in the stream. Position of transects was determined at random and the points to be sampled along them were determined using a random numbers table. As in 1987 depth, current velocity and distance to shore were recorded for each point. Then the percent cover of Cladophora was determined as before. Rocks were then removed into a dipnet lined with 1 mm^2 mesh, placed in individual buckets and returned to the laboratory where subsamples of Cladophora (three per rock) were removed from known areas for ashing. Again, samples were preserved in Lugols. Invertebrates were also removed from all rocks. All visible Cladophora was removed by eye and then the subsampled area was examined under a dissecting scope to remove any remaining small thalli. Total exposed surface area of the rocks (i.e. above the sediment surface and therefore available for algal colonization) was estimated by measuring the surface with a flexible ruler in 1988.

Blum (1957) demonstrated that there was seasonal variation in the abundance of Cladophora at some sites on the Saline R. in Michigan. Blum (1957) found that Cladophora would decline in abundance 3 - 4 weeks after water temperatures rose above 15^{o} C. He attributed this summer die-off to higher water temperatures. In Augusta Creek, however, Cladophora can be found throughout the summer, at least in shallow microhabitats (Creed, pers. obs., also see results of surveys). To demonstrate that water temperature is not the primary determinant of Cladophora abundance in Augusta Cr. during the summer, I conducted a survey of Cladophora abundance during the summer/early autumn of 1989. Cladophora distribution, measured as percent cover, was evaluated at HRS at roughly three week intervals. HRS was chosen for this survey for two reasons. First, two fairly extensive

(approximately 100 m^2 surface area), shallow (less than 20 cm) riffles occurred adjacent to a deeper pool so that a range of depths could be sampled. Second, current velocities across these two riffles rarely exceeded 40 cm/second at the substrate surface. Since this current velocity is probably not strong enough to dislodge crayfish from the substrate (Maude and Williams 1983), it is unlikely that this factor would restrict crayfish access to the riffles. Nagel's Site was not chosen because only a small portion of the streambed is in water less than 17-20 cm deep, i.e., the shallow habitat is not very extensive. Snyder Site does have fairly extensive shallow riffle habitat but current velocities are much swifter than those at HRS, often exceeding one meter per second.

The 1989 transects at HRS were placed across the shallow and deep areas upstream of the bridge, with a new starting point for the transect selected each time. The transect line was a rope marked off at 0.5 m intervals. Three samples were taken a each point on the rope (at 1 m intervals for the first transect, at 0.5 m intervals for later transects) for 10 points along the rope. The three readings were taken either 50 cm to the right or left of the point or directly beneath the point for a total of 27 - 30 points for each sample date. Percent cover of Cladophora for the rock directly beneath each sample point was estimated as before using a grid of 1/4 inch hardware cloth. After percent cover had been determined, current velocity (at substrate level) was recorded for all central sample points on the transect, i.e., one third of the samples.

All samples of Cladophora collected for AFDW determination were treated in the following manner. Samples with small amounts of Cladophora were filtered onto precombusted, Whatmans GF/F filters while larger quantities of the alga were placed into ceramic crucibles. All samples were dried at 105° C for 24 hours (Vollenveider 1969), cooled in a dessicator and weighed, and then combusted for one and a half hours at 550° C (APHA 1976). Ashed samples were then weighed again after cooling in the dessicator. Filtered samples were weighed on a Cahn C-31 microbalance to the nearest microgram. Crucible samples were weighed on a Sartorius 1265 MP electrobalance to the nearest mg. Ash free dry weights were then converted to grams Cladophora AFDW per m^2 for each rock using the total AFDW for 1987 samples and the mean of the three AFDW subsamples in 1988.

Orconectes propinquus

Crayfish density and distribution samples were initiated in early July 1988 at NS, approximately 2 weeks after YOY became free-swimming, and were taken once a month into the autumn. One intensive sample was taken at HRS on 2 August 1988. For these samples a 0.5 X 0.5 m quadrat sampler that resembled a Surber sampler was used. The device consisted of a square metal frame which rested on the bottom. Attached to the downstream end was a wooden frame (52 X 32 cm) which supported a net made of fiberglass window screen. Long pieces of foam were wrapped around the metal frame and held in place with sheets of window screen fastened with plastic cable ties. This created a tight seal between the sampler and the rugged bottom preventing crayfish from crawling out of the area to be sampled. When employed the device was placed on the bottom and all obvious crayfish on the surface were driven into the downstream net. Then the substrate was turned over to

a depth of 5-10 cm and all remaining animals were washed into the net by rapidly waving a hand over the substrate. Sampled crayfish were then measured for carapace length (CL, defined here as the distance from the tip of the rostrum to the posterior margin of the cephalothorax). (Note: size frequency data and crayfish growth data are discussed in Appendix D). All crayfish gathered on a given sample date were retained in a bucket after being measured and were released after collecting was completed. Since *O. propinquus* is active both day and night (Hay 1918, Van Deventer 1937, Creed pers. obs.), collections were made during the day. In a preliminary survey at NS in 1986 I did not find a significant difference in the number of active large crayfish (i.e., moving about on the surface) per m^2 between night and day samples (day: mean = 2.20, night: mean = 2.67, $t = 0.7390$, df = 14, $p = 0.4721$).

Since observations had suggested that there might be segregation of different sized crayfish by depth, shallow ($\leq$ 20 cm) and deep habitats were compared. In addition, at NS the shallow areas were subdivided into (1) midchannel areas of intermediate to swift currents having cobble substrates and (2) nearshore areas with slower currents and a substrate of cobble/gravel largely covered by macrophyte beds. Substrate in the deeper water was primarily cobble/gravel. These three habitats were sampled using a stratified design. Four samples were taken from each habitat on each date. Points for the center of each sample were selected at random using a set of three ropes which were marked a 0.5 m intervals. Two ropes were run along each bank and stretched across the stream connecting points on the streambank ropes. The first number drawn from a random number table determined the location of the transverse rope on the streambank ropes. The second

number determined the point on the transverse rope that was the point to be sampled. The spot was marked with a small, solid brick. To reduce the potentially disruptive effect of establishing sample points on crayfish, the points were determined the day before sampling. Water depth was determined as the sample was taken (there was a cm scale on the side of the sampler). After all points had been sampled, current velocity and distance to shore were determined for each point. As before, current velocity measurements were taken just above the substrate. The same sampling techniques were used at HRS on 2 August 1988. Only two habitats were present at HRS, 1) shallow, cobble with Cladophora and Potamogeton and 2) deep, cobble/gravel. Crayfish densities (YOY and adults separately) for each habitat at NS were compared using a one-way ANOVA and Tukey's HSD test.

Macroinvertebrates

A survey of the taxonomic and functional structure of the macroinvertebrate community on deep (>20 cm deep) substrates at Nagel's Site was initiated on July 14, 1986. Casual observations of crayfish during the day and night suggested that while large crayfish occasionally will move into shallow water at night, their activity was concentrated in deep water. Furthermore, filamentous algae did not appear to be very abundant on these deep substrates. Thus, I wanted to quantify the abundance of filamentous algae in this habitat and the macroinvertebrates associated with these substrates, and see if either algal abundance or macroinvertebrate distributions (either species or functional groups) changed over the course of the summer.

Three rocks were sampled (except on July 14 when n=2) throughout

July and August and into early September. Rocks were selected at random from the deep section downstream from the bridge at NS and were collected approximately once a week from July 14 - September 5. Rocks were retrieved by placing a dipnet lined with window screen (1 mm^2 mesh size) immediately downstream of the rock. The rock was then placed in the net. The window screen was then unclipped from the net frame and both the rock and the screen were placed in a sealable container containing stream water. Rocks were returned to the lab where all visible Cladophora thalli were counted and then removed under a dissecting scope. Cladophora samples were preserved in 2% Lugols until they were ashed. As Cladophora was not very abundant, samples were filtered onto GF/F filters. Methods for drying and ashing are the same as those described above for Cladophora surveys. All animals were removed by scrubbing the rock with a stiff nylon bristle toothbrush and preserved in 70% ethanol. Animals were later identified to the lowest taxonomic level (usually genus, species if possible) under a dissecting scope. Rock surface area was determined by making a foil impression of the exposed surface of the rock. This impression was then cut and flattened and area was determined by dividing up the impression into several geometric shapes, determining their area and then summing these together (note: these impressions were later run on the leaf area meter and the results of both methods were very similar). As mentioned in the section on Cladophora surveys, animals were removed from all rocks sampled for the survey of 28 July 1988 at HRS. Methods for removing and processing animals were the same as those just described for 1986. Finally, the density of the snail Goniobasis was determined during one of the Cladophora surveys at HRS in 1989. Densities of Goniobasis are often

considerably lower than those of the other invertebrates, thus it needed to be sampled on a larger scale. I quantified the abundance of Goniobasis using a 0.2 x 0.2 m quadrat at the same points where I sampled Cladophora.

RESULTS

Cladophora glomerata

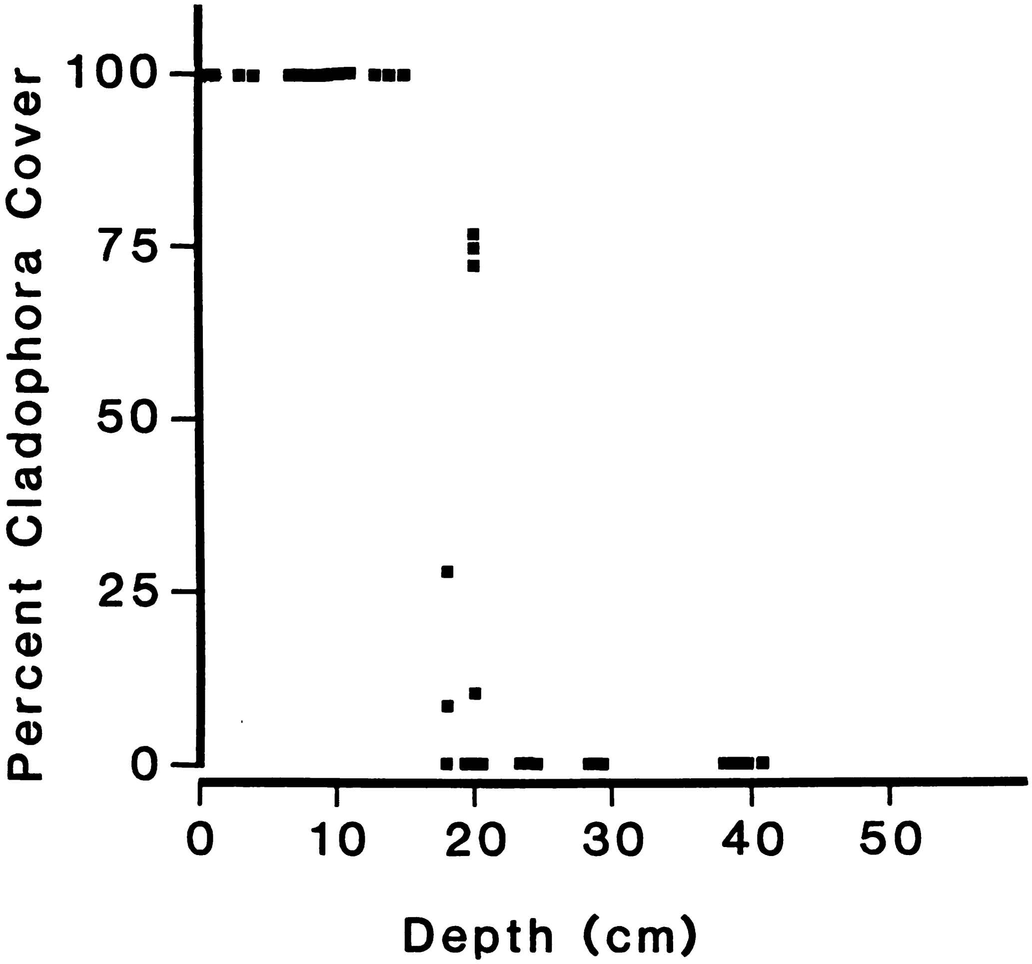
Strong negative correlations were observed between Cladophora biomass and both depth and distance to shore in 1987 (Table 1A, Figures 2B and 4B). Both correlations were highly significant ($p<0.001$). A non-significant correlation was found between biomass and current velocity (Table 1A, Figure 3). Similar patterns were observed with percent cover (Table 1A, Figures 2-4). The negative relation between Cladophora abundance and distance to shore makes little sense at first glance. If anything, one would anticipate Cladophora abundance to increase with increasing distance from the stream bank due to less shading by riparian vegetation. The positive correlation between depth and distance to shore ($r = 0.891$) probably accounts for this pattern at NS and SS in 1987.

The transects at HRS in 1988 produced a pattern of Cladophora biomass with depth similar to that seen at NS and SS in 1987. Cladophora was very abundant in water less than about 15-20 cm deep (Table 1A, Figure 5). Cladophora was twenty times less abundant on deeper substrates. The patterns of Cladophora abundance with respect to current velocity and distance to shore were different than those observed in 1987. In 1988 there was a positive correlation between

Figure 2. A. The relationship between percent *Cladophora* cover and depth for samples taken at Nagel's Site and Snyder's Site in 1987.

B. The relationship between *Cladophora* biomass and depth for samples taken at Nagel's Site and Snyder's Site in 1987.

Figure 2A.


Percent Cladophora Cover
100
75
50
25
0
0
10
20
30
40
50
Depth (cm)

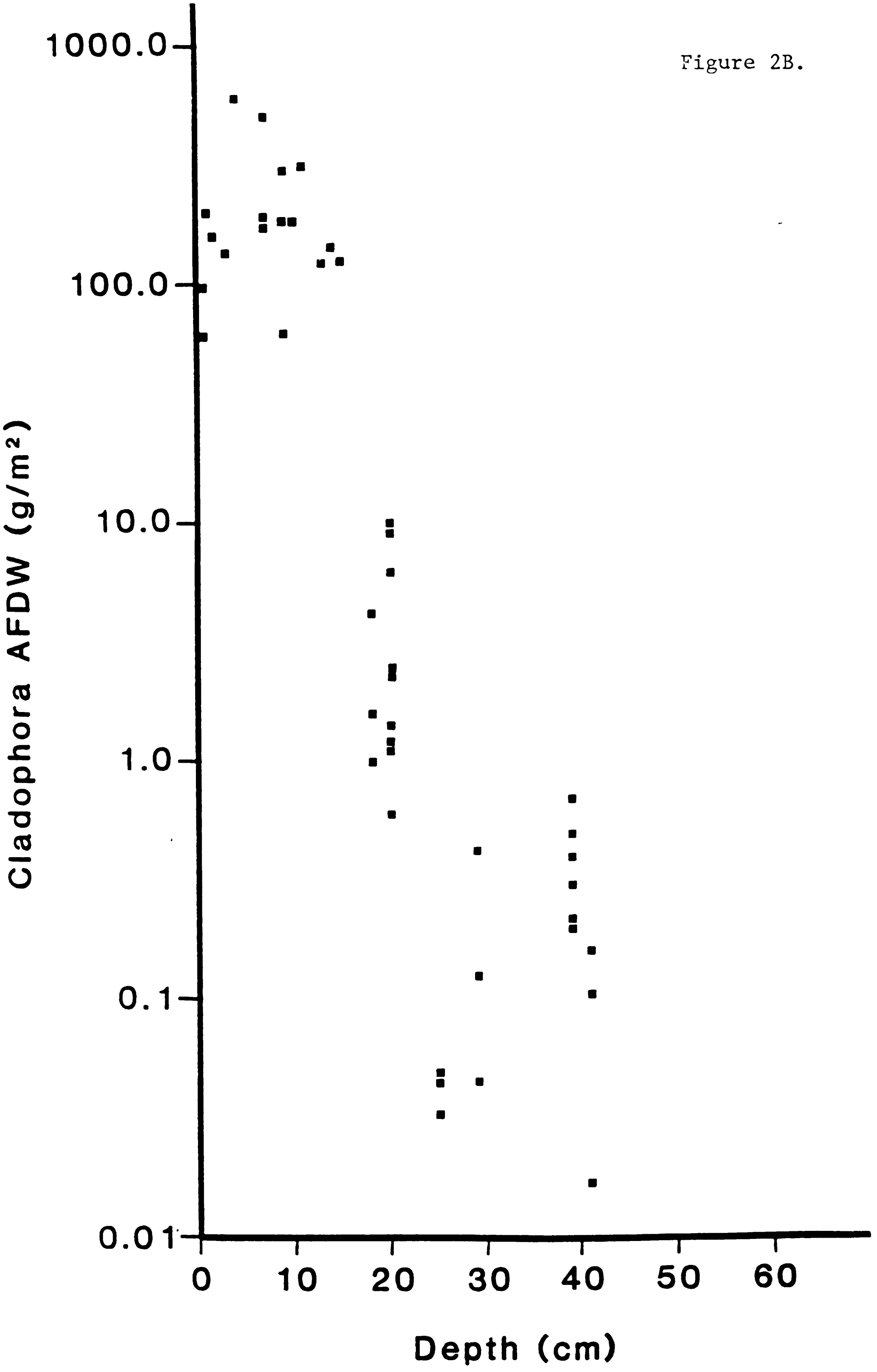

1000.0
100.0
10.0
1.0
0.1
0.01
Cladophora AFDW (g/m²)
0
10
20
30
40
50
60
Depth (cm)

Figure 2B.

Figure 3. A. The relationship between percent *Cladophora* cover and current velocity for samples taken at Nagel's Site and Snyder's Site in 1987.

B. The relationship between *Cladophora* biomass and current velocity for samples taken at Nagel's Site and Snyder's Site in 1987.

Figure 3A.

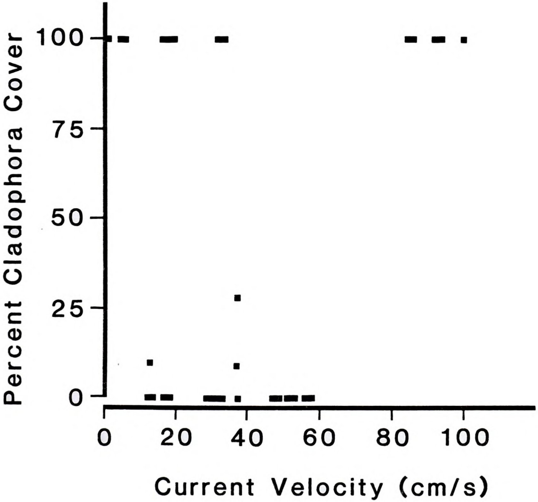

Percent Cladophora Cover
100
75
50
25
0
0
20
40
60
80
100
Current Velocity (cm/s)

Figure 3B.

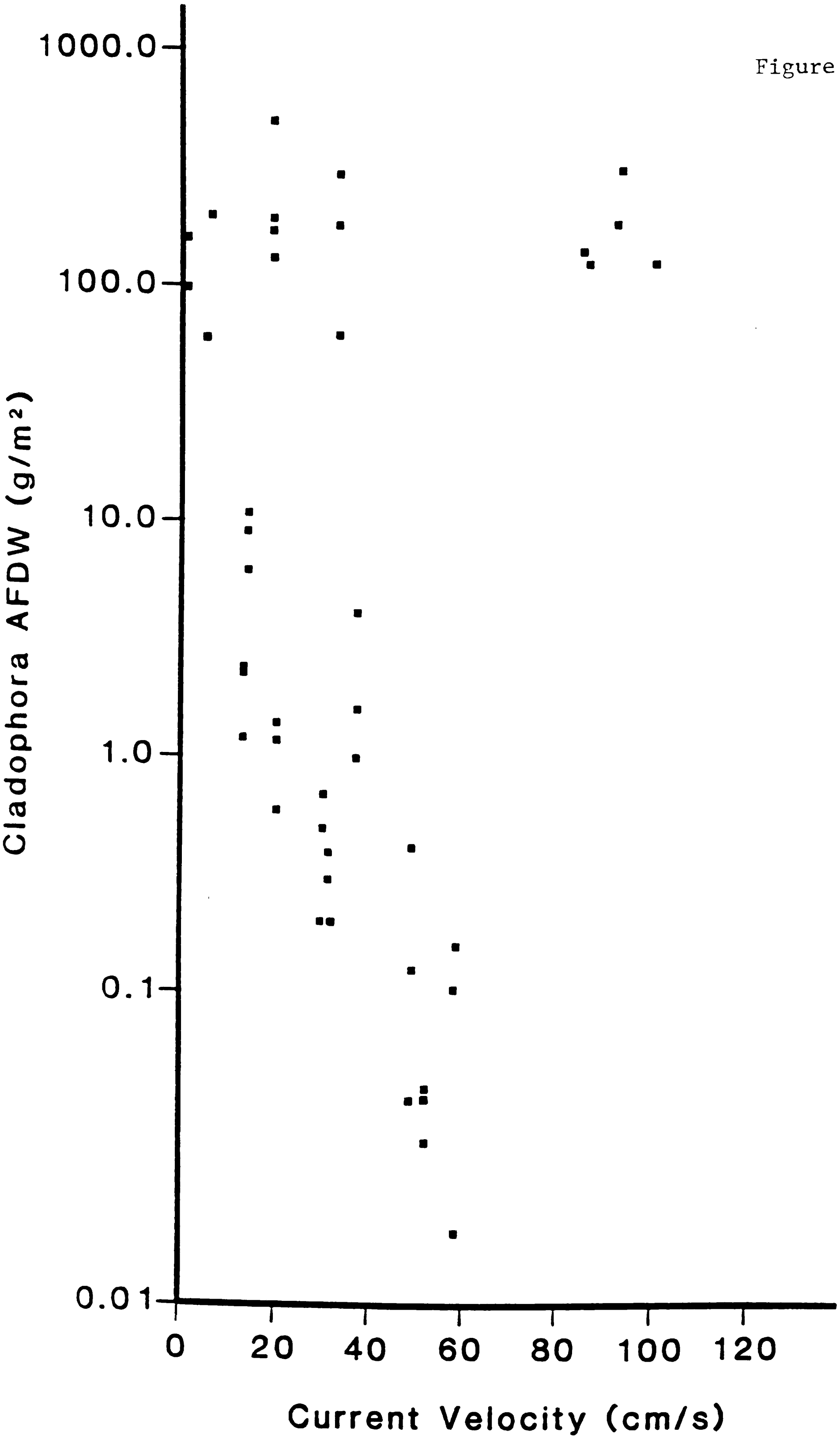
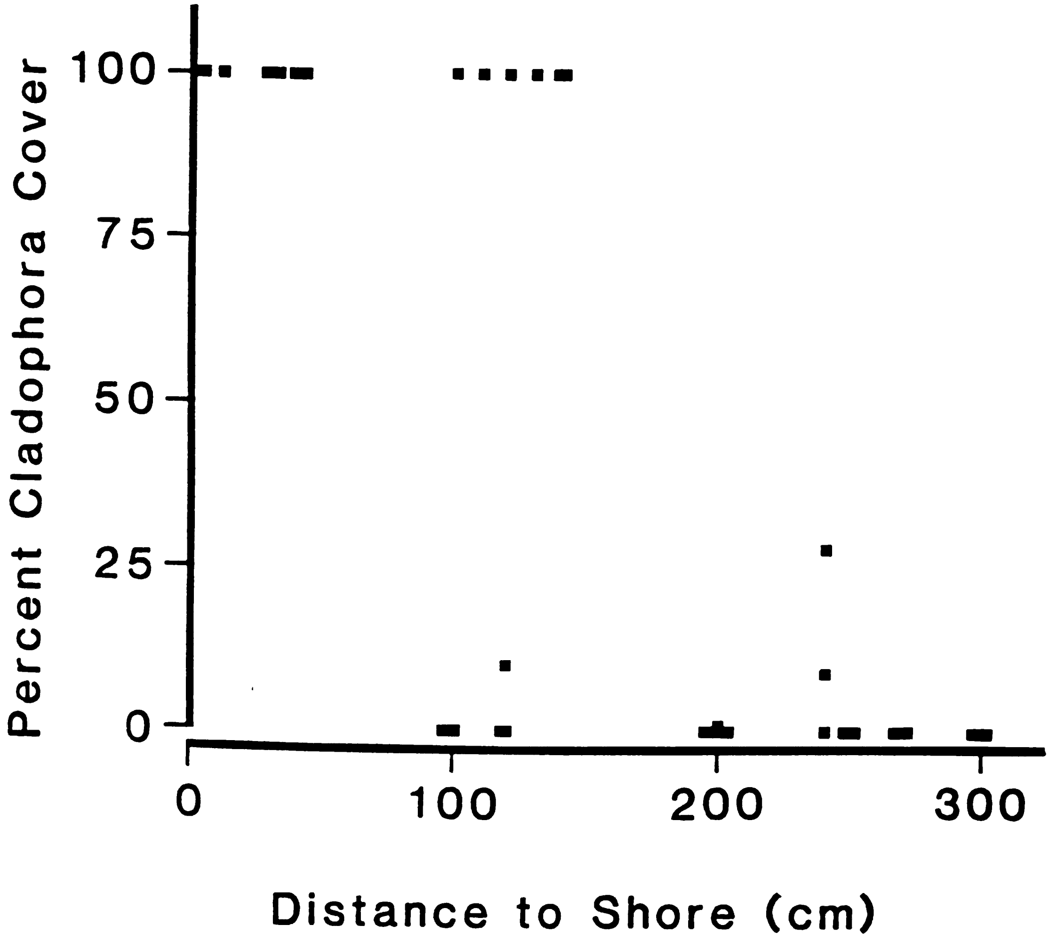

1000.0
100.0
10.0
1.0
0.1
0.01
Cladophora AFDW (g/m²)
0
20
40
60
80
100
120
Current Velocity (cm/s)

Figure 4. A. The relationship between percent Cladophora cover and distance to shore for samples taken at Nagel's Site and Snyder's Site in 1987.

B. The relationship between Cladophora biomass and distance to shore for samples taken at Nagel's Site and Snyder's Site in 1987.

Figure 4A.


Percent Cladophora Cover
100
75
50
25
0
0
100
200
300
Distance to Shore (cm)

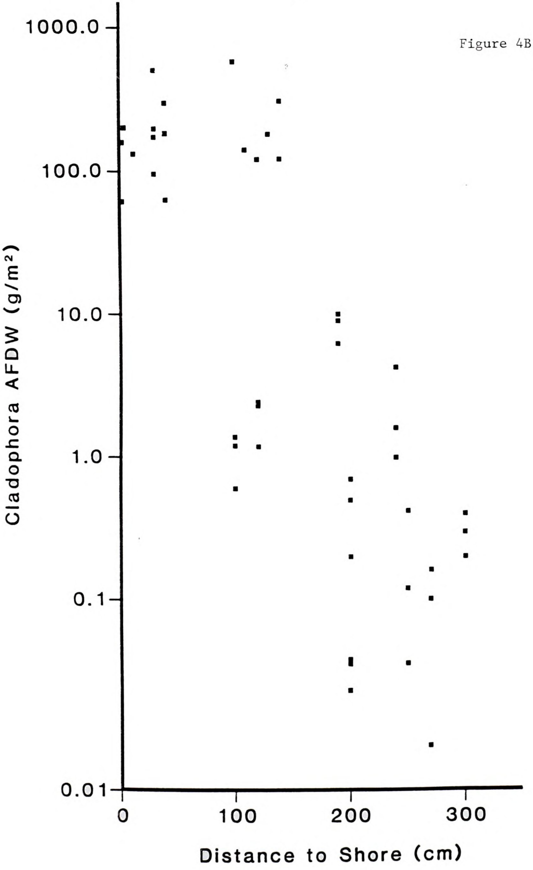

1000.0
100.0
10.0
1.0
0.1
0.01
Cladophora AFDW (g/m²)
0
100
200
300
Distance to Shore (cm)

Figure 4B.

Table 1. A. Pearson's product-moment correlation coefficients for *Cladophora* distribution (biomass) by depth, current velocity and distance to shore for 1987 (Nagel's and Snyder's Sites) and 1988 (Hickory Road Site) surveys.

Variable	Cladophora Biomass	
	1987	1988
Depth	-0.841 ***	-0.881 ***
Current Velocity	-0.056 n.s.	0.556 *
Distance to Shore	-0.793 ***	-0.183 n.s.

n.s.- not significant
* - $p<0.05$
** - $p<0.01$
*** - $p<0.001$

Table 1. B. Results of a stepwise multiple regression analysis of the relationship between *Cladophora* abundance and depth, current velocity and distance to shore for pooled data from 1987 and 1988 surveys.

Variable	Model R^2	F Value	P Value
Depth	0.7091	146.2591	0.0001
Current Velocity	0.7437	7.9719	0.0065
Distance to Shore	0.7555	2.7852	0.1005

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Variable	Model R^2	F Value	P Value
Depth	0.7091	146.2591	0.0001
Current Velocity	0.7437	7.9719	0.0065
Distance to Shore	0.7555	2.7852	0.1005

current velocity and Cladophora biomass (Table 1B, Figure 6B). There was no relation between Cladophora abundance and distance to shore (Table 1A, Figure 7). The positive response to current has two potential causes. First, Whitford and Shumaker (1961) have shown that there is a positive relation between nutrient uptake by filamentous algae and current velocity. This is thought to be due to the increased supply rate of nutrients in faster currents in conjunction with a decrease in the size of the diffusion zone around an algal filament. Alternatively, this pattern could simply be due to the fact that current is negatively correlated with depth ($r = -0.523$, $p<0.02$). The lack of a relation between distance to shore and Cladophora abundance appears to be due to the fact that fewer midchannel sites at HRS are in water greater than 10-15 cm deep as compared to NS and SS. When the data from the two years are combined and analyzed using multiple regression, depth is clearly the most important factor in determining Cladophora abundance in Augusta Cr. (Table 1B). In conclusion, depth was the only factor consistently related to Cladophora abundance over these two years.

The 1989 surveys at HRS demonstrated that this relation between Cladophora abundance and depth persisted throughout the summer (Figure 8A-D). For each sample date, Cladophora was consistently abundant in shallow water and not very abundant in deep water. It is interesting to note that the transition between the shallow habitat where Cladophora is abundant and the deep, Cladophora-free zone varies between sample dates. For example, in early July the transition occurs between the 20 and 25 cm depth intervals (Figure 8A). Daytime stream temperatures at this time were between 18 and 20° C. By early August water temperatures were in the low to mid-twenties (23° C. on

Figure 5. A. The relationship between percent Cladophora cover and depth for samples taken at Hickory Road Site in 1988.

B. The relationship between Cladophora biomass and depth for samples taken at Hickory Road Site in 1988.

Figure 5A.

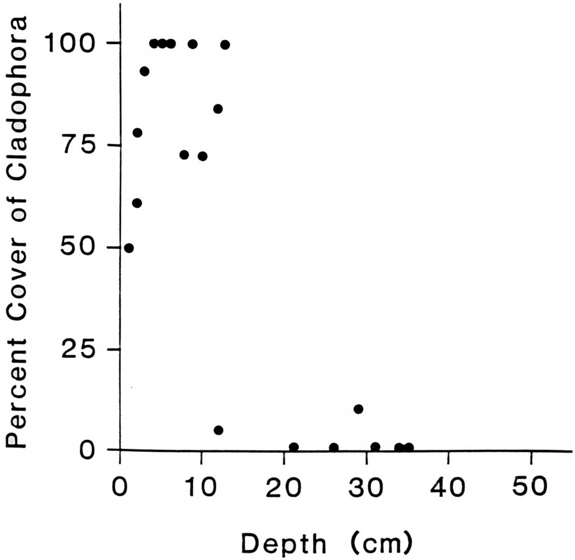

Percent Cover of Cladophora
100
75
50
25
0
0
10
20
30
40
50
Depth (cm)

Figure 5B.

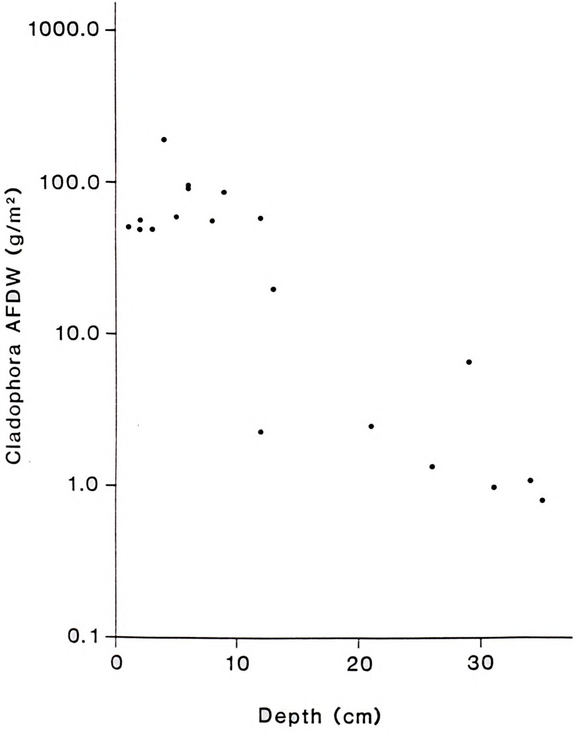


Figure 6. A. The relationship between percent *Cladophora* cover and current velocity for samples taken at Hickory Road Site in 1988.

B. The relationship between *Cladophora* biomass and current velocity for samples taken at Hickory Road Site in 1988.

Figure 6A.

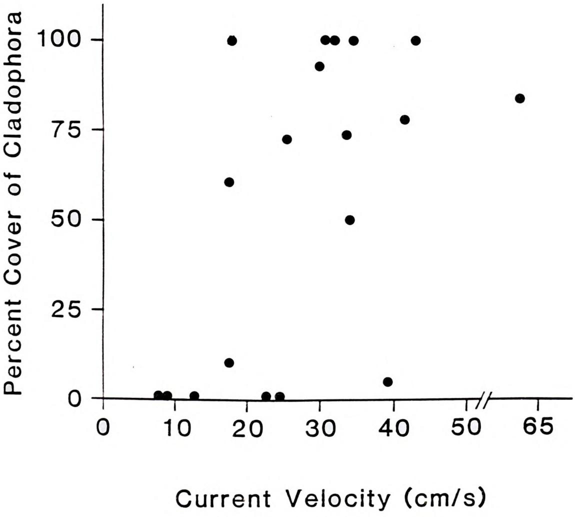

Percent Cover of Cladophora
100
75
50
25
0
0
10
20
30
40
50
65
Current Velocity (cm/s)

Figure 6B.

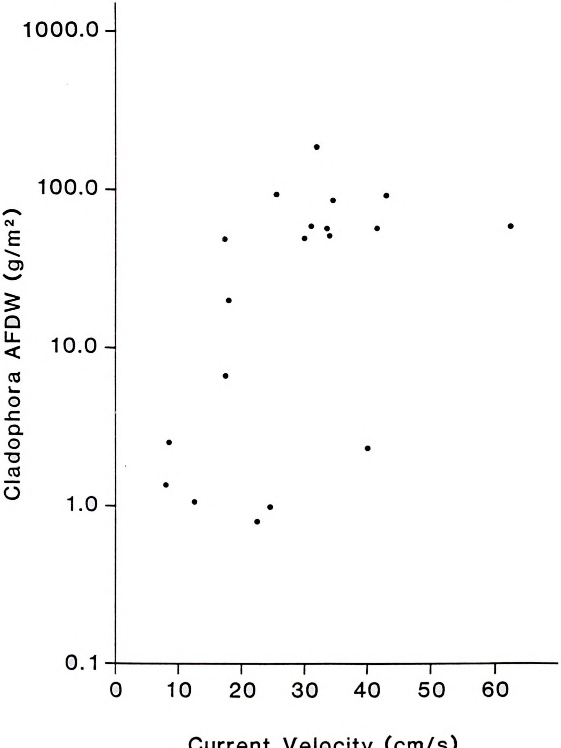

Cladophora AFDW (g/m²)
1000.0
100.0
10.0
1.0
0.1
0
10
20
30
40
50
60
Current Velocity (cm/s)

Figure 7. A. The relationship between percent *Cladophora* cover and distance to shore for samples taken at Hickory Road Site in 1988.

B. The relationship between *Cladophora* biomass and distance to shore for samples taken at Hickory Road Site in 1988.

Figure 7A.

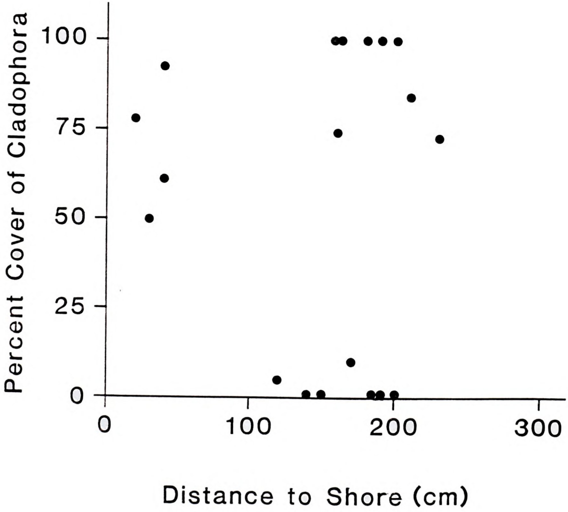
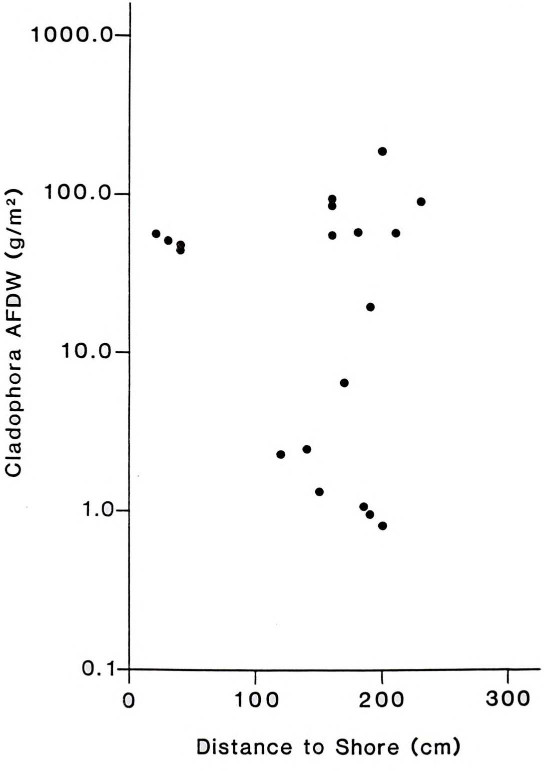

Percent Cover of Cladophora
100
75
50
25
0
0
100
200
300
Distance to Shore (cm)

Figure 7B.


Cladophora AFDW (g/m²)
1000.0
100.0
10.0
1.0
0.1
0
100
200
300
Distance to Shore (cm)

sample date) and the transition occurred from 17-20 cm (Figure 8B). By late August the transition is at 20 cm depth and the water temperature was 21° C. (Figure 8C). Finally, in October water temperatures had cooled to 17° C. and the transition was between 20 and 23 cm (Figure 8D).

Orconectes propinquus

Striking differences in the distribution and abundance of YOY versus large (1+ and 2+) crayfish were observed at both NS and HRS (Figures 9 and 10). YOY were most abundant in the shallow, cobble/Valisneria habitat at NS for most of the summer (Figure 9, A-C) and in the shallow, cobble/Cladophora/macrophyte habitat at HRS (Figure 10). At NS from early to midsummer YOY were much less abundant (from 4-20X less abundant) in the shallow, midchannel habitat and the deep habitat. On July 1 and August 2 YOY densities were significantly higher in the SCV (Shallow, Cobble/Valisneria) habitat than the other two habitats (Tukey's HSD test, $p<0.05$). However, as can be seen in Figure 9A-D, over the course of the summer as YOY became less abundant overall, their densities in the shallow, cobble/Valisneria habitat became identical to those in deep water (on October 1, SCV = DCM (Deep, Cobble, Midchannel) which were significantly higher than SCM (Shallow, Cobble, Midchannel) (Tukey's HSD test, $p<0.05$). This apparent shift in habitat utilization corresponds to the increasing size of the young-of-the-year. Large crayfish were most abundant in deeper water at both sites (Figures 9 and 10). At NS they maintained fairly constant densities (mean = 3 - 5 inds./m^2) over the course of the summer in deep water. Differences

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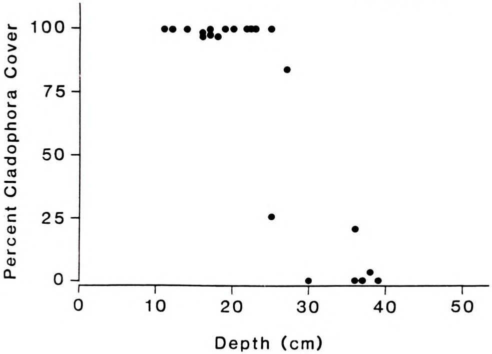
Figure 8 A - D. The relationship between percent Cladophora cover and depth for four different dates from the summer and early autumn of 1989. Samples taken at Hickory Road Site.

Figure 8.

A. July 8



B. August 3

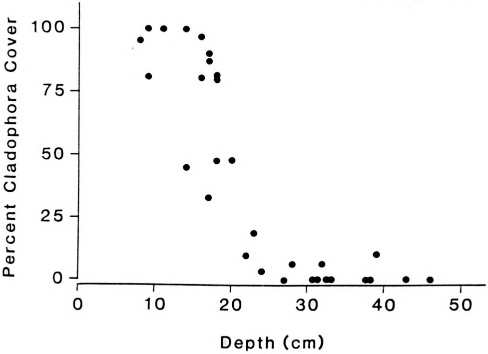
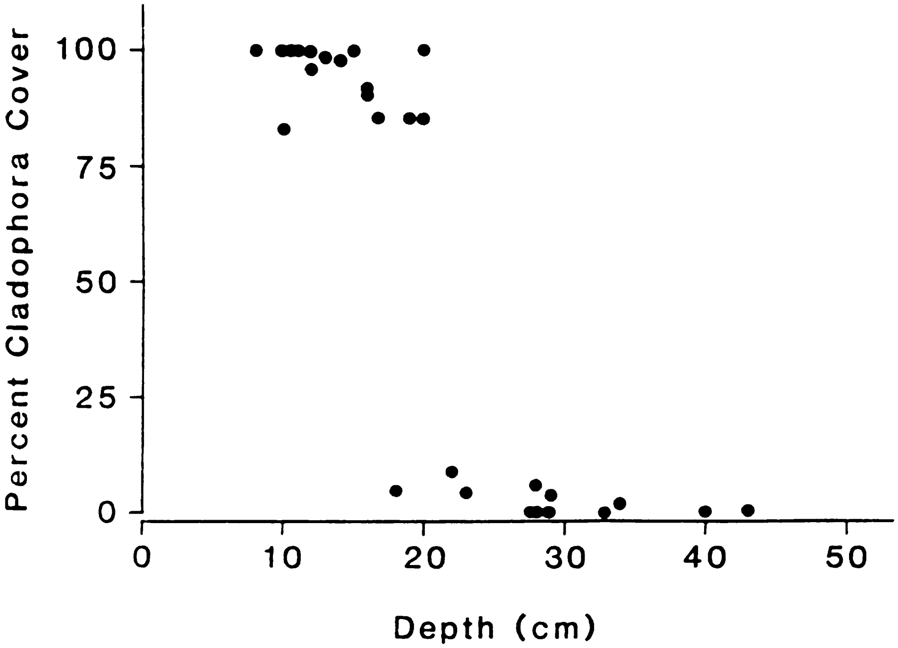


Figure 8.

C. August 25



D. October 2

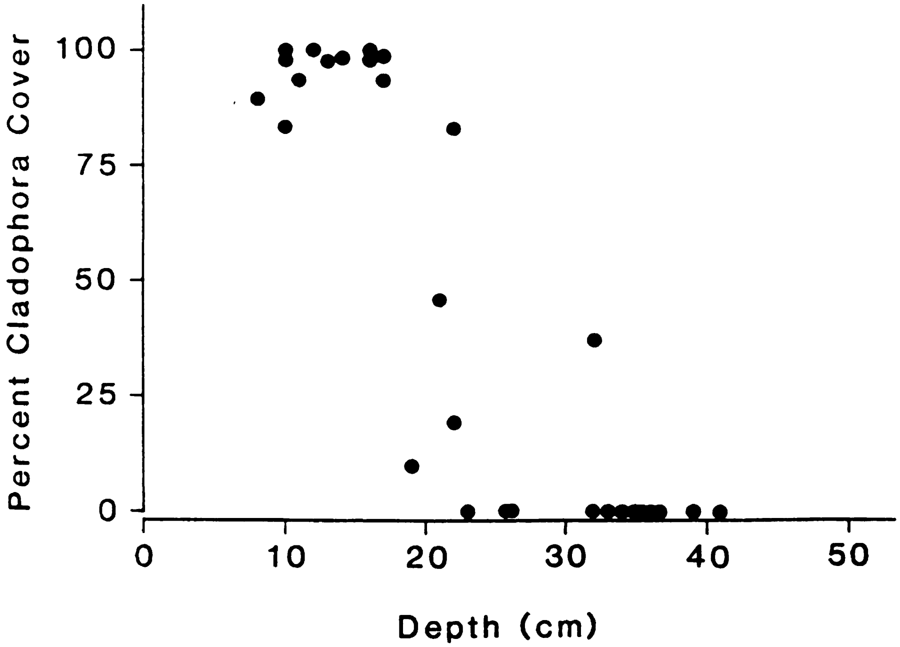


Figure 9 A - D. The distribution of young-of-the-year (open bars) and adult crayfish (shaded bars) by habitat at Nagel's Site. Habitats differ with respect to depth, current velocity and/or macrophyte cover. Shallow habitats have depths ≤ 20 cm; deep habitats have depths > 20 cm. Values are mean densities (± 1 S.E.). SCV - Shallow, cobble/*Valisneria* habitat; SCM - Shallow, cobble, midchannel habitat; DCM - Deep, cobble, midchannel habitat. A. Sample taken on July 1, 1988. B. Sample taken on August 2, 1988. C. Sample taken on September 2, 1988. D. Sample taken on October 1, 1988.

(1- On October 1, 1988 water levels were higher than normal. Mean depth for the SCV habitat was 28.0 cm)

Figure 9.

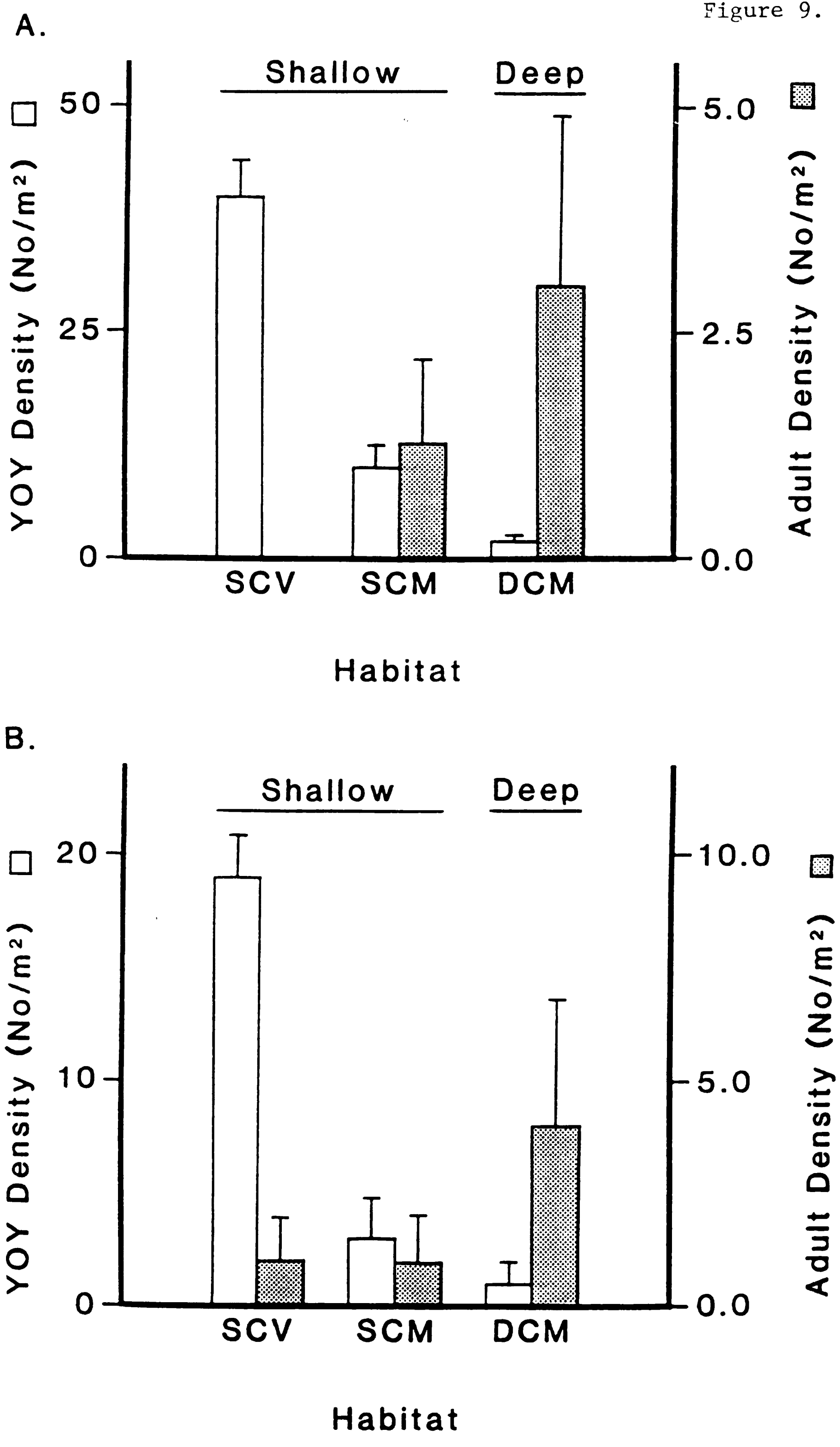

A.
Shallow
Deep
YOY Density (No/m²) □
50
25
0
Adult Density (No/m²) ▨
5.0
2.5
0.0
SCV
SCM
DCM
Habitat
B.
Shallow
Deep
YOY Density (No/m²) □
20
10
0
Adult Density (No/m²) ▨
10.0
5.0
0.0
SCV
SCM
DCM
Habitat

Figure 9.

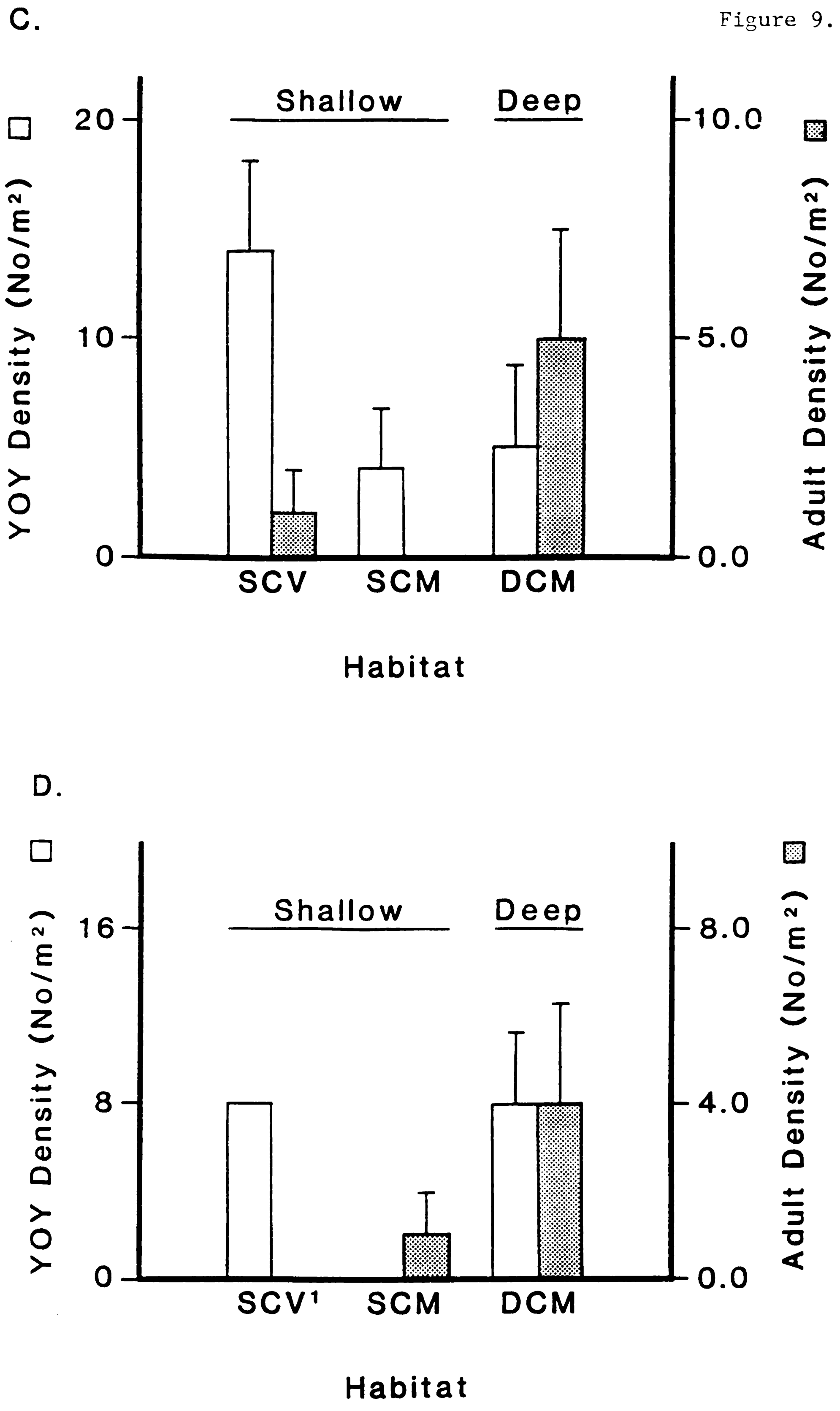
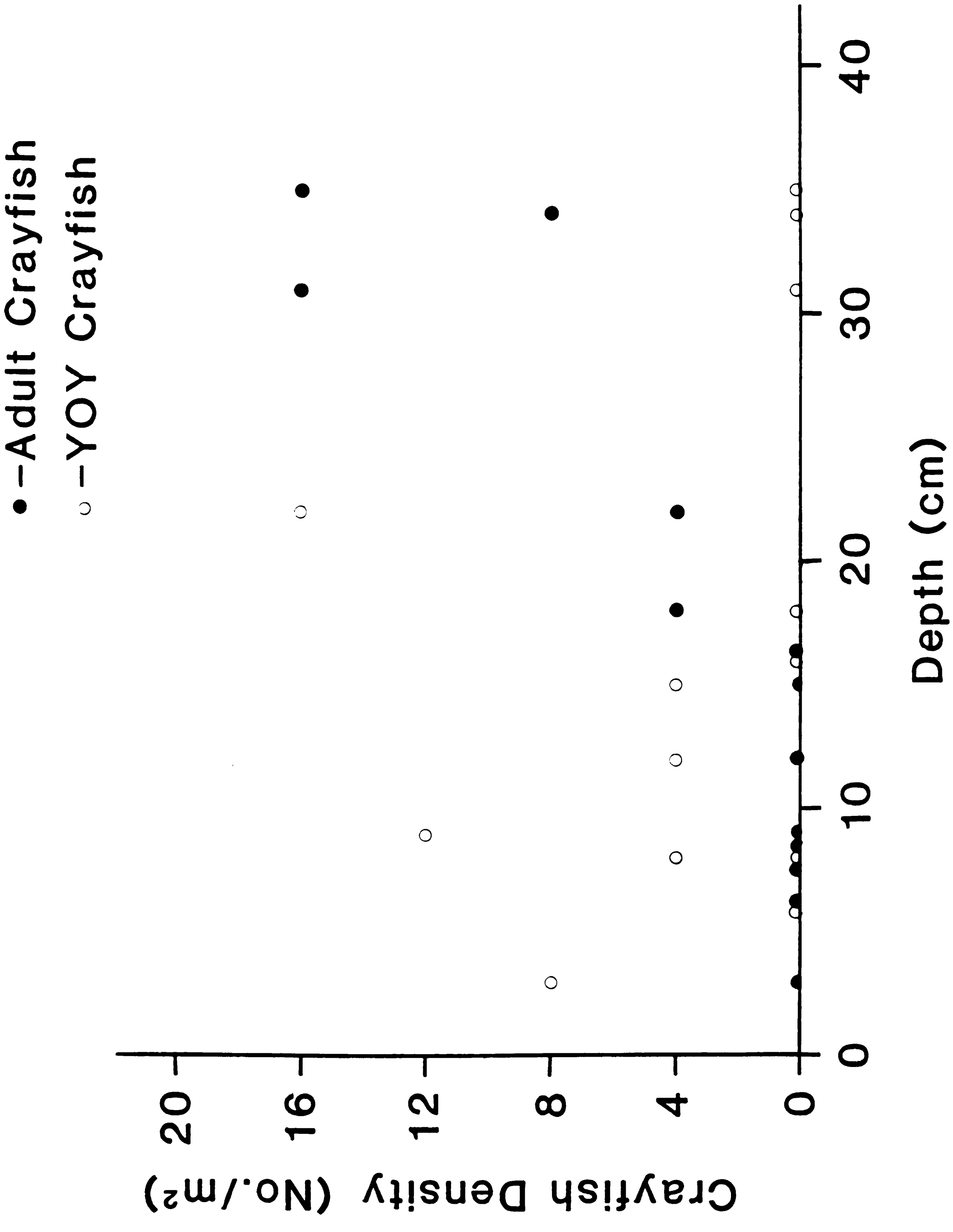

C.
Shallow
Deep
YOY Density (No/m²) □
Adult Density (No/m²) ▨
20
10
0
10.0
5.0
0.0
SCV
SCM
DCM
Habitat
D.
Shallow
Deep
YOY Density (No/m²) □
Adult Density (No/m²) ▨
16
8
0
8.0
4.0
0.0
SCV¹
SCM
DCM
Habitat

Figure 10. Distribution of crayfish by depth at Hickory Road Site on August 2, 1988.

Figure 10.


●–Adult Crayfish
○–YOY Crayfish
Crayfish Density (No./m²)
0
4
8
12
16
20
Depth (cm)
0
10
20
30
40

in density between habitats were never significant for adults though. Notice that large crayfish were always less abundant or absent in either shallow habitat at NS, but particularly the shallow, nearshore, cobble/Valisneria habitat (SCV) (Figure 9). When crayfish carapace lengths are converted into biomass (see Appendix D) a pattern of greater crayfish biomass in deep water is evident (Table 2).

The shallow, midchannel habitat and the deep, midchannel habitat only differed in depth, current velocities were very similar (Table 3). These data suggest, that for the range of current velocities measured for these habitats, that depth of the water is the best predictor of the distribution of large crayfish. Current velocity, in addition to depth, may be an important factor influencing the distribution of YOY crayfish. Current velocities were considerably slower in the shallow, cobble/Valisneria habitat compared to the other two habitats at NS (Table 3). However, at HRS, current velocities in the shallow habitat (33.5 ± 3.5 cm/s) were similar to those for the shallow and deep midchannel habitats at NS (Table 3). In conclusion, large crayfish appear to distribute themselves primarily with respect to depth, being more abundant in deeper water. Young-of-the-year crayfish, on the other hand, while much more common in shallow water, may also seek out areas of slower current velocity.

Macroinvertebrates

The deep water macroinvertebrate community (not including chironomids) at NS was dominated by members of the micrograzer guild throughout the summer of 1986 (Figure 11). From July through early September micrograzers accounted for approximately eighty percent of

Table 2. Mean crayfish biomass (g wet weight/m^2) for each of the three habitats sampled at Nagel's Site, Augusta Creek, Michigan during 1988. Young-of-the-year and adults are combined. Values in the table are means ± 1 standard error. Values with the same letter are not significantly different at the 0.05 level. Comparisons made using ANOVA with Tukey's HSD test on log(x+1) transformed data. N = 4.

Date	Habitat					
	SCV		SMC		DMC	
July 1	5.186 (1.156)	a	0.880 (0.424)	a	21.920 (13.440)	a
August 2	12.072 (3.280)	a	9.820 (9.119)	a	31.884 (21.832)	a
September 2	17.316 (7.412)	ab	3.580 (2.560)	b	44.068 (15.148)	a
October 1	7.304 (0.944)	a	9.767 (9.767)	a	28.248 (14.096)	a
Habitat Means (for entire season)	10.467 (2.203)	ab	6.012 (3.206)	b	31.529 (7.656)	a

Table 3. Depth and current velocity for habitats sampled for crayfish at Nagel's Site during the summer of 1988. Values in table are means (± 1 S.E.). Depths are in cm; current velocities are in cm/s. N = 4 for each habitat on each date.

Date	Habitat					
	Shallow				Deep	
	SCV		SMC		DMC	
	mean depth	mean C.V.	mean depth	mean C.V.	mean depth	mean C.V.
July 1	17.5 (1.3)	11.6 (2.3)	19.8 (0.5)	36.8 (2.4)	32.3 (2.9)	30.7 (5.6)
August 2	18.0 (0.8)	4.6 (1.2)	19.0 (0.4)	24.1 (2.5)	26.8 (1.3)	39.0 (8.3)
September 2	18.5 (0.9)	11.3 (3.7)	19.5 (0.5)	31.5 (1.6)	31.5 (1.6)	31.8 (2.9)
October 1	28.0 (1.1)	17.1 (1.6)	18.3 (0.9)	31.6 (5.3)	38.5 (0.7)	31.6 (4.3)

SCV = Shallow (< 20 cm) with Cobble/*Valisneria* substrate.
SCM = Shallow with Cobble substrate, Midchannel.
DCM = Deep (> 20 cm) with Cobble substrate, Midchannel.

the individuals on the rocks. The remaining twenty percent was largely split between filter feeders and predators, with detritivores rarely contributing more than five percent of the individuals (Figure 11). Figure 12 shows the dominant taxa for the same time period. One taxon, the sessile, micrograzer, caddisfly larva Psychomyia flavida, dominated the community throughout this period. P. flavida usually accounted for 40 - 50 percent of the individuals on the rocks (Figure 12). Two other sessile caddisfly groups were common on these substrates, the micrograzer Leucotrichia pictipes and the filter-feeding Hydropsychidae (Hydropsyche and Cheumatopsyche). Together with P. flavida they accounted for between 50 and 75% of the individuals on the rocks. The mobile, micrograzer mayflies Baetis and the Heptageniidae (primarily the genus Stenonema), consistently comprised about ten percent of the taxa. Chironomids generally accounted for about ten percent of the individuals as well except for two dates, August 11 and September 5, when their contribution increased to 31.5% and 22.0%, respectively. Overall, the relative abundances of all taxa changed little during this two month period. Mean densities of these taxa for this same period are shown in Table 4. As can be seen from the upper part of Figure 11, Cladophora was not particularly abundant on these rocks. Cladophora AFDW remained fairly constant over this period and averaged about 0.03 g/m^2. The thalli on these rocks were not particularly long either; 88.0% were less than 4 mm long (none were longer than 10 mm). The scarcity of thalli much longer than 4 mm suggests that Cladophora becomes vulnerable to crayfish when it exceeds this length.

At HRS in 1988 the abundance of various macroinvertebrate taxa was correlated with the abundance of Cladophora. Psychomyia, the dominant

Figure 11. Lower panel. Relative abundance of macroinvertebrates with respect to functional groups (not including chironomids) over the course of the summer at Nagel's Site in 1986. Samples are from rocks taken from water greater than 20 cm deep.

Upper panel. The biomass of *Cladophora* from the same rocks from which the macroinvertebrates were sampled.

Figure 11.

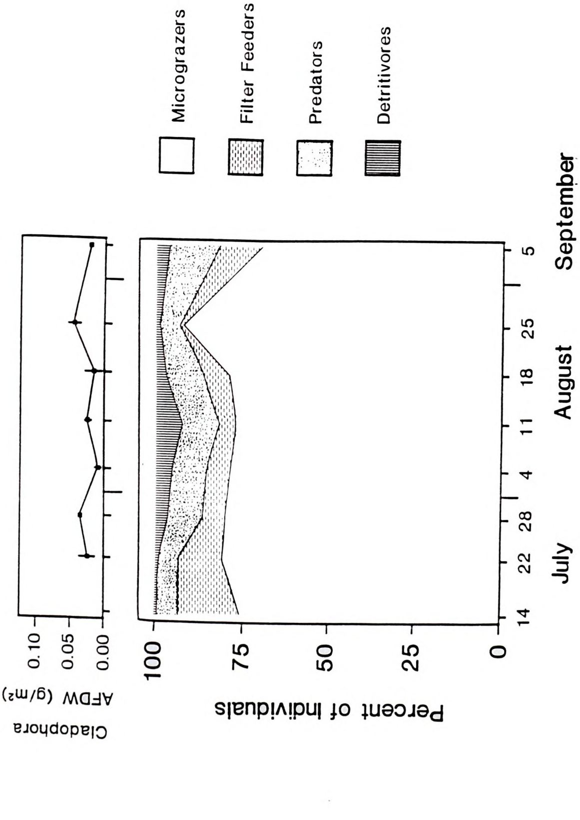

Cladophora AFDW (g/m²)
0.10
0.05
0.00
Percent of Individuals
100
75
50
25
0
14
22
28
4
11
18
25
5
July
August
September
Micrograzers
Filter Feeders
Predators
Detritivores

Figure 12. Relative abundance of macroinvertbrates with respect to major taxa over the course of the summer at Nagel's Site in 1986. Samples are from same rocks for which functional groups are described in Figure 11.

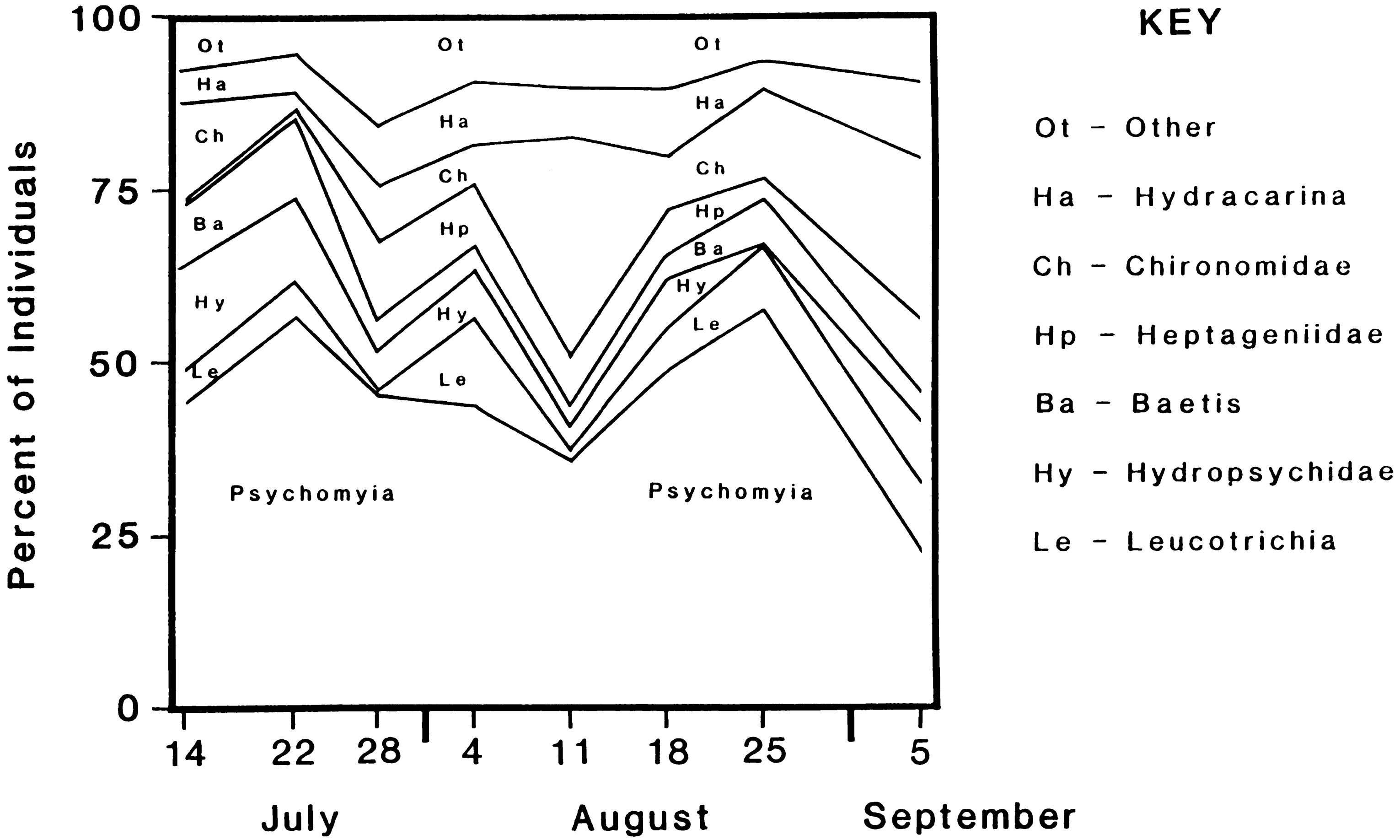

100
75
50
25
0
Percent of Individuals
14
22
28
4
11
18
25
5
July
August
September
Ot
Ha
Ch
Ba
Hy
Le
Ot
Ha
Ch
Hp
Hy
Le
Ot
Ha
Ch
Hp
Ba
Hy
Le
Psychomyia
Psychomyia
KEY
Ot - Other
Ha - Hydracarina
Ch - Chironomidae
Hp - Heptageniidae
Ba - Baetis
Hy - Hydropsychidae
Le - Leucotrichia

Figure 12.

taxa at NS on deep substrates, was also very abundant (mean = 12,973/m^2 ± 1065) on the deeper Cladophora-free substrates at HRS. However, as Cladophora biomass increased the density of this species dropped off precipitously (Figure 13); densities on shallow substrates with lots of Cladophora averaged about 499/m^2 ± 138. Psychomyia and Goniobasis (see below) were the only taxa to show this striking negative relation with Cladophora biomass. All other taxa either increased with increasing Cladophora abundance or showed little difference in abundance across this range of algal abundance. Among the groups that were positively associated with Cladophora were the filter-feeding Hydropsychid larvae (Figure 13), the caddisfly Ochrotrichia which feeds on filamentous algae, Gammarid amphipods (Figure 14), the micrograzer Baetis and the deposit-feeding Tricorythodes (both Ephemeroptera) (Figure 15). When Hydropsychid larvae are separated into large (>3mm total body length) and small individuals, both size classes show a similar pattern of increase with increasing Cladophora abundance. Heptageniidae (Ephemeroptera), Elmid larvae (Coleoptera), Helicopsyche borealis (Trichoptera) and Triclads showed no relation with Cladophora biomass (Table 4). The distribution of the snail Goniobasis, like Psychomyia, showed a strong negative relation with Cladophora at HRS in 1989 (Figure 16).

With respect to functional groups (not including chironomids) the deep substrates were dominated by micrograzers (86.4% of the individuals - a value very similar to that for NS in 1986), with Psychomyia again being the dominant member of this group (Figure 17A). Baetis and Heptageniidae were the next most common micrograzers with mean densities of 1085.5 (± 590) and 819 (± 321) per square meter, respectively. Filter-feeders were the other abundant group (primarily

Figure 13. Densities of the micrograzer <u>Psychomyia</u> (Trichoptera) and both large (> 3 mm long) and small filter-feeding Hydropsychidae (Trichoptera) with respect to <u>Cladophora</u> biomass at Hickory Road Site in 1988.

Figure 13.

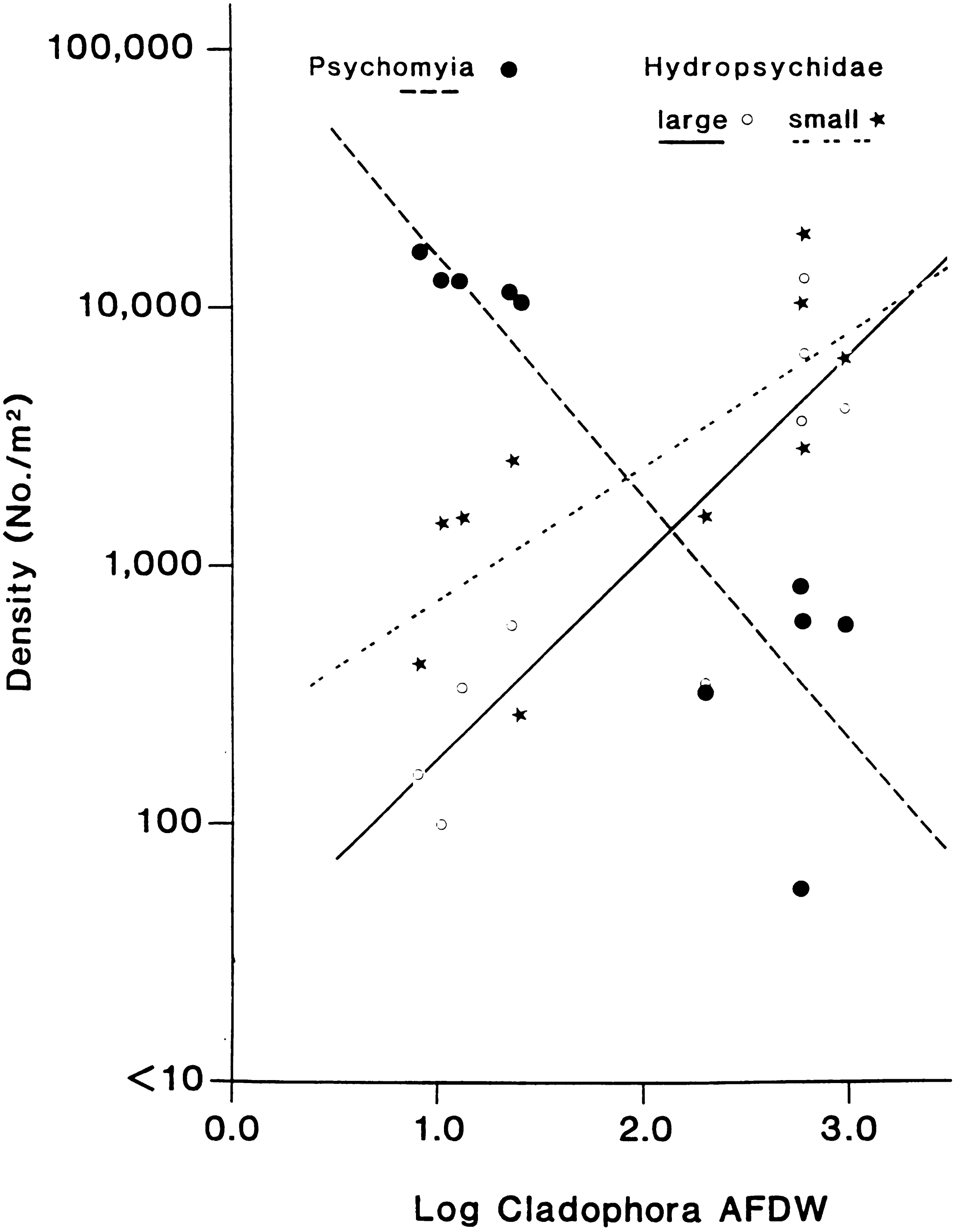

Psychomyia ●
Hydropsychidae
large ○
small ★
100,000
10,000
1,000
100
<10
0.0
1.0
2.0
3.0
Density (No./m²)
Log Cladophora AFDW

Figure 14. Densities of Amphipods and the piercer Ochrotrichia (Trichoptera) with respect to Cladophora biomass at Hickory Road Site in 1988.

Figure 14.

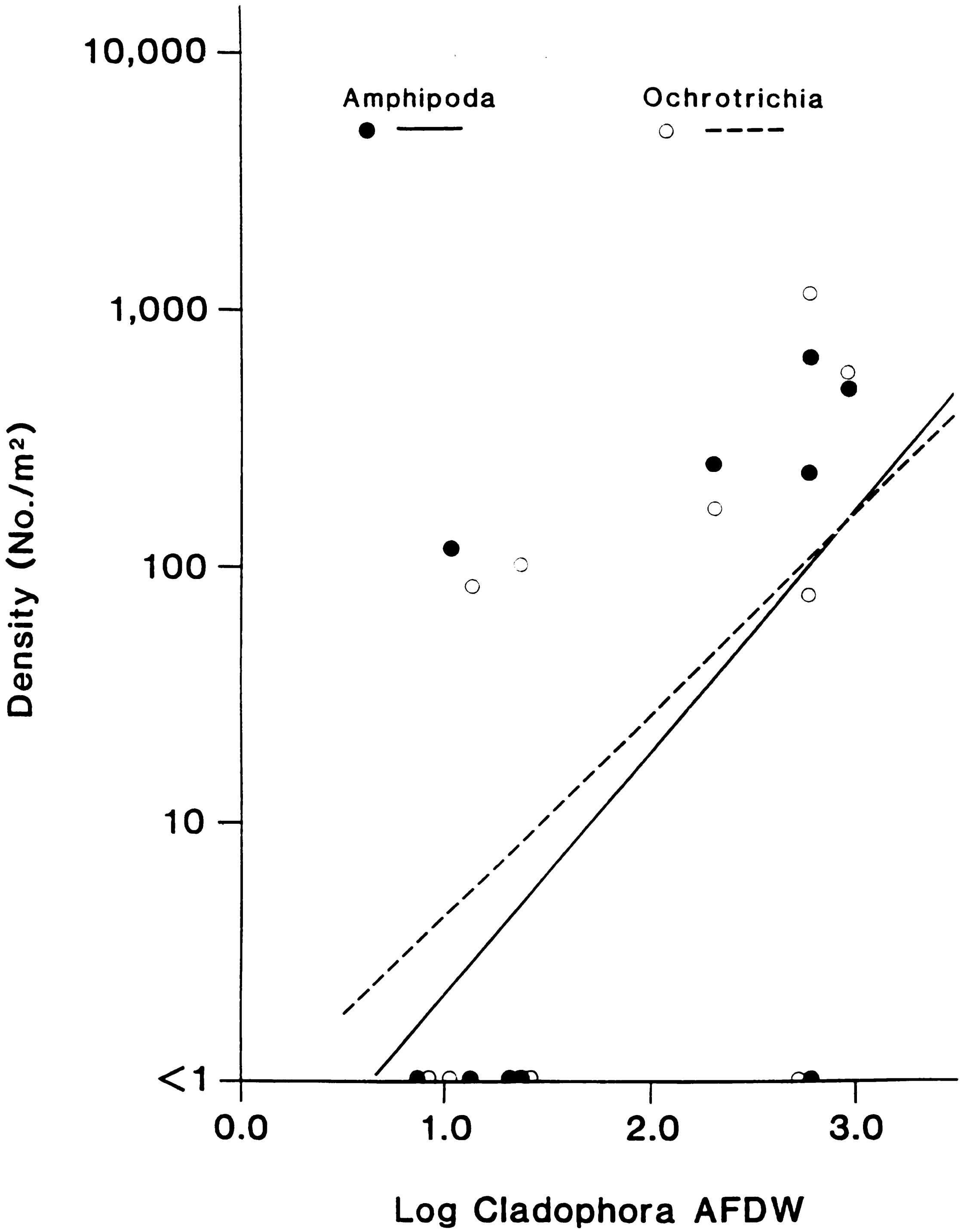

10,000
1,000
100
10
<1
Density (No./m²)
Amphipoda
Ochrotrichia
0.0
1.0
2.0
3.0
Log Cladophora AFDW

Figure 15. Densities of the micrograzer *Baetis* and the deposit-feeder *Tricorythodes* (both Ephemeroptera) with respect to *Cladophora* biomass at Hickory Road Site in 1988.

Figure 15.

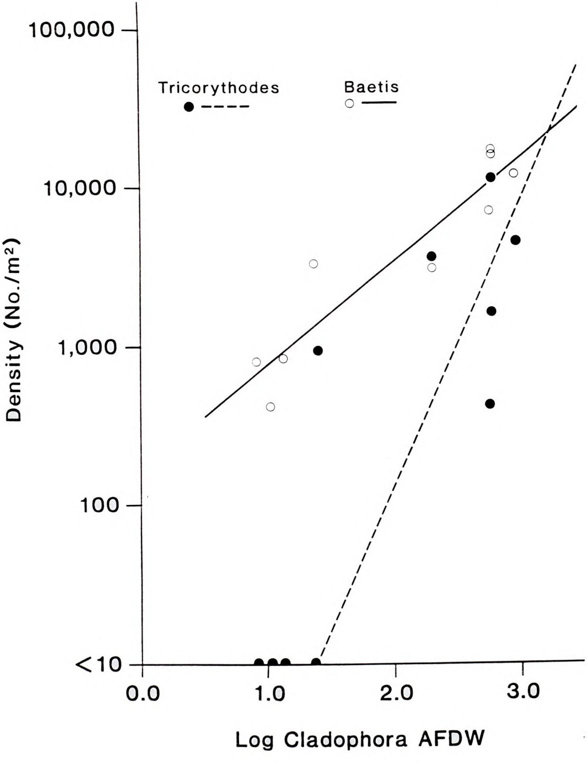

Tricorythodes
●
Baetis
○
100,000
10,000
1,000
100
<10
Density (No./m²)
0.0
1.0
2.0
3.0
Log Cladophora AFDW

Figure 16. Percent cover of Cladophora (filled squares) and the density of the grazing snail Goniobasis (open triangles) with respect to depth at Hickory Road Site on July 8, 1989.

Figure 16.

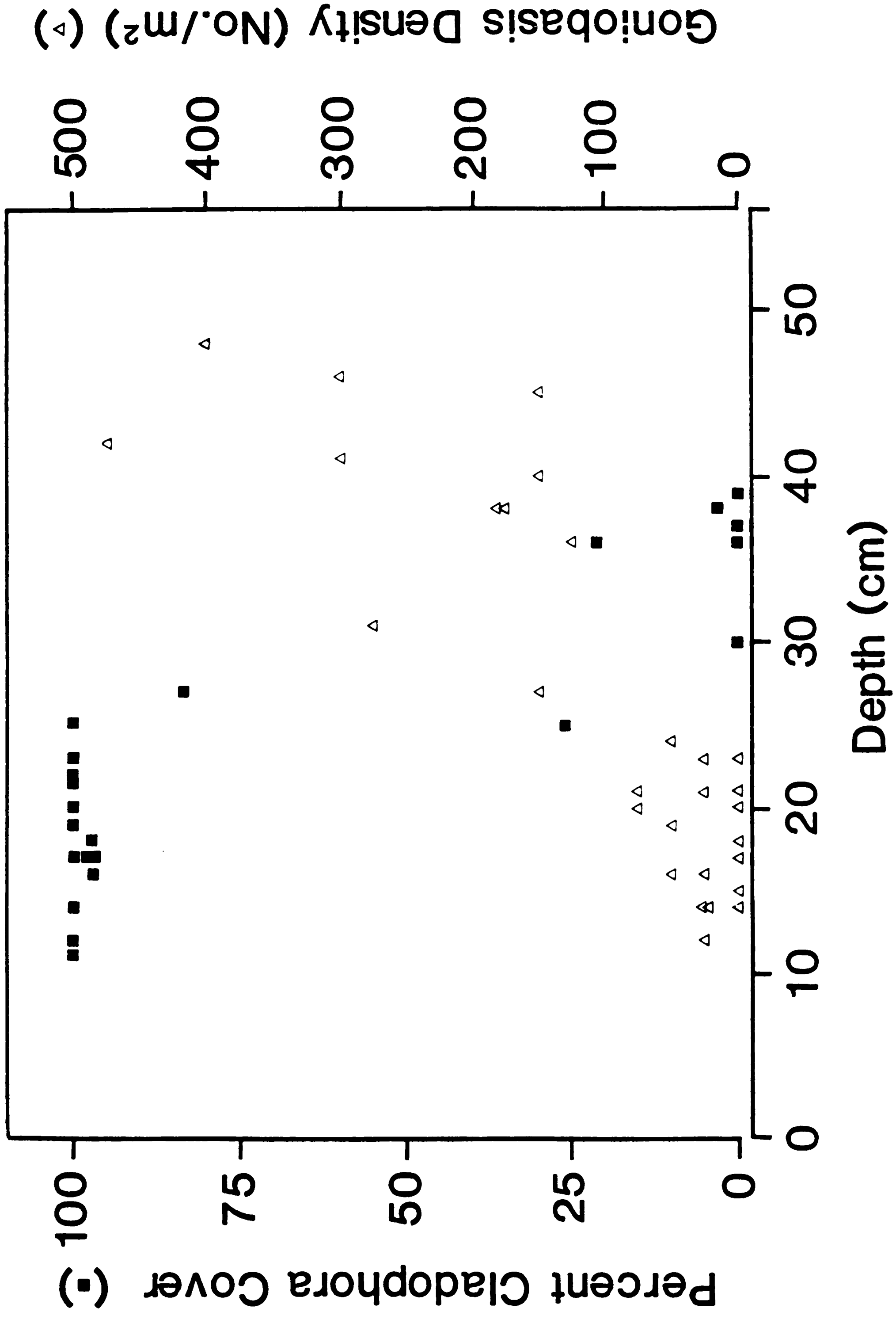

Goniobasis Density (No./m²) (◁)
500
400
300
200
100
0
Percent Cladophora Cover (■)
100
75
50
25
0
Depth (cm)
0
10
20
30
40
50

Table 4. Equations for regression lines of invertebrate density (No./m^2) on *Cladophora* biomass (g AFDW/m^2) and coefficients of determination (adjusted values) for dominant macroinvertebrate taxa collected on substrates at Hickory Road Site, Augusta Creek on July 28, 1988.

Taxon	Regression Equation	N	R^2 (adj.)	P^1
Diptera				
Chironomidae	$\text{LogD}^2 = 4.161 + 0.039\text{LogAFDW}$	9^3	-0.10	n.s.
Trichoptera				
Psychomyia	$\text{LogD} = 5.147 - 0.934\text{LogAFDW}$	10	0.79	***
Hydropsychidae - T*	$\text{LogD} = 2.310 + 0.618\text{LogAFDW}$	10	0.60	**
Hydropsychidae - L*	$\text{LogD} = 1.471 + 0.778\text{LogAFDW}$	9	0.76	**
Hydropsychidae - S*	$\text{LogD} = 2.344 + 0.525\text{LogAFDW}$	10	0.53	**
Ochrotrichia	$\text{LogD} = -0.142 + 0.791\text{LogAFDW}$	10	0.19	n.s.
Helicopsyche	$\text{LogD} = 1.680 + 0.375\text{LogAFDW}$	9	0.26	n.s.
Ephemeroptera				
Baetis	$\text{LogD} = 2.239 + 0.653\text{LogAFDW}$	9	0.84	***
Heptageniidae	$\text{LogD} = 3.057 - 0.072\text{LogAFDW}$	9	-0.10	n.s.
Tricorythodes	$\text{LogD} = -1.522 + 1.823\text{LogAFDW}$	10	0.72	**
Coleoptera				
Elmidae	$\text{LogD} = 1.806 + 0.298\text{LogAFDW}$	9	0.27	n.s.
Crustacea				
Amphipoda	$\text{LogD} = -0.604 + 0.950\text{LogAFDW}$	10	0.29	(0.06)
Tricladida	$\text{LogD} = 1.310 + 0.245\text{LogAFDW}$	10	-0.10	n.s.

1 - * $p<0.05$; ** $p<0.01$; *** $p<0.001$; n.s. not significant
2 - D = Density.
3 - For N <10 outliers were removed. Outliers tested using Dixon's method (Sokal and Rohlf 1981).
* - T = Total, L = Large (>3mm long), S = Small (<3mm long).

Hydropsychidae) but their densities (1500 ± 509 per square meter) were one tenth that of micrograzers.

Filter-feeders (35.4%) and micrograzers (47.7%) were codominant on the shallow, Cladophora-covered substrates (Figure 17B). Detritivores/deposit feeders accounted for 14.3% of the individuals. The filter-feeders were dominated by the Hydropsychidae (13,902/ m^2 ± 5419). Other filter-feeders included Simuliidae larvae (388 ± 164) and the caddisfly Chimarra (Philopotamidae) (280 ± 158). Micrograzers were dominated by Baetis (11,441 ± 2810). Other common micrograzers were Heptageniidae nymphs (1015 ± 349), Helicopsyche borealis (506 ± 89), Psychomyia (499 ± 138) and Elmid (Coleoptera) larvae (481 ± 104).

DISCUSSION

Young-of-the-year and adult Orconectes propinquus were found to overlap little with respect to habitat use. Adult crayfish were consistently more abundant in deep water. As current velocity and substrate were similar for the two midchannel habitats at NS, depth appears to be the main factor influencing their distribution. Their absence from the nearshore, shallow, cobble/macrophyte habitats suggests an avoidance of areas with low current velocities and macrophyte cover. However, they were most abundant in deep water at HRS which had slower currents than the shallow habitat, suggesting that current velocity (at least at velocities less than 60 cm/s) has little influence on adult habitat use. Also, casual inspection of macrophyte beds in deep water found adults to be as abundant in the beds as on cobble substrates. Young-of-the-year O. propinquus, on the other hand, were most abundant in the shallow, cobble/Valisneria

Figure 17. A. Relative abundance (percent individuals) of different macroinvertebrate functional groups for substrates from deep water at Hickory Road Site in 1988.

B. Relative abundance (percent individuals) of different macroinvertebrate functional groups for substrates from shallow water at Hickory Road Site in 1988.

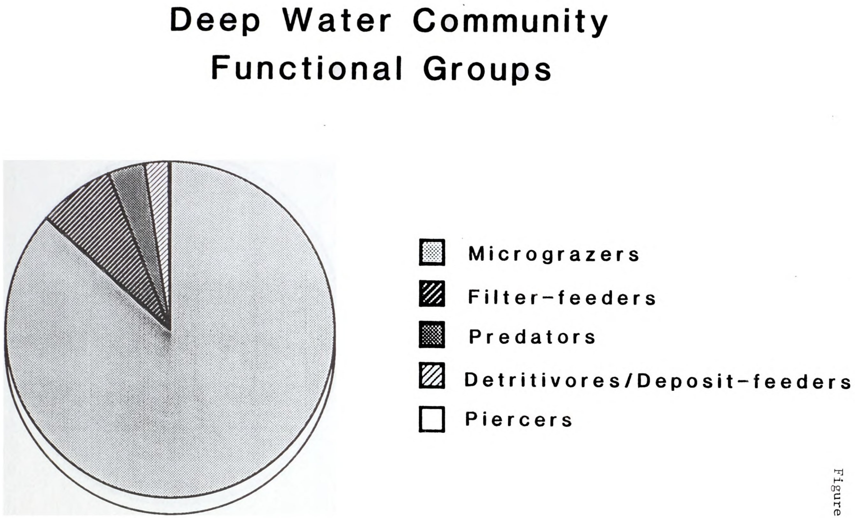

Deep Water Community
Functional Groups
Micrograzers
Filter-feeders
Predators
Detritivores/Deposit-feeders
Piercers

Figure 17A.

Shallow Water Community
Functional Groups

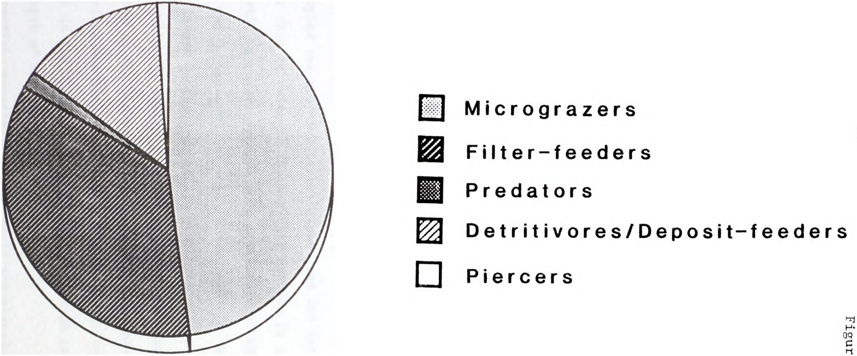


Figure 17B.

habitat at NS, especially in early to mid summer. This habitat had slower current velocities than either of the midchannel habitats suggesting that YOY prefer or simply aggregate in areas with slower currents as they may be more readily swept away than adults. In addition, the macrophyte cover in this habitat probably provided greater protection from predators than just cobbles. The data from HRS suggest that current velocity may not be as important a factor as depth in YOY distribution. Current velocities across the shallow habitat were comparable to those for the two midchannel habitats at NS. However, the YOY may experience lower current velocities if they remain beneath the Cladophora/Potamogeton mat. I should point out that there were slow current velocities in deep water at HRS which supports the idea that YOY O. propinquus avoid deep water regardless of current velocity.

This study is only the second to demonstrate a pronounced size-specific, depth distribution in a stream-dwelling crayfish population. While Van Deventer (1937) observed a similar segregation, he qualitatively sampled the crayfish with a dipnet and did not quantify depth other than to refer to the habitats as deep or shallow. Butler and Stein (1985), however, documented a preference of YOY Orconectes rusticus and O. sanborni for shallow streambanks. They also found that the larger O. rusticus adults preferred deeper pools but found that the smaller O. sanborni adults preferred streambanks over pools, especially in the presence of O. rusticus. An important feature of the distributions described here is the fact that there is a fairly sharp break in the distributions of small and large crayfish which occurs at a depth of approximately 20 cm. Small, young-of-the-year crayfish, especially in the early and midsummer periods, were most abundant in water less than 20 cm deep. Large crayfish (those greater than 20 mm CL) were most commonly encountered in water greater than 20 cm deep. These disjunct distributions suggest that the two size classes are avoiding one another and possibly other habitat-specific predators.

A number of studies have found that size classes of stream fishes often segregate by depth (Power 1984, 1987, Mahon and Portt 1985, Matthews et al. 1986, Schlosser 1982, Lobb and Orth 1988) or that smaller species are found in shallow water while larger taxa are more abundant in deep habitats (Schlosser 1987). Risk associated with two different groups of predators appears to be responsible for this pattern. Small species or individuals are more abundant in shallow water where the risk of predation by larger piscivores is reduced (Power 1984, Schlosser 1987, 1988). On the other hand, the larger species, including the piscivores, appear to be confined to deeper water as their size makes them more visible and therefore more vulnerable to terrestrial predators, particularly fish-eating birds such as herons and kingfishers (Power 1984, 1987). These terrestrial predators thus appear to generate a shallow water refuge for smaller fish. Large and small Orconectes propinquus may be responding in a similar fashion to this same sort of dual predator regime in Augusta Creek.

Large aquatic predators (brown trout, Salmo trutta, and creek chub, Semotilus atromaculatus) were most frequently seen in deeper pools and occasionally in runs (=raceways) if there was sufficient cover (J. Dexter, Michigan DNR, pers. comm., Creed, pers. obs.). These observations of large piscivores in deeper water is consistent with those made by other researchers (Barber and Minckley 1971,

Newsome and Gee 1978, Power 1984, 1987, Matthews et al. 1986, Schlosser 1988). Other common fish species, the mottled sculpin, *Cottus bairdi*, johnny darters, *Etheostoma nigrum*, and blacknosed dace, *Rhinichthyes atratulus*, were also more commonly encountered in water greater than 20 cm deep. White suckers, *Catostomus commersi*, were only seen in deeper water and this species was patchily distributed in Augusta Cr. All of these species could easily consume YOY crayfish and may account for the reductions in YOY abundance over the summer.

While creek chub and brown trout are known to consume crayfish to some extent (Pentelow 1932, Penn 1950, Barber and Minckley 1971, Newsome and Gee 1978), only very large brown trout could possibly consume large (> 20 mm CL) crayfish. Momot (1967) noted that only trout longer than 23 cm fed on crayfish and they were consuming only YOY crayfish. Gowing and Momot (1979) also found that trout only consumed YOY's in three Michigan lakes. Indeed, Stein (1977) found that 30 cm smallmouth bass, a crayfish specialist, had difficulty consuming adult *O. propinquus*. Brown trout, particularly large fish (>30 cm Total Length), do not appear to be exceedingly abundant (0.15 total trout/meter of stream, or 0.021/m^2) in Augusta Cr. (Coon and Watkins, unpublished report, Creed, pers. obs). Only 2 trout longer than 37 cm were found in Augusta Cr. Hopkins (1970) reported that brown trout consumed no crayfish in a New Zealand stream despite crayfish being abundant. Large creek chub (105 - 140 mm standard length) sampled by Newsome and Gee (1978) contained crayfish with carapace lengths ranging from 10 - 20 mm, i.e., they were only consuming young-of-the-year crayfish. Common terrestrial predators in the Augusta Creek watershed include great blue herons, green herons, kingfishers and racoons (Creed, pers. obs.). All of these predators

are known to prey on crayfish (Barbour and Davis 1974, Dearborn 1932, Lagler and Lagler 1944, Eipper 1956, Martin et al. 1961, M. Johnston, pers. obs.), especially green herons and racoons. Other potential predators of crayfish observed in or around Augusta Creek include Northern water snakes (*Nerodia s. sipedon*), Queen snakes (*Regina septemvittata*), snapping turtles (*Chelydra serpentina*), map turtles (*Graptemys geographica*), bowfin (*Amia calva*) rock bass (*Ambloplites rupestris*) (T. Coon, pers. comm), and mink (*Mustela vision*). All of these predators were rarely encountered (i.e., not seen on more than one or two occasions) during the four summers that I worked on Augusta Cr. with the exception of *N. sipedon*. A few northern watersnakes (1-3) were seen each summer except in 1989 when I saw 15. Finally, one additional predator of *O. propinquus* deserves mention and that is *O. propinquus* itself. Large crayfish will readily cannibalize smaller individuals and the reduced overlap between these size classes is probably as much an avoidance of cannibalism as of predation by larger fish.

Cladophora abundance was consistently related to depth in both sets of surveys. Shallow waters are generally characterized as having increased light levels and faster currents than deeper waters. In a clear stream like Augusta Creek where depths of cobble-bottomed riffles and runs rarely exceed 50 cm, differences in penetration of light to shallow and deep substrates is probably minor. Current regime is obviously important to an alga as it influences the rate at which nutrients are replenished in the surrounding water (Whitford and Schumacher 1961) and the amount of sedimentation to which the algal mat is subjected. While there was a positive correlation between current velocity and *Cladophora* abundance in 1988 this correlation was weaker than that for depth. This was due to substrates under similar current regimes but at different depths varying considerably in the amount of attached Cladophora. The primary importance of depth was confirmed in the multiple regression analysis, although current velocity had a small but significant contribution to the regression model. These patterns of Cladophora cover and biomass strongly suggest that some biological interaction that is correlated with depth is controlling Cladophora abundance.

The pattern of Cladophora distribution with respect to depth that I have observed in Augusta Creek is similar to patterns of algal abundance seen in Panamanian and Oklahoma streams (Power 1984, 1987). The patterns observed by Power resulted from large herbivores avoiding areas of high predation risk which were often shallow habitats. This suggests that the pattern of Cladophora distribution in Augusta Creek may be a consequence of the differential habitat use recorded for large Orconectes propinquus. If this is indeed the case, then crayfish may also influence the distribution and abundance of macroinvertebrates in the stream since macroinvertebrate communities that differ with respect to relative abundance of various taxa and functional groups were associated with these distinct differences in Cladophora distribution. The role of crayfish in influencing the distribution and abundance of Cladophora and other benthic algae will be addressed in the next chapter. The consequences for the macroinvertebrates will be explored in Chapter Four.

Chapter Three

DIRECT AND INDIRECT EFFECTS OF CRAYFISH ON BENTHIC ALGAE

INTRODUCTION

The patterns of distribution and abundance of crayfish, *Cladophora*, and macroinvertebrates described in Chapter Two are consistent with the hypothesis that the positive association between crayfish and several micrograzer taxa is the result of crayfish essentially excluding *Cladophora* from deep water. However, being consistent does not prove causation. An alternative explanation is that physical factors correlated with depth, i.e., decreasing light intensity or current velocity, were actually responsible for this pattern of *Cladophora* distribution. It is crucial then to evaluate the relative effects of these alternative processes, crayfish vs. abiotic factors, in generating these patterns in Augusta Creek before examining the other interactions in the system. In this chapter I will focus on the interaction between crayfish and *Cladophora* and the consequences of this interaction for the remainder of the benthic algal community, specifically the epilithic diatoms.

MATERIALS AND METHODS

Crayfish-Cladophora Interactions

Two field experiments were conducted to evaluate the effect of

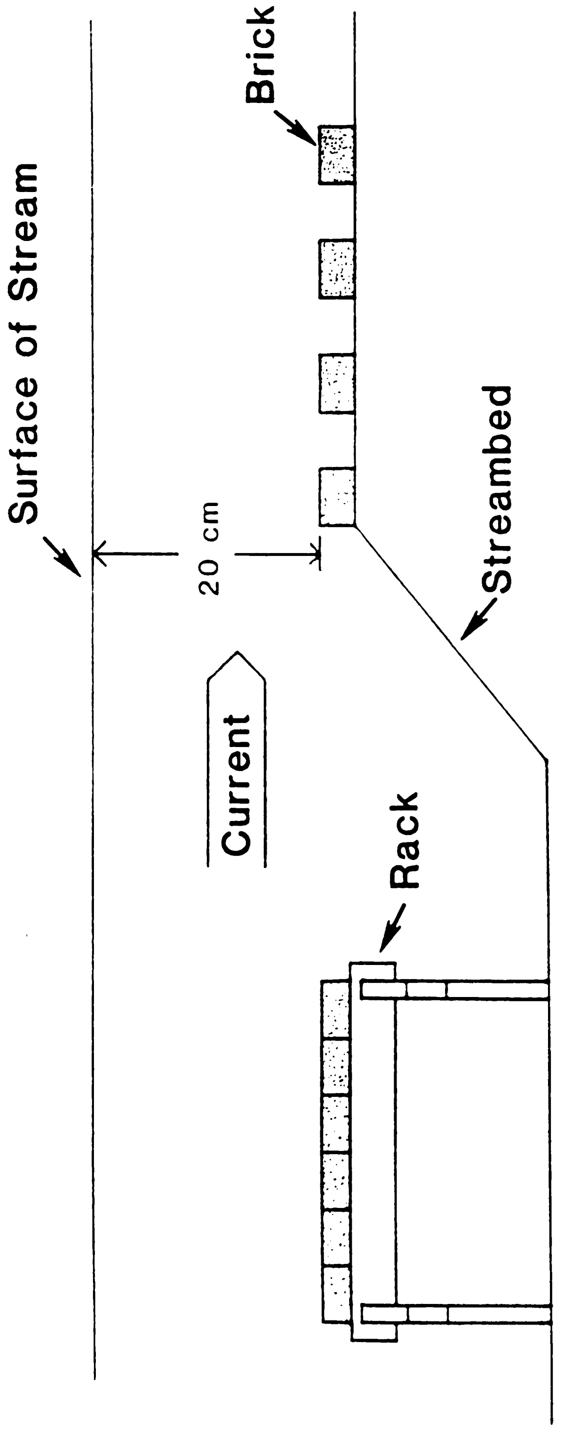
crayfish grazing on the distribution and abundance of *Cladophora*. The experiments differed by the fact that one (Experiment 1) examined the response of *Cladophora* to the exclusion of crayfish when abiotic factors (current velocity and depth) were held constant. The second (Experiment 2) was designed to compare the relative importance of these same environmental factors *versus* crayfish grazing in determining the distribution and abundance patterns of *Cladophora*.

EXPERIMENT 1. This experiment was conducted in the late summer/early autumn of 1987. Initially, 18 conditioned (i.e. they had well-developed marl layers), concrete bricks (9 X 9 X 9 cm) were scrubbed clean with a stiff, nylon bristle toothbrush which removed all visible *Cladophora* and macroinvertebrates. Three of these bricks were selected at random and sampled for initial percent cover, density and biomass of *Cladophora*. The remaining 15 bricks were placed on the stream bottom in a 35 cm deep reach (mean depth to top of bricks was 24.5 cm initially) with current velocities that ranged from 27-42 cm/s during the course of the experiment. After one week, three of these bricks were sampled. Of the remaining 12 bricks, 6 were removed to a crayfish-free rack (Figure 18). The rack was placed in deeper water so that depths of all bricks were similar. Crayfish were excluded by wrapping the legs of the rack with 10 cm long sheets of smooth, aluminum sheet metal. Depth of the water to the top of the bricks in the rack was initially 20 cm. Current velocities around the rack at brick level were very similar to those of the streambed site (range 29-44 cm/s). I picked up and replaced the 6 streambed bricks to insure that all bricks had been treated similarly. *Cladophora* was sampled from just the uppermost surface of the bricks.

In order to determine the extent to which the response of

Figure 18. Layout of Experiment 1 conducted at Nagel's Site in 1987.

Figure 18.



Cladophora was due to regrowth by existing thalli vs. colonization by new individuals, new (=unconditioned) bricks were placed in rows in the rack and on the stream bed. These bricks were treated in the same manner as the others except that they were sampled the day after conditioned bricks for all three sample dates.

A row of three bricks was sampled from both the streambed and the rack at two and four weeks for percent cover, density and biomass of Cladophora on the upper surface of the bricks. Percent cover was determined by laying a grid of 1/4 in mesh hardware cloth on top of the brick and counting the number of squares which were more than half covered by Cladophora. Biomass as AFDW was ascertained in the same fashion as for the surveys; all thalli were removed from the tops of the bricks and preserved in 2% Lugols. Again, small amounts of Cladophora were placed on GF/F filters while larger quantities were placed in ceramic crucibles. All sediments (material remaining on brick after Cladophora was removed) from the brick tops were removed to assess silt accumulation in the presence and absence of Cladophora. Sediments were ashed at 550^{o} C and the remaining material (the inorganic sediment) was considered silt. Finally, numbers of two sessile, grazing caddisflies, Leucotrichia pictipes and Psychomyia flavida, on all brick tops were recorded. Treatment effects were compared using a one-tailed t-test (PROC TTEST, SAS Institute). Percent cover data were arcsine transformed; AFDW data were log transformed.

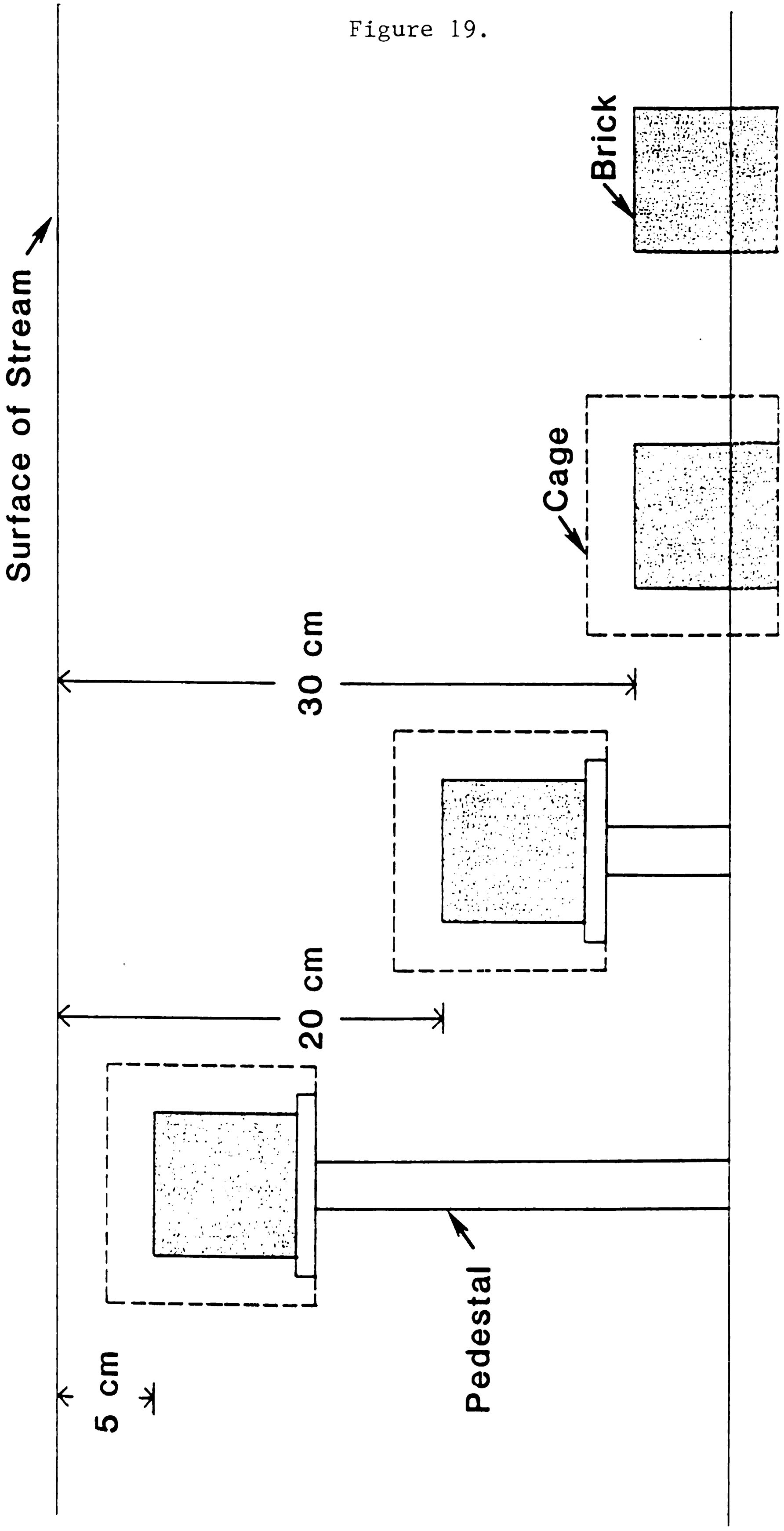
EXPERIMENT 2. Since physical factors such as current velocity and light intensity could influence the distribution and abundance of Cladophora, I designed a second experiment to compare their importance relative to crayfish grazing. The impetus for this experiment came

from the results of the 1987 Cladophora surveys which showed a strong negative relation between Cladophora abundance and depth (see Chapter Two). Since both light intensity and current velocity decrease with depth, it was possible that the observed pattern of Cladophora abundance was simply due to an inability of Cladophora to grow in deep water. Alternatively, if large crayfish spend most of their time in deeper water in an attempt to avoid terrestrial predators (e.g. Power 1987), this could also result in the observed pattern of Cladophora distribution.

This experiment was conducted in late June/early July of 1988. There were four treatments that spanned the range of depths in the stream (see Figure 19). Conditioned, concrete bricks were placed at 5, 20 and 30 cm deep (depth to top of brick). The 5 and 20 cm deep bricks were placed on wooden pedestals, the two 30 cm deep bricks were on the bottom. Crayfish were excluded from the 5, 20 and one set of the 30 cm deep bricks by enclosing the bricks in cages constructed of 1/4 in mesh hardware cloth. The fourth treatment was simply uncaged bricks placed on the bottom. Cages permitted access to all small invertebrates including young-of-the-year crayfish. Only large crayfish and fish were excluded from the substrates. At the initiation of the experiment twenty seven bricks were scrubbed with a stiff, nylon bristle toothbrush. Three bricks were chosen at random for an intial sample. The remaining 24 bricks were placed into 6 rows which contained each of the four treatments. The cages were cleaned two or three times a day. Current velocity (at the depth of the rock top) was measured at Rows 1, 3, and 5 when the experiment was initiated (22 June 1988) and at two weeks (5 July 1988). Mean current velocities in cm/s (± 1 S.E.) at shallow (5 cm), intermediate (20 cm)

Figure 19. Layout of Experiment 2 conducted at Nagel's Site in 1988.

Figure 19.



and above the bottom (30 cm), respectively, were as follows: 22 June - 21.0 (2.5), 8.7 (1.9) and 7.0 (0.6); 5 July - 20.5 (1.7), 13.5 (2.1) and 9 (1.6).

The experimental design was a randomized complete block design with four treatments and three replicates per treatment. I intended to collect three rows of bricks at two and four weeks after the initiation of the experiment. However the drought of 1988 resulted in the exposure of the 5 cm deep treatment by week three so I discontinued the experiment. Bricks were placed in individual containers on a sample date and returned to the laboratory. Percent cover was estimated as before using a grid of 1/4" mesh hardware cloth. Then all thalli were removed from the top of the brick and placed in individual vials and preserved in a 2% Lugols solution. Cladophora AFDW was also determined as before. Data for percent cover and AFDW were all analyzed using an ANOVA (PROC ANOVA, SAS) with planned, orthogonal contrasts to determine treatment effects. Percent cover data were arcsine transformed; AFDW data were log transformed for ANOVA.

Crayfish Cafeteria Experiments

To insure that crayfish were indeed consuming Cladophora and ascertain the amount they were able to ingest in a 24 hr period, I conducted two, simple cafeteria experiments. Large (>20 mm CL) and young-of-the-year crayfish were tested in separate experiments. Twenty four hours prior to the intiation of each experiment, 4 crayfish, either large adults or young-of-the-year, were collected, measured and weighed to the nearest milligram on a Sartorius

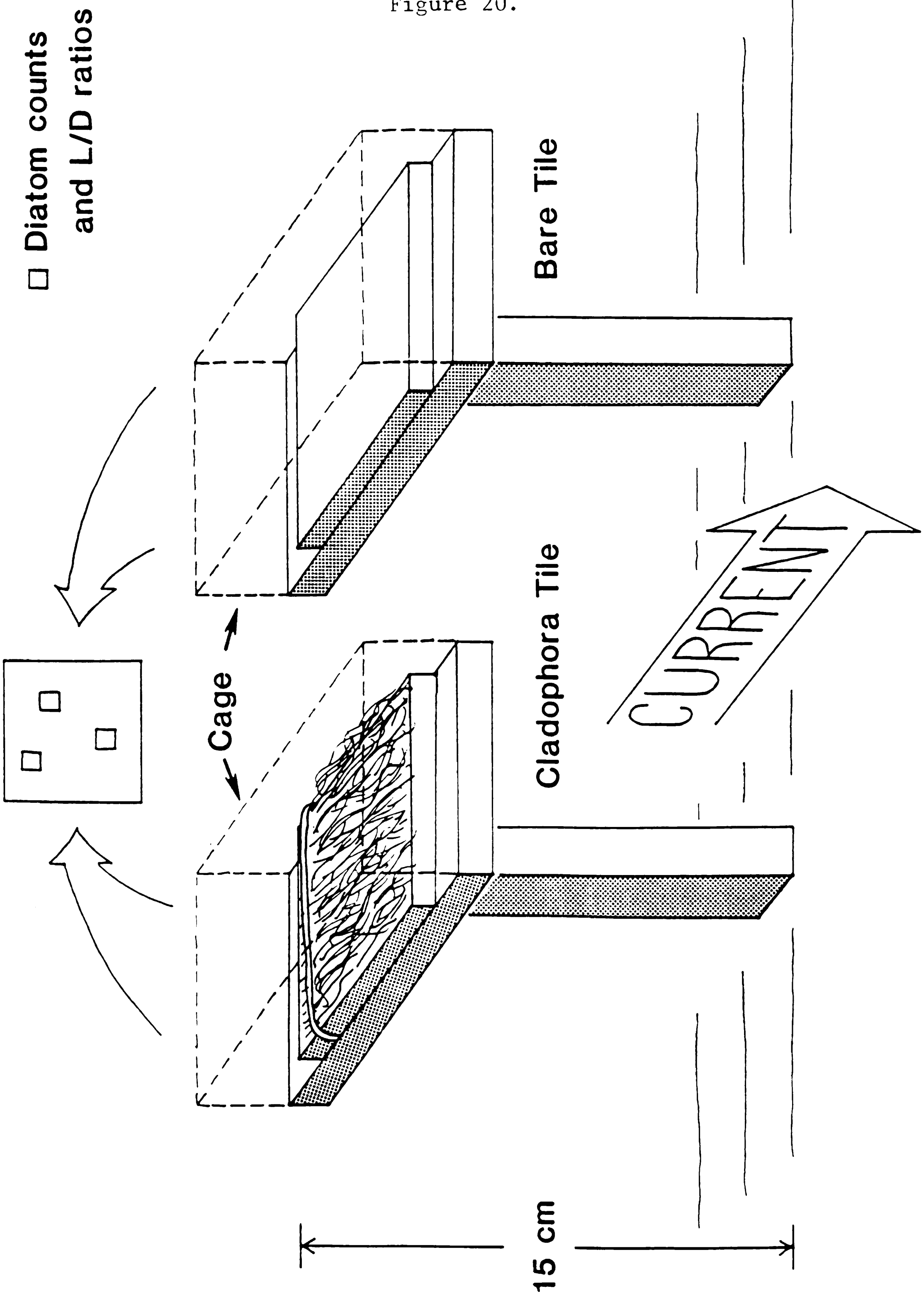
electrobalance (blotted wet weight), and then placed into separate flow-through containers in a single, well-aerated aquarium (light:dark schedule 16:8). Large crayfish used in the experiment were 27-29 mm CL, mean weight ($\pm$ 1 S.E.) = 7.669 $\pm$ 0.1705 g; YOY were 13-15 mm CL, mean weight ($\pm$ 1 S.E.) = 0.619 $\pm$ 0.034 g. Crayfish were starved for 24 hours prior to the the intiation of the experiment. The following day I collected a large quantity of Cladophora from Snyder's Site. The Cladophora was separated into 8 equal clumps, blotted dry for 45 seconds, and then weighed on a Sartorius electrobalance. Equal amounts of Cladophora were placed into eight flow-through containers, four of which already contained the starved crayfish. Crayfish were allowed to feed for 24 hours. Then all containers were removed and the Cladophora was reweighed. The amount of Cladophora remaining was compared using a one-tailed t-test (PROC TTEST, SAS). Water temperature in the aquaria during these trials was 18° to 20° C.

Cladophora - Diatom Experiment

One of the potential consequences of Cladophora overgrowing stream substrates is a reduction in the abundance of other epilithic algae such as diatoms, which are a principle food source for many aquatic grazers (Shapas and Hilsenhoff 1976, Merritt and Cummins 1978, Oemke 1983, Gregory 1983). In this experiment I evaluated the effect of Cladophora "mats" on colonization of hard substrates by lotic diatom taxa. The substrates used in this experiment were new, 9 X 9 cm, unglazed, ceramic tiles. Tiles were placed on top of 15 cm high pedestals which were situated in the long reach above the bridge at Nagel's Site (Figure 20). Depth of the water to the tiles generally

Figure 20. Layout of *Cladophora*-Diatom interaction experiment conducted at Nagel's Site in 1988. Square above pedestals represents a sampled tile with three 1 cm^2 subsamples removed for analysis of diatoms.

Figure 20.


□ Diatom counts
and L/D ratios
Bare Tile
Cage
Cladophora Tile
CURRENT
15 cm

ranged from 25 - 30 cm, although it did increase to 45 cm deep during one storm. Current velocity was not measured for this experiment. The rationale for elevating the substrates was that confounding effects of sedimentation and invertebrate grazing on diatom abundances were reduced. However, micrograzers still had access to the tiles but only Baetis were commonly observed on them; Goniobasis were observed on the tiles occasionally.

On half the tiles (the Cladophora tiles), an artificial Cladophora mat was created by tying down a standard amount of Cladophora to the upstream end of the tile. (note: these "mats" averaged about 1.1 - 1.2 g dry weight Cladophora. Estimates of weights were based on three extra "mats" returned to the lab and ovendried at 105° C. Assuming an ash weight that is 45% of dry weight, these amounts translate to approximately 80 g/m^2, a value well within the range of natural Cladophora abundance for shallow, ungrazed substrates in Augusta Creek). The remaining tiles were left bare (Bare tiles). A total of 8 tiles was used in this experiment. To prevent crayfish from eating the Cladophora "mats", cages were placed around all 8 tiles. Tiles were arranged in a randomized block design with a tile from each treatment in each of four rows. The experiment was initiated on 4 September 1988, and terminated 18 days later, which is enough time for development of a considerable diatom mat in Augusta Creek. Tiles were placed in individual containers full of water, placed in a cooler and returned to the laboratory. Lugols was added to each container and then the containers were placed in a refrigerator until the tiles were processed.

Three one cm^2 areas from each tile were selected for diatom samples using a random number table and a grid. Each area was

carefully scraped with a scalpal, followed by a dissecting probe, to remove as many of the diatoms as possible. This material was gathered onto the scalpel blade and then placed directly onto a drop of Karo^{TM} syrup mounting medium (20:1 syrup to formaldehyde, see Stevenson 1984) where it was swirled around in order to evenly distribute the diatoms throughout the mounting medium. Slides were allowed to sit until the mounting medium was fairly dry and then the edges of the slides were sealed with clear, nail polish.

Five rows were selected at random for each slide and every diatom was counted in a transect across the slide at 400X. This resulted in the enumeration of diatoms from approximately 10 - 12 percent of the slide surface area. Diatoms were identified to genus when possible. All diatoms encountered, whether live or dead, were noted, thus allowing me to assess the relative health of the diatom assemblage by calculating live/dead ratios. Mean densities of the more abundant taxa and live/dead ratios were calculated for each slide. These values were then combined to produce a mean value for each tile. Differences in densities of the dominant taxa and live/dead ratios between treatments were compared using ANOVA (PROC ANOVA, SAS Institute). Diatom density data were log transformed.

RESULTS

Crayfish - Cladophora Interaction: Experiment 1

<u>Cladophora</u> responded rapidly to the exclusion of crayfish. After two weeks mean percent cover for bricks from the exclusion rack was 62%; after four weeks all three exclusion bricks were almost entirely

covered (Figure 21A). For the same interval the percent cover of Cladophora never exceeded 6% for the streambed bricks. Differences between the two treatments were highly significant on both dates (t-test, 4 df: 2 weeks t = 9.5548, $p<0.0007$; 4 weeks t = 28.7466, $p<0.0001$). Cladophora biomass increased in both treatments relative to initial abundance (Figure 21B), however, AFDW for streambed bricks plateaued at a value of about 1 gram per m^2 while AFDW values for exclusion rack bricks averaged about 25 g per m^2 after 4 weeks. On both sample dates Cladophora AFDW was significantly greater on the exclusion rack bricks (t-test on log transformed data, 4 df: 2 weeks t = 5.6242, $p<0.0049$; 4 weeks t = 8.1670, $p<0.0012$). Density of Cladophora thalli (Figure 21C) was significantly higher on exclusion rack bricks for both sample dates (t-test, 4 df: 2 weeks t = 9.0671, $p<0.0008$; 4 weeks t = 9.2147, $p<0.0008$).

Both treatments showed a decline in thallus numbers from the 2 week to the 4 week sample. This decline in density is probably the result of two different processes. Most of the thalli that appeared on the bricks were probably regrowth from prostrate Cladophora tissue that remained in and on the rock surface after the scrubbing. As can be seen from Figure 21C, there is a marked increase in visible thalli abundance after the first week, however, all of these thalli were quite small with few more than 4 mm long (pers. obs.). On September 27 the number of thalli had continued to increase on the exclusion bricks while they had begun to decrease on the exposed streambed bricks. This appears to be the result of Cladophora thalli growing to a vulnerable size (> 4 mm high; see Chapter 2) on the streambed bricks at which point they were removed by crayfish. This trend continued over the following two weeks. While there was some colonization of

Figure 21. Results of Experiment 1.

A. Percent cover of *Cladophora* on rack and streambed bricks from Experiment 1 two and four weeks after manipulation. Means (± 1 S.E.) are shown.

B. Biomass of *Cladophora* on rack and streambed bricks from Experiment 1 two and four weeks after manipulation. Means (± 1 S.E.) are shown.

C. Number of *Cladophora* thalli on rack and streambed bricks from Experiment 1 two and four weeks after manipulation. Means (± 1 S.E.) are shown.

D. Abundance of silt on rack and streambed bricks from Experiment 1 two and four weeks after manipulation. Means (± 1 S.E.) are shown.

* $p<0.05$, ** $p<0.01$, *** $p<0.005$,

Figure 21A.

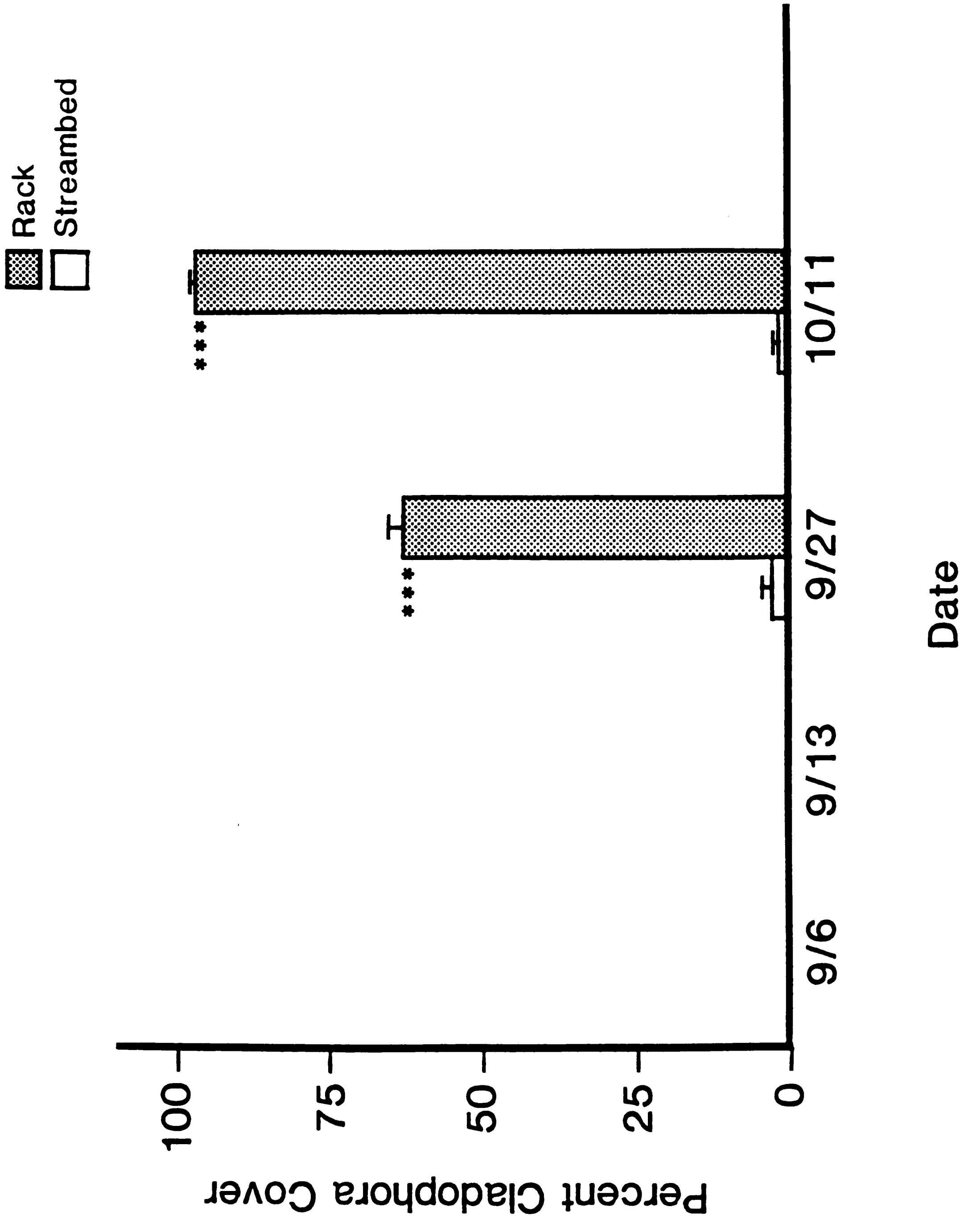

Rack
Streambed
Percent Cladophora Cover
100
75
50
25
0
9/6
9/13
9/27
10/11
Date
***
***

Figure 21B.

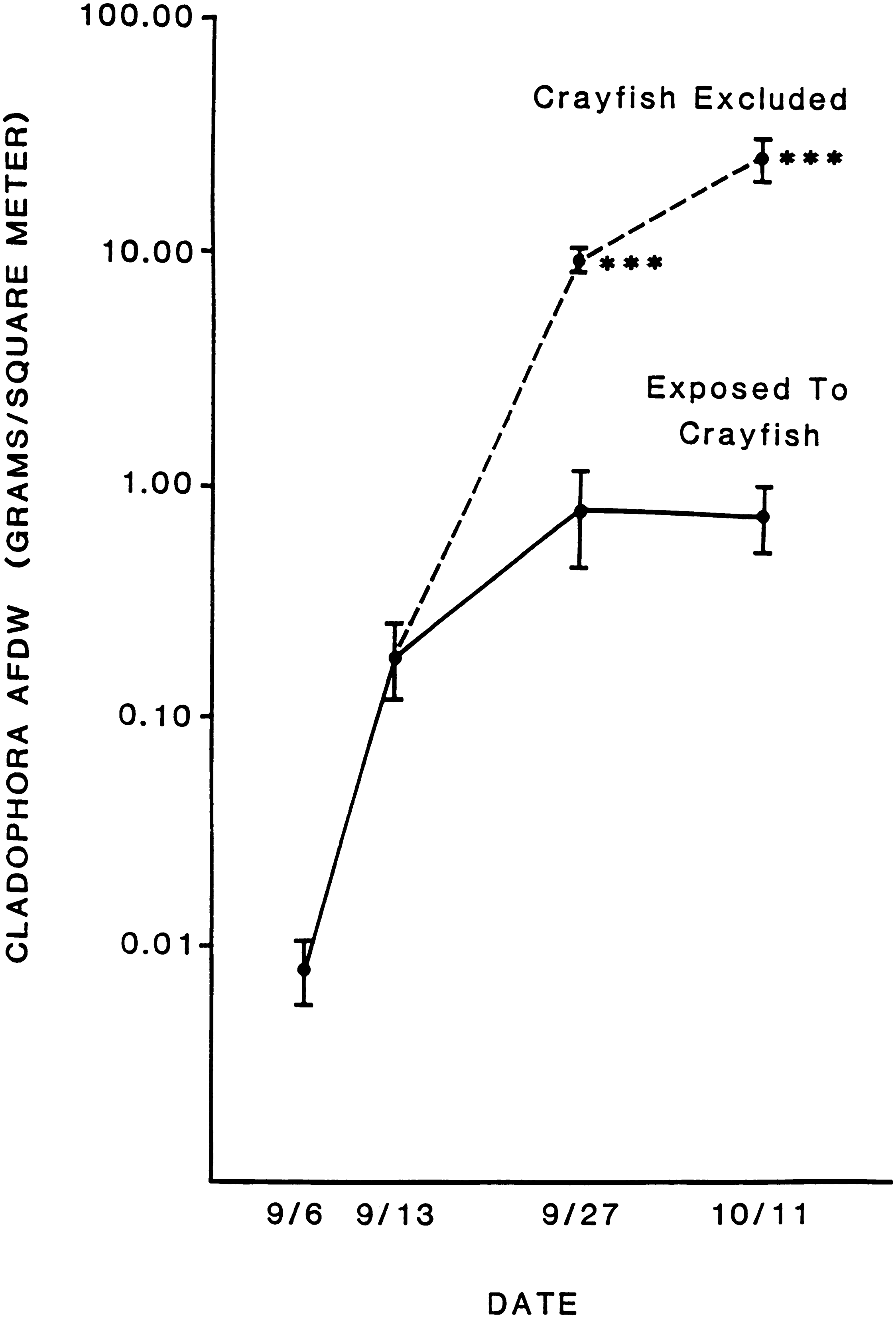

CLADOPHORA AFDW (GRAMS/SQUARE METER)
100.00
10.00
1.00
0.10
0.01
Crayfish Excluded
Exposed To Crayfish
***
***
9/6
9/13
9/27
10/11
DATE

Figure 21C.

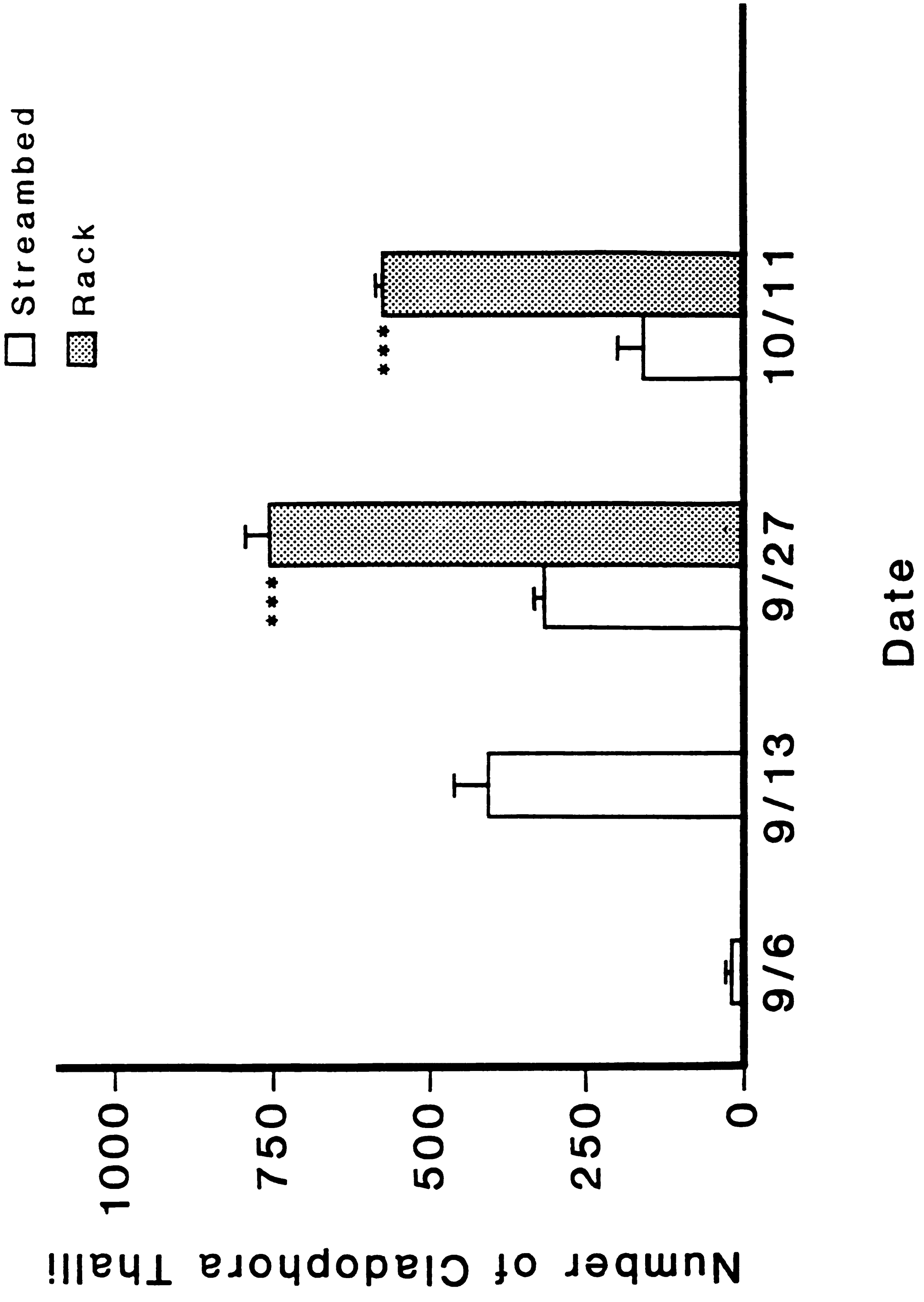
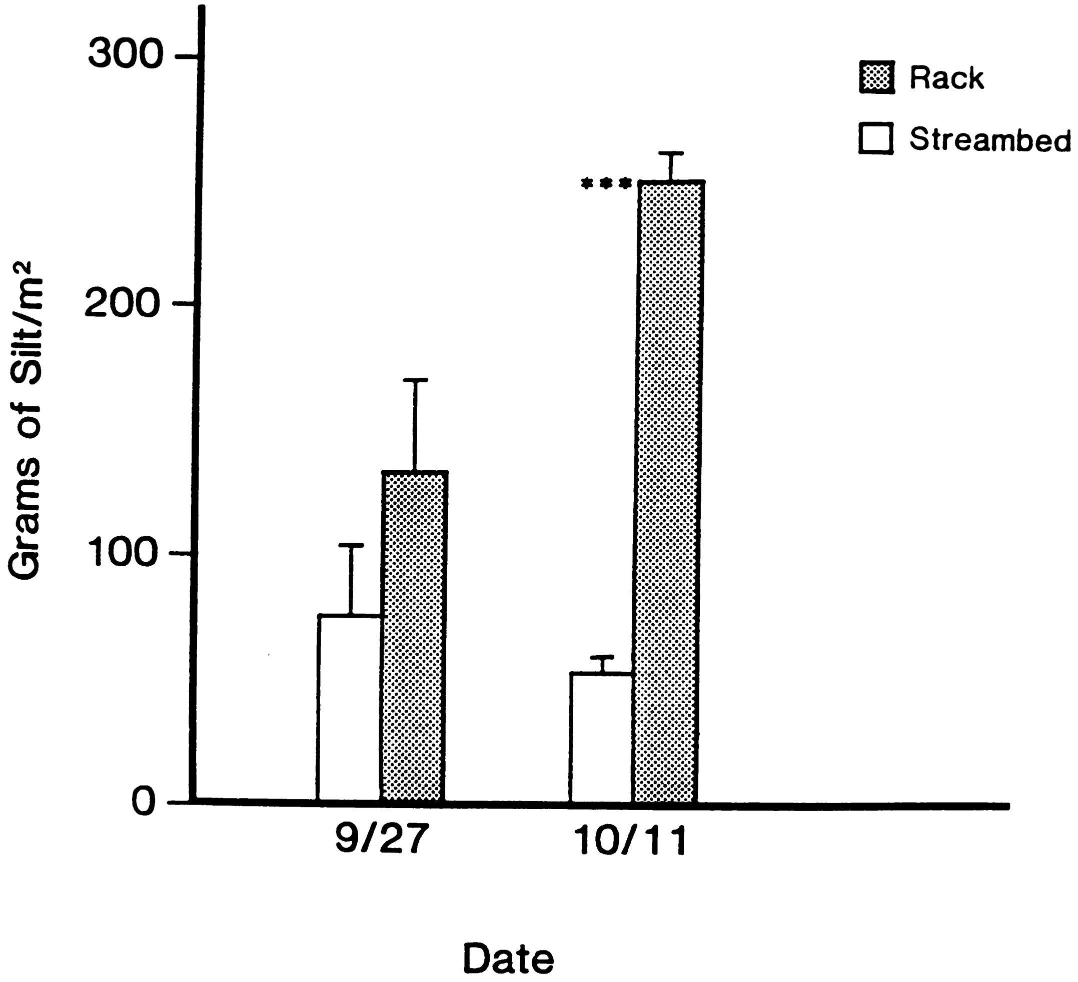

☐ Streambed
▨ Rack
Number of Cladophora Thalli
1000
750
500
250
0
9/6
9/13
9/27
10/11
Date
***
***

Figure 21D.



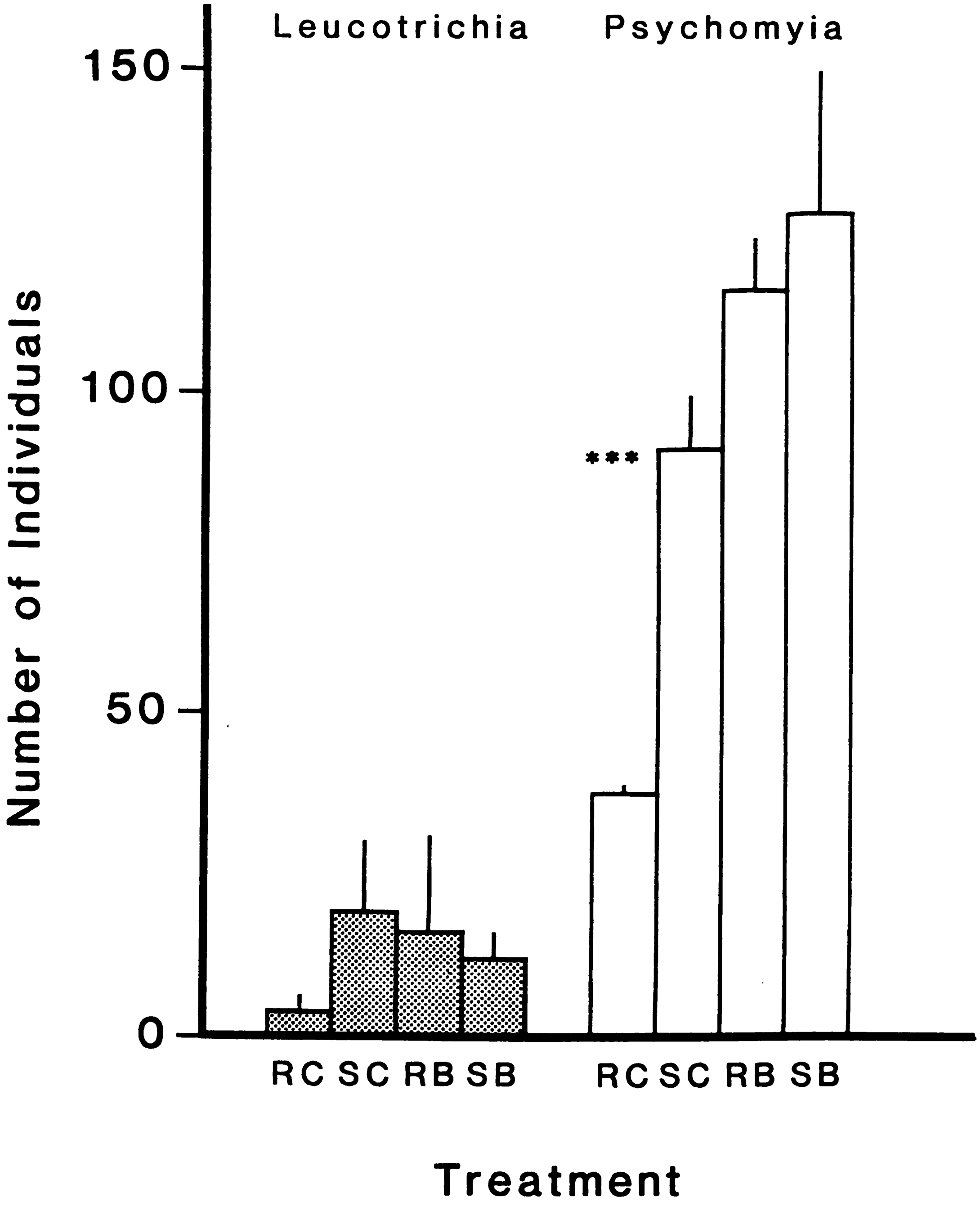
the bare bricks on the rack and the streambed (mean number of thalli per bare brick ranged between 34.3 - 51.7 for both treatments), the rate of colonization by Cladophora was obviously not great enough to counter the grazing losses. The decrease in thalli numbers on the exclusion rack bricks was probably due to both self-thinning of the Cladophora, i.e., large thalli shaded out small thalli as the mats developed, and a decrease in my ability to discriminate individual thalli from one another as the mat developed and individual thalli were closer together.

The presence of Cladophora on a rock surface had a significant effect on the accumulation of silt on the rock (Figure 22D). Cladophora-covered bricks on the rack had more silt than streambed rocks on both dates. The difference was significant after four weeks ($t = 14.9000$, $p<0.0001$) when the Cladophora-covered rack bricks had five times as much silt as the streambed bricks (Figure 21D). Even though the rack bricks were ~30 cm off the bottom they were able to accumulate more silt than the streambed bricks which were closer to the source of the sediment.

The two sessile micrograzers, Leucotrichia pictipes and Psychomyia flavida, were less abundant on the Cladophora-covered bricks of the exclusion rack after four weeks (Figure 22). Only the difference in Psychomyia abundance was significant, however (t-test, 4 df, $t = 6.3247$, $p<0.0032$). The reduced abundances of these two invertebrates on rack bricks was not a consequence of reduced immigration to the rack. The numbers of individuals of both species on the unconditioned bricks in the rack were similar to those for both brick types on the streambed (Figure 22). These two sessile species were thus avoiding substrates with substantial Cladophora cover. In fact, a number of

Figure 22. Numbers of *Leucotrichia* and *Psychomyia* larvae (Trichoptera) on the top of bricks after four weeks in Experiment 1. Means (± 1 S.E.) are shown. Treatments: RC - Rack, conditioned brick; SC - Streambed, conditioned brick; RB - Rack, unconditioned brick; SB - Streambed, unconditioned brick. * $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 22.


Leucotrichia
Psychomyia
150
100
50
0
***
RC SC RB SB
RC SC RB SB
Number of Individuals
Treatment

Leucotrichia had apparently colonized the conditioned rack bricks prior to the development of the Cladophora mats and later abandoned their cases (Creed, pers. obs.).

Crayfish - Cladophora Interaction: Experiment 2

Crayfish herbivory had a stronger effect on the development of Cladophora mats than any physical factors associated with increasing depth. Percent cover of Cladophora was 0% for the exposed bricks while it averaged 50% or greater for the other treatments (Figure 23A). While differences were observed in the percent cover of Cladophora over the range of depths, with greater cover on shallower bricks (Figure 23A), these differences were not significant ($F = 3.15$, $p=0.1509$). No statistical comparison could be made between crayfish exclusion treatments and the exposed treatment for percent cover due to the lack of variance for percent cover for the 30E treatment, i.e. all had 0% cover. A similar response was observed for Cladophora biomass (Figure 23B). While there was a trend toward decreasing Cladophora AFDW with depth in the exclusion treatments, the amount of Cladophora on the exclusion bricks at 30 cm was comparable to that on the 5 cm brick. The grazed brick, on the other hand, had almost two orders of magnitude less Cladophora biomass than the exclusion bricks (Figure 23B). The contrast between being exposed to crayfish or not accounted for the bulk of the sums of squares (98.8%, Table 5). Two additional observations suggest that these are fairly robust results. First, small one year old crayfish had access to the cages on the bottom (30 cm exclusion cages) and may have contributed to the reduced percent cover and biomass in this treatment. More importantly, I

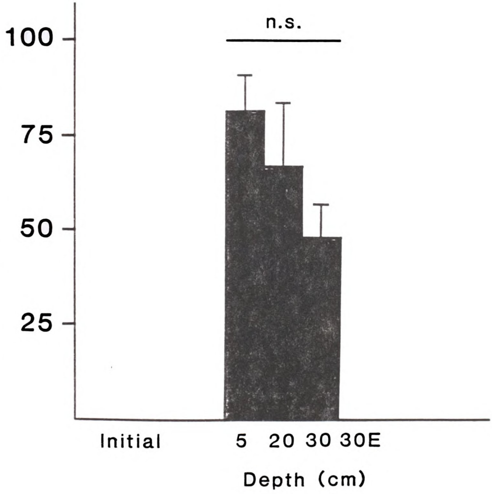
Figure 23. Results of Experiment 2.

A. Percent cover of Cladophora over a range of depths when crayfish are excluded (Treatments 5, 20 and 30 cm deep) compared to substrate exposed to crayfish (30E). Values are means (± 1 S.E.).

B. Biomass of Cladophora over a range of depths when crayfish are excluded (Treatments 5, 20 and 30 cm deep) compared to substrate exposed to crayfish (30E). Values are means (± 1 S.E).

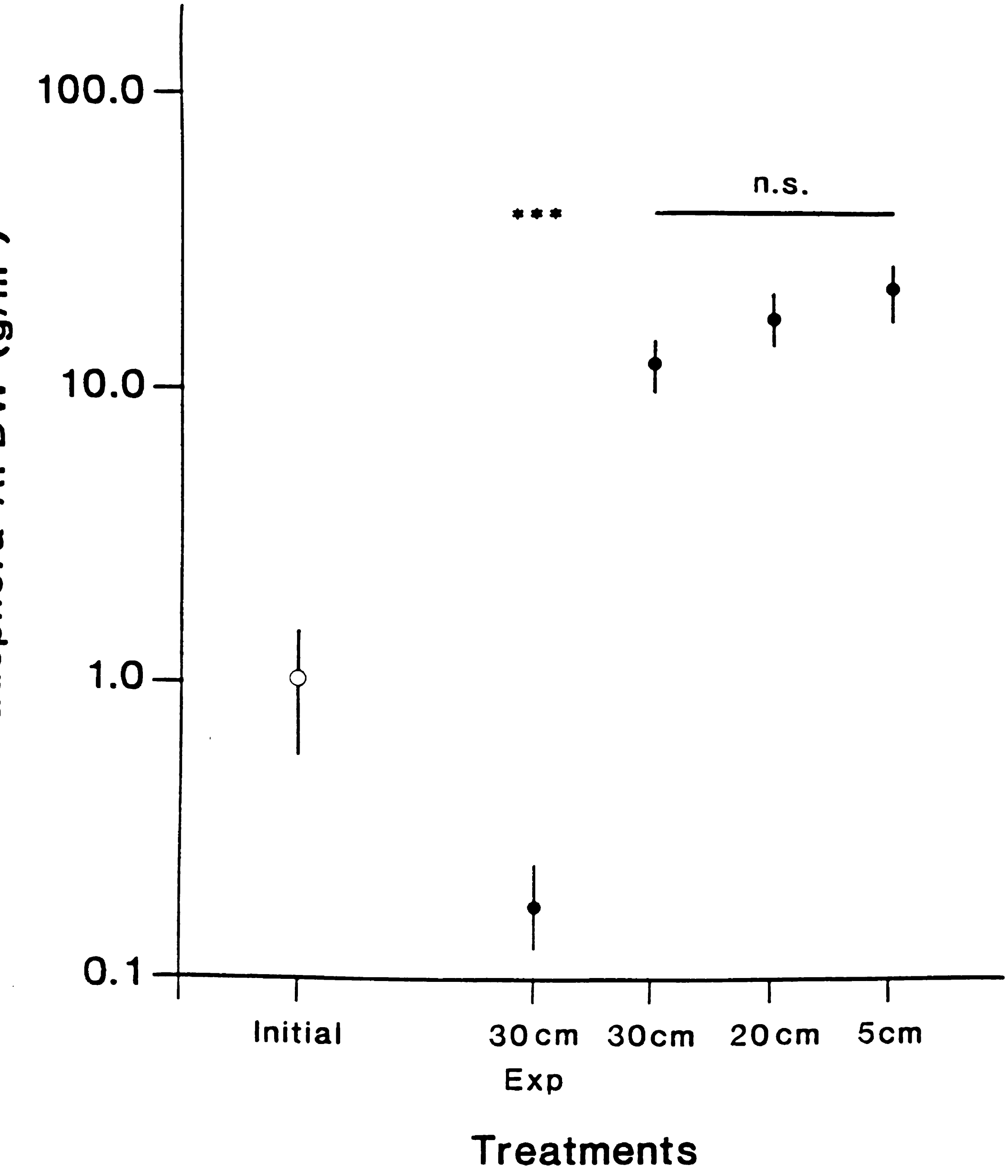
* p<0.05, ** p<0.01, *** p<0.005

Figure 23A.



E - Exposed to Crayfish

Figure 23B.



ble 5. ANOVA Table for *Cladophora* biomass (AFDW) from *Cladophora* owth by Depth Experiment (Experiment 2) with orthogonal contrasts.

urce	df	SS	MS	F
TAL	11	9.1223	----	
OCK	2	0.0173	0.0087	0.25 n.s.
EATMENT	3	8.8987	2.9662	86.27 ***
ONTRAST 1	1	8.7941	8.7941	256.38 ***
ONTRAST 2	1	0.0886	0.0886	2.58 n.s.
ONTRAST 3	1	0.0159	0.0159	0.46 N.S.
OR	6	0.2063	0.0344	

TRAST 1 = exposed to crayfish vs. crayfish excluded.

TRAST 2 = 5 and 20 cm substrates vs 30 cm (crayfish excluded).

TRAST 3 = 5 cm vs 20 cm substrates (crayfish excluded).

. $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.005$

lieve, was the location of the experimental site. Due to the fact at the stream level had already begun to fall when I selected the te, I chose as deep an area as I could find which turned out to be the downstream end of the pool above the reach at NS, which eloped a fairly heavy weed bed as the experiment progressed. The d bed slowed current velocities and this increased silt deposition, ecially on the deeper treatments, which undoubtedly inhibited dophora growth as well. Cladophora mats had to be "cleaned" iodically by waving a hand rapidly over the cage to remove some of s silt.

fish Cafeteria Experiment

Crayfish readily consumed Cladophora in these cafeteria-style riments. Large crayfish consumed approximately 90% of the ophora presented to them which was roughly 2.1 g apiece (Figure . This was about 30% of the animals body weight. YOY crayfish about 19% of the available Cladophora which averaged 0.181 g per ish (Figure 24B). This was 12 times less than the amount eaten rge crayfish. Again, the amount consumed was about 30% of the body weight. I should note that adults may be able to ingest than 30% of their body weight in 24 hours as 3 of the 4 boxes ined essentially no Cladophora at the end of the experiment.

hora - Diatom Experiment

e presence of a Cladophora mat had a strong, negative effect on atom community after eighteen days of colonization (Table 6).

Figure 24. A. Results of crayfish cafeteria experiment for adults. Values are mean amounts of Cladophora remaining (± 1 S.E.) after twenty four hours. W/O Cr - Without Crayfish, W/$\overline{C}$ - With Crayfish.

B. Results of crayfish cafeteria experiment for young-of-the-year. Values are mean amounts of Cladophora remaining (± 1 S.E.) after twenty four hours.

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 24A.

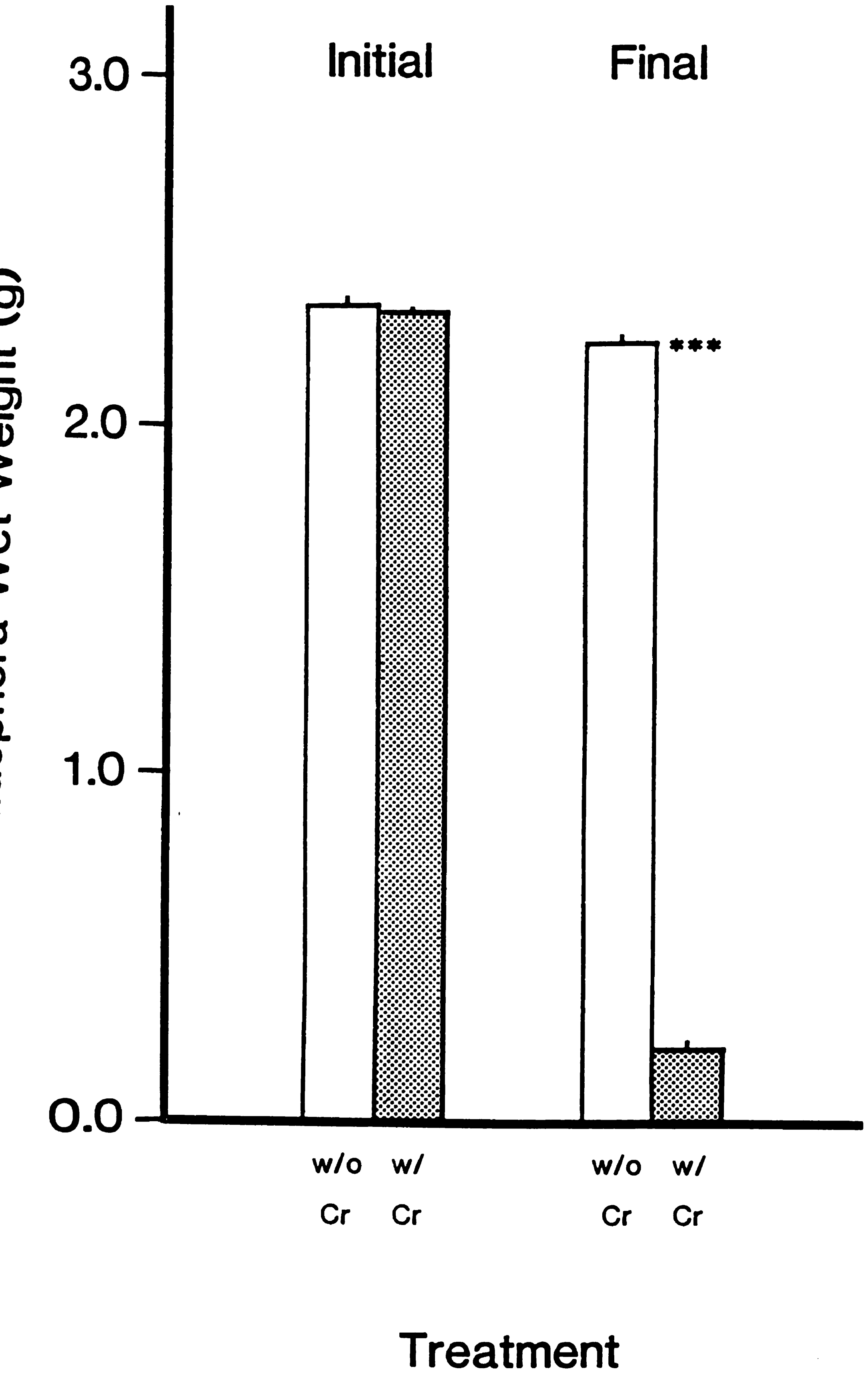
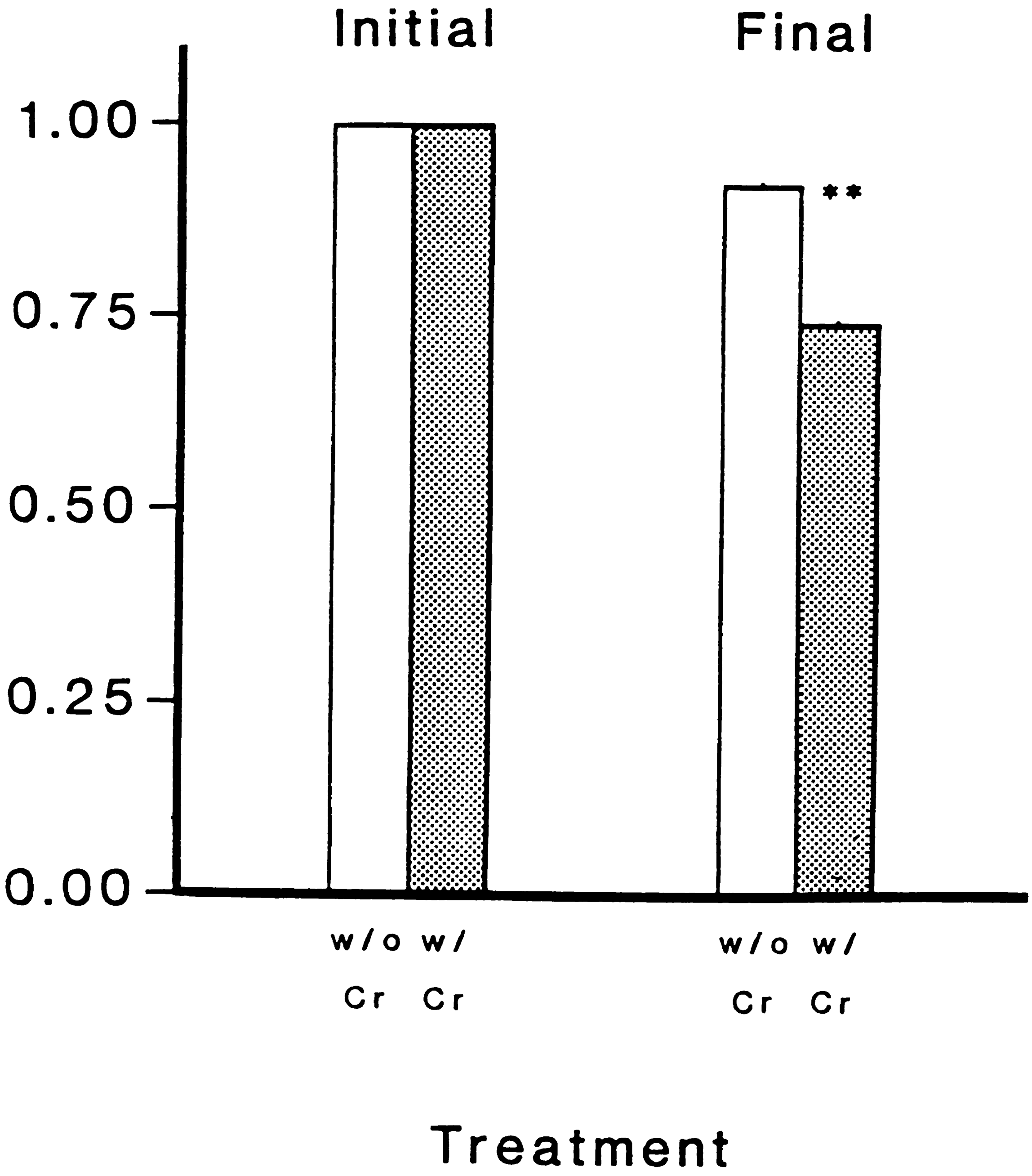


Figure 24B.


Initial
Final
1.00
0.75
0.50
0.25
0.00
**
w/o Cr
w/ Cr
w/o Cr
w/ Cr
Treatment

le 6. The influence of Cladophora on diatom colonization. Values the table, with the exception of the Live/Dead ratios, are diatom sities (No./mm^2) with one standard error in parentheses. The ANOVA performed on log transformed data.

iable	Cladophora Tile	Bare Tile	F Value	
al Live iatoms	24.6 (±7.1)	464.0 (±31.1)	47.17	**
e/Dead atios	2.9 (±0.4)	18.1 (±1.7)	120.57	***
coneis sp.	11.3 (±3.7)	314.8 (±32.0)	47.12	**
nanthes sp.	2.9 (±0.9)	120.5 (±11.1)	56.50	***
icula sp.	5.8 (±1.7)	8.1 (±1.5)	1.06	n.s.
toma sp.	0.3 (±0.1)	11.9 (±3.5)	28.93	**

. $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.005$

ısity of live diatoms was almost 20X less under *Cladophora* mats ıpared to bare tiles. Furthermore, the diatom community appeared to much healthier in the absence of *Cladophora* as there were nificantly more dead diatoms relative to live ones beneath the al mats. Three of the four most abundant diatom taxa (*Cocconeis*, *nanthes* and *Diatoma*) were also significantly more abundant in the ence of *Cladophora* mats (Table 8). *Navicula*, a mobile diatom, was only taxon to show no difference between treatments (Table 6).

DISCUSSION

Grazing by large crayfish (>20 mm CL) appears to be the primary tor influencing the distribution and abundance of *Cladophora* in the ısta Creek watershed. This conclusion is supported by the :ribution data for both crayfish and the alga and the experimental ılts. Survey results (Chapter 2) consistently showed a negative ıtion between the the percent cover and biomass of *Cladophora* with :h, with some influence of current velocity. Crayfish size class :ribution was also related to depth. Large crayfish were almost ys found in water deeper than 20 cm. When I did occasionally find ırge crayfish in shallow water they were almost always individuals had recently molted and still had soft exoskeletons (Creed, pers.). Young-of-the-year crayfish, on the other hand, were most dant in shallow water, especially early in the summer. Thus, *ophora* and large crayfish overlapped little in distribution but e was extensive overlap between *Cladophora* and YOY. This was cially evident at HRS and SS where considerable shallow habitat present. Unlike these two sites, at NS substrates less than 15 cm

leep are uncommon at normal water levels. Cladophora is consistently ibundant only on some large rocks which sit atop two dams at this ite. Current is fairly swift (>50 cm/s) across the top of these dams ind this, combined with large substrate size, make this an unsuitable iabitat for YOY.

The experimental results confirm the role of crayfish in creating this pattern of Cladophora distribution and abundance. Substrates inder almost identical environmental conditions (Experiment 1) that liffered only in exposure to crayfish had dramatically different ibundances of Cladophora. When substrates were exposed to different nvironmental factors that varied with depth, i.e., decreases in light ind current velocity with increasing depth, and crayfish were excluded (Experiment 2), an effect was observed but the magnitude of this ffect was small relative to crayfish grazing. Feminella et al. (1989) report similar results of effects of grazers vs. depth and current velocity on periphyton accrual in California streams. They concluded that differences between treatments in depth and current velocity had little effect on periphyton accrual relative to feeding by micrograzers.

The laboratory feeding trials demonstrated that crayfish would indeed consume Cladophora. Large crayfish are capable of consuming large quantities of Cladophora; the amounts they ingested in 24 hours were comparable to that which would cover a small to medium-sized rock. Small crayfish, while consuming roughly the same amount of Cladophora relative to their body weight (30%), ingested approximately 12 times less Cladophora than large individuals. The YOY crayfish used in this experiment were large YOY's, however, i.e., they were around the mean size for individuals captured late in the summer (see

ppendix D). Thus, the twelve-fold difference in the absolute amount ngested is the near the minimum difference that would be expected etween these size classes. Orzechowski (1973 cited in Momot et al. 978) found that adult crayfish consumed 50% of their body weight per ay while YOY consumed only 7%. The functional response for large rayfish therefore appears to be greater than that of small crayfish. his difference, combined with the fact that YOY may not be strong nough to rip Cladophora thalli off the rock surface and that YOY rayfish are thought to be more carnivorous than adults (Abrahamsson 966, Capelli 1980), probably allows for the overlap of small crayfish ith Cladophora in shallow water. Furthermore, Cladophora may be able o grow faster than small crayfish can remove it; this is obviously ot the case with large crayfish and Cladophora in deep water.

Despite the fact that the genus Cladophora has a world-wide istribution this study is only the second to demonstrate that rayfish grazing can be a major contributor to the pattern of istribution and abundance of this alga. Whitton (1970), in his xhaustive review of the biology of Cladophora, makes no reference to ny organism eating this alga let alone influencing its distribution. o my knowledge, only a handful of researchers have realized that nything might actually consume Cladophora, Coyle (1930), and D. Hart nd R. Patrick (D. Hart, pers. comm.). In an unpublished study, Hart ound a positive relation between Cladophora abundance and current elocity, with little Cladophora biomass present at current velocities ess than 50 cm/s. He attributed this pattern to crayfish avoidance f areas with faster currents (i.e., >50 cm/s). While I agree that rayfish will avoid areas of fast current, particularly YOY's, I elieve that the threshold lies more in the range of 100 cm/s for

dults. I have collected large crayfish from deeper waters where urrent velocities were on the order of 60 - 70 cm/s. I have even bserved one individual feeding in a spot that turned out to have a urrent velocity of 90 cm/s. More importantly, avoidance of areas ith current velocities >50 cm/s by large crayfish does not adequately xplain the patterns of *Cladophora* abundance. Considerable *Cladophora* iomass was observed on substrates where current velocities were often s low as 5 cm/s (see Chapter 2). A much more striking pattern of *ladophora* abundance was seen with depth. Blum (1957) also noted a imilar pattern of *Cladophora* distribution with depth, with *Cladophora* eing abundant in shallow riffles and on rocks in the shallow portion f pools. This pattern may be the result of the risk of predation eing considerably higher for large crayfish in shallow water relative o deep water (Chapter Two).

The results of the crayfish-*Cladophora* interaction studies are onsistent with the results of other large herbivore-algae interaction tudies (Power and Mathews 1983, Power 1984, 1987, Power et al. 1985, athews et al. 1986). These studies found strong inverse relations in e abundance of large herbivorous fishes and periphyton. They went to ascertain that these patterns were indeed caused by the grazing ctivities of the herbivorous fishes. Furthermore, Power and Mathews 983) and Power et al. (1985) demonstrated that variation in the undances of the algae and the herbivorous fishes (i.e. algae undant in deep water, minnows abundant in shallow water and vice ersa) could be attributed to the presence or absence of piscivorous ss. Power et al. (1989) demonstrated that shallow water was a risky bitat for large, conspicuous fishes in a Panamanian stream as they re susceptible to fish-eating birds. Considered all together, the

results of all these studies demonstrate that large crustacean or vertebrate herbivores play a direct role in structuring benthic algal communities in low gradient streams regardless of whether they are in tropical or temperate latitudes. The potential indirect effects of this apparently widespread interaction on stream communities deserve further attention by stream ecologists.

Cladophora definitely inhibits diatom colonization of the rock surface beneath its mats. This appears to be the consequence of at least three interacting processes. These are 1) shading, 2) siltation and 3) scouring. Shading and siltation are probably the overriding phenomenon at high thallus densities. The dense, heavily branched *Cladophora* thalli are bent over even in weak currents forming a heavy canopy over a rock. While I have not measured light above and beneath these mats, incoming light must surely be reduced by this canopy of interwoven thalli. Blum (1957) took several readings with a light meter beneath *Cladophora* mats in the Saline R. and frequently got values of 0.0 ft candles even at midday. There was some light penetration in less dense mats. Heavy epiphyte growth on the thalli would further reduce light penetration to the rock surface, and *Cladophora* can become heavily overgrown with epiphytes, especially at slower current velocities (Blum 1957, Creed, pers. obs.).

Cladophora mats are also very effective sediment traps, increasing the sediment-trapping ability of a rock surface by at least five fold (see results of Experiment 1, Blum 1957). *Cladophora* appears to be able to withstand moderate siltation at the base of the mats although heavy siltation undoubtedly would result in death of holdfast cells and lead to mat senescence. The moderate silt levels are probably effective at excluding sessile diatom taxa (e.g., *Cocconeis*,

Achnanthes) from the rock surface. It appears that mobile diatom taxa (e.g., Navicula) show little or no response to the presence of Cladophora mats with respect to silting and shading. It is likely that they stay above the accumulating sediments and move up near the surface of the mats where light intensities are higher. Indeed, there was no significant effect of Cladophora on Navicula in the Cladophora-diatom experiment.

Mobile diatoms, and the tube-dwelling forms such as Cymbella and taxa that form loose chains such as Melosira and Diatoma, may suffer adversely from the third process, scouring. Cladophora is a fairly stiff alga with a chitinous layer in its cell walls (Wurdack 1923, Whitton 1970). This stiffness, combined with the branched morphology of the alga, probably make it an effective brush even in moderate to weak currents. This effect was probably accentuated in my experiment where the Cladophora thalli were only attached at the upstream end of the tile. Under natural situations, as a Cladophora mat develops, widely scattered thalli probably reduce epilithic diatom abundance by scouring the surrounding rock surface. As mats develop and thalli grow together scouring probably diminshes in importance with respect to reducing diatom abundance and shading and siltation become more important. The interaction between Cladophora and diatoms may change with the size of the Cladophora thallus. Blum (1957) did find that the diatom Diatoma was quite abundant around the base of small Cladophora filaments which apparently anchor this chain-forming diatom.

In addition to these three processes, Cladophora may further inhibit diatom mat development by outcompeting diatoms for water column nutrients. Unlike terrestrial plant communities where possible

tradeoffs exist between a plants ability to capture light versus its ability to sequester soil nutrients (Tilman 1988), both of these essential resources come from above in most benthic aquatic communities, i.e., the water column (but see Pringle 1990). I would anticipate this to be particularly true of communities on large, hard substrata such as cobbles or bedrock. Cladophora has been shown to be very effective at sequestering nutrients in a desert stream (Fisher et al. 1982) and this may lead to nutrient depletion beneath its heavy mats. Again, this effect would favor mobile diatom taxa but would have a strong negative effect on sessile, understory taxa.

To summarize, many diatom taxa should suffer a strong negative effect due to the presence of a Cladophora canopy, in particular, sessile, tube and chain forms. Mobile forms may show little negative effect and maybe even benefit from the presence of the overstory alga, i.e., through reduced competition with other diatom taxa. At present, I am unable to compare these results to those of other researchers as I am unaware of any studies which examined the mechanism of the interactions between attached, filamentous algae and diatoms on substrates in freshwater. However, the patterns of succession of species and growth forms on artificial substrates are consistent with the idea that competition for space, light, and possibly nutrients, is occurring (Hoagland et al. 1982). Interactions between late-arriving filamentous algae and established diatom assemblages need to be investigated.

One further point needs to be made regarding the interaction between Cladophora and benthic diatoms. While Cladophora may reduce the abundance of understory algae on the rock surface, Cladophora itself can serve as a substrate for some algal taxa (Blum 1957,

Whitton 1970). This fact is important to the discussion of micrograzer feeding ability since it suggests that as Cladophora grows it replaces one substrate (the rock surface) with another (the algal filament). Apparently, this is not a preferred habitat for the sessile caddisfly taxa, Leucotrichia and Psychomyia, as they were much less abundant beneath Cladophora mats than on Cladophora-free surfaces. However, the presence or absence of Cladophora may have little effect on mobile grazers. This issue will be addressed in Chapter 4.

In summary, grazing by large crayfish excludes Cladophora from substrates in deep water. The consequence is that the algal component of the community appears to be kept in an earlier stage of succession, i.e., a predominance of diatoms and some small, filamentous forms (e.g. Stigeoclonium). This result is the opposite of that observed by Lubchenco (1983) in an intertidal system. Lubchenco found that grazing snails preferred the earlier successional species. The result of heavy snail grazing was a community dominated by late successional macroalgae. On the other hand, Dethier and Duggins (1984) reported that chitons prevented the establishment of late-successional macroalgae which resulted in increased abundances of microalgae. In many terrestrial systems, large herbivores appear to have an effect similar to crayfish and chitons; the community is kept in an earlier stage of succession (e.g. Tansley and Adamson 1925, Laws 1970, Harper 1977). The critical factor contibuting to these different patterns is which plant taxa are consumed by the dominant herbivore. This appears to be a function of either palatability (Lubchenco 1978) or the differential ability of the herbivore to handle different plant taxa, e.g., crayfish are not physically capable of feeding directly on small

Whitton 1970). This fact is important to the discussion of micrograzer feeding ability since it suggests that as Cladophora grows it replaces one substrate (the rock surface) with another (the algal filament). Apparently, this is not a preferred habitat for the sessile caddisfly taxa, Leucotrichia and Psychomyia, as they were much less abundant beneath Cladophora mats than on Cladophora-free surfaces. However, the presence or absence of Cladophora may have little effect on mobile grazers. This issue will be addressed in Chapter 4.

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diatoms (Creed, pers. obs.).

Grazer-induced changes in the composition of the plant community may have profound implications for the movement and cycling of nutrients if different taxa (or groups of taxa) have different abilities to sequester and/or store nutrients. It is quite likely that a stream covered by Cladophora would have very different patterns of nutrient spiralling (e.g., spiral length, retention time etc) as compared to a stream with diatom-covered substrates. The implications of plant-herbivore interactions for nutrient-spiralling in natural streams remains to be investigated.

Strong Interactions and Stream Community Structure

Until recently, the prevailing view was that streams were structured primarily by abiotic processes (Barnes and Minshall 1983, Ward and Stanford 1984, Reice 1985). This view has been supported by the fact that studies examining the role of fish predation, a strong force in lentic communities (e.g., Brooks and Dodson 1965, Sih et al. 1985, Thorp 1986, McPeek 1990), have generally demonstrated little or no effect of fish on the benthic macroinvertebrate community (Allan 1982, 1983, Reice 1984, Flecker and Allan 1984, Reice and Edwards 1986, Culp 1986, but see Griffiths 1981, Flecker 1984 and Gilliam et al. 1989. This perponderance of negative results may be the consequence of both the methodologies and the general approach employed by stream ecologists to understanding the role of predation. First, all of the above cited studies except Griffiths 1981 and Reice and Edwards 1986 evaluated the response of the invertebrate community by manipulating fish densities in sections of streams that already

contained fish. Thus, they were looking for a response by a fauna that already coexisted with fish and, in all likelihood, only weakly interacted with them in the first place (for a comparable example from lentic systems see McPeek 1990). Griffiths (1981) and Reice and Edwards (1986), on the other hand, introduced fish to previously fishless regions of watersheds. Griffiths observed a response in 5 out of 9 taxa to the introduction of fish; 3 species decreased in abundance while 2 increased in the presence of trout relative to controls. Reice and Edwards reported higher levels of prey consumption by fish introduced into a previously fishless stream. They also noted that the populations of several taxa declined in the presence of fish but that these were generally non-significant differences. Second, none of these studies reported the distribution of the invertebrate fauna with respect to physical factors such as depth to see if there were associated differences in the fauna which might suggest a refuge (e.g., shallow water) from fish predation (Gilliam et al. had demonstrated differential habitat use of the insectivorous predator, juvenile creek chubs, in earlier work, though). Finally, one of these studies (Allan 1982) did not appear to maintain an effective fish exclusion.

Unlike studies of fish predation, recent studies of large herbivores and omnivores have demonstrated strong biological interactions in stream communities (Power and Matthews 1983, Power 1984, 1987, Power et al. 1985, Matthews et al. 1986, this study) and I believe the approach holds promise for our efforts to understand the importance of fish predation in stream systems as well. All of these studies have demonstrated non-overlapping distributions of herbivores and vulnerable plant taxa and that these patterns are the result of a

strong interaction between these plants and herbivores. Furthermore, these patterns appear to be driven by forces that influence the distribution of the large herbivore, primarily risk of predation to either terrestrial or aquatic predators. Thus, spatially distinct refugia exist for both macroalgae and macroherbivores which results in their non-complementary distributions. It is my contention that these plant-herbivore interactions are not inherently different than other predator-prey interactions in streams, i.e., that insectivorous predators respond in a similar fashion to herbivores with respect to predation risk. This in turn creates refugia for benthic macroinvertebrates similar to those seen for macroalgae. This idea of spatial refugia within a fish-containing stream for vulnerable invertebrate taxa has yet to receive attention by stream ecologists studying the effects of fish predation. Gilliam et al. (1989) have initiated this effort indirectly by documenting spatial variation in habitat use by a predatory fish and then inferring that a refuge existed for the invertebrate prey. The results of Gilliam et al. (1989) - they saw strong fish effects - demonstrate that this approach holds considerable promise in interpreting fish effects in stream communities. Experimental evaluation of the behavior of stream invertebrates with respect to predation risk should also contribute to our understanding of the role of predation in these communities (see Kohler and McPeek 1989 for an excellent example of this approach).

To summarize, strong effects of large herbivores on the distribution and abundance of macroalgae have been demonstrated in both tropical and temperate streams. These results are important because they demonstrate a consistently strong biological interaction in systems thought to be dominated by abiotic forces. These results

do not preclude the importance of abiotic effects, however. It is quite likely that the relative importance of these forces may switch over the course of the year (e.g., wet vs. dry season in the tropics). In addition, these results suggest that before we rule out fish predation as an important force in streams we need to 1) document the distributions of macroinvertebrate and fish taxa both within and between stream systems (i.e., do spatial refugia exist for vulnerable taxa?) and 2) determine experimentally if predation by fishes is important in generating these patterns of macroinvertebrate distribution.

Strong Plant-Herbivore Interactions and Community Structure

A growing body of data points to strong plant-herbivore interactions being common in marine subtidal (Wharton and Mann 1981), marine intertidal (Lubchenco 1978, 1983, Dethier and Duggins 1984), lentic (Lodge and Lorman 1987, Sheldon 1987, Feminella and Resh 1989) and terrestrial (Tansley and Adamson 1925, Gillham 1955, Thomas 1960, 1963, Buechner and Dawkins 1961, Laws 1970, Lock 1972, Harper 1977, McNaughton 1976, Davidson et al. 1984, Brown et al. 1986) communities (see also results of review by Sih et al. 1985). A number of these studies examined the consequences of this interaction for other components of the community (other plant species: Tansley and Adamson 1925, Thomas 1960, 1963, Lock 1972, Dethier and Duggins 1984, Davidson et al. 1984, Brown et al. 1986); other herbivores: McNaughton 1976, Dethier and Duggins 1984, Davidson et al. 1984, Brown et al. 1986, this study). These results suggest that strong plant-herbivore interactions can play key roles in structuring communities in much the

same way as predation on sessile invertebrates in marine intertidal communities (Paine 1966, 1974). In other words, strong plant-herbivore interactions can potentially generate various indirect effects, e.g., mutualisms, facilitations etc. (Vandermeer and Boucher 1978, Vandermeer 1980), that are important in creating much of the structure we observe in many communities.

Chapter Four

DIRECT AND INDIRECT EFFECTS OF CRAYFISH ON BENTHIC MACROINVERTEBRATES

INTRODUCTION

The results presented in Chapter Three demonstrate the significant role crayfish play in determining the distribution and abundance of _Cladophora_ in Augusta Creek. These two species could be considered 'strong interactors' (sensu Paine 1980). Given the fairly strong associations of several invertebrate taxa with either _Cladophora_-covered or _Cladophora_-free substrates, such a strong effect undoubtedly influences the macroinvertebrate component of the community as well. The results of the _Cladophora_-diatom interaction experiment described in Chapter Three suggest that the removal of _Cladophora_ should lead to increased abundances of microalgae, the preferred food of many grazing stream invertebrates (Cummins 1973, Cummins and Klug 1979, Merritt and Cummins 1978), on many substrates and, subsequently, an increase in the invertebrates which feed on the microalgae. Other invertebrates may lose a preferred food or site for feeding with the removal of the _Cladophora_, e.g., piercers such as Hydroptilids (Trichoptera) which ingest the contents of individual cells of macrophytes and macroalgae (Cummins and Klug 1979) or deposit-feeding animals such as _Tricorythodes_ (Ephemeroptera) that feed on the organic matter (=FPOM) that accumulates among beds of macrophytes and macroalgae (Cummins and Klug 1979) (see Figure 1). In

addition to these effects on habitat structure and resource levels, crayfish, which are known to be omnivores (Crocker and Barr 1968, Capelli 1980), may exert an additional effect on the distribution and abundance of benthic invertebrates through direct predation. Thus many of the benthic animals that might otherwise benefit from the removal of *Cladophora* might still be excluded from the *Cladophora*-free substrates. In this chapter I will explore the response of various macroinvertebrate taxa in Augusta Creek to the activities of *Orconectes propinquus* in an attempt to determine the extent to which crayfish directly and indirectly influence both the taxonomic and functional structure of the macroinvertebrate component of this stream community.

MATERIALS AND METHODS

Brick Transplant Experiment

A brick transplant experiment was conducted to evaluate the response of both the macroinvertebrates and *Cladophora* to the effects of crayfish. In this experiment, concrete bricks were placed in a shallow habitat where they were allowed to develop *Cladophora* mats and be colonized by animals from the surrounding, ungrazed substrates. These bricks were then transplanted to the deep water habitat and the response of the macroinvertebrates and *Cladophora* to crayfish were evaluated. I anticipated the following responses based on the results of the surveys conducted in 1986 and other observations of the stream flora and fauna. Filter-feeding Hydropsychid caddisflies, which are abundant in *Cladophora* mats but not as common in deeper water, should

colonize the mats as they develop. Micrograzers, particularly sessile taxa such as Psychomyia and Leucotrichia, should not be very abundant. Once bricks were transplanted to deeper water where crayfish were present, Hydropsychid abundance should decrease as Cladophora was removed while the abundance of micrograzers, particularly mobile taxa, should increase.

This experiment was conducted in the late spring/early summer of 1987 at Nagel's Site. Twelve conditioned concrete bricks were scrubbed with a nylon bristle toothbrush to remove all visible Cladophora and animals. Nine of the bricks were then placed on the top of one of the rock dams, an area that appeared to be largely crayfish-free. Bricks on top of the dam were in about 14 cm of water (~3 - 5 cm to the top of the brick) and the mean current velocity was 55 cm/sec (range 34 - 92 cm/sec). The remaining three bricks (which will be referred to as the Reference bricks) were placed on the streambed in the area where six of the rock dam bricks were to be transplanted. Daytime water temperatures ranged from 19^{o} C at the beginning of the experiment to 23.5^{o} at the end. The experiment was intiated on May 1, 1987. Cladophora mats were allowed to develop on the nine rock dam bricks and be colonized by the fauna characteristic of this shallow habitat for six weeks.

After six weeks three of the rock dam bricks were sampled. Bricks were sampled by removing each brick from the dam into a dipnet lined with 1 mm^2 mesh net positioned immediately downstream. The brick and the net were then quickly placed into a sealable container containing stream water. The remaining six bricks were transplanted into either cages or cage controls arranged in three rows, two treatments per row, in the deeper water just upstream of the rock dam. These bricks were

first placed in a bucket, transported upstream and then set in the appropriate cage or cage control. Few animals came off of the bricks at this time (usually 2 - 3 <u>Baetis</u>). The experimental design was a randomized block design with three replicates per treatment. Selection of bricks for either sampling or manipulation was determined using a random number table. Cages and cage controls were constructed of 1/4 inch mesh hardware cloth. Cage controls were open on the downstream end. Water depth around cages and cage controls was 20 - 25 cm; depth to top of the bricks averaged 12 - 13 cm. Current velocity around the cages averaged 52 cm/sec (range 43 - 60). Cages and cage controls were cleaned of debris twice a day, once in the morning and at dusk.

The experiment was run for four days. At that time all six cage and cage control bricks plus the three reference bricks were sampled in the same manner as the three initial bricks. Bricks were returned to the lab where the abundance of <u>Cladophora</u> and the animals associated with the bricks were determined. Percent <u>Cladophora</u> cover was determined for just the top of the brick. Number of <u>Cladophora</u> thalli and biomass (AFDW) were determined for the top and four sides of each brick. <u>Cladophora</u> was removed using a dissecting scope set at 10X. Three 9 cm^2 areas were subsampled for <u>Cladophora</u> on the top of each brick; two subsamples were taken for each side unless <u>Cladophora</u> did not seem particularly abundant. Then the entire side was sampled. <u>Cladophora</u> AFDW was determined as before (see Chapter Two). All samples for this study were filtered onto precombusted Whatmans GF/F filters. After the <u>Cladophora</u> had been removed the brick was scrubbed in a bucket of water with a stiff, nylon bristle toothbrush to remove the animals. Animals were also washed off of the collecting net. The

wash water was then strained through a 250 um sieve and the animals were washed into a sample jar and preserved in 70% ethanol. Animals were later sorted and identified to the lowest taxonomic level under a dissecting microscope. Biomass for the more abundant invertebrate taxa was determined by drying animals for 24 hrs in preweighed aluminum pans at 60° C. Samples were weighed on a Cahn C-31 microbalance after cooling to room temperature in a dessicator. *Cladophora* and macroinvertebrate density and biomass data were analyzed using ANOVA (PROC ANOVA, SAS Institute). *Cladophora* and macroinvertebrate biomass and macroinvertebrate density data were log transformed; *Cladophora* percent cover data were arcsine transformed. Statistical comparisons were made between Exclusion Cage and Cage Control bricks only. The Initial and deep water Reference bricks served as unmanipulated, habitat controls against which the manipulated bricks could be compared.

Crayfish Predation Trials

Crayfish are omnivorous and thus can influence the distribution and abundance of various invertebrates through direct predation. The purpose of these experiments was to determine relative vulnerabilities of various macroinvertebrate taxa to crayfish predation. Three different types of trials were conducted, single micrograzer species trials, a trial pairing the two most abundant snail species, and a trial using the whole, deep water community.

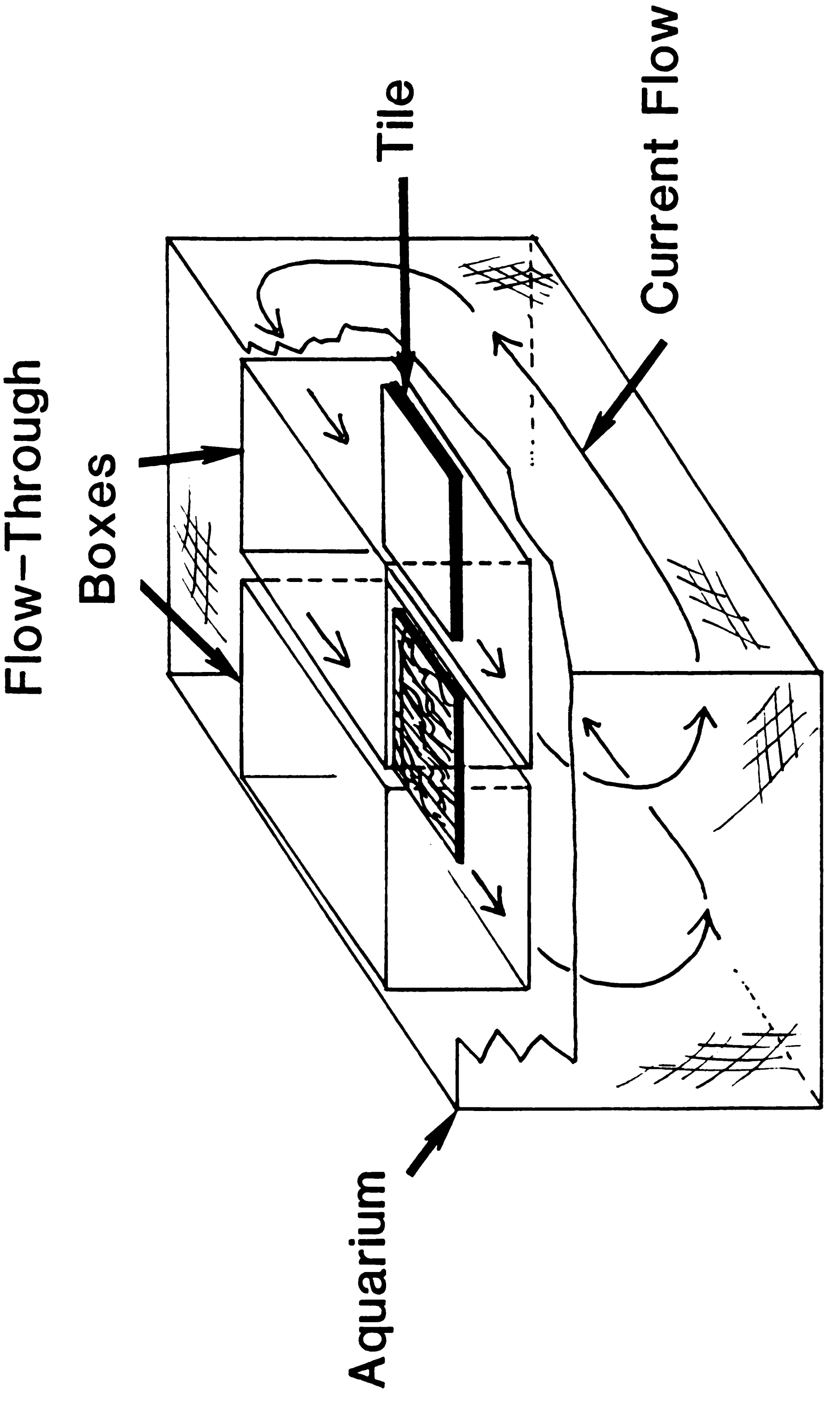
SINGLE SPECIES TRIALS. Four micrograzer taxa were tested in the single species trials. These included the two snails *Goniobasis* (Pleuroceridae) and *Physa* (Physidae), the mayfly *Baetis*, and the

sessile caddisfly Leucotrichia pictipes. Two of these taxa, Goniobasis and Leucotrichia, commonly co-occur with large crayfish on Cladophora-free substrates in deep water. Baetis is found in both shallow and deep habitats but tends to be more abundant in shallow water. Finally, Physa is only found in shallow water, either on Cladophora-covered substrates or on the stems of emergent plants (Creed, pers. obs.). The distributions of these four taxa suggest that they should represent the range of prey vulnerabilities to crayfish predation, i.e., Goniobasis and Leucotrichia should be least vulnerable while Physa should be highly vulnerable, if distributions are indeed indicative of vulnerability. These taxa also represent three different types of micrograzer morphology, 1) swift, mobile taxa (Baetis), 2) slow, mobile taxa (Goniobasis and Physa), and 3) sessile taxa (Leucotrichia).

The trials were conducted in 75.7 liter (20 gallon), recirculating aquaria modeled after those of Gee and Bartnik (1969). Water current was generated using a large airstone fixed at one end of the aquarium (Figure 25). The current was directed towards the containers by a plexiglass baffle set at a 45^{o} angle at the top of the aquarium above the airstone. A second plexiglass baffle separated deep water from shallow water which prevented mixing of the shallow and deeper currents and also provided a surface upon which to place containers. Current velocities of 15 to 20 cm/sec could be generated with this apparatus. All aquaria were filled with water from Augusta Creek. Water temperatures in these aquaria during these trials ranged from 18 - 21^{o} C. Chambers used in this apparatus were Rubbermaid^{TM} 2.8 L Servin' Saver^{TM} boxes with removable lids (overall dimensions: 24 cm L X 13.5 cm W X 10.5 cm H). The ends of each box were cut out and

Figure 25. Design of flow-through aquaria used in laboratory predation and macroinvertebrate feeding trials.

Figure 25.



covered with 1 mm^2 mesh plastic window screen which was glued in place using aquarium sealant. Window screen was also attached to the bottom of each chamber to provide a rough surface on which crayfish could walk. All four recirculating aquaria plus a holding tank were on a single shelf of a large rack. The aquaria were illuminated by six 24 inch flourescent bulbs mounted on the underside of the shelf above. The lights were on a common power supply and set for a 16:8 light:dark cycle using a timer. The entire setup was then enclosed in a shroud of dark plastic to minimize disturbance of animals by activities in the room and room lighting.

Both adult (>20 mm CL) and YOY crayfish were used in these trials. Crayfish were collected the day before the trial, placed in separate containers in the aerated holding tank and starved until the initiation of the experiment. On the day of the experiment the invertebrates were collected as well as a tile covered with diatoms to serve as a food source. Snails were collected by hand and Baetis were collected by washing them off of substrates into a dipnet. For trials involving these taxa, animals were returned to the lab, measured (shell height for the snails, head width and total body length for Baetis) and then equal numbers of similar-sized individuals were placed into each of eight boxes with a diatom-covered tile. As fifth instar Leucotrichia are sessile, I had to collect substrates which had already been colonized by this species. I used small concrete bricks which had been in the stream for at least one year. In the lab I counted the number of occupied cases for each rock under a dissecting scope. All occupied cases were then identified by scratching a mark into the rock surface next to the case. Different numbers of cases were present on each of the rocks. As all Leucotrichia used were

fifth instar individuals, they were assumed to be approximately the same size. Once the substrates and animals were in all of the boxes a single crayfish was added to four of them. Treatments (with and without crayfish) were paired by aquarium; there were four aquaria in all. The trial was run for another 24 hrs and then all surviving animals were recovered and measured for trials involving *Baetis*, *Goniobasis* and *Physa*. For trials involving *Leucotrichia* the number of occupied cases remaining was determined. As some of the *Baetis* had crawled out of the boxes into the aquaria in trials with adult crayfish (these individuals were counted as survivors), trials involving *Baetis* and YOY crayfish were conducted in 10.3 liter (2.75 gallon) buckets instead. Buckets contained 5 cm of water, a diatom-covered tile and an airstone which generated some current. The grooves on the underside of the tiles provided a potential refuge for *Baetis* and *Physa*; *Goniobasis* was too large to fit into these grooves.

TRIALS WITH *Goniobasis* AND *Physa*. The idea underlying both this experiment and the deep water community trials described below is that in the single species trials crayfish were not allowed to choose between prey thus forcing them to feed on the species presented to them. Crayfish might respond differently when presented with a range of prey types which could influence the resulting vulnerability of each prey species. The methods for these trials were identical to those described above for the single species trials. The only difference was that each box now contained equal numbers (4) of both *Goniobasis* and *Physa*. Trials were also run with only adult crayfish as neither snail species was found to be vulnerable to YOY crayfish in the single species trials.

DEEP WATER COMMUNITY TRIALS. As an alternative to running all

pairwise combinations of taxa, I ran a single set of trials using the whole array of taxa found associated with large crayfish on deep water substrates. Unglazed clay tiles which had been in the stream for a year (they had been on the bottom of the reach [40 - 45 cm deep] above the bridge at Nagel's Site) were brought into the lab. These tiles were covered with a maze of *Psychomyia* tubes. Other abundant taxa included chironomids, elmid larvae and adults (primarily *Stenelmis*), small Heptageniidae nymphs and oligochaets. After shaking these tiles vigorously in a pan of stream water in attempt to remove mobile grazers except *Ferrissia* (a limpet which is fairly easy to quantify by eye), I added known numbers of *Baetis*, *Goniobasis* and *Physa* to each chamber. Ambient densities of *Ferrissia* were used for each tile. *Physa* was used even though it is not found on these deep substrates to see if its vulnerability changed when in the presence of all these other invertebrates. Two tiles were placed in each flow-through chamber. One large crayfish was placed into half of the chambers and the trial was run for 24 hrs.

Macroinvertebrate Feeding Trials

Both *Cladophora* and cobbles can serve as substrate for microalgae. Consequently, the presence of *Cladophora* may have little effect on many micrograzers if they can feed equally well in both habitats. Alternatively, *Cladophora* might be a very difficult substrate either on or in which to forage. The brushing and scraping mouthparts of many stream micrograzers might not be suited to feeding on narrow algal filaments or in dense algal mats. If the latter is the case then crayfish would be facilitating these grazers by removing

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Cladophora mats.

I evaluated the ability of various mobile micrograzer taxa (Goniobasis, Physa, Baetis and Stenonema) to feed in these two distinct habitats in a series of laboratory trials. Sessile taxa were not tested as they were either rarely (Psychomyia) or never found (Leucotrichia) in or underneath Cladophora mats. Three of the four taxa (Goniobasis, Baetis and Stenonema) are among the most abundant mobile micrograzers in Augusta Creek either numerically (the mayflies) or with respect to biomass (Goniobasis). Physa was selected as it is known to be an efficient feeder on hard substrates (Barnese et al. 1990) yet it is almost never found on the deeper, Cladophora-free substrates in Augusta Cr. Larger individuals of all species were used due to both the ease of their collection and handling in the lab. Mean shell height (± 1 SE) for snail species was 14.7 ± 0.25 mm for Goniobasis (n = 21) and 6.67 ± 0.13 mm for Physa (n = 21). Mean head capsule widths and total body lengths (± 1 S.E.) for Baetis and Stenonema were as follows: Baetis - head capsule width = 1.07 ± 0.02 mm, body length = 7.36 ± 0.11 mm (n = 19); Stenonema - head capsule width = 3.18 ± 0.06, body length = 9.93 ± 0.25 mm (n = 19). The trials were conducted in the same recirculating aquaria used for the predation trials. Animals were collected from Augusta Creek 24 hours prior to the initiation of the experiment. They were placed in a holding chamber (water temperature 18^{o} - 21^{o} C.) and starved until the experiment began. The chamber was checked periodically during this period to remove accumulating feces (especially in the case of the snails) to reduce the incidence of reingestion. As Goniobasis can accumulate algae on their shells all snails were scrubbed with a stiff nylon toothbrush to prevent individuals from grazing each others

shells.

The day of the experiment, I collected the Cladophora thalli and clay tiles to be used for the experimental patches. The Cladophora was collected at HRS from a range of current velocities in an attempt to encompass the range of epiphytic algal abundances associated with the thalli. Clay tiles were incubated in the stream on top of 15 cm high wooden pedestals for three and a half to four weeks, which previous studies had shown was ample time for development of a considerable diatom mat. While diatom densities on these tiles were not determined all tiles had >80% diatom cover. The Cladophora patch was created by tying thalli to a clean clay tile, i.e., there were no diatoms on it, the idea being that a Cladophora mat prevents these grazers from feeding on the rock surface itself. In an attempt to mimic a natural mat, some thalli were tied down at the upstream end of the tile while others were attached near the middle. Thalli were tied down with cotton twine. Both tiles were then placed into separate, flow-through, Rubbermaid™ boxes in the same aquarium. At this time, one third of the particular grazer taxon being tested was removed to determine the inital weight of gut contents (see below for method of gut removal and determination of gut content weight). The remaining animals were measured and then equal numbers were placed onto each substrate type. Boxes were sealed and the trial started. As in the predation trials, aquaria were behind a dark plastic shroud to minimize disturbance and illuminated by six 24 inch flourescent bulbs on a 16:8 light:dark schedule. Water temperatures during the trial were 18^{o} - 21^{o} C.

After twenty four hours all animals were recovered and their gut contents were removed. Prior to removing the gut contents, gut

fullness was estimated using four levels of fullness: empty or with traces of food (0), 1/4 full, 1/2 full and 1 (full) (Yoshiyama 1980, Creed 1985). The mayflies were immersed briefly in boiling water which killed them instantly. Snails were not killed prior to dissection. The entire alimentary tract of mayflies was removed by pulling the animal apart at the juncture of the abdomen and thorax. The gut was then removed from the body. Then the contents separated from the gut tube itself and pipetted into a small, numbered, preweighed foil pouch open at one end. The snails were removed from their shells, the stomach and intestine isolated from the rest of the viscera and then the contents were removed and pipetted into a preweighed foil pouch. Foil pouches were then placed in a drying oven and dried for 24 hrs at 60^{o} C. Pouches were then removed to a dessicator, cooled to room temperature and weighed on a Cahn C-31 Microbalance. In order to standardize gut weights for different sized animals, gut content dry weight was divided by dry weight of body tissue. Dry weights for snails were determined using the experimental animals. Since the decision to standardize gut weight by body weight was made after running the two mayfly trials, dry weights for these two taxa were estimated using a length-weight regression for starved animals (Stenonema: Log(Body Weight) = -1.1823 + 1.7767Log(Body Length); Baetis: Log(Body Weight) = -0.9141 + 1.3107Log(Body Length). As snails produce readily identifiable feces, all feces from both treatments were also removed from each container and dried to determine overall processing rates of the two snail taxa in the different habitats. Feces were also dried at 60^{o} C in preweighed aluminum pans for 24 hrs and then weighed on a microbalance. Identifiable feces were not found for the mayflies.

RESULTS

Brick Transplant Experiment

Crayfish rapidly stripped exposed, cage control bricks (Cc) of their Cladophora cover. Two of the three bricks were stripped during the first 12 hours. The third brick was completely grazed within 48 hours. Changes in percent Cladophora cover, number of thalli per brick and biomass are shown in Figure 26. There was little difference in percent Cladophora cover between the initial sample and exclusion cage bricks (Ec) after four days. Cage controls, however, showed substantial reductions in percent Cladophora cover (Figure 26A). A similar pattern was observed for Cladophora biomass (Figure 26B), although this difference was not quite significant ($p=0.084$) due to the considerable variation in biomass displayed by the Ec bricks. There was no significant difference in the number of Cladophora thalli per brick between the Ec and Cc treatments (Figure 26C).

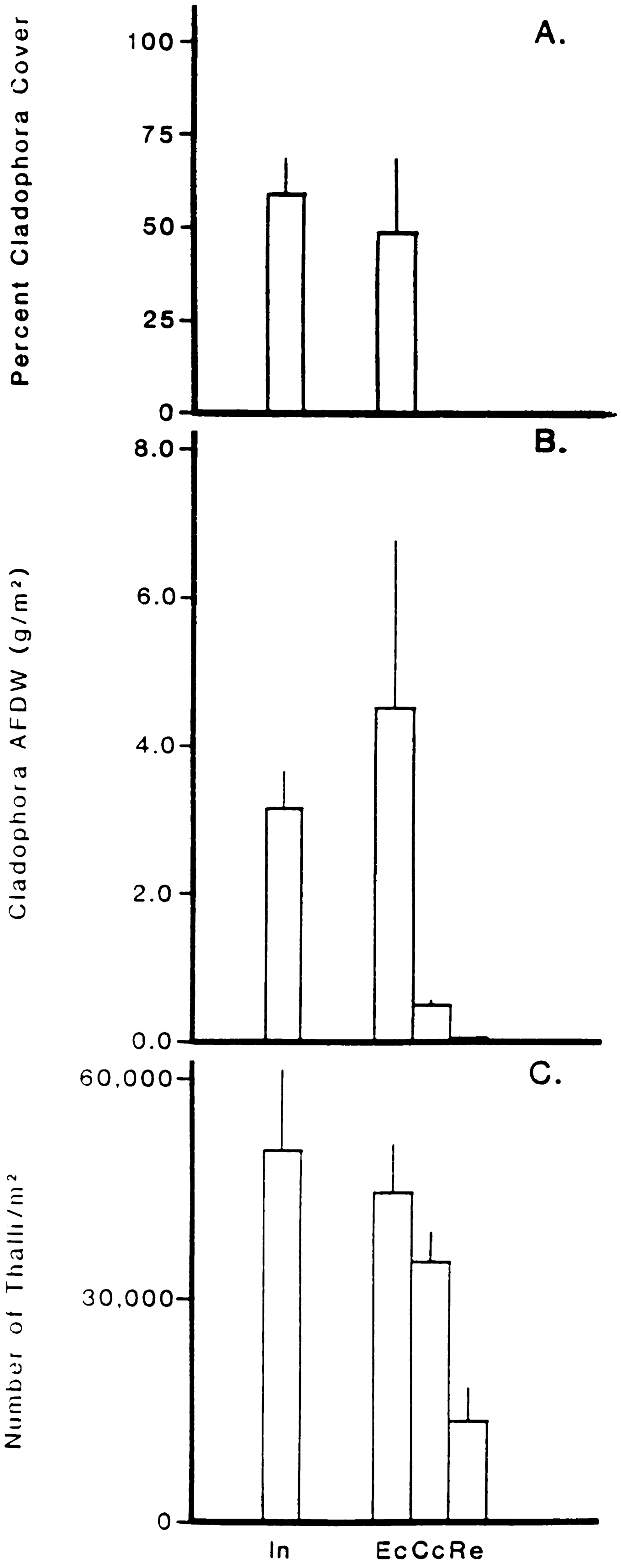
The lower than usual abundance of Cladophora in this experiment appears to be due to two factors. First, many of the bricks were wedged into crevices on top of the rock dam, thus the amount of light reaching several of the sides was reduced. Often only one or two sides of any given brick had appreciable Cladophora cover. Consequently, Cladophora biomass has been averaged over brick surface area that produced little Cladophora growth. When Cladophora biomasses are calculated for just the tops of the bricks the values are higher and more similar to those obtained in other experiments (Initial Bricks 8.08 ± 0.89 g/m^2 and 13.91 ± 6.67 for Exclusion Cage Bricks). Nevertheless, these values are still lower than those for

Figure 26. A. Percent cover of *Cladophora* on the tops of bricks from the Brick Transplant Experiment. Values are mean percent cover (± 1 S.E.). Treatments: In - Initial Bricks from top of rock dam; Ec - Exclusion Cage Bricks; Cc - Cage Control Bricks; Re - Reference Bricks from deeper water where Exclusion Cages and Cage Controls were located.

B. *Cladophora* biomass for bricks from the Brick Transplant Experiment. Values are mean biomass (± 1 S.E.).

C. Density of *Cladophora* thalli (No./m^2) for bricks from the Brick Transplant Experiment. Values are mean density (± 1 S.E.).

Figure 26.


A.
Percent Cladophora Cover
100
75
50
25
0
B.
Cladophora AFDW (g/m²)
8.0
6.0
4.0
2.0
0.0
C.
Number of Thalli/m²
60,000
30,000
0
In
EcCcRe

Experiment 1 in Chapter Three. This additional difference appears to be the result of crayfish grazing. After initiating the experiment I noticed crayfish coming up from inside the rock dam to graze some of these bricks on a couple of occasions. Crayfish may move into shallow water if they have ready access to a refuge such as the crevices in these rock dams.

A number of macroinvertebrate taxa responded to the removal of Cladophora by crayfish (Table 7). There was a significant decrease in the density of animals on cage control bricks (28,848 ± 2770 per m^2) compared to exclusion cage bricks (49,918 ± 3467 per m^2). This was due primarily to significant decreases in the densities of chironomids and Hydropsychid caddisflies (both large and small individuals). The only other taxon to display a significant difference in density between treatments were the Oligochaets (Table 7). Antocha and the Hydracarina appeared to decrease in abundance but the difference was not significant. A number of micrograzer taxa appeared to be more abundant on the grazed cage control bricks (e.g., Psychomyia, Protoptila, Leucotrichia, Baetis, Heptageniidae, and Elmids) but none of these differences were statistically significant either. The high densities of many micrograzer taxa (particularly Psychomyia and Leucotrichia) on both the initial and exclusion cage bricks compared with rocks sampled during surveys is probably a consequence of the reduced Cladophora cover on the sides of these bricks. Finally, four taxa were found almost exclusively on the Cladophora-covered Ec and In bricks. These were the deposit-feeding mayfly Tricorythodes, the microcaddisfly Ochrotrichia (Hydroptilidae), Gammarid amphipods and Harpacticoid copepods. Densities (mean #/m^2 ± 1 S.E.) of these taxa for the In, Re, Cc and Ec treatments, respectively, were:

Table 7. Densities (No./m^2) of the major macroinvertebrate taxa from the Brick Transplant Study conducted at Nagel's Site, Augusta Creek in the Spring of 1987. Values in the table are means (± 1 S.E.). ANOVA comparisons between manipulated bricks (CC and EC treatments) only. ANOVA performed on log transformed data. N = 3.

Taxon	Treatment[1]				F value	P value
	In	Re	Cc	Ec		
Diptera						
Chironomidae	22280	6311	6033	21161	24.94	0.0378
	(4183)	(1343)	(307)	(4560)		
Antocha	2617	271	1259	2115	3.75	0.1926
	(943)	(145)	(264)	(176)		
Ephemeroptera						
Baetis	4749	883	2025	1737	0.25	0.6683
	(1220)	(161)	(307)	(359)		
Heptageniidae	206	242	749	436	5.08	0.1529
	(22)	(117)	(70)	(100)		
Trichoptera						
Psychomyia	8304	8490	7679	6831	0.10	0.7777
	(2442)	(1277)	(1997)	(1999)		
Hydropsychidae (T)*	17893	1781	1778	6856	118.33	0.0083
	(2549)	(382)	(238)	(386)		
Hydropsychidae (L)*	4913	43	700	2839	25.28	0.0374
	(1765)	(0)	(100)	(765)		
Hydropsychidae (S)*	12980	1752	1078	4017	55.97	0.0174
	(2880)	(388)	(139)	(402)		
Protoptila	0	86	1399	749	0.03	0.8736
	(0)	(43)	(713)	(92)		
Leucotrichia[2] (Sessile)	173	470	749	280	0.92	0.4390
	(94)	(85)	(400)	(105)		
Leucotrichia[2] (Mobile)	815	1581	675	370	3.53	0.2011
	(399)	(150)	(502)	(260)		

Table 7. Continued.

Coleoptera Elmids (T)*	239 (86)	541 (38)	305 (206)	222 (51)	0.01	0.9219
Hydracarina	5202 (1062)	3547 (561)	4749 (394)	6420 (1614)	2.13	0.2816
Oligochaeta	617 (79)	128 (128)	519 (76)	288 (54)	246.24	0.0040
Total Number of Animals	64453 (9524)	24943 (1775)	28848 (2770)	49918 (3467)	69.19	0.0141

1- Treatments: In=Initial, Re=Reference, Cc=Cage Control, Ec=Exclusion Cage.

2- Instars 1 - 4 in Leucotrichia are mobile; fifth instars are sessile.

*- Symbols: T=Total, L=Large (>3 mm long), S=Small (<3 mm long).

Tricorythodes - 0 (0), 0 (0), 0 (0) and 50 (38); Ochrotrichia - 50 (25), 0 (0), 0 (0) and 33 (22); Amphipoda - 8 (8), 33 (33), 0 (0) and 41 (30); Harpacticoida - 8 (8), 0 (0), 0 (0), 66 (41).

With the removal of Cladophora, the cage control bricks became more similar to the reference bricks (Re) with respect to the associated fauna. The mean number of animals on the In bricks was 64,453 individuals per square meter. Compared to this initial estimate, there was a decrease of 14,535 individuals on the Ec bricks vs 35,605 individuals on the Cc bricks. Notice that the density of animals on the Cc bricks (28,848) was very similar to that on the Re bricks (24,943). These decreases in density with respect to In bricks were almost entirely attributable (approximately 97%) to three taxa: chironomids, Hydropsychids and Baetis. The decrease in Baetis densities is about the same for both treatments - 2724 for Cc vs 3012 for Ec. Differences between treatments were seen in the decline in the numbers of chironomids and Hydropsychids, however. There is almost no decrease in chironomids for the Ec treatment (1119) vs a decrease of 16,247 chironomids on the Cc bricks. Hydropsychids decrease by 16,115 individuals for Cc bricks as opposed to 11,037 for Ec bricks.

There is a six fold difference in the density of Baetis on the shallow In vs the deeper Re bricks (Table 7). This pattern is similar to that described at HRS in 1988. Baetis thus appear to congregate on shallower substrates, at least during the day. While the densities of Baetis on Ec and Cc bricks are lower than on In bricks they are still higher than Re bricks. Obviously, Baetis are disappearing from these bricks regardless of Cladophora cover and exposure to crayfish and fish suggesting that this taxon does not prefer deeper substrates,

during the day at any rate. If the experiment had run a few more days Baetis densities on Ec and Cc bricks might have equilibrated with those on Re bricks. Decreases in Hydropsychid densities appear to have two causes. The decrease on the Ec bricks (~11,000 animals) was probably due to emigration in response to lowered current velocities combined with increased sedimentation in the cage. Even though the cages were cleaned three times a day there was still an obvious silt accumulation on these substrates. As more than 16,000 Hydropsychids disappeared from the Cc bricks, i.e. ~5,000 more animals than Ec bricks, this additional decline was undoubtedly a combination of loss to predation (fish and crayfish) and emigration. Note the very similar densities of hydropsychids on Re and Cc bricks. Deeper habitats where crayfish and fish are more abundant do not appear to be safe habitats for hydropsychids, regardless of their size, even when currents suitable for their filter-feeding lifestyle (~40 -60 cm/s) are present. The decline in chironomids appears to be almost entirely the result of consumption/habitat loss due to crayfish grazing. Densities of chironomids on Ec and In bricks were very similar suggesting that very few chironomids, unlike Baetis and hydropsychids, emigrated from the Cladophora-covered Ec bricks when they were moved to deeper water. Notice the very similar densities of chironomids on Cc and Re bricks (Table 7). While the survey data from HRS showed little relationship between chironomid abundance and Cladophora cover, the results of this experiment suggest the reverse, i.e., that the presence of Cladophora increases the amount of available habitat for chironomids over a bare rock surface.

Significant differences in biomass between Ec and Cc treatments were observed for Baetis and Hydropsychids (Table 8). Chironomids,

Table 8. Biomass (mg dry weight/m^2) of the major macroinvertebrate taxa from the Brick Transplant Study conducted at Nagel's Site, Augusta Cr. in the Spring of 1987. Values in the table are means (± 1 S.E.). ANOVA comparisons between manipulated bricks (Cc and Ec Treatments) only. ANOVA performed on log transformed data. N = 3.

Taxon	Treatment[1]				F value	P value
	In	Re	Cc	Ec		
Diptera						
Chironomidae	109.0 (17.0)	30.0 (11.9)	43.7 (6.7)	94.3 (32.8)	5.03	0.1540
Antocha	55.8 (6.6)	8.8 (5.1)	35.7 (14.5)	42.1 (9.0)	1.90	0.3017
Ephemeroptera						
Baetis	49.7 (18.3)	15.2 (4.6)	76.6 (12.8)	16.1 (6.5)	27.11	0.0350
Heptageniidae	52.6 (21.9)	9.8 (8.3)	151.3 (57.2)	64.7 (31.1)	0.92	0.4383
Trichoptera						
Psychomyia	146.7 (42.6)	358.8 (54.9)	193.1 (50.7)	110.5 (41.1)	0.78	0.4691
Hydropsychidae (T)*	1027.8 (278.6)	24.2 (8.2)	28.1 (6.9)	358.4 (30.5)	233.09	0.0043
Protoptila	0.0 (0.0)	2.9 (0.8)	48.4 (26.9)	21.5 (9.0)	0.25	0.6682
Glossosoma	0.0 (0.0)	0.0 (0.0)	60.7 (30.7)	25.4 (18.4)	2.10	0.2842
Leucotrichia[2] (Sessile)	9.1 (4.7)	13.9 (1.8)	43.0 (18.4)	16.5 (6.9)	0.77	0.4722
Leucotrichia[2] (Mobile)	5.9 (3.6)	5.7 (0.3)	6.7 (3.5)	2.2 (0.7)	12.28	0.0727
Plecoptera						
Paragnetina	491.0 (290.0)	2.0 (2.0)	13.5 (8.1)	20.6 (18.6)	0.03	0.8775

Table 8. Continued.

Pteronarcys	0.0	250.1[3]	0.0	0.0	----	------
	(0.0)	(250.1)	(0.0)	(0.0)		
Coleoptera						
Elmidae	27.6	101.7	84.8	47.3	0.29	0.6428
	(15.0)	(21.1)	(43.2)	(9.6)		
Hydracarina	54.8	58.8	60.1	66.3	1.52	0.3433
	(1.9)	(8.6)	(3.3)	(8.4)		
Oligochaeta	6.4	1.6	3.2	2.6	2.70	0.2420
	(0.6)	(1.6)	(0.6)	(0.5)		
Other Taxa	26.0	28.4	33.8	20.1	0.99	0.4249
	(9.8)	(21.0)	(11.5)	(6.3)		
Total Animal						
Biomass	2062.4	911.9	882.7	908.5	0.02	0.9115
	(475.4)	(284.2)	(95.3)	(107.4)		

1- Treatments: In=Initial, Re=Reference, Cc=Cage Control, Ec=Exclusion Cage.

2- Instars 1-4 in Leucotrichia are mobile; fifth instars are sessile.

3- Biomass due to one individual.

*- Symbol: T=Total.

oligochaets and the total number of animals, which showed significant treatment effects for density, showed no significant differences in biomass. Baetis, which showed no significant difference in density between Cc and Ec bricks, had a significantly higher biomass on Cc bricks. This was due to a higher proportion of large animals on Cc bricks. Baetis biomass on Cc bricks was also greater than that for In bricks. The biomass of mobile Leucotrichia (i.e. instars 1 - 4) was higher on Cc bricks and this difference was marginally significant (p=0.0727). Chironomid and Hydropsychid biomasses were highest on Cladophora-covered In bricks, although In and Ec bricks were fairly similar with respect to chironomid biomass. Psychomyia biomass on the Cladophora-free Re bricks was 2 - 3 times greater than that observed on other treatments. Biomass of Elmid larvae was highest on Re and Cc bricks. Total animal biomass was quite similar for Re, Cc and Ec treatments. Animal biomass on In bricks was at least twice that of the other treatments, largely due to the much greater biomass of Hydropsychids on these bricks.

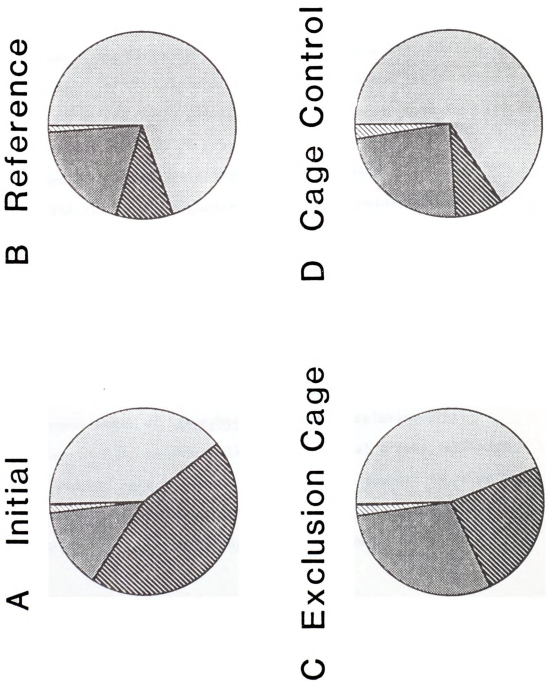
With respect to functional groups based on percent of individuals, Cladophora-free cage control bricks were dominated by micrograzers (65.8% of the individuals) (Figure 27). Predators, filter-feeders and detritivores/deposit-feeders accounted for 23.4%, 8.2% and 2.6%, respectively. Micrograzers dominated Ec bricks as well (44.1%) with filter-feeders (24.3%) and predators (29.8%) being about equal (Figure 27). Detritivore/deposit-feeders and piercers accounted for only 1.8% of the individuals. Notice that Cc and Re bricks are very similar with respect to functional groups based on densities. Ec bricks are more similar to In bricks although In bricks have more filter-feeders (44.8% vs 24.3%) and fewer predators (13.8% vs 29.8%). The

Figure 27. Composition of the macroinvertebrate community with respect to functional groups (based on percent of individuals) for the four different treatments (Initial sample of bricks from the top of the rock dam, Exclusion Cage, Cage Control and Reference Bricks from deeper water) from the Brick Transplant Experiment. A. Initial Bricks; B. Reference Bricks; C. Exclusion Bricks; D. Cage Control Bricks.

KEY

░ Micrograzers
▨ Filter-feeders
▓ Predators
▧ Deposit-feeders/Detritivores
☐ Piercers

Figure 27.



percentages of micrograzers (39.7% vs 44.1%) and piercers and detritivore/deposit-feeders combined (1.7% vs 1.8%) are quite similar, however. When functional groups based on biomass are compared similar patterns emerge (Figure 28). Re and Cc bricks are dominated by micrograzers, 84.4% and 84.5% respectively. When the effect of one *Pteronarcys*, a large, detritivorous stonefly, is included the percent of micrograzers for Re bricks is only 70.2% (Figure 28). Ec and In bricks are also fairly similar. The only differences are a higher percentage of micrograzers (42.2% vs 23.7%) and fewer predators (11.8% vs 23.6%) on Ec bricks vs In bricks.

In summary, substantial changes were observed in both the taxonomic and functional organization of the macroinvertebrate component of the community when bricks from shallow water were exposed to large crayfish in deep water. Much of the change could be attributed to three taxonomic groups: chironomids, Hydropsychids and *Baetis*. Macroinvertebrate associations on cage control bricks, from which *Cladophora* was removed, became more similar to the deep water control bricks (Re). When crayfish were excluded, bricks that retained their cover of *Cladophora* (Ec) had macroinvertebrate associations similar to the shallow water Initial bricks, although some cage effects were observed. These results support the hypothesis that large crayfish are important in generating the patterns of macroinvertebrate distribution and abundance observed in Augusta Creek.

Crayfish Predation Trials

SINGLE SPECIES TRIALS. No *Goniobasis* were eaten by either adult or

Figure 28. Composition of the macroinvertebrate community with respect to functional groups (based on percent of biomass) for the four different treatments (Initial sample of bricks from the top of the rocks dam, Exclusion Cage, Cage Control, and Reference Bricks from deeper water) for the Brick Transplant Experiment. A. Initial Bricks; B. Reference Bricks (not including one *Pteronarcys* nymph); C. Reference Bricks (including one *Pteronarcys* nymph); D. Exclusion Cage Bricks; E. Cage Control Bricks.

KEY

░ Micrograzers

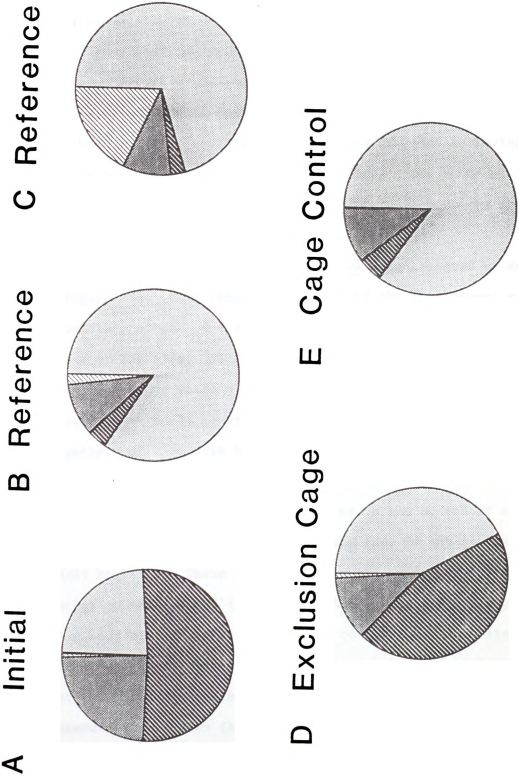
▨ Filter-feeders

▓ Predators

▧ Deposit-feeders/Detritivores

□ Piercers

Figure 28.


A Initial
B Reference
C Reference
D Exclusion Cage
E Cage Control

young-of-the-year crayfish (Figure 29). As this species has a fairly heavy shell and an operculum this result is not too surprising. However, individuals in boxes with adult crayfish did have several gashes in the marl covering their shells where crayfish had chewed on them. One large crayfish was observed chewing on a snail when the trial was terminated. While Goniobasis were too large to fit underneath the tiles they could seek refuge from crayfish by moving to the top of the boxes out of reach of the crayfish. Only 2 out of 32 snails in both trials were found on the sides of the boxes, the rest were either grazing on the tile or the bottom of the box.

In contrast to Goniobasis, almost all Physa were consumed by adult crayfish (Figure 29). None remained in three of the four boxes; all four remained in one box. The survivors were found in the grooves on the underside of the tile. No Physa were consumed by YOY crayfish. In the three treatments where all Physa survived (with and without YOY crayfish and without adult crayfish), the snails showed no clearcut avoidance pattern of high risk habitats, i.e., the top of the tile or the bottom of the box (Table 9). On the contrary, at least half of the snails were actually on top of the tile or on the bottom of the box. This response is most interesting in the case of the treatment without adult crayfish. These snails were in the same aquaria in boxes adjacent to those where their conspecifics were being devoured and yet only half of the individuals sought refuge under the tile or high on the sides. This result is contrary to those of Covich and his colleagues; they have documented various avoidance behaviors of snails in the presence of predators (A. Covich, pers. comm.).

Baetis were captured by both large and YOY crayfish although a slightly higher percentage (52.2 ± 4.9%) survived in the presence of

Figure 29. Results of the single species predation trials conducted in the recirculating aquaria. Values shown are mean percent surviving (± 1 S.E.). Open bars are controls. Shaded bars are treatments with crayfish. The upper panel shows results for adult crayfish. The lower panel shows results for young-of-the-year crayfish.

Figure 29.

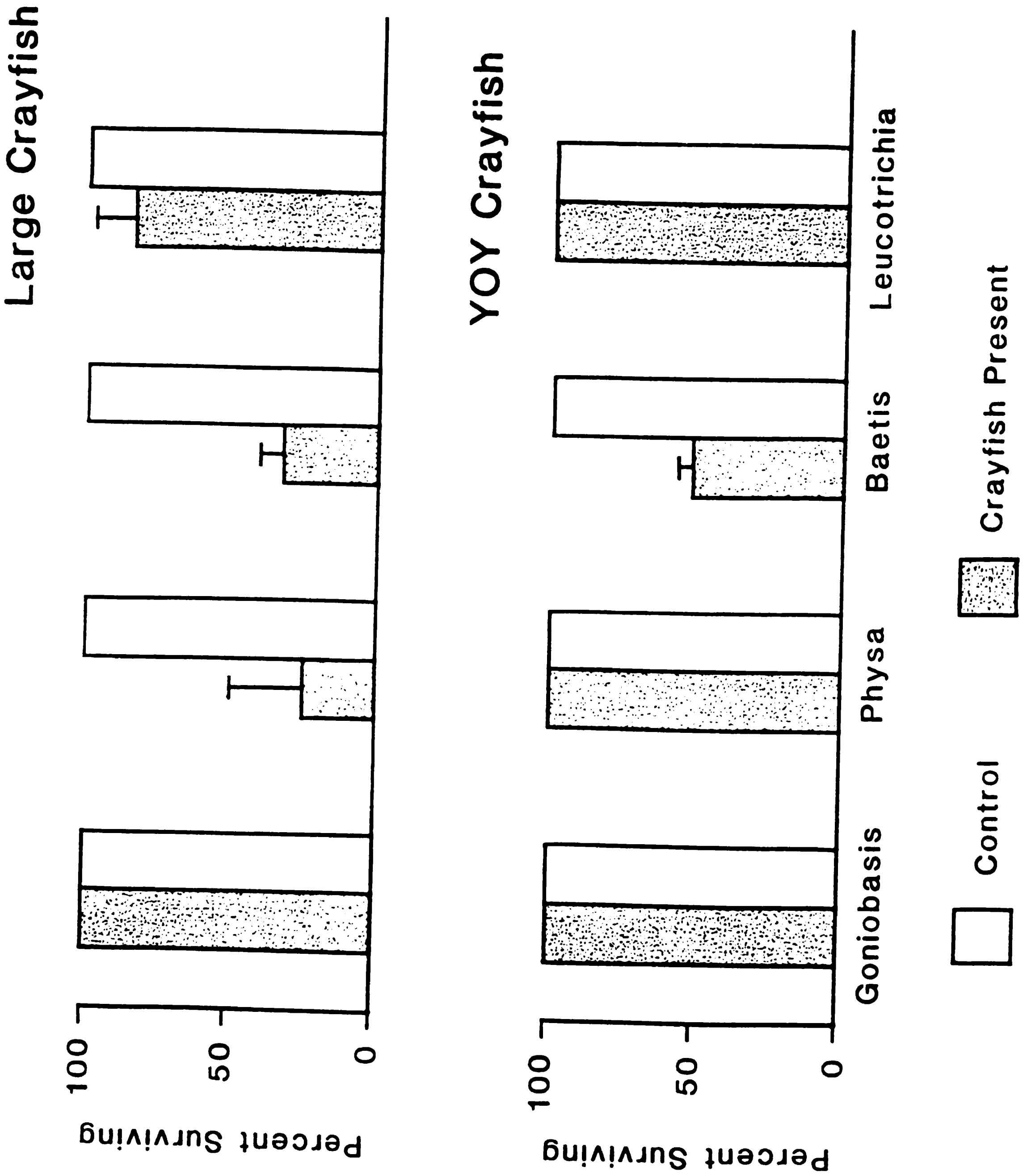

Large Crayfish
YOY Crayfish
Percent Surviving
100
50
0
Percent Surviving
100
50
0
Goniobasis
Physa
Baetis
Leucotrichia
Control
Crayfish Present

Table 9. Distribution of surviving Physa in boxes with and without crayfish in the single species predation trials. Values in table are means (± 1 S.E.). N = 4.

Treatment	Exposed to[1] crayfish	In refuge[2]	
		On Sides	Under Tile
With YOY[3]	3.25 (0.48)	0.75 (0.48)	0.00 (0.00)
Without YOY	2.00 (0.91)	0.50 (0.29)	1.50 (0.87)
Without Adults	2.00 (0.71)	0.50 (0.29)	1.50 (0.65)
With Adults	0.00 (0.00)	0.00 (0.00)	1.00 (1.00)

1- These snails considered within reach of crayfish.

2- These snails considered inaccessible to crayfish by either being out of reach on the sides or in grooves on the underside of the tiles.

3- YOY=Young-of-the-year crayfish.

Table 9. Distribution of surviving Physa in boxes with and without crayfish in the single species predation trials. Values in table are means (± 1 S.E.). N = 4.

Treatment	Exposed to crayfish[1]	In refuge[2]	
		On Sides	Under Tile
With YOY[3]	3.25 (0.48)	0.75 (0.48)	0.00 (0.00)
Without YOY	2.00 (0.91)	0.50 (0.29)	1.50 (0.87)
Without Adults	2.00 (0.71)	0.50 (0.29)	1.50 (0.65)
With Adults	0.00 (0.00)	0.00 (0.00)	1.00 (1.00)

1- These snails considered within reach of crayfish.

2- These snails considered inaccessible to crayfish by either being out of reach on the sides or in grooves on the underside of the tiles.

3- YOY=Young-of-the-year crayfish.

YOY crayfish (33.3 ± 6.8% survived with adults). No Leucotrichia were eaten in the boxes with YOY crayfish. A few were consumed in the trials with adult crayfish. Leucotrichia cases were removed in two of the four replicates. In one box a case was removed along with a piece of marl. In the other replicate, however, 4 cases were cleanly removed from the brick. These cases were situated on a groove in the brick surface. The crayfish may have been able to grab hold of the cases by sliding the claws on their walking legs along this groove. In summary, Goniobasis and Leucotrichia appear to be largely invulnerable to predation by both YOY and adult Orconectes propinquus. In the case of Leucotrichia, however, vulnerability is influenced by the location of the case on the rock, i.e., edges or similar discontinuities on a rock surface may be riskier places for this taxon to construct a case. While Physa were not eaten by YOY crayfish they were highly vulnerable to adults. While Baetis were eaten by both adult and YOY crayfish they appeared to be more susceptible to adults.

Goniobasis AND Physa TOGETHER. The results of these trials were similar to those of the single species trials. All Goniobasis survived regardless of treatment. Only 31.3% (± 23.7%) of the Physa survived in the presence of large crayfish. All individuals survived in the controls. Four out of the five (80%) surviving Physa in boxes containing crayfish had crawled out of reach of the crayfish. However, only 1 out of 15 (6.7%) (one box contained only 3 Physa) of the Physa in the control boxes crawled out. No Goniobasis displayed this crawl-out behavior in this set of trials.

DEEP WATER COMMUNITY TRIALS. All individuals of stocked taxa survived in the controls for this experiment (Table 10). As in the previous two experiments, all Goniobasis survived regardless of

Table 10. The percent of stocked taxa remaining on control and crayfish tiles in the multitaxa laboratory predation trial. The values in the table are means (± 1 S.E.). These taxa were on the same tiles described in Table 11. See text for further details. N = 4.

Taxon	Treatment	
	Control	Crayfish
Goniobasis	100.0 (0.0)	100.0 (0.0)
Physa[1]	100.0 (0.0)	93.3 (6.7)
Baetis	100.0 (0.0)	52.5 (9.5)
Ferrissia	100.0 (0.0)	95.7 (4.3)

1- N = 3 for Physa.

treatment. The limpet Ferrissia also had a fairly high survivorship (95.7%) as did Physa (93.3%). The low mortality for Physa was surprising given the results of the previous two experiments. Also interesting was the fact that at the time the experiment was sampled only 7 Physa were out of reach of the crayfish, either high on the side of the box or on the underside of the lid. The remaining 17 animals were either on the upper surface of the tiles or the bottom of the box. All Goniobasis were exposed to crayfish. All Ferrissia had remained on the tiles. Only about half of the Baetis survived the experiment, a value somewhat higher than the results for the single species trials involving adult crayfish.

Only two of the unstocked taxa, chironomids and Psychomyia, showed significant declines in the presence of crayfish (Table 11). The tiles in two of the boxes with crayfish had definitely been grazed. The upper layer of epilithon had been scraped off in places. The densities for chironomids on these two pairs of tiles were 3547 and 2991 per m^2, respectively. The lowest chironomid density observed on Control tiles was 4744. These tiles also had lower denities of Psychomyia (3761 and 3419) compared to the lowest density of $6154/m^2$ for an ungrazed tile. These results demonstrate that crayfish can remove sessile animals from rock surfaces. The effect is probably exaggerated in this experiment as I used smooth tiles. In Augusta Cr. Psychomyia often builds all or part of its tubes in natural depressions in the rock surface which undoubtedly enhances its survival in areas where crayfish are actively grazing. The fact that these tiles came from an area where crayfish are common also suggests that crayfish rarely engage in this sort of feeding behavior, i.e. scraping the rock surface extensively, when other foods such as

Table 11. The effect of crayfish on the density (No./m^2) of several co-occurring, deep water taxa in the multitaxa laboratory predation trial. These taxa had colonized the tiles while they were on the bottom of the upstream run at Nagel's Site. Values in the table are mean densities ($\pm$ 1 S.E.). The effect of crayfish compared using ANOVA. ANOVA performed on log transformed data; means compared using Tukey's HSD test (p = 0.05). Means with the same letter are not significantly different. N = 4. See text for further details.

Taxon	Treatment	
	Control	Crayfish
Chironomidae	6795 a (698)	4263 b (585)
Antocha	150 a (37)	64 a (41)
Elmidae L.*	224 a (81)	257 a (97)
Elmidae A.	96 a (56)	460 a (212)
Heptageniidae S.	459 a (112)	738 a (170)
Psychomyia	6688 a (370)	4648 b (628)
Oligochaeta	2190 a (566)	2190 a (363)

*- L. = Larvae, A. = Adults, S. = small (< 1 mm long)

detritus are available. Indeed, the only time I have seen them scraping rock surfaces is when they have consumed all other available food in an aquarium (Creed, pers. obs.). I am unable to explain why the crayfish resorted to this mode of feeding prior to consuming all of the *Physa* in the boxes. It is possible that *Physa* had avoided the tiles for much of the trial and had begun to move down to the high risk part of the box as hunger levels increased. Sih (1987) has observed similar behaviors in starved stream salamanders. For taxa such as *Baetis* and *Physa* trials such as these may need to be sampled at shorter time intervals or the animals' behaviors recorded on film (Wiley and Kohler 1981, Kohler and McPeek 1989).

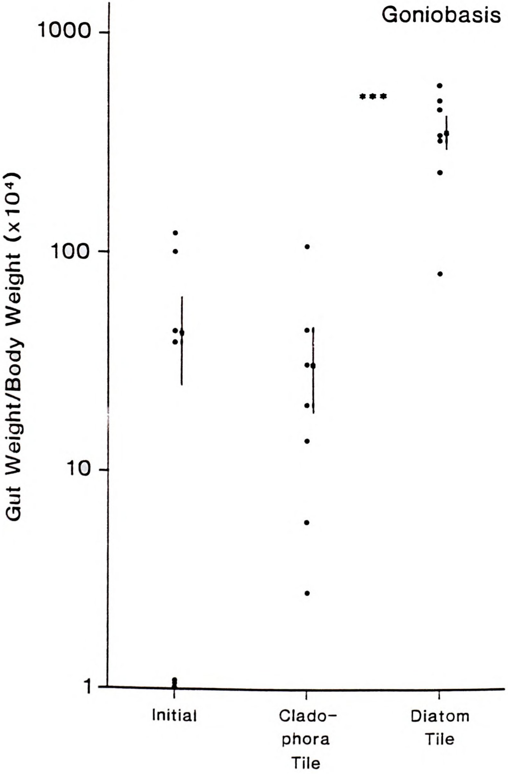
Macroinvertebrate Feeding Trials

The four taxa tested in the feeding trials displayed a range of abilities to feed in the *Cladophora* and diatom patches. With respect to gut contents, the two snails, *Goniobasis* and *Physa*, appeared quite different in their abilities to feed in the two patches. *Goniobasis* contained ten times more food per unit body mass when feeding on the diatom tile as compared to individuals feeding on the *Cladophora* (Figure 30). Individuals feeding on the *Cladophora* actually contained less food on average then those that had been starved for the first 24 hours. The difference between patches was highly significant ($t=5.3243$, 12 df, $p<0.0002$). Gut fullnesses differed between patches as well; mean (± 1 SE) for foregut: diatom - 0.39 ± 0.11, *Cladophora* 0.00 ± 0.00; intestine: diatom - 0.68 ± 0.11, *Cladophora* - 0.18 ± 0.07. Clearly, this species is more successful foraging on *Cladophora*-free substrates. There was no significant difference in

Figure 30. Results of the Goniobasis feeding trials. Treatments are as follows: Initial - Gut contents after animals were starved for 24 hours; Cladophora and Diatom tiles - Gut contents of animals feeding on either Cladophora-covered or diatom tiles for 24 hours after having been starved. Filled circles represent gut contents for each individual. Filled squares represent mean for treatment (± 1 S.E.).

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 30.


Goniobasis
Gut Weight/Body Weight (x10⁴)
1000
100
10
1
***
Initial
Clado-phora Tile
Diatom Tile

the amount of food contained in the guts of Physa from the two patches after 24 hours (Figure 31). Nor was there much difference in gut fullnesses; foregut: diatom - 0.96 ± 0.04, Cladophora - 0.96 ± 0.04; intestine: diatom - 1.00 ± 0.00, Cladophora - 0.86 ± 0.05. Physa did produce more feces while feeding on the diatom patch, however, (diatom - 75.829 mg dry weight feces vs Cladophora - 11.922 mg dry weight feces) as did Goniobasis (diatom - 47.334 mg dry weight feces vs Cladophora - 1.664 mg dry weight feces). For Physa this translates into approximate egestion rates (mg DW feces/hr) of 3.159 (for all 7 individuals) for diatom patches vs 0.496 for Cladophora. Egestion rates for Physa on the diatom tile were 6.4X greater than for individuals on the Cladophora tile. Comparable values for Goniobasis are 1.972 (diatom) vs 0.069 (Cladophora), a 28 fold difference. Thus, despite the similarity in the amount of food in the guts of Physa from both patches at the time of sampling, Physa, like Goniobasis, had much higher ingestion rates on the diatom tiles. The previous statement assumes that ingestion rate is correlated with egestion rate. If this is indeed the case, Physa had higher ingestion rates than Goniobasis in both patches, particularly in the Cladophora patch.

The striking difference observed in the feeding abilities of these two taxa is probably due to differences in radular morphology. Pulmonates such as Physa have a radula with numerous small teeth (50+) in a row (Pennak 1978, Barnese et al. 1990). Goniobasis (Pleuroceridae) has only seven, large teeth in a radular row (Pennak 1978, Barnese et al. 1990). Indeed, Barnese et al. (1990) have demonstrated that Pulmonates (including Physa) are significantly more efficient at removing periphyton from hard substrates than Goniobasis. This difference in radula design also appears to allow Physa to

Figure 31. Results of the Physa feeding trials. The treatment descriptions are in legend of Figure 30. Filled circles represent gut contents for each individual. Filled squares represent mean of treatment (± 1 S.E.).

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 31.

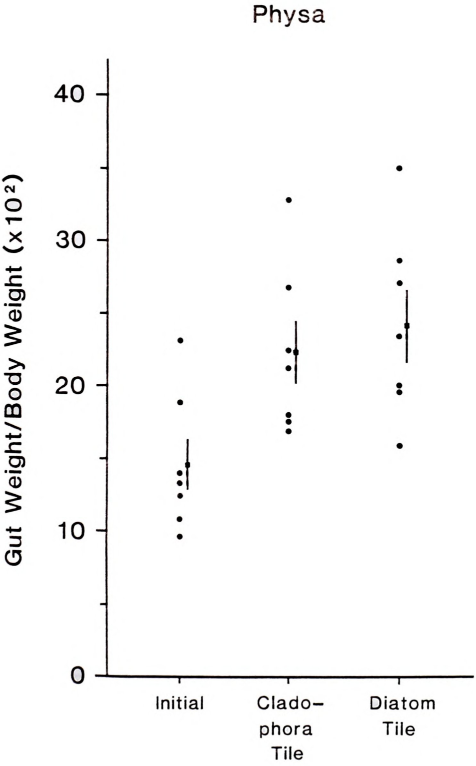
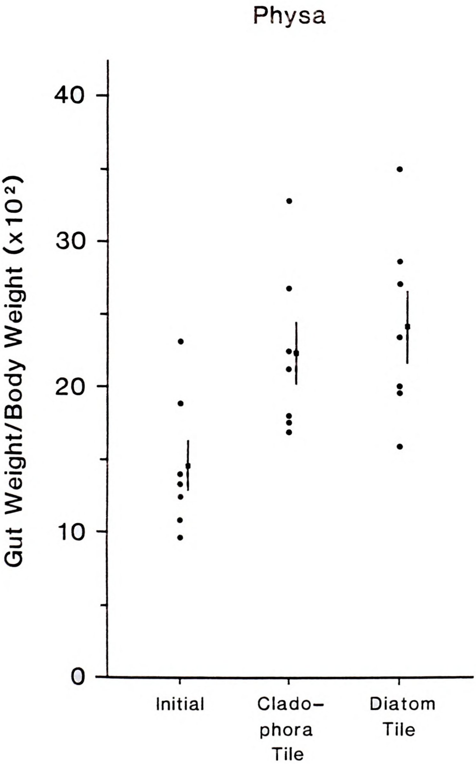

Physa
Gut Weight/Body Weight (x10²)
40
30
20
10
0
Initial
Clado–
phora
Tile
Diatom
Tile

Figure 31. Results of the *Physa* feeding trials. The treatment descriptions are in legend of Figure 30. Filled circles represent gut contents for each individual. Filled squares represent mean of treatment (± 1 S.E.).

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 31.


Physa
Gut Weight/Body Weight (x10²)
40
30
20
10
0
Initial
Clado-
phora
Tile
Diatom
Tile

exploit more marginal habitats such as Cladophora more effectively than Goniobasis.

The responses of Baetis and Stenonema were similar to those observed for the two snail species (Figures 32 and 33). Stenonema ingested three times as much food per unit body mass on the diatom tile compared to the Cladophora tile (t = 4.6800, 10 df, $p<0.0009$). Like Goniobasis, the mean amount of food/body weight for Stenonema on the Cladophora tile was slightly less than that for individuals starved for 24 hours (Figure 33). Mean gut fullness for Stenonema on the diatom tile was 0.88 ± 0.13 vs 0.21 ± 0.10 for animals feeding on the Cladophora tile. Baetis, on the other hand, while ingesting significantly more food on the diatom tile (t = 2.6635, 8 df, $p<0.0287$), was able to ingest some food on the Cladophora tile and increase the mean amount of food/body weight over starved individuals (Figure 32). There was little difference in mean gut fullness for the two patches (0.70 ± 0.05 diatom tile; 0.65 ± 0.13 Cladophora tile) although there was greater variation in gut fullnesses for individuls from the Cladophora tile.

DISCUSSION

Direct and Indirect Effects of Crayfish on Macroinvertebrates

The field and laboratory experiments presented above, considered along with the results discussed in Chapter Three, further demonstrate that crayfish can have strong direct and indirect effects on the benthic biota of Augusta Creek. In addition to the potential indirect effects of crayfish on many invertebrate taxa (primarily micrograzers)

Figure 32. Results of the Baetis feeding trials. The treatment desriptions are in legend of Figure 30. Filled circles represent gut contents for each individual. Filled squares represent mean of treatment (± 1 S.E.).

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 32.

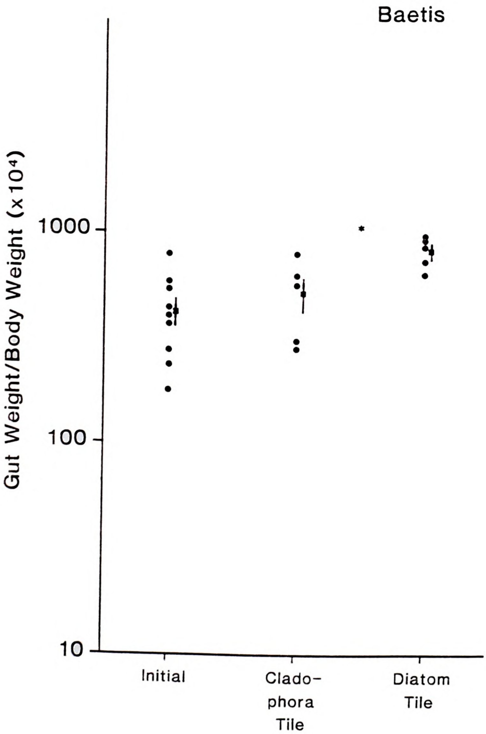
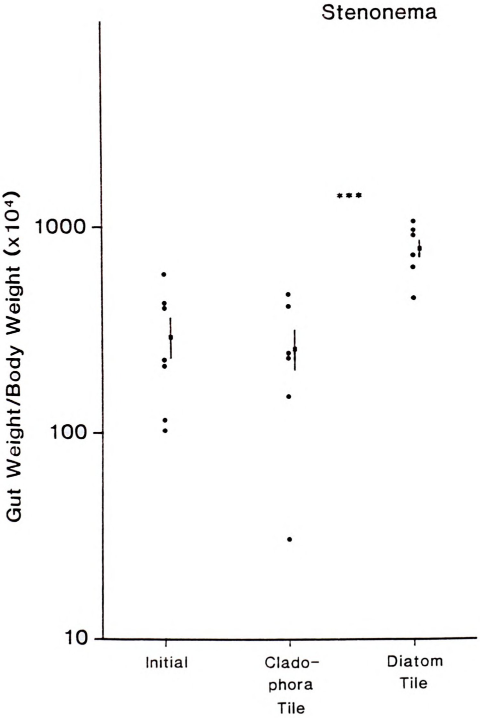

Baetis
Gut Weight/Body Weight (x10⁴)
1000
100
10
*
Initial
Clado-
phora
Tile
Diatom
Tile

Figure 33. Results of the Stenonema feeding trials. The treatment descriptions are in legend of Figure 30. Filled circles represent gut contents for each individual. Filled squares represent mean of treatment (± 1 S.E.).

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Figure 33.


Stenonema
Gut Weight/Body Weight (x10⁴)
1000
100
10
***
Initial
Clado-
phora
Tile
Diatom
Tile

mediated through changes in the benthic algae, the field and laboratory experiments described in this chapter suggest that crayfish can exert direct effects on several taxa as well. These direct effects can be manifested either as predation, direct disturbance of the animal and/or its retreat or a combination of both processes. As the response of the benthic algae has already been discussed in some detail in the previous chapter, the following discussion will focus primarily on the response of the various macroinvertebrate taxa.

Results from Chapter Three demonstrate that when large crayfish are absent or excluded from a portion of the streambed Cladophora dominates the substrate. This result was also observed in the Brick Transplant Experiment. Bricks transplanted to deeper water maintained their Cladophora cover when crayfish were excluded but were rapidly stripped of Cladophora when exposed to crayfish in the cage controls. Cladophora exhibited a much greater range of abundance on the rock dam bricks prior to manipulation then in the experiments described in Chapter Three, however. This appears to be a result of the positioning of the rocks on the rocks dam (i.e., shading) and forays by the crayfish up through the inside of the rock dam to graze some of these substrates. There was also considerable variation in current velocities across the top of the dam (34 - 92 cm/sec). Swifter currents could be either be limiting grazing by crayfish on certain bricks (Maude and Williams 1983, Hart 1984) or increasing Cladophora growth rates by enhancing the rates at which nutrients reach the algal thallus. All of these factors undoubtedly contributed to the observed variation in Cladophora cover on these bricks.

In Augusta Creek, the micrograzers appear to be incapable of excluding Cladophora, at least at the densities observed during these

studies (but see Chapter Five). All micrograzer taxa had access to these bricks, although some taxa (*Glossosoma*, *Protoptila* and *Goniobasis*) were absent from the bricks when they were on the rock dams. Since the presence of *Cladophora* on substrates can reduce densities of epilithic diatoms, an important food for many stream invertebrates (although some diatom taxa, e.g., *Cocconeis*, *Navicula*, are abundant on or among the *Cladophora* thalli), *Cladophora*-free substrates in Augusta Creek are dominated by diatoms with the only obvious filamentous algae being *Stigeoclonium* and occasionally *Oedogonium* (Creed, unpubl. data and pers. obs). The creation and maintenance of these two habitats, a shallow habitat with *Cladophora*-covered rocks and a deep, *Cladophora*-free habitat with abundant microalgae, by large crayfish has direct and indirect effects on various macroinvertebrate taxa.

Surveys found that there is a diverse guild of micrograzers in Augusta Creek. Micrograzers, which feed by brushing or scraping epilithon off of substrates, were found on both shallow, *Cladophora*-dominated habitats and on deeper substrates free of this macroalga. Deeper, *Cladophora*-free substrates were dominated by *Psychomyia*, *Leucotrichia*, *Glossosoma* and *Protoptila* (Trichoptera), *Baetis* and Heptageniidae (*Stenonema*, *Stenacron* and *Heptagenia*) (Ephemeroptera), Chironomid larvae and *Antocha* (Diptera), Elmid larvae and adults (Coleoptera) and *Goniobasis* and *Ferrissia* (Gastropoda). *Psychomyia*, *Leucotrichia* and *Goniobasis* were particularly abundant on *Cladophora*-free substrates. Some of these taxa (Heptageniidae, Elmids, *Antocha*) were found to have comparable densities on *Cladophora*-covered rocks. *Baetis* was actually found to have higher densities in *Cladophora* mats (also see Chapter Five). Finally, *Physa*

has only been found in shallow, nearshore waters at NS and SS with mean densities of 200 - 300 per m^2. Thus, there appear to be three groups of micrograzers (excluding chironomids) with respect to habitat distribution in Augusta Cr. There are sessile and mobile forms (*Psychomyia*, *Leucotrichia*, *Goniobasis*, *Glossosoma* and *Protoptila*) that are found primarily on *Cladophora*-free substrates in deeper water. Micrograzers found in both habitats include *Baetis*, Heptageniidae, *Antocha* and Elmid larvae. Finally, there was one micrograzer taxon, *Physa*, found only on shallow substrates with *Cladophora* or on the stems of emergent plants.

Taxa such as *Psychomyia*, *Leucotrichia* and *Goniobasis* appear to be indirectly facilitated by crayfish. The sessile caddisflies depend on crayfish to continually crop back *Cladophora* that would otherwise overgrow their retreats and foraging areas. They appear to be incapable of excluding *Cladophora* themselves. Hart (1985) has shown that *Leucotrichia* can directly inhibit the development of a bluegreen alga in its foraging area. However, this caddisfly had no effect on the alga beyond the boundaries of its territory. Due to *Cladophora's* immense size relative to other stream organisms it can influence plants and animals that are not in the immediate proximity of its holdfast. The presence of *Cladophora* would reduce light levels reaching the rock surface both through direct interception in the canopy (Blum 1957) and through increased siltation at the rock surface (Blum 1957, Chapter 3). These processes would in turn result in lowered abundances of microalgae such as diatoms. Indeed, abandoned *Leucotrichia* cases were found beneath fully developed *Cladophora* mats in the first crayfish exclusion experiment described in Chapter Three. As the rocks had been thoroughly scrubbed at the beginning of the experiment, these cases were built after the initiation of the experiment and prior to the mat covering the entire rock. When Leucotrichia and Psychomyia are found on rocks with substantial Cladophora cover they are almost always located in areas where algal cover is minimal, e.g., the leading edge of the stone (Creed, pers. obs).

Psychomyia, Leucotrichia and Goniobasis can benefit indirectly from the strong effect of crayfish on Cladophora by being largely invulnerable to direct crayfish predation. This was demonstrated in the laboratory trials for Goniobasis and Leucotrichia. In the case of Psychomyia, laboratory trials suggested that crayfish could capture this taxon, at least from certain substrates. As the tiles used in this experiment were taken from deep water where crayfish are common the effect on Psychomyia may be a function of the availability of alternative foods for crayfish. Observations of foraging O. propinquus in the stream over the last four summers indicate that the primary mode of feeding involves grabbing objects with the claws on the first two pairs of walking legs. Food is then passed to the maxillipeds, which pass it to the mandibles where it is ingested. Crayfish feeding in this fashion probably pass over the retreats of Psychomyia and Leucotrichia. As long as detritus and Cladophora are present on and around the substrates these sessile insects will probably be consumed infrequently. Indeed, Psychomyia was the most abundant taxon (both density and biomass) on the deepwater Re bricks in the Brick Transplant Experiment at NS. Gut contents of large crayfish captured in deeper water consist almost entirely of detritus. Cladophora fragments and animals generally comprise a small fraction of the ingested material (Appendix C). While Psychomyia larvae were

found in 8 of 19 large crayfish guts, rarely were more than 1 or 2 larvae present. Given that Psychomyia has densities ranging from 6,000 - 13,000 individuals/m^2 at NS suggests that large crayfish, whose densities average about 2 - 3/m^2 at NS, consume a small percentage of this species. Only one Leucotrichia was found in all of the 19 adult crayfish guts.

While the effect of crayfish on Psychomyia is probably consistent over the duration of larval phase of this species it may vary for Leucotrichia and Goniobasis. Both large and small Psychomyia build meandering sand tubes on the upper surface of rocks. The larger tubes of larger larvae may be more prone to being removed by crayfish. However, these larvae often build all or part of their tubes in a depression in the rock surface which undoubtedly minimizes their susceptibilty to crayfish. Also, the size distribution of Cladophora thalli from deep water substrates (generally <4 mm long, see Chapter 2) suggests that a refuge exists for animals or their structures that do not project more than 3 - 4 mm from the rock surface. Most Pyschomyia tubes and all Leucotrichia cases are less than 4 mm high. Leucotrichia, however, switches from being mobile (instars 1 - 4) to being sessile in the final instar. Goniobasis undergoes a considerable increase in size over the course of its life. Mobile Leucotrichia and young Goniobasis may be quite vulnerable to crayfish. Results of the Brick Transplant Experiment suggest that early instars of Leucotrichia, like fifth instars, are also largely invulnerable to crayfish predation as they had higher densities on Cc and Re bricks than on Ec bricks. Early instars of Leucotrichia were never found in crayfish guts.

The Goniobasis encountered in Augusta Creek are usually 8 - 17 mm

in shell height. The smallest Goniobasis that I ever collected in this stream was 3 mm in shell height. Small snails may be vulnerable to large crayfish and thus utilize a safe habitat (which I have yet to find) until they reach a large enough size (~6 - 8 mm) when they can move into deep water. Large Goniobasis were consistently invulnerable to crayfish in laboratory predation trials. The laboratory feeding trials suggest that large Goniobasis are much more efficient at foraging on Cladophora-free substrates. These large individuals are therefore very much dependent on crayfish to maintain more profitable Cladophora-free habitats. It is likely that at much higher densities Goniobasis might be able to reduce the density of a filamentous alga like Cladophora, or even exclude it (e.g., Gregory 1980 cited in Steinman et al. 1987, Brönmark 1989). At the densities recorded in Augusta Cr., however, Goniobasis appears to have little direct effect on Cladophora abundance. Goniobasis did not appear to ingest Cladophora in the laboratory feeding trials. However, large thalli may not be as vulnerable to this snail as very small thalli. Large Goniobasis can easily move through the 1/4" mesh hardware cloth that I used to build my cages so they have had access to substrates from which crayfish were excluded. Their effect on Cladophora in Augusta Cr., if any, appears to be small compared to that of the crayfish.

Other mobile grazers such as the limpet Ferrissia and the caddisflies Glossosoma and Protoptila, should benefit indirectly from the exclusion of Cladophora by crayfish. As these taxa all tend to plow along the surface of a rock as they feed they may be physically inhibited from feeding effectively in or on dense algal mats. Oemke (1983) observed that Glossosoma larvae avoided substrates with filamentous algal cover. Dudley (1986), however, noted that another

Glossosomatid, *Agapetus*, perched on *Cladophora* filaments in a California stream and appeared to be feeding on epiphytic diatoms. *Ferrissia* appears to be largely invulnerable to crayfish predation. *Glossosoma* and *Protoptila*, on the other hand, may be vulnerable. Oemke (1983) found densities of *Glossosoma* in Augusta Cr to be 5 - 10X less than nearby Spring Brook where crayfish are uncommon. Summer densities (No./m^2) of this taxon were estimated at 42.55 for Augusta Cr. and 566.04 for Spring Brook (Oemke 1983). I have recorded densities of *Glossosoma* as high as 3648/m^2 (mean 2319/m^2, range 1608 - 3648/m^2) on shallow substrates in another nearby stream, Seven Mile Cr. (see Chapter Five, Table 12). Densities of *Glossosoma* in deeper water, where large crayfish were more abundant, in Seven Mile Cr. averaged 64/m^2. These data suggest that *Glossosoma*, and possibly *Protoptila*, are vulnerable to crayfish predation. In an experiment evaluating the vulnerability of *Glossosoma* from Seven Mile Cr. to large crayfish, I observed higher survivorship in the absence of crayfish (54% vs 17%). Poor survivorship in the controls appears to have been due to water temperature differences between the stream and the lab. Thus, populations of these Glossosomatid grazers may suffer a cost through direct predation by crayfish which mitigates the indirect benefit of *Cladophora* removal. However, the few individuals that do manage to survive appear to be benefitting as fifth instars and pupae in Augusta Cr. are approximately 3X heavier than those from Spring Brook (Oemke 1983), which may be the result of reduced intraspecific competition.

Several taxa, e.g. *Baetis*, Heptageniidae, *Antocha* and Elmidae, were found on both *Cladophora*-covered and *Cladophora*-free substrates. *Baetis* densities were actually greater on the shallow, Cladophora-covered substrates both in the surveys and the brick transplant experiment. These results are interesting in light of the laboratory feeding trials which suggest that Cladophora-free substrates are more profitable for Baetis and Stenonema (Heptageniidae). However, the laboratory predation trials suggest that Baetis is vulnerable to crayfish predation. Heptageniidae nymphs may be vulnerable to crayfish as well. Baetis nymphs, which are generally found on the upper surface of stones, appear to avoid crayfish (and fish) by taking refuge in shallow water during the day. Heptageniidae nymphs, especially large individuals, on the other hand, move to the underside of large rocks during the day. As samples for both the surveys and the experiment were taken during the day, it is possible that the Baetis and Stenonema nymphs found in shallow water during the day may move into deeper water at night to feed on the Cladophora-free rocks. Even though Orconectes propinquus are also active at night the risk of predation in this habitat may be reduced if visually feeding fishes are not active. If these mayflies are "flushed" from the rock surface by crayfish at night there is a reduced probability that they might be consumed by fish before returning to the bottom.

Field observations and the contents of crayfish guts support the idea that fish have a stronger negative effect on these mayflies than crayfish in Augusta Cr. and that fish are also facilitated by crayfish with respect to prey capture. During the day several small fish, primarily blacknose dace (Rhynichthes atratulus) and creek chub (Semotilus atromaculatus) were often seen swimming immediately behind foraging crayfish. On a number of occasions the fish were observed to dart in around the crayfish, apparently consuming prey dislodged from

the stream bottom. These fish responded similarly to any disturbance I created on the stream bottom. Also, these mayflies were rarely (1 out of 25 guts for each taxon) found in crayfish guts (Appendix C) suggesting that it is not so much direct predation by crayfish that these mayflies are avoiding but being made more vulnerable to insectivorous fish by crayfish movements. Several studies report Baetidae nymphs being commonly consumed by a number of stream fish (e.g., Pentelow 1932, Allen 1941, Gerald 1966, Barber and Minckley 1971, Creed and Reice 1990). Furthermore, Kohler and McPeek (1989) found that the presence of sculpin strongly affected the behavior of *Baetis* during the day but had little effect on this mayfly's behavior at night. Overall, crayfish may have a positive effect on these mayfly taxa by providing a habitat where they can forage more effectively, especially *Stenonema*. The indirect benefit derived by these mayflies may be reduced, however, due to the presence of insectivorous fish. The preference displayed by *Baetis* for shallow water, during the day at least, may be a response to increased predation risk from fish in deep water. The degree to which the vulnerability of benthic invertebrates to fish is influenced by crayfish deserves further study.

Physa was the one taxon of micrograzer that was found exclusively in shallow water. *Physa* were found on shallow substrates at NS and SS; they were never seen at HRS. The laboratory feeding trials demonstrated that, unlike *Goniobasis*, *Physa* can ingest equal amounts of food on either *Cladophora*-covered or *Cladophora*-free substrates, although the rate at which food is processed is higher on *Cladophora*-free substrates. Thus crayfish have a slight positive indirect effect on *Physa* as a consequence of their strong interaction

with *Cladophora* in Augusta Cr. However, there is still a considerable proportion of the streambed on which *Physa* could be feeding. Two of the three laboratory predation trials suggest that crayfish are one agent, if not the primary one, excluding this snail taxon from deeper waters. Unlike the mayflies, *Physa* is unable to respond as quickly to the approach of a crayfish making coexistence between these taxa less likely. Certain large, benthic feeding fish such as white suckers (*Catostomus commercsi*) may also be involved in excluding *Physa* from deep water. The exclusion of *Physa* from deep water may benefit many of the other micrograzers found in that habitat as *Physa* appears to be a very efficient grazer on epilithon (Barnese et al. 1990). Barnese et al. (1990) found that *Physa* generally reduced levels of attached algae to a much greater extent than *Elimia* (=*Goniobasis*). These results suggest that *Physa* could outcompete *Goniobasis* as it can feed more efficiently on reduced levels of diatoms, possibly driving levels of diatoms below that which *Goniobasis* can utilize. *Goniobasis* may thus benefit from the combined effects of *Cladophora* and *Physa* exclusion.

The above discussion suggests that the degree to which a micrograzer taxon was indirectly facilitated by crayfish grazing depends on its vulnerability to either crayfish or fish. Taxa which are vulnerable to one or the other predator are not predicted to exploit the *Cladophora*-free substrates to the same extent as invulnerable taxa. The distribution data suggest that fairly mobile taxa may circumvent the problem of fish predation by exploiting the deeper habitat at night when visually-feeding, insectivorous fish may not be as effective at capturing individuals 'flushed' from the substrate by crayfish. Slower taxa such as *Physa* may not have this

option as crayfish feed both day and night and can orient towards prey using chemical (Motyka et al. 1985), visual and tactile cues (Creed, pers. obs.). Taxa which reap the greatest benefits are those that are invulnerable to both predators. Psychomyia, for example, appears to be largely invulnerable to fish predation. Barber and Minckley (1971) rarely found this sessile caddisfly in the guts of creek chub. It is likely that Leucotrichia and large Goniobasis are also relatively invulnerable to fish predation although this remains to be tested.

Crayfish appeared to have direct and indirect negative effects on several filter-feeding and deposit-feeding taxa. Filter-feeding Hydropsychidae larvae (Hydropsyche sp., Cheumatopsyche sp., Symphitopsyche bifida and S. sparna) were found to be more abundant on shallow, Cladophora-covered rocks in both the surveys and on both the shallow In bricks and the transplanted Ec bricks in the Brick Transplant Experiment. The experimental results demonstrate that much higher densities of hydropsychid larvae can occur in deeper water than are normally found there. While hydropsychid larvae will commonly utilize mats of algae and moss for the construction of their capture nets they are by no means limited to this habitat. They can just as easily use pieces of detritus and small stones for placing their nets. It is possible, though, that higher densities of hydropsychids could be supported in algal mats due to the increase in both attachment points for nets and the increase in available surface area. Current velocities in the deeper water often appeared suitable for filtering as well. Their much lower densities in deeper water appear to be a consequence of direct predation by crayfish and disturbance.

The sessile nature of hydropsychid caddisflies, along with a net and retreat with a higher profile than those of Psychomyia and

Leucotrichia, probably contribute to the vulnerability of these animals to crayfish. Given the manner in which crayfish forage, it is likely that the crayfish are simply consuming the net and the supporting materials (often detritus) and accidentally capture the animal on occasion. Smaller hydropsychids may have fewer encounters with crayfish if they build their nets and retreats in crevices or cracks between two rocks. This would account for their higher densities in deeper water. Nevertheless, the disturbance created by crayfish combined with the increased risk of capture (by either fish or crayfish) would make deeper waters a less profitable habitat overall. Hydropsychids were only found in 4 of the 25 crayfish guts examined (Appendix C). This fact, combined with the survey and experimental data which show this taxon to have much higher densities on shallow, *Cladophora*-covered substrates, supports the idea that hydropsychids, particularly large larvae, avoid deeper substrates. In the absence of crayfish, much greater densities of hydropsychids would be expected on substrates in deeper water. Even with insectivorous fish present, the *Cladophora* mats that would be present in Augusta Cr. would probably afford considerable refuge for these caddisflies from the fish.

Crayfish appear to have negative indirect effects on deposit-feeders such as *Tricorythodes* and *Amphipods*, and piercers such as *Ochrotrichia*. Rocks with *Cladophora* mats accumulate considerably more silt and organic matter (FPOM) than *Cladophora*-free rocks. The result is an environment rich in food and possibly with a reduced risk of predation for deposit-feeding taxa. When *Cladophora* is removed the amount of silt on a rock will probably decline if there is any water movement around the rock. Obviously, silt will accumulate on any

substrate where there is little or no current so these taxa are not dependant on crayfish to create appropriate feeding habitats. *Tricorythodes* were collected on silt-covered substrates which had little *Cladophora* cover. Mullen (pers. comm.) has also found *Tricorythodes* to be abundant on rocks with lots of silt but little macroalgal cover. However, the presence of *Cladophora* on shallow, riffle substrates does create additional habitat for these deposit-feeders to exploit. In the case of the piercing caddisfly *Ochrotrichia*, which feeds on *Cladophora*, crayfish appear to be involved in an exploitative competition interaction. At NS crayfish exclude *Cladophora* from all but a few shallow substrates which leaves a limited amount of resources for *Ochrotrichia*. Consequently, *Ochrotrichia* is quite rare at this site. At SS and HRS where there are more extensive shallow areas, *Ochrotrichia* was much more abundant with densities reaching $1000/m^2$. Dudley et al. (1986) also found that the abundance of *Ochrotrichia* was positively related to *Cladophora* abundance. Thus production of this caddisfly is greatly inhibited by crayfish in Augusta Cr. due to the substantial reduction in a major resource.

This diverse array of direct and indirect effects is summarized in Figures 34A and B. One of the major implications of this network of interactions is that the positive association of several micrograzer taxa with adult crayfish is seen to be an indirect consequence of a series of direct interactions, most importantly the strong negative interaction between crayfish and *Cladophora*. The importance of crayfish in inadvertently promoting this association would not be apparent without an understanding of how *Cladophora* can potentially influence habitat quality for these micrograzers when it

Figure 34. Representation of the web of direct and indirect interactions generated by large crayfish in Augusta Creek.

A. The effect on micrograzers.

B. The effect on Hydropsychidae (the dominant filter-feeders) and deposit-feeders.

Figure 34A.

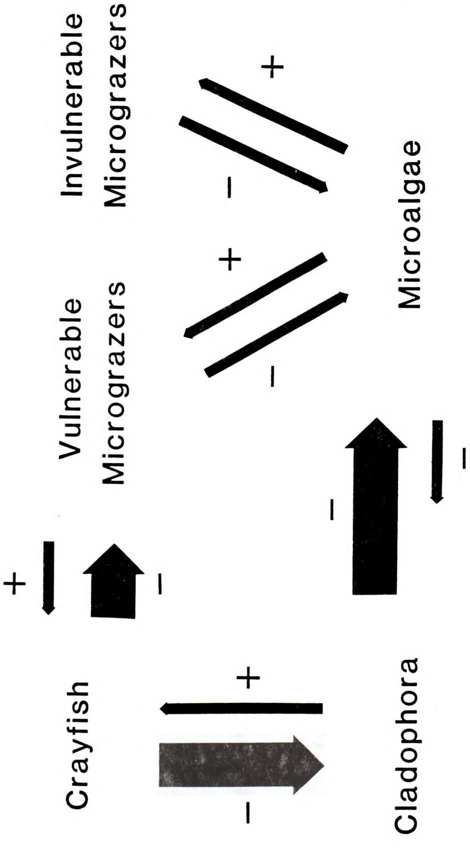
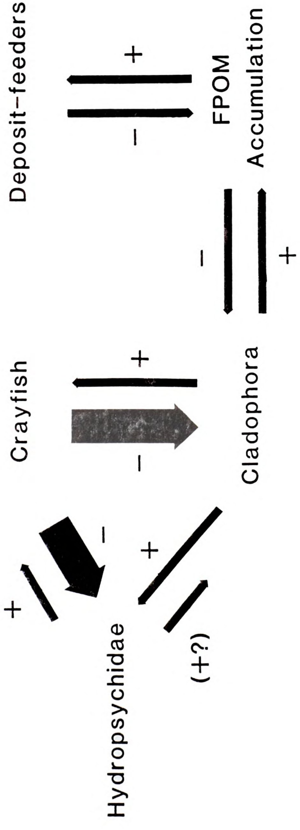

Crayfish
Vulnerable Micrograzers
Invulnerable Micrograzers
Cladophora
Microalgae
+
−
+
−
−
−
+
−
+
−

Figure 34B.


Deposit-feeders
+
−
FPOM
Accumulation
−
+
Crayfish
+
−
Cladophora
−
+
+
Hydropsychidae
(+?)

is very abundant. At first glance, large crayfish and the invulnerable micrograzers in deep water would appear to interact very little as they consume different foods (crayfish: primarily detritus and occasionally *Cladophora* and invertebrates; micrograzers: epilithic microalgae and associated FPOM) and these micrograzers rarely appear in the stomach contents of crayfish. This initial attempt to dissect this network of interactions has demonstrated that a co-occurring set of taxa which appear to interact little is not a random association of organisms at all but a community that does indeed have a 'limited membership' (sensu Elton 1933). When crayfish are excluded from this community *Cladophora* dominates the substrate with the result that the abundance of a number of micrograzer taxa (*Psychomyia*, *Leucotrichia* and *Goniobasis*) decreases dramatically. Alternatively, a number of macroinvertebrate taxa which are facultatively associated with *Cladophora* (e.g., Hydropsychids, *Tricorythodes*, Amphipods and possibly *Baetis*) increase in abundance. Analysis of the interactions that arise from excluded species like *Cladophora* may thus provide a considerable amount of insight into why particular associations of species exist in nature. In the case of Augusta Cr., these results also demonstrate why a community with one type of function (micrograzers) is dominant while a community dominated by filter-feeders is relegated to a refuge. My results, along with those of other researchers (e.g., Paine 1966, 1980, Lubchenco 1978, Dethier and Duggins 1984, Davidson et al. 1984, Power et al. 1985, Brown et al. 1986, Kerfoot and Sih 1987) demonstrate that community ecologists must evaluate the importance of indirect interactions, particularly those generated by strong, direct interactions, if we wish to understand how many communities are structured and function.

Implications for the River Continuum Concept View of Stream Community Organization

In 1980 Vannote et al. (1980) proposed a comprehensive framework within which to visualize stream community structure. They referred to this framework as the River Continuum Concept (RCC). The basic premise of the RCC was that the structure of communities of stream organisms was primarily a reflection of local geomorphological processes and the development of the riparian vegetation. Furthermore, communities along this continuum of streams in a watershed should display predictable changes in composition as various factors (e.g., allochthonous inputs, percent canopy cover and thus the amount of shading, current velocity, depth, turbidity etc) changed with increasing stream size (=order) (see Vannote et al. 1980, Figure 1). While there have been a number of challenges to the validity and/or usefulness of the RCC since its publication (e.g., Winterbourne et al. 1981, Stazner and Higler, 1985), one point which has received little or no attention is the role of biological interactions in modifying these predicted patterns of community composition. The work I have described above (along with that of Power and Mathews 1983, Power et al. 1985, Gilliam et al. 1988, for example) has important ramifications for our interpretation of stream community structure within the framework of the RCC.

With respect to the functional organization of the macroinvertebrate component of stream communities Vannote et al. (1980) visualized three fairly distinct community types along this gradient (Vannote et al. 1980, Figure 1). Headwater streams (orders 1 - 3), characterized by small size, dense or closed canopies and large

inputs of allochthonous inputs, were felt to be largely heterotrophic (P/R < 1). These streams were thought to be dominated (with respect to biomass) by shredding organisms, i.e., those animals whose primary source of nutrition was derived from detritus and the associated microbial fauna, and collectors (note: Vannote et al. combine filter-feeders and deposit-feeders into their collector category). Predatory and grazing invertebrates were predicted to be much less abundant comprising approximately 10% and 5% of the community respectively. In medium-sized streams the riparian canopy is predicted to open with a concomitant increase in autotrophic production and a decrease in allochthonous inputs. The predicted dominant invertebrate functional groups for these streams are collectors and grazers (~85 - 90% of invertebrate biomass). Shredders and predators comprise the remaining 10 - 15%. Large rivers, which receive significant quantities of fine particulate organic matter, are predicted to be dominated (~90%) by the collector functional group. Predators make up the remaining 10%. Shredders should be absent due to minimal inputs of coarse particulate organic matter (CPOM). Grazers are not expected to be very abundant due to lack of hard substrate on which to feed in addition to reduced primary production due to the combined effects of increasing depth and turbidity. As my research has been conducted in second and third order reaches of Augusta Creek which have essentially open canopies (similar to orders 3 - 6 depicted in Vannote et al. 1980, Figure 1) my discussion of these interactions is only applicable to streams of this order (or those with similar abiotic attributes and open canopies).

The results of the surveys and experiments described in this and the preceding chapters demonstrate that one of two alternative

communities, micrograzer vs collector dominated, could dominate the benthos along much of the course of Augusta Creek. The community dominated by micrograzers on the abundant, deep substrates at Nagel's and Snyder's Sites arises as an indirect consequence of crayfish excluding *Cladophora* from this habitat. With the exclusion of *Cladophora*, filter-feeding Hydropsychids and deposit-feeders such as amphipods and *Tricorythodes* are rare, being abundant only in shallow water refuges. Functional and taxonomic organization of the macroinvertebrate component of the community in Augusta Creek is thus dependant on the strong interaction between crayfish and *Cladophora*. While a grazer component of the community would still be present in the absence of crayfish, it would consist largely of mobile taxa (*Baetis*, *Physa*) that are capable of grazing epiphytes from *Cladophora* thalli. It is likely that there might be some heterogeneity in *Cladophora* cover if, in the absence of crayfish, *Cladophora* goes through stages of growth and senescence and patches of bare substrate open up periodically. This would benefit micrograzers such as *Psychomyia*, *Leucotrichia*, *Goniobasis*, *Glossosoma*, *Protoptila* and *Stenonema* that avoid *Cladophora*-covered substrates. I should note that this discussion is relevant only to the structure of summer communities in Augusta Creek. However, as some of these invertebrates have summer and winter generations (e.g., *Glossosoma*) it is possible that there could be a carryover effect. Lack of good habitat for feeding and growth of grazer species would result in reduced levels of recruitment to winter populations and possibly to the exclusion of that species in the winter if no individuals can survive during the summer. Taxa which pupate during the summer (e.g., *Neophylax*; Trichoptera) or aestivate would probably not be affected by changes in

the summer community.

The interactions described above should not be limited to just Augusta Creek. In addition to occurring in similar lotic environments in the Great Lakes region it is quite likely that these sorts of direct and indirect effects could be influencing stream community structure in many temperate and tropical streams. Research conducted in tropical and temperate streams over the last decade has demonstrated that strong interactions between plants and large herbivores occur in both temperate and tropical streams (e.g., Power and Mathews 1983, Power 1984, Power et al. 1985, Power 1987). Other researchers have focused on the associations of various invertebrate taxa with different types of macrophytes (McAuliffe 1983) or macroalgae (Neel 1968, Hart 1984, Dudley et al. 1986) and have found fairly distinct invertebrate associations on substrates free of macroalgae vs those with macroalgal cover. The preference of various micrograzers for microalgae and their influence on the distribution and abundance of these algal taxa has also received considerable attention in recent years (e.g., Oemke 1983, Gregory 1983, Lamberti and Moore 1984, Steinman et al. 1987, Lamberti et al. 1989, Barnese et al. 1990). All of these data collected from around North and Central America suggest that similar sorts of interactions between large herbivore (omnivores) and various macroinvertebrate taxa may be occurring in many stream systems.

In summary, strong biological interactions, at least plant-herbivore interactions, have the potential to influence the kind of macroinvertebrate community present in a particular stretch of stream due to their direct and indirect effects on substrate structure and resource availability. Large omnivores can further modify

community composition by feeding on vulnerable invertebrate taxa as well. This is not to say that abiotic effects are not important in streams. Abiotic factors may directly influence many of the macroinvertebrate taxa in a given stream (e.g., scouring flood). Alternatively, while change in a particular abiotic factor may have little direct effect on most taxa, if it changes the abundance and/or behavior of one of the members of a strong pairwise interaction then it can still have a significant impact on community structure. The recent classification of North American streams by Poff and Ward (1989) with respect to streamflow variability and predictability certainly provides a starting point from which to evaluate the relative effects of biotic vs abiotic effects on several stream communities.

Chapter Five

THE INFLUENCE OF TEMPERATURE AND MICROGRAZER COMMUNITY ON THE CRAYFISH-CLADOPHORA INTERACTION

INTRODUCTION

In the previous chapters large crayfish and *Cladophora* have been shown to be 'strong interactors' (sensu Paine 1980) in Augusta Creek. This strong interaction results in a negative association between these two organisms in Augusta Creek and indirectly affects a number of other benthic taxa. However, the interaction between crayfish and *Cladophora* takes place against the backdrop of the abiotic environment and Augusta Creek represents only one combination of the enviromental factors that might impinge on this interaction. As various aspects of the biology of *Cladophora* and crayfish are sensitive to abiotic factors, e.g., nutrient concentrations (growth rate of *Cladophora* - Pitcairn and Hawkes 1973) and water temperature (growth rate of *Cladophora* - Bellis 1968; and crayfish - Momot 1984, Huryn and Wallace 1987, Mundahl and Benton 1990; feeding rate of crayfish - Huryn and Wallace 1984) it is reasonable to presume that the nature and/or strength of the interaction between these two species might change with changes in the physical environment. Associated changes in the composition of the biotic community can possibly influence this interaction as well. The results of the previous chapters imply that modification of the interaction between these two species can in turn have profound consequences for other members of the community.

As mentioned above, temperature and nutrient availability are two aspects of the environment that could influence the crayfish-Cladophora interaction through effects on the relative growth and/or feeding rates of these species. An extensive data set does not yet exist for the water chemistry of local streams other than Augusta Creek (USDA 1977, Mahan and Cummins 1978, Bachman, unpublished data). However, we do have water temperature records for Augusta Creek (Morofsky, unpublished data, Mahan 1980, King 1982, Oemke 1983) and two nearby streams, Spring Brook (Oemke 1983, Kohler, unpublished data) and Sevenmile Creek (Kohler, unpublished data). It is apparent from these data that Augusta Creek is warmer during the summer months than the other two streams. Maximum summer water temperatures of 28° - 30° C have been recorded in Augusta Creek at (Mahan 1980, King 1982) or just upstream (Oemke 1983) of Nagel's Site. The maximum temperature recorded to date in Sevenmile Creek (Kirby Road Site) is 21.7° C (Kohler, unpublished data). Oemke (1983) obtained maximum temperature values of 16.7° C in Spring Brook (C Avenue Site). Kohler (unpublished data) recorded a maximum temperature of 20.0° C in Spring Brook for the DE Avenue Site. These differences in thermal regimes are probably due to Augusta Creek having more stretches of stream with open canopy as well as extensive wetlands (USDA 1977) where surface waters may be warmed prior to reentering the stream above Nagel's Site. These data lead to the inevitable question: Do different thermal regimes alter the interaction between Orconectes propinquus and Cladophora glomerata in local streams?

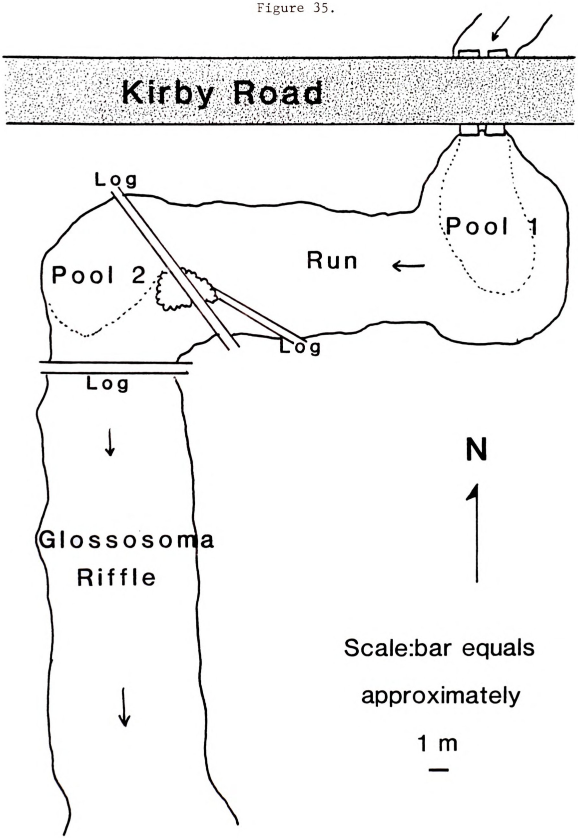
A casual inspection of Cladophora distribution at the Kirby Road Site on Sevenmile Creek revealed that Cladophora was present on some shallow substrates (concrete by culverts and on logs) as one would expect from the Augusta Creek studies. Unlike Augusta Creek, however, turfs of Cladophora were also seen on cobbles present in deeper water as well. Furthermore, all of the rocks in an extensive, shallow riffle were devoid of Cladophora cover. Large Orconectes propinquus were also observed in the pool where Cladophora was present. These observations of obvious Cladophora in deep water and limited abundance in shallow water are not consistent with observations in Augusta Creek. Indeed, they suggested that the interaction between these taxa in Sevenmile Creek was negative but weak or, alternatively, had reversed and become a positive one. They also suggested that the positive, indirect effect of crayfish on invulnerable macroinvertebrates, particularly micrograzers such as Psychomyia, Leucotrichia and Goniobasis, observed in Augusta Creek might be diminished or not occur at all. Below I describe the results of surveys and a rock transplant experiment that attempt to assess the nature of the interaction between O. propinquus and Cladophora in Sevenmile Creek and its consequences for the macroinvertebrates.

STUDY SITE

Sevenmile Creek at Kirby Road is a third order stream located in Calhoun and Barry Counties, Michigan. It is the next watershed to the east of Augusta Creek in the Kalamazoo drainage basin. The stream is approximately 5 - 7 m wide at the Kirby Road Site. There is a deep pool (100+ cm) immediately downstream of the road (see Figure 35). This pool (Pool 1) is partially shaded by the riparian vegetation during the summer. Substrate in Pool 1 is a mix of cobble, gravel and sand with gravel and sand predominating. The water becomes quite shallow (often less than 10 cm) at the downstream end of this pool

Figure 35. A map of Seven Mile Creek at the Kirby Road Site. Dotted lines approximate the boundaries of water deeper than 20 cm for the two pools during normal flow conditions. Arrows indicate the direction of flow in the stream.

Figure 35.


Kirby Road
Log
Pool 1
Run
Pool 2
Log
Log
Glossosoma Riffle
N
Scale:bar equals approximately 1 m

where it flows into a shallow (primarily < 20 cm) run approximately 10 m long which has a gravel/sand bottom. This run and the pool just below it (Pool 2) have a fairly open canopy and receive direct sunlight during the summer from mid-morning to mid-afternoon (Creed, pers. obs.). Pool 2 has a maximum depth of approximately 50 cm and has a substrate of cobbles and gravel with some sand. Immediately downstream of Pool 2 there is a long (~20 m), shallow (< 20 cm) riffle with a cobble/gravel substrate which is somewhat more shaded than Pool 2, primarily by trees on the west bank. The east bank is fairly open with only grasses and scattered shrubs.

Sevenmile Creek has a water chemistry very similar to that of Augusta Creek. Both streams have similar values for pH (8.0 - 8.2), alkalinity (212 - 242 mg $CaCO_3$/l) and specific conductance (443 - 475 uS/cm) (Appendix B). Concentrations of NO_3-N are somewhat higher in Augusta Creek (3.82 - 6.68 mg/l) vs Sevenmile Creek (2.54 - 2.58 mg/l); total P is similar (Augusta Cr. 0.0105 - 0.0268 mg/l vs Sevenmile Cr. 0.0086 - 0.0411 mg/l) (Appendix B). Admittedly, these comparisons are based on a small number of samples. A comparison of maximum water temperatures demonstrates that Augusta Creek consistently has warmer temperatures than Sevenmile Creek during the summer (Figure 36). Differences in the maximum temperatures of the two streams ranged from 0.1° C - 4.4° C in 1989.

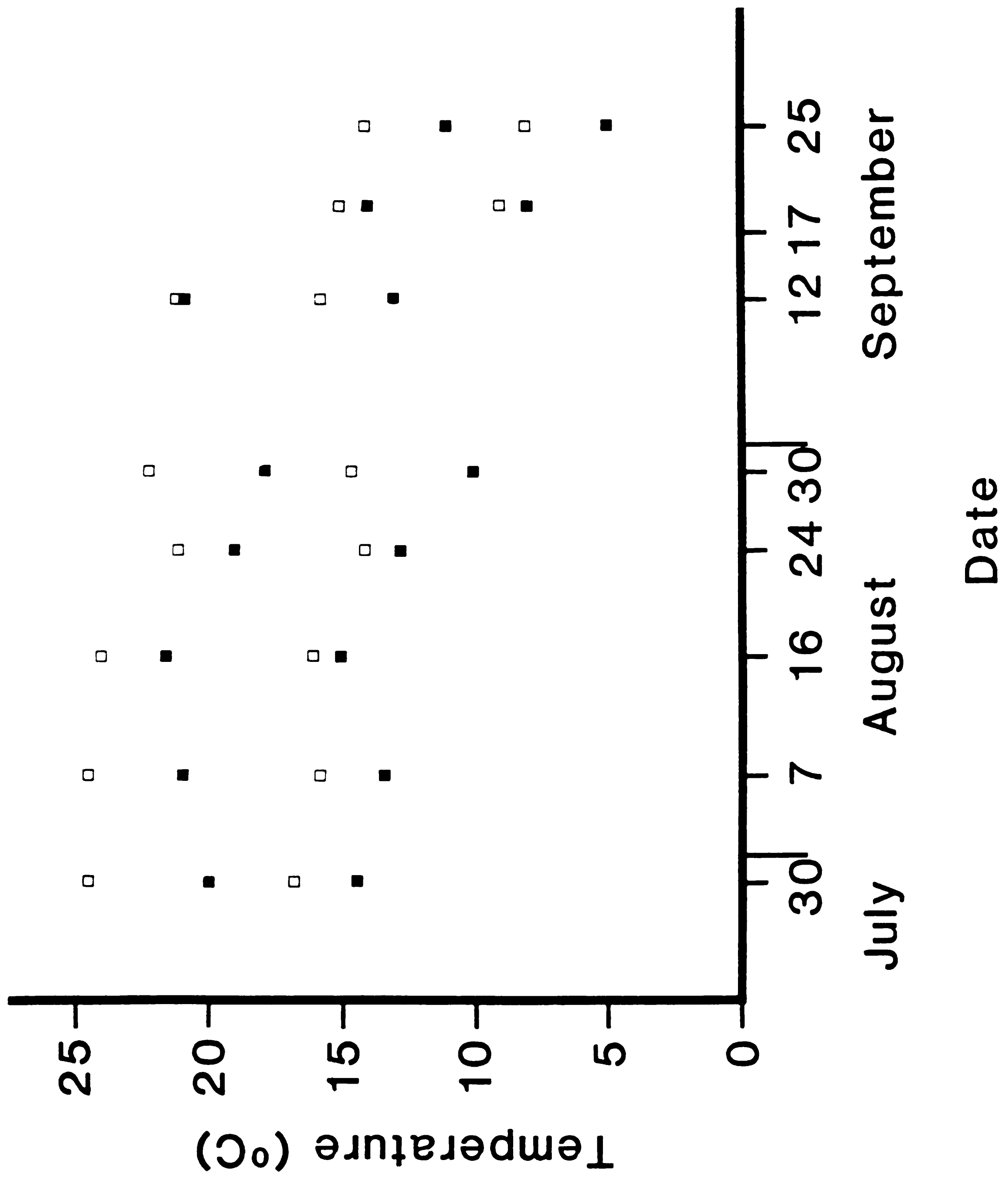
SURVEYS

Materials and Methods

The purpose of the surveys was to quantify substrate type and

Figure 36. Maximum and minimum water temperatures (^{o}C) for Augusta Creek, C Avenue (open squares) and Seven Mile Creek, Kirby Road Site (filled squares) during the summer and early autumn of 1989. Minimum temperatures for both streams for the last two sample dates estimated by extrapolation. Data provided by Steve Kohler.

Figure 36.


Temperature (oC)
0
5
10
15
20
25
Date
July
30
August
7
16
24
30
September
12
17
25

Cladophora distribution down the middle of the channel. If large substrates were only available in deep water this might partly explain the occurrence of Cladophora there. The transect was established and sampled on August 31, 1989. The transect line consisted of a rope marked off at 0.5 m intervals. The transect was located approximately in mid-channel and the upstream attachment point was determined at random. Readings were taken at 0.5 m intervals through much of the run between Pools 1 and 2, Pool 2 and 10 m into the riffle downstream of Pool 2 (Note: as the grazing caddisfly Glossosoma nigrior was extremely abundant in this riffle I will refer to this habitat as the 'Glossosoma riffle'). At each point I recorded the depth (cm), substrate type (sand, sand/gravel, gravel, or cobble/gravel) and the percent cover of Cladophora was estimated (0, 25, 50, 75 or 100%). A total of 50 points was sampled.

Crayfish were surveyed on September 28, 1989 using a 0.25 m^2 quadrat sampler. The survey was conducted during the day as crayfish, particularly large individuals, were seen moving about during the day as in Augusta Cr. The sampling methods were similar to those described in Chapter Two. A total of 15 samples was taken. Four were taken along the banks of the shallow run between Pools 1 and 2 where there were roots and piles of debris and two were taken in midchannel where there was little obvious cover for crayfish. Five were taken in Pool 2 and four more samples were taken in the Glossosoma riffle. Crayfish were counted and measured for carapace length (CL, defined here as the length from the tip of the rostrum to posterior margin of the carapace). Captured crayfish were released when sampling was completed. As these habitats differed by either depth and/or substrate the resulting crayfish densities will be presented separately for each habitat.

Results

The substrate composition of the run between Pools 1 and 2 was predominantly sand and gravel (Figure 37), a substrate that is largely unsuitable for Cladophora growth due to its instability. Much of the substrate in Pool 2 and the Glossosoma riffle consisted of cobbles mixed with gravel. Indeed, all of the values for shallow cobble/gravel substrate are from the Glossosoma riffle. Thus suitable substrate for Cladophora attachment was present in both deep and shallow habitats. Cladophora was found to be most abundant in the deeper waters along the midchannel transect (Figure 38). With respect to the transect, this alga was not abundant in shallow water regardless of substrate type. Remember that Cladophora had been found on some shallow substrates, e.g., some logs and a piece of concrete near the culverts.

Crayfish distributions were similar to those observed in Augusta Creek. Young-of-the-year crayfish were more abundant in shallow water, especially the nearshore habitat where there often were accumulations of detrital debris (Figure 39). Densities of YOY in deep water were about half that for the shallow, nearshore habitat. YOY were not found in the shallow, midchannel regions of the run between Pools 1 and 2, probably due to the lack of suitable cover. Nor were they found in the shallow, Glossosoma riffle. Adult crayfish were most abundant in the deeper habitat, Pool 2. Deep water abundances of adults were similar to those observed in Augusta Cr. One adult was found in the shallow, nearshore habitat; none were found

Figure 37. Distribution of substrate types by depth at the Kirby Road Site, Seven Mile Creek. Data are from a transect extending from the run between Pools 1 and 2 into the Glossosoma riffle. Substrate types: S - sand, G/S - mixture of gravel and sand, G - gravel, C/G - mixture of cobbles and gravel. Sand defined as particles less than 1 mm in diameter; gravel defined as greater than 1 mm but less than 30 mm in diameter; cobbles defined as having a maximum diameter greater than 30 mm.

Figure 37.

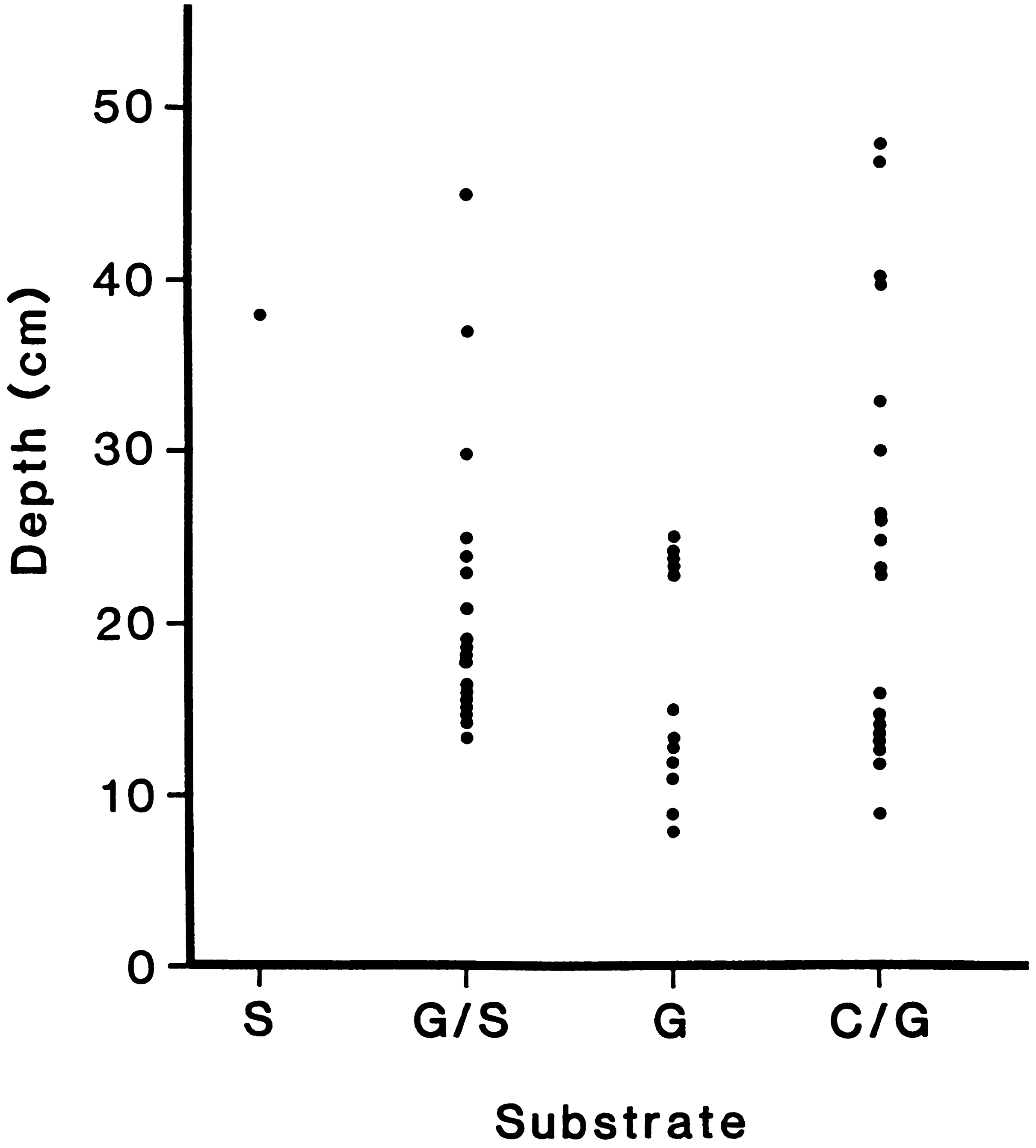


Figure 38. Distribution of <u>Cladophora</u> (measured as percent cover) from transect at Kirby Road Site, Seven Mile Creek.

Figure 38.

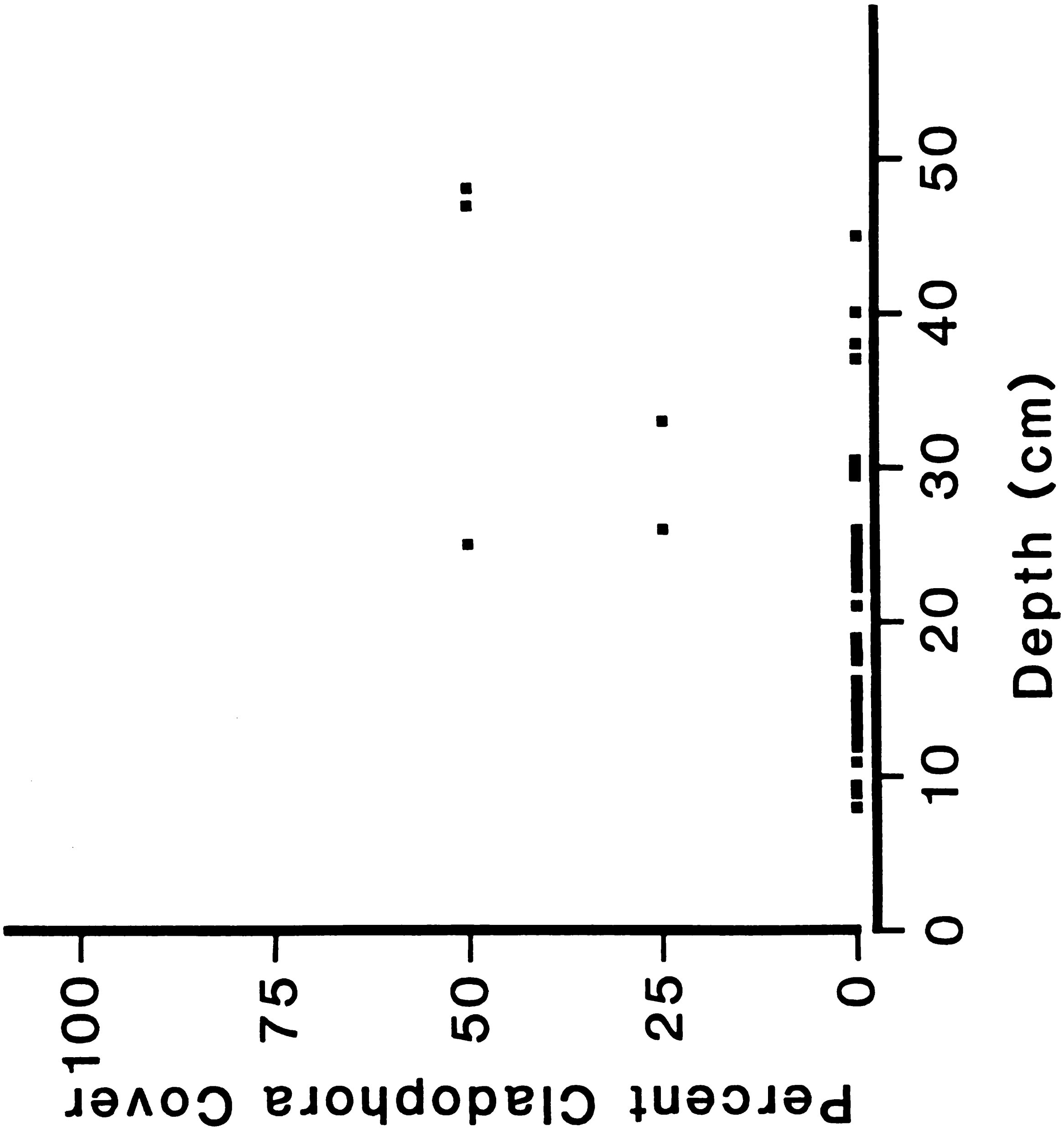
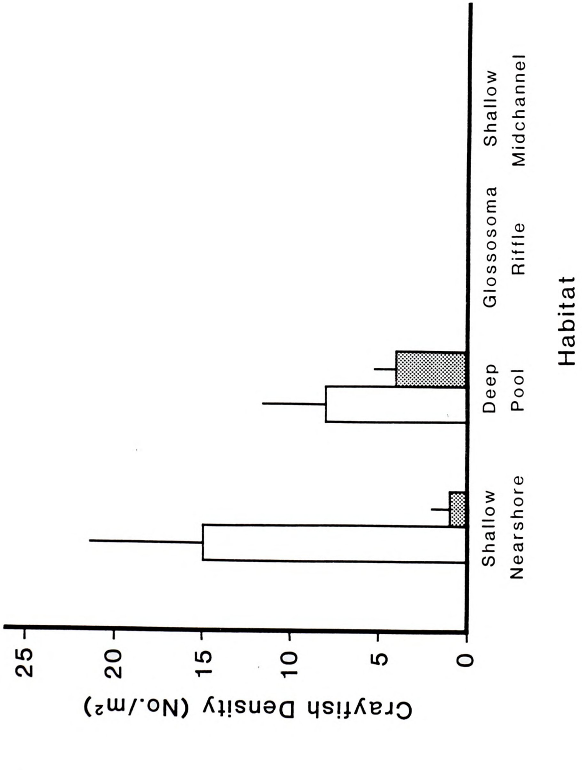

Percent Cladophora Cover
100
75
50
25
0
Depth (cm)
0
10
20
30
40
50

Figure 39. Distribution of adult (C.L. > 20 mm) (shaded bars) and young-of-the-year (open bars) *Orconectes propinquus* by habitat at Kirby Road Site, Seven Mile Creek on September 28, 1989. The habitats are described in the text.

Figure 39.



Crayfish Density (No./m²)
25
20
15
10
5
0
Shallow Nearshore
Deep Pool
Glossosoma Riffle
Shallow Midchannel
Habitat

in the Glossosoma riffle or in the shallow, midchannel regions of the run. While the size range of the crayfish (9 - 32 mm CL) collected was similar to those of O. propinquus collected in Augusta Cr., the YOY were quite a bit smaller than comparable YOY in Augusta Cr. for that time of year (see Appendix D). Mean CL (± 1 S.D.) for YOY was 11.04 ± 1.27 mm for the Sevenmile Cr. sample. Mean CL (± 1 S.D.) for YOY from Nagel's Site, Augusta Cr. on October 1, 1988 was 15.8 ± 2.65 mm.

In summary, the distributions of adult and YOY crayfish with respect to depth were similar to those observed in Augusta Creek, i.e., large adults were more abundant in deeper water and YOY were more abundant in shallow water. The distribution of Cladophora, on the other hand, was different. While Cladophora was seen on some shallow substrates, a considerable portion of the shallow substrates, which appeared suitable for Cladophora establishment, were devoid of obvious algal cover. Obvious Cladophora cover was most frequently observed in deeper water in close proximity to several large crayfish.

TRANSPLANT EXPERIMENT

Materials and Methods

The distributions of Cladophora and large crayfish in Sevenmile Creek suggested one of two possible scenarios. First, large crayfish were consuming little or no Cladophora and thus having no effect on its distribution in this stream. Alternatively, large crayfish were consuming Cladophora in deep water. However, due to the cooler water temperatures in Sevenmile Cr., crayfish were consuming the alga at rates slow enough that *Cladophora* could regrow as a turf before being cropped back again. In other words, *Cladophora* growth rates exceeded crayfish ingestion rates. If large crayfish were indeed consuming *Cladophora* in deep water then transplanting rocks from the deep waters of Pool 2 to shallow water should result in increases in the percent cover and biomass of *Cladophora*. Neither scenario explains *Cladophora's* absence from the *Glossosoma* riffle, however (see discussion).

On August 31, 1989 twelve rocks were selected at random from Pool 2. Four rocks were immediately sampled using a dipnet lined with 1 mm^2 mesh and placed in sealable containers with stream water. Of the remaining 8 rocks, 4 were lifted up and replaced on the bottom of Pool 2 (mean depth = 38 cm) serving as a control while the remaining four rocks were moved to a shallow gravel bar (mean depth = 8 cm). Both sets of rocks were placed in a square pattern (each rock ~10 cm apart) and marked. Horizontal distance between the two groups of rocks was approximately 1 m. Rocks were checked periodically to insure that they had not been moved. A flood halfway through the experiment (September 10) completely covered two of the shallow rocks with sediment and deposited some sediment on the other two. Rocks were 'cleaned' of accumulated sediment by gently waving a hand over them. Although there was little sediment on the deep rocks they were 'cleaned' in the same fashion. The 8 manipulated rocks plus 4 additional rocks from the *Glossosoma* riffle were sampled on September 25, 1989. Current readings were taken for each rock (at the level of the rock top) using a Scienfic Instruments pygmy meter.

Rocks were returned to the lab where percent *Cladophora* cover was determined using a grid of 1/4 inch mesh hardware cloth. Openings

more than half covered by *Cladophora* were considered covered. Then, all *Cladophora* thalli were removed from the rock surface using a dissecting scope at 10x. *Cladophora* was preserved in a 2% Lugols solution. After animals had been sorted from the *Cladophora*, algal samples were either placed in ceramic crucibles or filtered onto precombusted Whatman's GF/F filters, dried at 60^{o} C for 24 hours, weighed and then ashed at 550^{o} C for 1 and 1/2 hours to determine ash free dry weight (AFDW). Animals were removed from the rock surface by brushing the rock with a stiff, nylon bristle toothbrush in a bucket of water. Wash water was then filtered through a 250 um sieve. All animals and debris retained on the sieve were placed in a jar and preserved in 70% ETOH. Animals were later separated from the debris under a dissecting microscope and identified to the lowest possible taxonomic level (usually genus, species when possible). Exposed surface areas of rocks (i.e., above sediment and thus suitable for colonization by algae) were determined by making a foil impression. The impression was removed, cut and flattened with a minimal amount of distortion. Impressions were then run through a leaf area meter to determine surface area. Surface areas (in cm^2) used are the mean of three readings for each impression. Differences in *Cladophora* and animal abundance for the two treatments were compared using ANOVA (PROC ANOVA, SAS Institute). *Cladophora* biomass and animal densities were log transformed; percent *Cladophora* cover was arcsine transformed. As differences in the amount of marl ($CaCO_3$ precipitate) covering rocks from the *Glossosoma* riffle were noticed this was also measured using the foil method. On rocks with little marl, pieces of foil were cut until they matched the dimensions of the marl patch. For rocks with considerable marl buildup, marl-free areas were measured. Marl accumulation was expressed as percent of entire exposed, rock surface area.

Results

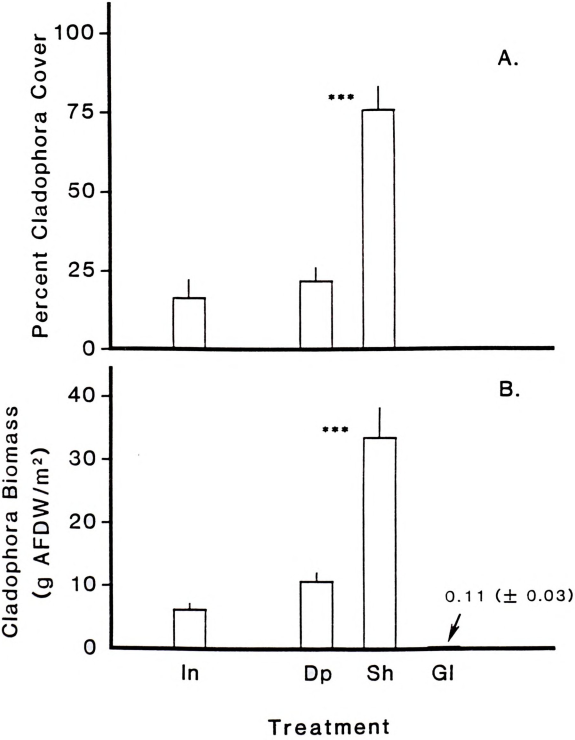
Transplanting rocks to shallow water resulted in significant increases in both the percent cover (F = 30.82, $p<0.0014$) and biomass (F = 33.29, $p<0.0012$) of Cladophora for these rocks compared to deep control rocks (Figure 40). Mean percent cover for shallow rocks (Sh) was 76.1% vs a mean of 22.0% for deep rocks (Dp) (Figure 40A). Mean percent cover on Dp rocks had increased since the intiation of the experiment but the increase was slight (from 16.8% to 22.0%). There was no Cladophora cover on Glossosoma (Gl) rocks. Cladophora biomass was approximately three times greater on Sh rocks compared to manipulated deep rocks and five times greater than initial deep rocks (Figure 40B). Cladophora biomass had almost doubled on the Dp rocks over the course of the experiment. Biomass of Cladophora on Glossosoma rocks was considerably lower than either the initial (In), Dp or Sh rocks (58X, 97X and 303X, respectively, Figure 40B). Deposition of sand appeared to have a negative effect on Cladophora abundance as the Sh rocks that were buried after the flood had lower values of percent Cladophora cover (63.6% and 64.1% vs 93.0% and 83.5%) and biomass (25.2 and 24.5 vs 40.5 and 43.2 g/m^2 respectively). These significant differences in Cladophora abundance between treatments are probably not related to current velocity as readings taken adjacent to the Dp, Sh and Gl rocks (mean ± 1 S.E.: 19.3 ± 1.1, 23.6 ± 0.9 and 23.4 ± 2.1 cm/s, respectively) on September 25 are almost identical. Nor are they simply due to higher light intensities

Figure 40. Response of Cladophora to the rock transplant experiment. In - Initial sample; Dp - Deep control rocks; Sh - Shallow, transplanted rocks; Gl - rocks sampled from Glossosoma riffle at time experimental rocks were sampled. * $p<0.05$, ** $p<0.01$, *** $p<0.005$

A. Percent cover of Cladophora.

B. Cladophora biomass.

Figure 40.


Percent Cladophora Cover
100
75
50
25
0
A.
***
Cladophora Biomass
(g AFDW/m²)
40
30
20
10
0
B.
***
0.11 (± 0.03)
In
Dp
Sh
Gl
Treatment

in shallow water as Sevenmile Cr., like Augusta Cr., has fairly clear water. Percent marl cover was not significantly different between Dp (90.8 ± 3.0%) and Sh (87.5 ± 1.6%) rocks ($F = 0.96$, $p<0.3646$). However, there was almost no marl deposition on the Gl rocks (0.4 ± 0.3%).

Significant responses to the transplant experiment were observed in three macroinvertebrate taxa (Table 12). Chironomids, *Baetis*, and Hydropsychids (Total and Large) were all significantly more abundant on Sh rocks. Mean chironomid density on Sh rocks was ~10,000 individuals per m^2 greater than on Dp rocks. Notice that chironomid densities on In rocks were similar to those on Sh rocks at the conclusion of the experiment. Chironomids were approximately an order of magnitude less abundant on Gl rocks compared to the other three habitats (Table 12). *Baetis* densities on Sh rocks were 20X greater than those observed on Dp and Gl rocks and 11X greater than on In rocks. Total Hydropsychidae were about twice as abundant on Sh rocks as on Dp rocks (Table 12). Notice that the densities of Hydropsychids, regardless of size, had increased since the beginning of the experiment. While the difference in densities of large Hydropsychids was significant, the difference was marginally significant ($p<0.08$) for small individuals. Hydropsychids were the most abundant taxon in the *Glossosoma* riffle with densities of almost $5000/m^2$. Unlike the other habitats, densities of large and small Hydropsychids are almost equal in the *Glossosoma* riffle. In the remaining three habitats small Hydropsychids outnumbered large individuals from 2.5:1 - 7.8:1. Densities of *Glossosoma* were greater on Sh rocks than Dp rocks (despite the greater percent *Cladophora* cover of the former) and the difference was marginally significant

Table 12. Densities (No./m^2) of major macroinvertebrate taxa from the rock transplant study at Sevenmile Creek conducted in the Fall of 1989. Values in the table are means (± 1 S.E.). ANOVA comparisons between manipulated rocks (Sh and Dp) only. ANOVA performed on log transformed data. N = 4.

Taxon	Habitat[1]				F value	P value
	In	Sh	Dp	Gl		
Diptera						
Chironomidae	25111.4 (2141.3)	26632.2 (1506.6)	16317.5 (1538.7)	2283.3 (111.4)	17.78	0.0056
Antocha	3968.4 (1075.5)	3431.4 (513.4)	3725.3 (747.7)	362.1 (211.4)	0.03	0.8595
Ephemeroptera						
Baetis	495.6 (74.6)	5408.7 (1235.8)	272.8 (60.9)	261.1 (101.2)	84.26	0.0001
Ephemerellidae	983.6 (253.5)	3021.9 (390.0)	3125.5 (847.4)	598.3 (202.0)	0.05	0.8308
Trichoptera						
Glossosoma	0.0 (0.0)	254.1 (61.1)	63.8 (36.9)	2318.5 (453.6)	4.44	0.0797
Hydropsychidae (T)*	5427.5 (1493.8)	20789.2 (1697.0)	11261.4 (3220.1)	4989.0 (1437.3)	6.72	0.0411
Hydropsychidae (L)*	614.6 (202.5)	5899.3 (667.4)	2463.8 (724.8)	2202.2 (807.1)	9.01	0.0240
Hydropsychidae (S)*	4812.9 (1300.6)	14889.9 (1869.0)	8797.7 (2532.5)	2786.8 (711.7)	4.50	0.0781
Brachycentrus	336.4 (238.6)	792.4 (155.9)	943.0 (267.0)	123.6 (72.6)	0.03	0.8609
Psychomyia	50.6 (50.6)	163.5 (55.4)	350.3 (99.0)	133.7 (77.9)	1.45	0.2743
Coleoptera						
Elmidae larvae	1159.2 (256.5)	1903.7 (800.9)	894.1 (170.5)	257.2 (87.6)	1.33	0.2929

Table 12. Continued.

Oligochaeta	1376.5	2173.2	2060.5	146.9	0.31	0.5974
	(274.6)	(743.1)	(1044.9)	(90.7)		
Hydracarina	3442.2	6102.0	3024.2	977.9	2.16	0.1918
	(430.9)	(2122.5)	(870.0)	(582.4)		

1- Habitats: In=Initial, Sh=Shallow, Dp=Deep, Gl=Glossosoma

*- Symbols: T=Total, L=Large (>3 mm long), S=Small (<3 mm long)

(p<0.0797). Glossosoma densities for the Glossosoma riffle were 9X and 36X greater than those for Sh and Dp rocks, respectively. No other taxon showed significant differences between the Sh and Dp treatments. Psychomyia, the dominant micrograzer in Augusta Cr., was not very abundant in Sevenmile Cr. (Table 12). While densities of Psychomyia were higher on the Dp rocks which had more Cladophora-free surface area this species was less abundant on the Cladophora-free Gl rocks. Many taxa that displayed little difference in densities between Sh and Dp treatments were much less abundant in the Glossosoma riffle (e.g., Chironomidae, Antocha, Ephemerellidae, Brachycentrus, Elmidae, Oligochaets and Hydracarina).

Inclusion of Gl rocks in the evaluation of animal distributions with respect to Cladophora abundance implicated depth as an important factor in the distribution of Baetis. If Baetis were responding to just Cladophora abundance then they should be more abundant on Dp than Gl rocks. An ANCOVA for depth with Cladophora biomass as the covariate found that depth was indeed the primary factor to which Baetis were responding (F = 30.76, p<0.0087). Depth was not found to be significant for any other taxon using ANCOVA. Inclusion of Gl rocks further emphasized the relationship between Cladophora biomass and other abundant taxa such as chironomids and Hydropsychids. These taxa generally showed strong positive correlations with Cladophora biomass (Chironomids r = 0.971, Total Hydropsychids r = 0.839, Large Hydropsychids r = 0.624, Small Hydropsychids r = 0.859) and weaker correlations with depth (Chironomids r = 0.033, Total Hydropsychids r = −0.273, Large Hydropsychids r = -0.450, Small Hydropsychids r = −0.134).

DISCUSSION

The increase in Cladophora abundance on the shallow rocks in the transplant experiment suggests a similarity in the interaction between large crayfish and Cladophora in Sevenmile Cr. with that observed in Augusta Cr. Large crayfish were more abundant in deeper water where they would thus concentrate their feeding on the alga. Unlike Augusta Cr., where only small (< 4 mm long) Cladophora thalli are found on rocks in deep water, Cladophora abundances in deep water are higher in Sevenmile Creek (compare Figure 40B with upper panel, Figure 11, Chapter Two). Since the transplant experiments suggest that crayfish are consuming Cladophora, the greater relative abundance of Cladophora in deep water in Sevenmile Cr. could be the result of (1) higher growth rates of Cladophora in Sevenmile Cr. relative to Augusta Cr., (2) decreased crayfish ingestion rates or (3) changes in both of these factors.

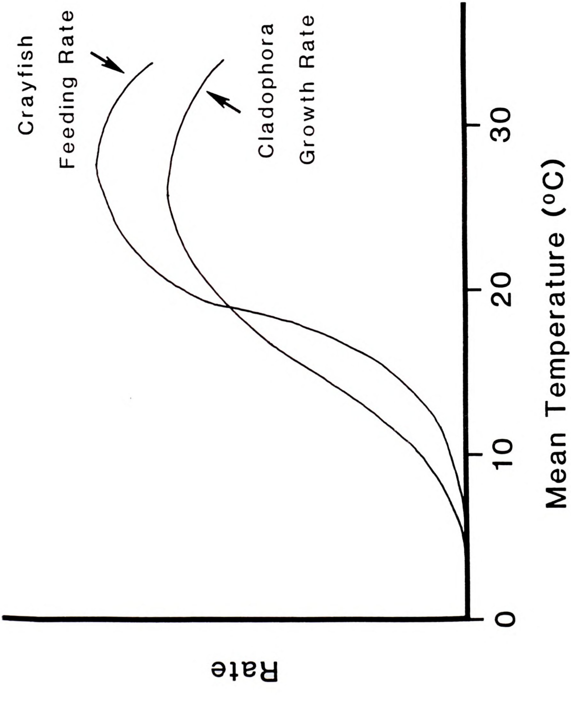
Higher Cladophora growth rates could result from increased nutrient levels in Sevenmile Cr. However, the water chemistry data (Appendix B) suggest that concentrations of nitrate nitrogen and total P are similar for these two streams. Augusta Cr. actually appears to have higher nitrate concentrations. As current velocities in deep water were only about 20 cm/s, nutrient supply rates (Whitford and Shumaker 1961) should not be greater in Sevenmile Cr. A decrease in crayfish ingestion rates could result from (1) increased predation risk, (2) swifter currents in deeper water and/or (3) cooler water temperatures. Similar suites of predatory fishes (e.g., brown trout, creek chub and sculpin) are found in both streams. As discussed in Chapter Two, these fish prey primarily on YOY crayfish and thus should

have little effect on the behavior of large crayfish. Current velocities in deep water (~ 20 cm/s) are comparable to those in Augusta Cr and should not prohibit crayfish feeding. Therefore, the most likely cause of this reduction in crayfish feeding rates is the lower water temperatures in Sevenmile Cr. (Figure 36). While Cladophora growth rates might also be slower at these lower temperatures, the relative change might be less than that in crayfish ingestion rates.

This proposed relationship between crayfish ingestion rate and Cladophora growth rate is illustrated in Figure 41. Both crayfish ingestion rate and Cladophora growth rate are depicted as increasing with increasing water temperature up to a threshold whereupon they decline. The general shape of these curves is supported by the data of Bellis (1968), Whitton (1970), Huryn and Wallace (1987) and Mundahl and Benton (1990). Cladophora's growth rate is postulated as increasing more rapidly at lower temperatures, though. In this proposed relationship, Cladophora growth rate exceeds crayfish ingestion rate at mean temperatures of approximately 10^{o} - 17^{o} C with the result that Cladophora mats will be present with crayfish, at least as patchy, low turfs such as those seen in Sevenmile Cr. As the average water temperature continues to increase Cladophora growth rate is exceeded by crayfish ingestion rate and Cladophora would now be removed faster than it can regrow. The result would be that only small Cladophora thalli invulnerable to crayfish grazing would be found in habitats with adult crayfish. As these small thalli grow into a vulnerable size they will be removed by crayfish. The latter scenario may well explain the interaction observed in the deeper waters of the warmer Augusta Cr. While the relative positions of

Figure 41. Proposed relationship between *Cladophora* growth rate (biomass produced per unit time) and crayfish feeding rate (biomass ingested per unit time) with respect to temperature.

Figure 41.


Crayfish
Feeding Rate
Cladophora
Growth Rate
0
10
20
30
Mean Temperature (°C)
Rate

these hypothetical growth and ingestion rate curves are based on observations from only Augusta Cr. and Sevenmile Cr. they are consistent with both the information on the distribution of Cladophora in a number of habitats over a range of latitudes and the knowledge of the influence of temperature on crayfish growth and feeding.

Cladophora has been shown to grow in water with temperatures ranging from 10° - 30° C (Bellis 1968, Whitton 1967, 1970). Bellis (1968) found that Cladophora growth rate increased over a range of temperatures from 15° to 30° C. Whitton (1967) observed that rapid growth of Cladophora occurred between temperatures of 15° - 25° C, with the lower and upper limits to detectable growth being 6° and 30°, respectively. Contrasting with these data for temperature tolerance in Cladophora are conflicting reports regarding the temporal abundance of Cladophora in many streams. Cladophora was considered to be a winter dominant in Texas with growth maxima in March and November (Thurman and Kuehne 1952). Thurman and Kuehne attributed the disappearance of Cladophora in the summer months to an inability of the alga to tolerate water temperatures of 24° C or higher. Bellis and McLarty (1967) observed growth maxima in May and August in populations of Cladophora in Medaway Cr., Ontario. These authors found that the alga persisted throughout the summer on rocky substrata in shallow riffles. Reported summer water temperatures in Medaway Cr. ranged from 21.0° - 22.5° C. Blum (1957) noted a midsummer decline in Cladophora abundance in the Saline R. in Michigan at one site but not at another (both sites were unshaded). Both sites were riffles although specific depths were not reported. Blum attributed the persistence of Cladophora at the latter station to cooler temperatures recorded there at night although he provided no mechanism for this

phenomenon. In general, water temperatures in the Saline R. during the summer ranged between 20° - 30° C (Blum 1957). My own work in Augusta Cr. has shown that *Cladophora* can persist in shallow water or in deep water when grazing crayfish are excluded. Water temperatures during these studies have ranged from 20° - 25° C. Also notice that in Sevenmile Cr. *Cladophora* abundance increases in deep water over the course of the experiment (Figure 40). In general, stream temperatures were declining during this same period.

In summary, two studies, Blum (1957) and Thurman and Kuehne (1952) report a disappearance of *Cladophora* from waters with temperatures otherwise suitable for the growth of this alga while others (Bellis and McLarty 1967, Whitton 1970 and myself) have reported *Cladophora* persisting in warmer water, although usually in shallow water. I believe that in many cases these contrary results can be explained by covariance of algal growth rates and consumption rates of co-occuring, endothermic grazers (crayfish and fish) with temperature. In addition, Blum (1957), Bellis and McLarty (1967) and myself have observed *Cladophora* persisting throughout the summer in shallow waters, further supporting the idea that grazers avoiding high risk shallow habitats are influencing the distribution and abundance of *Cladophora* in many streams.

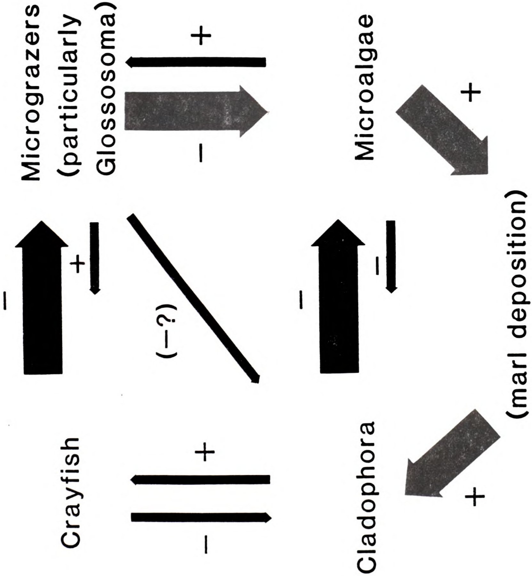
The absence of *Cladophora* from the shallow, *Glossosoma* riffle does not appear to be due to crayfish grazing. Instead, the micrograzer *Glossosoma nigrior* may be excluding *Cladophora* from these substrates through a combination of direct and indirect effects. *Glossosoma* occur at very high densities in this riffle, densities which are 9X and 36X higher than those on Sh and Dp rocks, respectively. At such high densities it is likely that *Glossosoma* may be able to remove

Cladophora thalli before they reach an invulnerable size. In addition, as *Glossosoma* has two cohorts a year in local streams (Oemke 1983, Kohler and McPeek 1989, Creed, pers. obs.), individuals are continuously grazing rocks and keeping epilithic diatom abundances at low levels. An indication that this is indeed occurring are the minor accumulations of marl on the rocks in the *Glossosoma* riffle. Photosynthesis by attached algae can result in the accrual of a marl layer on a surface (Wetzel 1983). A thick, epilithic algal mat can precipitate a layer of marl onto introduced substrates within a matter of months in Augusta Cr. (Creed, pers. obs.). The substantially greater development of marl on the deeper rocks suggests that micrograzers, particularly *Glossosoma,* are not having as strong an impact on epilithon abundance in deeper waters. *Cladophora* readily colonizes marl-encrusted surfaces. In addition, as the basal cells of the alga penetrate the marl it can rapidly grow back if it is grazed. Thus, by preventing the development of a marl layer on rocks, *Glossosoma* appears to be exerting an indirect, negative effect on *Cladophora* mediated by its effect on the epilithon in addition to a possible direct negative effect (herbivory). The *Cladophora* thalli that were found on these Gl rocks were almost always associated with either Hydropsychid retreats or *Neophylax* puparia. The rougher surfaces of these structures may be more difficult for *Glossosoma* to graze effectively. Also, Hydropsychids might prevent *Glossosoma* from grazing near or on their retreats.

When these effects are considered in conjunction with the effect of crayfish on *Cladophora* described above, it appears as if the net effect of crayfish on *Cladophora* is positive (Figure 42). Crayfish have a direct, negative effect on *Cladophora* abundance through

Figure 42. Representation of the web of interactions between crayfish, micrograzers, *Cladophora* and microalgae in Seven Mile Creek.

Figure 42.


Crayfish
Micrograzers (particularly Glossosoma)
Cladophora
Microalgae
(marl deposition)
+
−
(−?)

consumption. However, this consumption seems to be occurring at a slower rate than in Augusta Cr. allowing for the accumulation of patchy turfs of Cladophora in deep water. Distribution patterns of micrograzer taxa such as Baetis and Glossosoma are consistent with the idea that these taxa avoid deeper water and the direct (or indirect) mortality associated with the presence of large crayfish. Epilithon levels can thus remain higher allowing for the development of a marl layer which is colonized by Cladophora. Results of my studies in Augusta Cr. demonstrate that Cladophora basal cells can quickly produce new thalli after exposed tissue has been grazed by crayfish. Shallow substrates have dense populations of micrograzers, particularly Glossosoma, which severely reduce the standing crop of epilithic algae and prevent the development of a marl layer. This effect, in combination with potential, direct herbivory on small Cladophora thalli, may effectively exclude Cladophora from this habitat.

The idea that temperature is influencing feeding rates and thus growth rates of crayfish is supported by the smaller size of YOY in Sevenmile Cr. compared to August Cr. YOY differed by almost 5 mm in CL at the end of the growing season. Assuming equal relations between length and wet weight in both populations this translates into a difference of 0.72 g in the mean weight of YOY (1.03 g wet weight in Augusta Cr. vs 0.31 g in Sevenmile Cr.). Mundahl and Benton (1990) found O. rusticus juveniles to be smaller in a cooler, spring-fed stream in June compared to individuals collected from a warmer stream. Obviously, other factors such as higher predation risk could also be influencing the growth rates of YOY in Sevenmile Cr. While I have no comparative information on predation risk for the two streams, similar

suites of predatory fish (e.g., brown trout, creek chub and sculpin) were present in both Augusta and Sevenmile Creek (Creed, pers. obs.).

Macroinvertebrate taxa in Sevenmile Cr. displayed responses to the crayfish-*Cladophora* interaction similar to those observed in Augusta Cr. Taxa such as Chironomidae and small Hydropsychidae appeared to be responding primarily to the amount of *Cladophora* present on a rock. While these taxa were more abundant in shallow water there was no clear avoidance of deeper substrates; instead their densities were correlated with the abundance of *Cladophora*. *Baetis*, and to a lesser extent *Glossosoma*, exhibited distributions strongly suggestive of preference for shallow water and avoidance of deep water regardless of *Cladophora* cover. Analysis of covariance clearly demonstrated this response for *Baetis*. Depth and *Cladophora* abundance are highly correlated in Augusta Cr. thus obscurring this pattern. While I believe that crayfish are at least partly responsible for this distribution pattern of *Baetis* I believe that they exact a small, direct toll on this species. It is my suspicion that crayfish probably capture *Baetis* infrequently but make them more visible and vulnerable to insectivorous fishes by "flushing" them from the substrate (see Chapter Four). I should note that the experiment was sampled during the day. *Baetis* might well move out into deeper waters at night to feed and only seek refuge in shallow habitats during the day. If they do not move out into deeper water to feed then this refuging behavior might increase intraspecific competition for *Baetis*. Dudley et al. (1986) suggest that *Baetis* prefer *Cladophora* mats as food levels might be higher in the mats. Results from Chapter Four, however, suggest that *Baetis* are not as effective at feeding in *Cladophora* as on *Cladophora*-free surfaces. The low abundances of

Psychomyia in Seven Mile Cr. (~30X less abundant than in Augusta Cr.) may simply be due to a marginal thermal environment in this stream. Alternatively, it may well be a result of a breakdown in the indirect facilitation observed between crayfish and this sessile caddisfly in Augusta Cr. as crayfish are not as effective in excluding *Cladophora* from deeper substrates.

In summary, the data from the survey and the transplant experiment suggest that cooler water temperatures and a more abundant *Glossosoma* population in Seven Mile Creek influence the nature of the interaction between *Cladophora* and *O. propinquus*. While crayfish still appear to be consuming *Cladophora*, the magnitude of this effect does not appear to be as great as in Augusta Cr. Overall, the direct and indirect effects of grazing *Glossosoma* larvae appear to outweigh the negative effect of *Cladophora* consumption by crayfish. The result is an apparently weak, positive interaction between crayfish and *Cladophora*. This apparent change in the nature of this potentially strong interaction can weaken or negate the indirect facilitation of many taxa by crayfish, particularly sessile grazers such as *Psychomyia* and *Leucotrichia*. While the above data implicate water temperature as the primary factor producing the different pattern of *Cladophora* abundance in Sevenmile Cr., further studies are required before we can rule out the contribution of alternative factors such as changes in predation risk and nutrient concentration.

APPENDIX A. Checklist of macroinvertebrates from the Augusta Creek drainage, Barry and Kalamazoo Counties, Michigan. The functional group of each taxon is also presented and the reference(s) that supports this categorization. Animals were collected from routine samples and from experiments. Individuals of almost every taxon are represented in a reference collection. This should not be considered a complete list of the macroinvertebrate fauna of Augusta Creek as I focused my research in areas with gravel to cobble substrate and usually moderate (>15 cm/s) to swift currents. It should be a fairly complete list for these areas, however.

Taxon	Functional Group[1]	Reference[2]
Arthropoda		
Insecta		
Coleoptera		
Elmidae		
Macronychus	Gr	3
Optioservus	Gr	1
Stenelmis	Gr	1,3
Eubriidae		
Ectopria	Gr	3
Psephenidae		
Psephenus herricki	Gr	1,3
Diptera		
Chironomidae larvae		
Empididae		
Hemerodromia	P (Dt?)	1,3
Psychodidae		
Pericoma	Dp	3
Simuliidae		
Cnephia *	Ff	3
Prosimulium *	Ff	3
Simulium	Ff	3
Tipulidae		
Antocha	Gr	1,3
Tipula	Dt	3
Heleidae		
Ephemeroptera		
Baetidae		
Baetis	Gr	2,3,
Caenidae		
Caenis	Gr	1,3
Ephemerellidae		
Attenella	Gr	3
Dannella	Gr	3
Ephemerella	Gr	1,3
Serratella	Gr	3
Heptageniidae		
Heptagenia	Gr	2,3
Stenonema	Gr	1,2,3
Stenacron	Gr	2,3

APPENDICES

Appendix A. Continued.

Leptophlebiidae		
Oligoneuridae		
Isonychia	Ff (P)	1,3
Polymitarcydae		
Ephoron	Dp (?)	3
Tricorythodidae		
Tricorythodes	Dp	2,3
Megaloptera		
Corylidae		
Corydalus cornutus	P	3
Sialidae		
Nigronia	P	1,3
Odonata		
Anisoptera		
Gomphidae		
Hagenius brevistylus	P	3
Zygoptera		
Calopteryx	P	3
Plecoptera		
Paragnetina	P	2,3
Perlesta *	P	2,3
Pteronarcys	Dt	3
Trichoptera		
Glossosomatidae		
Glossosoma nigrior	Gr	1,2,3,5
Protoptila	Gr	2,3
Helicopsychidae		
Helicopsyche borealis	Gr	2,3
Hydropsychidae		
Cheumatopsyche	Ff	3
Hydropsyche betteni	Ff	3
Hydropsyche sp.	Ff	3
Symphitopsyche bifida	Ff	3
Symphitopsyche alhedra *	Ff	3
Symphitopsyche sparna *	Ff	3
Hydroptilidae		
Leucotrichia pictipes	Gr	2,3
Ochrotrichia	Pi	3
Leptoceridae		
Oecetis	P	2,3
Limniphilidae		
Neophylax	Gr	2,3
Pycnopsyche	Dt	3
Philopotamidae		
Chimarra	Ff	3
Polycentropidae		
Nyctiophylax	P	1,3
Psychomyiidae		
Psychomyia flavida	Gr	1,2,3

Appendix A. Continued.

Arachnida		
Hydracarina		
(Suborder Trombidiformes)	P	4
Crustacea		
Decapoda		
Reptantia		
Astacidae		
Orconectes propinquus	Dt (Gr,P)	6,7
Amphipoda		
Gammaridae	Dp	4
Copepoda		
Cyclopoida		
Harpacticoida		
Canthocamptidae *	Dp	4
Mollusca		
Gastropoda		
Mesogastropoda		
Pleuroceridae		
Goniobasis	Gr	4,7,8
Viviparidae		
Campeloma	Gr	4
Basommatophora		
Physidae		
Physa	Gr	4,7,8
Planorbidae		
Helisoma	Gr	4
Ancylidae		
Ferrissia	Gr	1,4
Bivalvia		
Unionidae	Ff	4
Platyhelminthes		
Turbellaria		
Seriata		
Tricladida	Gr	1
Nematoda		
Annelida		
Oligochaeta	Dp	4
Branchiobdellida	P (?)	1
Hirudinea	(P ?)	

Appendix A. Continued.

1- Definition of functional groups. Grazers (Gr) are animals that feed by moving across the surface of the substrate ingesting diatoms and fine particles of organic matter (FPOM) by brushing or scraping the surface with their mouthparts. Filter-feeders (Ff) are animals that feed by straining food material from the water column. This can be accomplished using body structures (e.g., Simuliidae, Isonychia) or a capture net (e.g., Hydropsychidae). Detritivores (Dt) feed on fragments of decaying vegetation which are shredded by their mouthparts. Deposit-feeders (Dp) feed on FPOM that accumulates in depositional areas. Predators (P) are primarily carnivorous, ingesting living prey. Piercers (Pi) feed by piercing individual cells of macrophytes and macroalgae and sucking out the contents.

2- References. 1 - Coffman et al. 1971. 2 - Shapas and Hilsenhoff 1976. 3 - Merritt and Cummins 1978. 4 - Pennak 1978. 5 - Oemke 1983. 6 - Capelli 1980. 7 - This thesis. 8 - Barnese et al. 1990.

*- Identification not positive.

APPENDIX B. Water chemistry data for some local streams.

Stream (Site)	Date	pH	Alkalinity (mg/l $CaCO_3$)	Conductance[1] (uS/cm)	NO_3-N (mg/l)	Total P (mg/l)
Augusta (NS)	6/23/89	8.20	218	.443	4.63	0.0268
Seven Mi. (Kirby Rd)	6/23/89	8.23	212	.450	2.54	0.0411
Wabascon (Kirby Rd)	6/23/89	8.23	170	.371	0.06	0.0417
Cedar	6/26/89	7.82	142	.319	0.11	0.0547
High Bank	6/26/89	8.07	198	.412	1.42	0.1325*
Augusta (HRS)	10/2/89	7.96	222	.456	3.82	0.0118
Augusta (NS)	10/2/89	8.18	242	.475	6.68	0.0105
Seven Mi. (Kirby Rd)	10/2/89	8.16	230	.471	2.58	0.0086
Wabascon	10/2/89	8.23	194	.398	0.18	0.0132

Note: Augusta Cr., Sevenmile Cr. and Wabascon all drain into the Kalamazoo River. Cedar Cr. and High Bank Cr. drain into the Thornapple River (both are in the vicinity of Hastings).

1- Conductance standardized to 25° C.

*- This value was outside the range of the standard curve and therefore is suspect.

Methods. Samples were collected, placed on ice and returned to the lab within 3 hours. Fresh samples were used for determination of pH, alkalinity and conductance. pH was measured on an Orion model SA520 pH meter. Alkalinity was determined by colorimetric titration using bromo-cresol green and methyl-orange indicator. Conductivity was determined using a YSI model 32 Conductance meter. Part of each sample was acidified with sulfuric acid and stored at 5° C until analysis for nitrate and total phosphorus concentrations. Nitrate and total phosphorus were measured on a Perkin Elmer Lambda 6 UV/VIS Spectrophotometer.

APPENDIX C. Stomach contents of Orconectes propinquus from Augusta Creek.

Materials and Methods

Crayfish were collected from Nagel's Site on three different dates, July 6, 1986 (day sample, n = 6), September 1, 1986 (night sample, n = 11), and July 1, 1988 (day sample, n = 8). Crayfish collected on the second two dates were collected during distribution surveys. Nineteen of the 25 crayfish collected were adults (C.L. > 20 mm, all but 3 had a C.L. greater than 25 mm). All large crayfish were collected in deep water (>20 cm deep). In addition, 6 YOY (C.L ranging from 11 - 17 mm) were collected during the night sample from waters ranging from 15 - 25 cm deep. Crayfish collected in 1986 were preserved in 70% ETOH until gut analysis. Crayfish collected in 1988 were placed on ice after capture and then frozen upon return to the laboratory. Crayfish sample sizes were intentionally small in order to minimize my impact on their population.

Crayfish were sexed, and then measured for C.L. and Total length prior to gut content evaluation. Then the carapace was cut along both sides just above the gills. The carapace was then carefully separated from the underlying organs using a blunt probe. The stomach (both the cardiac and pyloric regions) was then removed and placed in a dish. The stomach was carefully opened and gut fullness was evaluated visually using the methods of Yoshiyama (1980) and Creed (1985). Four levels of fullness were used: 0 (empty or with traces of food), 1/4 full, 1/2 full and 1 (full). Gut contents were then washed out of the

gut and identified as either animal, Cladophora or detritus. Animals were identified to the lowest possible taxon. The proportion of the gut contents attributable to one of these three categories was also estimated visually. Contents were separated into these three categories and preserved in 70% ETOH.

Results and Discussion

The most abundant food item in all the guts sampled was detritus (Table A1). Detritus occurred in 24 of the 25 guts sampled. In 23 of the 24 guts containing detritus it accounted for approximately 85% or more of the gut contents. In one gut detritus was approximately equal in volume with animals. Cladophora was found in 17 of the 25 stomachs. Cladophora comprised a very small proportion of the gut contents. Many of the pieces of Cladophora appeared to be intact thalli, often including a piece of the holdfast. These thalli were never more than 5 - 6 mm in length. While a number of animal taxa were consumed they rarely accounted for more than 1 - 2% of the gut contents. The most frequently consumed animals were chironomids (28 consumed) and Psychomyia (16). These taxa were found in a total of 12 and 8 stomachs, respectively. All other prey occurred in 4 or less stomachs. All stomachs from crayfish collected at night had fullness values of 1. Stomach fullness was more variable for daytime collections (mean fullness $\pm$ 1 S.E. - 7/6/86: 0.833 $\pm$ 0.105; 7/1/88: mean fullness 0.625 $\pm$ 0.157) although still fairly high.

In summary, crayfish fed during the day and night although there was less variation in gut fullness at night suggesting somewhat more

active feeding. By far the most abundant food item in the guts was detritus, a result similar to that reported by Momot et al. (1978). Animals and *Cladophora* accounted for only a small portion of the gut contents.

Table A1. Crayfish stomach contents from Nagel's Site, Augusta Creek. The first column (N.) lists the total number of animals found in crayfish guts on a given sample date. The second column (No. of guts) lists the total number of crayfish stomachs in which that prey item was found.

Food Item	Sample Date						Total	
	7/6/86		9/1/86		7/1/88			
	N.	No. of guts	N.	No. of guts	N.	No. of guts	N.	No. of guts
Animals								
Diptera								
Chironomids	3	2	19	7	6	3	28	12
Antocha pupae	–	–	2	2	–	–	2	2
Trichoptera								
Psychomyia	3	2	11	4	2	2	16	8
Oecetis	–	–	1	1	–	–	1	1
Hydropsychidae	–	–	–	–	8	4	8	4
Protoptila	–	–	–	–	1	1	1	1
Leucotrichia	–	–	1	1	–	–	1	1
Pupae	1	2	1	1	–	–	2	3
Unidentified	–	–	–	–	5	4	5	4
Ephemeroptera								
Baetis	–	–	2	1	–	–	2	1
Heptageniidae	–	–	1	1	–	–	1	1
Megaloptera								
Nigronia	–	–	1	1	–	–	1	1
Hydracarina	–	–	3	2	–	–	3	2
Cladophora*	–	5	–	7	–	5	–	17
Detritus	–	6	–	11	–	7	–	24

*- Due to possible fragmentation of Cladophora thalli (i.e., one thallus could fragment into several pieces in the gut) counts of thalli are not presented.

APPENDIX D. Growth of Young-of-the-year *Orconectes propinquus* and length-weight relationships for both young-of-the-year and adults.

Materials and Methods

The methods employed for the collection of the crayfish over the course of the growing season for 1988 are described in Chapter 2. Collections were made at NS. Crayfish were measured for carapace length (CL). To increase the sample size of crayfish for the size-frequency diagrams and the growth data, more crayfish were collected and measured in addition to the individuals already sampled for the distribution data. These data were used to generate size-frequency diagrams and to determine growth rate of the young-of-the-year crayfish.

To generate a length-weight curve, I sampled 124 crayfish from Snyder Site on 16 November, 1987 which is the end of the growing season for *O. propinquus* in Augusta Creek. To provide data for the lower end of the curve 8 YOY (CL = 6 mm) collected on 15 June, 1988 were also weighed. Crayfish were brought into the laboratory where they were measured for carapace length and total length and then blotted dry on paper towels for 45 s and finally weighed on a Sartorius 1265 electrobalance to determine wet weight. I chose to measure live, wet weights over dry weights in order to minimize my impact on the crayfish population.

Results and Discussion

Young of the year crayfish were first observed in the stream on

May 31, 1988, when they were 4.5 mm in carapace length (Figure A1). Only 3 individuals could be found on that date, however. Over the course of the summer the YOY steadily increased in size, reaching a mean carapace length of 15.8 mm by October 1. As the YOY increased in size there was a concomitant increase in the range of sizes within the cohort (Figures A1 and A2). In July most individuals were 6 - 9 mm long; by October young of the year ranged from 11 - 22 mm long (Figure A2). Since O. propinquus can be sexually mature upon attaining a carapace length of 20 mm (Crocker and Barr 1968, Momot et al. 1978), individuals from the same cohort may differ in the season of their first reproduction by a year.

The resulting variation in size of the young-of-the-year cohort makes it difficult to accurately determine length-age relationships for the older crayfish; the following interpretations are tentative at best. By July, 1+ individuals appear to range in size from approximately 15 - 24 mm. By the end of the growing season in October they appear to range from 24 - 30 mm in length. While a number of 2+ individuals were found dead in the early summer (apparently after a spring mating period), some individuals appear to survive the summer and reach lengths of 30 - 35 mm. The 40 mm female collected in October (Figure A2) may have been a 3 year old. In general, large crayfish ranged from 20 - 32 mm CL over the course of the summer.

These changes in length translate to substantial changes in weight for the crayfish over the course of the summer as illustrated by the length-weight curve in Figure A3. Small crayfish (i.e. 6 mm CL) have a mean wet weight of 0.039 g (± 0.0014). By the end of the summer the

Figure A1. Increase in carapace length for young-of-the-year Orconectes propinquus collected at Nagel's Site over the course of the late spring, summer and fall of 1988. Values in figure are mean (± 1 S.E.). Numbers in parentheses above each sample are sample size.

Figure A1.

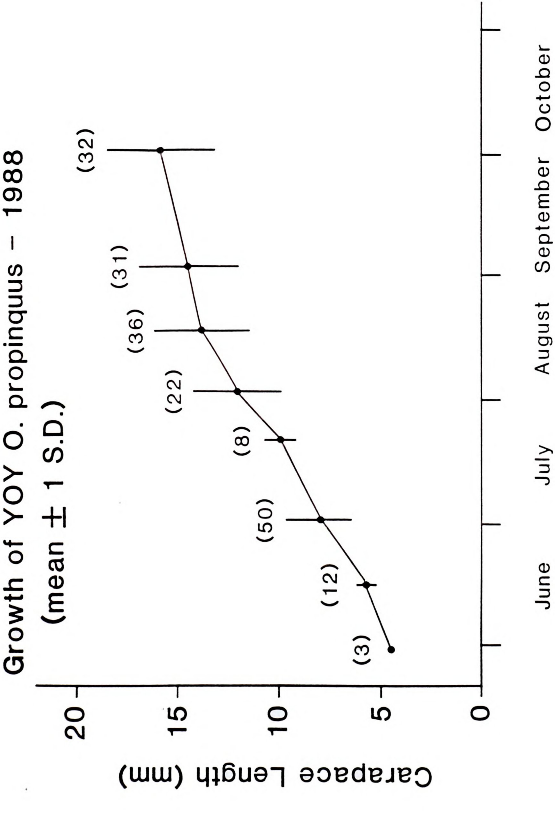

Growth of YOY O. propinquus – 1988
(mean ± 1 S.D.)
Carapace Length (mm)
0
5
10
15
20
June
July
August
September
October
(3)
(12)
(50)
(8)
(22)
(36)
(31)
(32)

Figure A2. Length-frequency diagram for young-of-the-year and adult Orconectes propinquus collected at Nagel's Site on four dates in 1988. Bars above histograms, labeled YOY, 1+, 2+, and 3+, approximate the range of sizes for young-of-the-year (YOY), one year olds (1+), two year olds (2+), and three year olds (3+).

Figure A2.

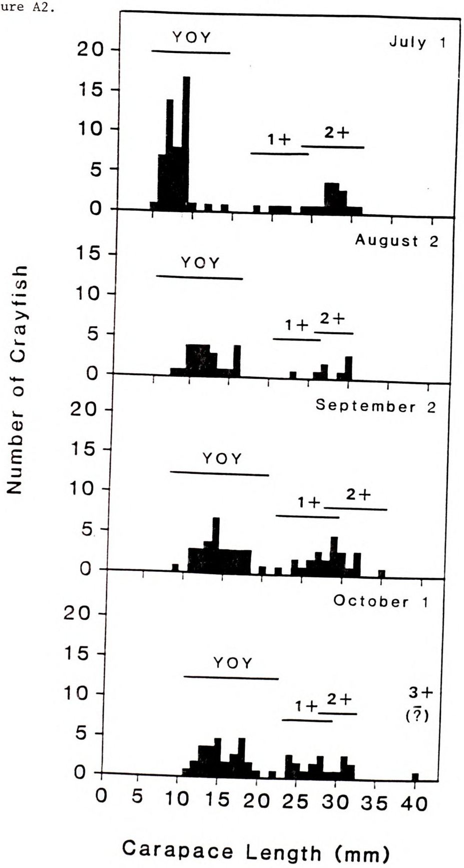
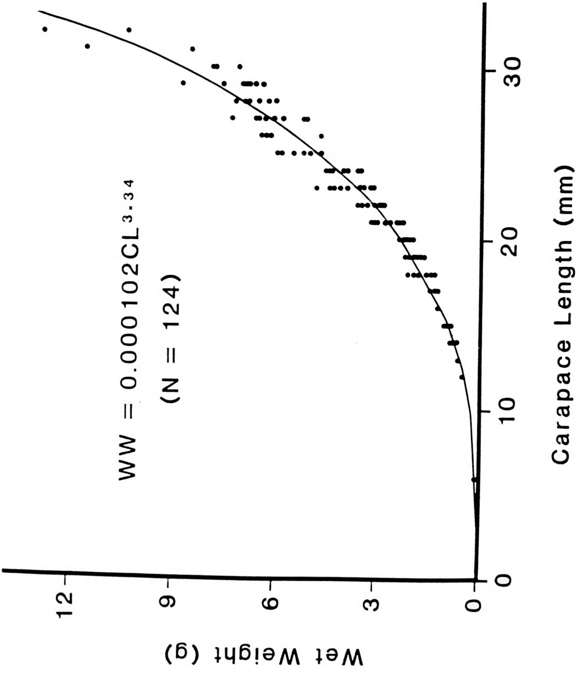

YOY
July 1
1+
2+
August 2
YOY
1+
2+
September 2
YOY
1+
2+
October 1
YOY
1+
2+
3+
(?)
20
15
10
5
0
Number of Crayfish
0
5
10
15
20
25
30
35
40
Carapace Length (mm)

Figure A3. Length-weight relationship for Orconectes propinquus collected in Augusta Creek, Michigan. Data are for males and females combined.

Figure A3.


WW = 0.000102CL$^{3.34}$
(N = 124)
Wet Weight (g)
0
3
6
9
12
Carapace Length (mm)
0
10
20
30

same individuals may have a CL of 15 to 20 mm and weigh anywhere from 1.7 to 2.3 grams. Thus, a 2 - 3 fold increase in length results in 40 - 60 fold increase in wet weight. Momot (1984) reports that juvenile *Orconectes virilis* weight can increase by a factor of 100 from release to maturity. A 1+ individual increasing in length from 20 to 26 mm CL may triple its weight. In addition, these animals are increasing in girth. These changes in size should have important consequences for both the visibility and vulnerability of crayfish to different predators they encounter, i.e., both aquatic and terrestrial predators. As crayfish are omnivorous, small crayfish are susceptible to predation by larger individuals. Avoidance of large crayfish, in addition to large fish, in deeper water may be the primary factor underlying the disjunct distributions of large and small crayfish in streams.

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