1993

The Effects of Crayfish Grazing on Benthic Algal Community Dynamics in Southwestern Lake Michigan

Kristi A. Zenchak
Loyola University Chicago

LOYOLA UNIVERSITY OF CHICAGO

THE EFFECTS OF CRAYFISH GRAZING ON BENTHIC ALGAL COMMUNITY DYNAMICS IN SOUTHWESTERN LAKE MICHIGAN

A THESIS SUBMITTED TO
THE FACULTY OF THE GRADUATE SCHOOL
IN CANDIDACY FOR THE DEGREE OF
MASTER OF SCIENCE

DEPARTMENT OF BIOLOGY

BY

KRISTI A. ZENCHAK

CHICAGO, ILLINOIS

JANUARY 1993

ACKNOWLEDGEMENTS

My sincere thanks are extended to all of the people who made significant contributions to this project.

My advisor, Dr. Nancy Tuchman introduced me to the science of ecology; because of her, my background in ecology has been greatly enhanced. Her continual enthusiasm and refreshing approach was always appreciated.

Dr. John Janssen continually shared his vast knowledge of the field with me. The field component of this research was always a fun and learning experience because of him. His help throughout my research was invaluable. (You were right John, variation was more interesting than means.)

Dr. Robert Hamilton provided input in experimental design; his thorough and objective review of this thesis was extremely helpful. I always appreciated his optimistic attitude.

Statistical analysis of this research was made possible because of Dr. Chris Peterson who willingly gave of his time and expertise to help me translate tremendous amounts of data into something meaningful. Dr. Ian Boussy also provided statistical input.

My dive buddy Tony Root helped greatly with the field component of this research, and shared his underwater

photography for use in seminars and in this thesis. Audrey Whang bailed me out on a cold October 27, 1990 by making a crucial dive for me when due to unforeseen circumstances, I was unable to dive. Mike Bert helped with the setup of both crayfish grazing experiments. Patsy Krema assisted in algal taxonomy and provided continual moral support.

Al Young donated a computer to this cause and allowed me to use his laser printer, fax machine and other such typical "household items" at all hours of the day and night.

Throughout my entire life, my mom and dad instilled in me the value of education. They always encouraged me to pursue my goals. I know Dad would be very proud to know that I finally accomplished this goal.

Even though I can't really say that my little Jessie was a whole lot of help, she was very instrumental in urging me on to the completion of this project.

And lastly, my very best friend, John Zenchak provided continual encouragement and had confidence in me throughout this endeavor. He was truly an inspiration for me and always kept me going even during my times of peak frustration. I will always be grateful for him...

This work was partially supported by Grant #NA89AA-D-SG058 from the National Sea Grant College Program of the

National Oceanic and Atmospheric Administration to the Illinois-Indiana Sea Grant Program. The views expressed herein are those of the author and do not necessarily reflect the views of NOAA or any of its sub-agencies.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Algae, present as either free-floating phytoplankton or attached benthic algae are the dominant primary producers in most aquatic ecosystems (Goldman and Horne 1983). Compared to phytoplankton, very little information on benthic algae and its interactions with other organisms is available (Wetzel 1983, Goldman and Horne 1983). The problem with studying benthic algae seems to center on "... the extreme heterogeneity in distribution of the algae across an exceptionally variegated spectrum of microhabitats, which in turn are subjected to much more variable environmental physicochemical and biotic parameters than usually occur in the open water" (Wetzel 1983).

Two species of crayfish, Orconectes virilis Hagen and O. propinquus Girard, inhabit the rocky areas of the littoral zone of southwestern Lake Michigan (Janssen and Quinn 1985). In the same area, grazers such as snails and caddisflies are relatively scarce. Because of the relatively high biomass of crayfish in these rocky areas, it appears that crayfish are an important component of the benthic community (Janssen and Quinn 1985). Benthic algae is likely to be a primary nutritive source for the crayfish of southwestern Lake Michigan since other food sources such as submerged macrophytes, detritus, and benthic macroinvertebrate prey are scarce. Preliminary studies have

shown benthic algae to be a major component of the crayfish diet (approximately 58% of gut contents), particularly in the late summer months (Tuchman, unpublished data). Crayfish, in turn, were found to be the most important prey of yellow perch (Perca flavescens Mitchill) in the late summer months in this habitat (Abrant 1988).

The benthic algae - crayfish - yellow perch food chain is a relatively short one compared to other Lake Michigan food chains which include aquatic invertebrates and forage fishes as intermediate links. In other Lake Michigan food chains, yellow perch are the top carnivores of a longer food chain which includes smaller fishes and other macroinvertebrates (Schaefer 1973). The small number of links in the southwestern Lake Michigan food chain makes it more energy efficient for the top consumers (yellow perch) as less energy is lost in the successive transfer between trophic levels (Odum 1983). Thus, in terms of food chain efficiency, it seems that benthic algae are a very important component of this southwestern Lake Michigan food chain.

The literature available on the relationship of benthic algae to other organisms is derived from studies of both marine and freshwater systems, however, the scope of these studies has been very limited. Studies of marine systems demonstrate the impact of herbivory on benthic algal community structure in littoral zones [e.g., sea urchin herbivory (Paine and Vadas 1969), gastropod herbivory

(Nicotri 1977), snail herbivory (Lubchenco 1978)], however, these studies focused primarily on macroalgae. Studies which have focused on the impact of herbivory on benthic algal community dynamics in freshwater systems have mainly been done in lotic systems (e.g.,snail herbivory McCormick and Stevenson 1989, Lamberti *et al.*, 1989). Very little information is available on the effects of crayfish herbivory on freshwater benthic algal community dynamics in lakes. The present study investigates the relationship between benthic algae and crayfish in a large freshwater lake focusing on the effects of crayfish herbivory on the benthic algal community.

The purpose of this study is to examine the relationship between benthic algae and crayfish. Three objectives are proposed:

(1) determine *in situ* densities of *O. virilis* and *O. propinquus* at the study site.

(2) determine *in situ* physical parameters including temperature, light, and dissolved oxygen at the study site.

(3) experimentally investigate the effects that different intensities of crayfish grazing have on benthic algal community dynamics including primary productivity, community composition and standing crop.

The results of this study may allow for a better

understanding of the trophic dynamics involved in a Lake Michigan benthic food chain, as well as provide information about a largely uninvestigated component of Lake Michigan food chains (i.e., benthic algae). Results of this study would also contribute specific information on the effects that crayfish herbivory may have on freshwater benthic algal community dynamics in large lakes.

CHAPTER II

LITERATURE REVIEW

Benthic Algae

Benthic algae (periphyton) are algae which grow attached to submerged substrates. The benthic algal community in the Great Lakes is commonly composed of diatoms, as well as green and blue-green algae. In general, unicellular pennate forms of diatoms predominate in the benthic community over filamentous and centric forms (Goldman and Horne 1983).

Benthic algal community development in a lentic system without disturbance generally begins with low profile, prostrate, or apically attached pioneer species, and proceeds to a more complex three-dimensional community dominated by stalked and/or filamentous cells (Murray and Littler 1978, Hudon and Bourget 1981, MacLulich 1986). Hoagland et al.(1982) examined the changes in three-dimensional structure of periphyton communities during community development in two reservoirs. They found a predictable algal colonization sequence starting with an organic film coating the substrate, followed by a variety of bacteria, low profile diatoms and finally an upperstory of long stalked and large rosette diatoms and filamentous green algae. In another study conducted in a lake, it was noted that large, overstory diatoms such as Synedra ulna var. danica Kutz. were early colonizers, and smaller motile or

understory forms were late colonizers (Tuchman and Stevenson 1991).

Benthic Algal/Herbivore Interactions

An interactive grazing system is one in which the rate of change of plants is a function of the density of herbivores present in the system and the rate of change of herbivores is a function of plant density (Caughley and Lawton 1981). Herbivory in an aquatic system may be analogous to terrestrial grazing systems in that,"... differential herbivory influences the abundance, species composition, and succession of freshwater phytoplankton ..."(Porter 1977).

Most of the studies addressing the effects of grazing on various community dynamics of both phytoplankton and periphyton have been conducted in marine intertidal zones (e.g., Paine and Vadas 1969, Lubchenco 1978, Nicotri 1977, Castenholz 1961), and in streams using snails and/or aquatic insects as grazers (e.g., Cooper 1973, Lamberti et al. 1989, McCormick and Stevenson 1989, Steinman et al. 1987).
In order to assess the overall health of the algal community, one community parameter that is commonly examined is primary productivity. In some studies, grazing has been found to have a stimulatory effect on benthic algal community primary productivity. Cooper (1973) examined the role of fish grazing intensity on net primary productivity and found that net primary productivity was enhanced with

increasing herbivore density up to a certain density. Similarly, Lamberti et al. (1989) observed that grazing by snails caused an increase in net primary production of stream periphyton in low and intermediate irradiance treatments. In another study conducted by Lamberti et al. (1987), the effects of grazing on stream algal assemblages by three different herbivores were examined. Grazing by mayflies (Centroptilum elsa Traver) changed the algal community slightly, but had little effect on periphyton chlorophyll a and biomass. A reduction in periphyton biomass and chlorophyll a, with an increase in primary productivity resulted when grazed by snails (Juga silicula Gould) at a density of $350 \cdot m^{-2}$. However, grazing by caddisflies (Dicosmoecus gilvipes Hagen) reduced periphyton biomass and chlorophyll a, as well as primary productivity. Hargrave (1970) observed that enhancement of algal primary production in experimental microcosms occurred within the range of natural densities of amphipods (Hyalella azteca Saussure); however, production declined at higher densities. A density study involving nine treatments of increasing densities of snails (density range = 13 - 504 snails$\cdot m^{-2}$) was conducted by Hunter and Russell-Hunter (1983). Intermediate levels of grazing increased algal productivity by 88% over the control.

Differential effects of grazing on algal standing crop have also been documented. Some studies noted that grazing

had a stimulatory effect on algal standing crop. For example, McDonald (1985) found that grazing fish increased algal population densities, compared to ungrazed populations. In a study conducted by Connor et al. (1982), respiration and gross photosynthesis, as well as chlorophyll concentration (biomass per square centimeter), significantly increased in low density treatments of snail grazing. Algal standing crop (total cell density and community biovolume) increased at low grazing pressure from snails in a phosphate-enriched environment (McCormick and Stevenson 1989). On the other hand, grazing has also been found to result in decreased standing crop. Steinman et al. (1987) observed that intermediate densities of snail grazing ($125 \cdot m^{-2}$ and $250 \cdot m^{-2}$) resulted in low algal biomass accumulation after day 16 of the experiment, and caddisfly grazing resulted in low algal biomass in all grazed treatments. Grazing by the herbivorous caddisfly, Helicopsyche borealis Hagen resulted in low amounts of algae but a high algal turnover rate (Lamberti and Resh 1983). When caddisfly larvae were excluded, higher amounts of algae were present, but the algal turnover rate declined. Hunter and Russell-Hunter (1983) observed that at nine densities of snail grazing, standing crop biomass was reduced when compared to the control, however, nutritional quality of the aufwuchs was improved with increased grazing intensities; carbon and nitrogen per unit dry mass of aufwuchs was higher

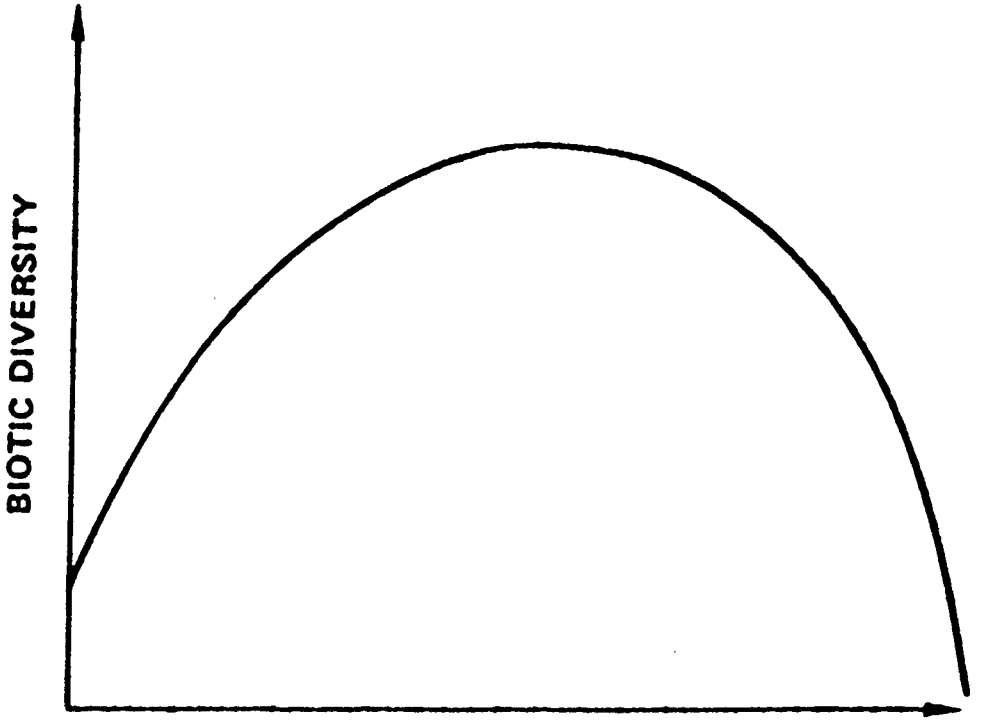
at all grazer densities than in the controls.

One of the first major studies of the impact of crayfish herbivory in lakes was conducted in Lake Tahoe by Flint and Goldman (1975). In their study, the effect of crayfish grazing on primary productivity of periphyton was investigated in field and laboratory enclosures. The ratio of crayfish to substrate area was varied in order to create treatments of different grazing intensities. Crayfish biomasses below 131 $g \cdot m^{-2}$ caused a stimulation in primary productivity of periphyton, whereas crayfish biomasses above 203 $g \cdot m^{-2}$ caused a decline in periphyton primary productivity.

Effects of Herbivory on Algal Community Diversity

The intermediate disturbance hypothesis states that a greater diversity may be maintained in communities which are subjected to intermediate levels of disturbance than in communities subjected to high or low levels of disturbance (Figure 1) (Ward and Stanford 1983). Connell (1978) provided evidence that the intermittent occurrence of tropical storms was responsible for the high diversity observed in tropical rainforests and coral reefs. Other researchers have also provided evidence in support of the intermediate disturbance hypothesis. For example, low and high levels of snail herbivory were shown by Lubchenco (1978) and Tuchman (1988) to result in low community diversity, whereas, intermediate levels of grazing resulted

Figure 1. Effects of intensity of disturbance on biotic diversity. (From Ward and Stanford 1983)



FREQUENCY OF DISTURBANCE
INTENSITY OF DISTURBANCE
PREDICTABILITY OF DISTURBANCE
TIME SINCE DISTURBANCE
PREDATION INTENSITY
RESOURCE VARIABILITY
ENVIRONMENTAL HETEROGENEITY

in increased levels of community diversity. Similarly, Paine and Vadas (1969) observed that removal of sea urchin grazers caused the algal community to eventually be dominated by a brown macroalgal species which didn't exist in areas where sea urchins were present. They suggested that intermittent sea urchin grazing might lead to a substantial increase in the number of algal species capable of coexisting. The "weeding" behavior of herbivore grazing prevented an algal mat from being overgrown and dominated by the blue-green filament, Microcoleus (Hart 1985). Tuchman and Stevenson (1991) suggested that the increased diversity observed in their grazed treatments was due to a decrease in abundance of predominate taxa.

Other studies which focused on the impact of grazing on algal community diversity demonstrated decreased diversity with increased grazing intensity. Cyanobacterial mats were overgrown by benthic diatoms when protected from grazing minnows; these diatom turfs were stripped off and replaced by cyanobacterial felts when exposed to grazing minnows (Power et al. 1988). In an experiment done by Sumner and McIntire (1982), the effects of grazing on community diversity seemed to be a function of the initial community structure. When relatively small, nonfilamentous algal species were dominant in the community, an increase in grazing decreased diversity. However, when larger, overstory species were dominant, grazing tended to result in

increased diversity. Dickman (1968) reported that tadpole grazing caused a reduction in periphyton species diversity which promoted a secondary succession in the algal community. Consequently, the grazed community attained a much lower level of maturity than the ungrazed community. In Hunter and Russell-Hunter's (1983) study, algal abundance and richness decreased as grazing intensity increased. It was observed that grazing reduced the number of taxa to 50% of the control at low grazing densities, and to less than 30% of the control at high grazing densities.

Susceptibility of Algae to Grazing; Preferential Feeding by Grazers

Susceptibility of benthic algae to grazers has been found to be a function of size and security of attachment (Sumner and McIntire 1982). Caddisfly grazers had more success ingesting large, high-profile diatom taxa and were less successful at removing small, adnate taxa (Peterson 1987). Bert (unpublished data) observed a preferential selection of a large green filamentous algae (Mougeotia sp.) by crayfish. Furthermore, increased gut retention time with large size crayfish appeared to negatively influence the viability of cells after gut passage.

Other studies have also documented a preferential selection of certain algal taxa because of size, mode of attachment or susceptibility to grazing. For example, grazing by snails reduced the relative abundance of erect

non-attached algae and increased the abundance of adnate diatoms (Lamberti et al. 1989, Tuchman and Stevenson 1991). Horizontal growth forms, as in the diatom genera, Achnanthes and Cocconeis, predominated on highly disturbed substrates whereas large, vertically positioned species of Navicula were most abundant on less disturbed substrates (Robinson and Rushforth 1987). Grazed treatments contained a larger percentage of non-motile as compared to motile forms of diatoms (Connor et al. 1982). Selective grazing on three diatom species by four species of intertidal gastropods was observed by Nicotri (1977) where the degree of digestibility among algal species was found to be related to a shift in algal community composition due to grazing. These three diatom species were long chains of cells that formed the upper story within the algal mat; diatoms with tighter adhesion to the substrate such as Achnanthes spp. were less affected by the grazers. Scanning electron micrographs revealed that even at high density grazing, neither snails nor caddisflies were capable of removing the entire algal assemblage (Steinman et al. 1987). In an algal mat of low lying diatoms interspersed among thick mats of a filamentous blue-green alga, caddisfly larva were found to remove, but not ingest the blue-green alga (Hart 1985). Four different taxa of pennate diatoms (including the genera Achnanthes, Amphora, Cocconeis, and Nitzschia) comprised 73% of the cells on highly grazed substrates compared to 7.5% of the

cells on ungrazed substrates (Hunter and Russell-Hunter 1983). This may indicate that these four taxa are resistant to grazing.

Role of Nutrient Recycling in Benthic Algal/Herbivore Interactions

Many studies have demonstrated the importance of grazers in influencing nutrient dynamics in aquatic ecosystems (Flint and Goldman 1975, Connor et al. 1982, Mulholland et al. 1983). Nutrient cycling in streams (and in other ecosystems) includes the release of soluble nutrients from cell lysis or consumption and excretion by heterotrophic organisms (Mulholland et al. 1991). Aquatic animals release dissolved phosphorus as inorganic orthophosphate (Pomeroy et al. 1963), and dissolved nitrogen as ammonia, free amino acids and a variety of other organic compounds (Nicol 1960). Nitrogen or phosphorus addition to streams can increase algal biomass and rates of primary production (Hill and Knight 1988) as well as affect the composition of algal communities (McCormick and Stevenson 1989).

The relationship between nutrients and grazing is complex since the type of nutrient, the trophic status of the water, the taxonomic structure of the benthic algal community, and the type and density of grazer all play a role in this relationship and its effects on the benthic algal community (Mulholland et al. 1991). However, there is

agreement that grazers may have a stimulatory effect on algal growth in nutrient limited systems since they can recycle nutrients as they feed (Cuker 1983, Sterner 1986).

Crayfish

Crayfish are the largest and longest-living members of the freshwater crustacea in North America (Momot 1967). They are common inhabitants of a wide variety of environments including most running waters, shallow areas of lakes, ponds, sloughs, swamps and wet meadows (Pennak 1989). They constitute an important source of food for many fish such as perch and trout (Momot et al. 1978). It is also known that crayfish eat benthos and vegetation. ~~According to Rickett (1974),~~ crayfish may be considered the dominant species within a benthic community in that feeding and reproductive behaviors associated with crayfish can have a strong impact on the growth and feeding behaviors of other species within the community. The success of crayfish has been attributed to their lack of specialization in feeding adaptations; they are able to utilize many different sources of food (Lorman and Magnuson 1978). Because of this characteristic, Lorman and Magnuson (1978) suggest that crayfish play a very complex and important role in the trophic interactions within aquatic ecosystems. The ultimate fate of energy and nutrients may be influenced in part, by the opportunistic feeding activities of crayfish (Momot et al. 1978).

Current information on crayfish ecology focuses on the harvest and culturing of crayfish for human consumption and the use of crayfish as fish bait (Hanson et al. 1990, Brown et al. 1990); relatively little information is available concerning the ecological role of crayfish in littoral communities of lakes. It has been shown however, that crayfish cannot be assigned to any one trophic level; they appear to belong to several trophic levels including herbivores, carnivores, and detritivores. In this regard, they occupy a unique niche in freshwater ecosystems (Mozley and Howmiller 1977, Momot et al. 1978). It has been observed that plant material constitutes a large portion of the crayfish diet in ponds (Rickett 1974). The structure of the mouth apparatus allows crayfish to eat both soft and hard plants (Momot et al. 1978). Stomachs of crayfish from the Grand Traverse Bay area of Lake Michigan (where aquatic macrophytes were relatively scarce) were full of algae (Mozley and Howmiller 1977). Similarly, benthic algae were observed to be a major component (58%) of the crayfish diet in Lake Michigan in the late summer months (Tuchman, unpublished data). In an early study done by Momot (1967), the contents of 57 crayfish stomachs were examined. Green algae, fragments of higher plants, and other miscellaneous organisms were found. These observations seemed to indicate that the crayfish in this study area (a marl lake ecosystem with little or no higher aquatic vegetation and a limited

abundance of aquatic insects) were primarily herbivorous, and at times, facultative scavengers. Other researchers have also determined that crayfish are mainly herbivorous (e.g., Chidester 1908, Norton 1942).

In a stream study done by Prins (1968), submerged aquatic macrophytes, and the roots, stems, bark and leaves of terrestrial plants were a major dietary component for Orconectes rusticus rusticus Girard; vascular plants and filamentous algae constituted the main food source for another species of crayfish, Cambarus tenebrosus Hay.

Budd and Lewis (1977) observed that crayfish are capable of filter feeding due to the presence of an extensive filtering apparatus. It is thought that juvenile crayfish obtain a large portion of their nutrients by filter feeding, whereas adult crayfish are opportunistic feeders.

Evidence indicating predatory behavior by crayfish also exists. Algae, as well as significant quantities of animal remains including midge larvae, mayfly nymphs, and other crayfish were found in crayfish stomachs from a mesotrophic lake (Capelli 1980). Momot et al. (1978) found a variety of animal material in the stomachs of juvenile crayfish including chironomid larvae, cladocerans, ostracods, small dragonfly naiads, chironomid eggs, chitinous fragments from the shells of crayfish and other arthropods.

Detritus is also thought to be a major component of the crayfish diet. Prins (1968) observed that detritus,

particularly that resulting from allochthonous leaf litter (i.e., organic input from sources outside the lake or stream), formed the most important part of the diet of O. rusticus. Detritus, especially amorphous organic and inorganic material, was a major component in the stomachs of O. virilis in a lake study conducted by Momot et al. (1978).

Lake Michigan

Lake Michigan has an average depth of 85 meters and a maximum depth of 281 meters; the thermocline depth is 10-15 meters ~~(Goldman and Horne 1983)~~. It has a very low surface area to drainage basin ratio (approximately 1:2) and a very long hydraulic retention time (104 years). The cold water temperatures (18-20°C summer temperatures) and the relatively high levels of dissolved silica contribute to the success of diatoms (Bold and Wynne 1985).

~~According~~ to Norby and Collinson (1977), bare glacial till is most likely the common bottom type of sediment in the Illinois portion of Lake Michigan. Geologic cross sections and sediment core data indicate that sediments of the lake floor consist of silicious sand with spotty areas of gravel and sand in the littoral and sublittoral zones at depths of 4.5 to 7.5 meters.

Lake Michigan is an oligotrophic lake having a low watershed area to lake area ratio, which results in low levels of allochthonous input and ultimately leads to relatively low productivity within the lake. Results of the

1984 Water Quality Survey of Lakes Erie, Huron and Michigan classify Lake Michigan as an oligotrophic lake based on the amount of particulate phosphorus and chlorophyll-a in the surface waters (Lesht and Rockwell 1987). Secchi depth was also a criteria for this determination. Blue-green algae indicative of oligotrophic conditions such as Lyngbya and Oscillatoria were also present.

CHAPTER III

MATERIALS AND METHODS

The Study Site

The Lake Michigan study site from which all collections were made was located at approximately Touhy Avenue, Evanston, IL and approximately 0.8 km offshore. The water depth was 5.5 - 6.4 m. The site was characterized by numerous rock piles which shelter crayfish (O. virilis and O. propinquus) and support benthic algal colonization (Figure 2). Two components of the study site examined were (1) in situ crayfish population and (2) in situ physical parameters. These components were examined so that the laboratory crayfish grazing experiments that followed could best simulate field conditions for benthic algae and crayfish.

In situ Crayfish Population

Between 20 June and 4 September 1990, 10 dives were conducted in order to estimate the density of crayfish at the study site. SCUBA divers collected all crayfish by hand along 11 different transects. During each dive, two divers attempted to collect all crayfish within one meter on each side of the transect line. The length of 10 of the 11 transects was 10 meters; one of the transects was 36 meters. The divers were reasonably certain that the same area was not sampled twice because rocks turned over on previous

Figure 2. The southwestern Lake Michigan study site

sampling days were never encountered.

The crayfish density range in these 11 transects was 0.3-2.3 crayfish·m^{-2} [average density =0.839 crayfish·m^{-2}; 0.575 (1 s.d.)]. The number of O. propinquus was higher than the number of O. virilis on all but one of the transects; the average O. propinquus to O. virilis ratio was 2.2 : 1. Other studies reported an average O. propinquus to O. virilis of 3.6:1 (Janssen and Quinn 1985), and 3.7:1 (Quinn and Janssen 1989) at a similar site in southwestern Lake Michigan.

In situ Physical Parameters

In order to simulate field conditions in the laboratory, the following measurements were taken during midday at the study site:

Measurement	Instrument	Mean values
light (Photosynthetically Active Radiation, PAR at water surface)	Licor Quantum Photometer (Model 910 A19)	2,373 $\mu E \cdot m^{-2} \cdot sec^{-1}$
light (PAR at sediment/water interface)	Licor Quantum Photometer (Model 910 A19)	192.15 $\mu E \cdot m^{-2} \cdot sec^{-1}$
water temperature (°C at sediment/water interface)	Oxygen meter with temperature probe (YSI Model 57)	12.94 °C
dissolved oxygen (mg $O_2 \cdot L^{-1}$ at water surface)	Oxygen meter (YSI Model 57)	10.22 mg $O_2 \cdot L^{-1}$
dissolved oxygen (mg $O_2 \cdot L^{-1}$ at sediment/water interface	Oxygen meter (YSI Model 57)	9.79 mg $O_2 \cdot L^{-1}$

There were two laboratory crayfish grazing experiments conducted in this study. The purpose of these experiments was to investigate the effects of different intensities of crayfish grazing on a variety of benthic algal community parameters including primary productivity, community composition, and standing crop. The preliminary crayfish grazing experiment was conducted between 5 August and 7 September 1990. Primary productivity measurements were made throughout the experiment, however, additional samples were not further analyzed because of problems encountered throughout the experiment (see p.32). The main crayfish grazing experiment (conducted between 26 November and 26 December 1990) was designed based on modifications of the preliminary experiment. Brief descriptions of the methods used for the preliminary experiment are included in the next section; detailed descriptions of the methods used are included in the main crayfish grazing experiment section.

Preliminary Crayfish Grazing Experiment

Colonization of Benthic Algae

Using SCUBA, divers collected rocks from the study site and an algal slurry was prepared by scraping algae from the rock surfaces and diluting the algae in water. The algal slurry was placed into a large, circular plastic chamber which was lined on the bottom with unglazed clay quarry tiles (24.01 cm^2) used as algal colonizing substrates. The purpose of using these tiles as algal colonizing substrates

was that they provided a flat, uniform surface to allow for even colonization of algae which is important when doing quantitative sampling. After 56 days, microscopic examination of the algal community on the tiles revealed many species of healthy diatoms (cells were golden-brown in color and the cytoplasm filled the entire cell).

The grazing experiment was initiated at this time. Tiles were transferred to the experimental grazing tanks located in a greenhouse. In order to attain a cool temperature in the greenhouse so that Lake Michigan water temperatures could be simulated in the tanks, the windows were painted with a sun shield (Kool Ray^{R}) which lowers total light intensity without selectively filtering photosynthetically active radiation (PAR) wavelengths. Air conditioners were also used to maintain a cool room temperature.

Experimental tanks

Twelve plastic tanks (150 liter) were filled with dechlorinated tap water which was maintained at a temperature between 13 and 17.5 °C and continually oxygenated with five high-output airstones. Into the bottom of each tank was placed autoclaved Lake Michigan sand, scrubbed and autoclaved Lake Michigan rocks (one rock per crayfish), and 11 of the algal tiles.

Treatments

Five treatments (2 replicates each) of grazing

intensities ranging from 2.37 - 28.41 crayfish·m^{-2} were constructed (Table 1). Although this density range was somewhat higher than that measured *in situ* (0.839 crayfish·m^{-2}), treatment tank size constraints allowed for a minimum density of 2.37 crayfish·m^{-2},(i.e., 1 crayfish in the treatment tank yielded a density of 2.37 crayfish·m^{-2}). It was therefore decided to use progressively higher crayfish densities while maintaining the *in situ* ratio of the two crayfish species. The ratio of the two species used in this experiment was 3 *O. propinquus* : 1 *O. virilis* which approximated the mean of the ratio obtained in the present study (2.2:1) and that obtained by Janssen and Quinn (1985) at a similar site (3.6:1) and Janssen and Quinn (1989) (3.7:1). Only adult male crayfish of a given size range (*O. propinquus* carapace length = 12-24 mm; *O. virilis* carapace length = 15-30 mm) were selected for use in this experiment.

Sampling

The experiment was conducted for 31 days. For primary productivity measurements, an entire tile was collected and all attached algae were removed for analysis. Primary productivity was measured *in vitro* using the dissolved oxygen method (light/dark bottle, APHA 1985) on days 1, 10, 20 and 31. On days 1, 2, 4, 6, 8, 10, 15, 20, 26 and 31, additional samples were collected by removing at least a 2 mm^2 section of the algal mat from a clay tile and preserving the algae in 2% glutaraldehyde. These samples were later

Table 1. Experimental design of preliminary crayfish grazing experiment.

Treatment	Crayfish density (no. crayfish·m^{-2})	Realized density (no. crayfish· cm^{-2} algae)	No.crayfish per chamber, (*O. propinquus*: *O. virilis*)
1(control)	0	0	0,(0:0)
2	2.37	0.0040	1,(1:0)
3	2.37	0.0040	1,(0:1)
4	9.47	0.150	4,(3:1)
5	18.94	0.030	8,(6:2)
6	28.41	0.045	12,(9:3)

used to determine microscopic community composition and turnover rates. On these same sampling days, an additional 2 mm^2 section of the algal mat was removed from the clay tile for chlorophyll a (standing crop) determinations. The chlorophyll was extracted in 90% aqueous acetone (APHA 1989). The tile was returned to its experimental tank so as to maintain the original realized density of each treatment.

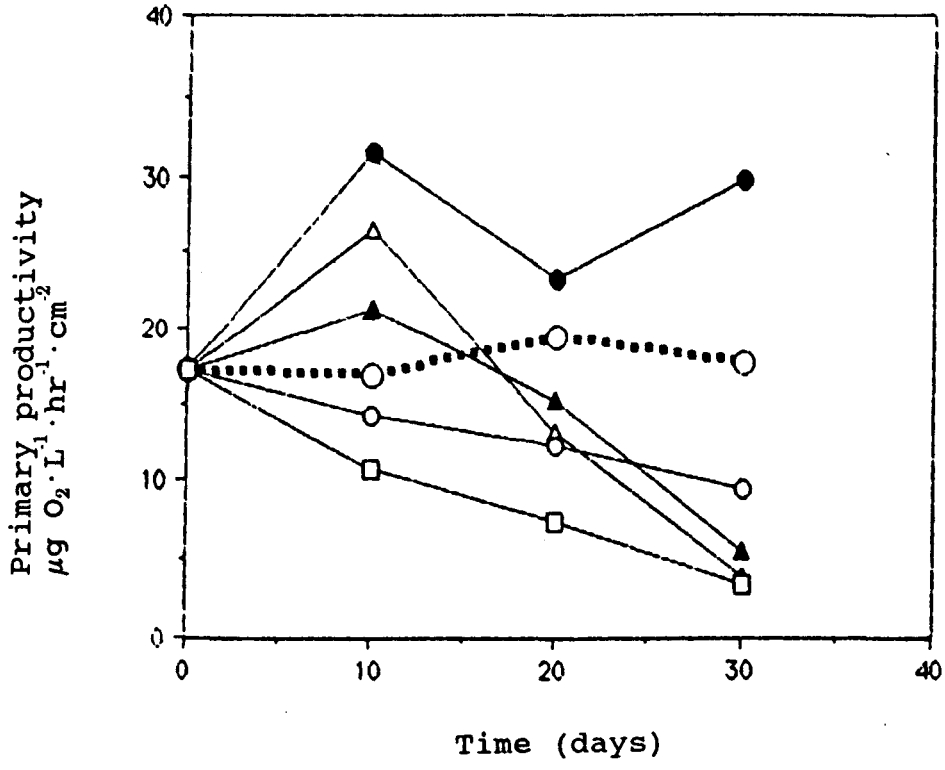
Preliminary results-Primary productivity

Crayfish densities of less than 10 crayfish$\cdot m^{-2}$ chamber (treatments 2,3 and 4) stimulated algal primary productivity until day 10 (Figure 3). A significant treatment effect (ANOVA; $P<.0001$) revealed that the low density treatment of O. propinquus (treatment 1) maintained higher levels of primary productivity than all other treatments throughout the experiment (Tukey test; $P<.005$). The same density of O. virilis (treatment 2) resulted in decreased primary productivity after day 10. High densities of crayfish (treatments 5 and 6) resulted in a substantial decline in primary productivity throughout the experiment. A significant time effect (ANOVA; $P<.0001$) revealed that primary productivity was higher on day 10 than on days 20 and 30 (Tukey test; $P<.01$).

Preliminary Results-Community Composition, Turnover Rate and Standing Crop

These parameters were not further considered because of

Figure 3. Preliminary experiment: average primary productivity for 5 treatments and control.



•••○•• control (0 crayfish·m^{-2})

—●— 1 O. propinquus (2.37 crayfish·m^{-2})

—▲— 1 O. virilis (2.37 crayfish·m^{-2})

—△— 3 O. propinquus : 1 O. virilis (9.47 crayfish·m^{-2})

—○— 6 O. propinquus : 2 O. virilis (18.94 crayfish·m^{-2})

—□— 9 O. propinquus : 3 O. virilis (28.41 crayfish·m^{-2})

problems encountered with the sampling technique.

Problems Encountered

There were two main problems with this experiment. The first problem was that starting on sampling day 8, many of the tiles began to look very "patchy", i.e., some areas of the tile appeared to be very heavily grazed, whereas other areas appeared to be minimally grazed. Because of this patchiness, it was difficult to obtain a representative sample from each treatment by using such a small subsample size (at least 2 mm^2). A second problem dealt with sampling technique. The 2 mm^2 samples were obtained by measuring sections of algae (with a millimeter ruler), and cutting out the small, square section with a razor blade. These samples were then preserved in 2% glutaraldehyde or 90% aqueous acetone for community composition analysis and chlorophyll *a* measurements, respectively. This method of obtaining the algae samples proved to be very crude, therefore, consistency in sample size was questionable. When estimating cell densities$\cdot mm^{-2}$ and chlorophyll *a* concentration$\cdot mm^{-2}$, even minute errors in the area of the samples collected can result in substantial discrepancies for these estimates. Because of these problems, it was decided to terminate this experiment and redesign the grazing experiment to incorporate necessary improvements.

Modifications for subsequent study based on problems encountered with preliminary experiment

In the main grazing experiment, two major modifications of the preliminary experiment were incorporated. Sample areas in the preliminary experiment for primary productivity measurements were large enough to account for heterogeneity; therefore, it was decided that these data would be useful in modifying the grazing experiment. Results from the preliminary experiment indicated a stimulatory effect on primary productivity at low grazing densities, and an inhibitory effect at higher grazing densities. The first modification of the main experiment was to focus on the region of the crayfish density continuum that stimulated primary productivity (see Figure 3).

The second modification was an improvement in the sampling technique to allow for more accurate sampling of the algae from tiles. In the preliminary experiment, small algal samples (2 mm^2) were used so that the realized densities (no. crayfish$\cdot cm^{-2}$ algae) in each treatment chamber were maintained as close as possible to the original realized density throughout the duration of the experiment. Removing small samples from each treatment would not significantly change the total amount of algae in each treatment chamber; therefore, the integrity of the original experimental design would be maintained. However, because of the inaccuracy among sample sizes, an improvement in the

technique was necessary. The second modification was to have duplicate chambers for each treatment running parallel with the experimental chambers for the sole purpose of supplying tiles to use as replacements for those tiles removed for samples. With this modification, an entire tile could be removed on each sampling day rather than a small section from a tile, and replaced by a tile which was in the same "condition" (i.e., subjected to the same periodicity and intensity of grazing) from the replacement chamber.

Main Crayfish Grazing Experiment

Colonization of Benthic Algae

On 27 October 1990, benthic algal-colonized rocks were collected using SCUBA from the study site and transported back to the laboratory in coolers filled with Lake Michigan water. The rocks were scrubbed with a stiff bristle brush to remove attached algae. The resulting algal slurry was placed into a colonizing chamber which was lined on the bottom with 200 unglazed clay quarry tiles (24.01 cm^2) to be used as algal colonizing substrates.

An algal colonizing chamber was established in the laboratory. The physical parameters were as follows:

chamber composition = plastic

chamber size: diameter = .9 meter; volume = 108 liters

light: 4, 40 watt wide spectrum bulbs (14 hour photoperiod)

water current: generated by 1 submersible pump; a plastic funnel was fitted on the pump output and a plastic mesh screen was stretched across the radius of the chamber in an effort to more evenly disperse the water flow.

temperature: 15-16 °C

nutrients: Guillard's F-1 algal media (James, 1978) was added on the following days:

day 5 - 600ml
day 12 - 300 ml
day 14 - 300 ml
day 17 - 300 ml
day 20 - 300 ml
day 24 - 300 ml
day 25 - 300 ml

water exchange: approximately 25 liters of surface water was removed and replaced with 25 liters dechlorinated tap water three times throughout the 30-day colonization period.

In a previous attempt to colonize clay tiles with algae (early October 1990), chironomid larvae contaminated the colonizing chamber and destroyed the integrity of the developing algal mat with their tube-building and algal grazing behavior on tiles. Therefore, in order to avoid this problem in this algal colonizing attempt, an insecticide, temephos ("Abate"; Clark Outdoor Spraying, Roselle, IL) was added according to the protocol described by Yasuno et al. (1985). On day 5 of the colonizing period, sufficient temephos was added to yield a concentration of 5 $mg \cdot L^{-1}$, which eliminated the chironomid larvae without noticeably affecting the health of the algae.

On day 17, the sides of the colonizing chamber were

scraped. The algae fragments that sloughed off were homogenized and resuspended in the water column to facilitate higher rates of algal colonization on the tiles. Microscopic examination of the algae was done three times throughout the colonization period to make sure the cells looked healthy, i.e., cells were golden-brown in color and the cytoplasm filled the entire cell. After a 30-day colonization period, dense algal mats of healthy cells had developed so the algae tiles were transferred to the grazing treatment tanks in the greenhouse for experimentation.

Experimental tanks

Twelve plastic experimental tanks were used (dimensions = 96.0 cm x 44.0 cm x 35.6 cm; volume = 150 liters; bottom area = 0.42 m^2) as treatment and replacement tanks and 2 circular plastic tanks (diameter = 0.9 meter) were used for the controls since the number of rectangular tanks available was limited. In order to remove organic debris and attached algae, the sand was sterilized in an electric soil sterilizer (Pro-Grow Model SS-15, Pro-Grow Supply Corp. Brookfield, WI) at 200°F for 26 hours and was then transferred into the treatment tanks. Rocks were scrubbed, and autoclaved for the same reasons as described above (to remove any potentially additional food sources such as attached algae and organic debris), and put on the bottom of each treatment tank. It was thought that if each crayfish had its own shelter, aggressive behavior would be minimized;

therefore, each tank contained one rock (approximately 20 cm x 15 cm x 10 cm) for each crayfish. The tanks were filled with 130 liters dechlorinated tap water; five high-output airstones were used continually throughout the 25-day experiment in each tank to oxygenate the water. The tanks were fitted with lids made of cloth which was stretched over a wooden frame (Figure 4); the light reading in the tanks with these lids on was 72 $\mu E \cdot m^{-2} \cdot sec^{-1}$ (as compared to the average of 192 $\mu E \cdot m^{-2} \cdot sec^{-1}$ as measured at the Lake Michigan study site; see p.24).

Treatments

Four treatments of grazing intensities ranging from 2.37 - 9.47 crayfish$\cdot m^{-2}$ were used (Table 2). In this experiment, it was decided to use one species of crayfish (O. propinquus) because the preliminary experiment indicated that grazing by the two species of crayfish had differential effects on the algal community; in this experiment, the intent was to focus on the effects of grazing at low densities without introducing the variability caused by the two different species of crayfish. Adult males (carapace length = 12 - 24 mm) were used and care was taken not to use crayfish which were about to molt (identified by a darkened carapace) or which had recently molted (identified by a soft, thin carapace)(Figure 5).

Each treatment had 2 replicates and 1 replacement tank. The replacement tank contained tiles which were in the same

Figure 4. The experimental tanks in the greenhouse.

Table 2. Experimental design of main crayfish grazing experiment.

Treatment	Crayfish density (#crayfish·m^{-2})	Realized density (#crayfish·cm^{-2} algae)	No. crayfish	No. tiles
control	0	0	0	8
1	2.37	0.0015	1	28
2	4.73	0.0050	2	17
3	7.10	0.0100	3	12
4	9.47	0.0200	4	8

Figure 5. Adult male O. propinquus.


O. propinquus

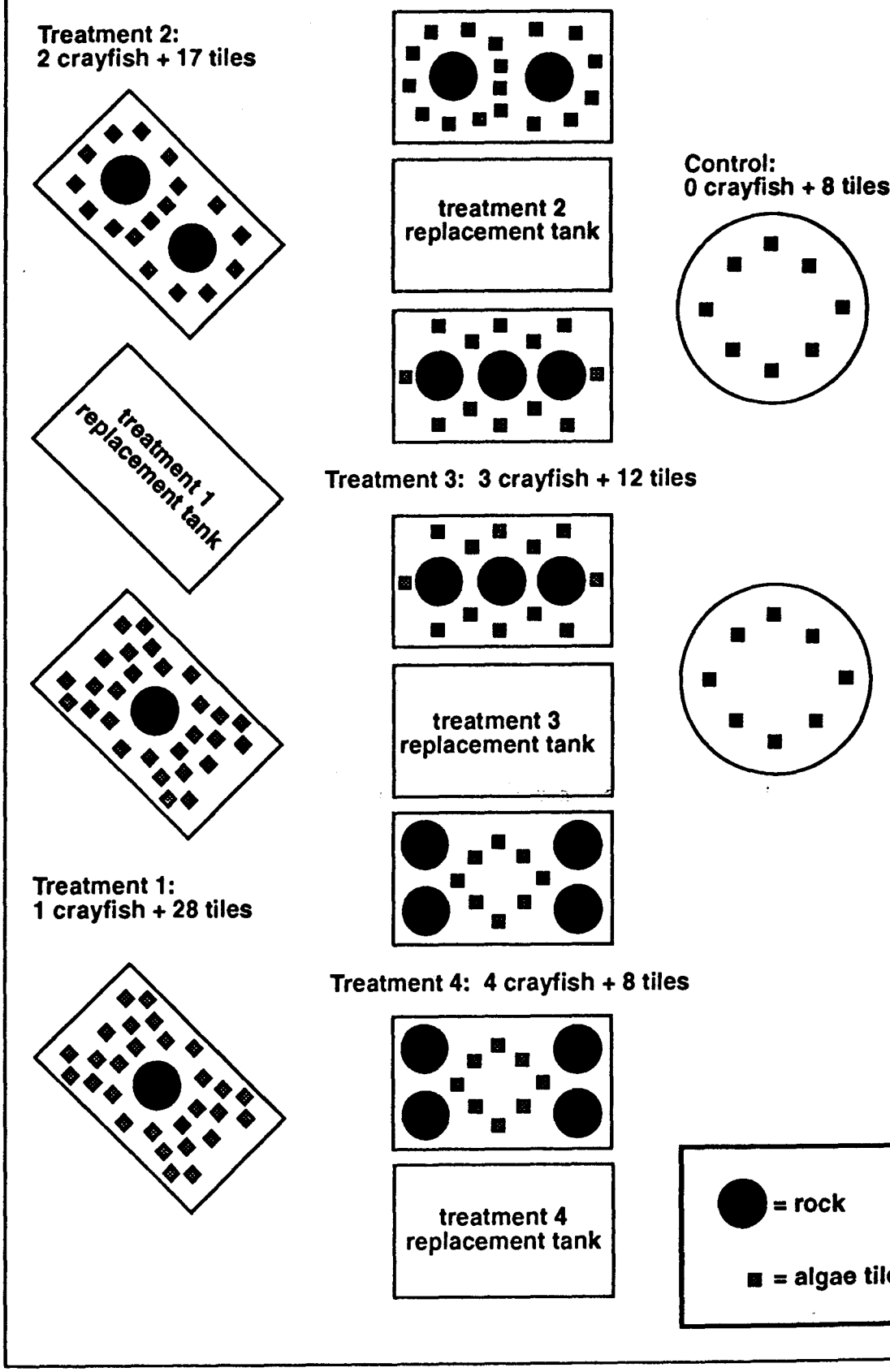
"condition" (in terms of periodicity and intensity of crayfish grazing) as the tiles in the treatment tanks; the replacement tank tiles were used to replace the tiles which were removed from the treatment tanks for samples. Since the number of tiles in the replacement tanks continually decreased with each successive sample, the tiles were kept in the same "condition" as the treatment tank tiles by maintaining a consistent number of grazing units (no. crayfish/no. tiles x no. days) in the replacement tank. After each sample, tiles were removed from the replacement tank to replace the tile removed from each treatment tank. The replaced tiles were marked so that they would not be used for subsequent samples. Therefore, they acted only to maintain the original crayfish to algae ratio. The number of grazing units in the replacement tank would remain the same as that in its respective treatment tank by adjusting the number of crayfish and/or the amount of time crayfish were allowed to remain in the replacement tank.

The arrangement of tiles and rocks in each treatment tank is depicted in Figure 6. Attempts were made to place tiles equidistant from rock shelters so that crayfish had equal access to the tiles. This was possible in all treatments except treatment 1.

Sampling

The experiment was conducted for 25 days at which time most of the tiles in the highest density treatment

Figure 6. Physical arrangement in the greenhouse of treatment tanks showing tile/rock arrangement.


Treatment 2:
2 crayfish + 17 tiles
treatment 2
replacement tank
Control:
0 crayfish + 8 tiles
treatment 1
replacement tank
Treatment 3: 3 crayfish + 12 tiles
treatment 3
replacement tank
Treatment 1:
1 crayfish + 28 tiles
Treatment 4: 4 crayfish + 8 tiles
treatment 4
replacement tank
= rock
= algae tile

(treatment 4) were nearly devoid of algae. One tile was removed from each treatment chamber for sampling on days 1, 4, 8, 12, 16, 20, and 25. Algae from the entire tile was scraped, homogenized and diluted to 600 ml with autoclaved, distilled water that contained 2% Guillard's F-1 algal media.

Primary productivity was measured *in vitro* using the dissolved oxygen method (light/dark bottle, APHA 1989). The 600 ml sample was divided so that both the light and dark bottle each contained 300 ml of the sample. Measurements of primary productivity were taken at 3 different time intervals during a 20 - 24 hour period. Primary productivity was calculated as follows:

$$\text{Net primary productivity (NPP) (light bottle)} = \frac{DO(final) - DO(initial)}{time}$$

$$\text{Respiration (R) (dark bottle)} = \frac{DO\ (final) - DO\ (initial)}{time}$$

DO = dissolved oxygen ($\mu gO_2 \cdot L^{-1} \cdot hr^{-1}$)

$$GPP = NPP - |R|$$

Standing crop of the algae was estimated as the concentration of chlorophyll *a* in each sample on each sampling day. Samples for chlorophyll *a* analysis were obtained by vacuum filtering 10 ml of the light bottle sample onto a piece of filter paper (pore size = .45 μm) (APHA 1989). The filter paper was then placed into an

opaque Nalgene 25 ml dark bottle with 8 ml 90% acetone (buffered with $MgCO_3$) and stored in a freezer. In order to analyze these samples, they were allowed to warm to room temperature and were then sonicated to lyse all cells and chloroplasts and centrifuged to remove cell wall fragments and undissolved filter from the extract. Analysis of these samples was done on a Turner Spectrofluorometer (Model 430) set at the following wavelengths: 430 nm excitation and 663 nm emission. Readings were taken before and after acidification in order to correct for the presence of phaeophytin (a degradation product of chlorophyll). Chlorophyll *a* concentration in each sample was calculated as follows (U.S.E.P.A. 1989):

$$\text{chl } a \ (\mu g \cdot L^{-1}) = F_s \frac{r_s}{r_s - 1} (R_b - R_a)$$

F_s = conversion factor for sensitivity level "s"
r_s = before:after acidification ratio
R_b = fluorometer reading before acidification
R_a = fluorometer reading after acidification

Chlorophyll *a* concentrations were then standardized for the volume filtered:

$$\frac{\text{chl a}}{\text{volume filtered}} = \frac{\text{standardized chl a}}{\text{proportion of tile area}}$$

To prepare slides for community composition analysis, the light bottle sample was rehomogenized, and 1 ml was extracted to be vacuum filtered and fixed with 50% and 95%

ethanol respectively. The filter paper was placed on a glass slide and cleared by adding 5-8 drops of clove oil. Each slide was microscopically examined three times: (1) to count and identify at least 500 diatom cells (using Nomarski optics, 1000x) (2) to count and identify at least 500 soft algae (green and blue-green) cells (using phase-contrast, 1000x); (cyanophyte filaments were standardized by counting cell units in which a 10 μm length was equal to one unit). and (3) to measure the dimensions of 15-20 cells of each taxon for biovolume calculations; biovolume calculations were done based on the geometric shape of the cells. Biovolume calculations for filamentous forms were done based on cell units. Turnover rates (T=number of new cells$\cdot cm^{-2}\cdot day^{-1}$) for selected species were calculated as follows:

$$T = \frac{\text{density (day final)} - \text{density (day initial)}}{\text{days}}$$

Per capita turnover rates (number new cells$\cdot cell^{-1}\cdot day^{-1}$) were calculated as follows:

$$\text{per capita } T = \frac{T \text{ (number new cells}\cdot cm^{-2}\cdot day^{-1})}{\bar{x} \text{ species cell density}}$$

Statistical Analyses

The diatom and soft algal (green and blue-green algae) components of this study were analyzed separately for the following reasons. (1) Diatoms and soft algae have different physiologies whereby diatoms are eukaryotic and

blue-green algae are prokaryotic. (2) Although diatoms and soft algae occupy the same habitat, they have different growth requirements (e.g., light, nutrients). (3) Diatoms and soft algae are different in cell size. It is thought that because of these differences, the two groups of algae may respond differently to the same grazing pressure (Tuchman and Stevenson 1991).

Analyses of the data were done using the five Algae Programs from the University of Louisville, Twin (Mosaic Software, Inc.), Mystat (1992) and Statistical Analysis Systems (SAS 1990) on the Loyola University mainframe computer. Abundance was described in terms of number of cells per mm^2.

Bartlett's test was used to test for homogeneity of treatment total variances (total variance = day-to-day variance plus inter-tile variance) followed by a Tukey-type multiple comparison test to determine which treatment variances were different (Zar 1984).

Primary productivity (standardized to standing crop estimates) data were tested for differences in treatments and time using 2-way ANOVA. A Tukey test was performed to determine which treatments or days were causing significant differences (Zar 1984). Chlorophyll *a* data were treated in the same manner as primary productivity data.

Seventeen taxa (see Appendix B) were selected for additional analyses on the basis of:

(1) occurrence in samples (were present in at least 25% of the counts)

(2) relatively large mean percent abundances

(3) large differences between minimum and maximum percent abundance (may indicate that a change is occurring over time or between treatments)

Growth rates of the 17 selected taxa were examined by natural-log-transforming cell count data and regressing with time. Slopes of these lines were examined to see if they were significantly different from zero.

Pearson's Correlation coefficients of the 17 selected taxa were calculated for the control and each treatment using Statistical Analysis Systems (SAS 1985).

Shannon's Diversity Indices were calculated as

$$H = - \sum_{i=1}^{s} P_i \ln P_i$$

where P_i is the fraction of all individuals in the community comprised by the i^{th} species, and s is the total number of species in the community (Vandermeer 1981).

Hurlbert evenness indices were calculated as:

$$V = \frac{D - D_{min}}{D_{max} - D_{min}}$$

where D is an observed diversity index and D_{min} and D_{max} are the minimum and maximum values, respectively, that D can obtain (Ludwig and Reynolds 1988). Species Richness was calculated as the total number of species (or taxa) in a sample.

Ruzicka's similarity Index (RI) was used to compare each individual treatment replicate to the mean of the two control replicates with identical assemblages approaching one. Ruzicka's Index was calculated as follows (Pielou 1984):

$$RI = \frac{\sum_{i=1}^{s} \min(x_{i1}, x_{i2})}{\sum_{i=1}^{s} \max(x_{i1}, x_{i2})} \times 100$$

where i is the species number, 1 and 2 are the samples being compared and s is the number of species.
Confidence limits using a jackknife method described in Smith et al. (1986) were used.

ANOVA and the Tukey test were performed to assess differences due to time and treatment for Shannon's diversity index, Hurlbert evenness index, species richness, and Ruzicka's similarity indices (Zar 1984).

Two different growth forms, canopy and adnate (Appendix C) were examined in order to determine if algal growth forms were differentially effected by grazing. Variances from canopy cell data and variances from adnate cell data were tested for homogeneity by using Bartlett's test; this was followed by the Tukey-type multiple comparison test to assess differences between treatment variances.

CHAPTER IV

RESULTS

Community Level Parameters

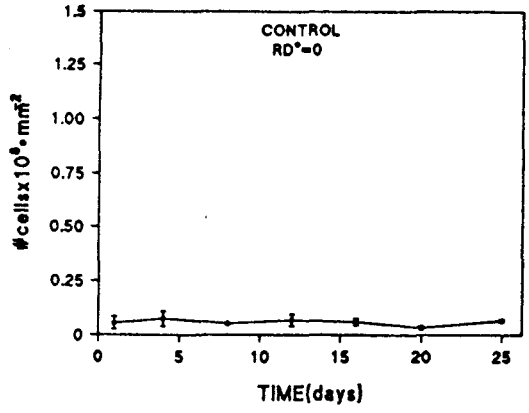
Overall effect of grazing on algal cell density

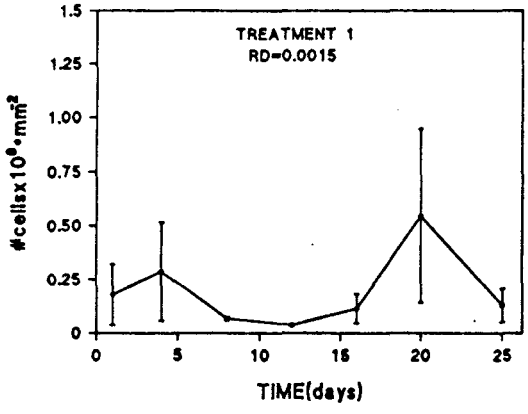
The overall effect of the increasing intensities of crayfish grazing on the entire algal community is depicted in Figure 7. The total number of algal cells in the control remained relatively constant whereas the total number of cells in the grazed treatments changed throughout the duration of the experiment and showed higher levels of variability. At the end of the 26 day experiment, all treatments (including the control) had similar total cell densities (range = $1.2 \times 10^6 - 2.1 \times 10^7$ cells$\cdot$mm^{-2}).

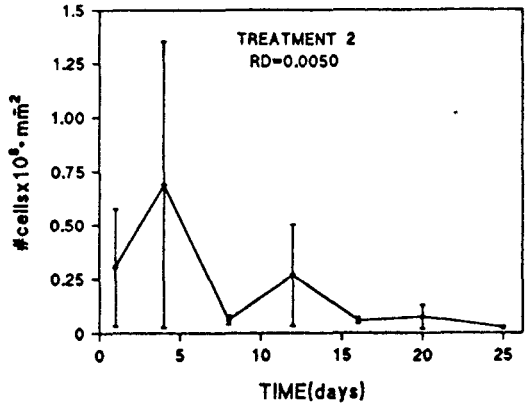
Since variability was one major difference between the control and grazed treatments, it was decided to examine variances about the mean of total cell density for all sampling dates in order to determine if the control and grazed treatments were significantly different in this regard. The 5 variances tested (control plus four grazing treatments) were not homogeneous (Bartlett's test; $P<.001$) (Table 3). Variances were not different among the four grazing treatments, however, variances for all four grazing treatments were significantly higher than the control variance (Tukey-type multiple comparison test; $P<.001$). Biovolume data for total cell abundances revealed the same results; i.e., the five variances tested were not

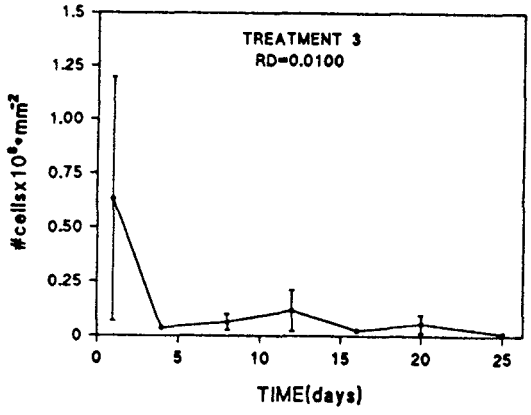
Figure 7. Mean cell density (± 1 s.d.) of total algal community (diatoms + soft algae).

(*RD=realized density: #crayfish·cm^{-2} algae)


CONTROL
RD°=0
#cellsx10⁶•mm⁻²
1.5
1.25
1.00
0.75
0.50
0.25
0
0
5
10
15
20
25
TIME(days)


TREATMENT 1
RD=0.0015
#cellsx10⁶•mm⁻²
1.5
1.25
1.00
0.75
0.50
0.25
0
0
5
10
15
20
25
TIME(days)


TREATMENT 2
RD=0.0050
#cellsx10⁶•mm⁻²
1.5
1.25
1.00
0.75
0.50
0.25
0
0
5
10
15
20
25
TIME(days)


TREATMENT 3
RD=0.0100
#cellsx10⁶•mm⁻²
1.5
1.25
1.00
0.75
0.50
0.25
0
0
5
10
15
20
25
TIME(days)

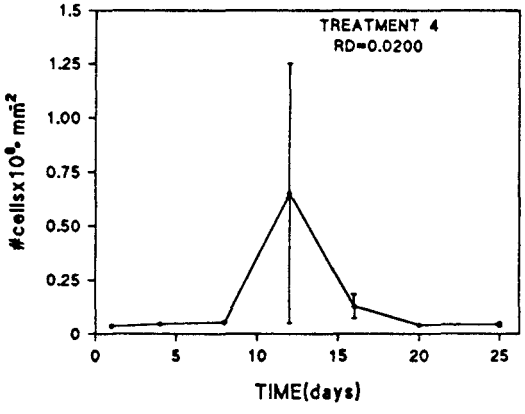

TREATMENT 4
RD=0.0200
#cellsx10⁶•mm⁻²
1.5
1.25
1.00
0.75
0.50
0.25
0
0
5
10
15
20
25
TIME(days)

Table 3. Total community variance about the mean (cell density and biovolumes) for all dates.

Treatment	Control	1	2	3	4
Variance[a] (based on cell density)	6.278×10^{12c}	6.587×10^{14d}	1.395×10^{15d}	9.632×10^{14d}	1.032×10^{15d}
Variance[b] (based on biovolumes)	5.549×10^{17c}	3.948×10^{19e}	3.028×10^{20e}	1.708×10^{20e}	7.599×10^{19e}

[a] variances were not homogeneous (Bartlett's test for homogeneity of variances: $B_c=133.655$, $X^2_{0.001,4}=18.467$, $P<.001$).

[b] variances were not homogeneous (Bartlett's test for homogeneity of variances: $B_c=181.561$, $X^2_{0.001,4}=18.467$, $P<.001$).

[c] control variance lower than all treatment variances (Tukey-type multiple comparison test: all q values greater than 3.858, $q_{0.05,\infty,5}=3.858$, $P<.05$).

[d] treatment variances not different from each other (Tukey-type multiple comparison test: all q values less than 3.858, $q_{0.05,\infty,5}=3.858$, $P>.05$).

[e] treatment 1 variance lower than treatment 2 variance (Tukey-type multiple comparison test: $q=5.199$, $q_{0.05,\infty,5}=3.858$, $P<.05$).
all other treatment variances not different from each other (Tukey-type multiple comparison test: all q values less than 3.858, $q_{0.05,\infty,5}=3.858$, $P>.05$).

homogeneous (Bartlett's test; P<.001) and all treatments had significantly higher variances than the control (Tukey-type multiple comparison test; P<.001) (Table 3).

Primary productivity

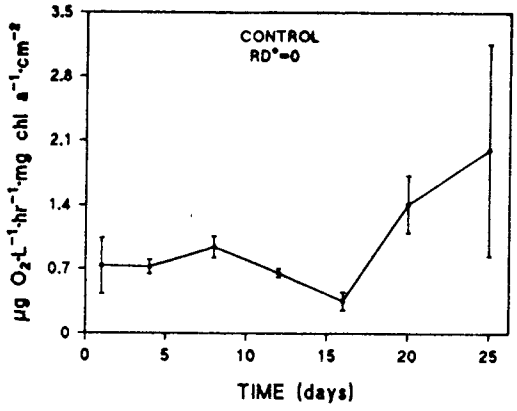
There were no significant differences in chlorophyll a-specific primary productivity rates among treatments (Figure 8), however, there was a significant time effect (ANOVA; P<.0001) within the treatments. In all treatments, primary productivity declined on day 16, and increased on day 20. When data from days 20 and 25 were disregarded for purposes of analysis (see p.98), there was a significant treatment effect (ANOVA; P<.001), a significant time effect (ANOVA; P<.001) and a significant interaction effect (ANOVA; P<.001). The lowest grazing intensity treatments (control, treatments 1 and 2) were not different and they all had significantly lower chlorophyll a-specific primary productivity rates than the highest grazing intensity treatment (treatment 4) (Tukey test; P<.005). Similarly, the control and treatment 1 had significantly lower chlorophyll a-specific primary productivity rates than treatment 3 (Tukey test; P<.025, P<.05, respectively), however treatments 2 and 3 were not significantly different.

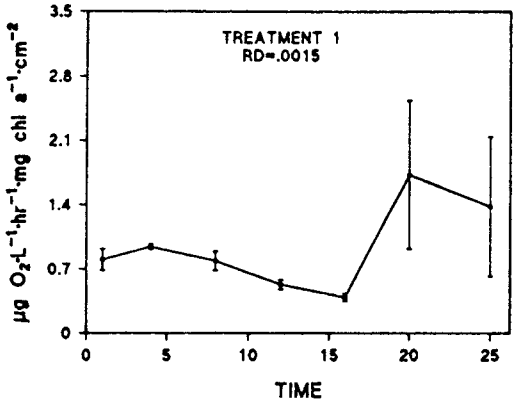
Standing crop

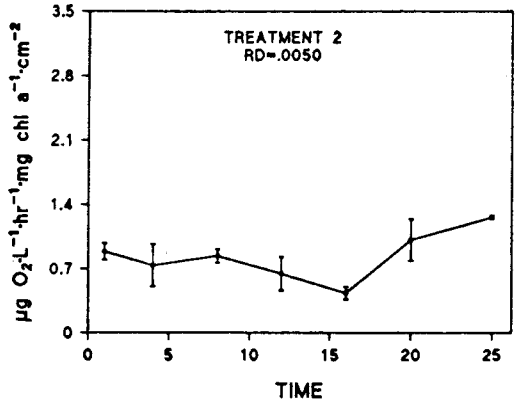
In general, there was an overall decrease in standing crop (estimated from chlorophyll a concentration) in all treatments throughout the 26 day experiment (Figure 9).

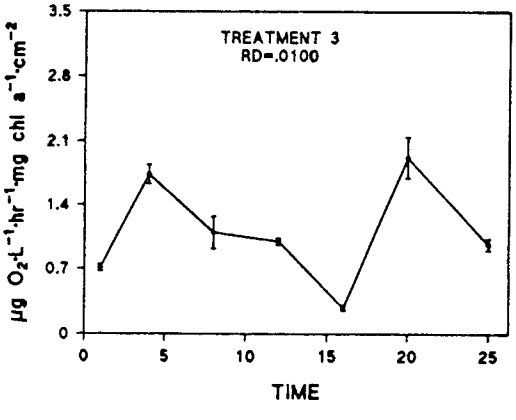
Figure 8. Mean chlorophyll a-specific primary productivity (± 1 s.d.).

($^{\bullet}$RD=realized density: #crayfish·cm^{-2} algae)


CONTROL
RD°=0
μg O2·L-1·hr-1·mg chl a-1·cm-2
TIME (days)


TREATMENT 1
RD=.0015
μg O2·L-1·hr-1·mg chl a-1·cm-2
TIME


TREATMENT 2
RD=.0050
μg O2·L-1·hr-1·mg chl a-1·cm-2
TIME


TREATMENT 3
RD=.0100
μg O2·L-1·hr-1·mg chl a-1·cm-2
TIME

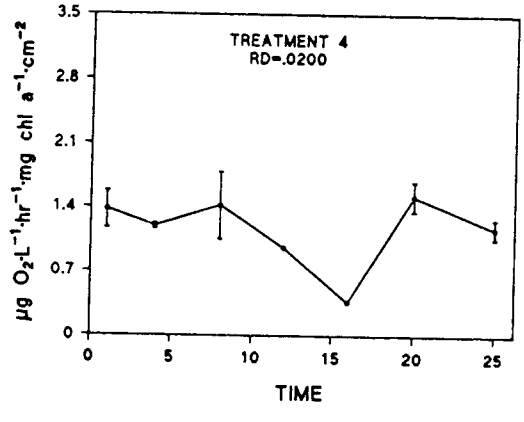
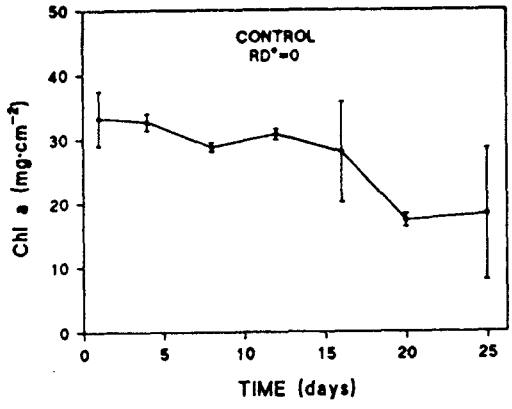
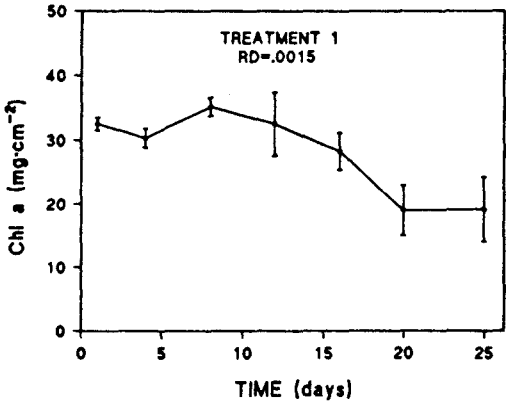
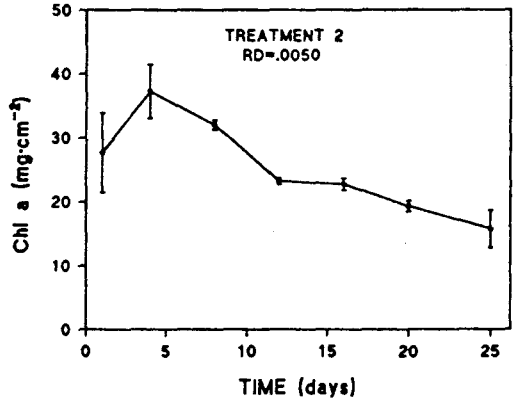

TREATMENT 4
RD=.0200
μg O2·L-1·hr-1·mg chl a-1·cm-2
TIME

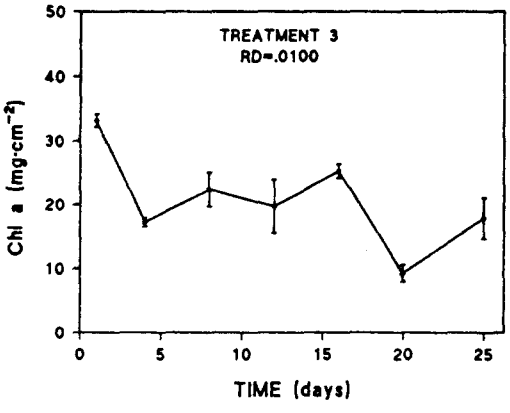
Figure 9. Mean standing crop (± 1 s.d.)(estimated from chlorophyll *a* concentration) in all treatments.

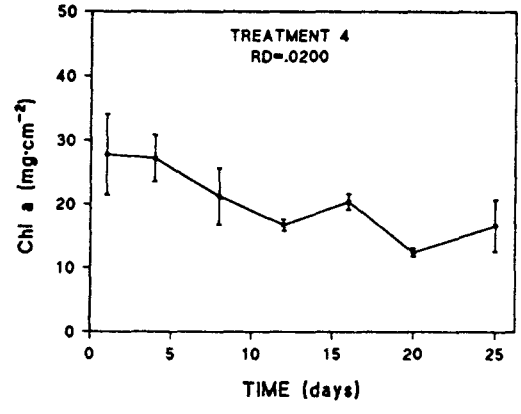
(*RD=realized density: #crayfish·cm^{-2} algae)


CONTROL
RD*=0
Chl a (mg·cm⁻²)
TIME (days)


TREATMENT 1
RD=.0015
Chl a (mg·cm⁻²)
TIME (days)


TREATMENT 2
RD=.0050
Chl a (mg·cm⁻²)
TIME (days)


TREATMENT 3
RD=.0100
Chl a (mg·cm⁻²)
TIME (days)


TREATMENT 4
RD=.0200
Chl a (mg·cm⁻²)
TIME (days)

There was a significant treatment (ANOVA; P<.0001) and time effect (ANOVA; P<.0001) on algal standing crop. The lowest intensity grazing treatments (control, treatments 1 and 2) had significantly higher concentrations of chlorophyll *a* than the two highest intensity grazing treatments (treatments 3 and 4) over all days (Tukey test; P<.025). The last two sampling days (days 20 and 25) had significantly lower chlorophyll *a* concentrations than some of the earlier sampling days (days 1, 4, 8, and 16) in the control and all treatments (Tukey test; P<.05). However, chlorophyll *a* concentration of the algal samples from the first five sampling days (days 1, 4, 8, 12, and 16) were not different.

Turnover and Growth rates

Turnover rates were calculated on a per cell per day basis. There was no obvious pattern in turnover rates on the total community level as the control and four grazed treatments had both positive and negative turnover rates throughout the experiment (Table 4). Mean cell turnover rate was positive in treatment 1 (0.037), slightly positive in treatment 4 (0.003), and negative in the control (-0.03), treatment 2 (-0.151) and treatment 3 (-0.249).

In order to compare growth rates of algal populations among treatments, total community cell densities were natural-log-transformed and regressed with time. The slope of this line is an indication of whether total community

Table 4. Per capita turnover rates (no. new cells·cell^{-1}·day^{-1}) for each sampling day.

Treatment	Control	1	2	3	4
day 4	0.530	0.185	0.605	-1.470	0.020
day 8	-0.4113	-0.285	-0.740	0.050	0.016
day 12	0.065	-0.038	0.240	0.099	1.050
day 16	-0.030	0.098	-0.980	-0.170	-0.920
day 20	-0.442	0.690	0.020	0.056	-0.150
day 25	0.107	-0.430	-0.050	-0.060	0.003
$\bar{x}$	-0.03	0.037	-0.151	-0.249	0.003

cell numbers are increasing (positive slope) or decreasing (negative slope) over time. The slope of the control (ANOVA: P=.75), treatment 1 (ANOVA; P=.499), treatment 2 (ANOVA; P=.096) and treatment 4 (ANOVA; P=.725) were not significantly different from 0 (Table 5) indicating a fairly consistent rate of new cell growth and cell removal/death; total community cell density in these treatments was not significantly changing throughout the duration of the experiment. The slope of treatment 3 was -0.17 and was significantly different from 0 (ANOVA; P<.02) indicating a slightly greater rate of cell removal/death than new cell growth.

Species Correlations

Correlations between the 17 selected taxa (see Appendix B) for the control and grazed treatments revealed that the twelve diatom taxa tended to be significantly correlated with each other, and the five soft algae taxa tended to be significantly correlated with each other in the control and all treatments (Table 6). Of the 330 possible diatom-to-diatom correlations, 282 (=85.5%) were statistically significant (P<.05); 80% of these significant correlations had correlation coefficients of at least .90. Similarly, 52% of the significant correlations between the soft algae taxa (23 out of 50 possible correlations = 46%) had correlation coefficients of at least .90. The diatom taxa were not significantly correlated with the soft algae taxa;

Table 5. Growth rates of algal populations.

Treatment	Slope	Probability of slope being different from 0
Control	0.0099	P=0.7541
1	0.0297	P=0.4993
2	-0.1075	P=0.0960
3	-0.1700	P=0.0191
4	0.0179	P=0.7246

Table 6. Pearson Correlation Coefficients for 17 selected diatom and soft algae taxa. Five rows of values following each algal group represent:

control
treatment 1
treatment 2
treatment 3
treatment 4

Column headings are abbreviations for algal groups listed in first column.

Significance levels for correlation coefficients are as follows:

.76-.999	P<.001
.64-.75	P<.01
.53-.63	P<.05

ALGAL GROUP	Acl	Acm	Amp	Cen	Fra	Nav	Nvr	Ntd	Ntf	Ntp	Nit	Syn	Blg	Coc	L+O	Pho	Sce
Achnanthes linearis	1.0	.63	.68	.44	.32	.64	.55	.65	.76	.53	.65	.59	.59	.18	-.2	.27	.31
	1.0	.99	.99	.99	.98	.98	.95	.98	.99	.99	.99	-.2	-.1	-.2	-.2	-.2	-.2
	1.0	.99	.97	.99	.96	.99	.69	.95	.99	.96	.98	-.1	-.2	-.1	-.1	-.2	-.1
	1.0	.99	.99	.99	.98	.99	-.3	.99	.99	.99	.99	.99	-.02	-.1	.31	.77	.24
	1.0	.99	.99	.98	.99	.99	.99	.99	.99	.99	.99	-.2	.10	-.1	.49	-.3	.50
Achnanthes minutissima	.63	1.0	.91	.65	.68	.95	.93	.91	.96	.79	.95	.94	.84	.56	-.1	-.2	.18
	.99	1.0	.99	.99	.97	.99	.98	.99	.99	.99	.99	-.2	-.1	-.1	-.2	-.2	-.2
	.99	1.0	.96	.99	.97	.98	.67	.95	.99	.95	.98	-.1	-.1	-.1	-.1	-.1	-.1
	.99	1.0	.99	.99	.98	.99	-.3	.99	.99	.99	.99	.99	-.01	-.1	.33	.78	.26
	.99	1.0	.99	.99	.99	.99	.99	.99	.99	.99	.99	-.2	.14	-.1	.51	-.3	.49
Amphora perpusilla	.68	.91	1.0	.73	.79	.98	.96	.83	.91	.61	.84	.92	.93	.54	-.1	-.1	.35
	.99	.99	1.0	.99	.96	.99	.99	.99	.99	.99	.99	-.2	-.1	-.1	-.2	-.2	-.2
	.97	.96	1.0	.95	.87	.99	.85	.99	.98	.99	.99	-.1	-.2	-.1	-.1	-.2	-.1
	.99	.99	1.0	.99	.98	.99	-.3	.99	.99	.99	.99	.99	-.04	-.1	.32	.77	.23
	.99	.99	1.0	.99	.99	.99	.99	.99	.99	.99	.99	-.2	.14	-.1	.52	-.3	.50
Centric spp.	.44	.65	.73	1.0	.74	.77	.77	.54	.67	.50	.58	.80	.78	.73	.37	.02	.33
	.98	.99	.99	1.0	.96	.99	.99	.99	.99	.99	.99	-.2	-.1	-.1	-.2	-.2	-.2
	.99	.99	.95	1.0	.98	.97	.64	.93	.99	.94	.97	-.1	-.1	-.1	-.1	-.1	-.1
	.99	.99	.99	1.0	.97	.99	-.3	.99	.99	.99	.99	.99	-.1	-.2	.30	.77	.17
	.98	.99	.99	1.0	.99	.99	.99	.99	.99	.98	.99	-.2	.18	-.1	.55	-.3	.50
Fragillaria crotonensis	.32	.68	.79	.74	1.0	.81	.82	.63	.63	.48	.62	.78	.76	.51	-.1	-.2	.23
	.98	.97	.96	.96	1.0	.95	.92	.95	.96	.96	.96	-.1	-.1	-.2	-.2	-.3	-.2
Fragillaria pinnata	.96	.97	.87	.98	1.0	.91	.48	.84	.96	.85	.90	-.1	-.1	-.1	-.1	-.1	-.1
	.98	.98	.98	.97	1.0	.97	-.3	.97	.98	.97	.97	.96	.11	-.00	.29	.78	.36
	.99	.99	.99	.99	1.0	.99	.99	.99	.99	.99	.99	-.2	.17	-.1	.52	-.3	.51
Navicula spp.	.64	.95	.98	.77	.81	1.0	.97	.87	.94	.70	.88	.96	.93	.59	-.1	-.2	.30
	.98	.99	.99	.99	.95	1.0	.99	.99	.99	.99	.99	-.2	-.1	-.1	-.1	-.2	-.2
	.99	.98	.99	.97	.91	1.0	.80	.99	.99	.99	.99	.99	-.1	-.1	.30	.77	.20
	.99	.99	.99	.99	.97	1.0	-.3	.99	.99	.99	.99	.99	-.1	-.1	.30	.77	.20
	.99	.99	.99	.99	.99	1.0	.99	.99	.99	.99	.99	-.2	.16	-.1	.52	-.3	.50
Navicula radiosa	.55	.93	.96	.77	.82	.97	1.0	.84	.87	.71	.86	.97	.91	.56	-.01	-.2	.23
	.95	.98	.99	.99	.92	.99	1.0	.99	.99	.99	.99	-.2	-.1	-.1	-.1	-.2	-.2
	.69	.67	.85	.64	.98	.80	1.0	.88	.71	.87	.81	-.1	-.2	-.1	-.1	-.1	-.1
	-.3	-.3	-.3	-.3	-.3	-.3	1.0	-.3	-.3	-.3	-.3	-.3	-.3	-.3	-.5	-.3	-.4
	.99	.99	.99	.99	.99	.99	1.0	.99	.99	.99	.99	-.3	.13	-.1	.52	-.3	.48
Nitzschia dissipita	.65	.91	.83	.54	.63	.87	.84	1.0	.89	.90	.97	.89	.82	.44	-.3	-.2	.07
	.98	.99	.99	.99	.95	.99	.99	1.0	.99	.99	.99	-.2	-.1	-.1	-.1	-.2	-.2
Nitzschia microcephala	.95	.95	.99	.93	.84	.99	.88	1.0	.96	.99	.99	-.1	-.2	-.1	-.1	-.2	-.1
	.99	.99	.99	.99	.97	.99	-.3	1.0	.99	.99	.99	.99	-.1	-.2	.32	.77	.18
	.99	.99	.99	.99	.99	.99	.99	1.0	.99	.99	.99	-.2	.13	-.1	.50	-.3	.50
Nitzschia fonticola	.76	.96	.91	.67	.63	.94	.87	.89	1.0	.73	.90	.91	.88	.60	-.1	-.1	.30
	.98	.99	.99	.99	.96	.99	.99	.99	1.0	.99	.99	-.2	-.1	-.1	-.2	-.2	-.2
	.99	.99	.98	.99	.96	.99	.71	.96	1.0	.96	.99	-.1	-.1	-.1	-.1	-.2	-.1
	.99	.99	.99	.99	.98	.99	-.3	.99	1.0	.99	.99	.99	-.04	-.1	.34	.78	.22
	.99	.99	.99	.99	.99	.99	.99	.99	1.0	.99	.99	-.2	.15	-.1	.51	-.3	.50
Nitzschia palea	.53	.79	.61	.50	.48	.70	.71	.90	.73	1.0	.92	.79	.62	.38	-.2	-.3	-.1
	.98	.99	.99	.99	.96	.99	.99	.99	.99	1.0	.99	-.2	-.1	-.1	-.1	-.2	-.2
	.96	.95	.99	.94	.85	.99	.87	.99	.97	1.0	.99	-.1	-.2	-.1	-.1	-.2	-.1
	.99	.99	.99	.99	.97	.99	-.3	.99	.99	1.0	.99	.99	-.1	-.2	.32	.78	.18
	.99	.99	.99	.98	.99	.99	.99	.99	.99	1.0	.99	-.3	.12	-.1	.49	-.3	.49
Nitzschia spp.	.65	.95	.84	.58	.62	.88	.88	.97	.90	.92	1.0	.91	.79	.46	-.2	-.2	.07
	.98	.99	.99	.99	.96	.99	.99	.99	.99	.99	1.0	-.2	-.1	-.1	-.2	-.2	-.2
	.98	.98	.99	.97	.90	.99	.81	.99	.99	.99	1.0	-.1	-.2	-.1	-.1	-.2	-.1
	.99	.99	.99	.99	.97	.99	-.3	.99	.99	.99	1.0	.99	-.1	-.2	.32	.77	.19
	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	1.0	-.2	.14	-.1	.50	-.3	.50
Synedra spp.	.59	.94	.92	.80	.78	.96	.97	.89	.91	.79	.91	1.0	.93	.66	-.1	-.2	.25
	-.2	-.2	-.2	-.2	-.1	-.2	-.2	-.2	-.2	-.2	-.2	1.0	-.2	-.2	.04	.002	-.04
	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	1.0	-.1	-.1	-.1	-.1	-.1
	.99	.99	.99	.99	.97	.99	-.3	.99	.99	.99	.99	1.0	-.1	-.2	.31	.77	.16
	-.2	-.2	-.2	-.2	-.2	-.2	-.3	-.2	-.2	-.3	-.2	1.0	-.4	.07	-.5	.45	.15
Chroococcus, Blue-green ovoids and spheres	.59	.84	.93	.78	.76	.93	.91	.82	.88	.62	.79	.93	1.0	.71	.05	-.2	.33
	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.2	1.0	.88	.86	.41	.87
	-.2	-.1	-.2	-.1	-.1	-.2	-.2	-.2	-.1	-.2	-.2	-.1	1.0	.98	.98	.92	.99
	-.02	-.01	-.04	-.1	.11	-.1	-.3	-.1	-.04	-.1	-.1	-.1	1.0	.90	.11	.04	.92
	.10	.14	.14	.18	.17	.16	.13	.13	.15	.12	.14	-.4	1.0	.42	.37	-.3	-.3
Coccoids	.18	.56	.54	.73	.51	.59	.56	.44	.60	.38	.46	.66	.71	1.0	.23	-.1	.47
	-.2	-.1	-.1	-.1	-.2	-.1	-.1	-.1	-.1	-.1	-.1	-.2	.88	1.0	.79	.51	.89
	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	.98	1.0	.97	.95	.99
	-.1	-.1	-.1	-.2	-.00	-.1	-.3	-.2	-.1	-.2	-.2	-.2	.90	1.0	.12	.05	.83
	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	.07	.42	1.0	-.1	-.3	-.02
Lyngbya limnetica	-.2	-.1	-.1	.37	-.1	-.1	-.01	-.3	-.1	-.2	-.2	-.1	.05	.23	1.0	-.2	-.2
	-.2	-.2	-.2	-.2	-.2	-.1	-.1	-.1	-.2	-.1	-.2	.04	.86	.79	1.0	.66	.97
Oscillatoria limnetica	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	.98	.97	1.0	.89	.98
	.31	.33	.32	.30	.29	.30	-.5	.32	.34	.32	.32	.31	.11	.12	1.0	.58	.36
	.49	.51	.52	.55	.52	.52	.52	.50	.51	.49	.50	-.5	.37	-.1	1.0	-.4	-.2
Phormidium tenue	.27	-.2	-.1	.02	-.2	-.2	-.2	-.2	-.1	-.3	-.2	-.2	-.2	-.1	-.2	1.0	.51
	-.2	-.2	-.2	-.2	-.3	-.2	-.2	-.2	-.2	-.2	-.2	.002	.41	.51	.66	1.0	.67
	-.2	-.1	-.2	-.1	-.1	-.2	-.1	-.2	-.2	-.2	-.2	-.1	.92	.95	.89	1.0	.94
	.77	.78	.77	.77	.78	.77	-.3	.77	.78	.78	.77	.77	.04	.05	.58	1.0	.38
	-.3	-.3	-.3	-.3	-.3	-.3	-.3	-.3	-.3	-.3	-.3	.45	-.3	-.3	-.4	1.0	.14
Scenedesmus spp.	.31	.18	.35	.33	.23	.30	.23	.07	.30	-.1	.07	.25	.33	.47	-.2	.51	1.0
	-.2	-.2	-.2	-.2	-.2	-.2	-.2	-.2	-.2	-.2	-.2	-.04	.87	.89	.97	.67	1.0
	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	-.1	.99	.99	.98	.94	1.0
	.24	.26	.23	.17	.36	.20	-.4	.18	.22	.18	.19	.16	.92	.83	.36	.38	1.0
	.50	.49	.50	.50	.51	.50	.48	.50	.50	.49	.50	.15	-.3	-.02	-.2	.14	1.0

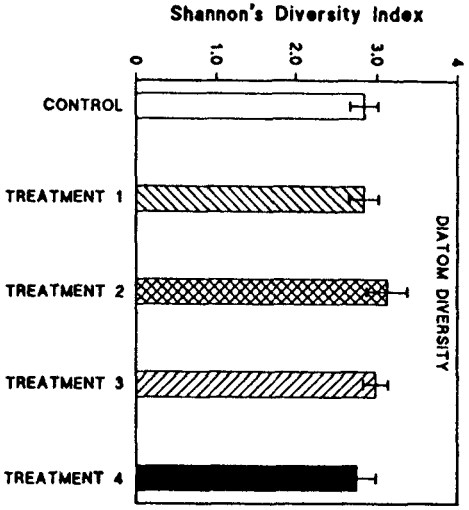
diatoms were negatively correlated with soft algae, although these negative correlations were not significant.

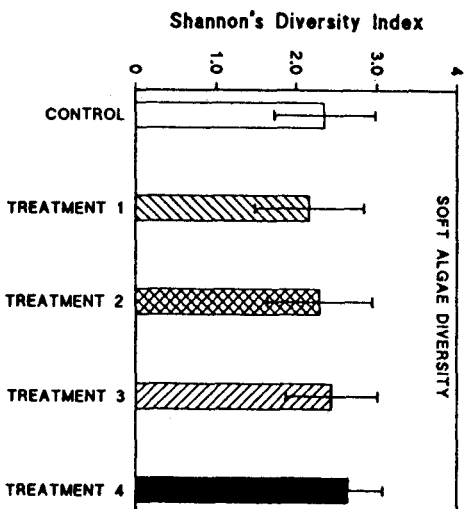
Community Diversity

In general, Shannon's Diversity Indices for the total algal community were lowest in the control, the lowest intensity grazing treatment (treatment 1), and in the highest intensity grazing treatment (treatment 4), and were slightly higher in the intermediate intensity grazing treatments (treatments 2 and 3) (Figure 10, Table 7). Treatments 2 and 3 had significantly higher diversity indices than treatment 1 (Tukey test; $P<.05$), but were not significantly different from the control or treatment 4. There were no significant differences among the other treatments. A significant time effect (ANOVA; $P<.0001$) revealed that total community diversity was significantly higher on days 4, 12, and 20 than on the other four sampling days (Tukey test; $P<.005$).

Average diatom diversity was higher than average soft algal diversity in all treatments (Table 7). Furthermore, diatom diversity indices tended to be higher than soft algal diversity indices on most days. Diatom diversity in treatment 2 was significantly higher than the control (Tukey test; $P<.05$), treatment 1 (Tukey test; $P<.05$) and treatment 4 (Tukey test; $P<.005$), but was not significantly higher than treatment 3. All other treatments were not significantly different.

Figure 10. Mean Shannon's diversity index (± 1 s.d.) for total community, diatom and soft algal components of the community.


Shannon's Diversity Index
0
1.0
2.0
3.0
4
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
DIATOM DIVERSITY


Shannon's Diversity Index
0
1.0
2.0
3.0
4
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
SOFT ALGAE DIVERSITY

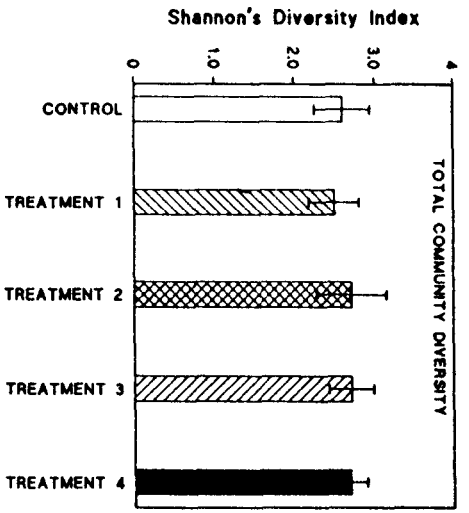

Shannon's Diversity Index
0
1.0
2.0
3.0
4
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
TOTAL COMMUNITY DIVERSITY

Table 7. Shannon's diversity indices for diatom, soft and total algal communities.

Day	Algal Community	Control	Trt. 1	Trt. 2	Trt. 3	Trt. 4
1	diatom	2.4976	2.75	3.0859	2.8917	3.1847
	soft	2.1338	1.9365	2.2562	1.6771	2.6834
	total	2.3157	2.3433	2.6711	2.2844	2.9341
4	diatom	2.9443	2.9988	3.41465	2.8603	2.3543
	soft	3.0662	3.0503	3.3494	3.2408	3.2972
	total	3.0053	3.0246	3.3820	3.0506	2.8258
8	diatom	3.0515	2.9473	2.9159	2.8016	2.6567
	soft	2.3301	1.6564	1.7299	2.3479	2.6282
	total	2.6908	2.3019	2.3229	2.5748	2.6425
12	diatom	2.8859	2.4682	3.2394	2.9426	2.8354
	soft	2.7865	3.2982	2.5458	3.0052	3.0259
	total	2.8362	2.8832	2.8926	2.9739	2.9307
16	diatom	2.9994	2.7789	2.6443	2.9542	2.8587
	soft	1.9227	1.3918	1.5294	2.3422	1.9721
	total	2.4611	2.0854	2.0869	2.6482	2.4154
20	diatom	2.7924	2.8887	3.3617	3.2006	2.6915
	soft	3.0311	2.1756	3.0066	2.7914	2.7710
	total	2.9118	2.5322	3.1842	2.996	2.7313
25	diatom	2.7465	3.0376	3.2316	3.218	2.7114
	soft	1.1926	1.645	1.6453	1.6697	2.2076
	total	1.9696	2.3413	2.4385	2.4439	2.4595
$\bar{x}$	diatom	2.845	2.8385	3.128	2.981	2.7561
	soft	2.352	2.165	2.295	2.439	2.6551
	total	2.599	2.5017	2.7112	2.7103	2.706

Soft algae diversity in treatment 4 was significantly higher than treatment 1 (Tukey test; P<.025), but was not significantly higher than the other treatments. All other treatments were not significantly different.

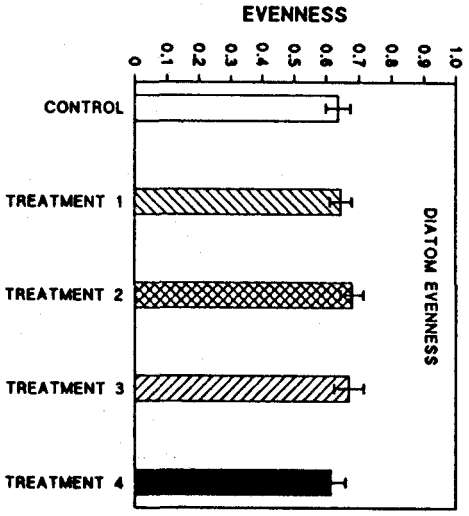
Evenness

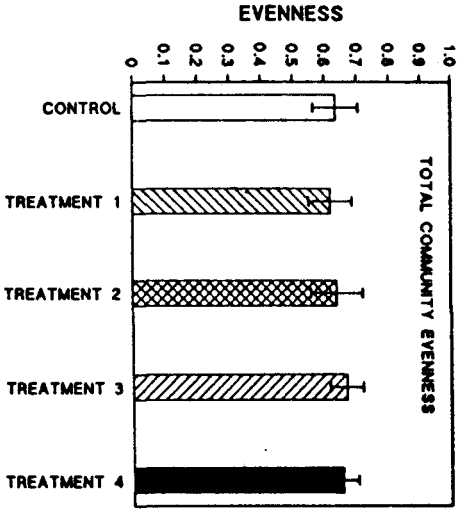
Total community evenness was not different among the control and four grazed treatments (ANOVA; P=.120)(Figure 11, Table 8). There was a significant time effect in total community evenness (ANOVA; P<.0001); community evenness was higher on day 4 than on day 25 (Tukey test; P<.001), day 16 (Tukey test; P<.005), day 1 (Tukey test; P<.025) and day 8 (Tukey test; P<.05). A similar pattern was noted with the soft algal community evenness. A significant treatment effect existed in diatom community evenness (ANOVA; P<.0001); treatment 2 had significantly higher evenness than treatment 4 (Tukey test; P<.001) and the control (Tukey test; P<.025). Treatment 3 was significantly higher than treatment 4 (Tukey test; P<.001).

Species Richness

Species richness was higher for diatoms than soft algae in all treatments on all sampling days (except treatment 1 on day 12) (Figure 12, Table 9). In general, total community species richness was not different among the control and four grazed treatments; i.e., increasing intensities of crayfish grazing did not affect species richness (ANOVA; soft algae P=.147, diatoms P=.284). There

Figure 11. Mean evenness (± 1 s.d.) for total community, diatom and soft algal components of the community.


EVENNESS
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
DIATOM EVENNESS


EVENNESS
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
TOTAL COMMUNITY EVENNESS

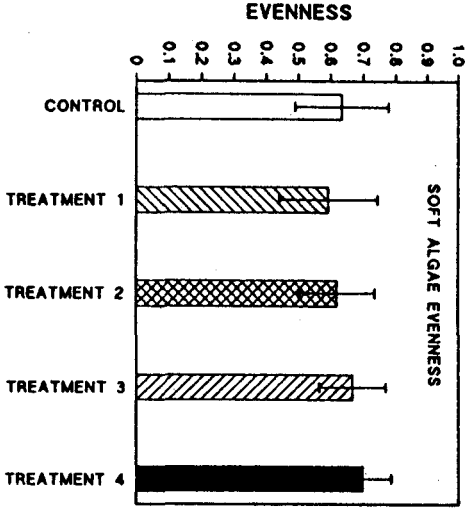
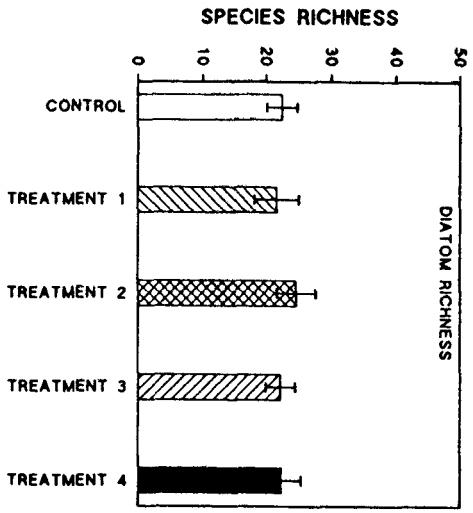
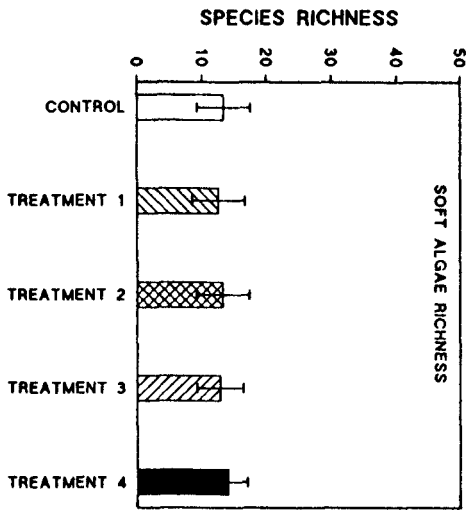

EVENNESS
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
SOFT ALGAE EVENNESS

Table 8. Hurlbert evenness values for diatom, soft and total algal communities.

Day	Algal Community	Control	Trt. 1	Trt. 2	Trt. 3	Trt. 4
1	diatom	0.5732	0.6172	0.6608	0.6345	0.6625
	soft	0.6412	0.5710	0.6097	0.5161	0.7659
	total	0.6072	0.5941	0.6353	0.5753	0.7142
4	diatom	0.6421	0.6274	0.7223	0.6674	0.5606
	soft	0.7658	0.7326	0.8033	0.7929	0.7908
	total	0.7040	0.6800	0.7628	0.7302	0.6757
8	diatom	0.6502	0.6658	0.6699	0.6711	0.6204
	soft	0.6563	0.5275	0.5208	0.6787	0.6904
	total	0.6533	0.5967	0.5954	0.6749	0.6554
12	diatom	0.6361	0.6115	0.6820	0.6550	0.6313
	soft	0.6603	0.7910	0.6196	0.7431	0.7332
	total	0.6482	0.7013	0.6508	0.6991	0.6823
16	diatom	0.6884	0.6629	0.6173	0.6511	0.6279
	soft	0.6065	0.4640	0.4970	0.7039	0.5791
	total	0.6475	0.5635	0.5572	0.6775	0.6035
20	diatom	0.6125	0.6302	0.7032	0.6935	0.6178
	soft	0.7199	0.5570	0.7312	0.6840	0.6930
	total	0.6662	0.5936	0.7172	0.6888	0.6554
25	diatom	0.6555	0.7013	0.6916	0.7135	0.5913
	soft	0.3868	0.5030	0.5534	0.5431	0.6468
	total	0.5212	0.6022	0.6225	0.6283	0.6191
$\bar{x}$	diatom	0.6369	0.6452	0.6782	0.6694	0.6160
	soft	0.6338	0.5923	0.6193	0.6660	0.6999
	total	0.6354	0.6188	0.6487	0.6677	0.6579

Figure 12. Mean species richness (± 1 s.d.) for total community, diatom and soft algal components of the community.


SPECIES RICHNESS
0
10
20
30
40
50
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
DIATOM RICHNESS


SPECIES RICHNESS
0
10
20
30
40
50
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
SOFT ALGAE RICHNESS

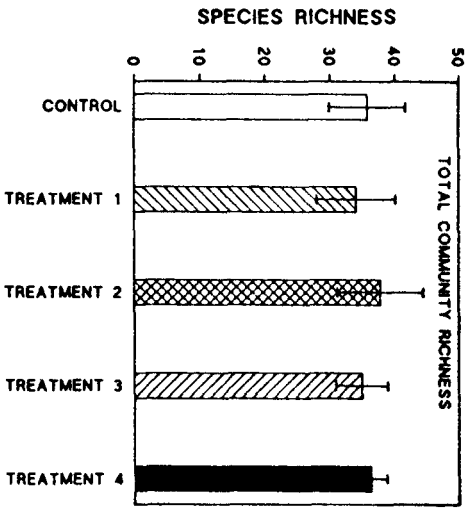

SPECIES RICHNESS
0
10
20
30
40
50
CONTROL
TREATMENT 1
TREATMENT 2
TREATMENT 3
TREATMENT 4
TOTAL COMMUNITY RICHNESS

Table 9. Species richness for diatom, soft and total algal communities.

Day	Algal Community	Control	Trt. 1	Trt. 2	Trt. 3	Trt. 4
1	diatom	20.5	22	25.5	24	28
	soft	10.5	10.5	13	9.5	11.5
	total	31.0	32.5	38.5	33.5	39.5
4	diatom	24	28	26.5	19.5	18.5
	soft	16	18	18	17	18
	total	40.0	46.0	44.5	36.5	36.5
8	diatom	26	21.5	20.5	18	19.5
	soft	11.5	8.5	10	11	14
	total	37.5	30.0	30.5	29.0	33.5
12	diatom	23.5	16.5	27	22.5	22.5
	soft	19	18	17.5	16.5	17.5
	total	42.5	34.5	44.5	39.0	40.0
16	diatom	20.5	18.5	19.5	23.5	23.5
	soft	9	8	8.5	10	10.5
	total	29.5	26.5	28.0	33.5	34.0
20	diatom	24	24	27.5	24.5	20.5
	soft	18.5	15	17.5	17	16
	total	42.5	39.0	45.0	41.5	36.5
25	diatom	19	20.5	25.5	23	24
	soft	8.5	9.5	8	8.5	11
	total	27.5	30.0	33.5	31.5	35.0
$\bar{x}$	diatom	22.5	21.6	24.6	22.1	22.4
	soft	13.3	12.5	13.2	12.8	14.1
	total	35.8	34.1	37.8	34.9	36.5

was a significant time effect on soft algae species richness for all treatments (ANOVA; P<.001). Although this effect showed no particular pattern, soft algae species richness was significantly higher on days 4, 12, and 20 than on the other four sampling days (Tukey test; P<.001). There was no significant time effect on diatom species richness in any treatment (ANOVA; P=.376).

Similarity Indices

Similarity indices were generated by comparing the community composition of each individual treatment replicate to the mean of the two control replicates for each sampling day. The intent of generating similarity indices was to see if algal communities on tiles from the treatment tanks which visually appeared to be grazed were less similar to the control tiles than tiles from the treatment tanks which visually did not appear to be grazed. There was not a large difference in diatom similarity indices between tiles which visually appeared to be grazed-vs-ungrazed (mean diatom similarity index-grazed = .718; mean diatom similarity index-ungrazed = .726). However, the mean soft algae similarity index of those tiles which visually appeared to be grazed was somewhat lower than the mean similarity index of ungrazed tiles (mean soft algae similarity index-grazed = .579; mean soft algae similarity index-ungrazed = .618).

In general, diatoms had higher similarity indices than soft algae (48 out of 56 cases) (Table 10). There was no

Table 10. Ruzicka's similarity indices: community of each individual treatment replicate was compared to the mean of the two control replicates.

	1A	1B	2A	2B	3A	3B	4A	4B
day 1	.345*	.802	.616	.747	.707	.859	.732	.613
	.624**	.657	.759	.704	.647	.654	.599	.553
day 4	.777	.823	.648	.748	.777	.783	.717	.698
	.500	.628	.521	.639	.588	.577	.533	.553
day 8	.718	.830	.651	.741	.757	.723	.750	.742
	.476	.572	.484	.535	.486	.503	.504	.506
day 12	.806	.762	.679	.715	.604	.598	.720	.713
	.559	.400	.545	.625	.340	.536	.296	.632
day 16	.789	.787	.730	.800	.647	.755	.795	.728
	.802	.544	.706	.680	.517	.797	.747	.612
day 20	.821	.858	.616	.677	.792	.593	.708	.783
	.586	.502	.550	.637	.673	.510	.522	.641
day 25	.716	.639	.680	.745	.699	.633	.829	.759
	.645	.836	.711	.705	.712	.821	.510	.406
$\bar{x}$	.710	.786	.660	.739	.712	.706	.750	.719
	.599	.591	.611	.646	.566	.628	.530	.558

*top number = diatom similarity index
**bottom number = soft algae similarity index

significant time effect (ANOVA; P=.559) or treatment effect (ANOVA; P=.412) in the diatom similarity indices. There was no significant treatment effect (ANOVA; P=.154), but there was a significant time effect (ANOVA; P=.001) in the soft algae similarity indices.

Population Level Parameters

In general, soft algal community densities were higher than diatoms in all treatments throughout the study (mean relative abundance in all treatments over all days; soft algae = 68.7%, diatoms = 31.3%) (Figure 13). In each of the four grazed treatments, there was one day in which this pattern of relative abundances was reversed; i.e., soft algae declined and diatoms increased. These "reversals" correspond to the peaks in community density (see Figure 7), therefore these peaks seem to be diatom peaks rather than soft algae peaks.

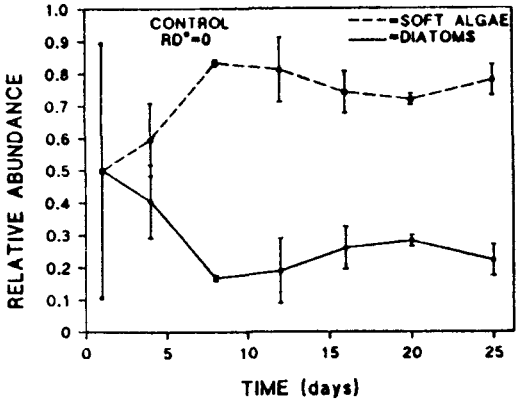
Relative abundance data of population densities indicate that Nitzschia spp. and Achnanthes minutissima Kutz. were the dominant diatoms, Phormidium tenue Menegh. Gomont was the dominant cyanophyte and Scenedesmus spp. was the dominant chlorophyte in the community in all treatments throughout the 26 day experiment (see Appendix A for a complete list of diatom and soft algal species from all samples in the study).

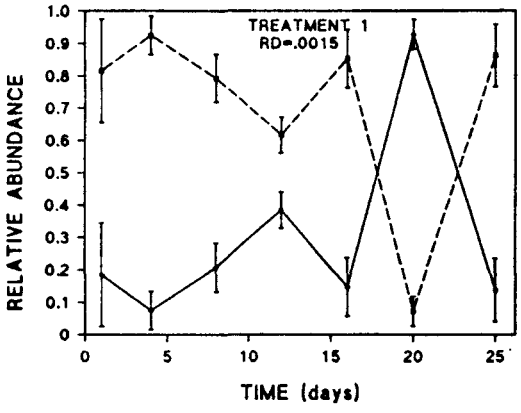
Growth forms

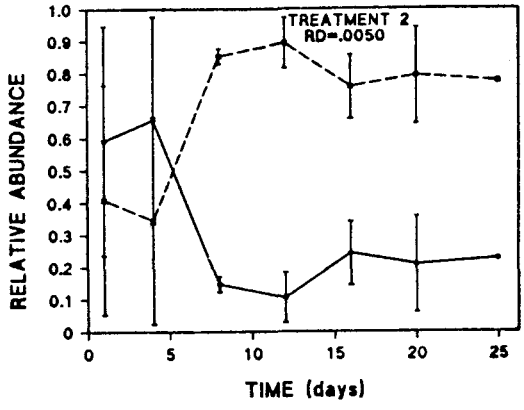
In order to examine if algal growth forms (canopy taxa-

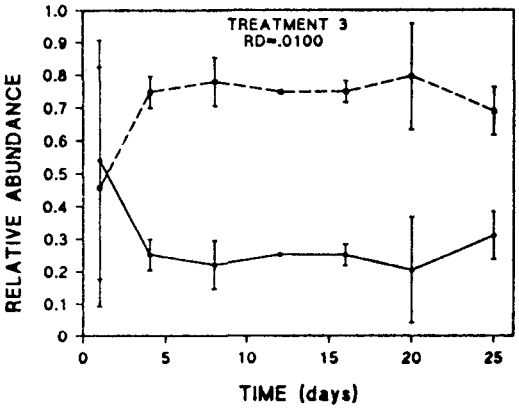
Figure 13. Mean relative abundance (± 1 s.d.) of soft algae and diatoms.

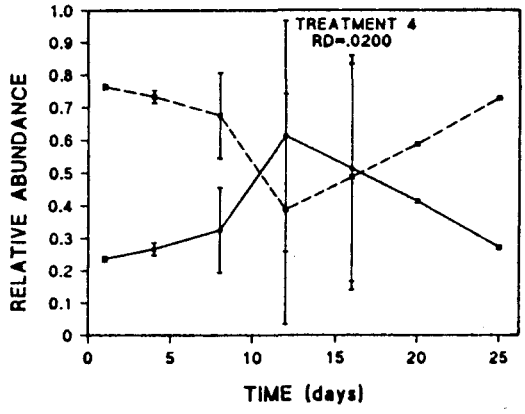
(*RD=realized density: #crayfish·cm^{-2} algae)


CONTROL
RD*=0
----=SOFT ALGAE
——=DIATOMS
RELATIVE ABUNDANCE
TIME (days)


TREATMENT 1
RD=.0015
RELATIVE ABUNDANCE
TIME (days)


TREATMENT 2
RD=.0050
RELATIVE ABUNDANCE
TIME (days)


TREATMENT 3
RD=.0100
RELATIVE ABUNDANCE
TIME (days)

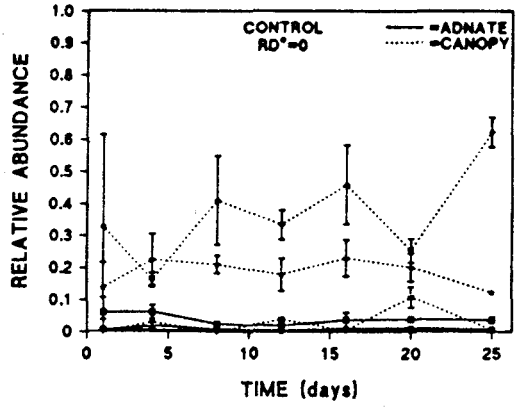

TREATMENT 4
RD=.0200
RELATIVE ABUNDANCE
TIME (days)

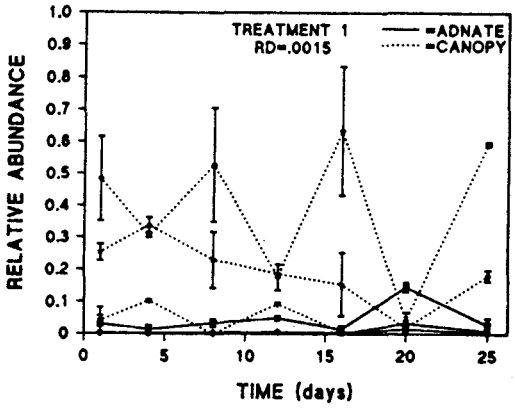
vs-adnate taxa) were differentially affected by crayfish grazing, three diatom taxa that are known to be adnate, (Achnanthes minutissima, A. linearis, Amphora perpusilla), as well as three species of filamentous cyanophytes (Oscillatoria limnetica, Lyngbya limnetica, Phormidium tenue), and one group of chlorophyte plankters associated with filaments in the canopy (Scenedesmus spp.) were selected for analysis. Of these six taxa, Phormidium tenue and Scenedesmus spp. were numerically dominant in the community in all treatments throughout the experiment (Figure 14). The three adnate species of diatoms appeared to be minimally affected by grazing (i.e., grazed treatment variances were not significantly different, Tukey-type multiple comparison test; $P>.05$), whereas higher levels of variation occurred among grazed treatments for the canopy species (Table 11).

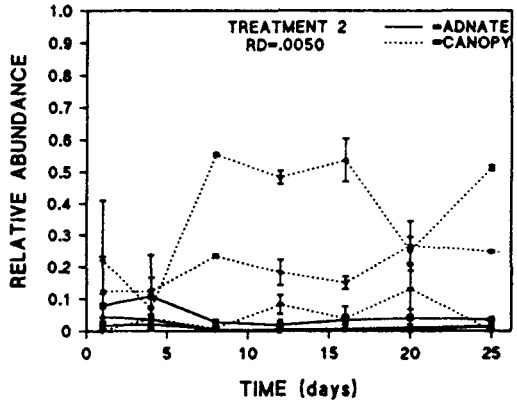
For the canopy species, intermediate intensity grazing treatments (treatments 1 and 2) had significantly higher variances than the control and highest intensity grazing treatments (treatments 3 and 4) (Tukey-type multiple comparison test; $P<.005$). However, for the adnate species, variances among treatments were not significantly different. This general trend within the canopy group and adnate group was evident when both cell density data and biovolume data were analyzed (Table 11).

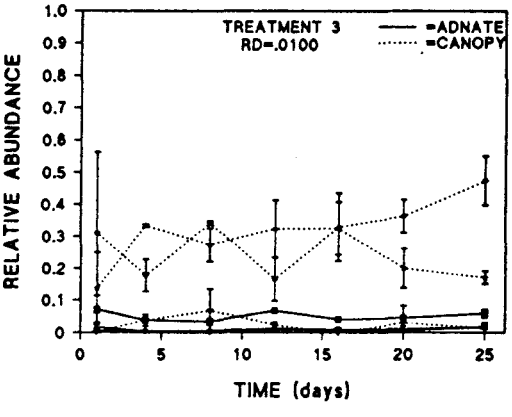
Figure 14. Mean relative abundance (± 1 s.d.) of canopy and adnate taxa.

(*RD=realized density: #crayfish·cm^{-2} algae)


CONTROL
RD°=0
=ADNATE
=CANOPY
RELATIVE ABUNDANCE
TIME (days)


TREATMENT 1
RD=.0015
=ADNATE
=CANOPY
RELATIVE ABUNDANCE
TIME (days)


TREATMENT 2
RD=.0050
=ADNATE
=CANOPY
RELATIVE ABUNDANCE
TIME (days)


TREATMENT 3
RD=.0100
=ADNATE
=CANOPY
RELATIVE ABUNDANCE
TIME (days)

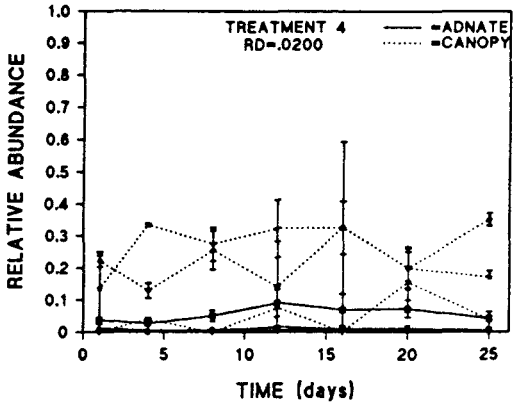

TREATMENT 4
RD=.0200
=ADNATE
=CANOPY
RELATIVE ABUNDANCE
TIME (days)

Table 11. Canopy and adnate variance about the mean for all dates.

Treatment	Control	1	2	3	4
Canopy variance[a,c] (based on cell density)	3.733×10^{13b}	1.464×10^{14b}	1.011×10^{14b}	1.395×10^{13b}	1.156×10^{13b}
Adnate variance[a,d] (based on cell density)	9.040×10^{10e}	1.921×10^{13e}	8.599×10^{12e}	2.326×10^{13e}	2.843×10^{13e}
Canopy variance[a,c] (based on biovolumes)	7.013×10^{15b}	6.904×10^{17b}	3.271×10^{17b}	7.095×10^{16b}	4.440×10^{16b}
Adnate variance[a,d] (based on biovolumes)	1.528×10^{16d}	3.043×10^{17d}	1.393×10^{18d}	3.713×10^{17d}	4.057×10^{17d}

[a] variances were not homogeneous (Bartlett's test for homogeneity of variances).
a[a]: B_c=200.502, $X^2_{0.001,4}$=18.467, P<.001
a[b]: B_c=261.085, $X^2_{0.001,4}$=18.467, P<.001
a[c]: B_c=225.417, $X^2_{0.001,4}$=18.467, P<.001
a[d]: B_c=185.957, $X^2_{0.001,4}$=18.467, P<.001

[b] treatments 1 and 2 variances were higher than the control, treatment 3 and treatment 4 variances (Tukey-type multiple comparison test: all q values greater than 3.858, $q_{0.05,\infty,5}$=3.858, P<.05).
treatment 3 variance was higher than treatment 4 variance (Tukey-type multiple comparison test: q=6.355 (cell density), q=7.071 (biovolume), $q_{0.005,\infty,5}$=4.886, P<.005).

[c] control variance lower than all treatment variances (Tukey-type multiple comparison test: all q values greater than 5.484, $q_{0.001,\infty,5}$=5.484, P<.001).

[d] control variance lower than all treatment variances (Tukey-type multiple comparison test: all q values greater than 5.484, $q_{0.001,\infty,5}$=5.484, P<.001).
treatment 1 variance lower than treatment 2 variance (Tukey-type multiple comparison test: q=3.880, $q_{0.05,\infty,5}$=3.858, P<.05).

CHAPTER V

DISCUSSION

In Lake Michigan, detritus, macrophytes and benthic macroinvertebrate prey are relatively scarce, therefore, it would seem that benthic algae may serve as a very important dietary component for crayfish. According to Momot et al. (1978), crayfish probably make major sources of energy such as detritus and benthic algae available to higher trophic levels at a faster rate than other consumers within the system. The energy transforming role of crayfish may be significant in terms of conserving energy within this system, i.e., crayfish may play an important role in increasing the ecological efficiency within this area of Lake Michigan. Momot et al. (1978) further suggested that much of the energy within the aquatic food web might be lost if crayfish were not present. It would seem that in the absence of crayfish, much of the energy reserve present in Lake Michigan (e.g., benthic algae) might not be utilized, resulting in a decrease of energy available to higher trophic levels as well as an overall decrease in community productivity and diversity.

Specific effects of crayfish on aquatic ecosystems have been studied by a variety of researchers (e.g., Rickett 1974, Flint and Goldman 1975, Momot et al. 1978, Capelli 1980, Lodge and Lorman 1987). Momot et al. (1978) suggested that crayfish provide stability to an ecosystem since they

are polytrophic and are able to utilize a variety of available food types. Because of this, they are not "using up" any one specific resource. In southwestern Lake Michigan, benthic algae were observed to be a major component of the crayfish diet. However, gut analyses also revealed the presence of additional available food types such as macroinvertebrates and detritus (Tuchman, unpublished data). This "intermediate" utilization of benthic algae may help provide stability to this ecosystem for the same reason Momot et al. (1978) suggested. Furthermore, crayfish may play a role in keeping the algal community in a highly productive state by decreasing interspecific competition within the algal community for limiting factors such as light and nutrients.

Effect of grazing on variability within algal communities

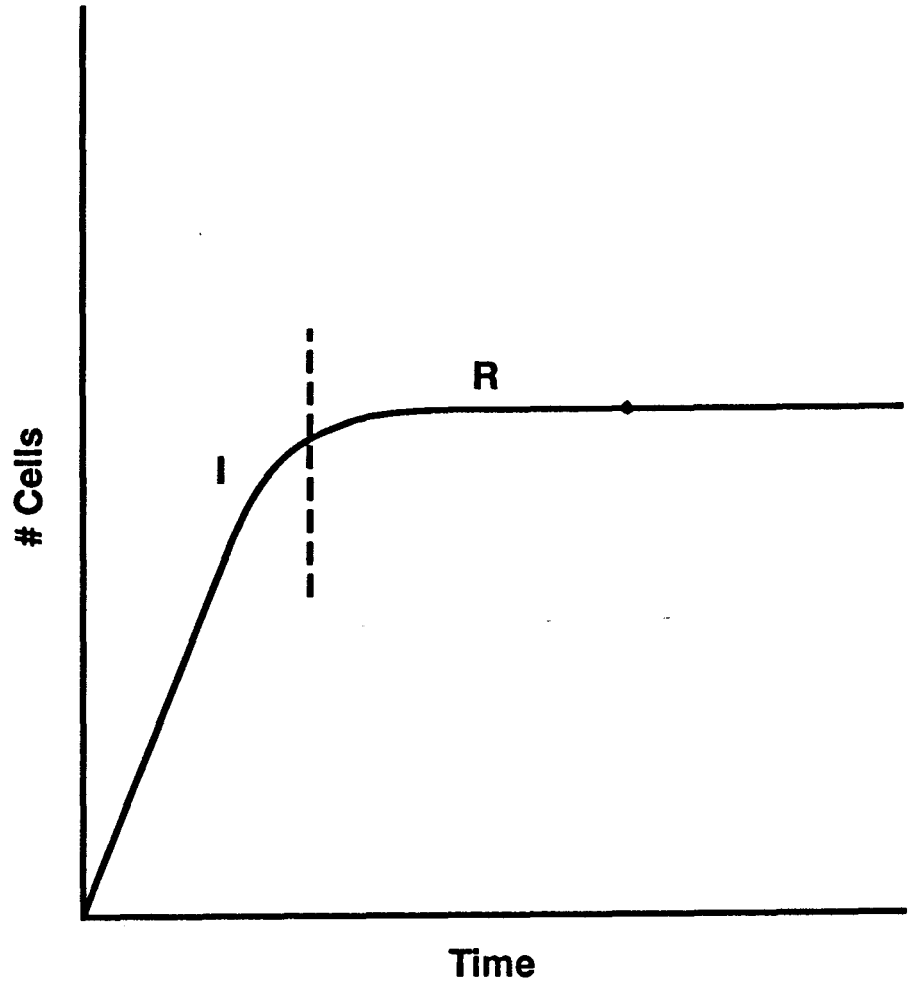
Data collected from individual sampling days were combined for this part of the analysis. Time was considered not to have an effect for the following three reasons:

1. As demonstrated by the control tiles, algal accrual appeared to be at a steady state, as population densities did not substantially change over the course of the experiment. Figure 15 depicts a hypothetical growth curve for benthic algal community development. Early stages of algal accumulation on substrates are characterized by immigration (I) of algal cells; cell numbers increase

Figure 15. Hypothetical growth curve for benthic algal community development (adapted from Stevenson 1984).

I=immigration of algal cells

R=reproduction of algal cells


R
I
Cells
Time

exponentially and immigration is the dominant process. The immigration stage is followed by a reproductive (R) stage where cell reproduction within the well established algal community becomes the dominant process. Immigration is still occurring, but since the community is well established, it's importance is diminished when compared to reproduction of existing cells. Prior to the start of the present experiment, exponential accumulation due to immigration and steady state population densities had already been established during the 30 day colonization period. Therefore, reproduction and death of algal cells maintained the densities of the populations at a steady state throughout the duration of the 26 day experiment. Since population densities in the control remained unchanged over time, time was not considered to be a variable, and samples collected on different dates were therefore treated as replicates.

2. Since the tiles were distributed over the entire bottom surface of the treatment tanks, the crayfish may not have visited every tile equally. Although in the original hypothesis it was assumed all tiles would be grazed equally, observations of crayfish feeding behavior throughout the experiment revealed that the tiles located nearest the crayfish rock shelters were regularly grazed whereas the more distant tiles were seldom, if ever, grazed by the crayfish. Therefore, it cannot be assumed that an increase

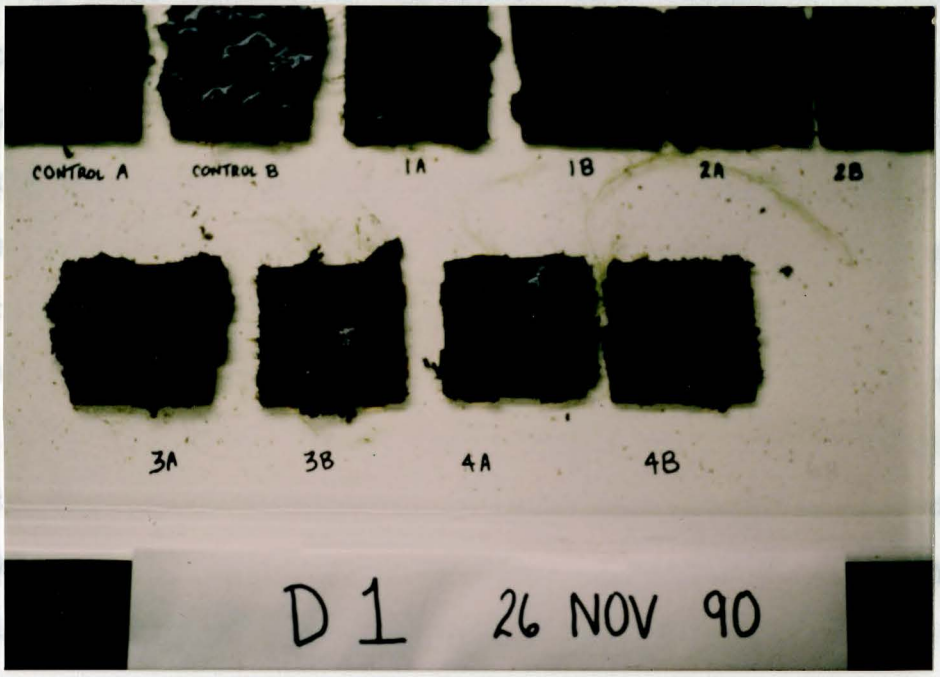
in crayfish numbers created a situation of increased grazing intensity on all tiles since all tiles may not have been visited equally by the crayfish. In one study, foraging crayfish wandered randomly around the tank, ingesting food as it was encountered; there was no evidence of direct searches for food (Capelli 1975). In the present study each crayfish had its own rock with algae tiles scattered about the rock. Day and night observations made throughout this experiment revealed that crayfish spent much of the time under rocks. Foraging crayfish appeared to venture only far enough from their rocks to encounter an algae tile to feed; crayfish were rarely observed at a distance greater than 20 - 25 cm from a rock shelter. Furthermore, a decrease in home range may be inversely related to crayfish densities; i.e., increases in crayfish density may result in a decrease in home range of the individual crayfish. Consequently, algae tiles which were placed farthest from the crayfish rocks might not have been visited by the crayfish (if at all) until the food supplies closer to the crayfish rocks were depleted. The fact that tiles were not visited equally by crayfish would intensify the variability of total algal cell densities found among randomly sampled tiles within a treatment tank. Variability in algal accrual may therefore be attributed to crayfish foraging behavior rather than the length of time the tiles were exposed to crayfish.

3. Crayfish may not necessarily feed consistently on a

24 hour basis; we were not able to determine whether crayfish actually fed every day, or if they were able to eat enough at one time to sustain them for several days. Daily observations (3-4 times throughout each day/night) revealed that crayfish typically remained hidden under rock shelters, or if on open sand, activity was minimal. Crayfish were rarely observed actively grazing.

Grazing resulted in higher levels of variation in total algal cell densities when all sampling days were averaged, analyzed by treatment, and then compared to the control. High levels of variation observed in the grazed treatments may have occurred because of the crayfish foraging behavior described above, and because crayfish are rather unique in their method of "grazing". Observations of crayfish actively involved in feeding revealed that crayfish were able to "grab" long filamentous algae with their pereiopods which sometimes resulted in patches of the algal mat being dislodged from the tile. These dislodged pieces of the algal mat were either completely or partially consumed by the crayfish. Furthermore, visual observations of the tiles collected during sampling (Figure 16) showed that the algal mat on some tiles was very patchy in appearance indicating crayfish had "grazed" or dislodged the algae on these tiles, whereas other tiles were covered with a uniform algal mat suggesting these were ungrazed tiles. Since patches were randomly distributed on tiles and were of all different

Figure 16. Algal tiles collected for sampling on days 1 and 20.


CONTROL A
CONTROL B
1A
1B
2A
2B
3A
3B
4A
4B
D 1 26 NOV 90


CONTROL A
CONTROL B
1A
1B
2A
2B
3A
3B
4A
4B
15 DEC 90 D20

sizes and shapes, numbers of cells from patchy tiles would have very high levels of variation when compared to the control tiles.

Other grazers such as snails generally remove large, overstory species of algae which allow the smaller, understory species of algae to increase in density (Sumner and McIntire 1982, Lamberti et al. 1989, McCormick and Stevenson 1989, Tuchman and Stevenson 1991). Nicotri (1977) found that intertidal limpets consumed proportionately more overstory species of diatoms than understory species of diatoms. The selectivity of overstory algal species by more familiar grazers (snails, limpets) results in a more uniformly grazed algal mat (i.e., these grazers seem to have a "mowing" effect on the algal mat).

Another unique feature of crayfish is that their activity appears to exert a "trampling" effect on the algal mat. Crayfish movement across an algae tile may bring deeper cells closer to the surface or completely dislodge cells from the algal mat (the dislodged cells may then become resuspended in the water column allowing them to immigrate onto other tiles). Observations of tiles partially or completely buried in the sand lend further support to the idea that crayfish activity was substantial. This "trampling" effect may be of importance since crayfish are approximately 1000 times larger than the cells they are consuming. By bringing deeper cells to the surface, or

completely dislodging cells, algal cells are exposed to new levels of resources such as light and nutrients that will likely stimulate the growth of these deeper lying cells.

Effects on primary productivity

The highest intensities of grazing (treatments 3 and 4) resulted in higher rates of chlorophyll *a*-specific primary productivity than was found in the lowest intensity grazing treatments (1 and 2) and the control. One possible explanation for the observed stimulation in chlorophyll *a*-specific primary productivity is that nutrient addition from crayfish waste products has a stimulatory effect on the cells. Furthermore, the patchiness of the algal mat caused by the grazing behavior of the crayfish may have allowed more light and nutrients to reach underlying cells. In this study, nutrients may have been particularly important since nutrient levels were a known limiting factor in the growth of the algal community. The fact that the diatom taxa in general were slightly negatively correlated with the soft algae supports the idea that competition for light and nutrients existed in this experiment. When conditions were suitable for diatom growth, they were less suitable for soft algal growth and vice-versa. Lamberti *et al*. (1989) suggested four explanations for stimulation of primary productivity by snail grazing: 1) removal of dead or senescent cells by consumption or dislodgement by grazers,

2) shifts in algal community composition to more photosynthetically active species, 3) increased light penetration and nutrient diffusion to underlying cells due to grazers creating spaces in the algal mat, 4) addition of nutrients from waste products of grazers. An alternative explanation was presented by Hunter and Russell-Hunter (1983). They found that an algal community disrupted by snail grazing may be dominated by rapidly growing species or grazer resistant species due to increased nitrogen content of the cells (increased nitrogen content presumably resulted from higher growth rates; rapid cell division results in maximum synthesis of new algal protein). Stimulation of primary productivity by grazing has also been demonstrated by several other researchers: crayfish grazing (Flint and Goldman 1975), sea urchin grazing (Paine and Vadas 1969), amphipod grazing (Hargrave 1970), fish grazing (Cooper 1973), snail grazing (Hunter and Russell-Hunter 1983, Lamberti _et al_. 1987).

In all treatments, as well as the control, chlorophyll _a_-specific primary productivity rates decreased slightly up to day 16 and greatly increased on the next two sampling days (day 20 and 25). Since this was a consistent observation in all treatments as well as the control, it seems necessary to understand why this deviation from the overall trend occurred on days 20 and 25. Conditions in the lab where primary productivity was being monitored might

account for these increases. Physical parameters such as external light conditions (sunny versus cloudy days), and air temperature were quite variable in this lab. Because these were not factors that could be controlled, it seemed reasonable to disregard data from these two questionable sampling days for purposes of analysis.

Effect of grazing on standing crop

As expected, high intensity crayfish grazing decreased algal standing crop in this study, however, the lowest intensity crayfish grazing treatment (treatment 1) had slightly higher standing crop than the control. Similar results were observed by Connor et al. (1982) where low levels of mud snail grazing stimulated algal standing stock and high snail densities inhibited algal standing stock. These researchers presented several mechanisms which may explain the stimulation at low grazer densities including feeding-induced changes in the diatom community, nutrient regeneration by the grazers as a means of fertilization, and stirring effects. Furthermore, above a certain grazing density threshold, they hypothesized that overgrazing may override the stimulation due to nutrient regeneration and changes in algal community composition resulting in a decline in algal standing crop.

In the present study, it seems that an overgrazing threshold does exist somewhere between the realized densities of treatment 2 (.0050 crayfish$\cdot cm^{-2}$) and treatment

3 (.0100 crayfish·cm^{-2}). Below this threshold, grazers either had a stimulatory effect on algal biomass (.0015 crayfish·cm^{-2}) or had no effect on algal biomass (.0050 crayfish·cm^{-2}). Above this threshold, overgrazing caused a decline in algal standing crop. Other researchers have found that low density grazing can result in an increase in chlorophyll a (biomass) (gastropod grazing; Jacoby 1985, snail grazing; Kehde and Wilhm 1972). More commonly, researchers have found that grazing in general results in a decrease in algal standing crop (snail grazing; Lein 1980, Sumner and McIntire 1982, Tuchman and Stevenson 1991, caddisfly grazing; Lamberti and Resh 1983, mayfly, snail and caddisfly grazing; Lamberti et al. 1987, intertidal gastropod grazing; Nicotri 1977, tadpole grazing; Dickman 1968).

The last two sampling days (days 20 and 25) had lower standing crop than the first five sampling days. The significantly lower chlorophyll a concentrations in samples from days 20 and 25 correspond to the increases observed in primary productivity on those same two sampling days. Relative to other sampling days, chlorophyll a concentration was lowest on days 20 and 25 in all treatments; yet it appears that the algal communities on these days were more productive. Similarly, Cooper (1973) observed that primary productivity was enhanced due to reductions in algal standing crop and increases in turnover rates of the algal

community. He suggested that a reduction in standing crop by grazing may initiate an increase in turnover rates; it seems that this may be a compensatory mechanism by primary producers in response to low level grazing. In the present study, the observed increase in turnover rate from day 16 to day 20 (in all treatments but the control), is an indication that the remaining algal community is at least somewhat compensating for decreased standing crop by increasing per capita productivity and reproduction. However, it is unlikely that this compensation could account for the dramatic increase in primary productivity observed on day 20 in the control and all treatments. As discussed above, variable physical conditions in the lab where primary productivity was being monitored most likely influenced the results on day 20.

Growth rate data lends further support to the fact that algal population densities in the grazed treatments (except treatment 3 which had a significant negative growth slope) were not changing over time; this lack of change in cell numbers over time may indicate that cells removed by grazing were being replaced by cells generated from increased reproductive capacities of the remaining cells. The algal community which remained on the tiles after grazing compensated for this removal since algal accrual in the grazed treatments did not decline.

Intermediate levels of grazing disturbance increased

total algal community diversity and diatom diversity as predicted by the intermediate disturbance hypothesis of Ward and Stanford (1983). Total algal community diversity tended to be higher in the two mid-intensity grazing treatments than in the control, lowest and highest intensity treatments (treatment 2 > treatment 3 > treatment 4 > control > treatment 1). Grazing at these mid-intensities may be enough disturbance to remove the potentially dominant species of algae, allowing the less dominant species to increase in abundance. For example, Phormidium tenue and Scenedesmus spp. were dominant in the community in all treatments, however, in the intermediate intensity grazing treatments (3 and 4), the relative abundance of these two taxa appeared to be lower than in the control and treatments 1 and 2 allowing other species (i.e., Achnanthes minutissima, Oscillatoria limnetica Lemm.and Lyngbya limnetica Lemm.) to increase in abundance. The number of species (species richness) did not significantly increase in these treatments, however, species richness was greatest in treatment 2. It seems that intermediate levels of grazing kept the dominant species at a level that allowed already existing species to increase in abundance.

The most accessible part of the algal mat to the crayfish was the blue-green filamentous algae and green plankters associated with the canopy. The soft algal community became less similar to the control as parts of it

were removed by the crayfish. Crayfish appeared to remove patches of algae while grazing, with the filaments most easily secured by their pereiopods. However, a patch of the algal mat may not have broken loose every time a crayfish removed filaments, therefore, it is probable that the filaments and algal cells associated with the filaments were more affected by the feeding of the crayfish than the tightly attached cells. The peaks observed in total diatom community density reinforce the idea that as crayfish removed filamentous algae, underlying diatoms were able to increase in abundance. The diatom component of the algal community was more similar to the control throughout the study than was the soft algal component. Furthermore, tiles which visually appeared to be grazed were less similar to the control for soft algae; this was not true for diatoms. This provides support to the idea that crayfish may be consuming/dislodging that part of the algal mat most accessible to them (e.g., the filamentous soft algae). Also, crayfish movement across tiles may dislodge filaments and the cells associated with the filaments. Additional evidence supports this suggestion. When algal growth forms were examined to see if they were differentially affected by grazing, much higher levels of variation were observed in the canopy group (primarily soft algae) than in the adnate group (diatoms). The increasing intensities of crayfish grazing had minimal effect on the adnate group.

Role of nutrient recycling

Although nutrient levels were not monitored in this study, it seems reasonable to assume that nutrients were a limiting factor since all treatment tanks were initially filled with water devoid of nutrients (dechlorinated tap water) and nutrients were not added at any time during the study.

In this study, the control tanks contained tiles with very thick (approximately 4 mm) algal mats; this could have potentially magnified the effect of nutrient limitation at the microhabitat level since in a thick mat, fewer cells are exposed to available nutrients and light than in a thinner algal mat. As benthic algal mats develop, cells at the base of the mat are the first cells to senesce from nutrient and light limitation as well as waste accumulation (Sumner and McIntire 1982).

In the present study, nutrient limitation was most likely a factor in algal productivity since chlorophyll *a* (standing crop) levels were inversely related to primary productivity. Mean primary productivity values were lowest in the control which had no nutrient supplement; mean primary productivity values were progressively higher as crayfish density increased and consequently nutrients from crayfish excretion increased (i.e., control < treatment 1 < treatment 2 < treatment 3 < treatment 4). Connor *et al.* (1982) found that the amount of nitrogen excreted from

snails in low densities was enough to account for the increase in algal production observed in their study. They concluded that at low snail densities, acceleration of nutrient cycling by grazing and excretion stimulated photosynthesis whereas at high snail densities, nutrient cycling was overshadowed by overgrazing and stirring inhibition. Flint and Goldman (1975) found that crayfish feces served as an important source of ammonia, which was then converted to nitrate by heterotrophic activity; this nitrate was therefore, directly available to the periphyton.

Algal cell removal rate and nutrient supply rate may have been directly related in the present study. At every density of crayfish, the removal of algal cells by crayfish was at a rate similar to the rate of growth stimulated by nutrient-rich excretory input. This was further substantiated since standing crop was lower in the high intensity grazing treatments, but primary productivity was increased and community growth remained relatively constant in these treatments. Highest densities of crayfish removed more cells, but also provided higher concentrations of nutrients which allowed remaining cells to have faster rates of replacement.

SUMMARY AND CONCLUSIONS

High levels of variability were observed in the algal population densities of the grazed treatments and were attributed to the unique characteristics of crayfish grazing and foraging behaviors. Crayfish selectively removed canopy forms of algae either directly by securing and ingesting the algae using their pereiopods, or indirectly by walking across an algal tile and dislodging the filaments. Additionally, observations of the tiles throughout the experiment provided evidence that crayfish removed the algae in patches rather than homogeneously. Furthermore, tiles closest to the crayfish rock shelters appeared to be grazed more heavily than distant tiles which may have also contributed to high variability in the algal community among tiles.

Algal standing crop was lowest in the highest intensity grazing treatment, yet chlorophyll a-specific primary productivity was stimulated in these same treatments. Nutrient limitation seemed to be directly related to the productivity of the algal community. Nutrient rich input from crayfish waste products, which increased as crayfish density increased most likely contributed to the increases in mean primary productivity rates. While crayfish removed algae by grazing, they also provided essential nutrients such as ammonia; the importance of the nutrient input was intensified since the water used in this study was nutrient

devoid. Although there were fewer algal cells in the high intensity grazing treatments, the remaining cells were able to maintain a steady-state growth curve (due to crayfish nutrient input) by increasing per capita productivity and reproduction. The existence of an overgrazing threshold (.0050-.0100 crayfish$\cdot cm^{-2}$ algae) in this study is supported by the fact that low intensity grazing had a stimulatory effect on standing crop. Below this threshold, algal standing crop was likely stimulated from increased nutrient levels, however, above this threshold, overgrazing may have caused the decline in algal standing crop.

As predicted by the intermediate disturbance hypothesis, algal community diversity was highest in the intermediate intensity grazing treatments. Intermediate levels of grazing tended to decrease the abundance of dominant taxa allowing less common taxa to increase in abundance.

APPENDIX A

Composite list of the diatom and soft algal species from all samples.

DIATOMS:

Achnanthes lanceolata (Eréb.) Grun.
A. linearis (W. Sm.) Grun.
A. minutissima Kütz
Achnanthes spp.
Achnanthes spp. girdle
Amphora perpusilla (Grun.) Grun.
Amphora spp.
Centrics spp. girdle
Cocconeis disculus (Schum.) Cl.
C. pediculus Ehr.
C. placentula Ehr.
Cocconeis spp.
Cyclotella bodanica Eul.
Cyclotella comensis var. 1 Grun.
Cyclotella comensis var. 2 rough Grun.
Cyclotella comensis var. 2 plain Grun.
Cyclotella glomerulata Bachmann
Cyclotella spp.
Cyclotella spp. girdle
Cymbella microcephala Grun.
Cymbella spp.
Denticula spp.
Diploneis spp.
Diatoma hiemale (Roth) Heib.
Diatoma spp.
Epithemia muelleri Fricke
Epithemia spp.
Eunotia spp.
Fragillaria crotonensis Kitton
F. leptostauren (Ehr.) Hust.
F. pinnata Ehr.
F. vaucheriae (Kütz.) Peters
Gyrosigma attenuatum (Kütz.) Rabh.
Gyrosigma spp.
Melosira islandica O. Mull.
Melosira spp.
Navicula cryptocephala Kütz.
N. exigua Greg. ex Grun.
N. radiosa Kütz.

APPENDIX A (cont'd)

Navicula spp.
Nitzschia fonticola Grun.
N. palea (Kütz.) W. Sm.
N. palea var. debilis (Kütz.) Grun.
N. microcephala Grun.
N. denticula Grun.
N. dissipita (Kütz.) Grun.
N. tryblionella Hantzsch
Nitzschia spp.
Nitzschia spp. girdle
Rhoicosphenia spp.
Rhopalodia spp.
Stephanodiscus alpinus Hust.
Surirella linearis W. Sm.
Surirella spp.
Synedra ulna (Nitz.) Ehr.
Synedra spp.
Tabellaria flocculosa (Roth) Kütz.
Tabellaria spp. girdle

SOFT ALGAE:

Agmenellum quadruplicatum (Menegh.) Bréb.
Anacystis incerta Lemm.
Anacystis montana f. minor Lightf.
Ankistrodesmus falcatus (Corda) Ralfs
Aphanocapsa spp.
Aphanothece clathrata G.S. West
Blue-green ovoids
Blue-green spheres
Chroococcus spp.
Coccoid-ovoids
Coccoid-spheres
Cosmarium spp.
Gomphosphaeria aponina Kuetzing
Lyngbya limnetica Lemm.
Merismopedia elegans A. Braun in Kuetzing
M. punctata Meyen
Microcystis flos-aquae (Wittr.) Kirch.
Microcystis spp.
Monoraphidium contortum (Thuret in Brebisson) Komarkova
Monoaphidium minutum (Nag.) Kom.-Legn.
Oscillatoria limnetica Lemm.
Ovoid-flagellate

APPENDIX A (cont'd)

Phormidium tenue Menegh.
Scenedesmus acuminatus (Lag.) Chodat
S. armatus (Chod.) G.M. Smith
S. bicaudatus (Hansgr.) Chod.
S. ecornis (Ralfs) Chod.
S. quadricauda Chod.
S. spinosus Chod.
Selenastrum gracile Reinsch
Sphere-flagellate
Tetraedron minimum (Eraun) Hansg.

APPENDIX B

Taxa selected for data analyses.

DIATOMS:

Achnanthes linearis
A. minutissima
Amphora perpusilla
Centric spp.
Fragillaria crotonensis and F. pinnata
Navicula cryptocephala, N. exigua and Navicula spp.
Navicula radiosa
Nitzschia dissipita and N. microcephala
N. fonticola
N. palea
Nitzschia spp. and Nitzschia spp. girdle
Synedra spp. and S. ulna

SOFT ALGAE:

Blue-green ovoids, Blue-green spheres and Chroococcus spp.
Coccoid-ovoids and Coccoid-spheres
Lyngbya limnetica and Oscillatoria limnetica
Phormidium tenue
Scenedesmus acuminatus, S. armatus, S. ecornis, S. quadricauda, and S. spinosus

APPENDIX C

CANOPY GROWTH FORMS:

Lyngbya limnetica and Oscillatoria limnetica
Phormidium tenue
Scenedesmus spp.

ADNATE GROWTH FORMS:

Achnanthes linearis
A. minutissima
Amphora perpusilla

LITERATURE CITED

Abrant, R.J. 1988. Feeding periodicity of yellow perch, Perca flavescens (Mitchill), in southwestern Lake Michigan. Master's thesis, Loyola University of Chicago. Chicago, Illinois. 28 pp.

APHA. 1985. Standard Methods for the Examination of Water and Wastewater. 16th ed. American Public Health Association. 1268 pp.

Bold, H.C. and M.J. Wynne. 1985. Introduction to the algae: structure and reproduction. Second Edition. Prentice-Hall, Inc., Englewood Cliffs, NJ 07632.

Brown, P.B., P. Tazik, M.L. Hooe and W.G. Blythe. 1990. Consumption and apparent dry matter digestibility of aquatic macrophytes by male and female crayfish (Orconectes virilis). Aquaculture 89: 55-64.

Budd, T.W. and J.C. Lewis. 1977. Filter feeding in crayfish. American Zoologist 17(4): 921.

Capelli, G.M. 1975. Distribution, life history, and ecology of crayfish in northern Wisconsin, with emphasis on Orconectes propinquus (Girard). Ph.D. Dissertation, University of Wisconsin. Madison, Wisconsin. 215 pp.

Capelli, G.M. 1980. Seasonal variation in the food habits of the crayfish Orconectes propinquus (Girard) in Trout Lake, Vilas County, Wisconsin, U.S.A. (Decapoda, Astacidea, Cambaridae). Crustaceana 38(1): 82-86.

Castenholz, R.W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42(4): 783-794.

Caughley, G. and J.H. Lawton. 1981. Theoretical Ecology: Principles and Applications. (Chapter 7). Second Edition. Sinauer Associates, Sunderland, MA 468 pp.

Chidester, F.E. 1908. Note on the daily life and food of Cambarus b. bartoni. American Midland Naturalist 42: 710-716.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Connor, M.S., J.M. Teal, and I. Valiela. 1982. The effect of feeding by mud snails, Ilyanassa obsoleta (Say), on the structure and metabolism of a laboratory benthic algal community. J. Exp. Mar. Biol. Ecol. 65: 29-45.

Cooper, D.C. 1973. Enhancement of net primary productivity by herbivore grazing in aquatic laboratory microcosms. Limnology and Oceanography 18: 31-37.

Cuker, B.E. 1983. Grazing and nutrient interaction in controlling the activity and composition of the epilithic algal community of an arctic lake. Limnology and Oceanography 28: 133-141.

Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49(6): 1188-1190.

Flint, R.W. and C.R. Goldman. 1975. The effects of a benthic grazer on the primary productivity of the littoral zone of Lake Tahoe. Limnology and Oceanography 20(6): 935-944.

Goldman C.R. and A.J. Horne. 1983. Limnology. McGraw-Hill, Inc., New York. 464 pp.

Hale, R.L. 1992. MYSTAT Statistical Applications, DOS Edition. Course Technology, Inc., Portions copyright 1990 SYSTAT, Inc.

Hanson, J.M., P.A. Chambers and E.E. Prepas. 1990. Selective foraging by the crayfish Orconectes virilis and its impact on macroinvertebrates. Freshwater Biology 24: 69-80.

Hargrave, B.T. 1970. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnology and Oceanography 15: 21-30.

Hart, D.D. 1985. Grazing insects mediate algal interactions in a stream benthic community. Oikos 44: 40-46.

Hill, W.R. and A.W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24: 125-132.

Hoagland, K.D., S.C. Roemer, and J.R. Rosowski. 1982. Colonization and community structure of two periphyton assemblages, with emphasis on the diatoms (Bacillariophyceae). American Journal of Botany 69(2): 186-213.

Hudon, C. and E. Bourget. 1981. Initial colonization of artificial substrate: community development and structure studied by scanning electron microscopy. Canadian Journal of Fisheries and Aquatic Sciences 38: 1371-1384.

Hunter, R.D. and W.D. Russell-Hunter. 1983. Bioenergetic and community changes in intertidal aufwuchs grazed by Littorina littorea. Ecology 64(4): 761-769.

Jacoby, J.M. 1985. Grazing effects on periphyton by Theodoxus fluviatilis (Gastropoda) in a lowland stream. Journal of Freshwater Ecology 3(2): 265-274.

James, D.E. 1978. Culturing Algae. Carolina Biological Supply Co., Burlington, North Carolina. 23pp.

Janssen, J. and J. Quinn. 1985. Biota of the naturally rocky area of southwestern Lake Michigan with emphasis on potential fish prey. Artificial Reefs. Marine and Freshwater Applications: 431-442.

Kehde, P.M. and J.L. Wilhm. 1972. The effects of grazing by snails on community structure of periphyton in laboratory streams. The American Midland Naturalist 87(1): 8-23.

Lamberti, G.A. and V.H. Resh. 1983. Stream periphyton and insect herbivores: An experimental study of grazing by a caddisfly population. Ecology 64(5): 1124-1135.

Lamberti, G.A., L.R. Ashkenas, S.V. Gregory, and A.D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society 6(2): 92-104.

Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, A.D. Steinman, and C.D. McIntire. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70(6): 1840-1856.

Lein, T.E. 1980. The effects of Littorina littorea L. (Gastropoda) grazing on littoral green algae in the inner oslofjord, Norway, Sarsia 65(2): 87-92.

Lesht, B.M. and D.C. Rockwell. 1987. The state of the middle great lakes: results of the 1984 water quality survey of lakes Erie, Huron, and Michigan. Pub. No. ANL/ER-87-1. Argonne National Laboratory, Argonne IL 60439 141 pp.

Lodge, D.M. and J.G. Lorman. 1987. Reductions in submerged macrophyte biomass and species richness by the crayfish Orconectes rusticus. Canadian Journal of Fisheries and Aquatic Sciences 44: 591-597.

Lorman, J.G. and J.J. Magnuson. 1978. The role of crayfishes in aquatic ecosystems. Fisheries 3(6):8-19.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. The American Midland Naturalist 112(983): 23-39.

Ludwig, J.A. and J.F. Reynolds. 1988. Statistical Ecology. John Wiley and Sons. New York. 337 pp.

MacLulich, J.H. 1986. Colonization of bare rock surfaces by microflora in a rocky intertidal habitat. Mar. Ecol. Prog. Ser. 32: 91-96.

McCormick, P.V. and R. J. Stevenson. 1989. Effects of snail grazing on benthic algal community structure in different nutrient environments. Journal of the North American Benthological Society 8(2): 162-172.

McDonald, M.E. 1985. Growth of a grazing phytoplanktivorous fish and growth enhancement of the grazed alga. Oecologia (Berlin) 67: 132-136.

Momot, W.T. 1967. Population dynamics and productivity of the crayfish, Orconectes virilis in a marl lake. The American Midland Naturalist 78(1): 55-81.

Momot, W.T., H. Gowing, and P.D. Jones. 1978. The dynamics of crayfish and their role in ecosystems. The American Midland Naturalist 99(1): 10-35.

Mozley, S.C. and R.P. Howmiller. 1977. Environmental Status of the Lake Michigan Region. Volume 6. Zoobenthos of Lake Michigan. Argonne National Laboratory Report Series ANL/ES-40. Argonne, IL 60439 148 pp.

Mulholland, P.J., J.D. Newbold, J.W. Elwood, and C.L. Hom. 1983. The effect of grazing intensity on phosphorus spiralling in autotrophic streams. Oecologia (Berlin) 53: 358-366.

Mulholland, P.J., A.D. Steinman, A.V. Palumbo, J.W. Elwood and D.B. Kirschtel. 1991. Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. Ecology 72(3): 966-982.

Murray, S.N. and M.M. Littler. 1978. Patterns of algal succession in a perturbated marine intertidal community. Journal of Phycology 14: 506-512.

Nicol, J.A.C. 1960. The Biology of Marine Animals. Pitman, London.

Nicotri, M.E. 1977. Grazing effects of four marine intertidal herbiovores on the microflora. Ecology 58: 1020-1032.

Norby, R.D. and C. Collinson. 1977. A preliminary evaluation of Lake Michigan "reefs" in Illinois as potential breeding sites for indigenous fish species. Illinois State Geological Survey.

Norton, E.M. 1942. The food of the crayfish of Reelfoot Lake. Rept. of the Reelfoot Lake Biol. Sta. 6: 51-54. (As cited by Momot, W.T. 1967. Population dynamics and productivity of the crayfish, Orconectes virilis in a marl lake. The American Midland Naturalist 78: 55-81.)

Odum, E.P. 1983. Basic Ecology. Saunders College Publishing. Philadelphia. 613pp.

Paine, R.T. and R.L. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnology and Oceanography 14: 710-719.

Pennak, R.W. 1989. Fresh-Water Invertebrates of the United States Protozoa to Mollusca. Third Edition. John Wiley & Sons. 769 pp.

Peterson, C.G. 1987. Gut passage and insect grazer selectivity of lotic diatoms. Freshwater Biology 18: 455-460.

Pielou, E.C. 1984. The Interpretation of Ecological Data: A Primer on Classification and Ordination. Wiley and Sons. New York. 263pp.

Pomeroy, L.R., Matthews, H.M. and Min, H.S. 1963. Excretion of phosphate and soluble organic phosphorus compounds by zooplankton. Limnology and Oceanography 8: 50-55.

Porter, K.G. 1977. The plant-animal interface in freshwater ecosystems. American Scientist 65: 159-170.

Power, M.E., A.J. Stewart and W.J. Matthews. 1988. Grazer control of algae in an Ozark Mountain stream: Effects of short-term exclusion. Ecology 69(6): 1894-1898.

Prins, R. 1968. Comparative ecology of the crayfishes Orconectes rusticus rusticus and Cambarus tenebrosus in Doe Run, Meade County, Kentucky. Int. Rev. Gesamten. Hydrobiol. 53(5): 667-714.

Quinn, J.P. and J. Janssen. 1989. Crayfish competition in Southwestern Lake Michigan: A predator mediated bottleneck. Journal of Freshwater Ecology: 5(1): 75-85.

Rickett, J.D. 1974. Trophic relationships involving crayfish of the genus Orconectes in experimental ponds. The Progressive Fish Culturist 36(4): 207-211.

Robinson, C.T. and S.R. Rushforth. 1987. Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. Hydrobiologia 154: 49-59.

SAS Institute, Inc. 1990. SAS/STAT user's guide. Fourth Edition. SAS Institute Inc., Cary, North Carolina.

Schaefer, W.F. 1973. A study of the growth patterns, food habits and seasonal depth distribution of the yellow perch, Perca flavescens, in southwestern Lake Michigan. Master's thesis, University of Wisconsin. Milwaukee, WI 55pp.

Smith, E.P., R.B. Genter and J. Cairns, Jr. 1986. Confidence intervals for the similarity between algal communities. Hydrobiologia. 1139: 237-245.

Steinman, A.D., C.D. McIntire, S.V. Gregory, G.A. Lamberti, L.R. Ashkenas. 1987. Effects of herbivory type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. Journal of the North American Benthological Society 6(3): 175-188.

Sterner, R. 1986. Herbivores' direct role and indirect effects on algal populations. Science 231: 605-607.

Stevenson, R.J. 1984. Mathematical model of epilithic diatom accumulation. 8th Diatom Symposium. pp. 323-335.

Sumner, W.T. and C.D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. Arch. Hydrobiol. 93: 135-157.

Tuchman, N.C. 1988. Effects of different intensities and frequencies of disturbance by snail herbivory on periphyton succession. Doctoral dissertation. University of Louisville, Louisville, Kentucky. 220 pp.

Tuchman, N.C. and R.J. Stevenson. 1991. Effects of selective grazing by snails on benthic algal succession. Journal of the North American Benthological Society 10(4): 430-443.

U.S. Environmental Protection Agency. 1989. Instructions for chlorophyll - spectrophotometric quality control samples. U.S.E.P.A. Environmental Monitoring Systems Laboratory, Cincinnati, Ohio.

Vandermeer, J. 1981. Elementary mathematical ecology. John Wiley & Sons, Inc., New York. 294 pp.

Ward, J.V. and J.A. Stanford. 1983. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. In: T.D. Fontaine III and S.M. Bartell (eds), Dynamics of lotic ecosystems. Ann Arbor Science press. pp. 347-356.

Wetzel, R.G. 1983. Limnology. Second Edition. Saunders College Publishing. Philadelphia. 767 pp.

Yasuno, M., Y. Sugaya and T. Iwakuma. 1985. Effects of insecticides on the benthic community in a model stream. Environmental Pollution (Series A) 38: 31-43.

Zar, J.H. 1984. Biostatistical Analysis. Second Edition. Prentice-Hall, Inc., Englewood Cliffs, NJ 07632. 718 pp.

VITA

The author, Kristi A. Zenchak, was born October 14, 1959 in Chicago, Illinois. She is the daughter of Edward and Beverly Anderson.

In 1981 she received a Bachelor of Arts degree with a Biology major from North Central College. She taught High School Biology from 1982 to 1989 in the Chicago Archdiocesan School System. In September 1989 she was awarded an assistantship in the Department of Biology at Loyola University of Chicago. The completion of a Master of Science degree is anticipated in January 1993.

APPROVAL SHEET

The thesis submitted by Kristi A. Zenchak has been read and approved by the following committee:

Dr. Nancy C. Tuchman, Director
Assistant Professor, Biology, Loyola University

Dr. Robert Hamilton
Professor, Biology, Loyola University

Dr. John Janssen
Professor, Biology, Loyola University

The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Masters of Science.

26 Aug 92
Date

Nancy C. Tuchman
Director's Signature