To the Graduate Council:

I am submitting herewith a thesis written by Carole Louise Hom entitled "The Effect of Grazing by the Snail, Goniobasis clavaeformis Lea, on Aufwuchs in Artificial Streams." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

T.G. Hallam, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

THE EFFECT OF GRAZING BY THE SNAIL, *GONIOBASIS CLAVAEFORMIS* LEA ON AUFWUCHS IN ARTIFICIAL STREAMS

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Carole Louise Hom

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DEDICATION

To my mom and daddy.

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ABSTRACT

The effects of grazing by snails on the biomass, primary productivity, chlorophyll *a* concentration, and species composition of aufwuchs were studied in once-through artificial stream channels. The snail, *Goniobasis clavaeformis* Lea, was stocked in three channels at densities of 1.4, 2.8, and 5.6 g AFDM $\cdot$ m^{-2} and a fourth channel was left ungrazed. These densities span the range of snail densities encountered in streams in the vicinity. Allochthonous detritus and other macroconsumers were excluded from the experimental system.

Over the six week experiment, grazing reduced aufwuchs biomass, chlorophyll *a* standing stock, and primary productivity per unit area and per unit chlorophyll. Chlorophyll *a* concentrations (µg chlorophyll *a* $\cdot$ mg $AFDM^{-1}$) however, tended to be higher in the grazed systems than in the ungrazed channel in the last 3 weeks of the experiment, indicating that grazing may have caused a change in the species composition of the aufwuchs community. This was supported by a decrease in the proportion of large diatoms observed in samples from the ungrazed system with a corresponding increase in the relative numbers of small diatoms. A similar change in the community composition of the grazed treatments was not observed.

Primary productivity per unit biomass was higher in the ungrazed treatment than in the grazed treatments throughout the experiment, although biomass-specific productivity actually increased relative to its initial value at the low grazing pressure. This suggests that the potential for grazer stimulation of aufwuch activity exists.

Analytical studies of a five-compartment non-linear aufwuchs-grazer stream model supplemented the empirical work. These studies imply that the stability of stream systems is determined by the growth rates of aufwuchs and fine particulate organic matter. This result, however, may be an artifact of 1) the inclusion of dissolved inorganic and organic carbon within a single compartment and 2) the lack of consideration of advection and diffusion effects. Additional modeling and experimental investigation are suggested in order to better clarify the role of grazers in stream systems.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

1. Literature Review

The role of grazers in maintaining floral communities has been well documented in a variety of ecosystems. Grazer influences include stimulating productivity through the secretion of growth factors (e.g., Dyer and Bokhari 1976), by removing senescent cells to leave room for further reproduction (e.g. Hargrave 1970, Cooper 1973, Flint and Goldman 1975) and by adding nutrients to the system via excreta (see Batzli 1978, Kitchell et al. 1979 for reviews). Grazers may also alter species diversity through selective removal of ecological dominants (e.g. Castenholz 1961, Paine and Vadas 1969) or non-selective clearing of substrate that results in opening potential colonization sites for opportunistic species (Lubchenco 1978).

In stream systems, the importance of grazing effects is unresolved. Interactions between stream consumers and their resources have been intensively investigated in recent years (Cummins 1974, Stockner and Shortreed 1977, Newbold et al. 1981, 1982a, 1982b, Elwood et al. 1981). Most of these studies have been conducted in heterotrophic systems and hence, have focused on the influence of benthic invertebrates on the decomposition of allochthonous detritus. Herbivore-primary producer interactions remain relatively unstudied in comparison.

Grazing processes in streams are of interest for two reasons. First, stream systems are strongly influenced by transport. Both the biota and the products of biotic activity tend to wash downstream at

potentially different rates (e.g. slowly for benthos, more rapidly for dissolved nutrients) that may be independent of the dynamics of the original community. As a result, trophic interactions in downstream reaches may be sensitive to the effects of grazing in upstream reaches, whereas most resource-consumer models, both conceptual and mathematical (cf. Caughley 1976), assume no spatial interdependency. Such models do not adequately describe stream structure and function. Further theoretical development is needed to reexamine the conclusions drawn from these models and to test their robustness to changes in spatial effects. Secondly, the low contribution of autochthonous primary production to the energy budget of many streams (e.g. Teal 1957, Nelson and Scott, 1962, Minshall 1967, Tilly, 1968, Fisher and Likens 1973) may be partially attributed to grazer reductions of producer standing stock (Elwood and Nelson 1972). In the absence of grazers, autochthonous production might contribute large quantities of algae to the detritus pool. Graders reduce this input and also alter the particle size distribution of stream detritus by reducing relatively large clumps of an algal mat to finely divided fecal pellets. The detritial food chain is thus potentially affected by this change in form and by the energy loss due to low transfer efficiency between trophic levels.

Stream ecologists use the term "grazer" or "scraper" to denote macroinvertebrates with morphological and behavioral adaptations for grazing upon food that adheres to surfaces (Cummins and Klug 1979). This food consists of aufwuchs, i.e., diatoms, green algae, blue-green algae, bacteria, and other microorganisms that attach to inorganic substrates (Ruttner 1964). American authors tend to refer to this

assemblage as "periphyton" rather than aufwuchs. Technically, this implies only the algae, but in practice, includes the heterotrophs as well, since the two cannot easily be separated. In this thesis, "aufwuchs" is used to mean the entire community; "periphyton" shall be reserved for the algal component only.

Stream aufwuchs is often the principal food resource for several species of gastropods, larval insects, and vertebrates (Hynes 1970, Anderson and Cummins 1979, Cummins and Klug 1979). Other organisms may also consume aufwuchs as a dietary supplement. Algal cells, with their low carbon to nitrogen ration (McMahon et al. 1974) are a higher quality food source than detritus derived from woody plant tissues (Ward and Cummins 1979). Detritus of algal origin may therefore have a role in satisfying the nutritional requirements of organisms with detritus-based diets (Hart 1981). Low aufwuchs biomass may be able to support relatively high standing crops of grazers because of the rapid turnover rates of algae in comparison to animals. In fact, a simulation model of periphyton dynamics by McIntire (1973) suggested that aufwuchs biomass of only 5.2 to 19.3 g glucose $\cdot$ m^{-2} was capable of supporting a grazer biomass of 115.4 to 118.9 g glucose $\cdot$ m^{-2}.

There is little experimental evidence with which to compare McIntire's modeling result. Most grazing studies have focused on the effects of grazers on aufwuchs rather than examining both aspects of the question. As a rule, these investigations reported increased aufwuchs productivity at low grazer biomass and decreased aufwuchs productivity at relatively high grazing pressure (Hargrove 1970, Cooper 1973, Flint and Goldman 1975, Pace et al. 1979). Similar trends

were observed for chlorophyll *a* concentration (Pace *et al*. 1979, Hunter 1980). A negative correlation between aufwuchs biomass and grazing pressure was another general result (Beyers 1963, Dickman 1968, 1977, Mason and Bryant 1975, Grechenberger 1975, Smrchek *et al*. 1976, Doremus and Harmann 1977, Eichenberger and Schlatter 1978).

In lacustrine systems, periphyton productivity (mg $C \cdot m^{-2} \cdot h^{-1}$) was shown to be enhanced by amphipod (Hargrave 1970) and crayfish (Flint and Goldman 1975) grazing at natural population densities and reduced by substantially higher grazing pressures. Similar results were obtained by Cooper (1973) with cyprinids in laboratory microcosms. Pace *et al*. (1979) reported higher mean chlorophyll *a* values in epipelic algae subjected to low levels of artificial grazing (wiping with lens tissue) than algae without artificial grazing. Algal primary productivity and chlorophyll *a* concentration were also significantly higher in ungrazed sediments than in sediments grazed by the snail, *Nassarius obsoletus*, at natural densities. These studies are summarized in Table 1.

Both Hargrave (1970), and Flint and Goldman (1975) hypothesized that grazing stimulated primary productivity through the effects of nutrient regeneration and by increasing turnover rate in the aufwuchs. They further suggested that the lower productivity observed at higher grazer densities was due to algal removal exceeding rates of biomass turnover. This was supported by Elwood and Nelson (1972) in an investiation of periphyton production (measured by differences in turnover of phosphorus associated with aufwuchs) and snail grazing rate in a

TABLE 1. Comparison of effects of grazing on aufwuchs productivity (or production), chlorophyll *a* concentration, and biomass in aquatic systems.

SOURCE	EXPERIMENTAL SYSTEM	AUFWUCHS PRODUCTION (UNITS)	AUFWUCHS CHLOROPHYLL *a*	AUFWUCHS BIOMASS
Hargrave 1970	Marion Lake, British Columbia	higher at low grazer densities, ($\mu l\ O_2 \cdot sample^{-1}\ h^{-1}$) lower at high grazer densities	----------	----------
Flint & Goldman 1975	Lake Tahoe, California	higher at low grazer densities, ($mg^{14}\ cm^{-2}\ h^{-1}$) , lower at high grazer densities	----------	----------
Cooper 1973	Static Laboratory Microcosms	higher at low grazer densities, ($g\ O_2\ m^{-2}\ day^{-1}$) , lower at high grazer densities	----------	----------
Pace *et al.* 1979	Salt Marsh Mudflat, Georgia	higher in ungrazed system ($mg^{14}\ C\ m^{-2}\ h^{-1}$)	----------	----------

TABLE 1 (continued)

SOURCE	EXPERIMENTAL SYSTEM	AUFWUCHS PRODUCTION (UNITS)	AUFWUCHS CHLOROPHYLL *a*	AUFWUCHS BIOMASS
Hunter 1980	pond, Michigan	----------	higher in grazed systems	lower in grazed systems
Kehde & Wilhm 1972	recirculating laboratory streams	no effect (g ash-free dry weight.m^{-2}.day^{-1})	higher in grazed systems	no significant effect
	recirculating laboratory streams, mixed effuents	decreased with increasing grazing pressure	----------	----------
Mason & Bryant 1975	*Typha* stems in Alderfen Broad, Great Britain	----------	----------	----------
Dickman 1968	Holly Lake, Quebec	----------	----------	lower in grazed systems
Dickman 1973	stream near Holly Lake, Quebec	----------	----------	----------
Eichenberger & Schlatter 1978	laboratory streams	----------	----------	
Eichenberger 1975	laboratory streams	----------	----------	lower in grazed systems

TABLE 1 (continued)

SOURCE	EXPERIMENTAL SYSTEM	AUFWUCHS PRODUCTION (UNITS)	AUFWUCHS CHLOROPHYLL *a*	AUFWUCH BIOMASS
Byers 1963	laboratory streams	----------	----------	lower in grazed systems
Smrchek *et al.* 1976	laboratory streams	----------	----------	lower in grazed systems
Doremus & Harmann 1977	static laboratory microcosms	----------	----------	decreased with increasing grazer density
Kesler 1981	pond, Rhode Island	----------	----------	lower in grazed systems

small woodland stream. Their results implied that Goniobasis clavaeformis limited periphyton production by reducing the standing crop of aufwuchs.

Cooper concurred in his endorsement of the turnover rate hypothesis but criticized the nutrient regeneration hypothesis. He argued that positive effects of nutrient regeneration on primary productivity should increase with increasing grazing pressure, which implies that biomass turnover rate should be greatest at extremely high grazer densities.

One of the few studies of grazer effects on primary productivity in streams illustrated the dependence of streams upon transport phenomena. Kehde and Wilhm (1972) found that net primary productivity (g ash-free dry mass $\cdot$ m^{-2} $\cdot$ day^{-1}) in recirculating laboratory streams was not affected by Physa gyrina grazing at densities of 0.012 snails $\cdot$ cm^{-1}. They also observed no difference in biomass between grazed and ungrazed systems, but a significant positive correlation between grazing and chlorophyll *a* concentration. Their index of primary productivity, however, was the instantaneous growth rate of aufwuchs obtained from plotting aufwuchs biomass against time (Kevern *et al*. 1968). This technique may be an unreliable estimator of the actual rates of productivity of the system because the rate of change in biomass reflects differences between rates of turnover plus colonization and rates of removal (sloughing plus grazing) rather than production rates (Wetzel 1963). Since the grazing rates used were different and the standing stocks in the grazed and ungrazed systems were the same, the two systems must have exhibited different turnover rates, and hence, different productivities. In addition, aufwuchs

standing crop includes bacteria, fungi, and detritus, as well as periphyton. Inclusion of the heterotrophic and non-living components in biomass determinations would therefore tend to magnify the inaccuracy of these types of productivity estimates.

Alternatingly, sloughing, often a major source of loss of standing crop in mature aufwuchs communities (Kevern et al. 1966, McIntire 1968) may have biased the data. If the rate of sloughing in the ungrazed systems was approximately equal to the rate of aufwuchs removal through grazing in the grazed systems, the average biomass in each system would tend to be the same.

Downstream regeneration of nutrients also may have enhanced periphyton productivity in such a way that the resultant growth compensated for reductions in aufwuchs standing crop. Consequently, no net changes in aufwuchs biomass would have been observed. Furthermore, this effect would have been magnified by the use of recirculating, rather than once-through, streams.

In comparison, an investigation that used four densities of grazers with complete mixing of water between all treatments yielded the opposite result. In this study Kehde and Wilhm (1972) obtained a negative correlation between grazing intensity and rate of change of aufwhchs biomass. Their observations were the result of the direct effects of grazing only, because mixing effluent water between channels caused all treatments to receive the same nutrient levels and eliminated difference in nutrient regeneration from treatment to treatment. This result thus indicates the potential importance of nutrient regeneration to aufwuchs productivity and also emphasizes the role of transport in streams.

The higher concentrations of chlorophyll *a* observed by Kehde and Wilhm in the grazed systems compared to the ungrazed systems raised further questions as to the effects of grazing upon aufwuchs. The increased chlorophyll *a* could have been the result of enrichment via nutrient regeneration by the snails, since similar additions of nutrients to experimental systems have been shown to elevate chlorophyll *a* concentrations in algal cells (Cooke 1967, Fraleigh 1968 , Wilhm and Long 1969, Rhee 1978). Alternatively, the snails could have been preferentially feeding on detritus or on algal species with a lower chlorophyll content. This selective grazing could serve to increase the relative abundance of algae or algal species with a higher chlorophyll concentration, and hence, increase the relative chlorophyll *a* concentrations in grazed aufwuchs compared to that in ungrazed aufwuchs.

Reductions in aufwuchs standing crop appear to be a general consequence of grazing. Mason and Bryant (1975) found that chironomid lavae were capable of almost totally eliminating the epiphytic algae in a eutrophic English lake. Similar results were obtained by Dickman (1968) with frog tadpoles. Furthermore, the decreases in algal biomass observed by Dickman were accompanied by reduction in algal species diversity.

Investigations in laboratory streams have produced similar conclusions. Eichenberger and Schlatter (1978) observed decreased aufwuchs biomass in once-through artificial streams as a result of grazing by herbivorous insects and increased sloughing presumably caused by mechanical damage. Midges similarly affected benthic algae (Eichenberger 1975). Physic and planorbid snails also reduced aufwuchs standing

crop to levels significantly below those of ungrazed systems (Beyers 1963, Smrchek et al. 1976, Doremus and Harmann 1977, Kesler 1981).

Other experimental evidence suggests that snails are capable of qualitative selection among food types. Calow (1973) observed that although satiated snails (Ancylus fluviatilis) prefer red diatoms to green or blue-green algae, and among diatoms, they preferred Gomphonema to Navicula or Achnanthes, these preferences were lost in starved individuals. Dickman (1973) noted that selective grazing by the oligochaete Stylaria lacustris on diatoms resulted in an increase in filamentous green algae. Moore (1977a, 1977b) has also observed selection against filamentous algae, and in addition, against the achnate diatom, Cocconeis, by amphipods and mayflies. Patrick (1970) noted that in the laboratory, the snail Physa heterostropha fed upon most species of diatoms but avoided Cocconeis placentula. Large Cocconeis populations developed and algal diversity of the algal community was greatly reduced.

Similar selectivity in feeding was observed by Kesler (1981) and Hunter (1980). Grazing by pond snails reduced the abundance of diatom species other than C. placentula. Furthermore, the relative abundance of Cocconeis was positively correlated with grazing pressure.

2. Objectives

There is a need for further investigation of the influence of grazers upon the aufwuchs community in streams (see Table 1, p. 5) . An inverse relationship between biomass and grazing is usually observed but several questions regarding grazer influences on aufwuchs productivity remain. Although the evidence is often contradictory, there

appears to be a tendency for grazing to increase aufwuchs productivity and chlorophyll *a* concentration at low grazer density and to decrease productivity at higher grazer density if the rate of cell removal exceeds the rate of algal turnover. The mechanism by which this may occur, however, is unclear. Several factors, including removal of senescent cells, nutrient regeneration, and changes in aufwuchs community structure as a result of selective grazing, may contribute. Since the majority of aufwuchs-grazer studies examined only one aspect of grazing effects (e.g. aufwuchs productivity or aufwuchs species composition), differentiation between these factors has not been possible. Furthermore, although one study (Kehde and Wilhm 1972) did consider grazer influences upon aufwuchs primary productivity, chlorophyll *a* , and biomass, their results are not definitive because of nutrient regeneration arising from the use of recirculation of stream water between treatments.

My objectives were:

1. simultaneous examination of the effects of grazing on aufwuchs productivity, pigment content, biomass, and species composition to elucidate the changes in these parameters attributible to grazing and the mechanisms by which these changes are produced.
2. construction and analysis of a general model of an aufwuchs-grazer systems to supplement the empirical work.

To avoid experimental bias, this research was done in laboratory stream systems. Their usefulness in ecological research has been demonstrated in numerous investigations (*inter al*. McIntire et al. 1964,

McIntire and Phinney 1965, McIntire 1966a, 1966b, Pfieffer and McDiffett 1975, Stockner and Shortreed 1976. See also Warren and Davis 1971 for a review). Artificial streams increase control of environmental variables, allow specification of system boundaries, and permit replication with ease that can rarely be equalled in the field. It is important, however, to relate investigations conducted in laboratory systems to the real world. Failure to do so may result in the aquisition of a wealth of information on the ecology of microcosms and artificial systems without a simultaneous increase in the understanding of natural systems.

Any researcher who studies primary productivity in streams must confront the methodological problems imposed by the nature of lotic systems. Streams are characterized by logitudinal transport and current, and they tend to be turbulent and spatially and temporally heterogeneous. Because of these features, open stream techniques that use changes in dissolved oxygen concentration, PG , biomass accural, or chlorophyll concentration do not yield reliable estimates of primary production rates.

Techniques that use ^{14}C-assimilation as an indicator of productivity are widely used and accepted in marine and lacustrine systems but have been infrequently used in streams. The standard incubation in closed bottles (Steeman-Nielsen 1952, 1963) may also yield inaccurate estimates of primary productivity due to the elimination of current flow (Whitford and Schumacher 1961, Blum 1963, Whitford 1960, Whitford and Schumacher 1961, 1964, McIntire 1966a, 1968, Rodgers and Harvey 1976, Horner and Welch 1981). Incubation of aufwuchs within a closed, recirculating photosynthesis-respiration chamber (Hansmann et al. 1971,

Thomas and O'Connell 1971, McIntire 1974, Pfeiffer and McDiffett 1975, Rodgers and Harvey 1976, Rodgers et al. 1978, Bott et al. 1978) reduces this source of error.

In this thesis, the terms "primary productivity" and "primary production rate" are used interchangably to denote carbon fixed per unit area per unit time. "Biomass-specific productivity" and "chlorophyll-specific productivity" denote carbon fixed per unit weight per unit time and carbon fixed per unit chlorophyll per unit time, respectively.

CHAPTER II

A MODEL OF A GRAZER-AUFWUCHS SYSTEM

I. Model Development

Unlike other functional components of stream ecosystems, few models of a grazer-aufwuchs subsystem have been developed. The general stream spiralling models (O'Neill et al. 1979, Newbold et al. 1982) do not specifically address the question of grazer effects upon the aufwuchs, whereas the botanically synoptic models of McIntire and his coworkers (McIntire 1973, McIntire et al. 1975, McIntire and Colby 1978) stress light and temperature effects but place less emphasis upon nutrient availability and grazing pressure. Consequently, neither type of model was deemed appropriate for the problems considered in this investiation.

A number of models have been developed for planktonic systems which include formulations that account for diffusion, advection, light and nutrient availability, sinking, and grazing pressure. Most of these models predict of changes in nutrient concentration and predator population size through time as well as changes in producer population size (see Patten 1968 for a review of the older literature; Wroblewski and O'Brien 1976; see also Hallam 1977, 1978). Models of this general form have been used as the basis for the general aufwuchs-grazer model developed here.

The model consists of a system of non-linear partial differential equations that describe the carbon dynamics within a simplified grazer-aufwuchs community. To make the model tractable, other functional groups and the associated biological processes are not considered here.

The model also does not incorporate the effects of exogenous physical phenomena, e.g. groundwater seepage or lateral inflows, and ignores changes in the form of inorganic carbon.

The grazer-aufwuchs system is divided into five compartments: 1) dissolved carbon (both organic and inorganic) in the water (C) ; 2) suspended particulates, i.e. seston (S) ; 3) attached particulates on the substrate, i.e. aufwuchs (A) ; 4) grazers (G) , and 5) unattached particulates on the substrate, i.e. fine particulate organic matter (F) .

The model can first be developed by considering a simple stream model, i.e. a system without aufwuchs or grazers. Carbon flux in such a system is dependent upon transport and the biological processes associated with fine particulate organic matter. These particulates take up dissolved organic carbon from the water for maintainance and growth, as, for example, in bacterial oxidation of glucose for respiration and biosynthesis. Some of this carbon is respired or excreted to the water at a later time while another fraction may be suspended in the water column and transported downstream in particulate form. If we assume the stream is a uniform cylinder, that water velocity is constant throughout, and that exchange with the atmosphere is at equilibrium, then this system can be modeled as

$$A\frac{\partial c}{\partial t} = AD\frac{\partial^2 C}{\partial x^2} + A\frac{v\partial C}{\partial x} + h_6 + h_7$$

$$\frac{\partial S}{\partial t} = AD\frac{\partial^2 S}{\partial x^2} + A\frac{v\partial S}{\partial x} + h_4 - h_5 \qquad (1.1a)$$

$$\frac{\partial f}{\partial t} = -h_4 + h_5 - h_6 + h_3$$

where A represents the cross-sectional area of the stream, D represents diffusivity, v represents the velocity of water, and w (used below) represents the width of the stream.

The first and second partial derivatives in the first two equations represent advective and diffusive forces in the transporting compartments. The other terms in the model are functions, h_i, that represent carbon fluxes between compartments (Table 2, Figure 1). Biologically reasonable values for the parameters are given in Table 3.

The release of dissolved organic carbon from fine particulates, is assumed to be a linear function of fine particulate organic water biomass:

$$h_6 = wa_6F$$

where a_6 is a positive constant. This is a gross oversimplication of carbon excretion and respiration but it is probably a reasonable approximation for our scale of analysis.

A generalized Michaelis-Menten term, h_7, is used to describe uptake of dissolved carbon by fine particulates:

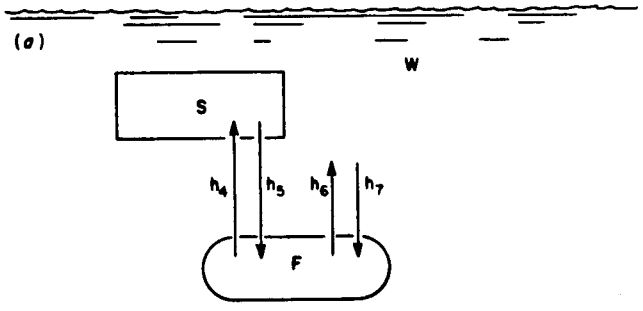
$$h_7 = \frac{wa_7 CF}{(1 + \ell_C C)(1 + \ell_F F)}$$

where a_7, ℓ_c, ℓ_F are positive constants. The form of the denominator here places a limitation on uptake by either dissolved carbon or FPOM. For example, when C is small relative to F, h_7 will become very small also. When C is large relative to F, however, its importance in determining the behavior of h_7 diminishes and the magnitude of h_7 will be governed by F.

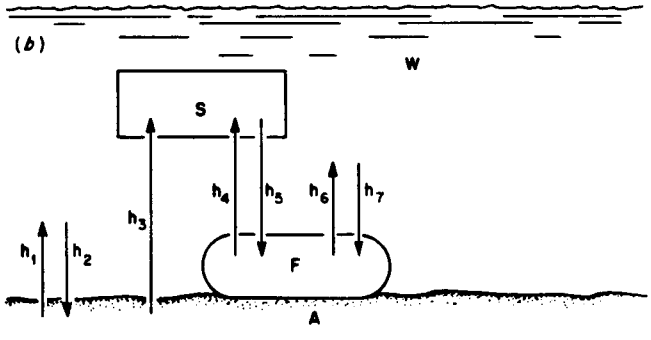
TABLE 2

Functions used in the aufwuchs-grazer model

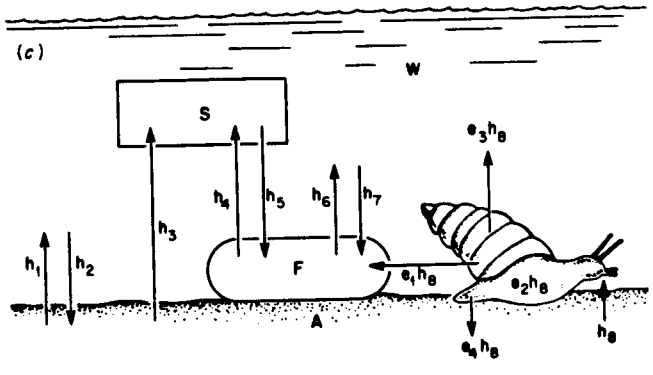
FUNCTION	BIOLOGICAL INTERPRETATION
$h_1 = wa_1A$	aufwuchs respiration
$h_2 = \frac{wa_2 CA}{(1 + k_c C)(1 + k_A A)}$	aufwuchs uptake of dissolved carbon
$h_3 = wa_3A^2$	aufwuchs sloughing
$h_4 = wa_4F$	fine particulates suspension
$h_5 = wa_5S$	seston settling
$h_6 = wa_6F$	fine particulates respriation
$h_7 = \frac{wa_7 CF}{(1 + \ell_C C)(1 + \ell_A A)}$	fine particulates uptake of dissolved organic carbon
$h_8 = \frac{w b_1 GA}{(1 + m_G G)(1 + m_A A)}$	snail grazing
$h_9 = w(b_2 + b_3 G)G$	snail mortality



a. the water-seston-fine particulates system



b. the water-seston-aufwuchs-fine particulates system



c. the water-seston aufwuchs-grazer-fine particulates system

FIGURE 1

Diagrammatic representation of stream models

TABLE 3

State variables and constants used in the aufwuchs-grazer model

TERM	DEFINITION	UNITS	VALUE	SOURCE
C	water	$g \cdot m^{-3}$	----------	----------
S	seston	$g \cdot m^{-3}$	----------	----------
A	aufwuchs	$g \cdot m^{-2}$	----------	----------
G	grazers	$g \cdot m^{-2}$	----------	----------
F	fine particulates	$g \cdot m^{-2}$	----------	----------
D	diffusion constant	$m^2 - sec^{-1}$	0.1	----------
w	stream width	m	0.25	obtained from this experiment
d	stream depth	m	0.07	obtained from this experiment
A	cross-sectional area of stream	m^2	0.019	obtained from this experiment
v	current velocity	$m \cdot sec^{-1}$	0.035	measured in this experiment
a_1	aufwuchs respiration rate	sec^{-1}	0.43×10^{-6}	McIntire 1973
a_2	aufwuchs uptake rate	$m^3 \cdot g^{-1}$ sec^{-1}	7.17×10^{-6}	McIntire 1973
a_3	aufwuchs sloughing rate	$m^2 \cdot g^{-1}$ sec^{-1}	2.3×10^{-6}	Newbold, pers. comm.

TABLE 3 (CONTINUED)

TERM	DEFINITION	UNITS	VALUE	SOURCE
a_4	fine particulates suspension rate	sec^{-1}	2.5×10^{-6}	Newbold et al. 1982a
a_5	seston settling rate	sec^{-1}	1.0×10^{-3}	Newbold et al. 1982a
a_6	fine particulate respiration rate	sec^{-1}	0.2×10^{-6}	Newbold et al. 1982a
a_7	time particulate uptake rate	$m^3 \cdot g^{-1} \cdot sec^{-1}$	1.0×10^{-7}	Newbold, pers. comm.
k_C	limitation on aufwuchs uptake by water	$m^3 \cdot g^{-1}$	3.2	McIntire 1973
k_A	limitation on aufwuchs uptake by aufwuchs	$m^2 \cdot g^{-1}$	0.25	McIntire 1973
ℓ_C	limitation on fine particulates uptake by water	$m^2 \cdot g^{-1} \cdot sec^{-1}$	0.25	Newbold, pers. comm.
ℓ_F	limitation on fine particulates uptake by fine particulates	$m^2 \cdot g^{-1} \cdot sec^{-1}$	1.0×10^{-6}	Newbold, pers. comm.
b_1	snail grazing rate	$m^2 \cdot g^{-1} \cdot sec^{-1}$	1.0×10^{-6}	Newbold, pers. comm.
b_2	density independent snail mortality rate	sec^{-1}	3×10^{-8}	Newbold, pers. comm.

TABLE 3 (CONTINUED)

TERM	DEFINITION	UNITS	VALUE	SOURCE
b_3	density dependent snail by mortality rate	$m^2 \cdot g^{-1} \cdot sec^{-1}$	3×10^{-9}	Newbold, pers. comm.
M_G	limitation on snail grazing by snail	$g \cdot m^{-2}$	0	Newbold, pers. comm.
M_A	limitation on snail grazing by aufwuchs	$g \cdot m^{-2}$	2×10^{-6}	Newbold, pers. comm.
e_1	defecated fraction by snail	----------	0.40	Kofoed 1975
e_2	fraction allocated to snail growth	----------	0.20	Kafoed 1975
e_3	fraction excreted by snail	----------	0.30	Kofoed 1975
e_4	fraction deposited as mucus	----------	0.10	Kofeod 1975, Denny 1980

The movement of stationary particulates from the stream bottom to the seston compartment, h_4, and the settling of seston back to the bottom, h_5, are assumed to be linear functions of the standing stock of fine particulates and seston concentration respectively:

$$h_4 = wa_4F$$

$$h_5 = wa_5 S \ .$$

Direct exchanges between water and seston are assumed negligible. Any exchanges between water and moving particulatse must therefore be mediated through uptake from the water by F, then transfer of these non-moving particulates to the transport compartment.

When aufwuchs are added to the system, the model (1.1a) becomes

$$A \frac{\partial C}{\partial t} = AD \frac{\partial^2 C}{\partial x^2} + Av \frac{\partial C}{\partial x} + h_1 - h_2 + h_6 - h_7$$

$$A \frac{\partial S}{\partial t} = AD \frac{\partial^2 S}{\partial x^2} + Av \frac{\partial S}{\partial x} + h_3 + h_4 - h_5$$

(1.1b)

$$w \frac{\partial A}{\partial t} = -h_1 + h_2 - h_3$$

$$w \frac{\partial F}{\partial t} = -h_4 + h_5 - h_6 + h_7 \ .$$

The schematic representation of this system is presented in Figure 18. In the above model, aufwuchs are assumed to behave dynamically much like fine particulates. Although excretion of dissolved carbon from

aufwuchs to the water, h_1 , can be better represented as a function of aufwuchs growth rate, for simplicity, it is assumed to be linearly dependent upon aufwuchs biomass only:

$$h_1 = wa_1 A$$

where a_1 is a positive constant.

Uptake of carbon by the aufwuchs, h_2 , is also described by a generalized Michaelis-Menten term similar to h_7:

$$h_2 = \frac{wa_2 CA}{(1 + k_C C)(1 + k_A A)}$$

where a_2, k_C, k_A are positive constants.

The function, h_3 , represents loss of aufwuchs to the seston compartment due to sloughing:

$$h_3 = wa_3 A^2$$

where a_3 is a positive constant. The quadratic form used here models the density dependence of sloughing upon aufwuchs biomass.

When grazers are added to the system, carbon dynamics may be affected through several mechanisms. Snails graze the substrate which tends to reduce the thickness of the algal mat which, in turn, decreases sloughing and increases the surface area for dissolved carbon uptake. Consequently, the aufwuchs would tend to be maintained in an actively growing condition, which could act to increase both primary production and the rate of biomass turnover.

The algae, measured here as carbon, ingested by a snail has several possible fates. It can either be assimilated or passed through its gut and egested as feces. When egested, the fecal pellets enter the system as finely divided FPOM. Assimilated carbon is further partitioned within the snail. A portion may be used for growth, another portion used to produce mucus that may be deposited on the substrate in locomotion, and a final portion degraded for maintainance then excreted into the water column as metabolic waste.

Incorporating these carbon pathways yields the model (Figure 1C)

$$A \frac{\partial C}{\partial t} = AD \frac{\partial^2 C}{\partial_x^2} + Av \frac{\partial C}{\partial x} + h_1 - h_2 + h_6 - h_7 + e_3 h_8$$

$$A \frac{\partial S}{\partial t} = AD \frac{\partial^2 S}{\partial x^2} + Av \frac{\partial S}{\partial x} + h_3 + h_4 - h_5$$

$$w \frac{\partial A}{\partial t} = -h_1 + h_2 - h_3 - h_8 + e_4 h_8$$

$$w \frac{\partial G}{\partial t} = e_2 h_8 - h_9$$

$$w \frac{\partial F}{\partial t} = -h_4 + h_5 - h_6 + h_7 + e_1 h_8 + h_9 \ .$$

A schematic representation of this system is given in Figure 1C.

The term, h_8 , represents loss from the aufwuchs compartment attributable to grazing by snails. It has the generalized Michaelis-Menten form

$$h_8 = \frac{wb_1 \, GA}{(1 + m_G G)(1 + m_A A)}$$

where b_1, m_G, m_A are positive constants. This type of function has been used to represent predatory interactions with saturation by the predator (cf. Holling 1959). The constants e_i, where $\sum_{i=1}^{4} e_i = 1$, $e_i > 0$, are constants of proportionality used to describe snail egestion, growth, excretion, and mucus production, respectively. Such a formulation assumes that snail feces, excretory wastes, and mucus do not differ from aufwuchs-derived fine particulates, dissolved carbon, and aufwuchs itself.

To facilitate model analysis, the model is scaled to obtain an equivalent non-dimensional form. This results in elimination of certain parameters and the need to carry units on each remaining parameter. Through substitution of the scaling variables

$$\tau = \frac{tv}{d} \qquad \alpha_1 = \frac{a_1 d}{v}$$

$$\chi = \frac{x}{d} \qquad \alpha_2 = \frac{a_2 d}{k_c v}$$

$$c = Ck_C \qquad \alpha_3 = \frac{a_3 d^2}{k_C v}$$

$$s = sk_C \qquad \alpha_4 = \frac{a_4 d}{v}$$

$$a = \frac{Ak_C}{d} \qquad \alpha_5 = \frac{a_5}{v}$$

$$g = \frac{Gk_c}{d} \qquad \alpha_6 = \frac{a_6 d}{v}$$

$$f = \frac{Fk_c}{d} \qquad \alpha_7 = \frac{a_7 d}{k_G v}$$

$$\beta_1 = \frac{b_1 d}{kev} \qquad \phi = \frac{m_A d}{k_C}$$

$$\beta_2 = \frac{b_2 d}{v} \qquad \psi = \frac{m_A d}{k_C}$$

$$\beta_3 = \frac{b_3 d^2}{k_C v} \qquad \eta = \frac{\ell_C}{k_C}$$

$$\mu_1 = \frac{k_A d}{k_C} \qquad \xi = \frac{\ell_F d}{k_C}$$

$$\delta = \frac{D}{vd}$$

we obtain the representation

$$\frac{\partial c}{\partial \tau} = \frac{\delta \partial^2 c}{\partial x^2} + \frac{\partial c}{\partial x} + \alpha_1 a - \frac{\alpha_2 ca}{(1 + c)(1 + \kappa a)} + \alpha_c f$$

$$- \frac{\alpha_2 cf}{(1 + \eta c)(1 + \xi f)} + \frac{e_3 \beta_1 ga}{(1 + \psi g)(1 + \phi a)}$$

$$\frac{\partial s}{\partial \tau} = \delta \frac{\partial^2 s}{\partial x^2} + \frac{\partial s}{\partial x} + \alpha_3 a^2 + \alpha_4 f - \alpha_5 s$$

$$\frac{\partial a}{\partial \tau} = -\alpha_1 a + \frac{\alpha_2 ca}{(1 + c)(1 + \kappa a)} - \alpha_3 a^2 - (1 - e_4) \frac{\beta_1 ga}{(1 + \psi g)(1 + \phi a)}$$

$$\frac{\partial g}{\partial \tau} = \frac{e_2 \beta_1 ga}{(1 + \psi g)(1 + \phi a)} - (\beta_2 + \beta_3 g) g$$

$$\frac{\partial f}{\partial \tau} = -\alpha_4 f + \alpha_5 s - \alpha_6 f + \frac{\alpha_7 cf}{(1 + \eta c)(1 + \xi f)} +$$

$$+ \frac{e_1 \beta_1 ga}{(1 + \psi g)(1 + \phi a)} + (\beta_2 + \beta_3 g) g \ .$$

This will be the form of the model used in subsequent analyses.

CHAPTER III

METHODS AND MATERIALS

I. Experimental Methods

The research reported here was conducted in artificial stream channels within the context of ongoing field studies of stream system dynamics conducted in Walker Branch. Like most lower order woodland streams, Walker Branch is spatially heterogeneous. Its upper reaches consist of small pools and zones with slow moving waters interspersed with riffle areas. Part of the stream flows directly over dolomite bedrock, but most of the substrate consists of sand, gravel, and rubble composed of weathered chert and dolomite (Elwood and Nelson 1972). Although the stream is covered by dense forest canopy from May to September (Elwood and Cushman 1975), aufwuchs still grow on inorganic substrates in the stream. Walker Branch supports over sixty species of benthic macroinvertebrates (Cushman et al. 1975), including the dominant primary consumer, Goniobasis clavaeformis.

The experiment reported here was conducted in four once-through artificial stream channels located in a greenhouse at Oak Ridge National Laboratory. Each stream consisted of eight fiberglas troughs connected in series with U-shaped modules to form a channel 0.25 m wide, 0.25 m deep, and slightly over 40 m long (see Figure 2).

These streams were maintained so as to approximate the current velocity and summer illumination of Walker Branch as closely as possible. Summer low flows in Walker Branch range from 4 to 5 l sec^{-1}

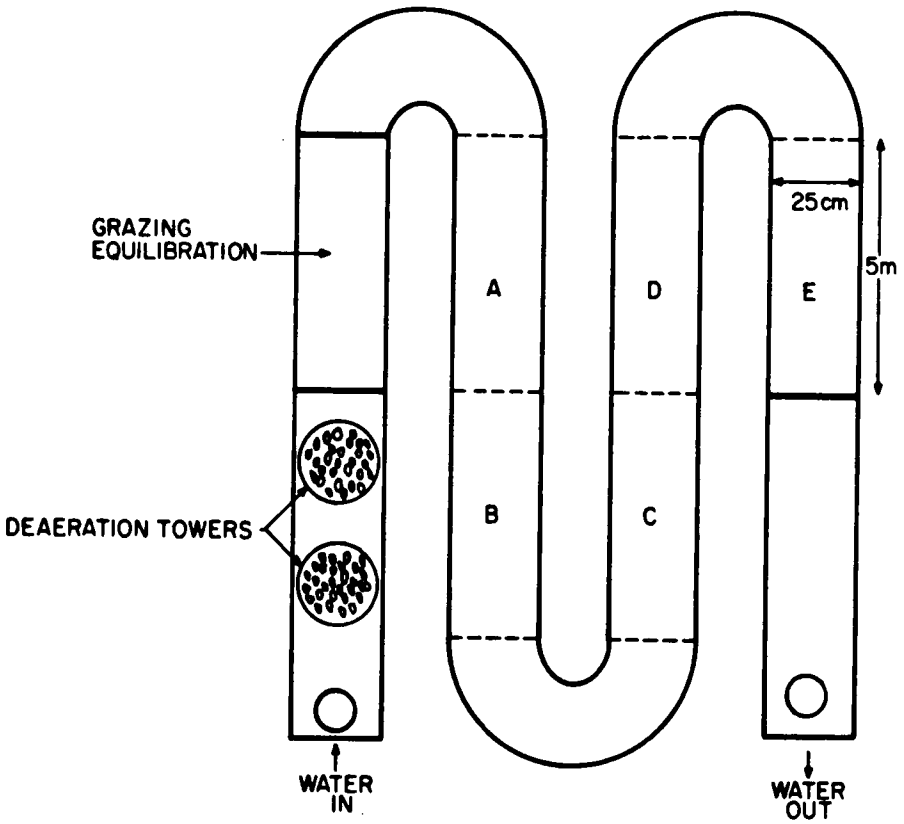


FIGURE 2

The artificial streams

and current velocities average 0.0366 m sec^{-1} . For this experiment, well water was pumped continuously to the streams at 0.67 to 0.70 l sec^{-1} . Low (8.9 cm) plexiglass dams placed approximately 5 m apart throughout the channels reduced the velocity of this water to obtain a final current velocity of 0.032 m sec^{-1} , similar to those in Walker Branch. The bottom of the channels were covered with chert cobble and gravel from Walker Branch. These functioned as substrates for aufwuchs growth and also increased the roughness of the artificial streambed. Finally, cheesecloth screens were placed above the channels to achieve light levels comparable to those of Walker Branch under full canopy (ca. 50 $\mu e \cdot m^{-2}$) , measured with a LiCor quantum flux meter.

Each stream was divided into three sections: an upstream section used for equilibration, as described below, a 25 m experimental section, and an unused downstream section. Hardware cloth with a mesh size smaller than the diameter of an average Goniobasis was used to restrict movement of snails between each of these sections.

The purpose of the equilibration reach was twofold: first, the incoming well water was supersaturated with oxygen and presumably with nitrogen and other atmospheric gasses during much of the experiment. In order to prevent snail mortality caused by gas bubble disease, dissolved gases in the water were allowed to equilibrate to saturation by agitating the incoming well water and dropping it through two gravel-filled columns (Figure 3). Secondly, the lower five meters of the equilibration section was maintained with grazers to reduce the possible effects of an abrupt system boundary in the upper portions of the experimental section.

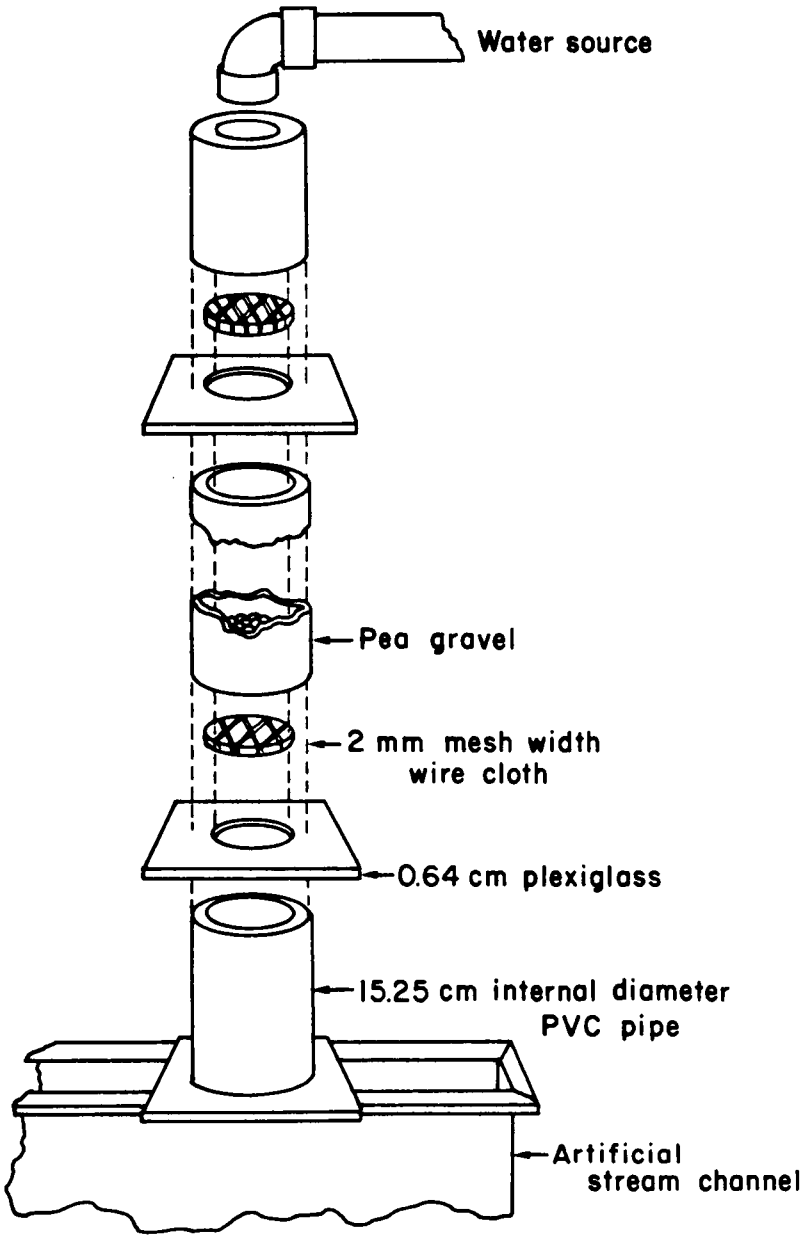


FIGURE 3

Deaeration towers

The experimental section of each stream was further divided into five reaches, each 5 m long reaches (referred to as reaches A, B, C, D, and E, from upstream to downstream) in order to partition out potential experimental variability due to longitudinal effects.

To examine quantitative effects of grazing, four grazer biomass levels were used in this experiment: high (5.6 g snails $\cdot$ m^{-2}), medium (2.8 g snails $\cdot$ g^{-2}), low (1.4 g snails $\cdot$ m^{-2}), and absent or ungrazed (0.0 g snails $\cdot$ m^{-2}). No attempt was made to maintain snail biomass at these densities after the initial stocking of the streams. Grazing treatments were randomly assigned to stream channels so that streams 1, 2, 3, and 4 contained the low, high, medium, and ungrazed treatments, respectively. All snails used in the experiment were Goniobasis clavaeformis Lea collected from a 50 m reach of Walker Branch. The snails were removed from the stream by hand, and held within the bottles at ambient stream temperature for no longer than 4 h prior to their introduction to the channels. Mean snail biomass was approximately 0.0009 g ash-free dry mass $\cdot$ $snail^{-1}$ although some smaller individuals (ca. 0.004 g ash-free dry mass $\cdot$ $snail^{-1}$) were used in reaches D and E of the medium and low treatments.

Four aufwuchs parameters -- primary productivity, ash-free dry mass, pigment concentration, and species composition -- were monitored throughout the experiment. To facilitate sampling, 9.0 $\times$ 3.8 $\times$ 0.5 cm plexiglas slides were used as artificial substrates for aufwuchs growth. Prior to the experiment, these were roughened on their upper surface, numbered, weighted with nails, and placed in each reach with their long axis parallel to the current flow. Several rocks from Walker Branch

were placed in the equilibration reach of each stream to seed both natural and artificial substrates with aufwuchs. Following an initial six week colonization period, the streams were sampled to provide baseline information on primary productivity, ash-free dry mass, chlorophyll *a* concentration, and species composition, and sampled weekly for six weeks following the introduction of the snails. Taxonomic composition was measured biweekly. For each sample, estimates of biomass, pigment concentration, and ^{14}C-assimilation were made using subsamples from a single slide; species composition was determined from a separate slide. Each sample was duplicated within each reach to provide an estimate of sample variability resulting from non-homogeneous aufwuchs growth. Although it would have been desirable to increase replication, the number of replicates was constrained by the total number of substrates available. A random scheme was used to select slides from each reach.

Dissolved oxygen, phosphate concentration (PO_4^{-3} - P), nitrate concentration (NO_3^{-2} - N), ammonia concentration (NH_4^{+} - N), and snail population numbers were also monitored weekly. The concentration of dissolved oxygen, used here as an indicator of gas saturation, was measured at the inlet, in the equilibration reach, and at several points in the experimental section using a YSI oxygen probe. Water samples for analysis of PO_4^{-3} - P, NO_3^{-2} - N, and NH_4^{+} - N were taken in acid-washed polyethylene bottles at the inlet and in reach D. Three replicates for each determination were taken at the inlet and two replicates for each determination were taken in reach D. All water chemistry samples were immediately frozen for later analysis with automated analytical chemistry methodology (Technicon 1974). Phosphate was

analyzed using the molybdenum blue method (EPA 1974), nitrate analyses were performed using the automated cadmium reduction method (EPA 1974), and ammonium was analyzed utilizing the automated colormetric phenate method (EPA 1974). The snail population was censused by a quadrat sampling (Tanner 1978). Two 100 cm^2 quadrats were randomly selected in each reach and all snails within the quadrats were counted, to obtain estimates of snail population density.

Primary productivity was estimated using standard ^{14}C-assimilation techniques in a recirculating incubation chamber. The chamber, modified from the design of Bott et. al. (1978), consisted of a 6.5 l plexiglas box connected to an in-line submersible pump that provided water circulation at approximately 0.5152 l sec^{-1} . For each incubation, slides were removed from the artificial streams and positioned in the chamber with minimal disturbance. The chamber was then placed immediately upstream of the outlet of channel 3, filled with stream water, and sealed. The volume of water used was always as close to 6.5 l as possible, but error due to the presence of air bubbles within the chamber, pump, or tubing may have reduced this volume by, at most, 200 ml (3.1 percent). This was measured during a preliminary incubation without ^{14}C-bicarbonate by noting the size of the air bubbles and the amount of water required to displace them. An incubation period was initiated by adding 30-100 microcuries (μ Ci) of ^{14}C-sodium bicarbonate solution (specific activity 59.7 μCi · μ $mole^{-1}$) to the water in the chamber and starting the pump. Each incubation lasted approximately 90 minutes and was done beneath the cheesecloth cover to maintain light conditions similar to those under which the algae had grown. The amount

of light that passed through the cheesecloth to reach the chamber was measured at the beginning and end of each incubation with a LiCor quantum flux meter. At the end of each incubation, the slides were removed from the chamber and either processed immediately or held in the dark at 4°C for no longer than two hours before processing.

Subsamples of aufwuchs for productivity estimates were scraped from a predetermined area of each substrate with a rubber spatula. These scrapings were filtered onto tared 0.4 µm poresize, 25 mm diameter Nuclepore polycarbonate filters under 380 mm Hg pressure. The remainder of the aufwuchs on the slide was processed for biomass and phytopigment determinates. Labelled inorganic carbonates were removed from the filters by either fuming with concentrated HCl or rinsing with 10 ml of 0.5 M HCl (Lean and Burnison 1979). To obtain the net dry weight of aufwuchs, the filters were dried at 60°C for 24 hours and weighed to the nearest 10 µg on a Cahn electrobalance. The samples were then oxidized on a Packard Tritium-carbon sample oxidizer and the evolved $^{14}CO_2$ trapped in Carbosorb placed in Permafluor scintillation cocktail. Samples were counted on a Packard 460 liquid scintillation counter. Procedural accuracy of the oxidizer, as measured by oxidizing 7.328 µCi of Packard standard ^{14}C-benzoic acid, was 92 ± 0.08 percent. This value was assumed constant for all determinations except as noted below in the results. Liquid scintillation counting efficiency was corrected using an external standard.

Productivity blanks to correct for incomplete removal of ^{14}C-carbonate from the filters after acidification were obtained by dipping several fresh unsterilized plexiglass slides into an incubation

solution of $H^{14}CO_3$ for 10 seconds then processing. Estimates of abiotic uptake of carbon-H from dark chamber or formalin-killed incubations could not be obtained because these techniques require a separate chamber for incubation of the blank, which was unavailable during this experiment.

The concentration of total inorganic carbon in the streams was determined by automatic potentiometric titration on a Fisher Titrimiter® II model 395 following Wetzel and Likens (1979).

Primary productivity was calculated using the following formulas

$$P(\text{mg C} \cdot \text{sample} \cdot \text{h}^{-1}) = \frac{(^{14}C_a)(^{12}C)(1.06)(0.001)}{(^{14}C_w)(E)(t)}$$

$$P_M(\text{mg C} \cdot \text{g}^{-1} \text{ dry weight} \cdot \text{h}^{-1}) = \frac{(P)}{M}$$

$$P_A(\text{mg C} \cdot \text{cm}^{-2} \cdot \text{h}^{-1}) = \frac{P}{A}$$

$$P_{Chl}(\text{mg C} \cdot \text{g}^{-1} \text{ chlorophyll } \underline{a}) = \frac{P_A}{Chl}$$

where

^{12}C = inorganic carbon concentration (mg l^{-1})

^{14}C = assimilated ^{14}C in sampled organisms (dpm)

$^{14}C_N$ = concentration of ^{14}C in incubation water (dpm · ml^{-1})

1.06 = correction for ^{14}C isotope effect

0.001 = conversion factor (ℓ to mℓ)

E = efficiency of recovery of ^{14}C in sample oxidizer

t = length of incubation (h)

M = dry weight of sample (g)

A = area sampled (cm)

Chl = concentration of chlorophyll *a*

(μg Chlorophyll *a* · cm^{-2})

A second subsample aufwuchs from the incubated substrates was scraped into a tared container, dried at 60° C for 18-24 h to obtain constant dry weight, weighed, combusted at 450° C , and reweighed to obtain ash-free dry mass by difference. All weight determinations were done to the nearest 10 μg on a Mettler H54AR analytical balance.

Chlorophyll *a* content of the aufwuchs also was used as an indicator of biomass of the periphyton component of the aufwuchs. Chlorophyll and phaeophytin concentrations were measured with a fluorometer following methanol extraction (Holm-Hansen and Riemann 1978).

Changes in the species composition of the aufwuchs was monitored by observation and enumeration of algal genera. Biweekly samples of aufwuchs from two replicate slides in each reach were scraped into separate 20 ml sample vials and preserved with Lugol's solution. Two

well-mixed 0.1 ml aliquots were later pipetted onto separate cover slips and permanent mounts prepared with the ethanol dehydration technique of Crumption and Wetzel (1981). Algae were identified to the genus level at 600x on a Nikon Diaphot microscope using the keys of Whitford and Schumacher (1973) and Weber (1971). Ten randomly selected microscope fields were counted on each slide (Kutkuhn 1958) for a total of 40 counts (10 fields × 4 subsamples) per sample.

II. Statistical Methods

A two-way analysis of variance (ANOVA) was used to determine the contribution of the treatment and reach sampled to the overall variance. Since the two samples within each reach were not independent estimates of each treatment-reach combination, it was necessary to test the significance of the main effects, treatment and reach, with the interaction term. This method assumes a non-significant two-way interaction and may be in error if it is indeed significant. In this case, however, the sums of squares due to the significant interaction would be larger than the sums of squares of a non-significant interaction. The F-statistic would be smaller and less likely to indicate a significant main effect. Thus, the F test would become more conservative. Normality of the error terms of the ANOVA also was checked by graphical examination of the residuals. A posteriori comparison of sample means was made with Duncan's multiple range test.

Differences in snail population biomass were tested with a two-way contingency table using the chi-squared (χ^2) statistic, while comparison of initial and final mean snail weights were made using a paired student's t-test. All analyses of variance and associated

tests were performed with SAS 79.5 with $\alpha = .10$. All other statistical tests were done using a hand calculator.

CHAPTER IV

RESULTS

I. Experimental Results

Initial aufwuchs colonization of the natural and artificial substrates proceeded rapidly. Within a week, a thin film of algae could be seen coating the rocks in all channels; by the end of a month, aufwuchs growth was well developed. Channel 4, however, appeared to have substantially heavier aufwuchs growth than did channels 2 and 3, while the aufwuchs in channel 1 was less well developed than in any of the other three channels. These differences in colonization appeared to be correlated with potential differences in light regieme. The four streams were located in two adjacent greenhouses, with channels 1 and 2 in the east greenhouse and channels 3 and 4 in the west greenhouse. The streams also were sequentially arranged from east to west. As a result of this configuration, channels 1 and 2 may have been shaded from the afternoon sun by the west greenhouse while channels 2 and 4 may have received more direct afternoon sun than did channels 1 and 3. Consequently, the heavy aufwuchs growth observed in channel 4 may have been associated with high light levels. Conversely, the sparse aufwuchs growth in channel 1 may have been associated with less light.

Unfortunately, I was unable to obtain reliable light readings for different positions in either greenhouse because of pipes and light fixtures suspended above the channels and variable afternoon light conditions. As a result, the light hypothesis could not be

tested. Alternative explanations, such as differences in temperature, current velocity, and nutrient concentration were rejected because the temperature in all four channels was constant (17° C), the flow rate and morphology of all four systems was the same, and the nutrient regimes did not significantly differ from channel to channel (see below).

Prior to the addition of snails, two coats of light-reducing greenhouse paint were applied to the lower portion of the western roof of the west greenhouse in an attempt to equalize the light regime. The effect of this treatment on aufwuchs growth were unclear because 1) no pre-paint data on aufwuchs biomass were available and 2) grazers were introduced into the system shortly thereafter.

The snails appeared to acclimate readily to laboratory conditions. Although collection, transport, and a 3-4 h holding period may have traumatized individual animals, mortality was not observed. Throughout the experiment, many snails were observed in the deaeration section of the grazed treatments. Presumably, these were snails that had crawled upstream from the grazed reaches and gone over or through the hardware cloth screen that separated the equilibration reach from the experimental reaches. A similar downstream movement into the overflow pipes leading from each channel also may have been occurring. Consequently, as a result of these movements, the average realized snail density (estimated by quadrat sampling) in each grazed treatment was lower than stocked levels (See Figure 4). The difference between stocked and measured density in each treatment, however, was not statistically significant (chi-squared test, see Table 4).

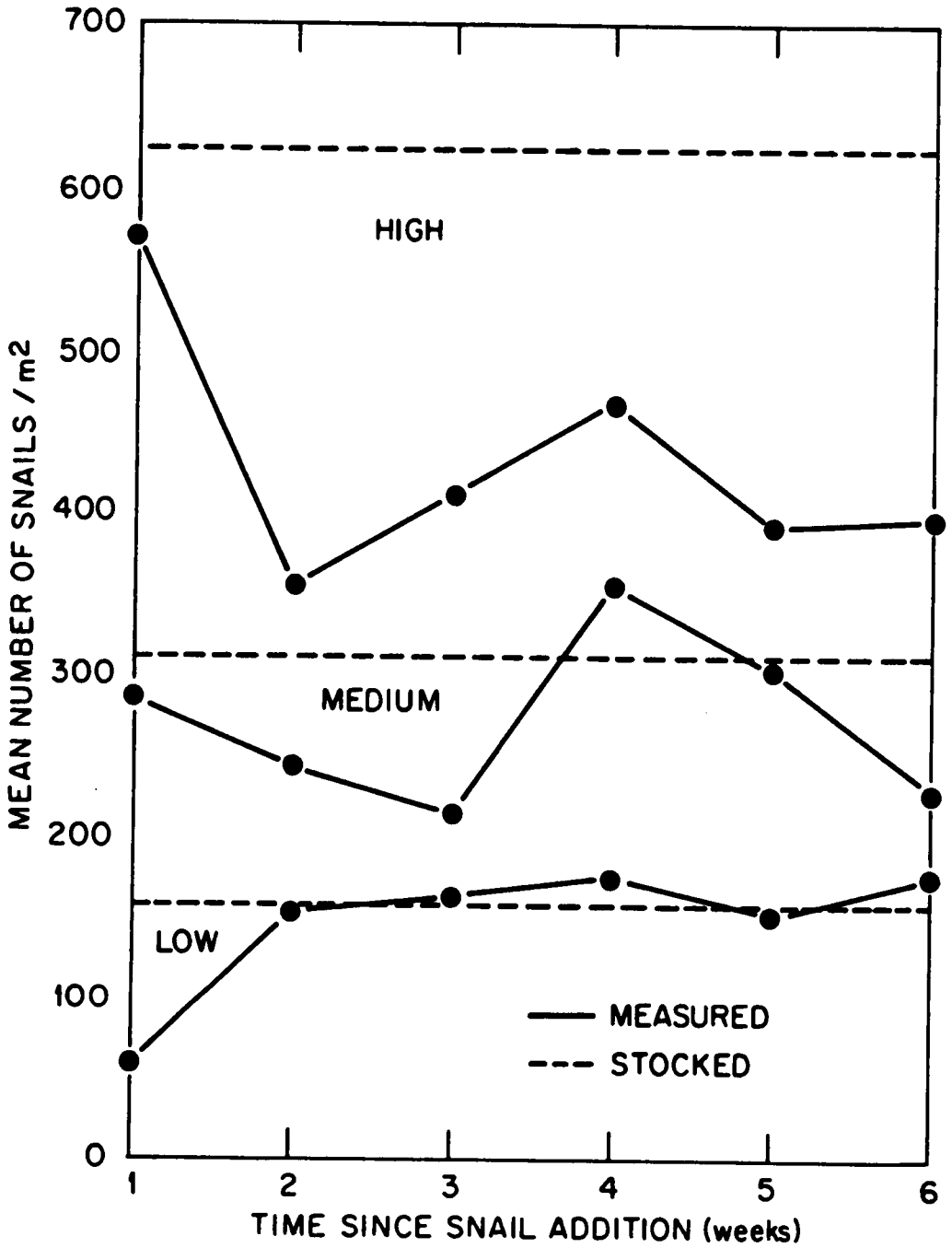


FIGURE 4

Mean density of snails versus time observed and stocked

TABLE 4

COMPARISON OF STOCKED AND MEASURED SNAIL DENSITY IN HIGH, MEDIUM, AND LOW TREATMENTS. THE CHI-SQUARE TEST STATISTIC WAS COMPUTED IN EACH REACH AND SUMMED OVER REACHES IN EACH STREAM.

SIGNIFICANT VALUE OF $\chi^2 = 7.78$,
$\alpha = .10$, d.f. = 4 .

WEEK	REACH	H	M	L
	A	.0153	.9402	.3703
	B	2.7751	.1621	.8626
1	C	1.0575	2.3614	1.5600
	D	2.5981	1.4315	.3703
	E	1.4633	.9402	.2010
	TOTAL	.8633	5.8354	3.3642
	A	1.4663	.9402	.0369
	B	.2860	.7332	.0001
2	C	2.3460	.1531	.0023
	D	1.4663	.1621	.0001
	E	.3242	.0836	.0831
	TOTAL	5.8888	2.0722	0.1225
	A	.6560	1.1730	.4523
	B	2.7006	1.2064	.3703
3	C	1.2785	3.2926	.3703
	D	0.0232	0.2663	.2626
	E	1.2785	0.0836	.1241
	TOTAL	5.9370	6.0319	1.5796
	A	.6560	0.2547	1.7241
	B	1.2785	0.3962	.0164
4	C	2.1068	0.0026	.0831
	D	0.3062	0.0772	.0831
	E	0.8610	0.2647	--
	TOTAL	4.4093	0.9854	1.9062

TABLE 4 (Continued)

WEEK	REACH	H	M	L
	A	.7293	.2547	.0369
	B	.9415	.0039	.0001
5	C	1.2785	.0836	.5408
	D	.2393	.0270	.1241
	E	.9415	.7332	.0001
	TOTAL	4.1931	1.1024	.7520
	A	.6560	.9402	.2626
	B	.2393	.5518	.1241
6	C	2.1068	.0309	.0831
	D	1.1036	.2663	.0164
	E	.5325	.0026	.1241
	TOTAL	4.6382	1.7910	.6103

An additional complication arose in weeks 2-6 when immature snails were observed in all reaches of the ungrazed stream. Initially, these snails were small and almost imperceptible to the unaided eye, however, by the end of the experiment, many were 0.5-1.0 mm long. Only two full-size snails were ever found in the ungrazed stream. Although it is impossible to ascertain the source of animals, the juveniles probably hatched from eggs that were either introduced on colonization rocks or deposited by adult snails that had crawled out of the grazed streams and into the ungrazed stream via the common system of outflow pipes.

Removal or census of the juveniles was not attempted since any manipulation of the rocks in the ungrazed channel dislodged relatively large clumps of algae. Consequently, neither an accurate estimate of juvenile snail biomass nor the extent of their grazing is known. After the termination of the experiment, an upper bound on the population biomass was obtained, by removing and weighing all the snails from several highly aggregated patches. The snail biomass in these patches was extremely low (mean ADFM Of 0.00021 g $snail^{-1}$, n = 22 snails in ca. $0.01m^2$), and the area of the patches was small compared to the entire channel bottom, thus the grazing pressure the juvenile snails exerted on the stream was probably insignificant.

Comparisons of final snail biomass to initial snail biomass shows that the snails in all treatments became larger, with greater increases corresponding to lower grazer densities (Table 5). In the low treatment, this represented sixty-seven percent increase in average snail mass in only six weeks.

TABLE 5

COMPARISON OF INITIAL AND FINAL MEAN SNAIL ASH-FREE DRY MASS.
N = NUMBER OF INDIVIDUALS SAMPLED, AFDM = MEAN ASH-FREE DRY MASS, S = STANDARD DEVIATION,
P = SIGNIFICANCE LEVEL FOR THE STUDENT'S t-TEST OF NO SIGNIFICANT DIFFERENCE BETWEEN
INITIAL AND FINAL ASH-FREE DRY MASS.

TREATMENT	INITIAL N	INITIAL AFDM	INITIAL S	FINAL N	FINAL AFDM	FINAL S	PERCENT INCREASE	P
LOW	9	.00855	.00259	7	0.01429	.00365	67.13	.005
MEDIUM	9	.00855	.00259	6	0.01281	.00346	49.82	.05
HIGH	9	.00855	.00259	10	0.01110	.00356	29.82	.05

The qualitative visual impact of grazing on the aufwuchs was striking. Grazing was patchy and without obvious selectivity. Freshly grazed surfaces appeared devoid of aufwuchs while adjacent substrates often retained a luxuriant algal mat. This spatial heterogeneity diminished with time as the snails grazed more of the stream bottom.

In the grazed treatments, aufwuchs biomass decreased immediately following the snail additions and, in general, continued to decline through the end of the experiment (Figure 5). Aufwuchs biomass in the ungrazed treatment also shows a similar, but less severe, drop in weeks 0 to 2 (Table 6), followed by a dramatic increase in biomass. The final biomass in the ungrazed system, although more than double its minimum value, was still less than its initial biomass.

It should be noted that the initial biomass values order from highest to lowest, ungrazed, high, medium, and low treatments, which correspond to channels 4, 2, 3 and 1, respectively. The visual observations of differing initial biomass described above were thus confirmed by qualitiative measurement. In addition, north-south differences that were not apparent upon casual inspection also may have existed. Ash-free dry mass data show that reaches B and C, located in the southern ends of the greenhouses, both tended to have higher initial aufwuchs biomass than the northern reaches, A, D, and E .

An analysis of variance on aufwuchs standing stock ash-free dry mass (as g ash-free dry mass $\cdot$ m^{-2}) showed that grazed treatments contained significantly less aufwuchs than did grazed treatments in weeks 3, 5, and 6 (Table 7, Figure 5). The effects of differential

TABLE 6

Initial change in aufwuchs ash-free dry mass. Values are expressed as percent decrease in ash-free dry mass from week 0 to week 0.

Treatment	Percent Decrease
ungrazed	77.07
low	69.48
medium	81.36
high	81.21

TABLE 7

Comparisons of effects of grazing treatment and reach on the ash-free dry mass in aufwuchs. Degrees of freedom, F-values, and their significance levels are from a two-way analysis of variance (α = .10). Treatment means are given in parentheses. Means underscored with the same line are not significantly different (Duncan's multiple range test, α = .10).

WEEK	F	P	MEAN ASH-FREE DRY MASS
0	3.30	0.0578	U(3.75) H(2.98) M(2.79) L(2.13)
1	1.88	0.1866	M(2.01) U(6.70) L(1.10) H(1.03)
2	0.72	0.5605	U(8.61) L(6.51) H(5.65) M(5.21)
3	7.23	0.0050	U(1.41) L(2.87) H(2.74) M(1.96)
4	1.21	0.3470	U(1.44) L(1.11) H(4.85) M(2.74)
5	109.83	0.0001	U(2.89) L(2.45) M(1.71) H(1.07)
6	55.74	0.0001	U(3.05) L(2.15) M(1.79) H(1.55)

grazing pressure upon biomass were less apparent. Comparison of mean aufwuchs ash-free dry mass among grazed treatments yielded varying results for different weeks (Duncan's multiple range test, $\alpha = .10$, Table 7). The low grazing pressure exhibited higher, but not significantly higher, biomass than did the medium and high grazing pressures in weeks 2 through 6. The medium treatment had slightly more biomass than did the high treatment in week 5, whereas the high treatment had more, but not significantly more, biomass than did the medium in weeks 3, 4, and 6.

The effects of reach were not significant for any week. No detectable patterns in the organic content of aufwuchs (as percent ash-free dry mass of the samples) emerged from an analysis of variance, although the effects of reach or treatment were significant for several of the weeks sampled (Table 8).

Chlorophyll and phaeophytin concentrations were extremely variable. In several cases, samples taken from adjacent slides within a treatment varied over as much as four orders of magnitude. Since these differences did not appear to be correlated with possible artifacts of sampling processing, it appeared that they were the result of heterogeneous distribution of algae. A logarithmic transformation was performed on the phytopigment data to normalize the sample variances (Sokal and Rohlf 1981) prior to statistical analyses. However, the results are reported as the anti-logarithms of the transformed data (Sokal and Rohlf 1981).

The concentrations of chlorophyll *a* ($\mu g \cdot mg\ AFDM^{-1}$) tended to be lower in the ungrazed treatment than in the grazed treatments

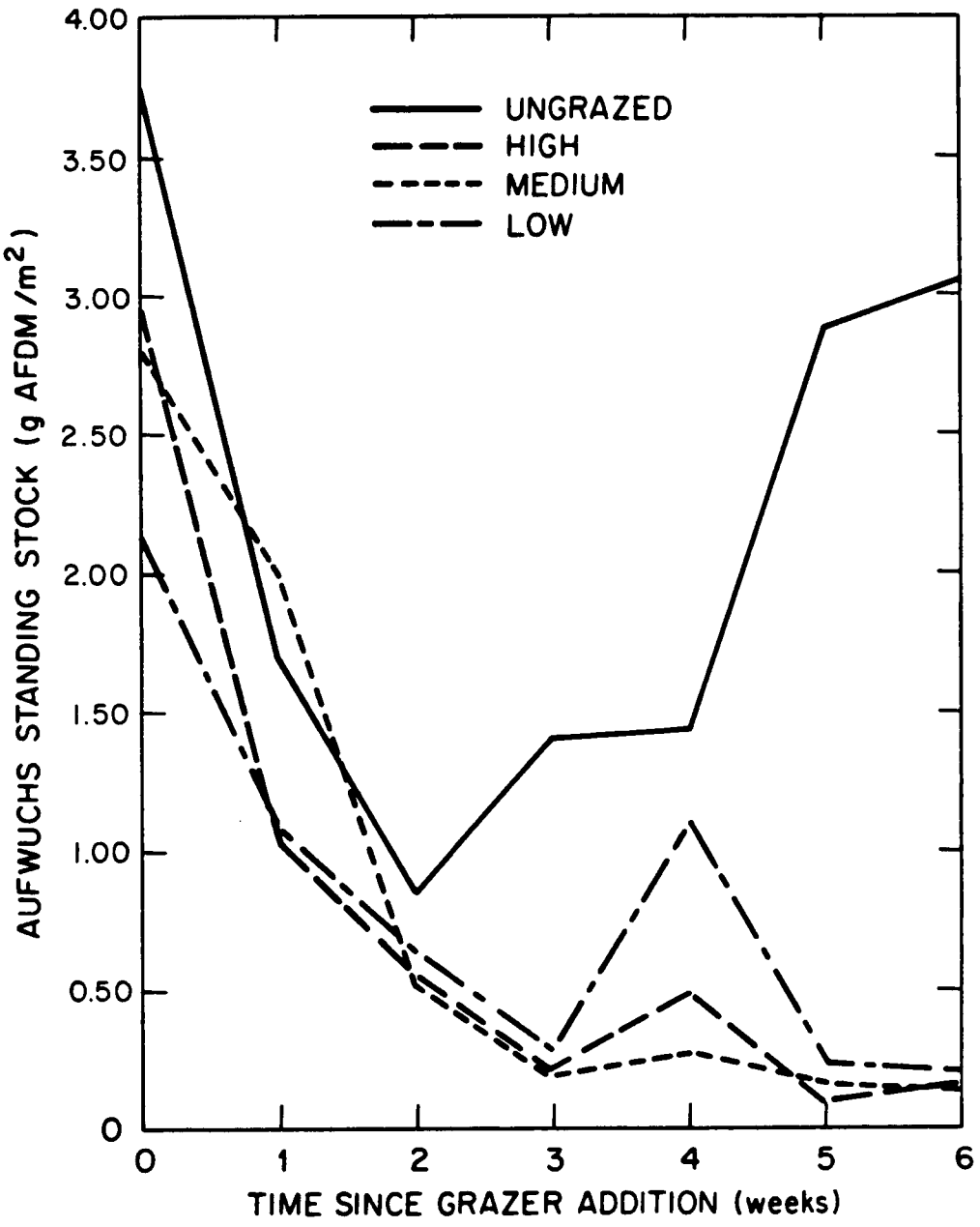


FIGURE 5

Aufwuchs standing stock versus time

TABLE 8

Comparisons of effects of grazing treatment and reach on the percent ash-free dry mass in aufwuchs. Degree of freedom, F-values and their significance levels are from a two-way analysis of variance (α = .10). Treatment means are given in parentheses. Means underscored with the same line are not significantly different (Duncan's multiple range test, α = .10).

WEEK	SOURCE	d.f.	F	P	MEAN PERCENT ASH-FREE DRY WEIGHT
0	TREATMENT	3	37.80	0.0001	L(80.06) M(74.99) U(73.12) H(70.74)
	REACH	4	4.42	0.0199	C(76.02) A(75.86) D(75.00) B(74.50) E(72.26)
1	TREATMENT	3	0.97	ns	L(80.90) M(75.16) H(74.65) U(69.90)
	REACH	4	0.37	ns	C(78.37) E(76.50) D(75.62) B(74.43) A(70.50)
2	TREATMENT	3	1.05	ns	L(80.61) M(79.08) U(78.40) H(71.88)
	REACH	4	1.41	ns	E(81.16) C(80.80) A(80.18) D(76.86) B(65.14)
3	TREATMENT	3	1.62	ns	H(76.09) L(75.10) U(74.44) M(55.90)
	REACH	4	1.52	ns	A(82.23) D(74.33) B(73.71) C(63.71) E(59.56)

TABLE 8 (continued)

WEEK	SOURCE	d.f.	F	P	MEAN PERCENT ASH-FREE DRY WEIGHT
4	TREATMENT	3	0.24	ns	M(80.23) U(77.92) H(76.05) L(71.08)
	REACH	4	0.90	ns	C(82.55) A(80.54) B(79.92) E(71.15) D(68.57)
5	TREATMENT	3	2.08	ns	L(76.41) H(73.61) U(65.94) M(59.61)
	REACH	4	2.87	0.0702	D(81.45) B(73.13) C(70.43) E(64.90) A(50.74)
6	TREATMENT	3	3.59	0.0465	L(93.60) M(79.54) H(78.60) U(64.38)
	REACH	4	1.34	ns	E(93.14) D(78.61) C(75.44) B(75.23) A(72.74)

(Figure 6) , and in week 6, chlorophyll concentrations were significantly lower in the ungrazed treatment than in the grazed treatments (Table 9).

There were no significant differences in chlorophyll *a* content among grazed treatments and no discernible trends as a result of differential grazing pressure (Duncan's multiple range test).

The results for phaeophytin *a* concentration per gram were similar (Table 10). In week 6, this value was significantly lower for ungrazed than for grazed treatments while effects of different snail densities did not significantly differ from each other (Figure 7). These differences were attributable to changes in phaeophytin *a* concentration, rather than differences in the concentrations of other pigments. Fluorometric methods for phaeophytin *a* measurement depend upon the absence of chlorophyll *b* from the samples because, after acidification, the fluorescence spectrum of chlorophyll *b* overlaps that of phaeophytin *a* and thus gives falsely high values for phaeophytin *a* (Yentsch *et al*. 1965, Loftus and Carpenter 1971; Holm-Hansen and Riemann 1978). This interference was probably negligible in this case because green algae were rarely observed in the aufwuchs (see below).

An analysis of variance for the logarithm of chlorophyll *a* standing stock (μg chlorophyll *a* $\cdot$ cm^{-2}) showed a significant reach effect in week 1 (Table 11). Reach was not significant in week 0 or weeks 2-6. Treatment was significant in weeks 1-3 and 5-6, with chlorophyll *a* standing stock much lower in the grazed treatments than in the ungrazed treatment (Figure 8).

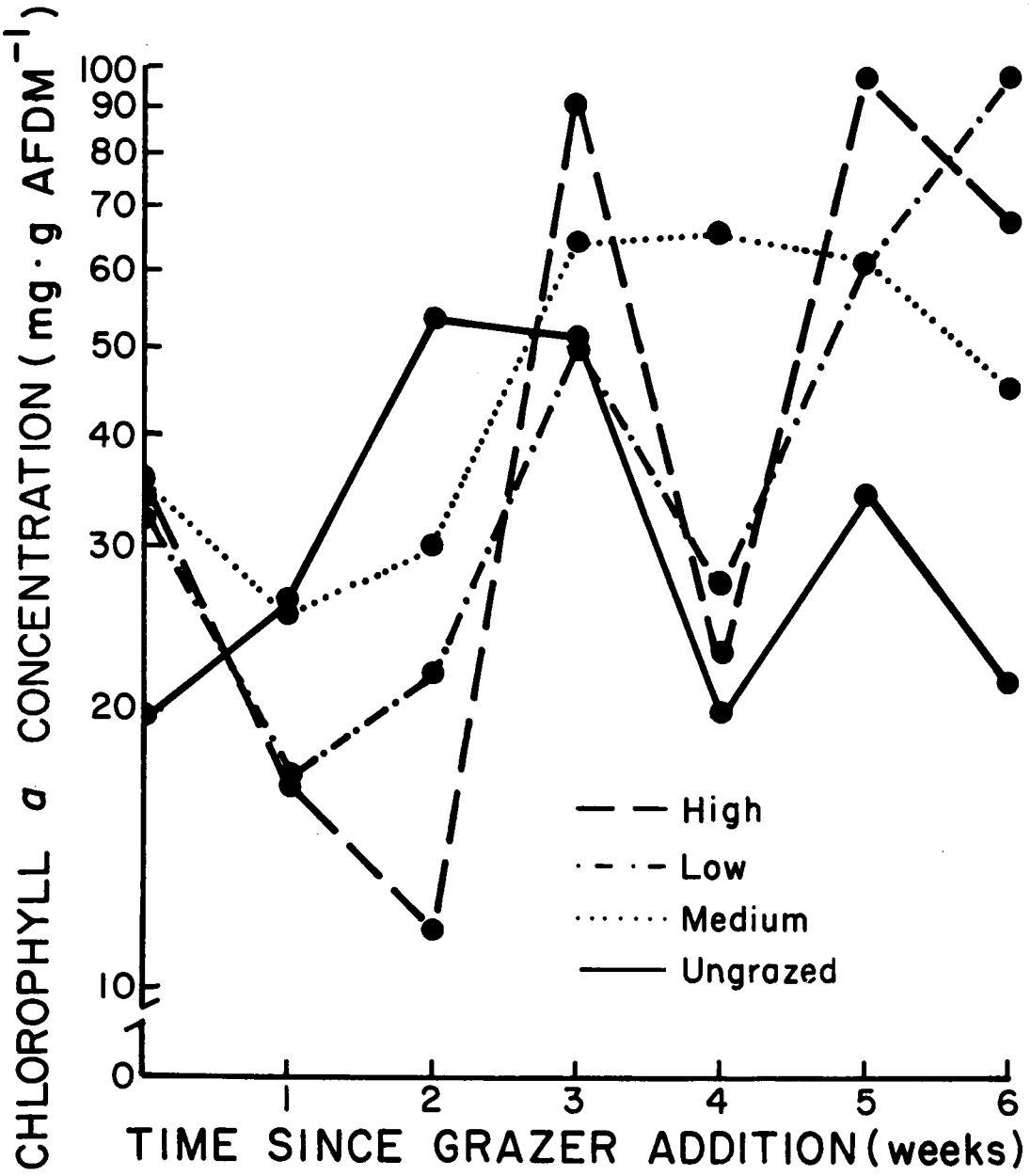


FIGURE 6

Chlorophyll *a* concentration versus time

TABLE 9

Effects of treatment on chlorophyll *a* concentration (mg chlorophyll *a* • g ash-free dry-mass^{-1}) in aufwuchs. F values and their significance levels are from a two-way analysis of variance, α = .10, = 9 degrees of freedom = 3. Treatment means are given in parentheses. Means underscored with the same line are not significantly different (Duncan's multiple range test, α = .10).

WEEK	F	P	MEAN CHLOROPHYLL *a* CONCENTRATION
0	0.41	ns	H(35.6) M(34.7) L(32.7) U(19.4)
1	0.94	ns	U(25.9) M(25.5) L(16.7) H(15.2)
2	4.76	0.0207	U(53.2) M(29.8) L(21.6) H(11.2)
3	0.37	ns	H(93.0) M(64.4) U(50.2) L(49.7)
4	0.91	ns	M(64.9) L(27.5) H(22.4) U(19.9)
5	1.18	ns	H(81.3) L(61.2) M(61.1) U(39.9)
6	3.45	0.0515	L(79.6) H(67.1) M(44.2) U(21.1)

TABLE 10

Effects of treatment on phaeophition *a* concentration (mg chlorophyll *a* • g ash-free dry mass^{-1}) in aufwuchs. F-values and their significance levels are from a two-way analysis of variance, $\alpha = .10$, degrees of freedom = 3 . Treatment means are given in parentheses. Means underscored with the same line do not significantly differ (Duncan's multiple range test, $\alpha = .10$)

WEEK	F	P	MEAN PHAEOPHYTIN *a* CONCENTRATION
0	1.04	ns	M(80.6) H(79.1) L(75.6) U(38.5)
1	1.15	ns	U(84.6) M(54.0) L(35.9) H(26.7)
2	3.24	0.0606	U(58.4) M(4.49) L(28.9) H(13.5)
3	0.28	ns	H(104.8) M(74.5) U(64.5) L(45.8)
4	1.02	ns	M(80.7) H(43.2) L(30.6) U(25.4)
5	1.40	ns	H(95.5) M(63.0) L(58.8) U(45.9)
6	4.29	ns	H(110.1) L(6.12) M(55.9) U(28.6)

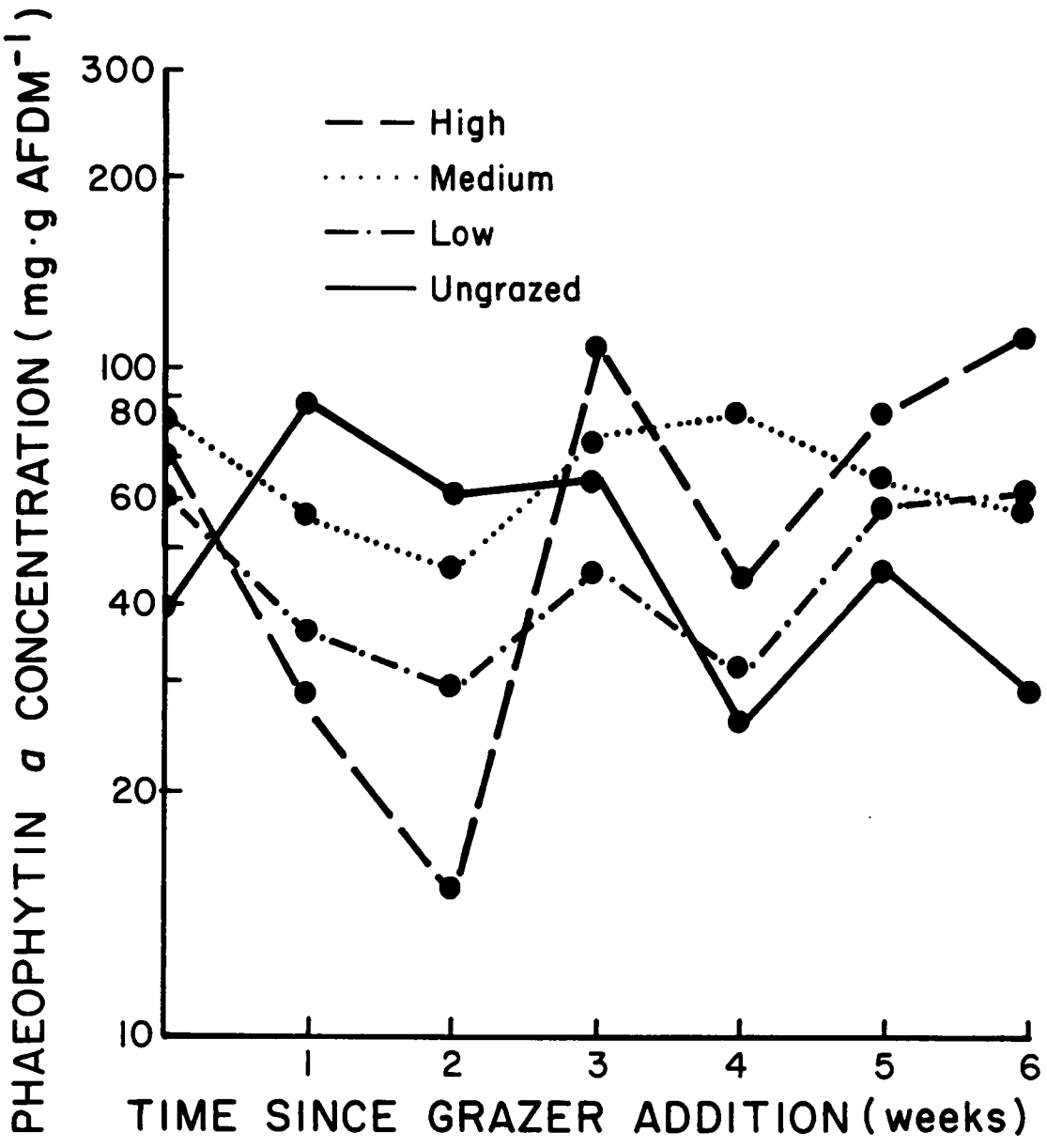


FIGURE 7

Phaeophytin a concentration versus time

TABLE 11

Effect of treatment and reach on chlorophyll *a* standing stock (μg chlorophyll *a* · cm^{-2}). F values and their significance levels are from a two-way analysis of variance, $\alpha = .10$. Sample means are given in parentheses. Means underscored with the same line do not significantly differ (Duncan's multiple range test, $\alpha = .10$).

WEEK	SOURCE	df	F	P	MEAN CHLOROPHYLL STANDING STOCK
0	TREATMENT	3	0.42	ns	M(8.900) H(8.257) U(6.364) L(5.800)
	REACH	4	0.42	ns	A(10.73) C(7.854) D(6.501) B(6.376) E(5.867)
1	TREATMENT	3	4.71	0.0214	U(4.043) M(2.807) L(1.569) H(1.187)
	REACH	4	2.60	0.0894	B(3.967) C(2.981) E(2.783) A(1.335) D(1.253)
2	TREATMENT	3	5.55	0.0127	U(4.182) M(1.128) L(0.913) H(0.431)
	REACH	4	0.61	ns	D(2.091) B(1.518) A(1.083) E(1.083) C(0.641)
3	TREATMENT	3	21.50	0.0001	U(4.877) L(1.190) H(0.555) M(0.448)
	REACH	4	0.51	ns	D(1.447) A(1.171) B(1.145) C(1.070) E(0.931)
4	TREATMENT	3	0.72	ns	U(1.421) L(0.939) M(1.047) H(0.491)
	REACH	4	0.54	ns	A(1.724) C(1.281) D(0.805) B(0.666) (E(0.616)
5	TREATMENT	3	9.43	0.0018	U(8.758) L(1.340) M(1.118) H(0.830)
	REACH	4	0.16	ns	C(2.161) D(2.003) A(1.906) B(1.582) E(1.514)

TABLE 11 (Continued)

WEEK	SOURCE	df	F	P	MEAN CHLOROPHYLL STANDING STOCK
6	TREATMENT	3	8.87	0.0023	U(5.182) L(1.412) H(0.756) M(0.637)
	REACH	4	0.28	ns	C(1.690) E(1.517) A(1.357) D(1.247) B(1.175)

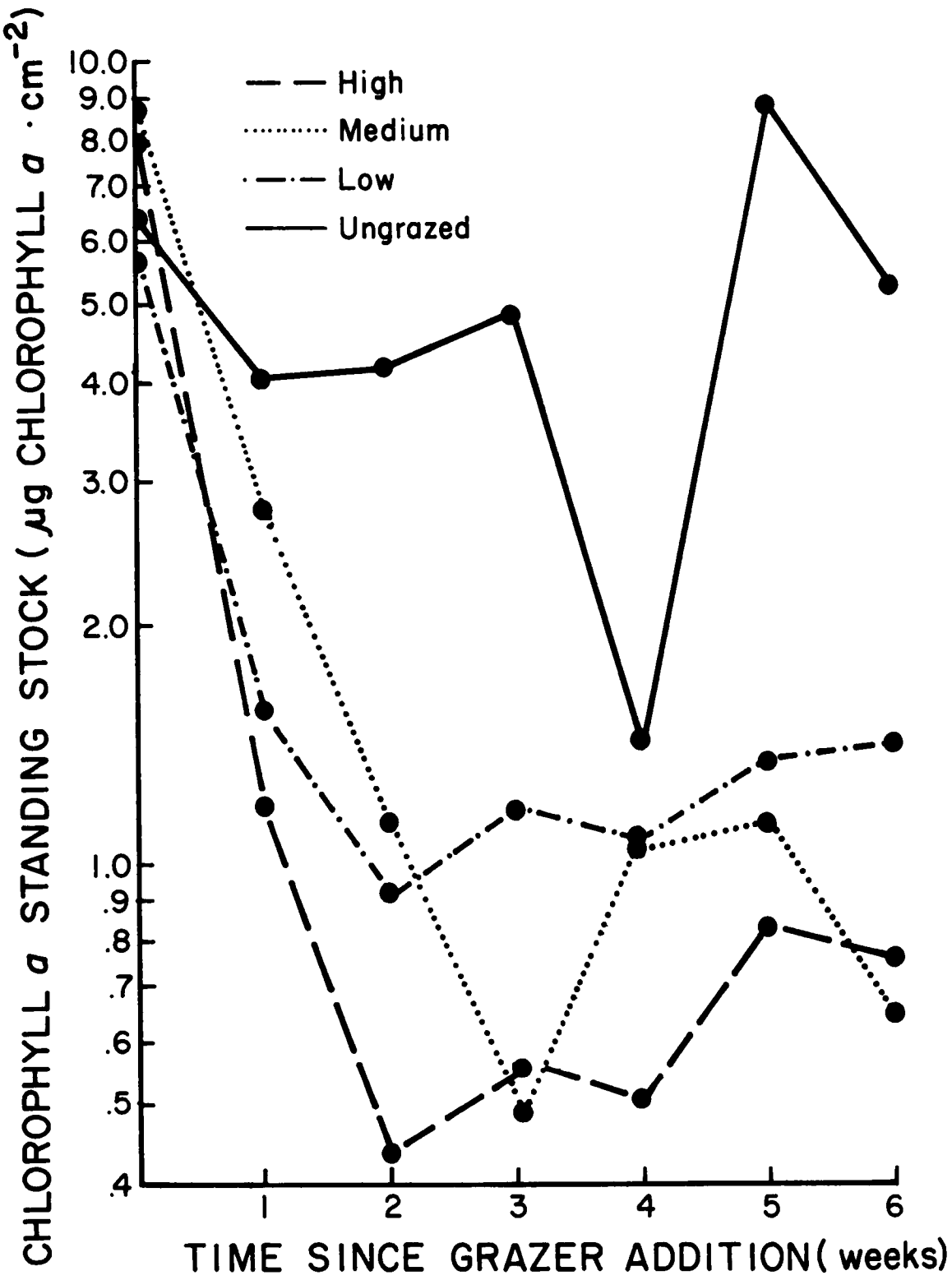


FIGURE 8

Chlorophyll a standing stock versus time

A two-way analysis of variance showed no significant reach effect on the logarithm of phaeophytin *a* standing stock (as µg phaeophytin *a* · cm^{-2}) (Table 12, Figure 9). In addition, there were no apparent general trends in the ordering of phaeophytin *a* standing stock (Duncan's multiple range test, Table 12) attributable to either treatment or reach.

Likewise, the arc-sine transformed ratio of chlorophyll *a* and phaeophytin *a* levels showed a significant reach effect in week 1 only, and a significant treatment effect in weeks 4 and 6 (Table 13, Figure 10). Since phaeopigment concentration is correlated with the standing stock of algal-derived detritus (Liaw and MacCrimmon 1977), this indicates that aufwuchs in the grazed treatments contained slightly fewer dead or senescent algal cells relative to living algae than did aufwuchs in the ungrazed treatments.

Data on aufwuchs productivity were available only for weeks 0-2 and 4-6. Samples for week 3 were lost in the oxidation step due to a malfunction in the oxidizer. Because the samples for the low, medium and high treatments from week 4 were processed shortly after repair of the oxidizer and prior to restandardization, the productivities obtained for grazed treatments in week 4 may also be lower than the actual values due to lower recovery of ^{14}C-carbon.

An analysis of variance on primary productivity (mg $^{14}C \cdot m^{-2}$) shows that productivity was higher in week 2 and significantly higher in weeks 4-6 in the ungrazed compared to grazed treatments (Table 14). In fact, productivity in the ungrazed system was often an order of magnitude greater than the productivities of the grazed systems

TABLE 12

Effect of treatment on phaeophytin *a* standing stock (μg phaeophytin *a* · cm^{-2}). F-values and their significance levels are from a two-way analysis of variance, $\alpha = .10$, d.f. = 3 . Treatment means are given in parentheses. Means underscored with the same line do not significantly differ (Duncan's multiple range test, ($\alpha = .10$).

WEEK	SOURCE	F	P	MEAN PHAEOPHYTIN *a* STANDING STOCK
0	TREATMENT	1.24	ns	M(21.223) H(19.289) U(13.183) L(11.863)
1	TREATMENT	5.47	0.0133	U(12.134) M(7.214) L(3.200) H(2.144)
2	TREATMENT	3.73	0.0420	U(4.344) M(1.944) L(0.999) H(0.534)
3	TREATMENT	25.73	0.0001	U(6.294) L(0.854) H(0.641) M(0.557)
4	TREATMENT	0.25	ns	U(1.819) M(1.308) L(1.150) H(0.986)
5	TREATMENT	31.20	0.0001	U(11.495) L(1.322) M(1.165) H(1.021)
6	TREATMENT	15.98	0.0002	U(7.744) H(1.321) L(1.076) M(0.809)

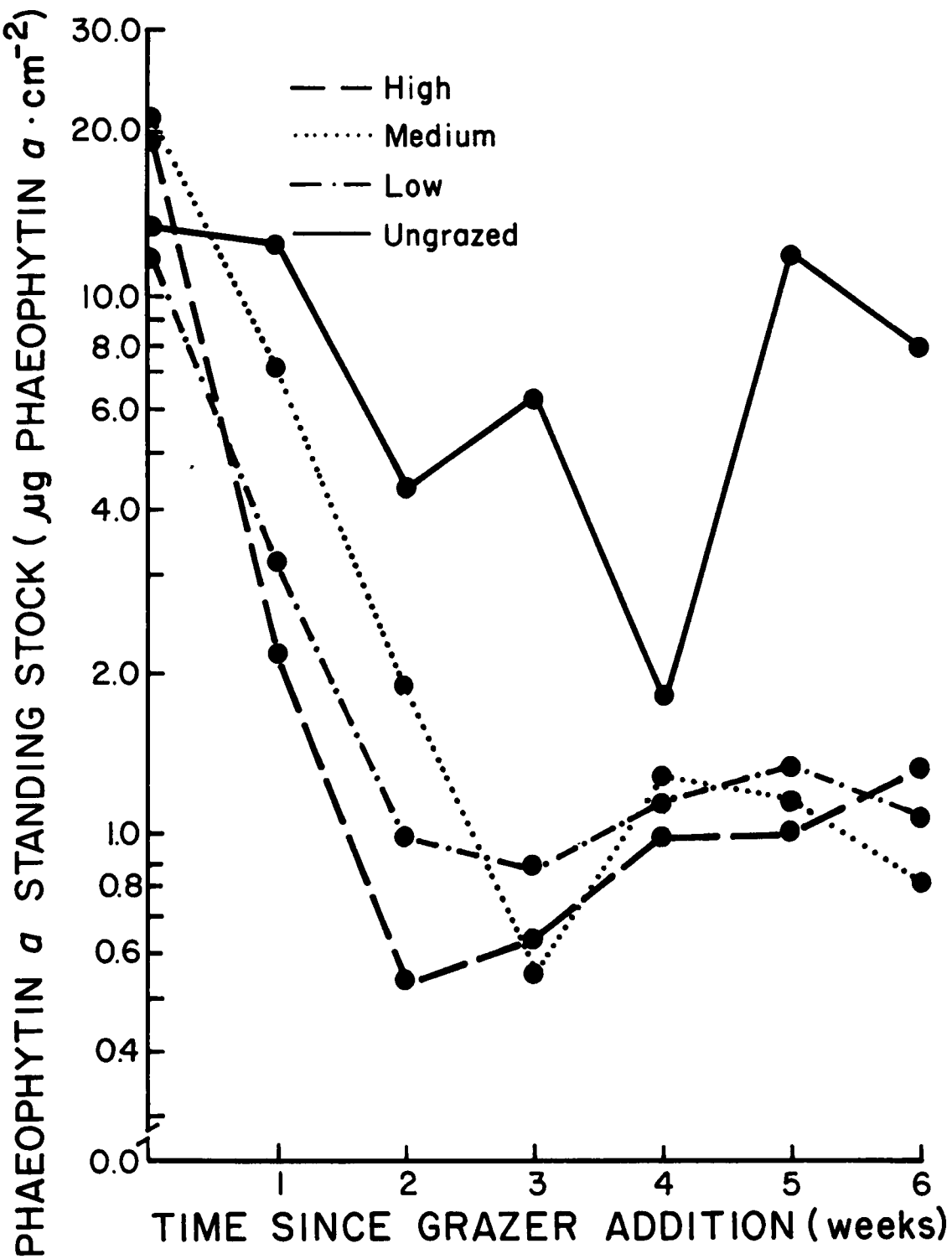


FIGURE 9

Phaeophytin a standing stock versus time

TABLE 13

Effects of grazing on the ratio of chlorophyll *a* to phaeophytin *a*. Degrees of freedom, F-values, and their significance levels are from a two-way analysis of variance (α = .10). Sampled means are given in parentheses. Means underscored with the same line are not significantly different (Duncan's multiple range test, α = .10).

WEEK	SOURCE	d.f.	F	P	MEAN RATIO
0	TREATMENT	3	0.29	ns	U(0.0110) M(0.0104) L(0.0095) H(0.0085)
	REACH	4	1.98	ns	C(0.0121) E(0.0118) A(0.0104) D(0.0095) B(0.0048)
1	TREATMENT	3	0.18	ns	L(0.0097) H(0.0092) M(0.0092) U(0.0086)
	REACH	4	3.15	0.0548	A(0.0124) C(0.0112) E(0.0110) B(0.0069) D(0.0043)
2	TREATMENT	3	.46	ns	H(0.0131) U(0.0124) L(0.0112) M(0.0100)
	REACH	4	.34	ns	D(0.0187) A(0.0100) B(0.0095) C(0.0042) E(0.0062)
3	TREATMENT	3	.54	ns	L(0.0122) U(0.0121) H(0.0120) M(0.0105)
	REACH	4	.20	ns	D(0.0140) E(0.0131) C(0.0128) B(0.0104) A(0.0085)

TABLE 13 (CONTINUED)

WEEK	SOURCE	d.f.	F	P	MEAN RATIO
4	TREATMENT	3	3.70	0.0464	M(0.0169) U(0.0134) L(0.0114) H(0.0089)
	REACH	4	1.05	ns	A(0.0146) C(0.0140) E(0.0125) D(0.0121) B(0.0101)
5	TREATMENT	3	1.19	ns	L(0.0144) M(0.0135) U(0.0108) H(0.0102)
	REACH	4	0.72	ns	A(0.0141) D(0.0128) C(0.0118) E(0.0100) B(0.0083)
6	TREATMENT	3	2.88	0.0953	L(0.0210) M(0.0109) H(0.0108) U(0.0096)
	REACH	4	0.12	ns	E(0.0163) C(0.0135) A(0.0122) D(0.0122) B(0.0118)

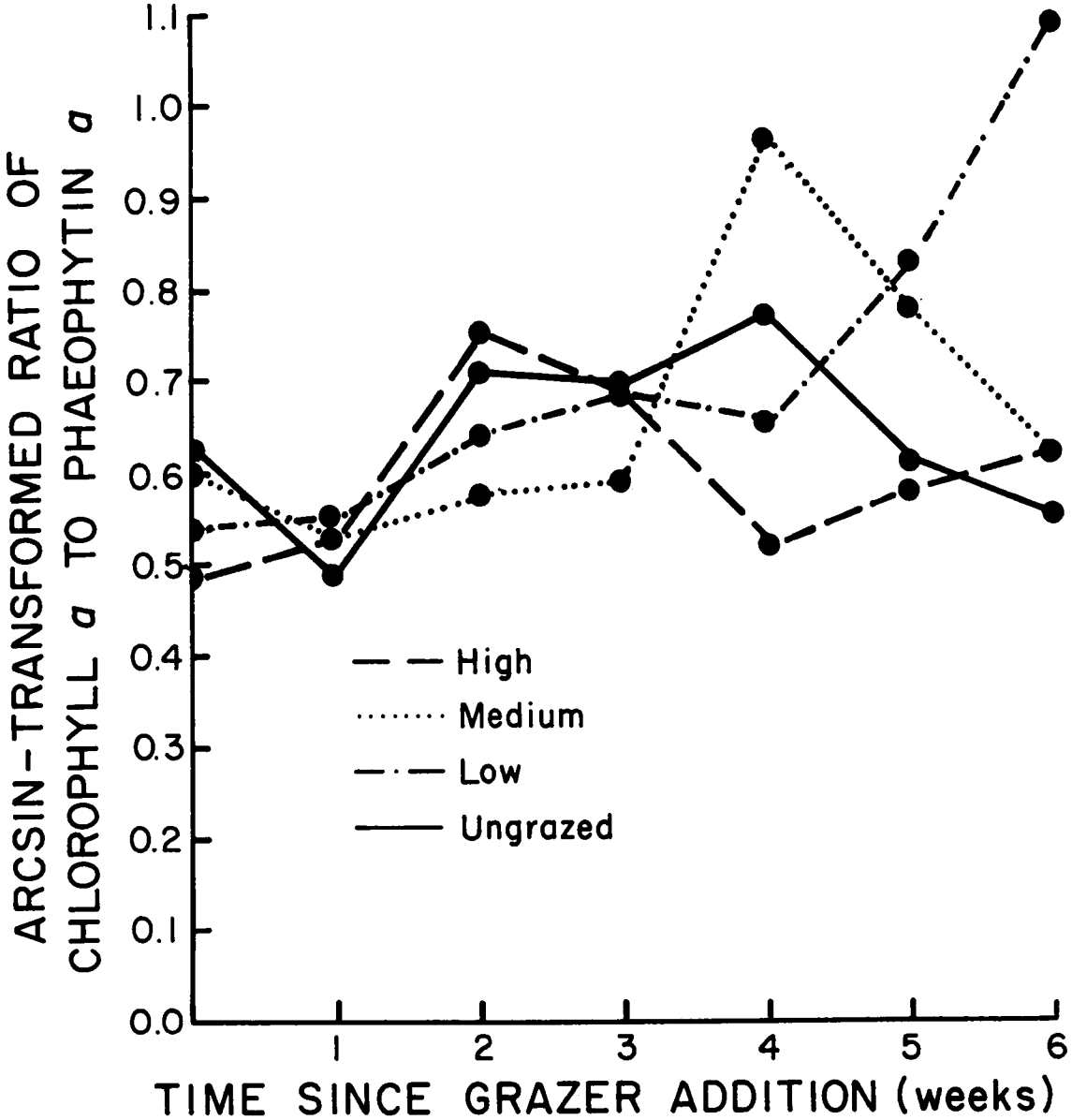


FIGURE 10

Arcsin-transformed ratio of chlorophyll *a* to phaeophytin *a* versus time

TABLE 14

Effects of treatment and reach on primary productivity (mg c $\cdot$ m^{-2} $\cdot$ h^{-1}) in aufwuchs. F-values and their significance levels are from a two-way analysis of variance, α = .10. Sample means are given in parentheses, means underscored with the same line do not significantly differ (Duncan's Multiple Range test, α = .10).

WEEK	SOURCE	d.f.	F	P	MEAN PRIMARY PRODUCTIVITY
0	TREATMENT	3	3.42	0.0525	M(43.6) U(34.4) H(32.5) L(24.0)
	REACH	4	58.97	0.0001	C(72.0) E(45.1) D(39.6) A(4.0) B(2.2)
1	TREATMENT	3	5.29	0.0168	U(25.2) M(25.1) L(11.8) H(8.2)
	REACH	4	3.94	0.0320	D(25.7) B(23.3) C(17.3) A(17.2) E(2.4)
2	TREATMENT	3	1.79	ns	U(10.5) M(4.5) H(3.4) C(2.7)
	REACH	4	0.47	ns	E(9.1) B(8.0) D(7.1) C(4.4) A(3.0)
4	TREATMENT	3	67.72	0.0001	U(25.4) L(2.0) M(1.2) H(0.9)
	REACH	4	1.19	ns	D(9.2) A(8.2) B(8.1) C(6.9) E(4.6)

TABLE 14 (CONTINUED)

WEEK	SOURCE	d.f.	F	P	MEAN PRIMARY PRODUCTIVITY
5	TREATMENT	3	13.91	0.0003	U(42.5) L(6.6) H(5.0) M(2.4)
	REACH	4	5.36	0.0104	E(34.5) A(11.2) D(8.5) C(7.9) B(4.0)
6	TREATMENT	3	84.13	0.0001	U(48.2) L(2.7) M(1.8) H(0.7)
	REACH	4	1.39	0.2957	D(16.5) E(16.4) C(16.2) B(10.3) A(9.4)

(Figure 10). Also, primary productivity under the low grazing pressure tended to be higher, but not significantly higher, than productivity under higher grazing pressure (Table 14). There were no discernible trends in productivities per area in the high and medium treatments.

The results of an analysis of variance on chlorophyll-specific primary productivity were similar. Differences between ungrazed and grazed treatments were highly significant in weeks 4 and 5 (Table 15). At these times, productivity in the grazed treatments was in order of magnitude smaller than in the ungrazed treatment (Figure 12) . No discernible trends in productivity per chlorophyll among the grazed treatments was discernible (Duncan's multiple range test (Table 15)).

Similar effects were observed for biomass-specific productivity. Although biomass-specific productivity increased through time in the low treatment, productivity in the ungrazed treatment remained higher than in all grazed treatments in weeks 4-6. These differences were significant in weeks 4 and 6 (Table 16). No trends in biomass-specific productivity emerged among the grazed treatments (Table 16, Figure 13).

The effects of grazing on nutrient concentration in the stream water were variable (Table 17). The effects of grazing treatment were not significant in any week for either PO_4^{-3} - P , NO_3^{-2} - N , or NH_4^{+} - N . Longitudinal factors, however, sometimes did have a significant effect (see Figures 13, 14, 15). In week 3, the inlet water contained significantly less NO_3^{-2}- N , and more, but not significantly more, PO_4^{-3}- P and NH_4^{+} - N , than did the downstream station (reach D). Similarly, NH_4^{+} - N was significantly higher downstream than upstream

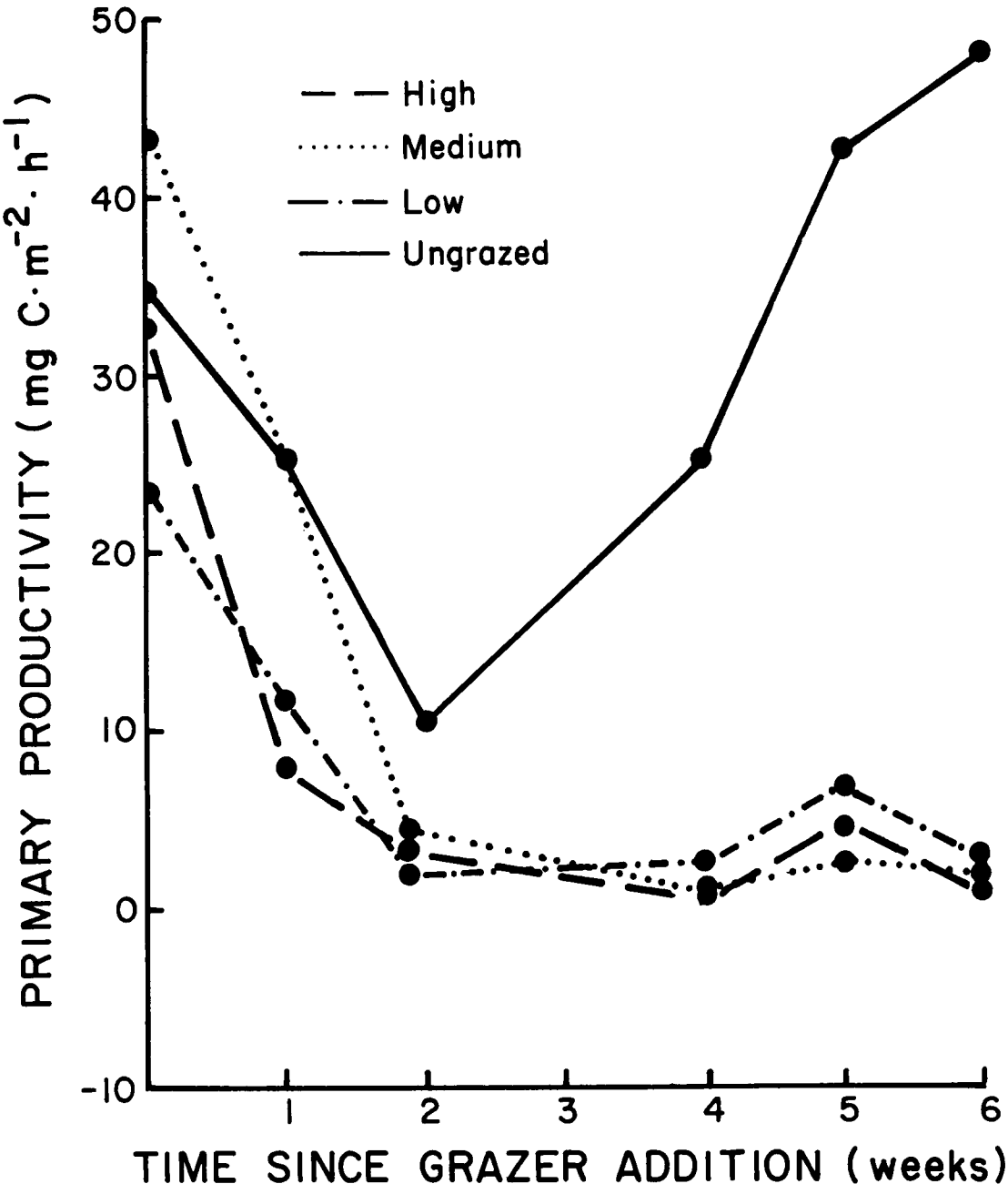


FIGURE 11

Primary productivity versus time

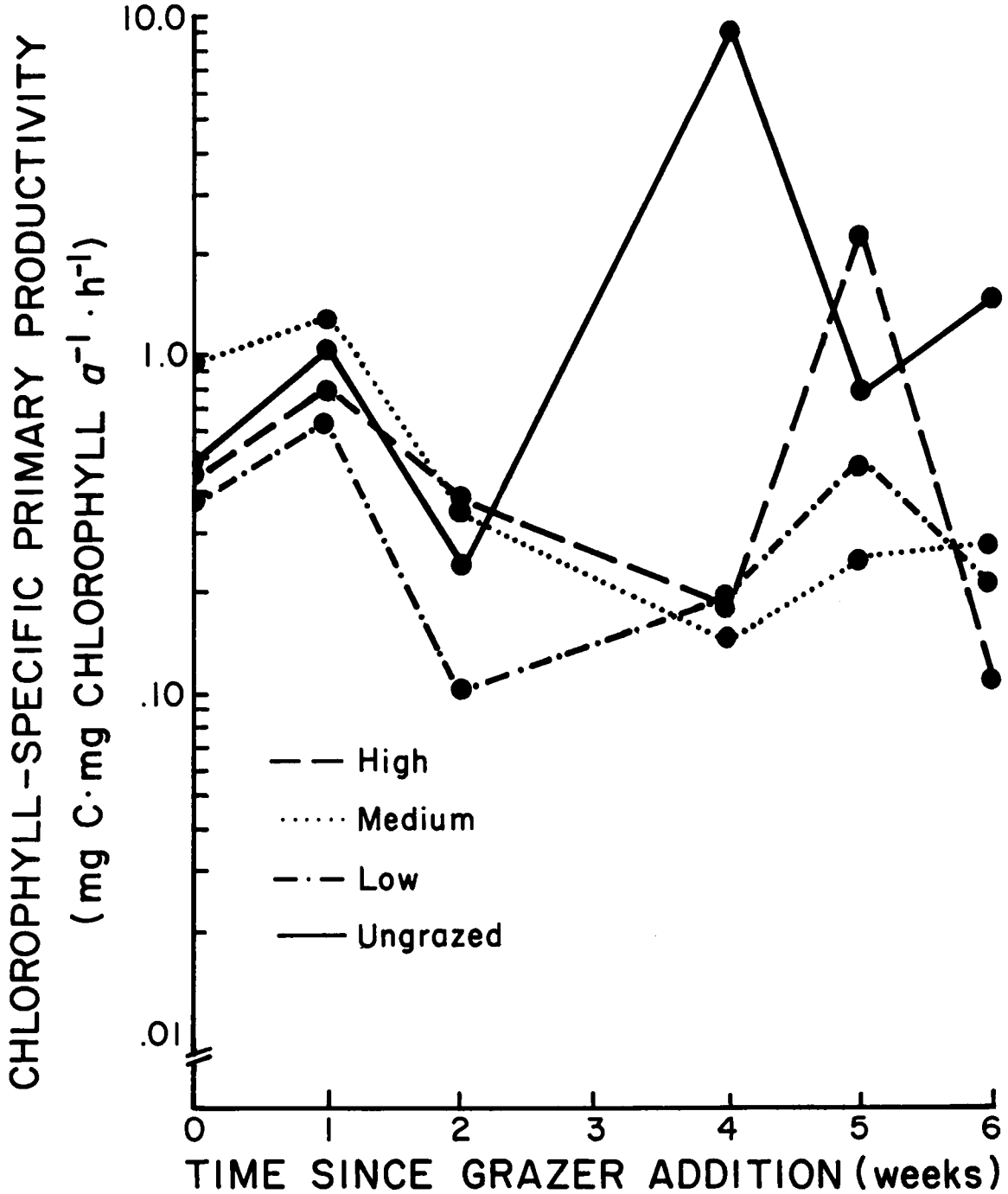


FIGURE 12

Chlorophyll a-specific primary productivity versus time

TABLE 15

Effects of treatment and reach on chlorophyll-specific productivity (mg C · mg chlorophyll *a* · n^{-1}) in aufwuchs. F-values and their significance levels are from a two-way analysis of variance, $\alpha = .10$. Sample means are given in parenthesis. Means underscored with the same line do not significantly differ (Duncan's multiple range test, $\alpha = .10$).

WEEK	SOURCE	d.f.	F	P	MEAN CHLOROPHYLL-SPECIFIC PRIMARY PRODUCTIVITY
0	TREATMENT	3	3.40	0.0533	M(0.980) U(0.495) H(0.440) L(0.369)
	REACH	4	10.64	0.0006	C(1.075) E(0.779) D(0.710) B(0.090) A(0.054)
1	TREATMENT	3	0.44	ns	M(1.331) U(1.036) H(0.808) L(0.650)
	REACH	4	3.55	0.0549	D(2.000) A(1.143) C(0.539) B(0.481) E(0.090)
2	TREATMENT	3	2.75	ns	H(3.087) M(3.049) U(2.401) L(1.049)
	REACH	4	0.35	ns	C(0.290) D(0.285) E(0.225) A(0.202) B(0.158)
4	TREATMENT	3	3.18	0.0633	U(91.300) L(1.953) H(1.897) M(1.473)
	REACH	4	0.92	ns	D(64.689) B(52.305) E(6.455) C(3.361) A(1.874)

TABLE 15 (CONTINUED)

WEEK	SOURCE	d.f.	F	P	MEAN CHLOROPHYLL-SPECIFIC PRIMARY PRODUCTIVITY
5	TREATMENT	3	0.173	ns	H(23.137) U(7.804) L(4.894) M(2.578)
	REACH	4	1.65	ns	E(36.554) B(5.986) D(2.056) A(1.847) C(1.418)
6	TREATMENT	3	2.98	0.792	U(15.212) M(2.796) L(2.021) H(1.043)
	REACH	4	0.79	ns	D(10.405) A(6.796) E(2.927) C(2.855) B(2.773)

TABLE 16

Effects of treatment and reach on biomass-specific productivity (mg C · g dry mass^{-1} · h^{-1}) in aufwuchs. F-values and their significance levels are from a two-way analysis, $\alpha = .10$. Sample means are given in parentheses. Means underscored with the same line do not significantly differ (Duncan's multiple range test, $\alpha = .10$).

WEEK	SOURCE	d.f.	F	P	MEAN BIOMASS-SPECIFIC PRIMARY PRODUCTIVITY
0	TREATMENT	3	3.21	0.0620	U(3.2924) H(3.2237) M(3.1463) L(1.3657)
	REACH	4	15.38	0.0001	E(5.0629) C(4.2564) D(3.5790) A(0.3686) B(0.1435)
1	TREATMENT	3	8.93	0.0022	M(3.4689) U(3.2232) L(2.1052) H(1.7371)
	REACH	4	17.45	0.0001	C(3.5735) D(3.2893) A(3.2162) B(2.8982) E(0.0831)
2	TREATMENT	3	1.34	ns	U(2.8774) M(2.7283) L(1.1912) H(0.8132)
	REACH	4	0.80	ns	C(3.5941) D(1.6709) A(1.227) B(0.8846) E(0.0031)
4	TREATMENT	3	13.61	0.0004	U(5.6974) M(1.7010) L(1.6581) H(1.3823)
	REACH	4	0.60	0.6728	A(2.9801) B(2.9730) C(2.9325) D(2.0862) E(2.0767)

TABLE 16 (CONTINUED)

WEEK	SOURCE	d.f.	F	P	MEAN BIOMASS-SPECIFIC PRIMARY PRODUCTIVITY
5	TREATMENT	3	2.11	ns	U(6.2242) H(5.0172) L(3.1025) M(3.7000)
	REACH	4	0.61	ns	E(22.438) A(13.887) C(2.445) D(2.349) B(1.736)
5	TREATMENT	3	18.41	0.0001	U(5.6043) L(4.1149) M(2.8453) H(1.6133)
	REACH	4	5.10	0.0123	D(4.8922) C(4.0813) E(3.5745) B(3.0372) A(2.3823)

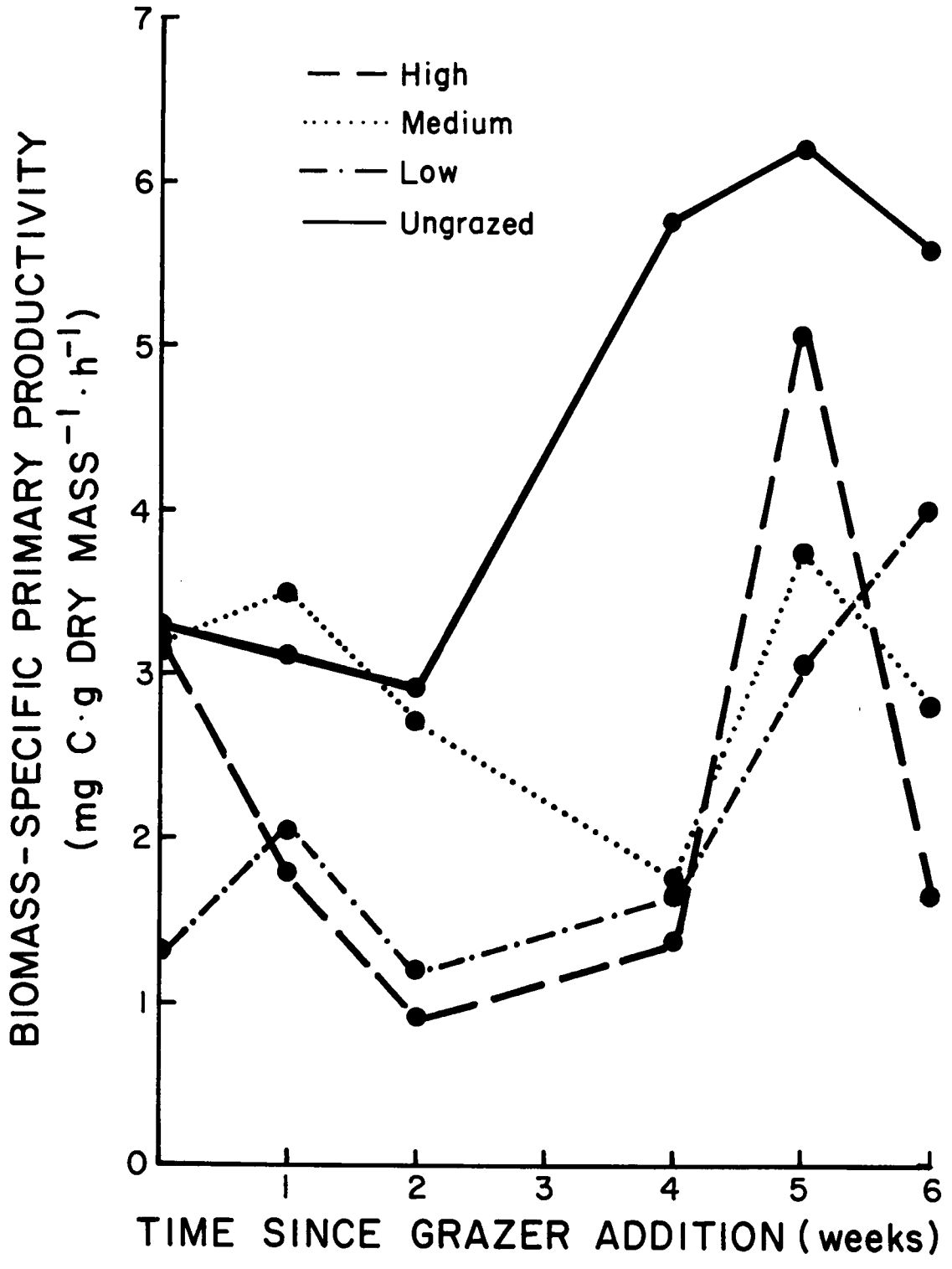


FIGURE 13

Biomass-specific primary productivity versus time

TABLE 17

Comparison of effects of grazing treatment on nutrient concentrations in streamwater. F-values and their significance levels are from a two-way analysis of variance (α = .10). Sample means are given in parentheses. Means underscored with the same line are not significantly different (Duncan's multiple range test, α = .10).
(H, M, L, U = high, medium, low & ungrazed treatments, I = water inlet, D = reach D).

NUTRIENT	WEEK	SOURCE	d.f.	F	P	MEAN NUTRIENT ($\mu g \cdot m\ell^{-1}$)
PO_4 - P						
	0	TREATMENT	3	1.00	ns	m(.00325) L(.00300) H(.00250) u(.00250)
		REACH	1	1.00	ns	I(.00300) D(.00225)
	1	TREATMENT	3	1.00	ns	L(.00100) m(.00075) H(.00050) u(.00050)
		REACH	1	.03	ns	D(.00075) I(.00067)
	2	TREATMENT	3	1.00	ns	u(.00767) H(.08667) m(.00600) L(.00567)
		REACH	1	11.57	.0424	I(.00800) (.00350)
	3	TREATMENT	3	1.00	ns	L(.00450) H(.00350) m(.00325) u(.00325)
		REACH	1	4.41	ns	D(.00550) I(.00300)

TABLE 17 (continued)

NUTRIENT	WEEK	SOURCE	d.f.	F	P	MEAN NUTRIENT ($\mu g \cdot m\ell^{-1}$)
PO_4 - P (con't)						
	4	TREATMENT	3	1.00	ns	H(.00275) u(.00275) L(.00250) M(.00250)
		REACH	1	27.00	0.0138	I(.00300) D(.00150)
	5	TREATMENT	3	1.00	ns	L(.00275) m(.00275) H(.00250) u(.00250)
		REACH	1	0.33	ns	I(.00267) D(.00250)
	6	TREATMENT	3	1.00	ns	H(.00433) m(.00433) u(.00400) L(.00360)
		REACH	1	6.82	0.0796	I(.00450) D(.00325)
NO_3 - N						
	0	TREATMENT	3	1.00	ns	L(.1545) M(.1532) u(.1512) H(1.430)
		REACH	1	5.68	0.0974	I(.1567) D(.1320)

TABLE 17 (continued)

NUTRIENT	WEEK	SOURCE	d.f.	F	P	MEAN NUTRIENT ($\mu g \cdot m\ell^{-1}$)
NO_3 - N (con't)						
	1	TREATMENT	3	1.00	ns	L(.1488) H(.1470) m(.1463) u(.1437)
		REACH	1	3.34	ns	I(.1483) D(.1407)
	2	TREATMENT	3	1.00	ns	m(.1647) L(.1642) H(.1623) u(.1580)
		REACH	1	10.69	.0468	I(.1673) D(.1472)
	3	TREATMENT	3	1.00	ns	u(.1420) L(.1412) H(.1410) M(.1363)
		REACH	1	17.39	.0251	D(.1565) I(.1347)
	4	TREATMENT	3	1.00	ns	H(.1525) L(.1515) M(.1515) u(.1475)
		REACH	1	69.61	.0036	I(.1600) D(.1230)
	5	TREATMENT	3	0.68	ns	H(.1370) L(.1365) u(.1352) M(.1228)
		REACH	1	1.57	ns	I(.1370) D(.1150)

TABLE 17 (continued)

NUTRIENT	WEEK	SOURCE	d.f.	F	P	MEAN NUTRIENT ($\mu g \cdot m\ell^{-1}$)
NO_3 - N (con't)						
	6	TREATMENT	3	1.00	ns	m(.1537) H(.1513) L(.1413) u(.1413)
		REACH	1	21.43	.0190	J(.1620) D(.1168)
NH_4^+ - N						
	0	TREATMENT	3	1.00	ns	L(.00575) m(.00500) H(.00435) u(.00425)
		REACH	1	0.75	ns	D(.00575) E(.00467)
	1	TREATMENT	3	1.00	ns	m(.00875) L(.00850) u(.00800) H(.00750)
		REACH	1	0.28	ns	I(.00833) D(.00775)
	2	TREATMENT	3	1.00	ns	L(.00725) m(.00725) u(.00700) H(.00650)
		REACH	1	14.22	0.0326	I(.00767) D(.00500)

TABLE 17 (continued)

NUTRIENT	WEEK	SOURCE	d.f.	F	P	MEAN NUTRIENT - P($\mu g \cdot m\ell^{-1}$)
NH_Y^+ - N (con't)						
	3	TREATMENT	3	1.00	ns	H(.00575) u(.00500) L(.00200) m(.00150)
		REACH	1	3.18	ns	D(.00925) I(.00167)
	4	TREATMENT	3	1.00	ns	H(.04350) m(.04275) u(.04100) L(.0400)
		REACH	1	22.74	0.0175	D(.0532) I(.0380)
	5	TREATMENT	3	1.00	ns	L(.01775) u(.01550) m(.01525) H(.01475)
		REACH	1	33.65	0.0102	I(.01967) D(.00425)
	6	TREATMENT	3	1.00	ns	L(.03667) m(.03633) H(.03533) u(.03532)
		REACH	1	2329.47	0.0001	I(.05250) D(.00275)

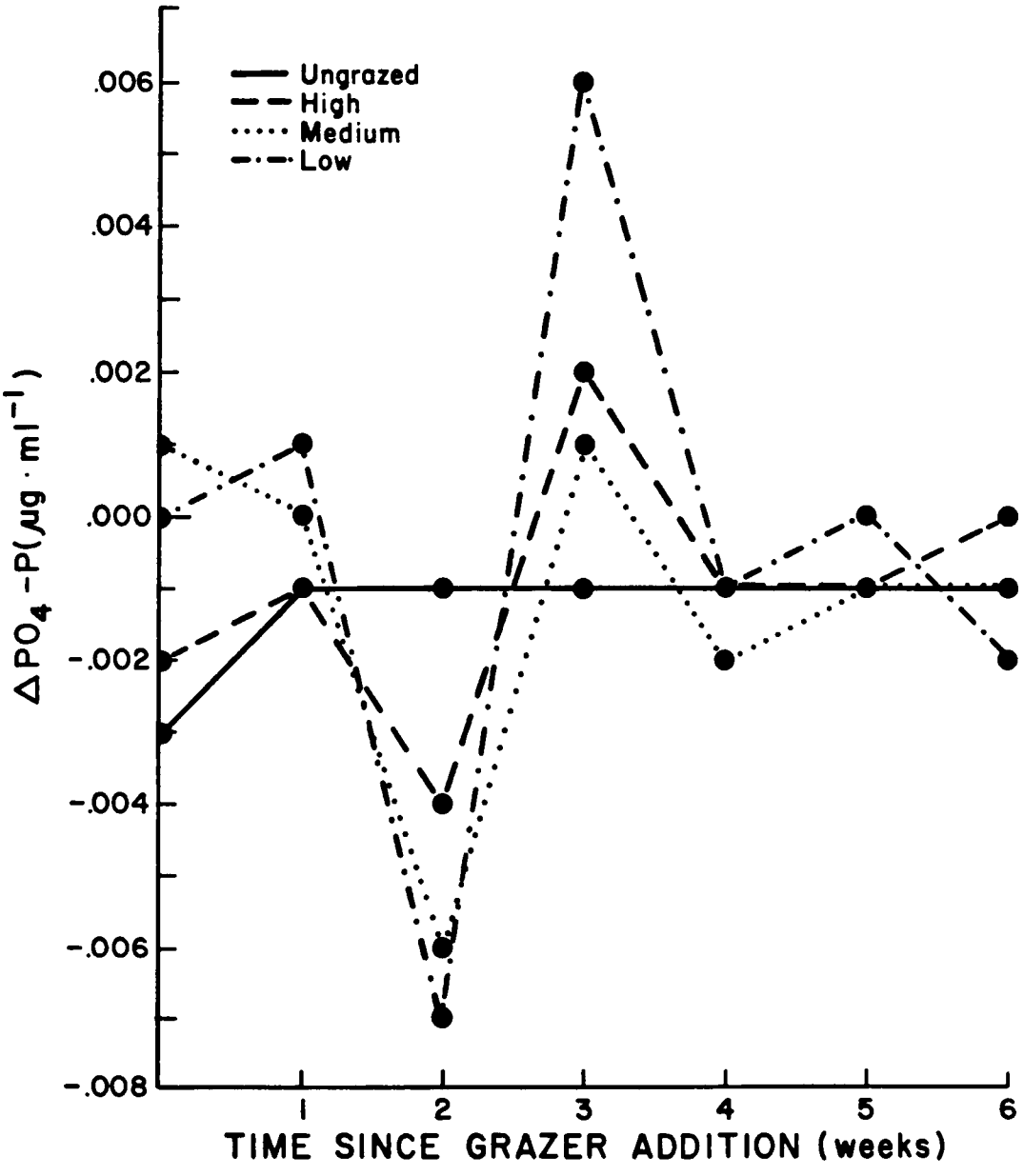


FIGURE 14

Change in phosphate concentration through time

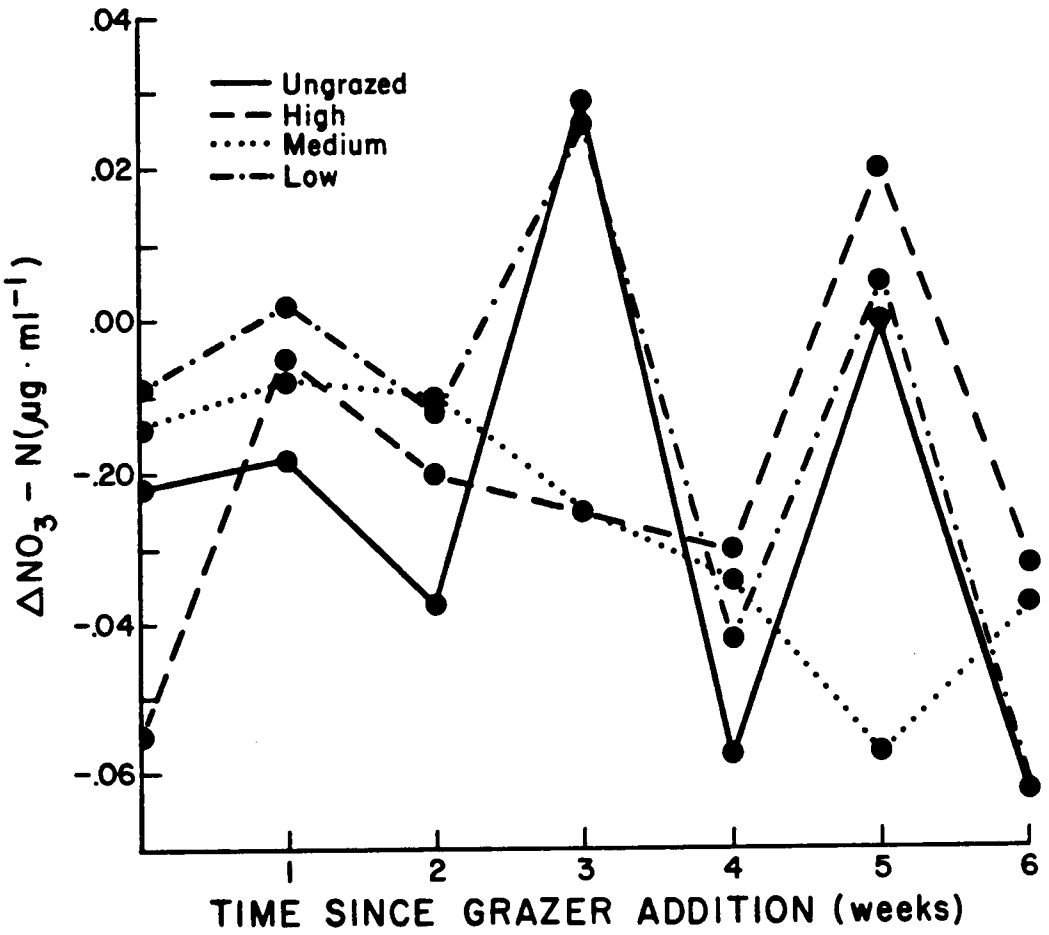


FIGURE 15

Change in nitrate concentration versus time

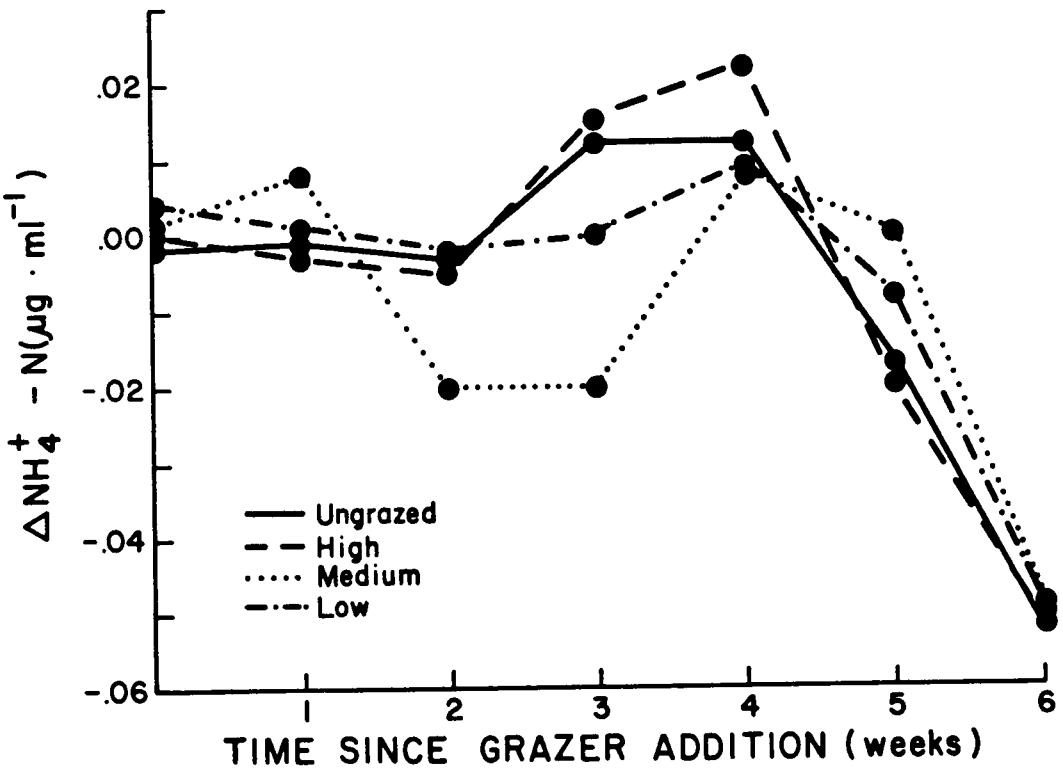


FIGURE 16

Change in ammonia concentration versus time

in week 4. The inlet and reach D did not differ significantly in weeks 1 and 5 for PO_4^{-3} - P and NO_3^{-2} - N , and in weeks 0 and 1 for NH_4^+ - N . In the remaining weeks, however, water from the downstream station contained significantly lower concentrations of PO_4^{-3} - P (weeks 2, 4, 6), NO_3^{-2} - N (weeks 0, 2, 4, 6) and NH_4^+ - N (weeks 2, 5, 6). This indicates that a net loss of nutrients from water may have occurred during at least part of the study. Some of the reach effects noted above thus may have been a result of nutrient depletion.

The reduction in aufwuchs standing stock that resulted from grazer activities was also reflected in the numbers of individuals in the algal taxa. Seventeen diatom genera, one unidentified green alga, and one unidentified blue-green alga were observed during the experiment. Diatoms were counted as individual cells, but green and blue-green algae were counted as colonies. Unidentifiable debris of diatom origin (classified by the presence of fragments of diatom valves) and clumps of cells too dense to identify or count were counted as detritus. This classification was probably biased in favor of Gomphonema, Cymbella, Cymatopleura, and Surilella because their highly distinctive morphology facilitated identification even when partially obscured by dense clumps, whereas smaller or more nondescript genera, such as Stauroneis or Navicula, would not have been recognizable.

In the ungrazed samples Fragilaria and Eunotia often formed long, ropy chains in the first weeks of the experiment. During the last few weeks, however, they were largely replaced by dense clusters of Achnanthes and Amphora. The densities of cells of these four genera in each microscope field was often too high (> 100) to obtain an accurate count in

a reasonable amount of time (< 10 min · genus^{-1} · field^{-1}). Consequently, in such cases, the number of individuals in these genera was estimated to the nearest 25 cells. This degree of precision was used when the number of individuals in these genera were much greater than the number of individuals in other genera. In addition, these estimates were verified occasionally by counting individual cells.

The effects of reach on abundance were rarely significant for any species (Table 18). In comparison, the number of cells of a given genus was significantly lower in grazed treatments than in the ungrazed treatment for Fragilaria, Meridion, Melosira, Synedra, Eunotia, Achnanthes, Stauroneis, Navicula, Gomphonema, Cymbella, Amphora, Nitzschia, Cymatopleura, the green alga, the blue-green alga, and detritus. Furthermore, the numbers of Cocconeis, Rhoicosphenia, Pleurosigma, and Surilella were not significantly affected by treatment. This implies that their frequency of occurrence relative to other genera increased in the grazed treatments compared to the ungrazed treatments.

Kesler (1981) suggested that Cocconeis is able to escape predation by snails through its ability to cement a valve to the substrate thus making it more resistant to grazers. It is quite possible that his mechanism enabled Cocconeis to maintain its relatively high population numbers here. The lack of change in the numbers of Rhoicosphenia, Pleurosigma, and Surilella is probably attributable to their rarity rather than to a similar predator avoidance strategy.

In addition to the analyses of variance on individual species, an analysis of variance was also performed on the total mean number of cells (calculated as the mean number of individuals of each genus

summed over all genera). Because no replicates were available for this analysis, the F-statistic was constructed using the error sums of squares, rather than the interaction term. Again, differences attributable to reach effects were not significant, however, the total mean number of cells in grazed treatments was significantly lower than the total mean number of cells in the ungrazed treatment (Table 19, Figure 16).

The relative abundance of large chain-forming diatoms (Melosira, Fragilaria, Meridion, Synedra, Eunotia, Gomphenema, and Nitzschia) decreased throughout the investiation in all treatments (Figure 17). Conversely, the abundance of small forms (Achnanthes, Stauroneis) drastically increased through time in the ungrazed treatment but remained relatively constant in the grazed treatments. The gradual increase in the relative abundance of medium-sized diatoms (Navicula, Cymbella, Amphora, Rhoicosphenia, Pleurosigma, Surilella, Cymatopleura) in the ungrazed treatment was probaly due to the higher numbers of Amphora in the latter part of the experiment. This increase was not observed in the grazed treatments.

As might be expected, the relative abundance of detrital particles increased through time in the grazed treatment, but remained at a fairly constant low level in the ungrazed treatment. Furthermore, in the last two weeks of the study, detrital particles composed a large portion (ca. 30 percent) of the aufwuchs in samples from the high and medium grazed treatments. In comparison, large and small sized diatoms remained more abundant than detritus in samples from the low grazer density.

TABLE 18

Effects of grazing on abundance of algal genera. F-values and their significance levels are from a two-way analysis of variance ($\alpha = .10$). Sample means are given in parentheses. Means underscored with the same line are not significantly different (Duncan's multiple range test, $\alpha = .10$).

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Melosira						
	0	TREATMENT	3	2.26	ns	U(9.1) M(7.3) L(5.9) H(3.2)
		REACH	4	1.21	ns	B(10.3) E(8.6) C(6.9) A(5.4) D(3.4)
	2	TREATMENT	3	0.75	0.0478	U(17.9) M(5.9) L(0.3) H(0.0)
		REACH	4	3.55	ns	E(10.4) A(9.6) C(5.8) B(2.3) D(1.1)
	4	TREATMENT	3	7.52	0.0052	U(7.2) H(1.5) M(0.1) L(0.0)
		REACH	4	1.41	ns	A(4.7) C(3.4) B(2.6) D(2.1) E(0.0)
	6	TREATMENT	3	34.04	0.0001	U(11.2) H(0.5) L(0.1) M(0.1)
		REACH	4	0.41	ns	z(3.6) C(3.5) D(3.2) B(2.5) A(2.1)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Meridion						
	0	TREATMENT	3	6.71	0.0045	H(110.5) M(80.7) U(59.1) L(49.8)
		REACH	4	7.40	0.0046	A(114.7) B(91.9) C(70.5) E(53.9) D(44.4)
	2	TREATMENT	3	3.8	0.0040	L(17.9) U(14.5) M(5.9) H(1.3)
		REACH	4	0.42	ns	E(14.1) C(11.1) D(8.8) A(7.8) B(7.7)
	4	TREATMENT	3	20.54	0.0001	U(3.7) H(0.7) L(0.4) M(0.3)
		REACH	4	1.52	ns	D(2.1) B(1.5) C(1.3) A(1.3) E(0.7)
	6	TREATMENT	3	11.74	0.0007	U(2.1) L(0.5) H(0.4) M(0.1)
		REACH	4	0.68	ns	B(1.1) A(0.9) D(0.7) E(0.6) E(0.5)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Fragilaria						
	0	TREATMENT	3	15.91	0.0002	U(1156.8) M(886.8) L(681.6) H(382.3)
		REACH	4	4.36	-.0209	C(985.1) B(858.7) A(825.5) E(710.5) D(487.9)
	2	TREATMENT	3	5.61	0.0122	U(204.3) L(103.9) M(54.1) L(12.4)
		REACH	4	1.37	ns	E(143.2) C(128.6) D(64.7) B(63.9) A(51.7)
	4	TREATMENT	3	41.20	0.0001	U(34.5) L(9.3) M(2.3) H(1.3)
		REACH	4	1.29	ns	E(15.5) C(13.5) D(13.3) A(10.0) B(7.3)
	6	TREATMENT	3	15.51	0.0002	U(42.8) H(2.4) L(2.5) M(1.2)
		REACH	4	1.40	ns	A(23.9) C(12.5) D(10.6) B(8.1) E(6.7)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Synedra						
	0	TREATMENT	3	1.37	ns	L(49.1) U(38.3) M(37.3) H(21.9)
		REACH	4	.71	ns	C(50.0) A(37.4) E(37.0) A(32.2) D(25.8)
	2	TREATMENT	3	3.96	0.0355	U(12.2) L(10.5) M(5.0) H(1.1)
		REACH	4	0.88	ns	C(10.7) E(9.3) B(6.1) D(5.0) A(4.4)
	4	TREATMENT	3	3.73	ns	U(2.4) L(1.3) H(0.8) M(0.1)
		REACH	4	1.83	0.0453	D(2.3) B(1.2) C(0.9) E(0.7) A(0.3)
	6	TREATMENT	3	30.44	0.0001	U(3.1) L(0.2) M(0.1) H(0.1)
		REACH	4	1.44	ns	C(1.3) A(1.0) B(0.9) D(0.8) E(0.3)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Eunotia						
	0	TREATMENT	3	11.96	0.0006	H(96.9) M(48.5) U(32.1) L(19.9)
		REACH	4	0.85	ns	A(63.7) Q(54.0) B(51.3) E(42.1) D(39.2)
	2	TREATMENT	3	4.19	0.0303	L(97.7) U(26.3) H(5.5) M(4.6)
		REACH	4	1.00	ns	E(65.5) C(49.8) D(29.9) A(12.1) B(10.4)
	4	TREATMENT	3	18.57	0.0001	U(69.6) H(5.4) L(3.9) M(2.5)
		REACH	4	1.09	ns	B(37.1) D(27.5) E(17.1) C(15.9) A(12.0)
	6	TREATMENT	3	74.97	0.0001	U(173.9) L(17.3) H(4.5) M(3.1)
		REACH	4	1.5	ns	A(64.9) C(57.1) A(52.7) E(43.3) 8(30.4)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Achmanthes						
	0	TREATMENT	3	27.11	0.0001	U(239.3) H(91.1) L(81.3) M(48.7)
		REACH	4	0.16	ns	E(128.9) C(115.4) A(114.4) B(113.7) D(106.1)
	2	TREATMENT	3	23.44	0.0001	U(105.5) L(29.3) M(4.5) H(2.1)
		REACH	4	0.52	ns	B(40.6) C(40.6) D(34.8) E(34.3) A(22.0)
	4	TREATMENT	3	19.45	0.0001	U(175.3) L(1.7) H(0.5) M(0.4)
		REACH	4	0.84	ns	C(87.6) B(55.1) D(49.1) E(29.8) A(23.7)
	6	TREATMENT	3	33.87	0.0001	U(290.8) L(6.0) M(3.6) H(2.8)
		REACH	4	0.88	ns	D(106.4) A(96.4) E(75.6) C(50.6) B(49.9)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Rhoicosphenia						
	0	TREATMENT	3	1.52	ns	H(0.3) L(0.3) u(0.3) m(0.1)
		WEEK	4	1.84	ns	B(0.3) D(0.3) C(0.2) E(0.1) A(0.1)
	2	TREATMENT	3	1.06	ns	L(0.2) M(0.1) (0.1) (0.0)
		REACH	4	1.05	ns	E(2.5) A(0.1) B(0.1) C(0.1) D(0.0)
	4	TREATMENT	3	.88	ns	H(0.6) L(0.0) M(0.0) U(0.0)
		REACH	4	.89	ns	D(0.7) A(0.0) B(0.0) C(0.0) E(0.0)
	6	TREATMENT	3	1.81	ns	U(0.3) H(0.1) L(0.0) M(0.0)
		REACH	4	1.54	ns	A(0.3) D(0.2) B(0.0) C(0.0) E(0.0)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Cocconeis						
	0	TREATMENT	3	5.47	0.0133	U(3.3) M(2.3) L(1.1) H(0.7)
		REACH	4	1.31	ns	E(2.3) C(2.3) D(2.3) A(1.4) A(0.9)
	2	TREATMENT	3	3.82	0.0394	U(1.3) M(0.9) L(0.5) A(0.5)
		REACH	4	0.89	ns	D(1.1) E(0.9) B(0.8) C(0.7) A(0.6)
	4	TREATMENT	3	1.94	ns	M(8.7) U(3.5) H(3.3) L(1.7)
		REACH	4	0.95	ns	D(7.1) E(5.9) B(4.0) C(4.0) A(0.7)
	6	TREATMENT	3	2.54	ns	U(8.7) M(6.3) L(4.5) H(4.3)
		REACH	4	1.26	ns	D(8.6) E(5.9) C(5.5) B(5.0) A(4.5)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Pleurosigma						
	0	TREATMENT	3	1.01	ns	H(0.1) M(0.1) L(0.0) U(0.0)
		REACH	4	2.37	ns	E(0.0) D(0.0) B(0.0) C(0.0) A(0.0)
	2	TREATMENT	3	0.0	ns	H(0.0) L(0.0) M(0.0) U(0.0)
		REACH	4	0.0	ns	A(0.0) B(0.0) C(0.0) D(0.0) E(0.0)
	4	TREATMENT	3	0.0	ns	H(0.0) L(0.0) M(0.0) U(0.0)
		REACH	4	0.0	ns	A(0.0) B(0.0) C(0.0) D(0.0) E(0.0)
	6	TREATMENT	3	0.0	ns	H(0.0) L(0.0) M(0.0) U(0.0)
		REACH	4	0.0	ns	A(0.0) B(0.0) C(0.0) D(0.0) E(0.0)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Stauroneis						
	0	TREATMENT	3	25.95	0.0001	U(271.7) L(125.2) H(111.3) M(46.9)
		REACH	4	0.66	ns	A(166.9) B(136.6) E(175.4) D(124.5) C(122.5)
	2	TREATMENT	3	10.12	0.0013	U(141.3) L(36.1) M(7.6) H(2.9)
		REACH	4	0.77	ns	B(65.0) C(63.1) E(50.1) D(28.2) A(21.3)
	4	TREATMENT	3	16.53	0.0002	U(198.1) L(2.7) M(1.4) H(0.9)
		REACH	4	0.97	ns	C(99.2) E(65.2) D(45.6) B(44.0) A(21.9)
	6	TREATMENT	3	44.14	0.0001	U(272.3) L(6.9) M(4.1) H(2.4)
		REACH	4	0.89	ns	D(107.4) A(70.9) B(67.9) C(56.4) E(54.6)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Navicula						
	0	TREATMENT	3	5.24	0.0153	U(89.7) M(87.3) H(63.6) L(47.7)
		REACH	4	0.54	ns	E(79.7) C(75.1) A(74.1) B(72.0) D(60.6)
	2	TREATMENT	3	11.91	0.0007	U(20.5) L(5.9) M(5.3) H(0.8)
		REACH	4	1.08	ns	E(11.1) C(9.9) B(8.7) A(5.3) D(4.6)
	4	TREATMENT	3	19.31	0.0001	U(9.0) H(0.9) M(0.7) L(0.5)
		REACH	4	0.07	ns	B(5.0) C(3.3) D(2.7) A(2.7) E(1.6)
	6	TREATMENT	3	14.66	0.0003	U(6.9) L(0.3) H(0.2) M(0.2)
		REACH	4	0.83	ns	B(3.2) E(2.1) A(1.9) C(1.9) D(0.7)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Cymbella						
	0	TREATMENT	3	0.13	0.0049	L(8.7) H(8.1) M(7.9) U(7.7)
		REACH	4	6.56	ns	A(12.2) B(8.6) C(8.5) E(7.6) D(3.5)
	2	TREATMENT	3	9.45	0.0017	U(5.0) M(1.3) L(1.1) H(0.2)
		REACH	4	0.56	ns	A(2.5) E(2.3) C(1.9) B(1.3) D(1.1)
	4	TREATMENT	3	7.49	0.0053	U(13.2) L(0.3) H(0.1) M(0.0)
		REACH	4	0.85	ns	D(7.4) C(4.7) A(2.8) B(2.3) E(1.1)
	6	TREATMENT	3	2.96	0.0748	U(1.0) L(0.6) M(0.1) H(0.0)
		REACH	4	0.96	ns	C(0.9) A(0.5) D(0.3) E(0.3) B(0.1)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Amphora						
	0	TREATMENT	3	0.39	ns	M(10.7) H(10.1) L(9.1) U(8.6)
		REACH	4	2.91	0.0675	B(12.9) C(10.7) A(9.6) E(9.4) D(5.5)
	2	TREATMENT	3	6.23	0.0085	U(5.6) L(3.8) H(0.8) M(0.8)
		REACH	4	2.08	ns	E(5.3) D(2.6) B(2.1) C(1.8) A(1.7)
	4	TREATMENT	3	11.82	0.0009	U(32.1) L(0.7) H(0.0) M(0.0)
		REACH	4	1.21	ns	E(16.1) C(10.9) D(7.6) B(5.1) A(3.4)
	6	TREATMENT	3	7.60	ns	U(181.6) M(1.5) L(1.2) H(1.0)
		REACH	4	1.01	0.0041	D(109.6) E(42.5) A(33.2) C(32.0) B(14.4)

TABLE 18 (CONTINUED)

GENUS	WEEK	SOURCE	d.f.	F	P	MEAN NUMBER OF CELLS
Nitzschia						
	0	TREATMENT	3	3.71	0.0426	(33.4) L(28.9) M(27.1) H(20.3)
		REACH	4	8.67	0.0016	C(35.4) A(34.6) B(30.4) E(18.3) D(16.8)
	2	TREATMENT	3	4.69	0.0217	L(15.3) U(9.6) M(3.8) H(1.2)
		REACH	4	1.22	ns	E(12.4) C(8.8) D(8.0) B(4.6) A(3.4)
	4	TREATMENT	3	24.26	0.0001	U(4.6) L(1.5) H(0.3) M(0.2)
		REACH	4	2.05	ns	D(2.7) B(1.5) E(1.4) C(1.4) A(1.1)
	6	TREATMENT	3	15.61	0.0002	U(9.6) L(0.9) M(0.6) H(0.4)
		REACH	4	1.17	ns	A(4.8) C(3.7) D(2.6) B(2.1) E(1.3)

TABLE 19

Analysis of variance for total mean number of cells.

WEEK	F	P	MEAN
0	0.02	ns	U(2498.24) M(1679.63) L(1448.27) H(1188.69)
2	8.62	.0050	U(550.34) L(345.35) M(115.70) H(36.43)
4	20.82	.0001	U(519.98) L(28.85) M(26.30) H(23.30)
6	79.50	.0001	U(1224.36) L(53.70) H(33.40) M(28.45)

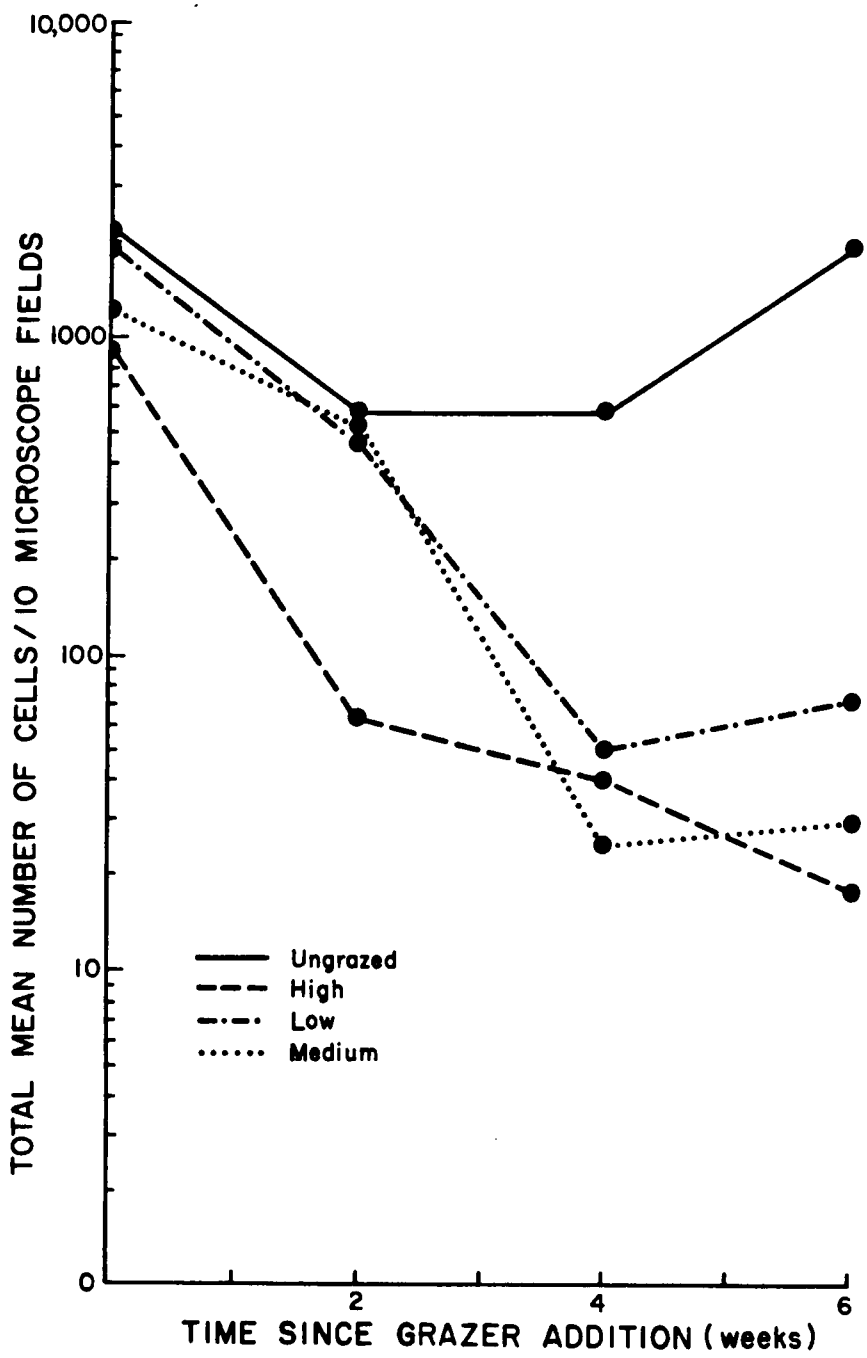


FIGURE 17

Total number of algal cells
per 10 microscope fields versus time

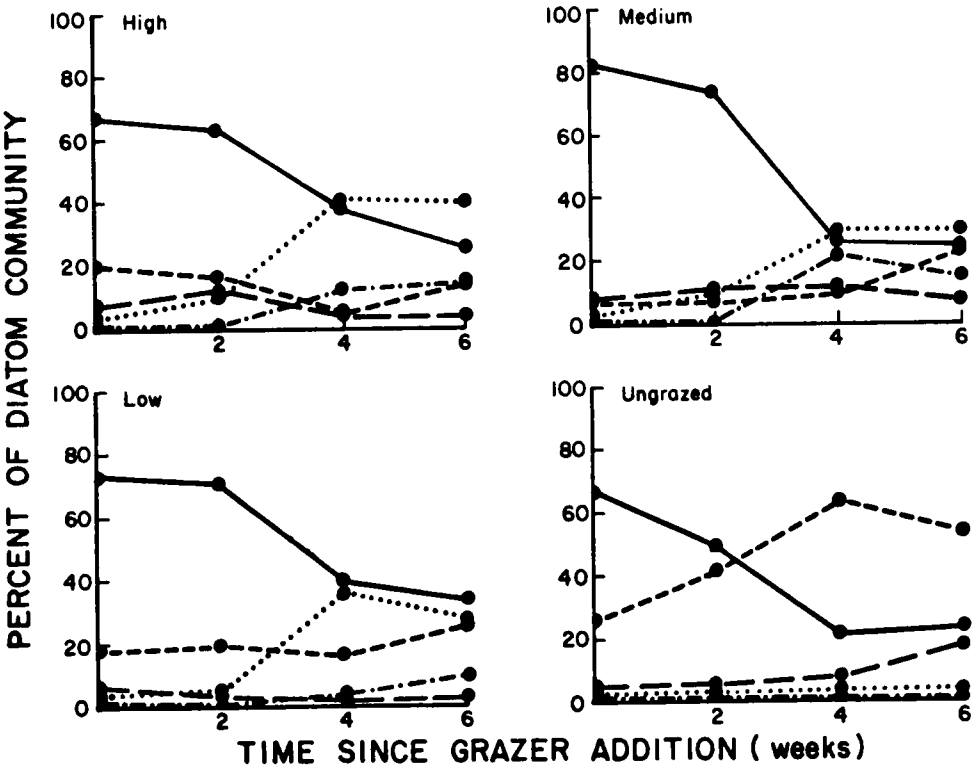


FIGURE 18

Diatom community composition through time

large diatoms ———

medium size diatoms — —

small diatoms - - - -

detritus .....

Cocconeis -.-.-.-

II. Stability Analysis

In order to determine the effects of diffusion and advection on the aufwuchs-grazer model (1.2) the stability properties of the spatially homogeneous system shall first be considered. By examining progressively complex models, that is, the three-equation (c, s, f) then the four (c, s, a, f) and five (c, s, a, g, f) equation models, more insight into the function of stream systems can be obtained than by investigating only the grazed system.

The (c, s, f) System

The spatially homogeneous three-equation system

$$\frac{\partial c}{\partial \tau} = \alpha_6 f - \frac{\alpha_7\, cf}{(1 + \eta c)(1 + \xi f)}$$

$$\frac{\partial s}{\partial \tau} = \alpha_4 f - \alpha_5\, s \tag{2.1}$$

$$\frac{\partial f}{\partial \tau} = \alpha_4 f + \alpha_5\, s - \alpha_6 f + \frac{\alpha_7\, cf}{(1 + \eta c)(1 + \xi f)}$$

is conservative, i.e.,

$$\frac{\partial c}{\partial \tau} + \frac{\partial s}{\partial \tau} + \frac{\partial f}{\partial \tau} = 0$$

so that

$$c + s + f = \hat{C} \tag{2.2}$$

where $\hat{C}$ is a constant that represents the total amount of carbon

in the system. We will use this additional constraint upon c, s, and f to find the equilibria of (2.1).

By setting the equations (2.1) equal to zero and applying condition (2.2), it can be shown that (2.1) has the unique interior equilibrium (c*, s*, f*) given by

$$c^* = \frac{(\alpha_6+\mu_1\alpha_7 - \alpha_6\eta\hat{C}-\alpha_6\eta\mu_1) + \sqrt{(\alpha_6+\mu_1\alpha_7-\alpha_6\eta\hat{C} - \alpha_6\eta\mu_1)^2 + 4\alpha_6\eta(\alpha_6\hat{C}+\mu_1\alpha_6)}}{2\,\alpha_6\eta}$$

$$g^* = \left(\frac{\alpha_4}{\alpha_5}\right) \frac{\alpha_7\hat{C} - \alpha_6(1 + \eta\hat{C})}{\alpha_6\,\xi(1 + \eta\hat{C})}$$

$$f^* = \frac{\alpha_7\hat{C} - \alpha_6(1 + \eta\hat{C})}{\alpha_6\xi(1 + \eta\hat{C})}$$

where $\mu_1 = \frac{1}{\xi}\left(\frac{\alpha_4}{\alpha_5} + 1\right)$, provided that

$$\alpha_6 + \mu_1\alpha_7 > \alpha_6\eta(\hat{C} - \mu_1)$$

(2.3)

$$\frac{\alpha_7\hat{C}}{1 + \eta\hat{C}} > \alpha_6 \quad .$$

These conditions can be interpreted as the requirement that the fine particulates compartment grow more than it respires and loses to seston transport. This is biologically reasonable, i.e., if the converse were true, then the fine particulates would evidently disappear. The parameter values in Table 3, however, do not satisfy these criteria.

The value for the F uptake parameter, h_7, used here is very small because the concentration of dissolved organic carbon in Walker Branch is very low (ca. 0-1.5 g m^{-3}, Comiskey (1978)). As a result (2.3) cannot hold for any biologically realistic parameter values obtained from streams like Walker Branch. An interior equilibrium for a system that contains only water, seston, and fine particulates therefore does not exist for such streams.

Under these circumstances, boundary equilibria are of great interest. Here, if we allow s or f to vanish, then (2.1) has the boundary equilibrium

$$(c^{**}, s^{**}, f^{**}) = (\hat{C}, 0, 0) .$$

On the other hand, if we allow c to vanish, then we find that $s = f = 0$, which contradicts the nutrient conservation condition (2.2). Thus c must always be nonzero and the system will always maintain at least some carbon in the water.

Now the stability of these equilibria must be examined. Linearizing (2.1) about (c^{**}, g^{**}, f^{**}) yields the Jacobian matrix

$$\begin{matrix} 0 & 0 & \alpha_6 - \dfrac{\alpha_7 \hat{c}}{1 + \eta\hat{c}} \\ 0 & -\alpha_6 & \alpha_4 \\ 0 & \alpha_5 & -\alpha_4 - \alpha_6 + \dfrac{\alpha_7 \hat{c}}{1 + \eta\hat{c}} \end{matrix}$$

with eigenvalues

$$\lambda_1 = 0$$

$$\lambda_2 = -\alpha_5$$

$$\lambda_3 = -\alpha_4 - \alpha_6 + \frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} \quad .$$

A necessary condition for instability of the boundary equilibrium is $\lambda_i > 0$ for some i. By hypothesis, $\alpha_5 > 0$, so $\lambda_2 < 0$. Thus, the instability criterion is $\lambda_3 > 0$, which implies that

$$\frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} > \alpha_4 + \alpha_6 \quad . \tag{2.4}$$

This is satisfied by the parameter values from Table 3. Furthermore, (2.3) cannot be satisfied whenever (2.4) holds, thus existence of a stable boundary equilibrium precludes the existence of an interior equilibrium for the (c, s, f) system. Conversely, it could be expected that the boundary equilibrium for the (c, s, f) system to be locally unstable whenever an interior equilibrium for the system exists (since $\frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} > \alpha_6 \Rightarrow \frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} > \alpha_4 + \alpha_6$) .

The (c, s, a, f) system

The non-dimensionalized spatially homogeneous model with water, seston, aufwuchs, and fine particulate organic matter is

$$\frac{\partial c}{\partial \tau} = \alpha_1 a - \frac{\alpha_2\, ca}{(1 + c)(1 + a)} + \alpha_6 f - \frac{\alpha_7\, cf}{(1 + \eta c)(1 + \xi f)}$$

$$\frac{\partial s}{\partial \tau} = \alpha_3 a^2 + \alpha_4 f - \alpha_5 s$$

(2.5)

$$\frac{\partial a}{\partial \tau} = -\alpha_1 a + \frac{\alpha_2\, ca}{(1 + c)(1 + a)} - \alpha_3\, a^2$$

$$\frac{\partial f}{\partial \tau} = -\alpha_4 f + \alpha_5 s - \alpha_6 f + \frac{\alpha_7\, cf}{(1 + \eta c)(1 + \xi f)} .$$

The additional constraint

(2.6) $\qquad c + s + a + f = \hat{C}$

is derived from the conservative nature of (2.5). Again, $\hat{C}$ represents the total carbon in the system at any time t.

The interior equilibrium of (2.5) can be found from the relationships

$$c^* = \frac{(\alpha_1 + \alpha_3 a)(1 + \kappa a)}{\alpha_2 - (\alpha_1 + \alpha_3 a)(1 + \kappa a)}$$

$$f^* = \{-[\alpha_6 - \alpha_3\, a^2 z + \frac{(\alpha_1 + \alpha_3 a)(1 + \kappa a)}{\alpha_2 - (\alpha_1 + \alpha_3 a)(1 + \kappa a)} (\alpha_6 \eta - \alpha_7 - \alpha_3 a^2 \eta\ )]$$

$$\pm [[\alpha_6 - \alpha_3\, a^2 \xi + \frac{(\alpha + \alpha_3 a)(1 + \kappa a)}{\alpha_2 - (\alpha_1 + \alpha_3 a)(1 + \kappa a)}$$

$$\cdot\ (\alpha_6\eta - \alpha_7 - \alpha_3 a^2\ \xi\eta)]^2$$

$$+ 4\alpha_3\alpha_6\ \xi a^2[1 + \eta(\frac{(\alpha_1 + \alpha_3 a)(1 + a)}{\alpha_2 - (\alpha_1 + \alpha_3 a)(1 + \kappa a)})]^2]^{1/2}$$

$$\frac{1}{2\alpha_6\xi[1 + \eta(\frac{(\alpha_1 + \alpha_3 a)(1 + \kappa a)}{\alpha_2 - (\alpha_1 + \alpha_3 a)(1 + \kappa a)})]}$$

$$s^* = \frac{\alpha_3}{\alpha_5}\ a^2 + \frac{\alpha_4}{\alpha_5}\ f$$

$$g^* = \hat{C} - c - s - f\ .$$

This general form, however, is too algebrically complex to be useful in further analysis. We therefore substitute parameter values from Table 3 to find a specific equilibrium for the system rather than using this general expression. This equilibrium is

$$(c^*,\ s^*,\ a^*,\ f^*) = (1.19,\ 0.16,\ 129.84,\ 568.81).$$

To find boundary equilibria, as previously, only s or f are allowed to vanish. This yields the unique boundary point

$$(c^{**},\ s^{**},\ a^{**},\ f^{**}) = (\hat{C},\ 0,\ 0,\ 0)\ .$$

The stability of these equations can again be analyzed by linearization. The Jacobian matrix for the boundary equilibrium is

$$\begin{bmatrix} 0 & 0 & \alpha_1 - \frac{\alpha_2 \hat{C}}{1 + \hat{C}} & \alpha_6 - \frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} \\ 0 & -\alpha_5 & 0 & \alpha_4 \\ 0 & 0 & -\alpha_1 + \frac{\alpha_2 \hat{C}}{1 + \hat{C}} & 0 \\ 0 & \alpha_5 & 0 & -\alpha_4 - \alpha_6 + \frac{\alpha_7 \hat{C}}{1 + \mu \hat{C}} \end{bmatrix}$$

with eigenvalues

$$\lambda_1 = 0$$

$$\lambda_2 = -\alpha_1 + \frac{\alpha_2 \hat{C}}{1 + \hat{C}}$$

$$\lambda_{3,4} = \frac{-(\alpha_4+\alpha_5+\alpha_6 - \frac{\alpha_7 \hat{C}}{1+\eta \hat{C}} \pm \sqrt{(\alpha_4+\alpha_5+\alpha_6 - \frac{\alpha_7 \hat{C}}{1+\mu \hat{C}})^2 - 4(\frac{-\alpha_5\alpha_7 \hat{C}}{1+\eta \hat{C}} + \alpha_5\alpha_6)}}{2}$$

The boundary equilibrium will therefore be unstable when $\lambda_2 > 0$ or $\lambda_2, \lambda_4 > 0$. The first condition, $\lambda_2 > 0$, requires that

$$\frac{\alpha_2 \hat{C}}{1 + \hat{C}} > \alpha_1 . \tag{2.7}$$

Biologically, this implies that the aufwuchs grows more than it respires. The second condition, $\lambda_3 > 0$ or $\lambda_4 > 0$ may be satisfied in one of two ways. If $(\alpha_4 + \alpha_5 + \alpha_6 - \frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}})^2 + \frac{4\alpha_5\alpha_7 \hat{C}}{1 + \eta \hat{C}} < 4\alpha_5\alpha_6$, then λ_3 and λ_4 are complex conjugates. In this case, the instability

condition reduces to

$$(2.8) \qquad \frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} > \alpha_4 + \alpha_5 + \alpha_6 .$$

This analogous to (2.4) of the (c, s, f) system, i.e., the fine particulates compartment must grow. If, on the other hand,

$$(\alpha_4 + \alpha_5 + \alpha_6 - \frac{\alpha_7 \hat{C}}{1 + \mu \hat{C}})^2 + \frac{4\alpha_5 \alpha_6}{1 + \mu \hat{C}} > 4\alpha_5\alpha_6$$ then λ_3 and λ_4 are

real, with λ_3 positive if either

$$(2.9) \qquad \alpha_7 > \alpha_6$$

$$\frac{\alpha_7 \hat{C}}{1 + \eta \hat{C}} > \alpha_4 + \alpha_5 + \alpha_6 .$$

So for the (c, s, a, f) system, the boundary equilibrium is unstable if either the aufwuchs or fine particulates compartments tend to grow. Conversely, reversal of the inequalities in (2.9) implies that the boundary equilibrium is locally stable.

Although the parameter values in Table 3 (p.20) satisfy (2.7), they also lead to λ_3 and λ_4 real and strictly positive by condition (2.9).

Similarly, the Jacobian matrix for the interior equilibrium is

$$
\begin{bmatrix}
-\alpha_2 \tilde{c}(c, a) & 0 & \alpha_1 - \alpha_2 \tilde{a}(c, a) & \alpha_6 - \alpha_7 \tilde{f}(c, f) \\
0 & -\alpha_5 & 2\alpha_3 a^* & \alpha_4 \\
\alpha_2 c(c, a) & 0 & -\alpha_1 + \alpha_2 \tilde{a}(c, a) - 2\alpha_3 a^* & 0 \\
\alpha_7 \tilde{c}(c_1 f) & \alpha_5 & 0 & -\alpha_4 - \alpha_6 + \alpha_7 \tilde{f}(c, f)
\end{bmatrix}
$$

where

$$\tilde{c}(c_1\ a) = \frac{a^*}{(1 + c^*)^2(1 + a^*)}$$

$$\tilde{c}\ (c_1\ f) = \frac{f^*}{(1 + \eta c^*)(1 + \xi f)}$$

(2.8)

$$\tilde{a}\ (c_1\ a) = \frac{c^*}{(1 + c^*)(1 + a^*)^2}$$

$$\tilde{f}(c_1\ f) = \frac{c^*}{(1 + \eta c^*)(1 + \xi f^*)^2}$$

A similar analysis can be conducted to find the eigenvalues for this matrix in order to determine the stability of the interior equilibrium of (2.7). This interior point should be locally stable whenever the boundary equilibrium is locally unstable.

The (c, s, a, g, f) System

The full nondimensionalized, spatially homogeneous aufwuchs-grazer model is described by the system of equations

$$\frac{\partial c}{\partial \tau} = \alpha_1 a - \frac{\alpha_2\, c}{(1 + c)(1 + a)} + \alpha_6 f - \frac{\alpha_7\, cf}{(1 + \eta c)(1 + \xi f)}$$

$$+ \frac{e_3\, \beta_1\, ga}{(1 + \psi g)(1 + \phi a)}$$

$$\frac{\partial s}{\partial \tau} = \alpha_3\, a^2 + \alpha_4 f - \alpha_s\, s$$

(2.9)
$$\frac{\partial a}{\partial \tau} = -\alpha_1 a + \frac{\alpha_2\, ca}{(1 + c)(1 + a)} - \alpha_3\, a^2 - (1 - e_4)\, \frac{\alpha_1\, ga}{(1 + \psi g)(1 + \phi a)}$$

$$\frac{\partial g}{\partial \tau} = \frac{e_2\, \beta_1\, ga}{(1 + \psi g)(1 + \phi a)} - (\beta_2 + \beta_3 g)g$$

$$\frac{\partial f}{\partial \tau} = -\alpha_4 f + \alpha_5 s - \alpha_6 f + \frac{\alpha_7\, cf}{(1 + \eta c)(1 + \xi f)}$$

$$+ \frac{e_1\, \beta_1\, ga}{(1 + \psi g)(1 + \phi a)} + (\beta_2 + \beta_3\, g)g$$

with the additional constraint

(2.10)
$$c + s + a + g + f = \hat{C}$$

where $\hat{C}$ is a constant that represents the total amount of carbon in the system.

Because of the algebraic difficulties in finding equilibria of (2.13), we assume the existence of feasible interior equilibria for certain values of the model parameters. Again, let $(c^*, s^*, a^*, g^*, f^*)$ denote this equilibrium.

The only variable that may vanish from this system is f. When $c = 0$ or $a = 0$, then $g < 0$ for all parameter values. Similarly, when $s = 0$ then $a < 0$ for all parameter values. A feasible boundary equilibrium is therefore obtained only when $f = 0$. This point is

$$(c^{**}, s^{**}, a^{**}, g^{**}, f^{**}) = (\hat{C}, 0, 0, 0, 0) .$$

To study the stability of the boundary equilibrium, linearization about $(\hat{C}, 0, 0, 0, 0)$ is performed. This results in the Jacobian matrix

$$\begin{bmatrix} 0 & 0 & \alpha_1 - \dfrac{\alpha_2 \hat{C}}{1 + \hat{C}} & 0 & \alpha_6 - \dfrac{\alpha_7 \hat{C}}{1 + \mu \hat{C}} \\ 0 & -\alpha_5 & 0 & 0 & \alpha_4 \\ 0 & 0 & -\alpha_1 + \dfrac{\alpha_2 \hat{C}}{1 + \hat{C}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & \alpha_5 & 0 & 0 & -\alpha_4 - \alpha_6 + \dfrac{\alpha_4 \hat{C}}{1 + \eta \hat{C}} \end{bmatrix}$$

This matrix has eigenvalues

$$\lambda_1 = 0$$

$$\lambda_2 = 0$$

$$\lambda_3 = \frac{-\alpha_1 + \alpha_2 \hat{C}}{1 + \hat{C}}$$

$$\lambda_{4,5} = -(\alpha_4+\alpha_5+\alpha_6 - \frac{\alpha_7 \hat{C}}{1 + \eta\hat{C}}) \pm$$

$$\pm \sqrt{(\alpha_4+\alpha_5+\alpha_6 - \frac{\alpha_7 \hat{C}}{1 + \eta\hat{C}})^2 - 4(-\frac{\alpha_5\alpha_7\hat{C}}{1 + \eta\hat{C}} + \alpha_5\alpha_6)} \quad .$$

These eigenvalues are exactly analagous to the eigenvalues for the (c, s, a, f) system boundary equilibrium, hence the conditions for local instability of $(\hat{C}, 0, 0, 0, 0)$ are the same as for $(\hat{C}, 0, 0, 0)$, and moreover, do not directly depend upon grazers.

Linearization of (2.13) about (c*, s*, a*, g*, f*) yields the Jacobian matrix

$$
\begin{bmatrix}
-\alpha_2 \tilde{c}(c_1\ a) - \alpha_7 \tilde{c}(c,\ f) & 0 & \alpha_1 - \alpha_2\tilde{a}(c,\ a) + e_3\ _1\ a(a,\ g) & e_3\ \beta_1\tilde{g}(a,\ g) & \alpha_6 - \alpha_7\ \tilde{f}(c,\ f) \\
0 & -\alpha_5 & 2\alpha_3\ a & 0 & \alpha_4 \\
\alpha_2\ \tilde{c}(c,\ a) & 0 & \alpha_1 + \alpha_2\ \tilde{a}(c,\ a) - 2\alpha_3 a - (1 - e_4)\beta_1\ \tilde{a}(a_1\ g) & (1 - e_4)\beta_1\tilde{g}(a,g) & 0 \\
0 & 0 & e_2\ \beta_1\tilde{a}(a,\ g) & e_2\beta_1\tilde{g}(a,g) - \beta_2 - 2\ \beta_3\ g & 0 \\
\alpha_7\ \tilde{c}(c,\ a) & \alpha_5 & e_1\ \beta_1\tilde{a}(a,g) & e_1\beta_1\tilde{g}(a,\ g) + \beta_2 + 2\beta_3\ g & -\alpha_4-\alpha_6+\alpha_7\ \tilde{f}(c,\ f)
\end{bmatrix}
$$

where

$$\tilde{c}(c, a) = \frac{a^*}{(1 + c^*)^2(1 + a)^*} \qquad \tilde{c}(c_1, f) = \frac{f^*}{(1 + \eta c^*)(1 + \xi f^*)}$$

$$(2.11)\quad \tilde{a}(c, a) = \frac{c^*}{(1 + c^*)(1 + a^*)^2} \qquad \tilde{a}(a_1, g) = \frac{g^*}{(1 + \psi g^*)(1 + \phi a^*)^2}$$

$$\tilde{g}(a, g) = \frac{a^*}{(1 + \psi g^*)^2(1 + \phi a^*)} \qquad \tilde{f}(c_1, f) = \frac{c^*}{(1 + \eta c^*)(1 + \xi f^*)^2}$$

The preceding analyses suggest that the stability or instability of boundary and interior equilibria of stream models is greatly dependent on the dynamics of aufwuchs and fine particulate matter. This suggests that the influence of grazers on the equilibrium behavior of the system may be mediated through either indirect effects upon the detrital pool or by direct effects upon aufwuchs growth rates.

It must be stressed, however, that these results were obtained for spatially homogeneous systems, and therefore, may not be directly applicable to streams.

Several investigations have shown that the addition of diffusion effects to spatially homogeneous models with asymptotically stable solutions can lead to the development of instability for certain parameter values (Okubo 1974, 1978, 1980, Levin 1977, Levin and Segel 1976). Addition of diffusion and advection terms to the model would affect the dynamics of seston and water. This might tend to increase the concentrations of carbon in seston and water relative to other compartments and thus, make carbon more available for the growth of

aufwuchs or fine particulates. Inclusion of spatial effects would also eliminate the total carbon restriction. This loss of the additional degree of freedom permitted by the conservation equation would eliminate (2.4), (2.7), (2.8), (2.9), and (2.12) and allow other factors to potentially affect the stability of equilibria. For example, preliminary analyses on the spatially heterogeneous model suggest that the relative sizes of the equilibrium values for different compartments could be important in determining the stability of the system. In addition, the zero eigenvalue present for the boundary equilibrium of all systems examined indicate that the models are structurally unstable, i.e. that inclusion of non-linear terms could greater alter the stability of the equilibria. Other oscillatory behaviors are also possible. These characteristics could also be an artifact of the total carbon restriction. Inclusion of diffusion and advection terms and the resultant effects upon the stability of equilibria will not be examined here but will be left for future investigations.

Another difficulty in applying this model to stream systems is the inclusion of both inorganic and organic carbon in the same compartment. This loss of compartmentalization is biologically and biochemically unrealistic due to the different sources and utilization of inorganic and organic forms of carbon. Future modelling efforts should also examine the properties of a six compartment model (i.e., dissolved organic carbon, dissolved inorganic carbon, seston, aufwuchs, grazers, and fine particulate organic matter) compared to this five compartment model.

CHAPTER V

DISCUSSION

In order to better understand the effects of snail grazing on aufwuchs observed in this experiment, it is necessary to consider the results as an integrated whole, rather than as isolated measurements of aufwuchs ash free dry mass, pigment concentration, and productivity.

Although aufwuchs biomass was inversely related to grazing pressure, chlorophyll *a* standing stock was not similarly affected, and in fact, tended to be higher at the low grazer density than in the ungrazed treatment. Consequently, the concentration of chlorophyll *a* per gram ash-free dry mass was much higher in the grazed treatments than in the ungrazed. This suggests that grazing 1) decreased the number of non-photosynthetic cells in the aufwuchs, 2) increased the abundance of either algal species containing high levels of chlorophyll *a* or the algal component relative to the heterotrophic component of the aufwuchs, or 3) increased the concentration of chlorophyll *a* in cells of any given algal species without changing community structure.

If the first mechanism was operative, then we could expect elevated concentrations phaeophytin *a* in the ungrazed, compared to the grazed, treatments. This, however, was not observed. In the last weeks of the experiment, the aufwuchs from grazed treatments contained more phaeophytin *a* per gram ash-free dry mass than did aufwuchs from the ungrazed treatments. This suggests that grazing either did not change the quantity of senescent algae or heterotrophic species in the aufwuchs,

or that decreases in algal senescence and heterotrophic were offset by an increase in the quantity of detritus of algal origin. The data presented in Figure 18 (p. 105) support the latter hypothesis. Proportionally more detrital material was observed in the medium and high grazed treatments than in the low treatment.

Further examination of Figure 18 (p. 105) shows that the aufwuchs in the ungrazed treatment did shift from a community dominated by Fragilaria, Eunotia, and other large chain-forming diatom genera, to a one dominated by Achnanthes and Stauroneis. There was no such shift in the community composition in grazed treatments (Figure 18, p. 105). This, however, is not sufficient to differentiate between the second and third hypotheses. Information on species-specific chlorophyll a concentrations under grazing pressure is needed to make this distinction. Thus, although this experiment has not conclusively established the mechanism by which grazing affects the biomass-specific chlorophyll a concentration in aufwuchs, it does suggest avenues for further investigation of this question. Primary production rates were markedly higher in the ungrazed treatment than in any of the grazed treatments. Grazing also resulted in lower biomass-specific productivity in grazed treatments relative to the ungrazed treatment. These results suggest that although grazing actually may have increased chlorophyll concentration per gram A FDM , this elevation of chlorophyll concentration was not sufficient to counteract the decrease in photosynthetic capability caused by the removal of cells at the grazing pressures used here.

Because of the dependence of algal growth rate on nurtient availability (Droop 1972, Tilman & Kilham 1976, Rhee 1978), phosphorus and nitrogen concentrations in the streamwater should also be considered

in the interpretation of the productivity data. Interrelationships between longitudinal changes in nutrient concentration and aufwuchs community metabolism, however, are not clear. The possible depletion of PO_4^{-3} - P , NO_3^{-2} - N , and NH_4^{+} - N in weeks 2 and 6 was correlated with low productivities in all treatments. The higher downstream levels of PO_4 - P , NO_3 - N , and NH_4^{+} - N in week 3 , however, could not be compared to aufwuchs productivity since no productivity data are available for that week. Consequently, any conclusions drawn regarding the relationships between changes in nutrient concentration and primary productivity are tenuous.

Throughout this experiment, I have assumed that observed differences between streams are, in fact, attributable to the presence or absence of grazers. The effects of treatment, however, potentially could be confounded by the influence of the stream channel itself and by channel-treatment interactions. The data thus reflect the effects of stream-treatment combinations. Furthermore, since the experiment was not replicated, it is impossible to partition variability due to these interactions from variability strictly due to grazer treatments, hence the experimental results must be interpreted cautiously.

One of the major confounding factors in this experiment was the difference in initial aufwuchs biomass between streams. Because of the lower aufwuchs standing stocks in the stream channels corresponding to the grazed treatments relative to the ungrazed treatment, the actual grazing pressures were probably (on a relative scale) high, medium high, and medium, rather than high, medium, and low, respectively.

This may have been especially critical with respect to the low grazer treatment. For example, initial primary productivity in the

aufwuchs from the low treatment was only slightly over half as large as the initial primary productivity in the other treatments. In the last three weeks of the experiment, however, the mean primary productivities for samples subject to low grazing pressure were higher than the mean productivities for aufwuchs under the medium and high grazing pressures. Furthermore, biomass-specific primary productivity actually increased through time in the low grazed treatment. Although the final mean value for biomass-specific productivity in the low treatment was still lower than the mean biomass-specific productivity in the ungrazed system, the increase suggests that the potential for grazer stimulation of aufwuchs productivity exists. It is conceivable that aufwuchs productivity in the low treatment could have been higher, and perhaps could have approached the productivity in the ungrazed channel, had the pre-snail biomass-specific primary production rate been higher. Similarly, chlorophyll *a* standing stock was initially lower, but subsequently tended to be higher at the low snail density than at higher grazing treatments.

In spite of the initial discrepancies between treatments, these results seem to indicate that aufwuchs activity may actually be enhanced at some low grazing pressure, as postulated by Cooper (1973), Flint and Goldman (1975), and Pace *et al*. (1979).

It must be noted that estimates of primary productivity obtained through the ^{14}C assimilation technique used here are subject to several sources of potential error that could contribute to sample variability and, thus, confuse the analysis. First, assimilation of radioactive carbon is dependent on the amount of $H^{14}CO_3^-$ available in the incubation

solution. The values used in the calculations were the amounts of $H^{14}CO_3^-$ added to the photosynthesis-respiration chamber; however, these may be erroneous for two reasons. If the chamber was not watertight, then $H^{14}CO_3^-$ water could have been lost from the chamber and been replaced by $H^{12}CO_3^-$ in stream water leading into the chamber. Such an exchange would not have been detectable by observation because the total volume of incubation water would remain approximately constant and would result in an underestimate of primary productivity. Samples of the incubation water were taken at the beginning and end of each incubation in order to check for this leakage and also for depletion of $H^{14}CO_3^-$. In several of these water samples, however, the activity of the samples was as much as 30 percent higher than the maximum theoretical activity of the incubation solution (μ Ci $^{14}CO_3$ added and corrected for dilution by the volume of stream water in the chamber). This discrepancy is too large to have been caused by pipetting error, and implies that the incubation solution was not well-mixed. This could have occurred if a higher concentration of $H^{14}CO_3$ had been localized in an eddy created by the port of the photosynthesis-respiration chamber or in droplets clinging to the port itself. In either case, carbon assimilation would have been underestimated. Since substrates were incubated by reach across all treatments (i.e., samples from a single reach of all treatments in a single incubation), both of these factors would contribute to the error attributable to reach-treatment interaction for any given day. This would have increased the possibility of accepting the hypothesis of no treatment effect when it would have been, in fact, false.

Additional error would have been introduced if nutrients had been depleted from the incubation water. This was unlikely, since a preliminary investigation showed that levels of PO_4^{-3} - P , NO_3^{-2} - N ,

and $NH_4^+ - N$, remained high throughout 120 minutes of incubation (Figure 19). Nutrient depletion cannot be entirely ruled out, however, due to the possible existence of microscale concentration gradients at the cell-water interface. Such gradients would not have been detectable with the sampling and analytical techniques used here.

Several errors associated with filtration of the samples also may have influenced the results. Loss of labeled organic compounds could have resulted from cell lysis during filtration (Steeman-Nielsen et al. 1975). Lysis was probably minimal since low vacuum pressures (< 380 mm Hg) were used throughout (Vollenweider 1974). Acid rinsing the filters to remove $H^{14}CO_3$ may also leach organic matter from cells (Steeman-Nielsen et al. 1975). Fuming with concentrated HCl was used in processing the initial and first week of samples to avoid both this problem and retention of inorganic ^{14}C by the edge of the filter clamped by the filter holder. I discovered, however, that it was difficult to accurately determine the dry mass of these samples. This may have been the result of formation of a hydroscopic residue from HCl fumes combined with the layer of algal cells on the filter. Acid rinsing was therefore used for filter decontamination throughout the remainder of the experiment.

Drying the filters also may have caused a loss of counts from the organic fraction (Wallen and Geen 1968, Lean and Burnison 1979). Drying, however, was necessary to obtain dry mass for the sample.

Snail growth rates exhibited a strong negative correlation with grazer density. This implies that snail growth was limited by food availability. This, in turn, has several implications for Goniobasis

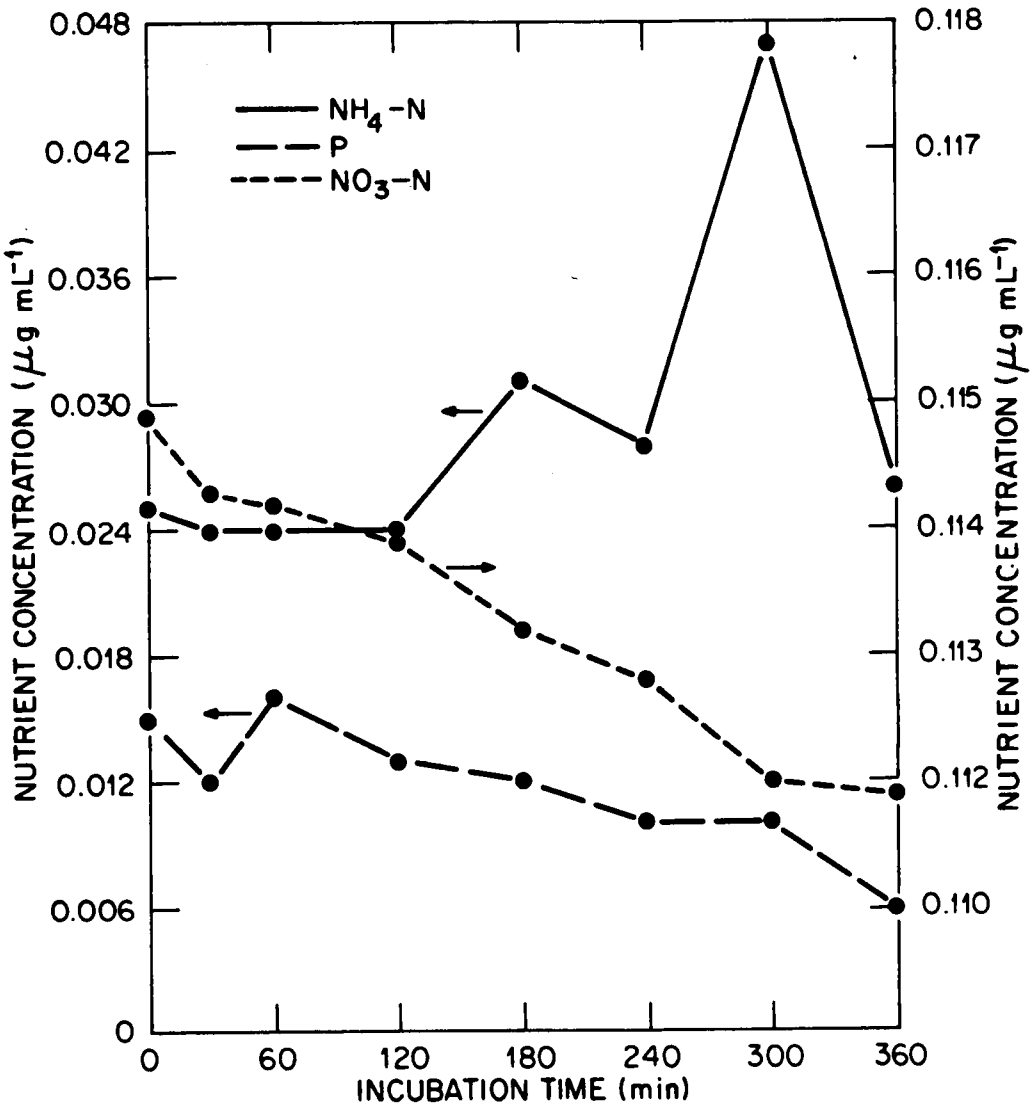


Figure 19

Nutrient concentration vs. time of incubation

population dynamics. Although the relationship between size and fecundity is not known in Goniobasis, large size usually enhances reproductive potential (Calow 1977). First, larger females tend to produce larger clutches of offspring (Calow 1977). Second, size may confer some immunity to predation (Calow 1977), and third, it may be an advantage in resource allocation. Larger snails would be more likely to displace small snails in competitive situations that involved direct interference. In addition, large individuals are more capable of ingesting food particles not available to small snails because of size limitations (Calow 1977, Kliban 1976, Wilson 1975). This may be particularly important during periods of food shortage. Examination of the frequency data in Figure 18 (p.105) indicates that this phenomenon may have occurred at the medium and high snail densities. During the last two weeks of the experiment, the frequencies of all but the large diatom size classes were lower in the high grazing treatment than in the medium grazing treatment. Conversely, large diatoms composed a smaller percentage of the community in the medium treatment than in the higher treatment. These data suggest that the slightly larger snails in the medium treatment were able to exploit large diatoms to a greater extent than could the smaller snails in the high treatment.

Consequently, if we assume that large size is associated with fecundity and thus potentially higher reproductive success than that attained by smaller individuals, then it could be selectivity advantageous for snails to grow large as rapidly as possible. The evidence from this experiment indicates that this might be achieved in systems with a high turnover rate of aufwuchs. This further implies that snails should be prudent predators (sensu Slobodkin 1961), i.e., that

they should cultivate the aufwuchs through mucus deposition (Calow 1974) and controlled grazing rates in order to maintain high biomass-specific productivity. Such a strategy, however, would increase the fitness of a given individual only if that individual were the sole reaper of the harvest. Territoriality is thus a prerequisite for prudent predation. Although territorial behavior has been demonstrated in several species of marine intertidal limpets (Branch 1976), similar defense of territory has not been observed in Goniobasis. Unless Goniobasis is genetically capable of evolving the suite of behaviors necessary for territoriality, and offsetting the costs of territorial behavior by increased food availability, its best foraging strategy is to eat as much as it can whenever it can.

Several authors (Owen and Wiegert 1976, 1981, Stenseth 1978) have suggested that grazers and plants may have coevolved a mutualism in which each participant increases the fitness of the other. If low grazing pressure were to enhance biomass-specific aufwuchs productivity, and thus, aufwuchs growth rate and fitness (sensu Cole, 1954), it could be argued that the aufwuchs-snail system exhibited this relationship. This, hosever, is unlikely for several reasons. First, the mutualism hypothesis assumes that only a part of a multicellular clone of algae is consumed (Stenseth 1978). The uneaten portion of the clone can then benefit from the effects of cropping, e.g. reduction of a potential diffusion limitation on nutrient uptake or increased availability of nutrients via mineralization. In chain-forming diatoms, however, snails graze at the substrate end, rather than at the floating end, of the chain. The cells that would presumably benefit from cropping are thus

the ones most likely to be eaten. In addition, snail fecal pellets and the uneaten segments of the chain would tend to be transported downstream and away from the site of grazing. The algae at the origional site of grazing would consequently tend to lose the nutrients that might be regenerated through mineralization of this detritus. Grazer effects on aufwuchs should therefore be considered with respect to the entire stream, rather than in spatially isolated patches.

The empirical evidence from this investigation implies that snail grazing reduces aufwuchs standing crop and thereby decreases the primary productivity of the entire stream system. The modeling results, however, suggest that this effect may be relatively minor and that growth rates of the aufwuchs community and fine particulate organic matter, rather than standing stocks, are of greater importance in determining the stability of the equilibrium stream community.

This experiment demonstrated that low grazing pressure increased biomass-specific primary productivity relative to its initial (i.e., pre-grazing) productivity. If the increases in productivity were a result of increased rates of nutrient uptake due, for example, to the removal of a diffusion limitation, then the rates of aufwuchs growth would also increase. Grazers could theoretically change an unstable aufwuchs-seston-fine particulates-water system to a stable community. Grazers could also potentially alter processes associated with fine particulates. Grazing may change the particle size distribution in the benthos by reducing relatively thick algal mats to finely divided fecal pellets. This may, in turn, act to increase the availability of nutrients previously tied up in algal biomass through enhanced rates

of mineralization (Barsdate et al. 1974), and also to affect transport rates through differential suspension and settling of large versus small particles. Furthermore, fecal pellets provide a large surface area of nutrient-rich substrate for bacterial colonization (Short and Maslin 1977). This would tend to stimulate growth of fine particulates and thus to increase the quantity and nutritive value of food for collectors (Kaushik and Hynes 1971).

Consequently, although this investigation has served to answer some of the most basic questions on grazer effects on stream aufwuchs, it has also indicated areas for further investigation. These inquiries involve both more reductionistic and more holistic lines of research. The reductionistic approach would entail investigating grazer effects upon signle genera of algae in order to more clearly elucidate the relationship between community composition and changes in chlorophyll-specific and biomass-specific production rates. The holistic approach would seek to integrate grazer activity with the detrital food chain by examining the effects of grazing on transport, nutrient dynamics, and metabolism of fine particulates of different particle sizes (large clump of algal mat vs. small fecal pellet) and origin (algal biomass vs. snail feces). Both of these types of investigation are like to answer meaningful questions on the role of snails in stream ecosystems and to thus further the basic understanding of streams.

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VITA

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In the fall of 1979, Ms. Hom eagerly continued her quest for knowledge at The University of Tennessee in Knoxville. Many hours of slime weighing, diatom counting, and pencil pushing, interspersed with a little Bach and a few culinary orgies, led to the receipt of a Master of Science in Ecology in August 1982.

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