PERIPHYTON COMMUNITY DYNAMICS IN A MOUNTAIN STREAM DURING WINTER

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ABSTRACT

Community ecology theory maintains that abiotic and biotic variables in the environment influence community taxonomic structure and community standing stock. Deficiencies and excesses in the abiotic environment have been shown to result in sub-optimal growth (stress) or loss of individuals from within the community (disturbance). Winter at high latitudes presents organisms with a number of potential stresses including low temperature, low light and sporadic high flow events associated with snow melt. The research presented here attempted to determine whether two abiotic factors, light and stream flow, cause algal community minima in winter as measured by chlorophyll *a* and ash free dry mass and if winter conditions effect changes in community taxonomic structure and diversity.

Periphyton samples were collected from rocks in Stevensville Brook, a 2nd order stream in the Green Mountains of Vermont. Fast flow and slow flow treatments, and high light and low light treatments, were created using a 2^2 factorial design for winter/spring 1994. Approximately 100 stream rocks were evenly distributed in an area of 1.0 m x 0.5 m in each treatment and 100 artificial substrata were added to the 1.0 m x 0.5 m area of stream bed next to the rocks to assess periphyton colonization. Rocks were collected about every two weeks from 4 February 1994 to 17 March 1994 and a clay tile collection occurred on 5 April 1994. Data from 4 February were analyzed using a two factor t-test to test for a significant difference between high and low flow samples. The remaining data were tested using the general linear model ANOVA. Rocks for fall/winter 1994/95 were collected on 4 August and 5 October 1994 and about every two weeks from 8 November 1994 to 5 January 1995. A periphyton suspension collected from the rocks was split for analysis of chlorophyll *a*, ash free dry mass and algal taxonomy. To determine if nutrients were limiting to periphyton, a nutrient enrichment experiment was performed from January 1995 to March 1995 using chlorophyll *a* and AFDM as indicators of response.

Results suggest that ash free dry mass responds to different parameters in the abiotic environment than chlorophyll *a*. Chlorophyll *a* was found to be influenced predominately by phosphorus concentration in the water whereas AFDM was more responsive to sample date, indicating that AFDM may be influenced by mid-winter spates. Relative abundance data showed an active community during the sampling period with a predominance of cyanophyta throughout most of the study period and three taxa - *Chamaesiphon* sp., *Lyngbya subtilis* and *Synechocystis* sp. - dominant out of a total of 52 taxa found. Neither individual taxon cell densities nor diversity were found to respond to the light treatment. Diversity for samples following the imposition of treatments was significantly affected by sampling date and flow, but no consistent pattern of flow mediated response could be seen across sampling dates. The hypothesis that lowest diversity occurs during winter was rejected since a mid-February sampling date had the highest diversity values for three of the treatments.

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INTRODUCTION

I. Winter Ecology

Although the biotic environment appears inactive to humans during winter, there is evidence that many components of ecosystems continue to function year round (Marchand 1991). Many terrestrial plant species retain their photosynthetic apparatus during this time and are able to restart as soon as conditions become favorable. Some studies of stream algal communities have found that complete algal assemblages are present throughout winter and that their abundances may actually be greater in winter than during other seasons of the year (Douglas 1958, Rounick and Gregory 1981).

Unfortunately, ecological aspects of the winter environment have often been neglected in field studies, especially in aquatic ecosystems. Two reasons for this are: 1) the lack of instrumentation able to withstand the rigors of the winter environment and 2) the inaccessibility of many areas to humans during the winter period (Marchand 1991). Nonetheless, changes occurring in the environment during winter are important to fully understand the mechanisms of an ecosystem (Resh *et al.* 1988).

The goal of this research is to determine the response of stream algal communities to changes in flow, light and nutrient concentrations which occur during winter in New England stream ecosystems. Variations in amounts of chl a and AFDM, and community taxonomic structure have been analyzed for differences resulting from treatment with a given level of flow, light or nutrients. Significant differences indicate community stress or disturbance which may result in successional changes. Current successional models provide a

framework for predicting the effects of winter conditions on community structure and function and would benefit from four season testing (Harper 1981). Algal communities are excellent model communities to test hypotheses about flow, temperature, and nutrients regimes *in situ* due to their small size and quick regeneration.

II. Definitions

Winter

Since this research is focused on algal community dynamics during a given part of the year it is appropriate to define what makes winter different from all other seasons. For the purposes of this research, winter is defined as a period from December 1 to March 31; a time during which mountain areas in Vermont maintain sub-freezing temperatures on average. Sub-freezing temperatures result from reduced solar exposure and radiation intensity caused by a change in the angle of the earth's surface in relation to the sun. Temperature is depressed further by the loss of long wave radiation from snow covering the ground surface during winter (Marchand 1991).

The definition proposed above does not correspond to our traditional astronomical concept of winter as the period of December 21 - March 21. It is proposed as defining a period of study in which the climatic conditions desired will have a high probability of occurring. These conditions are: sub-freezing temperatures, low light intensities, reduced photoperiod, stream ice formation and snowfall. Biotic conditions, such as leaf loss from deciduous species, are also important.

Another commonly used definition for winter is meteorological which charts winter as occurring December 1 - February 28 (Trenberth 1983). A four season structure is only useful in the mid-latitudes (22.5-67.5) since the poles and the equator have only two well defined seasons. Lag phases between the earth-sun distances and the resultant surface temperature changes occur in both hemispheres as a result of the moderating influence of the continents and the ocean. The lag phase is most pronounced in the Southern Hemisphere where the oceans comprise the bulk of the earth's surface while annual differences between high and low mean temperatures are greatest in the North.

Resh (1988) mentions that adaptation of algae to seasonal fluctuations in the environment needs to be studied. Any such studies must take into account the high variability of the seasons between and across distances.

Stress and Disturbance

A variety of definitions exist in the literature concerning stress and disturbance. Some authors use these terms synonymously (Odum 1981, Neuhold 1981), while other authors prefer to differentiate between the two (Menge and Sutherland 1987, Grime 1979). Although these different uses may be appropriate for a given study or model, the lack of consistent usage leads to confusion in the interpretation of study results and a breakdown of communication (Poff 1992). As used in common English and defined in any dictionary, stress and disturbance are two fundamentally different concepts, although they are not mutually exclusive in community and population ecology. In this research, these two terms will be used to describe different processes affecting algal communities.

White and Pickett (1985) defined disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". This definition was intended as a broad outline with the specifics to be determined relative to the system under study. A more specific definition is given by Menge and Sutherland (1987) who define a disturbance as the lethal effects of physical, chemical and biological stress.

An obvious disparity between these definitions results from the use of cause versus effect to determine disturbance. White and Pickett (1985) focus on the causal event which produces a given effect. Menge and Sutherland (1987) focus on the effect produced by an event. While this may seem to create a problem for an ecologist trying to study a system influenced by disturbance, the division is actually reconcilable. The effects that result from the event that Pickett and White describe are equivalent to Menge and Sutherland's lethal effects. However, Pickett and White's definition does not explicitly call for organism destruction, and although death would necessarily be included in possible effects, non-lethal outcomes are also possible.

Since Pickett and White's definition was designed to accommodate variable study conditions, I prefer a merger of their definition with Menge and Sutherland's: A disturbance is any relatively discrete event in time resulting in organism death causing a disruption of ecosystem, community or population structure and changes resources, substrate availability, or the physical environment. In short, a disturbance is an environmental event that causes organism mortality. This definition purposely excludes the use of stress. It is assumed that stress and disturbance are different points along the same continuum.

As mentioned above, stress is often used synonymously with disturbance resulting in the lumping together of many dissimilar events and subsequent community responses. The term stress derives from distress which refers to an event that induces a negative response. This is a relatively broad definition that would include disturbance. Odum *et al.* (1979) and Odum (1985) employ this line of thought calling stress an unfavorable alteration or deviation from what is usual or expected. These two papers develop models for stressed ecosystems and outline diagnostic features associated with such systems. As would be expected, some features parallel those associated with disturbance models while other features are unique to the stress model.

Barrett's and Rosenberg's (1981) compilation of papers on stress in a variety of ecosystems focused on a number of functional properties that are affected. In this work, Barrett (1981) defines stress as "a perturbation that is applied to a system by a stress which is foreign to that system or which may be natural to it but, in the instance concerned, is applied at an excessive level." In a later chapter, Ivanovici and Wiebe (1981) review past attempts to define stress including Bayne's 1975 work in which he determines stress to be an alteration from a steady-state caused by environmental change and resulting in a population or community more vulnerable to further change. Ivanovici and Wiebe propose using the adenylate energy charge (AEC-a ratio of ATP to AMP) as an indicator of stress. Stressed organisms convert a higher percentage of ATP to ADP and AMP in order to maintain cellular processes in sub-optimal conditions. A threshold value of AEC would be designated as indicative of stress.

Grime (1979) and Menge and Sutherland (1987) distinguish between stress and disturbance. Grime defines stress for plants as phenomena which restrict photosynthetic production. This definition, although still vague, establishes stress

as an agent and implies sub-optimal production (as opposed to deviation from normal) due to sub-lethal conditions. Menge and Sutherland define stress as a reduction in performance of an organism caused by physical stresses (produced by mechanical force) or physiological stresses (produced by biochemical reactions). While Menge and Sutherland refer to the effect as stress, their definition provides a useful base for a working definition in the proposed research.

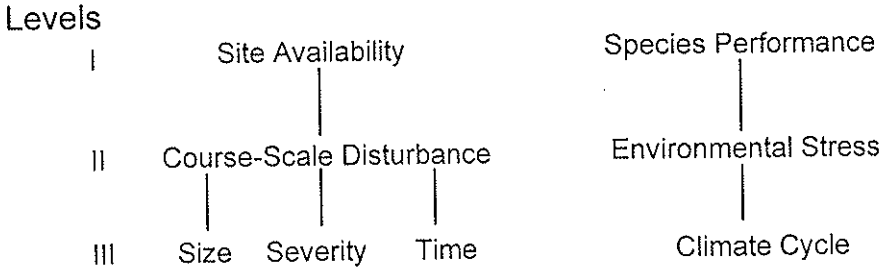
Drawing from the strengths of the existing definitions and broadening their scope to include populations and communities, I propose to define stress as: a factor external to the organism, population or community which causes a reduction in growth, reproductive and photosynthetic rates relative to the optimal rate for the process. The advantages of this definition are twofold. First, by defining stress in terms of an outside force, those conditions which produce stress can be quantified in a manner similar to disturbance so that predictions of lethal endpoints can be made. Second, there are a number of analyses which may be used to determine growth and reproduction so that effects can be quantified and results compared to control units.

III. Community Dynamics

Community dynamics have historically been explained by the theory of succession (Luken 1990). Algal communities are known to follow distinct succession patterns and are an excellent model for succession studies due to relatively short organismic life cycles (Power *et al.* 1988, Townsend 1989, McCormick and Stevenson 1991). The following sections examine succession

mechanisms can be sorted according to their role in promoting succession. The levels they provide - I) general cause of succession, II) contributing processes or conditions, III) modifying factors - move from general causes to detailed mechanisms of succession. The advantages of this concept include the allowance for mechanisms not presented by Connell and Slatyer, the explanation of successional sequences by multiple mechanisms, and the accommodation of individual community deviations from the "norm". Figure I depicts two categories from Pickett *et al.*'s (1987) framework which apply to winter algal community dynamics.

Figure 1 - Diagrammatic representation of 2 categories from Pickett *et al.*'s hierarchical model for causes of succession.



Site Availability

A site becomes available for colonization as a result of disturbance as defined above (Connell and Slatyer 1977, Grime 1979, White and Pickett 1985, Menge and Sutherland 1987, Petraitis *et al.* 1989). Recent work in stream biology has focused on disturbance as a controlling factor in lotic ecosystems (Resh *et al.* 1988, Pringle *et al.* 1988, Boulton *et al.* 1988, Townsend 1989, Grimm and Fisher 1989, Steinman *et al.* 1991). The reason for this emphasis is the

stochastic nature of the stream environment, especially with regard to water current which may significantly depart from the mean at any time during the year. There are two theories as to the effects of disturbance on communities: the intermediate disturbance hypothesis and the dynamic equilibrium model (Resh *et al.* 1988). Intermediate disturbance theory (Connell 1978) suggests that maximum species richness in communities will occur in environments where disturbance is frequent and intense enough to reduce competitive dominants before they exclude inferior competitors, but not frequent enough to prevent competitors from colonizing. Dynamic equilibrium (Huston 1979) is similar to Connell's hypothesis, but focuses on the disturbance in relation to organismic life cycles.

Streams under winter conditions are subject to three disturbance variables: light, temperature and flow (Rounick and Gregory 1981, Marchand 1991). Temperature can lead to disturbance through thermal shock or by ice formation which can scour channels or trap algae in a solid medium. Light extinction caused by temporary and long term snow deposits on ice across the stream surface may cause mortality. Increased flow rate resulting from snow melt is capable of removing algal biomass. Given the high potential for disturbance, it is likely that species richness in winter will remain low compared to spring, summer and fall. In this scenario the most likely type of algae present would be the ruderal from Grime's classification (1979). However, it is assumed that herbivory is absent during winter and that leaf litter from deciduous plants supply adequate nutrients. Thus, species subject to grazing pressures or nutrient shortages during other seasons may flourish during the winter period.

During any part, or over the entire length of its lifetime, an organism is likely to be subject to stress. As with disturbance, stress can affect a particular species population or it can subject entire communities to reduced productivity (Grime 1979). Although much of the literature does not differentiate stress from disturbance, the distinction is important in determining responses at all scales of study. Unlike disturbance, stress may endure any period of time. Potentially, stress may overlap disturbance, thereby affecting both pre- and post-disturbance communities. For example, low light intensities may inhibit algal production over long periods during the winter while short term spates occur at various intervals during the same time period. Since energy must be spent on photoacclimation, the organism would have less energy to allocate for disturbance adaptation (sensu Petraitis *et al.* 1991, Parsons 1993). It seems likely that under conditions resulting in multiple stresses, disturbance frequency should increase as a result of a decrease in the organism's range of tolerance to disturbance intensity.

Many authors refer to the general responses of both organisms and communities as stress (Odum *et al.* 1979, Grime 1979, Odum 1985, Parsons 1993). On the whole, responses can be lumped into one of the following categories: 1) net energy loss from an individual population which may result in a net energy loss from the community; 2) shifts in species relative abundance; or, 3) both 1 and 2 (Rapport *et al.* 1981, Odum 1985, Parsons 1993). Shifts in species relative abundances do not necessarily indicate disturbance, but rather, the need for one species to grow at a faster rate than the species which is inhibited by stress (Grime 1979, Menge and Sutherland 1987, Keely 1991).

However, any disturbance occurring during a period of stress is likely to enhance the rate of succession in a community.

In summary, both stress and disturbance influence the successional trajectory of a community. The physical and chemical phenomena may be quantified independently of the organisms affected, but it is the response of the organisms which determines whether stress and/or disturbance are influencing community composition. Responses of individuals or populations to either condition may be measured and correlated to overall community changes. The next section will address models which predict the outcomes of succession in disturbance and stress controlled systems. It is very likely that stress and disturbance will be closely linked in winter streams and that a given stress may cross the threshold to disturbance.

Models

Although some models of succession have been mentioned in the sections above, it is helpful to synthesize this information and formulate a single model that can be used as an experimental guide. Succession is a process of species replacement due to changes in relative species performances (Pickett *et al.* 1987). In choosing models to illustrate this process for winter, the important consideration has been the abiotic environment .

Menge and Sutherland (1987) proposed a model based on three trophic levels of interaction. Their basal level model (fig.3c in Menge and Sutherland) provides some useful predictions, although grazing in winter streams is assumed to be low during winter and predatory fish have not been observed in the reaches being investigated. According to that figure, basal level species (primary

producers) in the community existing under extremely high stress levels will be affected almost exclusively by physical factors rather than competition or predation. A study by Power (1990) analyzing the interaction of trophic levels in a California stream supports this aspect of the Menge and Sutherland model. She found that the importance of predation increases with decreasing environmental stress. As long as algal recruitment remains moderate to low in winter streams, competition and predation should be insignificant. Another prediction of the Menge and Sutherland model is that the importance of disturbance increases with increasing environmental stress, whereas species diversity, in the absence of competition (under low recruitment), is highest under moderate stress.

The Menge and Sutherland model is useful in formulating some broad scale assumptions relative to algal stream communities, but it lacks the resolution for determination of the effects of stress and disturbance in regulating succession within a single trophic level. A more useful model is that of Petraitis *et al.* (1989). In their presentation they mathematically connect equilibrium and non-equilibrium models such that immigration and extinction rates are based on probabilities of species numbers changing over time. For disturbance to effect a change in species numbers, it must cause a change in extinction and immigration rates. They offer numerous graphical examples of the differential effects of disturbance size and frequency upon species number. This model is especially useful for winter environments in streams since it is assumed that size and frequency of disturbance events are dependent on levels of stress prior to the event. Since stress will affect each population differently, species within a community should be differentially sensitive to changes in size and frequency of disturbance.

IV. Abiotic Factors

Light

Light is the most important source of energy for autotrophic organisms. Aquatic autotrophs are subject to large variations in fluence as a result of the depth and turbidity of the water column (Kirk 1983). Ice cover and snow deposition on that ice in mountain streams further reduces available solar radiation in the water (Marchand 1991, Wright 1964). Transmittance of light through snow occurs primarily in the wavelength range between 450-600 nm, although quantity and quality of light transmitted depend upon the age of the snow pack (Curl *et al.* 1972). Given typical weather conditions and the sun's position relative to the earth's surface, available solar radiation during winter in mountain streams is at the lowest level of the year.

The ability of algae to acclimate their photosynthetic apparatus to light intensity has been well documented in the physiological literature (Raps *et al.* 1983, Cunningham *et al.* 1990, Smith *et al.* 1990, Sukenik *et al.* 1990) for all algal classes and probably occurs in most algal species (Falkowski and LaRoche 1991). Two basic strategies have been proposed for photoacclimation in algae: 1) a change in the size (ratio of antenna pigments to reaction center pigments) of the photosynthetic unit or 2) a change in the total number of photosynthetic units per chloroplast (Falkowski and LaRoche 1991). These changes may be quantified directly by established methods and correlated with environmental variables.

The ecological significance of this process is not yet well defined though there is an established body of literature for phytoplankton (Ryther and Menzel 1959, Wright, 1964, Gallegos *et al.* 1983, Neori *et al.* 1984, Wood 1985). Changes in

photosynthetic apparatus have been cited to result in the chlorophyll maximum found in lakes and oceans at a depth where the light intensity is about 1% or less of the surface irradiance (Ryther and Menzel 1959, Wright 1964, Beers *et al.* 1975, Gallegos *et al.* 1983, Neori *et al.* 1984). For the chlorophyll maximum to occur, algae must remain at depth for a period of hours or days implying that stratification of the water column is necessary (Harris 1980). However, these studies have failed to rule out the possibility of successional changes within the community as a cause of the chlorophyll maximum.

Investigation of algal responses to light in lotic ecosystems has been primarily limited to laboratory streams and is almost non-existent for winter communities. Rounick and Gregory (1981) found a positive correlation between standing crop of periphyton and light for streams during winter in the Western Cascade Mountains, Oregon. Hill and Harvey (1990) found that productivity of algal communities during summer was positively correlated to photosynthetically active radiation (PAR), but that loosely attached algae showed only weak correlation as compared to tightly attached algae. This finding agrees with the necessity of stable positioning in phytoplankton. Experiments in laboratory streams have found that irradiance plays a significant role not only in the standing crop biomass, but also the composition of successional sequences (DeNicola and McIntire 1990). Recovery of lotic ecosystems following light elimination disturbance (which would be possible in winter if snow deposition occurred on stream surface ice) has also been studied under laboratory conditions and was found to be enhanced by nutrient input and deterred by grazing (Steinman *et al.* 1991).

Temperature

As stated earlier, temperature decline and increase in the environment generally follow solar changes with a lag period of about one month. Temperature is extremely important in any ecological study because it influences the rates of reactions both internal and external to organisms (Davison 1991). For example, Tilman *et al.* (1981) have found that algal cell quotas for nutrients are temperature dependent with the result that dominance in competitive interactions may vary at different temperatures. Low temperature has been found to limit either electron transport or carbon fixation in algal cells resulting in a lower light saturation value and increased photoinhibition at saturating light levels (Davison 1991). As temperature increases, the light level necessary to reach compensation irradiance increases, and the rate of net photosynthesis at sub-saturating light levels decreases (Davison 1991). Algae have been observed to acclimate photosynthetic apparatus and other metabolic functions to changes in temperature such that inferences concerning long-term growth based on short-term photosynthetic responses may be inappropriate (Davison 1991).

It is important to separate the effects of light and temperature on algal community functions since the similarities between light and temperature acclimation may obfuscate experimental results. Graham *et al.* (1982) were able to separate the two variables while analyzing *Cladophora glomerata* at temperatures between 1° and 35°C for 8 irradiance levels. The data indicate that *C. glomerata* is unable to attain positive net photosynthesis for any irradiance level at 1°C. Fawley (1984) measured carbon fixation and division rates at six temperatures between 14° and 25°C under five fluence rates for the diatom *Phaeodactylum tricornutum*. He found that both division rate and carbon fixation

for *P. tricornutum* decreased with decreasing light at all temperatures. The carbon:Chl a ratio is found to be influenced by temperature, whereby the ratio decreases exponentially with increasing temperature at a constant light level for microalgae and cyanobacteria (Geider 1987).

During winter the temperature in mountain streams is assumed to remain relatively constant. Therefore, winter populations should provide an excellent opportunity to study algal community response to light in the field without temperature interference. It is apparent that some algal populations will not be able to dominate or even survive at low temperatures, thus, winter community taxonomic structure is likely to be completely different from spring, summer and fall structure.

Flow

Stream flow has been increasingly noted as being an extremely important factor in periphyton community dynamics by researchers. Rounick and Gregory (1981) found that freshets during winter in the Western Cascades, Oregon, are correlated to a reduction of periphyton standing crop resulting in a winter minimum of periphyton. They noted that under abnormally low flows the winter minimum did not occur. Hydrological factors explained up to 63% of the variance in periphyton biomass in rivers at Canterbury, New Zealand (Biggs and Close 1989). However, they also found that the percent of time in flood was the single most important factor leading to loss of periphyton biomass while the actual rate of flow was less important. Uehlinger (1991) determined that chlorophyll and ash free dry mass were positively correlated with time since last flood in the Necker river, Switzerland. Stevenson (1990) observed that diatom assemblages in a

third order stream were able to survive all but the most intense discharge events and that increased flow may have actually enhanced growth by increasing nutrient supply to algal cells.

In addition to field studies, there have been a number of studies of the effects of flow on periphyton in laboratory streams. Horner *et al.* (1990) showed that sudden increases in flow above initial growth velocity can lead to increased algal loss rates and changes in dominance. These effects were only short term and reversed within a couple of days. Peterson and Stevenson (1990) monitored algal recovery for slow and fast current laboratory streams following a simulated flood event. Recovery of algal assemblages proceeded more rapidly in the slow current regime and maximum algal abundance at 33 days was greater in slow current than in fast. Peterson and Stevenson's results also suggested that autogenic changes were more pronounced in slow current streams.

Due to the stored water content in snow, impermeability of frozen soil to water and the lack of transpiration, periphyton communities will be subject to highly variable flow and frequent spates during winter. From results presented in the literature it is evident that flow patterns will be an important factor influencing community productivity and taxonomic structure.

V. Research Questions and Hypotheses

As stated previously, the overall goal of this research is to determine the response of stream benthic algal communities to flow, light and nutrient availability. More specifically, this research is intended to determine whether flow, light or nutrients control algal community activity at low temperatures during winter as measured by chlorophyll *a* (chl *a*), ash free dry mass (AFDM) and

taxonomic changes. The working hypothesis used was based on prior research found throughout the literature: Quantifiable changes in abiotic factors - light, water flow and nutrients- in mountain streams during winter result in stress and/or disturbance which influence the structure and function of algal communities during succession. The specific questions addressed in this study and my hypotheses are listed below:

Q1.1: Does algal community chl *a* and periphyton AFDM change in response to a reduction of daily solar energy during the winter in montane streams?

H1.1: Chl *a* and periphyton AFDM per unit area declines in communities subject to reduced daily solar energy input.

Q1.2: How does a reduction in daily solar energy affect algal community diversity?

H1.2a: Algal community diversity, as measured by the number of species and the relative abundances of each species, decreases as a result of reduced solar energy in streams under winter conditions.

Q2.1: How will algal community chl *a* and periphyton AFDM respond to an increase in flow during winter?

H2.1: Algal community chl *a* and periphyton AFDM decreases as water velocity increases during winter.

Q2.2: How will algal community diversity be influenced by stream flow during winter?

H2.2: Diversity decreases at higher flow.

Q3.1: What effect will increased nutrient concentrations have on algal community chl *a* and periphyton AFDM ?

H3.1: Nutrient increases have no effect on algal community chl *a* and periphyton AFDM during winter.

PERIPHYTON STANDING STOCK IN A MOUNTAIN STREAM DURING WINTER : IS THERE ANYTHING OUT THERE?

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ABSTRACT

We conducted two experiments to determine the activity of and factors which control periphyton during winter in Stevensville Brook, Vermont. The first experiment during Winter/Spring 1994 examined the effect of a 300-450% difference in light and doubling of flow (low and high light, slow and fast flow) on periphyton. Stream rocks were collected, the periphyton removed and then processed for chlorophyll *a* (chl *a*) and ash free dry mass (AFDM). In addition, 100 uncolonized clay tiles were added to each treatment and collected at the end of the experiment to determine the treatment effects on colonization. To determine the availability of nutrients in Stevensville Brook, stream water was sampled during Fall/Winter 1994/95 for nitrate (NO_3), ammonia (NH_4), soluble reactive phosphorus (SRP) and total phosphorus (TP). To test whether periphyton were nitrogen or phosphorus limited, clay saucers filled with agar containing N, P, N+P or no nutrients were attached to cinder blocks, submersed in the stream for two months (winter 1994/95) then sampled for chl *a* and AFDM.

Increases of up to 250% for AFDM and 600% for chl *a* during the first study indicated robust activity throughout the winter despite low temperatures and light. Flow had a negative effect and sampling date was found to have a significant effect on periphyton biomass (chl *a* and AFDM) while light was found to influence increases in AFDM on clay tiles only. Water analyses showed that SRP was less than 0.001 mg/L, NH_4 and TP were low and often undetectable, and NO_3 remained at about 0.20 mg/L. Results from the nutrient enrichment experiment showed a significant response of chl *a* to P but not N and no response of AFDM to enrichment with either N or P. In Stevensville Brook during winter, the algal community, as represented by the chl *a* concentration, is predominantly controlled by phosphorus concentrations and is impacted to a lesser extent by

flow; the periphyton community as a whole, represented by AFDM, is controlled mostly by stream flow and light.

KEYWORDS: algae, ash free dry mass, chlorophyll *a*, flow, light, nitrogen, nutrient limitation, periphyton, phosphorous, stream, winter.

INTRODUCTION

The winter environment provides a formidable barrier to scientific study resulting in a lack of complete information about stream ecosystems in winter. Some studies of stream algal communities have found that algal assemblages are present throughout the winter and that abundances may sometimes be greater in winter than during periods of the year with higher temperature and more sunlight (Douglas 1958, Rounick and Gregory 1981, Uehlinger 1991, Delong & Brusven 1992). It is imperative that stream ecosystems are analyzed during the winter in order to understand the temporal relationships of the system.

Winter is naturally associated with environmental minima (Marchand 1991) which may result in stress and/or disturbance. Stress is defined as: a factor external to an organism, population or community which causes a reduction in growth, reproduction and/or photosynthesis (*sensu* Grime 1979). A disturbance is any relatively discrete event in time resulting in the death or removal of an organism which causes a disruption of ecosystem, community or population structure and thereby changes resources, substrate availability, or the physical environment (*sensu* White and Pickett 1985). The most obvious environmental changes likely to cause stress or disturbance in streams during winter are a reduction in temperature caused by reduced solar radiation, reduction of light

intensity due to ice and snow cover, and erratic water flow resulting from freeze-thaw incidents.

Temperature is extremely important in any ecological study since it influences the rates of reactions both internal and external to the organism (Davison 1991). For example, Tilman *et al.* (1981) have shown that algal cell quotas for nutrients are temperature dependent. Ice and snow buildup over streams in winter reduce light levels within the water which may restrict algal growth (Wright 1964, Marchand 1991). Light can also interact with temperature: at low temperatures algal cells display a lower light saturation value and increased photoinhibition at saturating values (Davison 1991). Laboratory studies have shown that flow can influence the rate of recovery of periphyton following loss due to disturbance (Peterson and Stevenson 1990). Numerous field studies have demonstrated that stream velocity can be a significant factor in organizing stream communities (Rounik & Gregory 1981, Biggs and Close 1989, Uehlinger 1991).

A model proposed by Menge and Sutherland (1987) predicts that under conditions of high stress, such as those found in winter, biotic communities will be regulated almost exclusively by abiotic factors rather than competition or predation. This model provides the basis for our research which attempts to determine which, if any, changes in the physical abiotic environment control the periphyton community during winter.

The goals of this research were : 1) to establish the extent of the winter periphyton community as measured by ash free dry mass (AFDM) and chlorophyll *a* (chl *a*), and 2) to test the effect of flow and light on these community parameters under constant low temperature. Based on models and previous research it was hypothesized that the standing stock of periphyton, as measured by chlorophyll *a* and ash free dry mass, would decrease as a result of

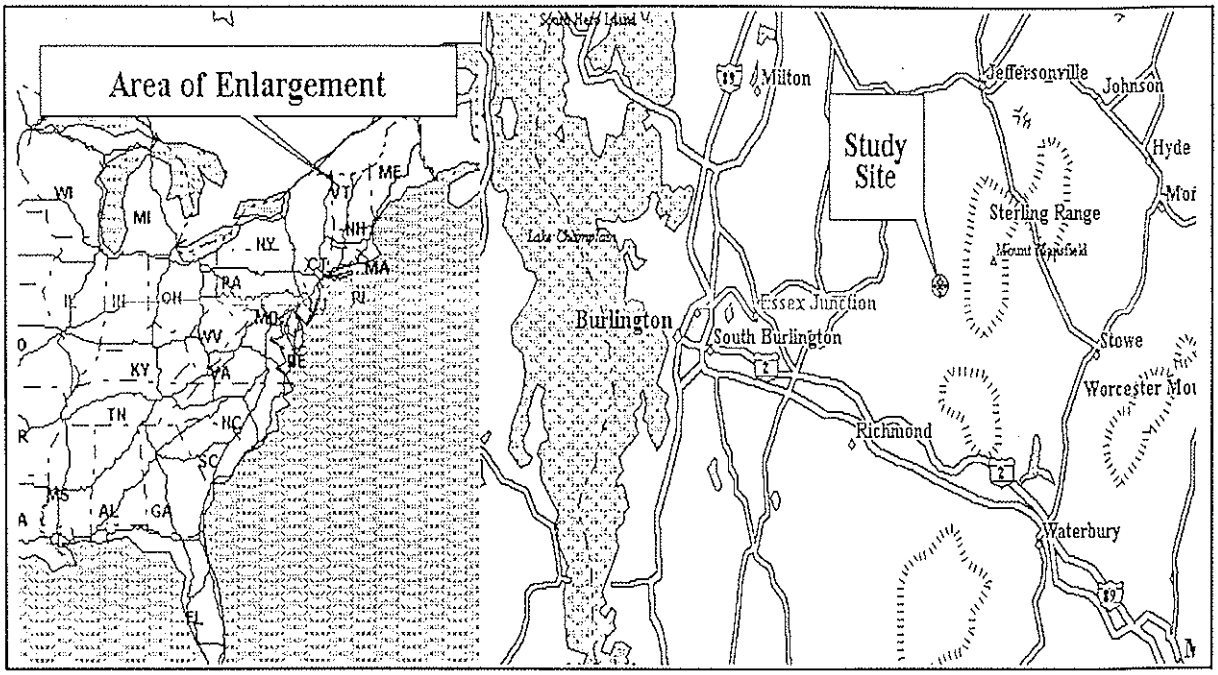
reduced light and that standing stock would be lower in fast flow areas than slow flow areas. It was assumed that nutrients are not limiting to periphyton at this time because of the increased detrital pool left by autumn leaf litter (Pomeroy 1980) and an increase in input to snow melt water caused by the reduction of terrestrial community activity.

MATERIALS AND METHODS

Site Location

Stevensville Brook is a 2nd order stream located in Underhill State Park, VT, USA (N44° 30', W72° 53', Fig.1). The stream drains an area of 5.2 km^2 in a forested watershed with a beech, maple and birch community predominating at the experimental site. Underlying bedrock is composed of complex highly metamorphosed rock, primarily schists, in the area of the study (USDA, 1974). The ground surface consists mostly of glacial till, remnants of the extensive glaciation that has occurred in the region. Total experimental reach area was 4 m long by 1 m wide and located at an elevation of about 425 m. While most of the trees and shrubs at the experimental site lose their leaves during winter, the branches and trunks of the trees shade about 10-15% of the stream surface in winter. The stream bottom at the site is composed of cobble-boulder material. Water depth and stream width vary considerably, but typically the depth was 0.5 m and the width 1.5 m. During the winters of 1994 and 1995 the stream did not freeze solid and diurnal water temperature change was less than 1°C (Tim Scherbatskoy, personal communication).

Figure 1: Location of Stevensville Brook.


Area of Enlargement
Study Site
Milton
Jeffersonville
Johnson
Hyde
Sterling Range
Burlington
Essex Junction
South Burlington
Stowe
Richmond
Waterbury
VT
ME
NH
MA
RI
CT
NY
PA
OH
MD
WV
VA
KY
TN
NC
SC
GA
AL
MS
FL
MI
WI
IL
IN

Winter/Spring 1994

A 2^2 factorial design was used with high and low levels for water velocity and light. Fast and slow flow regimes measuring 2 m in long by 1 m wide were constructed in-stream by building rock dams to separate and enhance existing flow differences. Flows were measured using rhodamine dye injected into the stream at the bottom of the water column and establishing its time of travel over a 1 m distance (Table 1). High and low light regimes with an area of 1 m^2 were created by blocking light with eight layers of plastic black mesh (9 mm^2 mesh area) screening for low light treatments and by keeping water clear of ice cover for high light. Light was measured on 12 March 1994 (Table 1) in bright sun using a Biospherical Instruments QSL-100 (San Diego, CA). Each treatment contained at least 100 stream rocks already present in the reach as well as 100 unglazed red quarry tiles (4.5 x 4.5 x 1.0 cm, 90% New Brunswick shale and 10% clay, American Olean, Quakerstown, PA) added as uncolonized substrata.

Five rocks were taken from high and low flow areas on 4 February 1994. Ten individual rocks were collected at approximately two week intervals at random for each sample from all treatments beginning on 19 February and ending 5 April 1994. Samples from 4 February to 17 March 1994 consisted of rocks with a mean surface area of 51.40 cm^2, SE, 1.33, n=130. Ten of the artificial substrata were collected from each treatment on 5 April 1994 and processed in the same way as stream rocks.

Rocks were cleaned in the lab using a stiff bristle toothbrush and rinsed with deionized/reverse osmosis water. The resulting suspension was homogenized for about five minutes in a 120 mL sample cup using a drill mounted tissue homogenizer with a teflon head (Wheaton Scientific, Millville, NJ). Homogenate

Table 1 a: Estimated mean stream velocity (n=10) in experimental reaches for Winter/Spring 1994 flow manipulation in Stevensville Brook. **b:** Estimated light intensity (PAR) for Winter/Spring 1994 light manipulation experiment. Readings were taken between 12:00 and 13:00 hours on 12 March.

1a)

Treatment	Mean Flow	SE
Slow Flow/Low Light	0.15 m/s	0.01
Slow Flow/High Light	0.15 m/s	0.02
Fast Flow/ High Light	0.30 m/s	0.03
Fast Flow/ Low Light	0.34 m/s	0.05

1b)

Treatment	Quanta·s^{-1}·cm^{-2}
High Light/ Slow Flow	0.9×10^{17}
High Light/ Fast Flow	0.8×10^{17}
Low Light/ Fast Flow	0.2×10^{16}
Low Light/ Slow Flow	0.3×10^{16}
Stream Surface	1.5×10^{17}

volume depended on rock size since larger rocks required more rinsing. Homogenized samples were split into separate aliquots: 25 mL for ash free dry mass analysis (AFDM), 25-50 mL for chlorophyll *a* (chl *a*) and 5-25 mL were preserved with Lugol's solution (APHA 1992). AFDM aliquots were poured directly into tared crucibles, oven dried at 90°C, and then ashed at 550°C for one hour (method 10300 C.5., APHA 1992). Chl *a* aliquots were filtered with glass microfibre filters (934-AH, 47mm, Whatman Inc., Clifton, NJ), the filters frozen and then extracted using 20 mL boiling (78°C) 90% ethanol (Sartory and Grobbelaar 1984). Spectrophotometer (Shimadzu UV160U) readings using a 1cm pathlength were taken 24 hours after extracting. Extracts were analyzed at 665 nm and 750 nm before and after acidification using 0.02 mL 1 N HCl in a 3 mL sample to account for phaeophytin. Rock area was estimated by wrapping the rock in aluminum foil and removing excess so that a single layer of foil covered the rock surface and weighing the foil (Sheely 1979). Standard curves were generated by regressing the area of aluminum foil pieces by their weight (r^2=100%). Discharge measurements were obtained from the Vermont Monitoring Cooperative (Tim Scherbotskoy, University of Vermont, School of Natural Resources, Burlington, Vermont) which maintains a gauging station located on a tributary about 100m upstream from the site.

Fall/Winter 1994-1995

To test the nutrient limitation assumption, water samples for nitrogen and phosphorus analysis were collected throughout fall 1994 and into January 1995. Separate 1 L samples were taken at the upstream end of the experiment and 4.5 m downstream at the end of the experimental reach. Nitrate was analyzed using the cadmium reduction method of Sechtig (1992). Ammonia was analyzed using

the salicylate method (Switala 1993) on a Lachat QuikChem AE (Lachat Instruments, Milwaukee, WI 53218). Soluble Reactive Phosphorus (SRP) was analyzed using method 4500-P E. outlined by the APHA (1992) for spectrophotometric analysis with a 10 cm pathlength. Total phosphorus samples (TP) were digested using the persulfate method 4500-P B. (APHA 1992) and then analyzed as SRP.

To further examine stream nutrient status, *in situ* nutrient enrichment experiments were used. Control (2% agar only), 0.5 M N ($NaNO_3$), 0.05 M P (KH_2PO_4) and N+P treatments were prepared in terra cotta saucers (10.5cm top and 6.5cm bottom diameter) as outlined by Fairchild *et. al.* (1985). One of each of the nutrient treatments was attached with silicone caulk to a 19 x 4 x 39 cm cement paving stone to prevent movement. Positions on the paving stone were randomly assigned. Four replicate paving stones with nutrient treatments were placed in the experimental reach on 30 December 1994 and retrieved on 7 March 1995. The exposed colonization surface (area = 33 cm^2) of each saucer was cleaned and the periphyton analyzed for chl *a* and AFDM as described above for winter-spring 1994.

Statistical Analyses

Samples collected on 4 February 1994 were tested for differences in chl *a* and AFDM between fast and slow flow reaches using a two factor t-test. The three sampling dates following 4 February were analyzed using a three-way ANOVA to determine the significant differences for AFDM, $\log_e$chl *a* and chl *a*/AFDM between flow and light regimes and among sampling dates. One value from the 7 March chl *a* data was discarded as an extreme outlier. The ratio chl *a*/AFDM was calculated in order to examine the change of the relative importance of

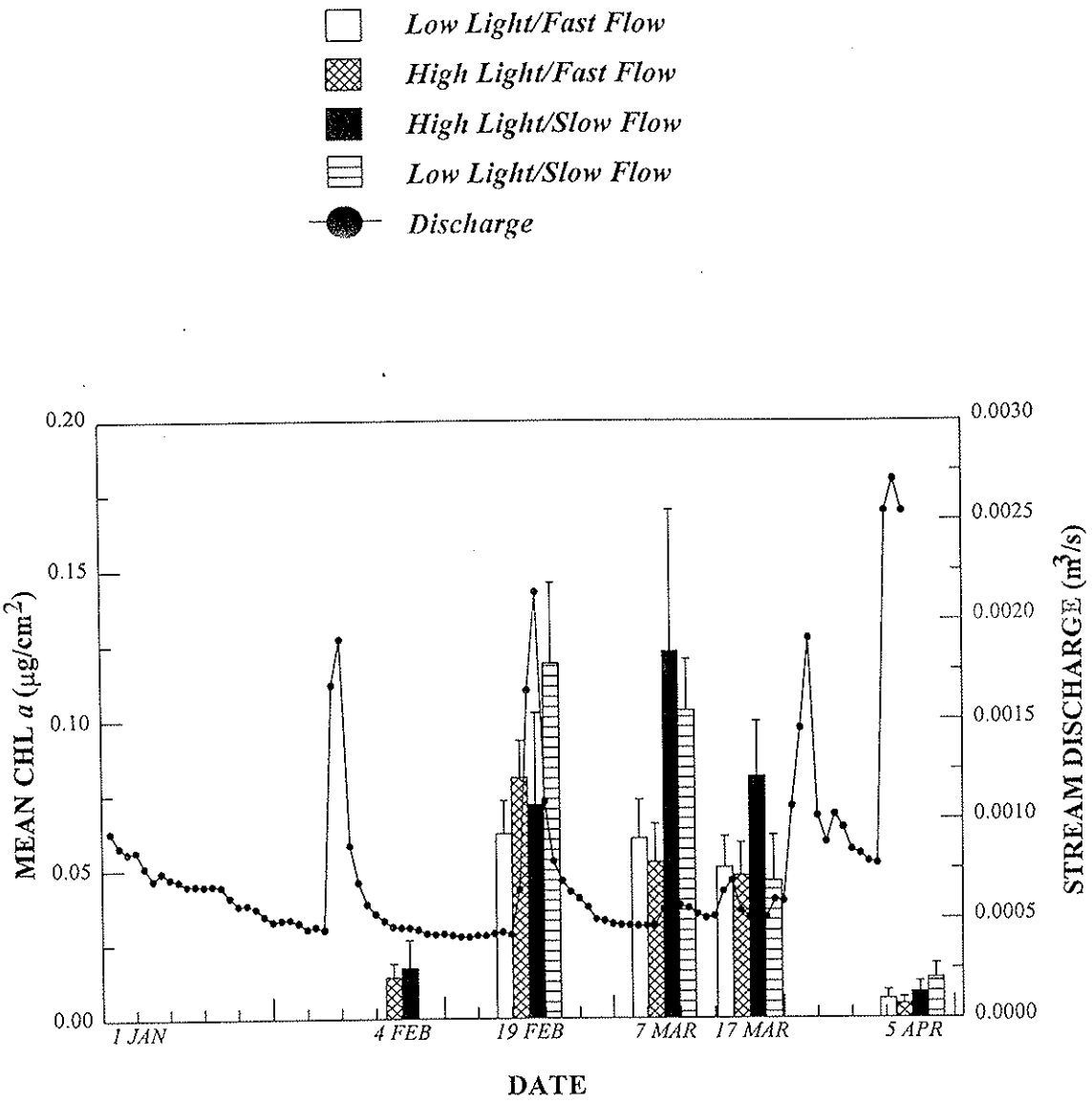
autotrophy to heterotrophy over time. Two-way ANOVAs were performed on each sampling date for the period from 19 February to 5 April to determine within date effect of flow and light treatments on chl *a*, AFDM and chl *a*/AFDM. Data were transformed as necessary to meet the assumptions of normality and equal variance. A one-way ANOVA was used to test chl *a*, AFDM and chl *a*/AFDM for significant differences among the four sampling dates during Winter/Spring 1994 and to test for treatment effects in the nutrient enrichment experiment. All statistical analyses were performed using Minitab for Windows version 10.2 (Minitab Inc., State College, PA).

RESULTS

Winter/Spring 1994

Stream discharge, measured in m^3/s, is shown for the period from 1 January to 5 April 1994 in figures 2, 3 and 4. Peak discharges during the winter were caused by periods of time with temperatures above freezing and were sometimes accompanied by rain. There were four distinct peak discharges which occurred on 29 January, 21 February, 25 March, and 4 April. The 29 January peak occurred six days prior to the start of the experiment when the stream discharge was 0.00191 m^3/s, four times higher than the discharge recorded on 27 January of 0.00045 m^3/s. By the 4 February collection, stream flow had receded from the peak on 29 January to 0.00046 m^3/s. The 19 February sample collection occurred at the beginning of another thaw with stream discharge at 0.00065 m^3/s. By 21 February, the stream peaked again at 0.00214 m^3/s. The discharges for the 7 and 17 March sample collections were 0.00046 and 0.00054 m^3/s respectively. No major runoff events were noted for these two collection

Figure 2: Mean chl *a* concentrations by treatment (n = 5 for 4 Feb., n = 10 for all others) and daily stream discharge data collected upstream in the watershed for Winter/Spring 1994 in Stevensville Brook. Date indicates the day on which the sample was collected. Error Bars = 1 SE

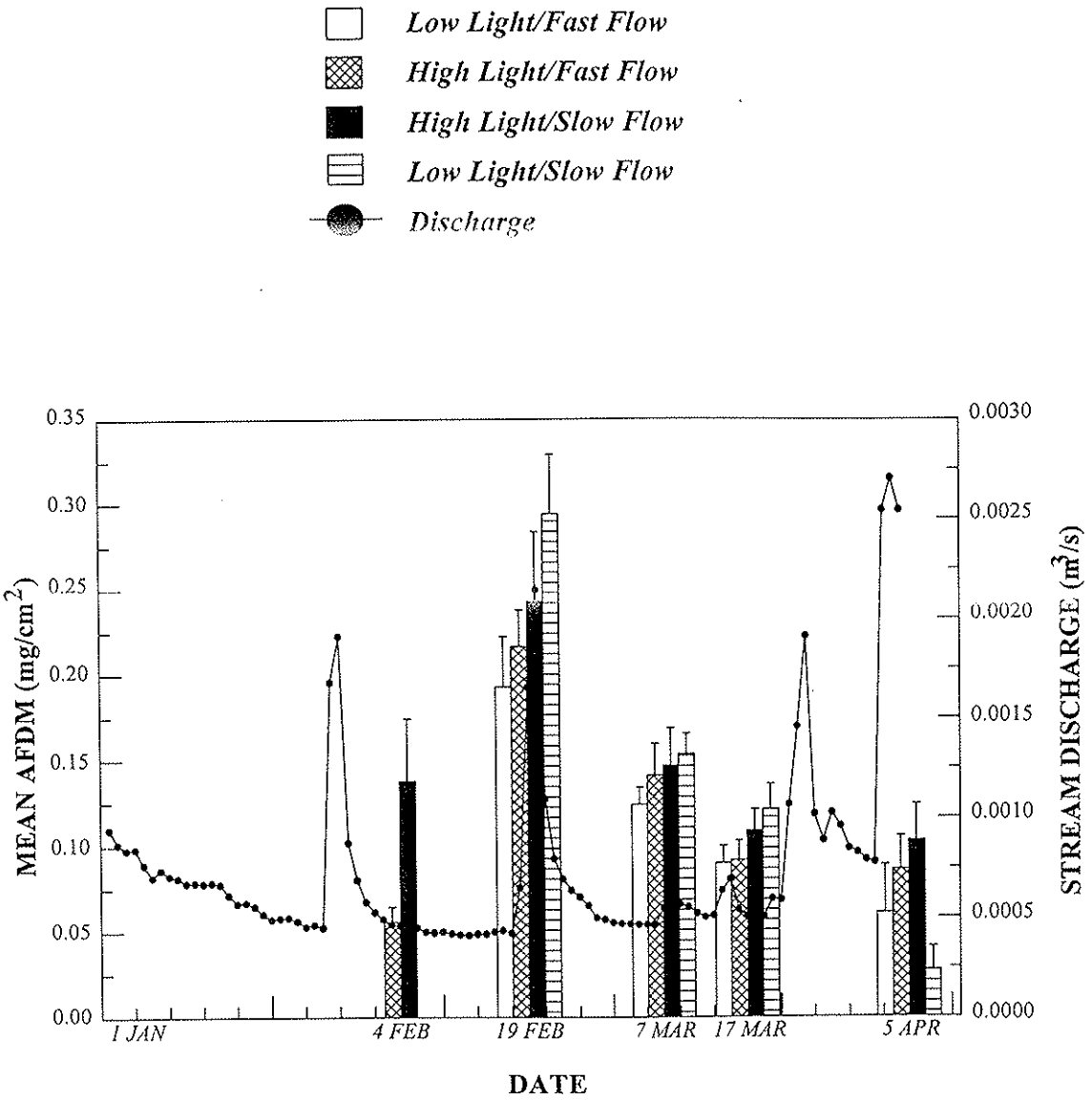

Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
Discharge
MEAN CHL a (µg/cm2)
STREAM DISCHARGE (m3/s)
0.20
0.15
0.10
0.05
0.00
0.0030
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
1 JAN
4 FEB
19 FEB
7 MAR
17 MAR
5 APR
DATE

periods. There were two major discharge events prior to the collection of clay tiles on 5 April including a discharge of 0.0191 m^3/s on 25 March and 0.00270 m^3/s on 4 April, which was the largest single runoff event over the period of the experiment.

Community chlorophyll values changed dramatically from week to week (Figure 2). During the 4 February collection, the mean chl *a* values were 0.014 $\mu g/cm^2$ and 0.017 $\mu g/cm^2$ for fast and slow flow stream sections respectively. By the 19 February collection, the first collection following the application of treatments, chl *a* values had increased by 350% for low light/fast flow and 500% for high light/fast flow over the 4 February fast flow value, while the high light/slow flow and the low light/slow flow treatments increased by 300% and 600% respectively over the slow flow chl *a* value of 4 February. Between 19 February and 7 March, chl *a* concentrations declined for all treatments except high light/slow flow. Chl *a* for high light/slow flow almost doubled going from 0.0718 $\mu g/cm^2$ on 19 February to 0.1228 $\mu g/cm^2$ on 7 March. All treatments showed a decrease in chl *a* between 7 March and 17 March, but the 17 March value for the high light/slow flow reach remained higher than the 19 February value. Mean chl *a* concentrations for clay tiles were lower than for stream rocks: all treatments had concentrations below 0.010 $\mu g/cm^2$ except for the low light/ slow flow treatment of 0.0134 $\mu g/cm^2$.

AFDM values for stream rocks were consistently higher for slow flow reaches than fast flow reaches during the experimental period (Figure 3). The AFDM for the slow flow reach on 4 February was 0.138 mg/cm^2 or two and a half times greater than the fast flow reach of 0.056. By 19 February, all treatments showed an increase in AFDM over their initial estimates and fast flow reaches exhibited a

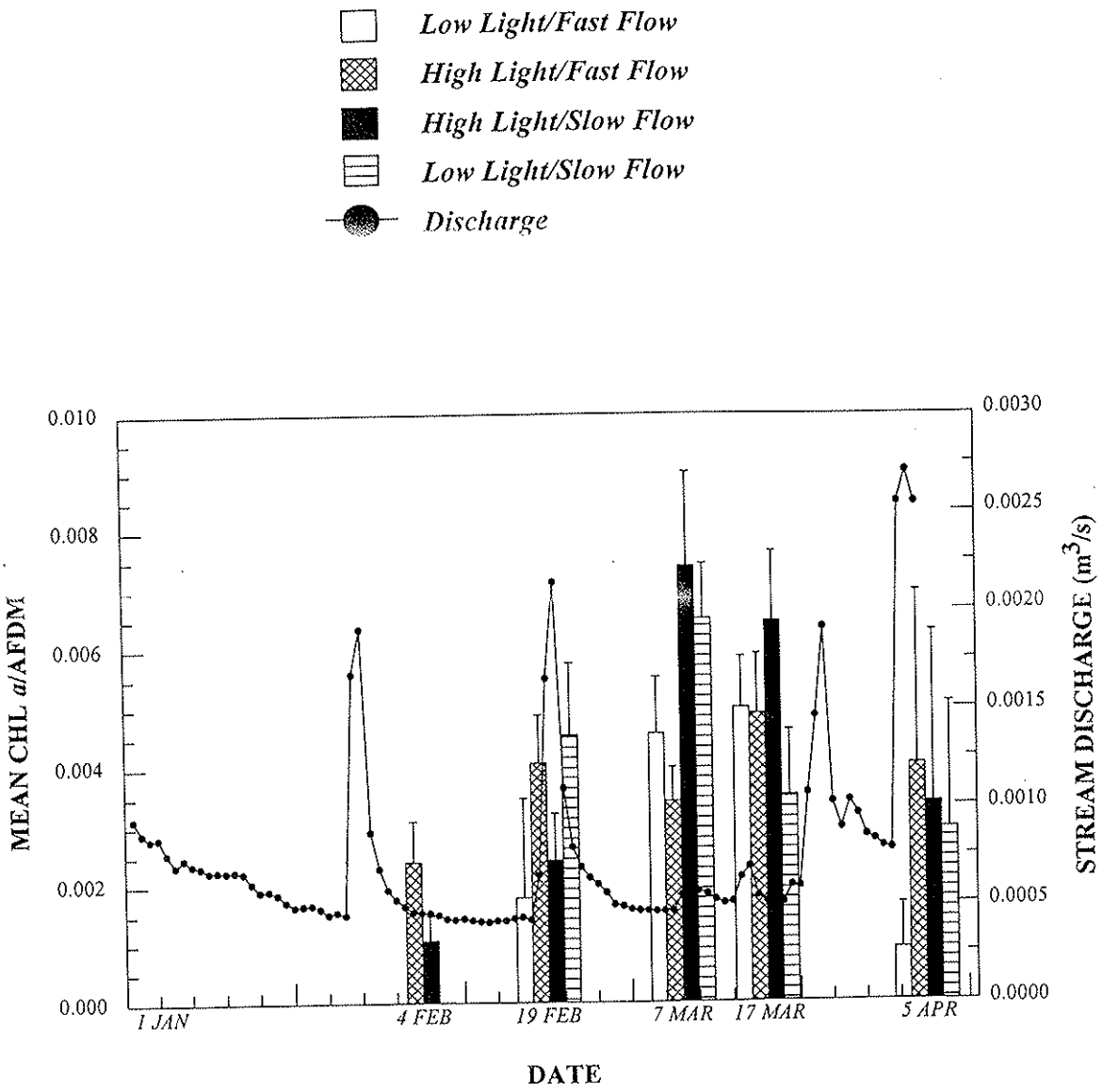
Figure 3: Mean AFDM by treatment (n = 5 for 4 Feb., n = 10 for all others) and daily stream discharge data collected upstream in the watershed for Winter/Spring 1994 in Stevensville Brook. Date indicates the day on which the sample was collected. Error Bars = 1 SE


Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
Discharge
MEAN AFDM (mg/cm^2)
STREAM DISCHARGE (m^3/s)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0.0030
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
1 JAN
4 FEB
19 FEB
7 MAR
17 MAR
5 APR
DATE

larger increase than slow flow reaches: low light/fast flow and high light/fast flow increased to 0.1930 and 0.2165 mg/cm^2 respectively over the 4 February fast flow value while high light/slow flow and low light/slow flow increased to 0.2435 and 0.2945 mg/cm^2 respectively over the 4 February slow flow. AFDM declined from the previous collections for all treatments on 7 March and 17 March. Clay tiles collected on 5 April did not follow the trend of slow flow yielding higher AFDM but instead had higher values for high light treatments over low light treatments. Unlike chl *a*, AFDM for the clay tiles was not much lower than AFDM for stream rocks from the previous collection.

The chlorophyll *a*/AFDM ratio indicates the percent contribution of autotrophs to the total biomass (Figure 4). Units for the ratio have been converted so that the number given is dimensionless. On the first collection date, 4 February, the fast flow reach had a ratio more than double the slow flow reach indicating a much larger contribution of autotrophs to the total biomass. By 19 February, the ratio had increased by more than a factor of one and a half for the high light/fast flow, two for high light/slow flow, and four for the low light/slow flow since 4 February, whereas, the ratio for low light/fast flow had declined by a quarter since the previous collection. Between 19 February and 7 March, the chlorophyll *a*/AFDM ratio had increased two and a half times to 0.0046 for low light/ fast flow, three times to 0.0074 for low light/slow flow and four and a half times to 0.0065 for low light/slow flow while declining by almost a fifth to 0.0034 for high light/fast flow. Both fast flow reaches showed increases in the relative autotroph contribution, low light by a tenth, high light by one and a half times, between 7 and 17 March while both slow flow reaches experienced a decline, 13% for high light and about 50% for low light. Among clay tile samples, the low light/fast flow had the lowest relative autotroph contribution to biomass with a ratio of less than

Figure 4: Mean chl *a*/AFDM (mg/mg) by treatment (n = 5 for 4 Feb., n = 10 for all others) and daily stream discharge data collected upstream in the watershed for Winter/Spring 1994 in Stevensville Brook. Date indicates the day on which the sample was collected. Error Bars = 1 SE


Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
Discharge
MEAN CHL a/AFDM
STREAM DISCHARGE (m3/s)
0.010
0.008
0.006
0.004
0.002
0.000
0.0030
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
1 JAN
4 FEB
19 FEB
7 MAR
17 MAR
5 APR
DATE

0.0009 and the two high light treatments had greater ratios than the low light treatments.

A t-test of the samples collected at the start of the experiment (4 February) shows that chl *a*, AFDM and chl *a*/AFDM were not significantly different ($p>0.05$) for the fast and slow flow treatments at the start of the experiment (Table 2a and 2b), although mean AFDM in the slow flow reach was more than two times greater than that of the fast flow reach. Analysis of variance tests for the effect of flow and light on AFDM for each sample date between 19 February to 17 March did not indicate a significant ($p\leq0.05$) effect for flow. The p-values, however, were less than 0.06 for 19 February and 17 March and the slow flow treatment means were consistently higher for natural rock samples (Figure 3). An ANOVA, including all three sample dates from 19 February to 17 March, indicated that flow and collection date had a significant effect on AFDM values during that time (Table 3). A one-way ANOVA testing the effect of sampling date on AFDM indicated a significant effect for the period from 4 February to 17 March (Table 4). Light did not significantly affect AFDM values.

ANOVAs for chl *a* for each day (19 February-17 March) showed a significant flow effect ($p<0.05$) on 7 March. A three-way ANOVA of sample date, flow and light for the same period showed that flow had a significant effect on chl *a* when all three days are included (Table 3). In addition, a one-way ANOVA for the effect of sampling date over the four sampling days (4 Feb.-17 Mar.) indicated that chl *a* on 4 February was significantly different from the other three sampling dates (Table 4). Analysis of the chl *a*/AFDM ratio shows a significant response to sampling date and the flow x light interaction for the period of 19 February to 17 March (Table 3). The ratio also showed a response to date for the four sampling dates from 4 February to 17 March (Table 4).

Table 2 a: Summary of t-test comparing means for chl *a* from fast and slow flow reaches collected on 2/4/94. **b:** Summary of t-test comparing means for AFDM from fast and slow flow reaches collected on 2/4/94. **c:** Summary of t-test comparing means for chl *a*/AFDM from fast and slow flow reaches collected on 2/4/94.

a)

Flow	N	Mean (µg chl *a*/cm^2)	SE
fast	5	0.0139	0.0046
slow	5	0.0170	0.0093

T= -0.30 **p**=0.77

b)

Flow	N	Mean (mg AFDM/cm^2)	SE
fast	5	0.0560	0.0086
slow	5	0.1378	0.0370

T=-2.17 **p**=0.096

c)

Flow	N	Mean(mg chl *a*/mg AFDM)	SE
fast	5	0.0024	0.069
slow	5	0.0011	0.043

T=1.65 **p**=0.15

Table 3: Analysis of variance summary for chlorophyll *a*, AFDM and chl *a*/AFDM ratio analyzed by flow, light and sampling date. Sampling dates included are 19 February, 7 March and 17 March.

	mg chl *a*/mg AFDM			mg AFDM/cm^2			$\log_e$µg chl *a*/cm^2		
Source	DF	F	P	DF	F	P	DF	F	P
flow	1	2.43	0.122	1	7.63	0.007	1	5.35	0.023
date	2	3.54	0.032	2	38.8	0.000	2	2.43	0.093
flow x date	2	3.05	0.052	2	1.31	0.275	2	0.36	0.699
light	1	0.10	0.748	1	0.13	0.717	1	0.24	0.625
flow x light	1	0.42	0.520	1	2.14	0.146	1	0.56	0.456
date x light	2	1.18	0.310	2	0.18	0.833	2	1.11	0.335
flow x date x light	2	2.33	0.102	2	0.54	0.585	2	2.31	0.105

Table 4: Summaries of ANOVA for Winter/Spring 1994 data analyzed by sampling date for the period from 4 February to 17 March. Fisher's pairwise comparisons follow the summary table.

Dependent variable	Source	df	*F*-ratio	p
log_eAFDM	Sampling Date	3	28.19	0.000
Chl *a*	Sampling Date	3	3.91	0.010
Chl *a*/AFDM	Sampling Date	3	4.98	0.003

Fisher's Pairwise Comparison

AFDM (mg/cm²)

Date	2/4/94	2/19/94	3/7/94	3/17/94
Mean	$0.095^{a,b}$	0.233^{c}	0.140^{a}	0.102^{b}

Chl a (µg/cm²)

Date	2/4/94	2/19/94	3/7/94	3/17/94
Mean	0.0154^{a}	0.0834^{b}	0.0846^{b}	$0.0562^{a,b}$

Chl *a*/AFDM

Date	2/4/94	2/19/94	3/7/94	3/17/94
Mean	0.1726^{a}	$0.3614^{a,b}$	0.5468^{c}	$0.4963^{b,c}$

Means denoted with the same superscript are not significantly different at the p=0.05 level. Arithmetic means shown.

Table 5 shows a summary of ANOVAs for the effect of light and flow on AFDM and chl *a* sampled from the artificial tiles collected on 5 April 1994. AFDM data have been transformed using square root. In this case, AFDM is significantly affected by light. Figures 2 and 3 show that the slow flow, low light treatment is responsible for this result with a large amount of chl *a* and small amount of AFDM. The chl *a*/AFDM data were not statistically analyzed due to the large number of missing points caused by values below the 0.0001 g detection limit for AFDM.

Fall/Winter 1994/95

Results from samples collected to determine phosphorus and nitrogen concentrations in the stream are listed in Table 6. All values for SRP were below the detection limit. TP was variable during this period with a high on 2 August 1994 of 0.025 mg/L and four samples below detection limit. Ammonia (NH_4) was also quite variable during the fall with maximum concentrations occurring on 8 November 1994 and only one other sample above the detection limit on 5 January 1995. Nitrate (NO_3) remained stable over the sampling period at about 0.2 mg/L except for the upstream sample on 29 November which was below the detection limit.

Phosphorus and nitrogen enrichment did not significantly affect AFDM values during early 1995 (Table 7). However, the control accumulated less mass on average than any of the enriched surfaces (Figure 5). Mean AFDM was 0.0437 mg/cm^2 for the control, 0.0701 mg/cm^2 for phosphorus, 0.0602 mg/cm^2 for nitrogen, and 0.0625 mg/cm^2 for phosphorus plus nitrogen enrichment. A comparison of the AFDM values shows that the nutrient enrichment experiment generally had lower AFDM than the spring 1994 collections.

Table 5: Summaries of 2-factor ANOVA for AFDM and chl *a* from clay tiles sampled on 5 April 1994.

Dependent variable	Source	df	*F*-ratio	p
$AFDM^{1/2}$	flow	1	0.05	0.832
	light	1	12.12	0.001
	flow x light	1	0.50	0.486
Chl *a*	flow	1	1.95	0.172
	light	1	0.99	0.326
	flow x light	1	0.11	0.742

Table 6: Concentrations of soluble reactive phosphorus (SRP), total phosphorus (TP), ammonia (NH_3) and nitrate (NO_3) by date for Stevensville Brook. All concentrations in mg/L. Values with * show the detection limit for that analysis and indicate that the sample was below that limit. Value with ** shows lower limit of calibration for that date and indicates that the sample was below this limit. N.A. indicates that samples were not available for those dates.

	DATE				
	8/2/94	11/8/94	11/29/94	12/19/94	1/5/95
SRP u	0.005*	0.001*	0.001*	0.001*	0.001*
d	N.A.	0.001*	0.001*	0.001*	0.001*
TP u	0.025	0.001*	0.010	0.009	0.002*
d	N.A.	0.001*	0.010**	0.006	0.003
NH_4 u	N.A.	0.29	0.02*	0.02*	0.02*
d	N.A.	0.08	0.02*	0.02*	0.04
NO_3 u	N.A.	0.15	0.10*	0.19	0.20
d	N.A.	0.15	0.21	0.21	0.21

u=samples taken at upstream end of site
d=samples taken at downstream end of site

Table 7: Summary of results for the nutrient enrichment experiment for Winter 1995.

Dependent variable	Source	df	*F*-ratio	p
log_eAFDM	Nutrient Type	3	2.00	0.173
log_eChl *a*	Nutrient Type	3	3.89	0.037

Fisher's Pairwise Comparison for Chl a

Phosphorus	Nitrogen+Phosphorus	Nitrogen	Control
0.4503^a	0.3389^a	0.1738^b	0.0937^b

Means denoted with the same superscript are not significantly different at the p=0.05 level. Arithmetic means shown; units=μg/cm².

Figure 5: Mean AFDM (n = 4 except nitrogen n = 3) for the nutrient enrichment experiment during Fall/Winter 1994/95 at Stevensville Brook. Control = substrates without nutrient addition, Nitrogen = substrate amended with nitrogen, Phosphorus = substrates amended with phosphorus and Nitrogen + Phosphorus = substrates amended with both nitrogen and phosphorus. Error bars = 1 SE.

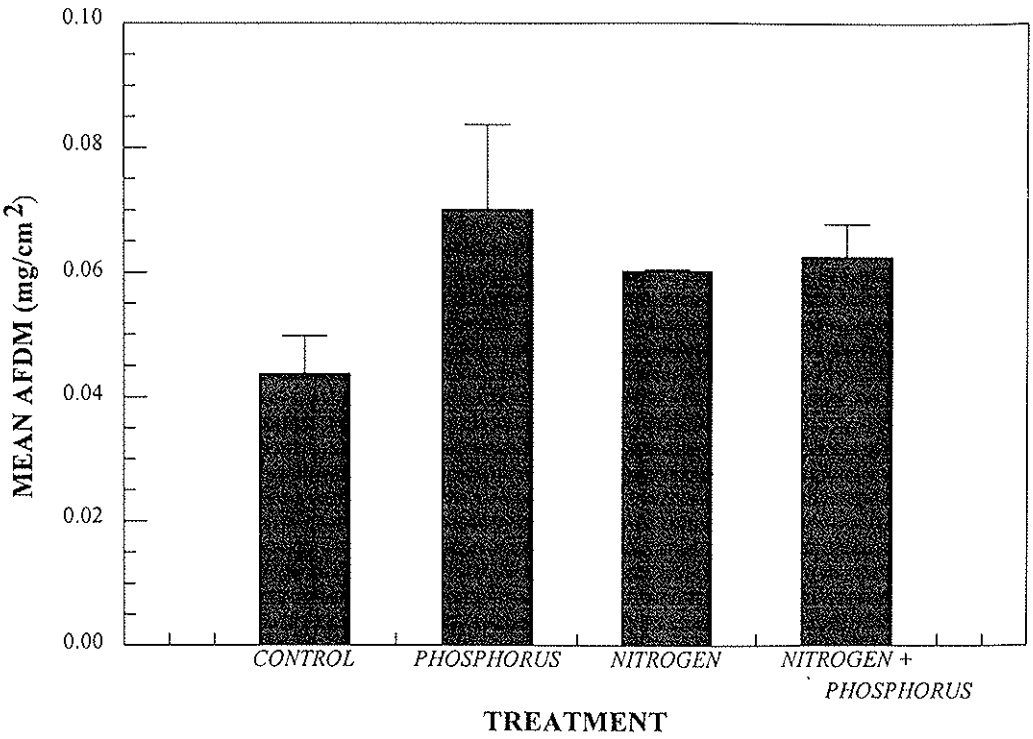
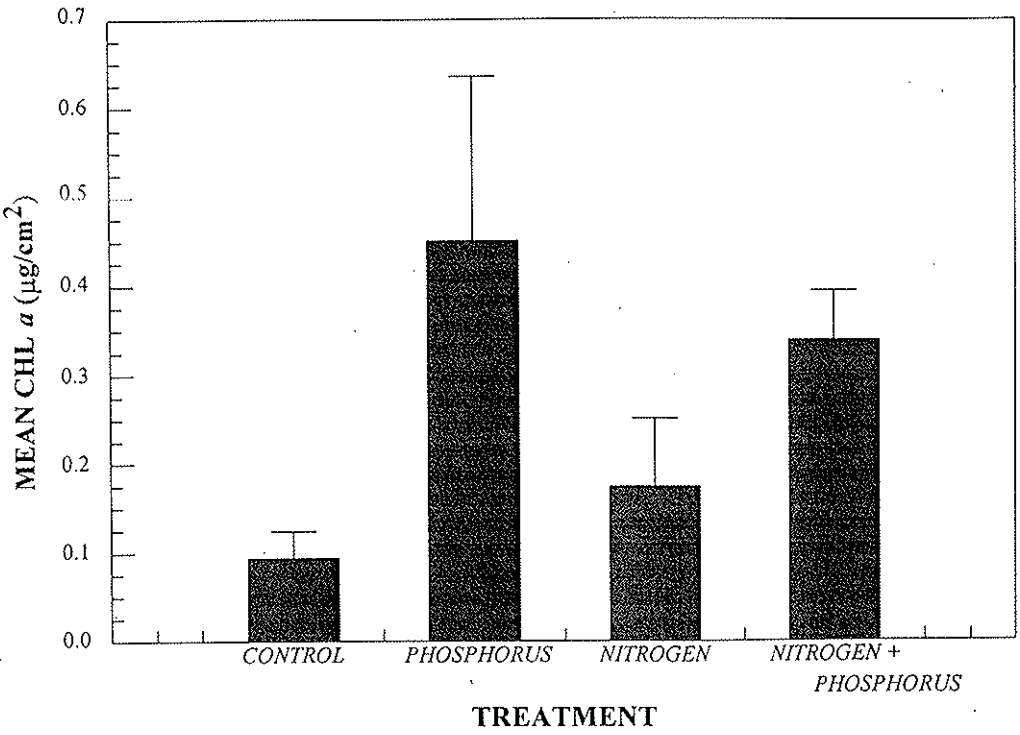

0.10
0.08
0.06
0.04
0.02
0.00
MEAN AFDM (mg/cm 2)
CONTROL
PHOSPHORUS
NITROGEN
NITROGEN + PHOSPHORUS
TREATMENT

Figure 6: Mean chl *a* (n=4) for the nutrient enrichment experiment during Fall/Winter 1994/95 at Stevensville Brook. Control = substrates without nutrient addition, Nitrogen = substrate amended with nitrogen, Phosphorus = substrates amended with phosphorus and Nitrogen + Phosphorus = substrates amended with both nitrogen and phosphorus. Error bars = 1 SE.


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MEAN CHL a (µg/cm2)
CONTROL
PHOSPHORUS
NITROGEN
NITROGEN + PHOSPHORUS
TREATMENT

The phosphorus and phosphorus plus nitrogen enrichments, with five and three and a half times more chl *a* respectively than the control (Figure 6), exhibited a significant positive effect on chl *a* standing stock (Table 7). The average chlorophyll value for nitrogen treated substrata was not significantly different from the control (Table 7), although the nitrogen mean was almost two times greater than the control mean(Figure 6). Chl *a* means were: 0.0937 $\mu g/cm^2$ for the control, 0.4503 $\mu g/cm^2$ for phosphorus, 0.1738 $\mu g/cm^2$ for nitrogen, and 0.3389 $\mu g/cm^2$ for the phosphorus plus nitrogen enrichment (Figure 6). Average chl *a* values were about two times higher for nitrogen, three and a half times higher for phosphorus and nitrogen, and five times higher for phosphorus than the highest chl *a* values for stream rocks collected in spring 1994.

DISCUSSION

The data verify the existence and dynamic nature of periphyton in Stevensville Brook during winter. Both AFDM and chl *a* clearly showed activity over the period from 4 February to 17 March 1994 (Figs. 2 & 3). A comparison of the data shows that Stevensville Brook chl *a* concentrations during winter were equal to and in some cases higher than similar Vermont streams sampled during summer (Scott 1982). Winter values for chl *a* reported by Scarsbrook and Townsend (1993) for two New Zealand streams are also comparable to Stevensville Brook as are chl *a* and AFDM concentration in nutrient poor catchments in New Zealand studied by Biggs (1995), winter concentrations of chl *a* and AFDM in the Rakaia and Waimakariri rivers in New Zealand (Biggs and Close 1989), and AFDM values found in streams in Oregon (Rounick and Gregory 1981). However, Stevensville Brook chl *a* and AFDM concentrations were up to an order of magnitude lower

than in streams studied by Liaw and MacCrimmon (1978) in Ontario, Canada; Grimm and Fisher (1989) in Arizona, USA; Uehlinger (1991) in Switzerland; Delong and Brusven (1992) in Idaho.

Even more interesting and unexpected than the existence of an active winter periphyton community were observed increases of up to 300% for AFDM and up to 600% for chl *a* between the 4 February and 19 February sampling dates. It is possible that the spate on 29 January reset the community and spurred the increase seen on 19 February. Uehlinger (1991), following bed moving spates in September, observed increases of about 300% for mean AFDM and about 400% for mean chlorophyll through winter to the end of January in the Necker River, Switzerland. It has been suggested that post spate communities can grow rapidly because dead cells are washed away decreasing any shade effect and faster flow can increase nutrient delivery across the viscous sub-layer (Horner *et al.* 1990, Stevenson 1990). The increases observed are in contrast to the findings of Biggs and Close (1989) and Rounick and Gregory (1981) who concluded that biomass development was higher in winter for rivers which did not experience high discharge events.

There did not appear to be a single factor controlling periphyton standing stock over the sampling period. The algal component, as represented by chl *a*, was found to be significantly phosphorus limited (Table 7) during winter 1994-95. This is not surprising given the phosphorus concentrations found in-stream during Fall/Winter 1994/95 and invalidates the initial assumption that no nutrient limitation exists during this portion of the year. During the fall and into winter 1994/95, SRP values were found to be consistently below a detection limit of 0.001 mg/L (Table 6). TP was variable for the sampling period, but generally comparable to concentrations found in other Vermont streams with similar

characteristics (Scott 1982). SRP and TP concentrations in Stevensville Brook are extremely low as compared to values found elsewhere in the literature (Rounick and Gregory 1981, Elwood *et al.*1981, Biggs and Close 1989, Winterbourn 1990, Mulholland 1992). Nutrient limitation during winter has been reported by Mulholland (1992) who found a winter minimum for phosphorus in streams in Tennessee, but he pointed out that this was contradictory to previous research in the northern USA. Winterbourn (1990) has reported an increase in chl *a* following nitrogen and phosphorus addition during winter in streams in New Zealand. Phosphorus limitation has also been demonstrated at other times of the year (Elwood *et al.* 1981, Peterson *et al.* 1985, Carrick & Lowe 1989).

The assumption that nutrients would not be limiting was based on the observation that leaf litter remains in the stream from autumn and the belief that it would continue to decompose and release nutrients throughout the winter. A likely reason that winter processing is not providing adequate phosphorus in Stevensville Brook is a reduction in bacterial and detritivore mineralization caused by low temperatures (Reice 1974, Webster and Benfield 1986), although, some studies have shown that significant breakdown can occur at 0^{0}C (Short *et al.* 1980, Sinsabaugh *et al.* 1981). Alternatively, it's possible that winter breakdown is occurring, but that decomposers are actually depleting stream phosphorus (Elwood *et al.* 1981, Webster and Benfield 1986). Low in-stream phosphorus also discounts the possibility that snow meltwater during the winter is providing adequate nutrients. It has been reported that runoff from snow melt can carry significant amounts of phosphorus (Gjessing and Johannessen 1987) derived largely from the forest floor (Barry and Price 1987). Most likely, the numerous melt events that occur during the winter in Vermont are either not

frequent enough to supply adequate phosphorus, or they are not of a great enough magnitude to leach organic materials at the forest floor.

Chl *a* was also significantly affected by flow and sampling date during the Winter/Spring 1994 sample period, but flow accounted for only 4% of the variance for the model in Table 3 while sampling date explained 9% of the variance for the model in Table 4. This is in contrast to the nutrient enrichment experiment in which nearly 50% of the variance was explained by the nutrient treatments. The significance of flow and date suggests that the periodic spates experienced as a result of snow melt in winter are responsible for the flow mediated response and that slow flow reaches are less affected than fast flow reaches. This finding contradicts that of Scarsbrook and Townsend (1993) who found that pools had a higher disturbance frequency than riffles based on bed movement.

It is unusual that AFDM did not show a response to nutrient treatment since chl *a* is a component of AFDM. In fact, chl *a* and AFDM response to nutrients, flow and sampling date were different, evidence that other components of the periphyton besides chl *a* dominated the AFDM response. A decoupling of these variables has been reported by Biggs and Close (1989) in a study of periphyton from nine streams in New Zealand. In Stevensville Brook, slow flow reaches accumulated a greater amount of organic matter than fast flow reaches. This would be expected since deposition is greater in slow flow reaches (Lau & Liu 1993). As with chl *a*, flow accounts for a small percentage (~4%) of the total variance for AFDM in the model in Table 4. The response of AFDM to sample date accounted for about 40% of the total variance for the three day (19 February - 17 March) and four day (4 February - 17 March) analyses (Tables 3 & 4). As with chl *a*, it seems that midwinter spates are controlling the periphyton

AFDM, although the change over time could also be a response to changing day length.

What is most surprising about these experiments is that reduced light level did not cause a significant response in periphyton communities except for AFDM accumulation on the clay tiles (Table 5). Other studies have shown that light elimination can result in a significant alteration of the periphyton community (Wright 1964, Bothwell *et al.* 1989, Steinman *et al.* 1991, Hill *et al.* 1995). Either the influence of light is negligible compared to other parameters, or the effect of light is being obscured by photoacclimation (Raps *et al.* 1983, Cunningham *et al.* 1990, Smith *et al.* 1990, Sukenik *et al.* 1990). In the latter situation, the loss of chlorophyll due to reduced growth or death of algae would have been offset by an increase in the chl *a* content per surviving cell. Since the response of chl *a* is not apparent in the AFDM response, photoacclimation could render invisible the effect of light on chl *a*. Alternatively, low temperature may have caused a depression of the compensation point so that reduced light treatment was not low enough to be limiting (Davison 1991). Results from the clay tile experiment suggest that light plays a role in colonization of open patches. Movement in response to light has been demonstrated by Bothwell *et al.* (1989) in streams and has been shown to occur among phytoplankton (Wright 1964). Light controlled immigration would profoundly impact ice covered streams and may explain the low standing crop of periphyton in Stevensville Brook.

Changes in the ratio chl *a*/AFDM through winter 1994 further support the existence of an active periphyton community and may indicate a community succession occurring between heterotrophs and autotrophs. Thomas *et al.* (1991) noted a similar occurrence in a subalpine California lake where the ratio of planktonic chlorophyll to bacterial biomass increased from January through

March. Autotrophy in Stevensville Brook peaked around the 7 and 17 March sampling dates which may signal algal community growth in response to changes in daylength. This change is confirmed by an analysis of variance showing that the ratio has a significant time response (Table 3 & 4). The ratio also showed a significant effect in the flow x date interaction term, but not to flow alone, supporting the hypothesis that short term flow processes (spates) have a significant impact on the periphyton community. The percentage of chlorophyll to AFDM found in Stevensville Brook compares well with figures reported for other mountain streams (Pontasch and Brusven 1987, Biggs and Close 1989).

The data from these experiments support the model put forth by Menge and Sutherland (1987) that physico-chemical factors control community dynamics under high stress conditions. That there is much unexplained variance in the data indicates the need for further research and reinforces the need to conduct research spanning all seasons of the year (Harper 1981, Resh *et al.*, 1988). Three areas to investigate in future research are: 1) the role of low temperature in controlling periphyton communities, 2) the interaction of flow, nutrients and temperature and 3) the possible interference of photoacclimation in quantifying a response of periphyton chl *a* to light.

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PERIPHYTON STANDING STOCK IN A MOUNTAIN STREAM DURING WINTER II: IS THERE ANYBODY OUT THERE?

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ABSTRACT

Numerous models of community dynamics predict low diversity in high stress ecosystems. While epilithic algae during winter provide appropriate test communities for such models, few studies of these systems have been made. This research tested the hypothesis that lowest diversity for algal communities will occur during the winter and that reaches with reduced light and fast flow would have a lower diversity than reaches with ambient light and slower flow. A 2^2 factorial experiment was established in Stevensville Brook, VT consisting of a combination of low light (0.8×10^{17} and 0.9×10^{17} Quanta$\cdot s^{-1} \cdot cm^{-2}$), high light ($0.3 \times 10^{16}$ and 0.2×10^{16} Quanta$\cdot s^{-1} \cdot cm^{-2}$) and slow flow (0.15 m/s), fast flow (0.30 and 0.34 m/s) treatments. Slow and fast flow reaches were created by constructing rock dams and light was controlled by removing surface ice to create high light areas or removing surface ice and shading with a black mesh to create low light areas. Algal samples were collected on three occasions during February and March 1994. Algal samples were also collected on three occasions between August 1994 and January 1995, but no light treatments were imposed during this period. Changes in cell densities showed an active community during the sampling period with three taxa, *Chamaesiphon* sp., *Lyngbya subtilis* and *Synechocystis* sp., dominant out of a total of 52 species found. Neither individual taxon cell densities nor diversity were found to respond to the light treatment. Diversity for samples following the imposition of treatments was significantly affected by sampling date and flow, but no consistent pattern of flow effect could be seen across all sampling dates. The hypothesis that lowest diversity occurs during winter was rejected since a mid-February sampling date had the highest diversity values for three of the treatments.

KEYWORDS: epilithic algae, flow, intermediate disturbance hypothesis, light, species diversity, streams, species cell densities, species relative abundance, Vermont, winter.

INTRODUCTION

The community ecology literature has attempted to explain changes in community diversity as a function of the mechanisms of predation, competition, and stress/disturbance (Menge and Sutherland 1987). Most ecologists hold that adaptation, long term genetic or short term phenotypic, in response to an environmental variable involves an energy expenditure which is not then available to use for other organismic functions (Petraitis *et al.* 1989, Parsons 1993). Some current models hypothesize that maximum diversity, based on richness of species and their evenness of distribution, will be achieved when the frequency and magnitude of disturbance keep later successional species from excluding early successional species, but still allow later successional species to colonize. The connection to energy allocation is that later successional species must invest in adaptations which make them superior competitors and, therefore, less resilient to perturbation (Petraitis *et al.* 1989).

Numerous authors have attempted to refine this hypothesis. Huston (1979) linked disturbance and growth rate to the maintenance of diversity. He argued that slower growth rates for the community as a whole will lengthen the period of coexistence among competitors, thereby maintaining higher diversity, since it will take longer for dominants to displace inferiors. Conversely, faster growth rates will result in a quicker convergence to competitive exclusion. Menge and Sutherland (1987) hypothesized that under low recruitment and high

environmental stress, physical factors will predominate, competition and predation will be minimal and diversity will subsequently be low.

Although much lotic research has been devoted to testing these models, there is a lack of such studies for temperate region streams during winter. We studied the effect of light and flow on algal community structure and diversity during winter, spring and fall in a mountain stream located in northwestern Vermont, USA. This stream experiences severe winter conditions for a period of about five months, from November to April, each year. Winter, on average, has the lowest temperature and light values of all the seasons. Accumulation of precipitation in the snowpack results in long term low flows interspersed with freshets caused by occasional mid-winter thaws. While Huston (1979) hypothesized diversity maintenance under low growth conditions such as these, we expect that the limiting physical environment will override this effect and that epilithic algal species diversity during winter will be lower than at other times of the year as predicted in the Menge and Sutherland model. Rather than selecting between competitive ability and resistance to perturbation, it is likely that algae must be prepared to resist numerous abiotic extremes. It would be expected that algal communities would be expending energy to increase growth under low temperature and that extremes of light or flow would result in decreased cell density from reduced growth and decreased diversity caused by local species extinctions.

MATERIALS AND METHODS

Samples were collected from Stevensville Brook in Underhill State Park, VT, USA which was described in the previous chapter. For Winter/Spring 1994, a 2^2

factorial design was used with high and low levels for water velocity and light (values given in previous chapter). During Fall/Winter 1994/95 (4 August 1994, 5 October 1994 and 5 January 1995), fast flow, slow flow and high light treatments were maintained, but low light treatments were not imposed. Rocks were collected from all light and flow treatments on 19 February, 7 March and 17 March 1994; from flow treatments only on 4 August 1994 and 5 January 1995; and from the high flow reach only on 5 October 1994. A description of sampling protocol and sample processing for Winter/Spring 1994 was given in the previous chapter and these were the same methods used for collections made during Fall/Winter 1994/95.

Samples collected from a single rock were homogenized and split into three aliquots as described in the previous chapter, one aliquot of which was preserved with Lugol's solution (APHA 1992). Two preserved aliquots out of ten from each treatment for each date were randomly selected to make permanent slide mounts. At the time of slide preparation, the entire preserved aliquot was twice drawn into and forced out of a syringe with a needle to break up clumps then manually mixed in the sample vial. Permanent slides were prepared as outlined by Stevenson (1984). Total volume for a slide was 700 µl of Type II H_2O + sample; the amount of water added depended on the initial concentration of the sample. Samples were concentrated as necessary by allowing the sample to settle for 24 hours and drawing off a known volume of water. Slides were analyzed at a magnification of 1000x under oil immersion using an Olympus microscope with phase contrast illumination. Cells were enumerated by counting along transects of 100µm width. At least 500 cells were counted on each slide (Stevenson and Lowe, 1986).

Algae were identified using Prescott (1982), Germain (1981), Bourrelly (1970) and Smith (1950). Cell densities were determined by calculating the number of cells for the area of slide counted and using this number to estimate the total number of cells per slide and, thus, per volume of sample used for the slide. The number of cells per volume of sample used was then scaled up to number of cells in the original sample volume and this number was then divided by rock surface area. Relative abundances were calculated by adding the number of cells counted for a given species from the two slides analyzed for each treatment on each sampling date and dividing by the total of all cells counted for the treatment and sampling date. Diversity was determined using Shannon's diversity index calculated as:

$$H' = - \Sigma p_i \log p_i$$

where p_i is the proportion of the total number of individuals occurring in species i or,

$$p_i = n_i / N;$$

(Brower and Zar 1984). H' was analyzed for response to flow and sampling date once excluding the 5 October sample which lacked a slow flow sample to balance the model, and once excluding both 5 October and 4 February. The sample from 4 February was excluded to determine the impact of the variables after the imposition of the treatment manipulations. An ANOVA was also performed on the diversity values from 19 February, 7 March and 17 March to include the light effect which was imposed during the Winter/Spring 1994 sampling date. All statistical analyses were performed using Minitab for Windows version 10.2 (Minitab Inc., State College, PA).

RESULTS

A total of 52 species were found in Stevensville Brook over the sampling period (Table1). The Cyanophyceae was the largest contributor of species and cell densities for the periods sampled. The diatoms provided the 2nd largest group of species, but only *Eunotia exigua* was found regularly and in substantial numbers. Other phyla represented were Chrysophyceae, Rhodophyceae and Zygnemaphyceae. There were three species which could not be identified; their physical appearance is described in Table 1. Although none of the unknown taxa gave a positive starch test, members of Zygnemataceae, which normally store starch, did not give a positive starch test either. Therefore, the unknowns cannot be ruled out as possible members of the Chlorophyta.

Taxon Relative Abundance and Cell Density

Figure 1 shows the relative abundances for 16 species which contributed greater than 3% of the total cells counted for at least one treatment on one day. Figures 2-17 show the densities (cells/cm^2) for species which appear in figure 1. Relative abundance plots (Figure 1) indicate that three taxa comprised 80% and greater of the total cells counted throughout the course of the study: *Chamaesiphon* sp., *Lyngbya subtilis* and *Synechocystis* sp.

Chamaesiphon cells accounted for greater than 50% of all cells for 4 February and 4 August high light/fast flow (HL/FF), 7 March low light/slow flow (LL/FF), and 17 March low light/fast flow (LL/FF) and high light/slow flow (LL/FF) treatments. *Chamaesiphon* cells also accounted for 30% or more of the total cells counted for 11 of 19 samples and never comprised less than 10% of the total cells counted for any treatment on any day (Figure 1). *Chamaesiphon* cell

Table 1: List of taxa found in Stevensville Brook during winter/spring 1994 and fall/winter 1994/95.

Bacillariophycae	*Acnanthes lanceolata* Bréb.			*Gomphonema angustatum* (Kütz) Rabh.
	Acnanthes marginulata Grun.			*Meridion circulare* Agardh.
	Cooconeis placentula (Ehrbg.) Cleve.			*Navicula cari*
	Cymbella affinis Kütz.			*Nitzschia gracilis*
	Diatoma hiemale (Ehrbg.) Grun.			*Nitzschia linearis*
	Epithemia sorex Kütz.			*Nitzschia* sp.
	Eunotia exigua (de Bébisson) Grun.			*Pinnularia appendiculata* (Agardh.) Cleve.
	Eunotia pectinalis (Kütz) Rabh.			*Tabellaria flocculosa* (Roth.) Kütz.
	Frustularia rhomboides (Ehrbg.) DeToni.			
Cyanophycae	*Anabaena* sp.	*Entophysalis* sp.	*Lyngbya* sp.3	*Plectonema* sp.1
	Aphanothece sp.	*Gleocapsa* sp.	*Lyngbya* sp.4	*Plectonema* sp.2
	Borzia sp.	*Gloeotilopsis* sp.	*Lyngbya* sp.5	*Rivularia* sp.
	Chaemosiphon sp.	*Hormidium* sp.	*Oscillatoria* sp.1	*Synechococcus* sp.
	Chroococeidiopsis sp.	*Lyngbya subtilis*	*Oscillatoria* sp.2	*Synechocystis* sp.
	Chroodactylon sp.	*Lyngbya* sp.2	*Pascherinema* sp.	
			Psuedoanabaena catenata Lauterb.	

Table 1: continued.

Chrysophyceae	*Peroniella* sp.		
Rhodophyceae	*Audouinella* sp.1	*Audouinella* sp2.	*Chroodactylon* sp.
Zygnemaphyceae	*Closterium leibleinii* Kütz	*Cosmarium* sp.2	
	Cosmarium sp.1	*Cylindrocystis brebissonii* Menegh. (Fontainebleu).	
Unknowns	1) Colonies of spherical, eukaryotic cells. Each cell ~10µm in diameter and surrounded by wall.		
	2) Filament with eukaryotic cells. Cells ~4µm in diameter and filament ~3um wide.		
	3) Single cells ~5µm diameter with no flaggelum and a parietal chloroplast.		

Figure 1: Plots of relative abundances for species found in Stevensville Brook which contributed greater than 3% of the total cells counted for at least one treatment on one date.

Legend for Figure 1:

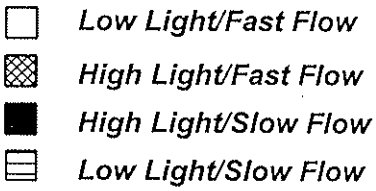


Figure 1

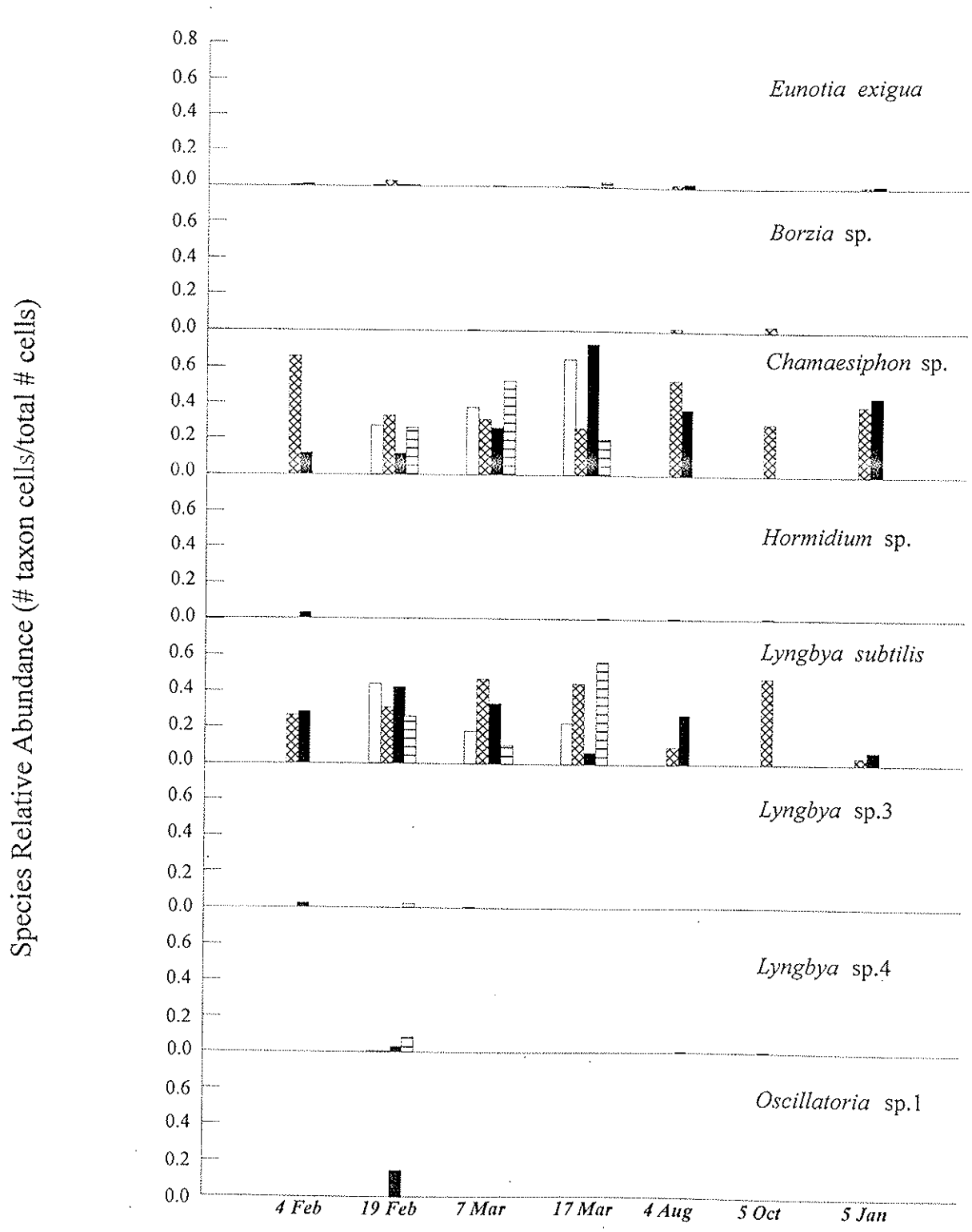
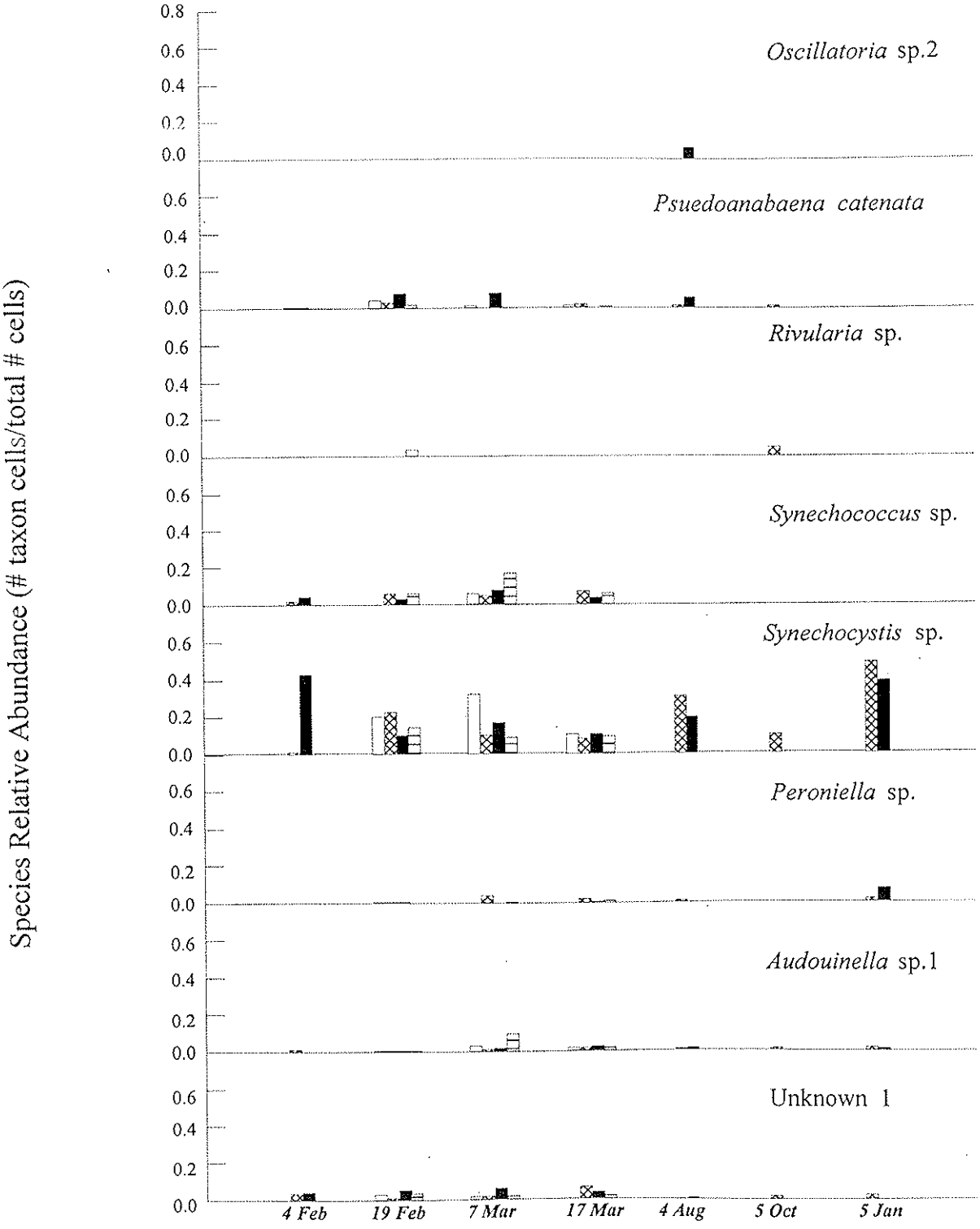

Species Relative Abundance (# taxon cells/total # cells)
0.8
0.6
0.4
0.2
0.0
Eunotia exigua
Borzia sp.
Chamaesiphon sp.
Hormidium sp.
Lyngbya subtilis
Lyngbya sp.3
Lyngbya sp.4
Oscillatoria sp.1
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 1 continued



densities peaked on 17 March for LL/FF and LL/FF with 7.9 x 10^5 and 4.4 x 10^5 cells/cm^2 in each treatment respectively (Figure 4). Cell densities for the HL/FF treatment were highest on 4 August at 4.5 x 10^5 cells/cm^2 and LL/SF were highest on 19 February at 2.9 x 10^5 cells/cm^2. Sampling date appeared to impact *Chamaesiphon* the most with cell densities being lowest on 5 January and 4 February and maximum density occurring on 17 March. There was no apparent effect of the light or flow treatments on *Chamaesiphon* density.

Lyngbya subtilis accounted for 30% and greater of the total cell abundance for 8 of 19 samples over the study period and dropped below 10% for four samples (Figure 1). The highest density of *L. subtilis* (Figure 6) occurred in the LL/FF treatment on 19 February with 5.8 x 10^5cells/cm^2. Two peak densities, 3.8 x 10^5 cells/cm^2 on 17 March and 3.7 x 10^5 cells/cm^2 on 5 October, occurred for *L. subtilis* in the HL/FF treatment. A peak of 2.1 x 10^5 cells/cm^2 for the LL/FF treatment and 2.9 x 10^5 cells/cm^2 for LL/FF both occurred on 19 February. Although the greatest combined density of *L. subtilis* occurred on 19 February, cell densities did not show any distinct pattern by date except that the 5 January and 4 February densities were very low compared to all other dates. The effect of flow appeared to control cell densities on 19 February and 4 August when slow flow reaches had greater densities than fast flow and on 17 March when fast flow reaches had higher cell densities. Combined high light treatments on 7 March had higher *L. subtilis* cell densities than low light treatments.

Synechocystis sp. accounted for 30% or more of the total cells in 5 of 19 samples and comprised more than 10% of the cells found for 15 of 19 samples (Figure 1). Except for 4 February HL/FF in which *Synechocystis* accounted for less than 1% of the total, it's relative contribution to the community was highest in mid-winter (4 February and 5 January). Cell densities for *Synechocystis*

(Figure 14) peaked for LL/FF at 2.0 x 10^5 cells/cm^2 on 7 March, for HL/FF at 2.6 x 10^5 cells/cm^2 on 4 August, for HL/SF at 1.4 x 10^5 cells/cm^2 on 19 February and for LL/SF at 1.6 x 10^5 cells/cm^2 on 19 February. *Synechocystis* densities appeared to be flow regulated over most of the sampling period. Samples for 4 February and 19 February show a higher number of cells on average in slow flow treatments. However, on 7 March, 4 August and 5 January, the fast flow densities were higher than slow flow densities. There was not any obvious effect of the light treatments on *Synechocystis* densities.

There were numerous other species which were found in smaller numbers than the ones above throughout the sample period. *Synechococcus* sp. represented 5% or more of the algal density for 8 of 19 samples including 10% of the cells counted for LL/FF on 7 March (Figure 1). *Synechococcus* was not found in samples after 17 March. Unknown 1 accounted for 5% or more of the total for only 3 out of 19 samples, but was found in all samples except HL/FF on 4 August and LL/FF on 5 January. Cell densities for unknown 1 were highest on 19 February, 7 March and 17 March. *Pseudoanabaena catenata* contributed to more than 5% of the total cell density on 19 February, 7 March and 4 August all in the HL/SF treatment. *P. catenata* was found in 14 out of 19 samples during the study, but was not found at all on 5 January and had very low densities on 4 February (Figure 11). Although not contributing 5% or more of the total cells for any sample, *Eunotia exigua* was present in every sample. There were two peak densities for *E. exigua* occurring on 19 February and 4 August (Figure 2). *Audouinella* sp.1 accounted for 9% of the total cells counted in the LL/FF treatment on 7 March, but did not contribute more than 3% in any other sample and was not found in HL/SF on 4 February (Figure 16). *Audouinella* sp.1 densities were highest on 7 and 17 March and lowest on 4 February and 5

Figure 2-17: Mean cell density (n=2) for individual taxa which contributed greater than 3% of the total cells counted for at least one treatment on one date. Cell densities were normalized to rock surface area.

Figure 2

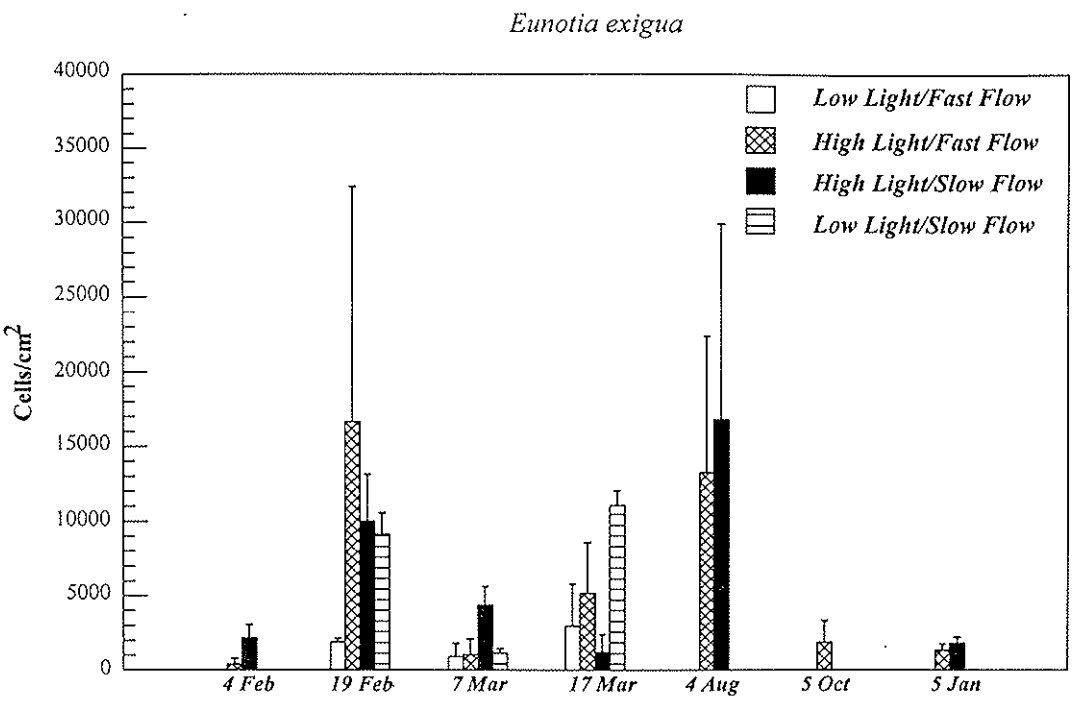

Eunotia exigua
Cells/cm2
40000
35000
30000
25000
20000
15000
10000
5000
0
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow

Figure 3

Borzia sp.

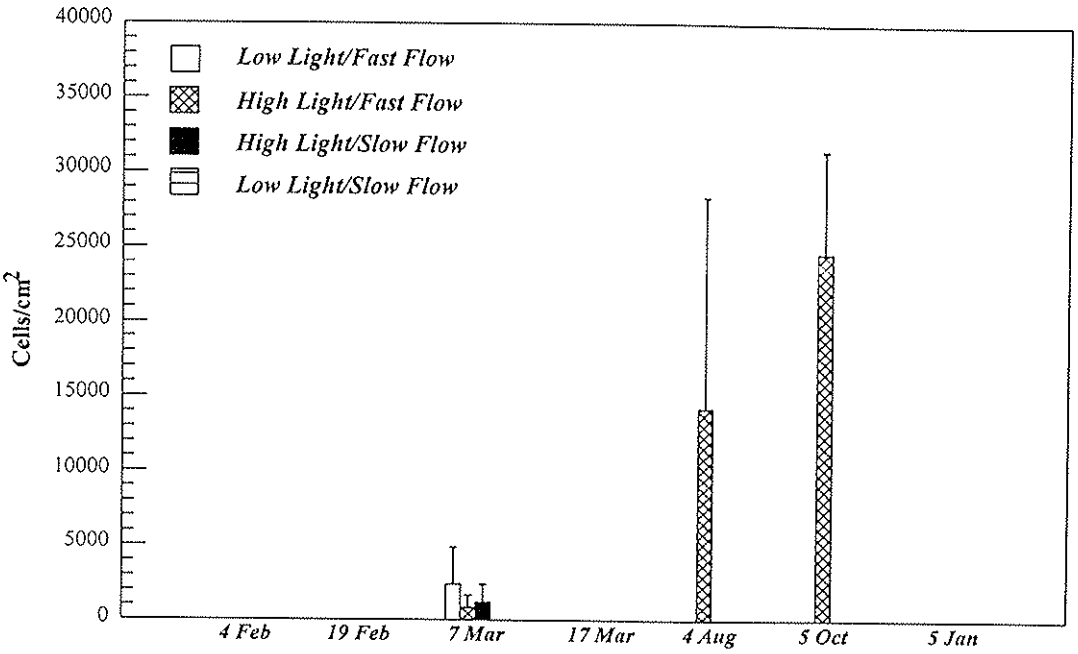


Figure 4

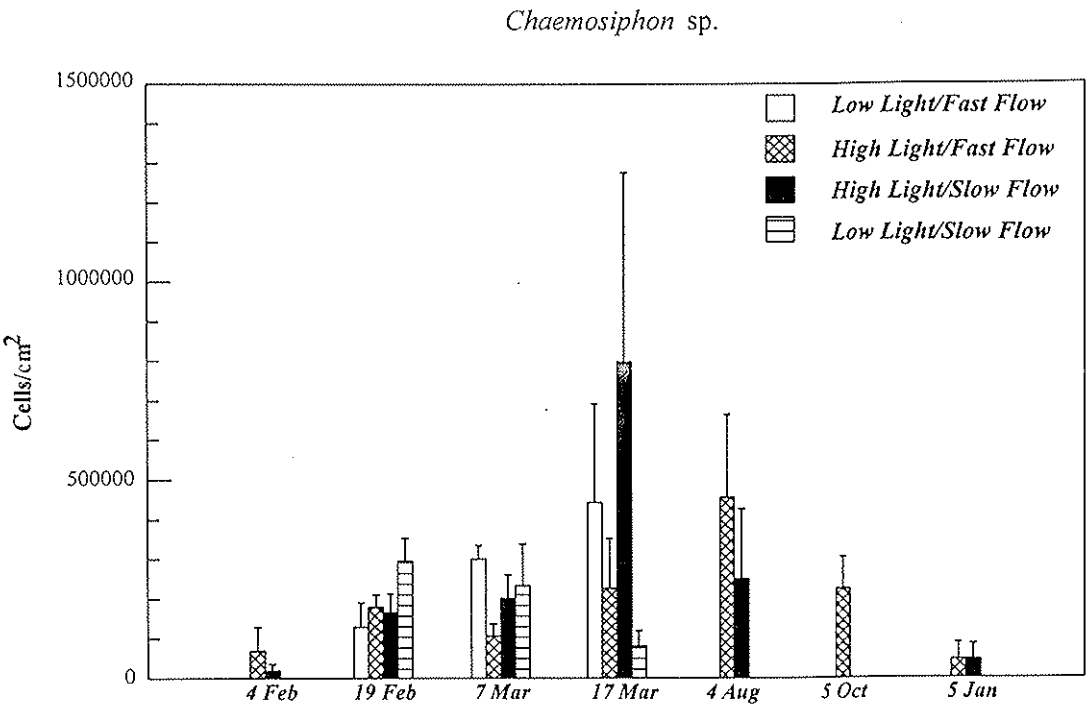

Chaemosiphon sp.
1500000
1000000
500000
0
Cells/cm^2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 5

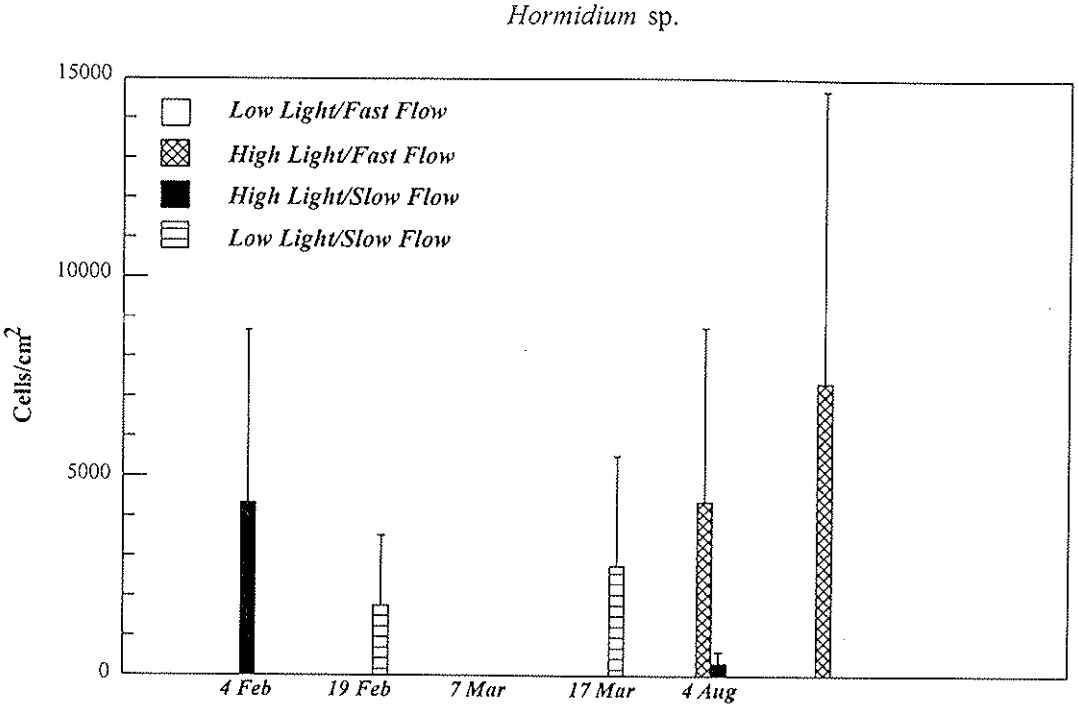

Hormidium sp.
15000
10000
5000
0
Cells/cm^2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug

Figure 6

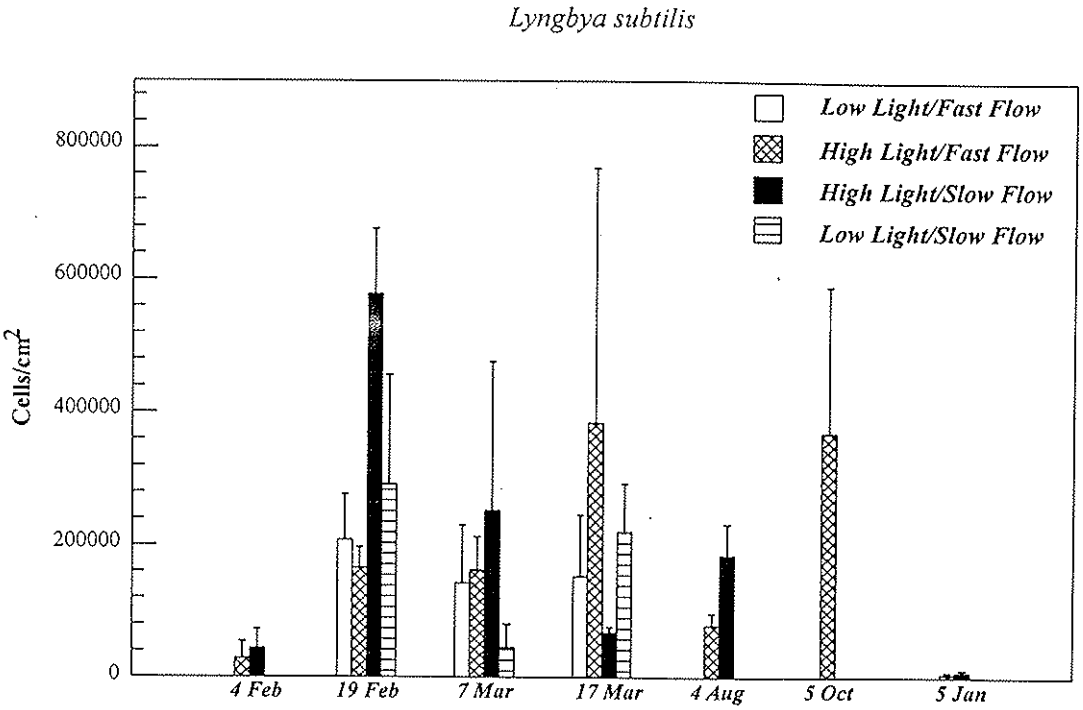

Lyngbya subtilis
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
Cells/cm2
800000
600000
400000
200000
0
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 7

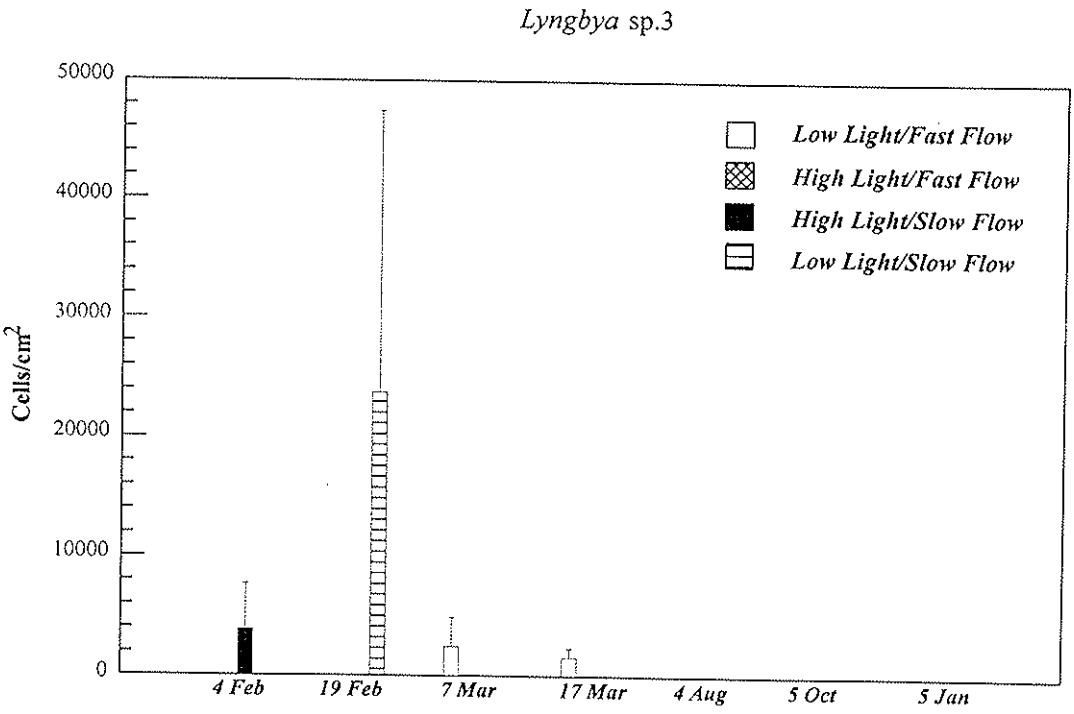

Lyngbya sp.3
50000
40000
30000
20000
10000
0
Cells/cm^2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 8

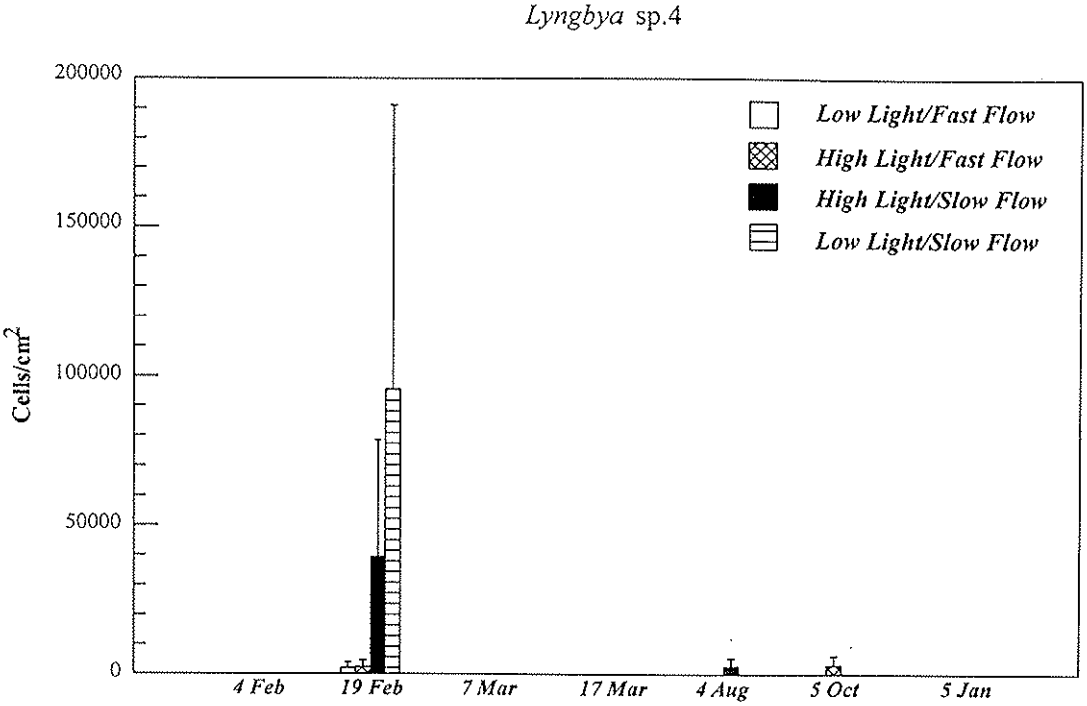

Lyngbya sp.4
200000
150000
100000
50000
0
Cells/cm^2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 9

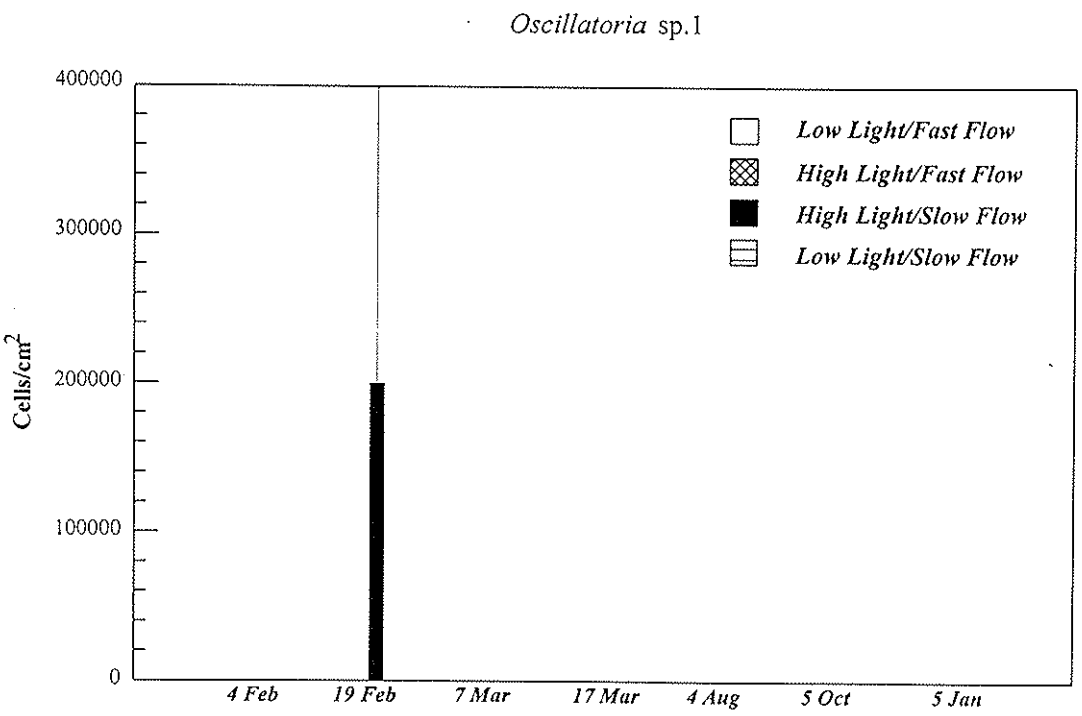

Oscillatoria sp.1
400000
300000
200000
100000
0
Cells/cm^2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 10

Oscillatoria sp.2

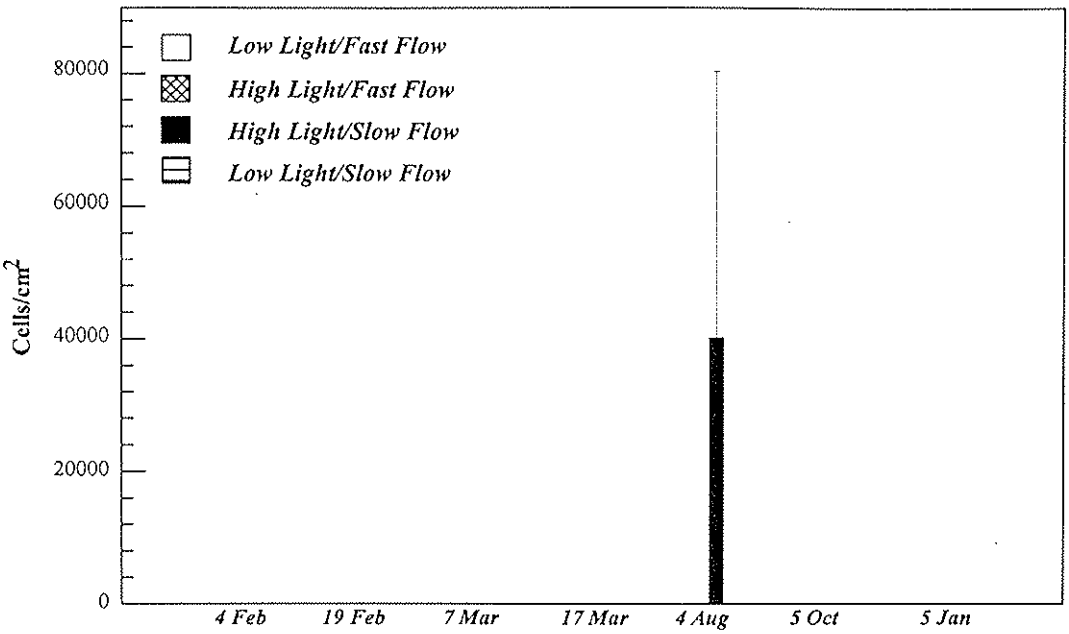


Figure 11

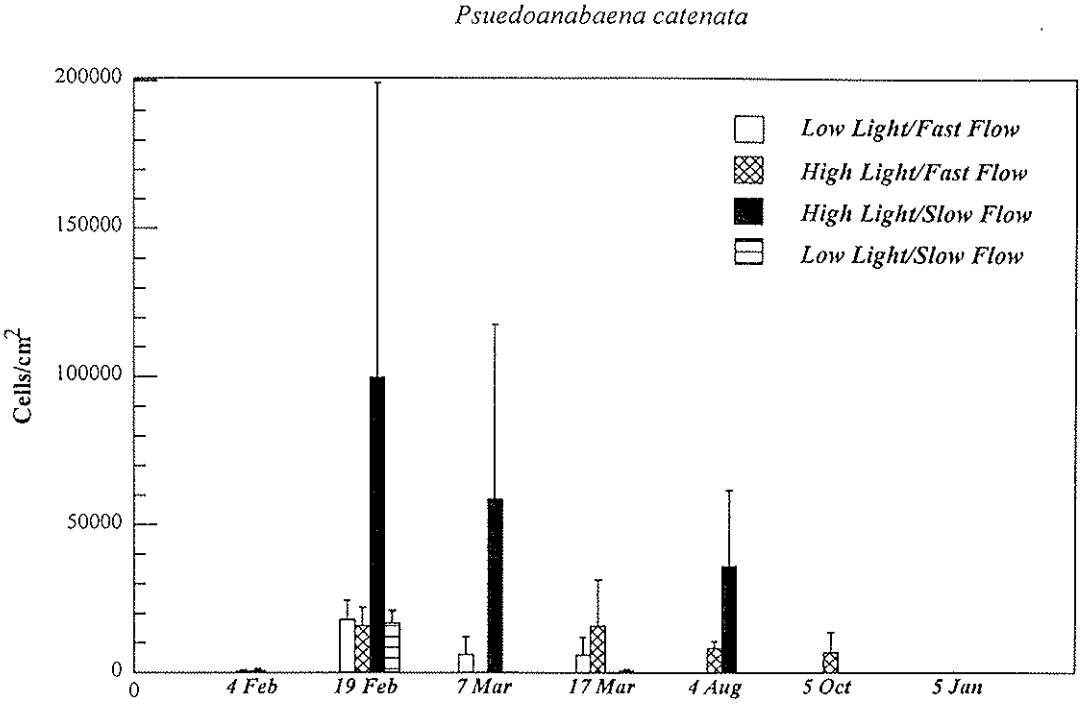

Psuedoanabaena catenata
200000
150000
100000
50000
0
Cells/cm2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
0
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 12

Rivularia sp.

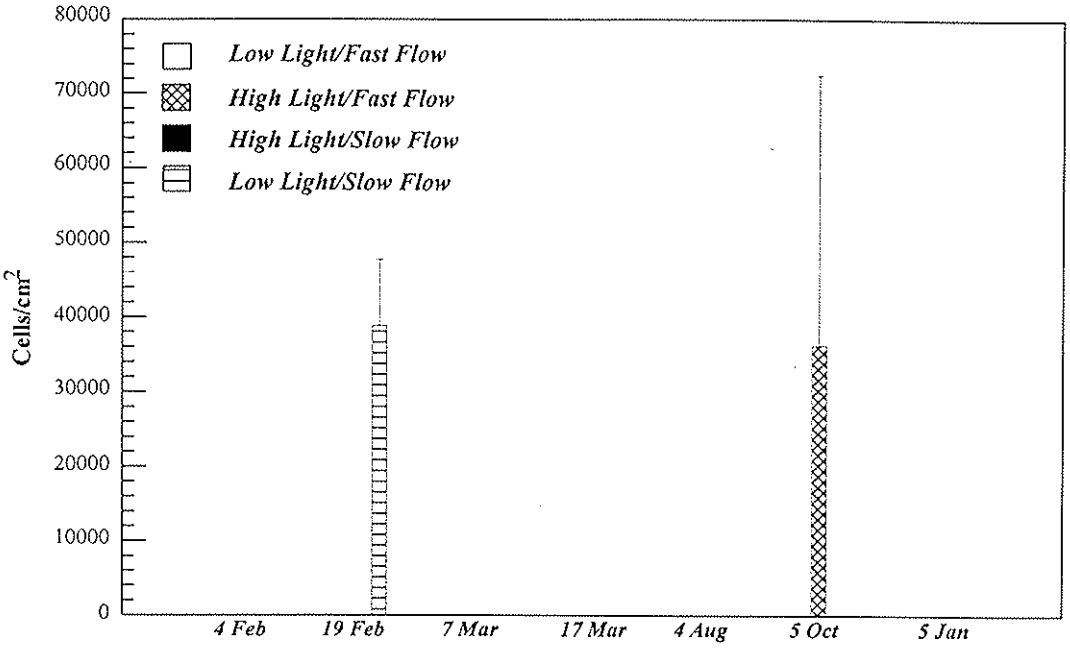


Figure 13

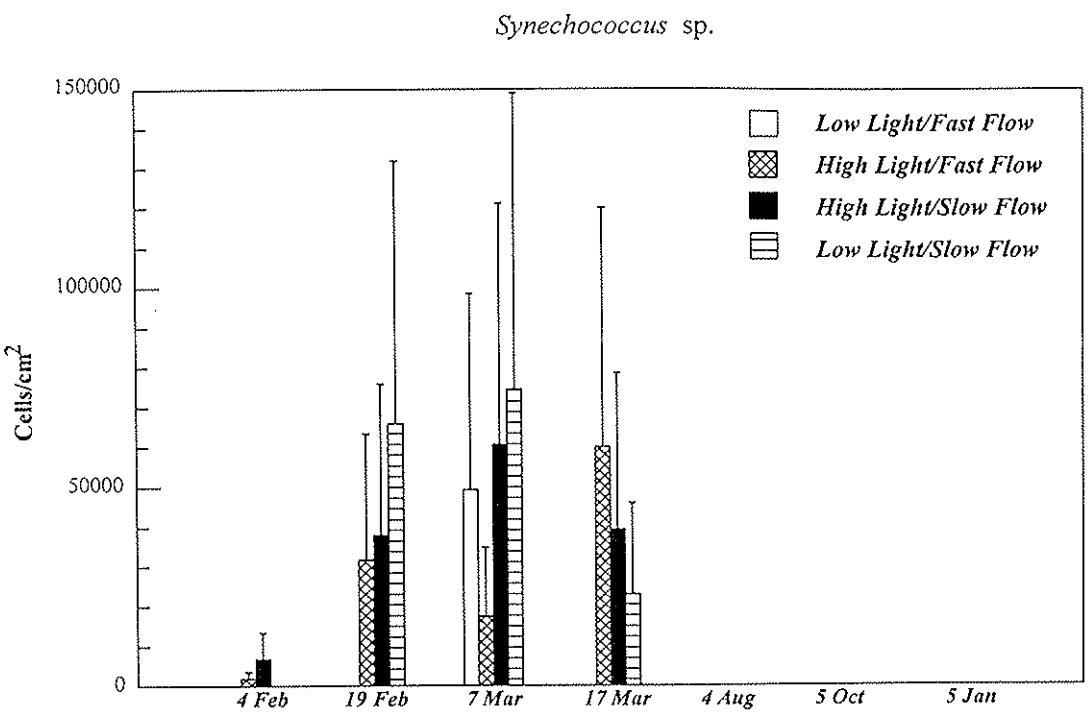

Synechococcus sp.
150000
100000
50000
0
Cells/cm^2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 14

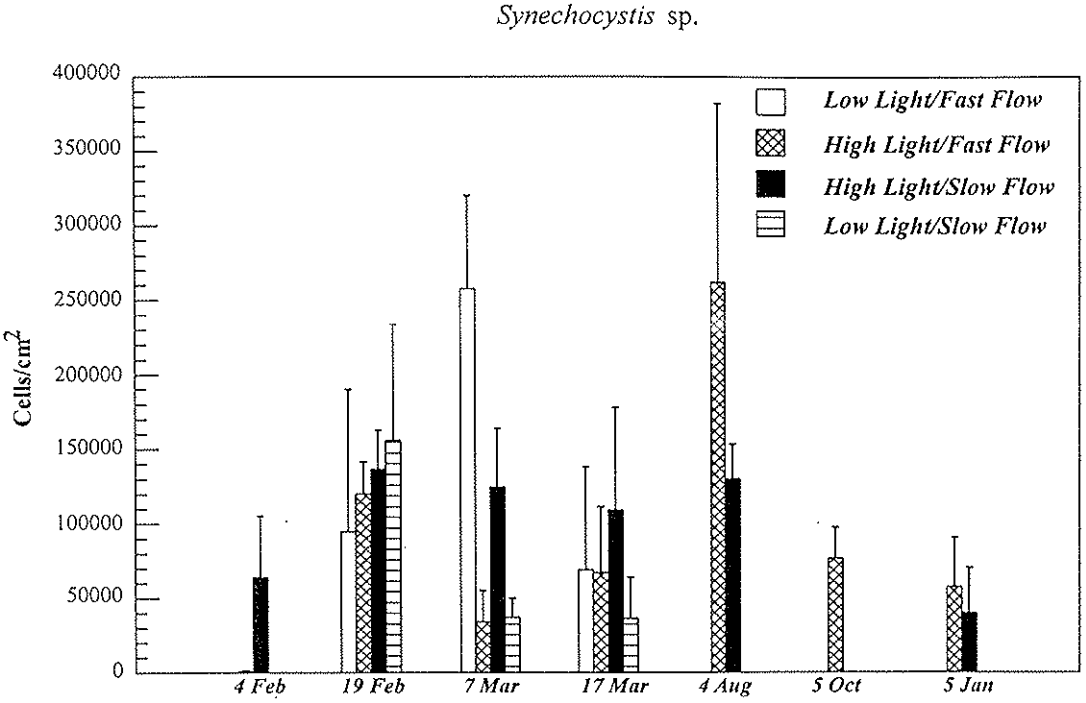

Synechocystis sp.
Cells/cm^2
400000
350000
300000
250000
200000
150000
100000
50000
0
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Figure 15

Peroniella sp.

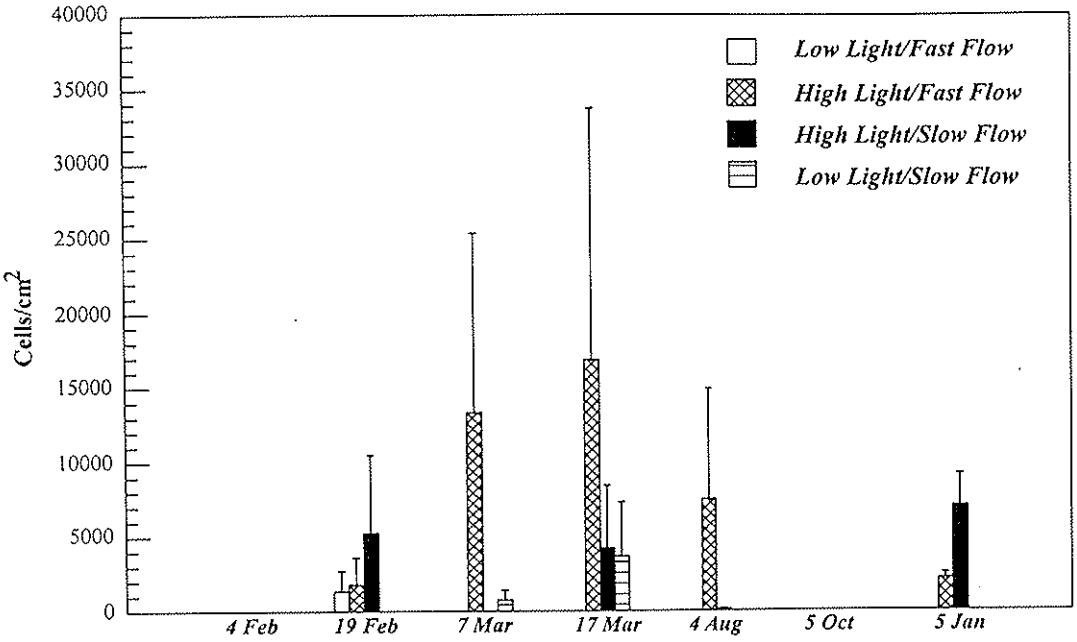


Figure 16

Audouinella sp.1

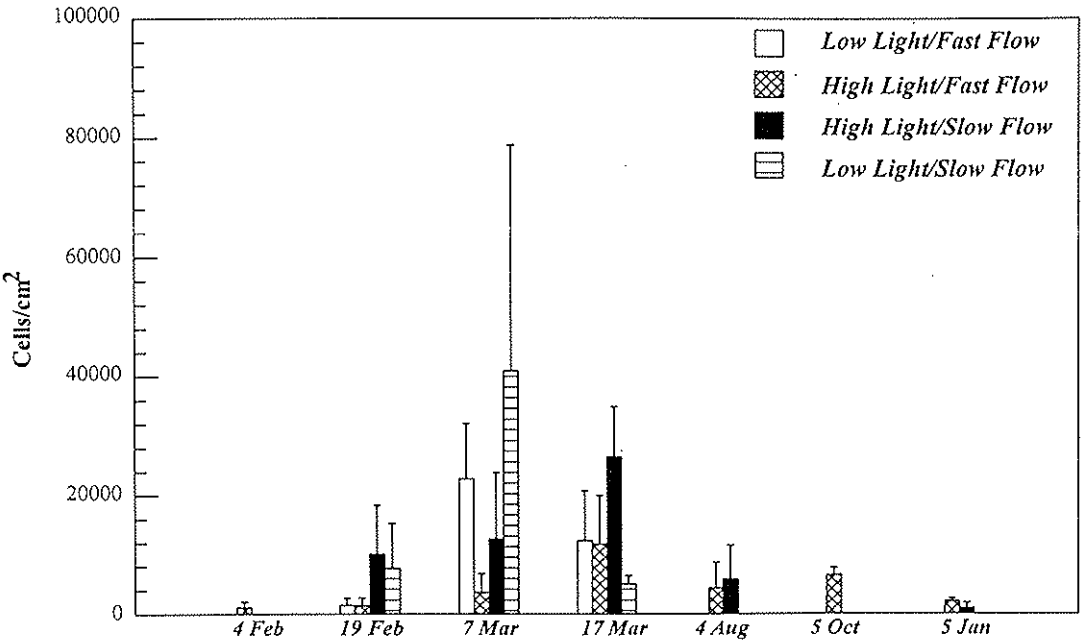
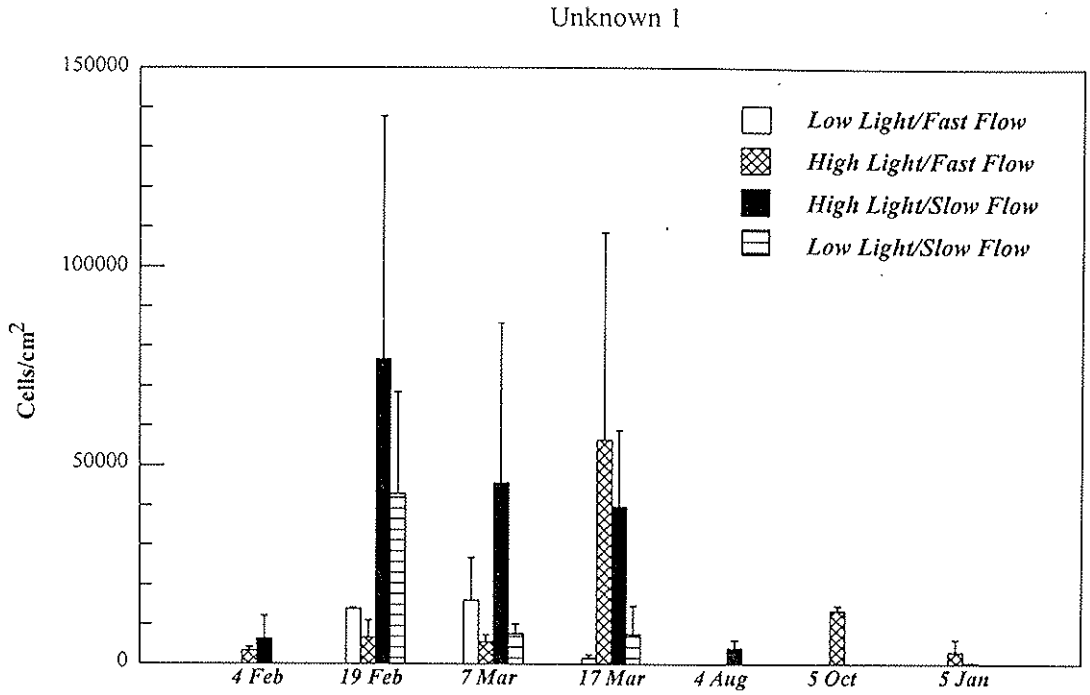


Figure 17


Unknown 1
150000
100000
50000
0
Cells/cm2
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

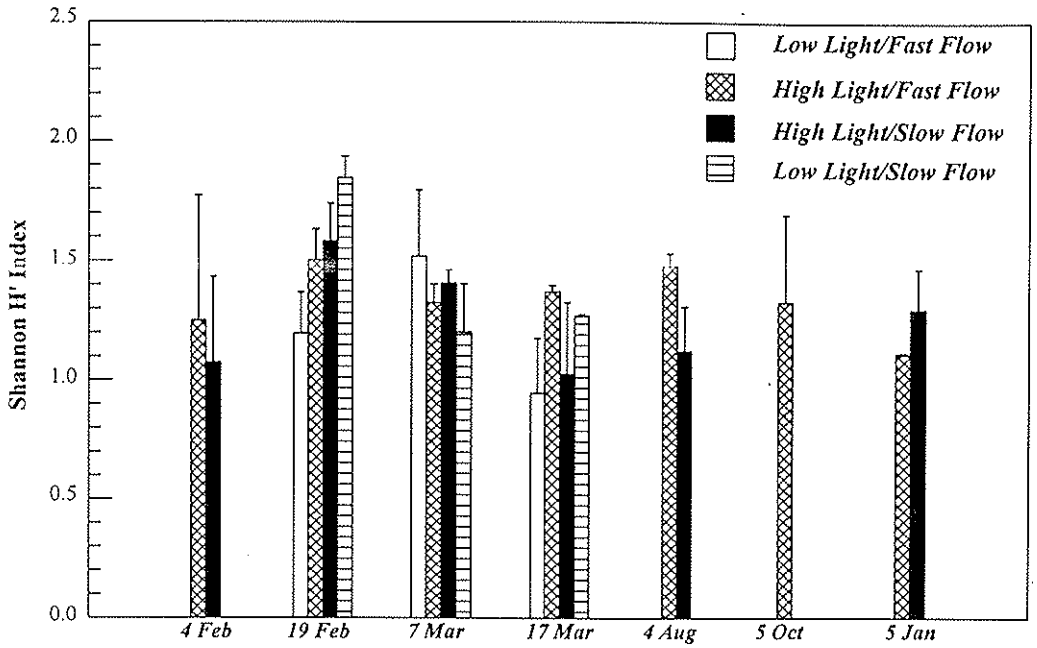
January. *Oscillatoria* sp.1 and sp.2, *Lyngbya* sp.1 and sp.2, *Rivularia* sp., *Peroniella* sp., *Borzia* sp., and *Hormidium* sp. generally did not exceed 1% of the total for most samples and often were not found outside of a few samples, but are shown in figure 1 because they accounted for at least 3% of the total cells in one sample.

Shannon H' *Diversity*

The Shannon *H'* diversity index is shown in Figure 18. Initial mean diversity values were 1.249 for fast flow reaches and 1.074 for slow flow. Between 4 February and 19 February, average diversity increased by 17% for HL/FF, 47% for LL/FF and 72% for LL/FF, constituting the largest increase and producing the largest diversity value for the sample period, while decreasing by 4% for LL/FF. Between 19 February and 7 March the changes in diversity were opposite to the previous sampling: diversity for the LL/FF reach had increased by 27% while it decreased by 12% for HL/FF, 11% for LL/FF and 35% for LL/FF reaches. Average diversity for the LL/FF reach declined by 37% between 7 March and 17 March constituting the largest decline in diversity and resulting in the lowest diversity value over the sampling period. The diversity of LL/FF treatment also declined by 17% while HL/FF and LL/FF increased by 4% and 5% respectively between 7 March and 17 March. The change in mean diversity between the last spring collection on 17 March and the first fall collection on 4 August was an 8% increase for HL/FF and a 10% increase for the LL/FF treatment. Mean diversity from 4 August to 5 October declined by 10% in the HL/FF reach and another 16% from 5 October to 5 January while the LL/FF treatment increased by 16% between 4 August and 5 January. The highest average diversity in all treatment reaches except LL/FF was attained on 19 February.

Figure 18: Plot of the mean (n=2) Shannon H' Diversity Index by date and treatment.

Figure 18


Shannon H' Index
2.5
2.0
1.5
1.0
0.5
0.0
Low Light/Fast Flow
High Light/Fast Flow
High Light/Slow Flow
Low Light/Slow Flow
4 Feb
19 Feb
7 Mar
17 Mar
4 Aug
5 Oct
5 Jan

Neither flow nor date were found to have a significant effect on diversity values when analyzed across sampling dates excluding 5 October due to lack of flow data for this date (Table 2a). However, when samples from 4 February were also excluded from the analysis, both flow ($p<0.10$) and sampling date ($p<0.05$) were found to have a significant effect (Table 2b). The ANOVA testing the effect of flow, light and sampling date for samples from 19 February, 7 March and 17 March show that only sample date was found to have a significant effect ($p<0.05$) on diversity (Table 2). Although there appeared to be a flow mediated effect, it was not significant over these 3 dates.

DISCUSSION

The data collected at Stevensville Brook for this research are, to the author's knowledge, the only taxonomic data available for periphyton in mountain streams during winter in Vermont, USA. The taxonomic changes occurring in Stevensville Brook throughout the winter months indicate an active algal community. As compared to values published for various aquatic systems in the literature, the total number of taxa found in this ecosystem in winter was small (Douglas and Smol 1995, Robinson *et al.* 1994, Hendey 1977, Moore, 1976, Sullivan 1976, Moore 1974). However, species richness is a function of area sampled and most of these studies examined a larger area than the present research. Richness values closer to those found in Stevensville Brook were reported from a study of 21 lakes in Antarctica where 66 species were identified (Hansson and Håkansson 1992) and a study of periphyton in a sewage clarifier in Vermont, USA where only 23 taxa were present over a 61 week sampling period (Davis *et al.* 1990).

Table 2: ANOVA tables indicating the response of the Shannon H' Index to experimental variables. a) Testing the effect of flow and sample date excluding 5 October samples. b.) Testing the effect of flow and sample date excluding 4 February and 5 October samples. c.) Testing the effect of flow, light and sample date for samples from 19 February, 7 March and 17 March 1994.

	Source	DF	Seq SS	Adj MS	F	P
a.)	flow	1	2.613	2.763	1.07	0.311
	date	5	22.666	4.494	1.74	0.162
	flow x date	5	16.223	3.245	1.26	0.314
	Error	25	64.600	2.584		
b.)	flow	1	0.9882	1.2467	3.21	0.087
	date	4	4.8604	1.2151	3.13	0.035
	flow x date	4	2.6855	0.6714	1.73	0.179
	Error	22	8.5353	0.3880		
c.)	flow	1	0.03645	0.03645	0.62	0.445
	date	2	0.57624	0.28812	4.92	0.028
	flow x date	2	0.25433	0.12716	2.17	0.157
	light	1	0.00865	0.00865	0.15	0.707
	flow x light	1	0.11891	0.11891	2.03	0.180
	date x light	2	0.00843	0.00422	0.07	0.931
	flow x date x light	2	0.34865	0.17433	2.98	0.089
	Error	12	0.70283	0.05857		

The predominance of Cyanophyceae in the stream is of interest. Bacillariophyceae have generally been noted as the dominant group present in steams and lakes in the presence of winter conditions of low temperature and light (Allen 1995). On Baffin Island, Moore found 200 out of 240 taxa of benthic algae in rivers to be diatoms. Winter phytoplankton communities in a sub-alpine lake in Colorado, USA were also dominated by diatoms (Spaulding *et al.* 1993) and sub-ice algal assemblages in the Barents sea were dominated by pennate diatoms (Hegseth 1992). However, Griffith and Perry (1995) found the cyanophyte *Chamaesiphon* sp. to be the dominant algae during winter for two out of three years in two streams in W. Virginia, USA. This indicates that the predominance of cyanophyceae in streams during winter may be a phenomenon occurring in the Appalachian mountain chain in the northeastern USA. Although the dominance of cyanophytes is a surprise based on the literature, the lack of studies during the winter may account for the disparity. In fact, members of the Cyanophyceae are known to exhibit some of the greatest capacity to resist extreme conditions including temperature (Fogg 1969).

Relative abundance plots indicate a stable community dominated by *Chamaesiphon* sp., *Lyngbya subtilis* and *Synechocystis* sp. during most of the experimental period. Changes in relative abundances among these three species did not necessarily represent increases in species density. For instance, peaks in relative abundance for *Chamaesiphon* sp. and *Synechocystis* sp. on 4 February and 5 January occurred when both species were actually experiencing some of their lowest cell densities. As a result of the extremely low densities of *Lyngbya subtilis* cells and the low relative abundances of other taxa, *Chamaesiphon* sp. and *Synechocystis* sp. were able to account for a much greater portion of the community.

An interesting pattern that appears in the cell density plots is the existence of some species which have two peak densities and some which peaked only once. Numerous species including *Audouinella* sp.1, *Chamaesiphon* sp., *Lyngbya* sp.4, *Lyngbya* sp.3, *Psuedoanabaena catenata*, *Peroniella* sp., *Synechococcus* sp., Unknown 2 and Unknown 1 had peak densities which occurred during the Winter/Spring 1994 sample period indicating a possible daylength mediated growth response. Other species peaked once during the Winter/Spring 1994 season and once during Fall/Winter 1994/95 which may be the result of changing nutrient status. Since data are not available from the summer, the 4 August peak may not represent a true peak density. However, the double peak pattern has been noted in other river studies (Allen 1995).

Among the three dominant taxa and most of the minor taxa, there did not appear to be any consistent pattern of response of cell density to either flow or light although there were distinct differences on some dates (Figures 2-17). For instance, almost all of the species which were found on 19 February had lower densities in fast flow reaches than in slow flow reaches except for *Eunotia exigua*. Such a pattern may be explained by the fact that during the 4 February sample there had been a period of very warm temperatures resulting in rain and high runoff. Species in slow flow reaches may have been subject to less scouring loss and also may have benefited from removal of debris resulting in higher nutrient availability. In an experiment in Kentucky, USA, Peterson and Stevenson (1992) found that communities in slow flow channels recovered more quickly than those in fast flow channels due to enhanced reproduction and greater accumulation of biomass due to lower shear stress. By 7 March, the pattern was still apparent only for *Psuedoanabaena catenata*, Unknown 1 and *Synechococcus* sp.

Four taxa provide evidence of a distinct treatment response: *Borzia* sp., *Oscillatoria* sp.1, *Oscillatoria* sp.2. and *Psuedoanabaena catenata*. Both *Oscillatoria* species were found only in LL/FF reaches with sp.1 occurring on 19 February and sp.2 occurring on 4 August (Figures 9 & 10). *Borzia* sp. had the greatest density of cells in the fall HL/FF treatment reach (Figure 3). *P. catenata* had distinctly higher cell densities in LL/FF than in any of the other treatments. It seems that *Oscillatoria* sp.1 and 2 and *P. catenata* were the only species present which conformed to our hypothesis that the extreme environment would result in more species taking advantage of slower flows and higher light. In general, species density plots show a strong relationship between time of year and most species densities. Cell densities were usually lowest on 4 February and 5 January and almost all species had a peak density in the Winter/Spring 1994 experiment. Winter minima and springtime maxima have been reported by many authors (Blomqvist *et al.*, 1994, Müller-Haeckel and Håkansson 1978, Moore 1977, Moore 1976), however, the large increase in the cell densities of many of the taxa occurring on 19 February is unusually early as compared to other studies. These results indicate that the flow and light treatments imposed were not a factor in controlling individual species densities or were not of the appropriate magnitude to influence individuals.

The most important predictors of algal diversity were sampling date and flow (Table 2). Contrary to our expectations, light did not have a significant effect on diversity. Although flow had a significant effect on diversity, there was no consistent pattern from sample date to sample date to provide evidence that slow flow or fast flow reaches have a greater diversity (Figure 18). It may be that the low and high flow regimes were at the extreme ends of the current spectrum of the stream and therefore both resulted in reduced diversity. In a summer study

of diatoms in Kentucky, USA, Molloy (1992) found that diversity peaked at intermediate currents and declined above and below the optimum. In fact, the range of values found in Stevensville Brook, 0.95 to 1.85 (Figure 18), are at the lower end of the range reported by Molloy and correspond to the faster and slower currents found in her study. A more obvious pattern can be seen for sample date where the average diversity was greater for all treatments (except LL/FF) on 19 February than on any other date sampled. This would not be expected given the harsh conditions which exist at the site during February, but it supports Huston's (1979) hypothesis that slower growth rates will maintain diversity by increasing the length of time necessary for competitive exclusion. Overall, diversity values for Stevensville Brook were at the low end of values reported in other studies. For instance, values for Shannon *H'* diversity reported by Molloy (1992) were between about 1.00 and 3.00, and in a study of diatoms from 14 sites in the Yellowstone Park Area, USA, Robinson *et al.* (1994) recorded a range of values for Shannon's *H'* from 1.00 up to 5.27 with few values below 2.00. However, Stevensville Brook values were intermediate to those reported by Hendey (1977) for diatom communities from six sites along the coast of Cornwall, England which ranged in value from 0.33 to 3.84. Although Molloy's findings suggest that extreme flow regimes may result in the lower diversity values found, Stevensville Brook periphyton were found to be phosphorus limited (previous chapter), and this may account for the low values.

The data from this research show that streams during winter have an active epilithic algal community and can provide excellent experimental systems to test theories regarding community dynamics and species diversity. Our results support the hypothesis that lower diversity will occur in ecosystems with extreme physical conditions such as exist during winter in the northeastern USA.

However, we were unable to determine the exact mechanism controlling the community. Since ambient light intensity does not appear to be a factor it would be best to focus on interactions of flow, nutrient status and daylength in future investigations.

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CONCLUSIONS

My initial goal in pursuing the research presented was to try to disprove the intermediate disturbance hypothesis as presented by Connell and Slatyer (1977). It seemed that a theory developed around tropical ecosystems would lack the ability to predict dynamics though seasonal changes associated with temperate climates. Furthermore, the language associated with the theory, such as "intermediate", is vague and cannot be quantified with accuracy. As the research progressed and results began to appear, I realized that I had not, in fact, designed my experiments to test intermediate disturbance.

While this research did not result in an earth shattering rebuke of the intermediate disturbance hypothesis, it did provide much needed periphyton community information from a previously unobserved ecosystem. The cornerstone of this research was the determination of factors which control stream periphyton in the mountains of Vermont during winter. A review of the literature turned up very few attempts to quantify periphyton during winter and no experiments to explain why communities are present or absent. However, there were numerous models which provided a hypothetical basis for examining these communities. From these models came the hypothesis that increases or decreases in magnitude of abiotic environmental variables away from the optimum in an ecosystem already subject to extremes will result in a decline of community biomass and species diversity. This is a very similar concept to the intermediate disturbance hypothesis, but it does not necessitate a disturbance as defined in the Introduction.

The most likely variables to have an immediate impact on community dynamics in winter were identified as temperature, flow and light. Since temperature is

difficult and expensive to control in a natural stream channel, I initially chose to focus on flow and light during winter/ spring 1994 and return to temperature later. The parameters chosen to measure community response were chlorophyll *a*, an indicator of algal biomass; ash free dry mass, an indicator of total periphyton biomass; algal species densities; and algal diversity. Studies were carried out *in situ* in Stevensville Brook.

Results Summary

Most of the results obtained were unexpected. It was found that not only did Stevensville Brook have a periphyton community during the winter, but that periphyton biomass over a two month period in February and March peaked in mid-February and declined into March, indicating active growth. The hypothesis that chl *a* and periphyton AFDM per unit area declines in communities subject to reduced daily solar energy input must be rejected since reductions in light mimicking ice cover did not affect algal biomass except for possibly influencing colonization rates on artificial tiles. There is weak support of the hypothesis that algal community chl *a* and periphyton AFDM decreases as water velocity increases during winter since differences in flow were found to have a significant effect on biomass, but the effect did not account for much of the variance observed. Sampling date was consistently a significant factor accounting for differences in periphyton biomass, but also left much of the variance unexplained.

Water sampling during the fall of 1994 and bioassay data not presented in the thesis indicated that nutrient deficiency may be responsible for controlling the periphyton in Stevensville Brook. So in January 1995, four nutrient treatments were introduced at the stream site to test the hypothesis H3.1 that nutrient

increases have no effect on algal community chl *a* and periphyton AFDM during winter. Results from this experiment confirmed the fact that the algal portion of the periphyton was phosphorus limited and therefore hypothesis H3.1 was rejected based on chl *a* data, but supported for AFDM data. I suggested that in addition to nutrient limitation, the significant flow and sampling date effects during Winter/Spring 1994 indicate that periodic spates have an impact on the periphyton community.

Algal taxonomic data collected during the Winter/Spring 1994 experiment and also in the Fall/Winter 1994/95 supported the chlorophyll *a* data and added detail to the changes observed. Three dominant taxa, all members of the Cyanophyceae, were observed out of a total of 52 species found. Based on the literature, I expected to find a predominance of diatoms, but blue green algae comprised the bulk of the species found both in numbers of taxa and cell density. Relative abundance plots show a dynamic community indicating that the high chlorophyll *a* values found on 19 February were the result of a bloom by *Lyngbya subtilis*. Density plots show that all but 16 of the most abundant species had peak densities occurring in February or March. Mean algal species diversity was highest for three treatments on 19 February and diversity was found to be significantly affected by flow and sampling date. These data do not support hypothesis H1.2a: Algal community diversity, as measured by the number of species and the relative abundances of each species, decreases as a result of reduced solar energy in streams under winter conditions; but there is not enough evidence to accept or reject H2.2: diversity decreases at higher flow. In general, species diversity in Stevensville Brook was found to be at the lower end of diversity value ranges reported for other streams. These results supported some

hypotheses put forth by Menge and Sutherland (1987) and Huston (1979), but do not entirely conform to any specific model.

Future Directions

The results point to some research possibilities for future investigators. Phosphorus limitation indicates the need to consider nutrient status in any benthic research conducted in mountain streams in Vermont. Although it is likely that many of these lower order streams are nutrient deficient, it would be interesting to test a number of streams throughout the Green Mountains. It is known that temperature affects algal minimum requirements for nutrients and it is likely that temperature affects in-stream nutrient availability. Experiments controlling stream temperature *in situ*, though difficult and expensive, are essential to fully understanding stream periphyton in Vermont. Flow must also be a consideration in future investigations and I propose designing factorial experiments which incorporate flow treatments and nutrient treatments. Significant sampling date effects raise the possibility of seasonal changes resulting from changes in daylength or stochastic processes such as spates. More frequent sampling would aid in obtaining samples as close to a high runoff event as possible providing before and after analysis capability. This is certainly not an exhaustive list, but it covers some of the most basic research questions for this system that remain for me.

Relevance

It is my view that the importance of this research is two fold: 1) it provides information necessary to establish the validity of theoretical models, and 2) it provides data to be considered when making determinations concerning

resource management. With regard to the former, this research has provided a direct test for some aspects of community succession models in the literature. It has also provided the basic data from which to launch further testing of these and other models. As regards the latter point, decisions concerning stream drawdown for snowmaking at ski resorts and plans to harvest northern forests could benefit from this data, too. As a result of the lack of seasonal studies, such management decisions are often made using anecdotal evidence. The results of this research show that anything short of quantitative evidence may be misleading and result in detrimental management decisions. I hope, as do many graduate students, that my thesis will provide useful information and analyses that will remain pertinent to future investigators.

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APPENDIX A

Table of chlorophyll *a*, ash free dry mass and rock area data for Winter/Spring 1994 flow and light experiments listed by date collected and treatment.

Notes on some Headings

Treatment: 1=Low Light/Fast Flow, 2= High Light/Fast Flow, 3=High Light/Slow Flow, 4=Low Light/Slow Flow.

Light: 1=High Light, 0=Low Light

Flow: 1=Fast Flow, 0=Slow Flow

date	treatement	flow	light	rock area (sqr. cm)	µg chl	µg chl/sqr. cm	mg afdm	mg afdm/sqr. cm	chl/afdm
20494	2	1	1	40.1	0.592	0.0147	2.1	0.0523	0.2819
20494	2	1	1	45.4	0.592	0.0130	3.9	0.0859	0.1518
20494	2	1	1	48.2	1.48	0.0307	3.0	0.0623	0.4933
20494	2	1	1	63.4	0.296	0.0047	2.7	0.0426	0.1096
20494	2	1	1	48.6	0.296	0.0061	1.8	0.0371	0.1644
20494	3	0	1	66.4	0.888	0.0134	5.7	0.0858	0.1558
20494	3	0	1	56.2	0	0.0000	3.2	0.0561	0.0000
20494	3	0	1	25.3	0.296	0.0117	6.0	0.2368	0.0493
20494	3	0	1	42.3	0.296	0.0070	4.1	0.0957	0.0731
20494	3	0	1	27.9	1.48	0.0530	6.0	0.2147	0.2467
21994	1	1	0	71.6	2.368	0.0331	11.3	0.1576	0.2099
21994	1	1	0	32.5	1.184	0.0364	6.2	0.1909	0.1906
21994	1	1	0	54.3	4.736	0.0872	8.9	0.1644	0.5305
21994	1	1	0	29.5	2.368	0.0804	5.1	0.1742	0.4613
21994	1	1	0	26.4	1.184	0.0449	4.1	0.1558	0.2883
21994	1	1	0	63.1	3.552	0.0563	17.8	0.2829	0.1990
21994	1	1	0	43.4	2.96	0.0683	14.7	0.3395	0.2011
21994	1	1	0	48.9	0	0.0000	0.0	0.0000	0.0000
21994	1	1	0	56.2	6.512	0.1159	10.3	0.1841	0.6298
21994	1	1	0	60.4	5.92	0.0980	16.9	0.2805	0.3495
21994	2	1	1	93.3	4.736	0.0508	15.2	0.1634	0.3107
21994	2	1	1	70.6	7.104	0.1006	9.6	0.1366	0.7362
21994	2	1	1	34.3	2.368	0.0691	5.9	0.1711	0.4036
21994	2	1	1	58.9	8.88	0.1508	9.8	0.1669	0.9037
21994	2	1	1	50.1	4.736	0.0946	18.9	0.3766	0.2511
21994	2	1	1	58.3	3.552	0.0609	13.9	0.2384	0.2554
21994	2	1	1	38.9	0.592	0.0152	7.6	0.1945	0.0783
21994	2	1	1	49.9	4.144	0.0830	12.8	0.2554	0.3250
21994	2	1	1	69.4	8.88	0.1280	15.1	0.2184	0.5863
21994	2	1	1	43.4	2.368	0.0546	10.6	0.2438	0.2240
21994	3	0	1	60.9	1.776	0.0292	9.2	0.1507	0.1936
21994	3	0	1	48.9	0.592	0.0121	4.4	0.0909	0.1333
21994	3	0	1	34.2	2.96	0.0866	14.2	0.4170	0.2078

date	treatement	flow	light	rock area (sqr. cm)	µg chl	µg chl/sqr. cm	mg afdm	mg afdm/sqr. cm	chl/afdm
21994	3	0	1	33.2	0	0.0000	7.2	0.2167	0.0000
21994	3	0	1	62.9	1.184	0.0188	7.4	0.1176	0.1602
21994	3	0	1	52.1	0.592	0.0114	9.6	0.1847	0.0616
21994	3	0	1	64.7	10.064	0.1556	30.5	0.4721	0.3295
21994	3	0	1	46.1	1.184	0.0257	11.1	0.2411	0.1065
21994	3	0	1	56.4	17.76	0.3148	19.8	0.3501	0.8991
21994	3	0	1	74.3	4.736	0.0638	14.4	0.1944	0.3280
21994	4	0	0	73.5	1.776	0.0242	17.0	0.2309	0.1047
21994	4	0	0	33.4	7.104	0.2125	17.6	0.5250	0.4047
21994	4	0	0	63.2	7.104	0.1125	16.5	0.2618	0.4296
21994	4	0	0	59.3	1.776	0.0299	20.4	0.3447	0.0869
21994	4	0	0	69.2	10.064	0.1454	13.1	0.1891	0.7685
21994	4	0	0	86.0	9.472	0.1101	15.2	0.1767	0.6232
21994	4	0	0	37.4	4.736	0.1265	11.3	0.3010	0.4202
21994	4	0	0	38.6	11.248	0.2911	8.3	0.2151	1.3533
21994	4	0	0	55.6	6.512	0.1172	23.7	0.4272	0.2744
21994	4	0	0	57.0	1.184	0.0208	15.6	0.2738	0.0758
30794	1	1	0	74.2	5.92	0.0797	8.4	0.1131	0.7048
30794	1	1	0	64.1	1.776	0.0277	9.5	0.1482	0.1870
30794	1	1	0	63.2	6.512	0.1030	8.0	0.1262	0.8160
30794	1	1	0	54.2	5.92	0.1093	7.6	0.1403	0.7790
30794	1	1	0	57.8	5.328	0.0921	9.7	0.1671	0.5516
30794	1	1	0	45.8	2.96	0.0646	7.2	0.1575	0.4100
30794	1	1	0	70.5	6.512	0.0923	8.8	0.1248	0.7400
30794	1	1	0	42.7	0	0.0000	3.0	0.0703	0.0000
30794	1	1	0	52.1	1.184	0.0227	4.4	0.0845	0.2691
30794	1	1	0	52.0	0.592	0.0114	5.8	0.1107	0.1028
30794	2	1	1	63.3	5.92	0.0935	14.5	0.2290	0.4083
30794	2	1	1	71.8	2.368	0.0330	8.3	0.1153	0.2860
30794	2	1	1	36.7	2.368	0.0646	8.0	0.2181	0.2960
30794	2	1	1	61.6	0.592	0.0096	2.8	0.0455	0.2114
30794	2	1	1	47.4	1.184	0.0250	4.2	0.0886	0.2819
30794	2	1	1	42.8	5.92	0.1382	7.2	0.1681	0.8222

date	treatement	flow	light	rock area (sqr. cm)	µg chl	µg chl/sqr. cm	mg afdm	mg afdm/sqr. cm	chl/afdm
30794	2	1	1	43.4	1.184	0.0273	5.8	0.1326	0.2056
30794	2	1	1	39.2	2.96	0.0756	7.2	0.1843	0.4100
30794	2	1	1	69.6	2.368	0.0340	9.7	0.1390	0.2446
30794	2	1	1	25.9	0.592	0.0229	2.3	0.0905	0.2530
30794	3	0	1	33.2	1.776	0.0535	5.1	0.1536	0.3482
30794	3	0	1	46.5	1.184	0.0254	5.5	0.1182	0.2153
30794	3	0	1	34.1	3.552	0.1043	2.7	0.0781	1.3353
30794	3	0	1	31.7	2.368	0.0746	3.1	0.0971	0.7688
30794	3	0	1	60.4	3.552	0.0588	5.0	0.0835	0.7048
30794	3	0	1	52.8	11.248	0.2130	11.2	0.2121	1.0043
30794	3	0	1	58.1	4.736	0.0815	11.4	0.1969	0.4140
30794	3	0	1	38.4	2.368	0.0616	6.0	0.1556	0.3960
30794	3	0	1	48.8	25.456	0.5215	14.1	0.2889	1.8054
30794	3	0	1	52.3	1.776	0.0339	4.5	0.0860	0.3947
30794	4	0	0	30.1	4.736	0.1574	4.0	0.1316	1.1960
30794	4	0	0	28.4	1.776	0.0626	4.2	0.1481	0.4229
30794	4	0	0	60.5	7.104	0.1175	13.0	0.2150	0.5465
30794	4	0	0	48.2	7.104	0.1474	9.7	0.2009	0.7339
30794	4	0	0	49.8	1.776	0.0357	6.1	0.1221	0.2921
30794	4	0	0	49.3	2.96	0.0600	5.6	0.1135	0.5286
30794	4	0	0	78.3	2.96	0.0378	8.2	0.1042	0.3627
30794	4	0	0	42.3	6.512	0.1538	6.8	0.1616	0.9521
30794	4	0	0	55.6	10.064	0.1809	10.8	0.1941	0.9319
30794	4	0	0	76.1	5.92	0.0778	11.0	0.1446	0.5382
31794	1	1	0	69.3	4.736	0.0683	7.9	0.1142	0.5980
31794	1	1	0	76.2	4.736	0.0622	5.5	0.0725	0.8580
31794	1	1	0	72.8	1.184	0.0163	5.3	0.0725	0.2242
31794	1	1	0	22.4	1.776	0.0793	2.9	0.1277	0.6210
31794	1	1	0	37.7	0	0.0000	1.1	0.0297	0.0000
31794	1	1	0	66.4	5.92	0.0891	7.1	0.1075	0.8291
31794	1	1	0	45.0	4.144	0.0921	5.8	0.1280	0.7194
31794	1	1	0	62.2	1.776	0.0286	4.8	0.0772	0.3700

date	treatement	flow	light	rock area (sqr. cm)	µg chl	µg chl/sqr. cm	mg afdm	mg afdm/sqr. cm	chl/afdm
31794	1	1	0	59.4	2.96	0.0498	6.4	0.1078	0.4625
31794	1	1	0	30.2	0.592	0.0196	1.9	0.0637	0.3083
31794	2	1	1	89.0	7.696	0.0865	6.5	0.0726	1.1913
31794	2	1	1	48.1	0.592	0.0123	2.1	0.0437	0.2819
31794	2	1	1	41.6	0.592	0.0142	2.9	0.0692	0.2056
31794	2	1	1	35.1	0	0.0000	2.3	0.0666	0.0000
31794	2	1	1	58.3	4.144	0.0711	7.6	0.1297	0.5482
31794	2	1	1	53.5	5.92	0.1106	8.7	0.1633	0.6774
31794	2	1	1	43.8	2.368	0.0540	4.3	0.0986	0.5482
31794	2	1	1	50.1	1.776	0.0354	4.4	0.0878	0.4036
31794	2	1	1	25.5	1.184	0.0464	1.9	0.0752	0.6167
31794	2	1	1	63.7	2.96	0.0465	7.1	0.1122	0.4146
31794	3	0	1	39.2	7.696	0.1965	6.4	0.1634	1.2025
31794	3	0	1	36.1	1.184	0.0328	3.7	0.1035	0.3166
31794	3	0	1	67.5	5.92	0.0878	9.7	0.1435	0.6116
31794	3	0	1	44.2	5.92	0.1338	5.6	0.1266	1.0571
31794	3	0	1	62.2	1.184	0.0190	4.0	0.0637	0.2990
31794	3	0	1	36.7	2.368	0.0646	3.9	0.1063	0.6072
31794	3	0	1	39.4	4.736	0.1201	5.9	0.1491	0.8054
31794	3	0	1	63.6	5.92	0.0931	6.2	0.0969	0.9610
31794	3	0	1	46.5	0	0.0000	1.6	0.0344	0.0000
31794	3	0	1	39.4	2.368	0.0601	4.0	0.1005	0.5980
31794	4	0	0	46.2	0.592	0.0128	3.4	0.0728	0.1762
31794	4	0	0	29.5	2.368	0.0804	4.4	0.1500	0.5358
31794	4	0	0	22.8	0.592	0.0260	4.7	0.2057	0.1265
31794	4	0	0	67.9	0	0.0000	8.4	0.1232	0.0000
31794	4	0	0	25.9	2.96	0.1144	4.4	0.1709	0.6697
31794	4	0	0	36.6	3.552	0.0971	3.8	0.1039	0.9347
31794	4	0	0	59.7	6.512	0.1091	8.4	0.1407	0.7752
31794	4	0	0	70.6	0	0.0000	7.9	0.1122	0.0000
31794	4	0	0	62.7	0	0.0000	4.0	0.0638	0.0000
31794	4	0	0	57.8	1.184	0.0205	4.0	0.0693	0.2960
40594	1	1	0	62.1	0.592	0.0095	6.8	0.1095	0.0871

date	treatement	flow	light	rock area (sqr. cm)	µg chl	µg chl/sqr. cm	mg afdm	mg afdm/sqr. cm	chl/afdm
40594	1	1	0	62.1	0	0.0000	0.9	0.0142	0.0000
40594	1	1	0	62.1	1.184	0.0191	0.0	0.0000	0.0000
40594	1	1	0	62.1	0.592	0.0095	0.8	0.0135	0.7048
40594	1	1	0	62.1	0	0.0000	5.8	0.0928	0.0000
40594	1	1	0	62.1	0	0.0000	1.3	0.0213	0.0000
40594	1	1	0	62.1	0	0.0000	2.4	0.0386	0.0000
40594	1	1	0	62.1	1.184	0.0191	0.0	0.0000	0.0000
40594	1	1	0	62.1	0	0.0000	16.1	0.2596	0.0000
40594	2	1	1	62.1	0.592	0.0095	2.4	0.0386	0.2467
40594	2	1	1	62.1	0	0.0000	6.0	0.0963	0.0000
40594	2	1	1	62.1	0	0.0000	3.2	0.0519	0.0000
40594	2	1	1	62.1	0.592	0.0095	0.8	0.0122	0.7790
40594	2	1	1	62.1	0	0.0000	6.7	0.1082	0.0000
40594	2	1	1	62.1	0	0.0000	4.4	0.0709	0.0000
40594	2	1	1	62.1	0	0.0000	11.6	0.1868	0.0000
40594	2	1	1	62.1	0	0.0000	7.8	0.1256	0.0000
40594	2	1	1	62.1	0.592	0.0095	10.4	0.1675	0.0569
40594	2	1	1	62.1	1.184	0.0191	0.4	0.0064	2.9600
40594	3	0	1	62.1	0.592	0.0095	8.6	0.1391	0.0685
40594	3	0	1	62.1	0	0.0000	1.9	0.0309	0.0000
40594	3	0	1	62.1	2.368	0.0381	0.8	0.0129	2.9600
40594	3	0	1	62.1	0	0.0000	11.3	0.1826	0.0000
40594	3	0	1	62.1	0	0.0000	7.6	0.1217	0.0000
40594	3	0	1	62.1	0.592	0.0095	4.2	0.0670	0.1423
40594	3	0	1	62.1	0.592	0.0095	11.8	0.1894	0.0503
40594	3	0	1	62.1	0.592	0.0095	10.5	0.1691	0.0564
40594	3	0	1	62.1	0.592	0.0095	5.9	0.0947	0.1007
40594	3	0	1	62.1	0	0.0000	1.4	0.0232	0.0000
40594	4	0	0	62.1	0	0.0000	2.4	0.0386	0.0000
40594	4	0	0	62.1	0	0.0000	0.0	0.0000	0.0000
40594	4	0	0	62.1	1.184	0.0191	5.5	0.0886	0.2153
40594	4	0	0	62.1	0.592	0.0095	0.0	0.0000	-0.6037
40594	4	0	0	62.1	0.592	0.0095	0.0	0.0000	0.0000

date	treatement	flow	light	rock area (sqr. cm)	µg chl	µg chl/sqr. cm	mg afdm	mg afdm/sqr. cm	chl/afdm
40594	4	0	0	62.1	0.592	0.0095	0.0	0.0000	0.0000
40594	4	0	0	62.1	0	0.0000	0.0	0.0000	0.0000
40594	4	0	0	62.1	0.592	0.0095	0.5	0.0077	1.2333
40594	4	0	0	62.1	1.776	0.0286	1.0	0.0167	1.7077
40594	4	0	0	62.1	2.96	0.0477	7.6	0.1217	0.3915

APPENDIX B

Table of chlorophyll *a* and ash free dry mass data for winter 1995 nutrient enrichment experiment listed by treatment type.

Notes on some Headings

Light: 1=High Light, 0=Low Light

Flow: 1=Fast Flow, 0=Slow Flow

date	Shannon	light	flow
204r	1.77215	1	1
204l	0.72499	1	1
04d	1.73203	1	0
04ff	0.99388	1	0
04ff	0.49491	1	0
219a	1.36793	0	1
219g	1.02695	0	1
219l	1.63133	1	1
219n	1.37323	1	1
19a	1.74022	1	0
219cc	1.41799	1	0
19e	1.75562	0	0
219ll	1.93685	0	0
307e	1.24031	0	1
307c	1.79654	0	1
307s	1.24542	1	1
307n	1.40296	1	1
307cc	1.46018	1	0
307v	1.3528	1	0
307kk	1.00099	0	0
307ff	1.40472	0	0
317i	0.71579	0	1
317g	1.17591	0	1
317p	1.39771	1	1
317r	1.34526	1	1
317z	0.72274	1	0
17b	1.32497	1	0
317ii	1.27641	0	0
317ff	1.26118	0	0
804s	1.52963	1	0
804sf	1.42707	1	0
804fg	1.30731	1	1
804ff	0.93587	1	1
1005j	1.69372	1	1
005	0.96459	1	1
105f1	1.1113	1	1
105f5	1.11665	1	1
105s	1.12518	1	0
105s	1.46855	1	0

APPENDIX C

Table of species densities (# cells/cm^2) for Winter/Spring 1994 and Fall/Winter 1994/95 listed by date collected and treatment.

Notes on some Headings

Light: 1=High Light, 0=Low Light

Flow: 1=Fast Flow, 0=Slow Flow

date	flow	light	julien	*Audouinella 1*	Unknown 1	*Eunotia exigua*
204rCL/cm	1	1	35	0	4282	789
204lCL/cm	1	1	35	2085	2502	0
204ddCL/	0	1	35	0	17998	2000
204ff1CL	0	1	35	0	277	692
204ff2CL	0	1	35	0	692	3808
219aCL/c	1	0	50	2715	13577	2112
219gCL/c	1	0	50	166	14277	1660
219lCL/c	1	1	50	2753	11011	918
219nCL/c	1	1	50	0	2401	32413
219aaCL/	0	1	50	18363	15740	13116
219ccCL/	0	1	50	1723	137826	6891
219eeCL/	0	0	50	15286	17196	7643
219llCL/	0	0	50	0	68514	10541
307eCL/c	1	0	66	32188	5365	1788
307cCL/c	1	0	66	13394	26789	0
307sCL/c	1	1	66	6790	7312	2089
307nCL/c	1	1	66	551	3817	0
307ccCL/	0	1	66	1432	85903	5602
307vCL/c	0	1	66	23834	5181	3109
307kkCL/	0	0	66	3096	5348	844
307ffCL/	0	0	66	78835	10034	1433
317iCL/c	1	0	76	20801	2311	5778
317gCL/c	1	0	76	3968	794	132
317pCL/c	1	1	76	20002	108584	8572
317rCL/c	1	1	76	3546	4433	1773
317zCL/c	0	1	76	34884	20349	0
317bbCL/	0	1	76	18038	58923	2405
317iiCL/	0	0	76	3657	522	12015
317ffCL/	0	0	76	6434	14706	10110
804sgCL/cm	0	1	216	0	1869	29909
804sfCL/cm	0	1	216	11545	6102	3661
804fgCL/cm	1	1	216	0	0	22387
804ffCL/cm	1	1	216	8626	0	4140
1005jCL/cm	1	1	278	5253	14709	385
1005bCL/cm	1	1	278	7786	12235	3337
1108s3CL/cm	0	1	310	2278	1519	2278
1108f10CL/cm	1	1	310	6227	9785	890
1129s6CL/cm	0	1	333	1628	8142	0
1129f9CL/cm	1	1	333	0	2591	0
1219s3CL/cm	0	1	353	5098	6118	0
1219f10CL/cm	1	1	353	2230	1115	0
105f1CL/cm	1	1	5	1571	0	943
105f5CL/cm	1	1	5	2619	6112	1746
105s3CL/cm	0	1	5	1833	367	2199
105s7CL/cm	0	1	5	0	0	1369

date	*Acnanthes marginulata*	*Meridion circulare*	*Eunotia pectinalis*
204rCL/cm	185	17	17
204lCL/cm	0	0	0
204ddCL/	0	0	0
204ff1CL	0	277	0
204ff2CL	0	0	0
219aCL/c	0	0	0
219gCL/c	0	0	0
219lCL/c	918	0	0
219nCL/c	2401	0	0
219aaCL/	2623	0	0
219ccCL/	0	0	0
219eeCL/	1911	0	0
219llCL/	0	0	0
307eCL/c	0	0	0
307cCL/c	1218	0	0
307sCL/c	1567	0	0
307nCL/c	0	0	0
307ccCL/	0	0	0
307vCL/c	0	0	0
307kkCL/	281	0	0
307ffCL/	0	0	0
317iCL/c	0	0	0
317gCL/c	794	0	0
317pCL/c	0	0	0
317rCL/c	1773	0	0
317zCL/c	0	0	0
317bbCL/	0	0	0
317iiCL/	0	0	0
317ffCL/	2757	0	0
804sgCL/cm	1869	0	0
804sfCL/cm	299	85	0
804fgCL/cm	0	0	0
804ffCL/cm	0	0	0
1005jCL/cm	770	0	0
1005bCL/cm	0	0	0
1108s3CL/cm	380	380	0
1108f10CL/cm	949	0	0
1129s6CL/cm	0	0	0
1129f9CL/cm	0	0	0
1219s3CL/cm	0	0	0
1219f10CL/cm	0	0	0
105f1CL/cm	0	0	0
105f5CL/cm	0	0	0
105s3CL/cm	0	0	0
105s7CL/cm	196	0	0

date	*Gomphonema angustatum*	*Lyngbya 2*	*Pinnularia appendiculata*
204rCL/cm	185	269	17
204lCL/cm	0	0	0
204ddCL/	0	0	0
204ff1CL	0	0	0
204ff2CL	0	0	0
219aCL/c	0	0	0
219gCL/c	0	0	0
219lCL/c	0	0	0
219nCL/c	0	0	0
219aaCL/	0	0	0
219ccCL/	5168	0	0
219eeCL/	0	0	0
219llCL/	0	0	0
307eCL/c	0	0	0
307cCL/c	0	0	0
307sCL/c	1045	0	0
307nCL/c	0	0	0
307ccCL/	0	0	0
307vCL/c	0	0	0
307kkCL/	0	0	0
307ffCL/	0	0	0
317iCL/c	0	0	0
317gCL/c	0	0	0
317pCL/c	0	0	0
317rCL/c	0	0	0
317zCL/c	0	0	0
317bbCL/	0	0	0
317iiCL/	0	0	0
317ffCL/	0	0	0
804sgCL/cm	0	0	0
804sfCL/cm	0	0	0
804fgCL/cm	0	0	0
804ffCL/cm	0	0	0
1005jCL/cm	0	0	0
1005bCL/cm	0	0	0
1108s3CL/cm	0	0	0
1108f10CL/cm	0	0	0
1129s6CL/cm	0	0	0
1129f9CL/cm	0	0	0
1219s3CL/cm	0	0	0
1219f10CL/cm	0	0	0
105f1CL/cm	0	0	0
105f5CL/cm	0	0	0
105s3CL/cm	0	0	0
105s7CL/cm	0	0	0

date	*Psuedoanabaena catenata*	*Lyngbya subtilis*	*Entophysalis*
204rCL/cm	840	1679	0
204lCL/cm	0	54200	0
204ddCL/	2000	101989	0
204ff1CL	0	8585	0
204ff2CL	0	18001	0
219aCL/c	24439	276977	0
219gCL/c	11289	138292	0
219lCL/c	22022	134882	0
219nCL/c	9604	196878	0
219aaCL/	199367	676799	0
219ccCL/	0	478946	0
219eeCL/	21018	456659	0
219llCL/	12297	126487	0
307eCL/c	0	230680	0
307cCL/c	12177	53578	0
307sCL/c	0	212573	0
307nCL/c	0	111213	0
307ccCL/	117649	476200	0
307vCL/c	0	27979	0
307kkCL/	0	8726	0
307ffCL/	0	80268	0
317iCL/c	0	245566	0
317gCL/c	11905	59526	0
317pCL/c	31432	768663	31432
317rCL/c	0	0	0
317zCL/c	0	75582	0
317bbCL/	0	58923	0
317iiCL/	1045	146788	0
317ffCL/	0	293198	0
804sgCL/cm	61688	231796	0
804sfCL/cm	10374	134865	0
804fgCL/cm	5970	61192	0
804ffCL/cm	10581	96149	0
1005jCL/cm	13659	147092	0
1005bCL/cm	0	590473	0
1108s3CL/cm	0	10632	0
1108f10CL/cm	8895	8895	0
1129s6CL/cm	0	226338	0
1129f9CL/cm	0	21156	0
1219s3CL/cm	7138	56080	0
1219f10CL/cm	1115	139178	0
105f1CL/cm	0	1257	0
105f5CL/cm	0	7858	0
105s3CL/cm	0	11730	0
105s7CL/cm	0	3128	0

date	*Chamaesiphon*	*Frustularia rhomboides*	*Synechocystis*
204rCL/cm	8563	0	1343
204lCL/cm	128516	0	0
204ddCL/	53494	0	50994
204ff1CL	0	0	0
204ff2CL	0	346	141238
219aCL/c	190082	0	190082
219gCL/c	67790	0	0
219lCL/c	144975	0	99097
219nCL/c	210083	0	141656
219aaCL/	212484	0	162642
219ccCL/	117152	0	110261
219eeCL/	238839	0	78339
219llCL/	351354	0	233650
307eCL/c	334397	0	320091
307cCL/c	265454	0	194829
307sCL/c	136600	0	13392
307nCL/c	76528	0	55056
307ccCL/	141926	0	164336
307vCL/c	260099	0	84972
307kkCL/	126672	0	49852
307ffCL/	338273	0	24367
317iCL/c	689924	0	0
317gCL/c	193657	0	138100
317pCL/c	351470	0	22860
317rCL/c	101070	0	111709
317zCL/c	1276170	0	40698
317bbCL/	312651	0	177971
317iiCL/	39178	0	64253
317ffCL/	119485	0	9191
804sgCL/cm	424336	0	153285
804sfCL/cm	74450	0	106793
804fgCL/cm	244769	0	382079
804ffCL/cm	662461	0	141463
1005jCL/cm	304690	0	97711
1005bCL/cm	144594	0	55613
1108s3CL/cm	23162	0	29237
1108f10CL/cm	185912	0	152110
1129s6CL/cm	480358	0	146550
1129f9CL/cm	19429	0	26769
1219s3CL/cm	228400	0	192713
1219f10CL/cm	286386	0	144531
105f1CL/cm	4713	0	24194
105f5CL/cm	88182	0	90802
105s3CL/cm	85773	0	70378
105s7CL/cm	5475	0	9190

date	*Aphanothece*	Unknown 3	*Hormidium*	*Lyngbya 3*	*Synechococcus*
204rCL/cm	0	0	0	0	3526
204lCL/cm	0	0	0	0	0
204ddCL/	0	0	12999	11499	19998
204ff1CL	1662	554	0	0	0
204ff2CL	0	0	0	0	0
219aCL/c	0	0	0	0	0
219gCL/c	0	0	0	0	0
219lCL/c	0	0	0	0	63312
219nCL/c	0	0	0	0	0
219aaCL/	0	7870	0	0	0
219ccCL/	0	0	0	0	75804
219eeCL/	0	0	0	0	131839
219llCL/	0	0	3514	0	0
307eCL/c	0	0	0	0	0
307cCL/c	0	0	0	4871	98632
307sCL/c	0	0	0	0	34820
307nCL/c	0	2202	0	0	0
307ccCL/	0	0	0	0	0
307vCL/c	0	0	0	0	121241
307kkCL/	0	0	0	0	0
307ffCL/	0	0	0	0	149069
317iCL/c	0	0	0	0	0
317gCL/c	0	0	0	0	0
317pCL/c	0	0	0	0	120014
317rCL/c	0	0	0	0	0
317zCL/c	0	0	0	0	78489
317bbCL/	0	0	0	0	0
317iiCL/	0	0	0	0	0
317ffCL/	0	0	5515	0	45956
804sgCL/cm	0	0	0	0	0
804sfCL/cm	0	0	610	0	0
804fgCL/cm	0	0	0	0	0
804ffCL/cm	0	0	8741	0	0
1005jCL/cm	0	0	14709	0	0
1005bCL/cm	0	0	0	0	0
1108s3CL/cm	0	0	0	0	0
1108f10CL/cm	0	0	0	0	0
1129s6CL/cm	0	0	0	0	0
1129f9CL/cm	0	0	0	0	0
1219s3CL/cm	0	0	0	3059	0
1219f10CL/cm	0	0	0	0	0
105f1CL/cm	0	0	0	0	0
105f5CL/cm	0	873	0	0	0
105s3CL/cm	0	440	0	0	0
105s7CL/cm	0	0	0	0	0

date	*Audouinella 2*	Unknown 2	*Lyngbya 4*	*Rivularia*	*Tabellaria flocculosa*
204rCL/cm	0	0	0	0	0
204lCL/cm	0	0	0	0	0
204ddCL/	500	0	0	0	0
204ff1CL	0	0	0	0	0
204ff2CL	0	0	0	0	0
219aCL/c	0	0	4073	0	0
219gCL/c	0	0	0	0	0
219lCL/c	0	0	4588	0	0
219nCL/c	0	0	0	0	0
219aaCL/	0	0	78698	0	0
219ccCL/	0	0	0	0	0
219eeCL/	0	0	191071	47768	0
219llCL/	0	0	0	29994	0
307eCL/c	0	0	0	0	0
307cCL/c	0	0	0	0	0
307sCL/c	0	0	0	0	0
307nCL/c	0	0	0	0	0
307ccCL/	0	0	0	0	0
307vCL/c	0	0	0	0	0
307kkCL/	0	0	0	0	0
307ffCL/	0	0	0	0	0
317iCL/c	0	0	0	0	0
317gCL/c	0	0	0	0	0
317pCL/c	0	0	0	0	0
317rCL/c	0	0	0	0	0
317zCL/c	0	0	0	0	0
317bbCL/	0	0	0	0	0
317iiCL/	0	0	0	0	0
317ffCL/	0	0	0	0	0
804sgCL/cm	0	0	5369	0	0
804sfCL/cm	0	0	0	0	0
804fgCL/cm	0	0	0	0	0
804ffCL/cm	0	0	0	0	460
1005jCL/cm	0	0	6304	72495	0
1005bCL/cm	0	0	0	0	0
1108s3CL/cm	0	0	0	0	0
1108f10CL/cm	0	0	0	0	0
1129s6CL/cm	0	0	0	0	0
1129f9CL/cm	0	0	0	0	0
1219s3CL/cm	0	0	0	0	0
1219f10CL/cm	0	0	0	0	0
105f1CL/cm	0	0	0	0	0
105f5CL/cm	0	0	0	0	0
105s3CL/cm	0	0	0	0	0
105s7CL/cm	0	0	0	0	0

date	*Pascherinema*	*Oscillatoria 1*	*Chroodactylon*	*Anabaena*
204rCL/cm	0	0	0	0
204lCL/cm	0	0	0	0
204ddCL/	0	0	0	0
204ff1CL	0	0	0	0
204ff2CL	0	0	0	0
219aCL/c	0	0	0	0
219gCL/c	0	0	0	0
219lCL/c	0	0	0	0
219nCL/c	0	0	0	0
219aaCL/	0	399191	0	0
219ccCL/	0	0	0	0
219eeCL/	0	0	0	0
219llCL/	0	0	0	0
307eCL/c	0	0	0	0
307cCL/c	6088	0	0	0
307sCL/c	0	0	0	0
307nCL/c	0	0	0	0
307ccCL/	0	0	0	0
307vCL/c	0	0	0	0
307kkCL/	0	0	0	0
307ffCL/	0	0	4300	0
317iCL/c	0	0	0	0
317gCL/c	0	0	0	0
317pCL/c	0	0	0	0
317rCL/c	0	0	0	0
317zCL/c	8721	0	0	0
317bbCL/	0	0	0	0
317iiCL/	0	0	0	0
317ffCL/	0	0	0	0
804sgCL/cm	0	0	0	0
804sfCL/cm	0	0	0	0
804fgCL/cm	0	0	0	9726
804ffCL/cm	0	0	0	0
1005jCL/cm	0	0	3152	0
1005bCL/cm	0	0	0	0
1108s3CL/cm	0	0	0	0
1108f10CL/cm	0	0	0	0
1129s6CL/cm	0	0	0	0
1129f9CL/cm	0	0	0	0
1219s3CL/cm	0	0	0	0
1219f10CL/cm	0	0	0	0
105f1CL/cm	0	0	0	0
105f5CL/cm	0	0	0	0
105s3CL/cm	0	0	0	0
105s7CL/cm	0	0	0	0

date	*Cosmarium 2*	*Borzia*	*Cocconeis placentula*	*Gloeotilopsis*
204rCL/cm	0	0	0	0
204lCL/cm	0	0	0	0
204ddCL/	0	0	0	0
204ff1CL	0	0	0	0
204ff2CL	0	0	0	0
219aCL/c	0	0	0	1509
219gCL/c	0	0	0	0
219lCL/c	0	0	0	0
219nCL/c	0	0	0	0
219aaCL/	0	0	0	0
219ccCL/	0	0	0	0
219eeCL/	0	0	0	0
219llCL/	0	0	0	0
307eCL/c	0	0	0	0
307cCL/c	0	4871	0	0
307sCL/c	0	0	0	0
307nCL/c	0	1652	0	0
307ccCL/	0	2386	0	2863
307vCL/c	0	0	0	0
307kkCL/	0	0	0	0
307ffCL/	0	0	0	0
317iCL/c	0	0	0	0
317gCL/c	0	0	0	0
317pCL/c	0	0	0	0
317rCL/c	0	0	0	0
317zCL/c	0	0	0	0
317bbCL/	0	0	0	0
317iiCL/	0	0	0	0
317ffCL/	0	0	0	0
804sgCL/cm	0	0	0	0
804sfCL/cm	0	0	0	0
804fgCL/cm	0	28357	0	0
804ffCL/cm	0	0	0	0
1005jCL/cm	0	31520	0	0
1005bCL/cm	0	17796	0	3337
1108s3CL/cm	0	0	0	0
1108f10CL/cm	0	56040	316	1779
1129s6CL/cm	0	16283	0	0
1129f9CL/cm	0	0	0	0
1219s3CL/cm	0	12236	0	0
1219f10CL/cm	0	14126	0	0
105f1CL/cm	0	0	0	0
105f5CL/cm	0	0	0	0
105s3CL/cm	0	0	0	0
105s7CL/cm	0	0	0	0

date	*Nitzschia gracilis*	*Nitzschia*	*Epithemia sorex*	*Acnanthes lanceolata*
204rCL/cm	0	0	0	0
204lCL/cm	0	0	0	0
204ddCL/	0	0	0	0
204ff1CL	0	0	0	0
204ff2CL	0	0	0	0
219aCL/c	0	0	0	0
219gCL/c	0	0	0	0
219lCL/c	0	0	0	0
219nCL/c	0	0	0	0
219aaCL/	0	0	0	0
219ccCL/	0	0	0	0
219eeCL/	0	0	0	0
219llCL/	0	0	0	0
307eCL/c	0	0	0	0
307cCL/c	0	0	0	0
307sCL/c	0	0	0	0
307nCL/c	0	0	0	0
307ccCL/	0	0	0	0
307vCL/c	0	0	0	0
307kkCL/	0	0	0	0
307ffCL/	0	0	0	0
317iCL/c	0	0	0	0
317gCL/c	0	0	0	0
317pCL/c	0	0	0	0
317rCL/c	0	0	0	0
317zCL/c	0	0	0	0
317bbCL/	0	0	0	0
317iiCL/	0	0	0	0
317ffCL/	0	0	0	0
804sgCL/cm	0	0	0	0
804sfCL/cm	109	0	0	0
804fgCL/cm	0	0	0	0
804ffCL/cm	0	0	0	0
1005jCL/cm	0	1051	0	385
1005bCL/cm	420	0	0	0
1108s3CL/cm	0	0	0	0
1108f10CL/cm	0	0	0	0
1129s6CL/cm	0	0	0	0
1129f9CL/cm	0	0	0	0
1219s3CL/cm	0	0	0	0
1219f10CL/cm	0	0	0	0
105f1CL/cm	0	0	0	0
105f5CL/cm	0	0	0	0
105s3CL/cm	0	0	0	0
105s7CL/cm	0	0	0	0

date	*Peroniella*	*Cymbella affinis*	*Lyngbya 5*	*Diatoma hiemale*
204rCL/cm	0	0	0	0
204lCL/cm	0	0	0	0
204ddCL/	0	0	0	0
204ff1CL	0	0	0	0
204ff2CL	0	0	0	0
219aCL/c	2715	0	0	0
219gCL/c	0	0	0	0
219lCL/c	0	0	0	0
219nCL/c	3601	0	0	0
219aaCL/	10493	0	0	0
219ccCL/	0	0	0	0
219eeCL/	0	0	0	0
219llCL/	0	0	8784	0
307eCL/c	0	0	0	0
307cCL/c	0	0	0	0
307sCL/c	1339	0	0	0
307nCL/c	25326	0	0	0
307ccCL/	0	0	0	0
307vCL/c	0	0	0	0
307kkCL/	1407	0	0	0
307ffCL/	0	0	0	0
317iCL/c	0	0	0	0
317gCL/c	0	0	0	0
317pCL/c	0	0	0	0
317rCL/c	33690	0	0	0
317zCL/c	0	0	0	0
317bbCL/	8418	0	0	0
317iiCL/	7313	0	0	0
317ffCL/	0	0	0	0
804sgCL/cm	0	0	0	0
804sfCL/cm	137	0	0	0
804fgCL/cm	14925	0	0	0
804ffCL/cm	0	0	0	0
1005jCL/cm	0	0	0	0
1005bCL/cm	0	0	0	0
1108s3CL/cm	39489	0	0	0
1108f10CL/cm	16901	0	0	0
1129s6CL/cm	0	0	0	0
1129f9CL/cm	9930	0	0	0
1219s3CL/cm	7138	0	6968	0
1219f10CL/cm	1115	0	0	0
105f1CL/cm	2514	314	0	0
105f5CL/cm	1746	0	0	0
105s3CL/cm	4838	0	0	0
105s7CL/cm	9190	0	0	0

date	*Chroococcidiopsis*	*Nitzschia linearis*	*Cosmarium 1*	*Oscillatoria 2*
204rCL/cm	0	0	0	0
204lCL/cm	0	0	0	0
204ddCL/	0	0	0	0
204ff1CL	0	0	0	0
204ff2CL	0	0	0	0
219aCL/c	0	0	0	0
219gCL/c	0	0	0	0
219lCL/c	0	0	0	0
219nCL/c	0	0	0	0
219aaCL/	0	0	0	0
219ccCL/	0	0	0	0
219eeCL/	0	0	0	0
219liCL/	0	0	0	0
307eCL/c	0	0	0	0
307cCL/c	0	0	0	0
307sCL/c	0	0	0	0
307nCL/c	0	0	0	0
307ccCL/	0	0	0	0
307vCL/c	0	0	0	0
307kkCL/	0	0	0	0
307ffCL/	0	0	0	0
317iCL/c	0	0	0	0
317gCL/c	0	0	0	0
317pCL/c	0	0	0	0
317rCL/c	15958	0	0	0
317zCL/c	0	0	0	0
317bbCL/	0	0	0	0
317iiCL/	0	0	0	0
317ffCL/	0	0	0	0
804sgCL/cm	0	0	488	80381
804sfCL/cm	0	0	0	0
804fgCL/cm	0	0	0	0
804ffCL/cm	0	0	0	0
1005jCL/cm	0	0	0	0
1005bCL/cm	0	0	0	0
1108s3CL/cm	0	0	0	0
1108f10CL/cm	0	0	0	0
1129s6CL/cm	0	0	0	0
1129f9CL/cm	0	0	0	0
1219s3CL/cm	0	0	0	0
1219f10CL/cm	0	0	0	0
105f1CL/cm	0	0	0	0
105f5CL/cm	0	0	0	0
105s3CL/cm	0	0	0	0
105s7CL/cm	0	0	0	0

date	*Plectonema 1*	*Gleocapsa*	*Plectonema 2*	*Navicula cari*
204rCL/cm	0	0	0	0
204lCL/cm	0	0	0	0
204ddCL/	0	0	0	0
204ff1CL	0	0	0	0
204ff2CL	0	0	0	0
219aCL/c	0	0	0	0
219gCL/c	0	0	0	0
219lCL/c	0	0	0	0
219nCL/c	0	0	0	0
219aaCL/	0	0	0	0
219ccCL/	0	0	0	0
219eeCL/	0	0	0	0
219llCL/	63244	10541	64723	0
307eCL/c	0	0	0	0
307cCL/c	0	0	0	0
307sCL/c	0	0	0	0
307nCL/c	0	0	0	0
307ccCL/	0	0	0	0
307vCL/c	0	0	0	0
307kkCL/	0	0	0	0
307ffCL/	0	0	0	0
317iCL/c	0	0	0	0
317gCL/c	0	0	0	0
317pCL/c	0	0	0	0
317rCL/c	0	0	0	0
317zCL/c	0	0	0	0
317bbCL/	0	0	0	0
317iiCL/	0	0	0	0
317ffCL/	0	0	0	0
804sgCL/cm	0	0	0	0
804sfCL/cm	0	0	0	0
804fgCL/cm	0	0	0	0
804ffCL/cm	0	0	0	0
1005jCL/cm	0	0	0	0
1005bCL/cm	0	0	0	0
1108s3CL/cm	0	0	0	0
1108f10CL/cm	0	0	0	0
1129s6CL/cm	0	0	0	0
1129f9CL/cm	0	0	0	0
1219s3CL/cm	0	0	0	0
1219f10CL/cm	0	0	0	0
105f1CL/cm	0	0	0	0
105f5CL/cm	0	0	0	0
105s3CL/cm	0	0	0	0
105s7CL/cm	0	0	0	0

date	*Cylindrocystis brebissonni*	*Closterium leibleinii*
204rCL/cm	0	0
204lCL/cm	0	0
204ddCL/	0	0
204ff1CL	0	0
204ff2CL	0	0
219aCL/c	0	0
219gCL/c	0	0
219lCL/c	0	0
219nCL/c	0	0
219aaCL/	0	0
219ccCL/	0	0
219eeCL/	0	0
219llCL/	0	0
307eCL/c	0	0
307cCL/c	0	0
307sCL/c	0	0
307nCL/c	0	0
307ccCL/	0	0
307vCL/c	0	0
307kkCL/	0	0
307ffCL/	0	0
317iCL/c	0	0
317gCL/c	0	0
317pCL/c	0	0
317rCL/c	0	0
317zCL/c	0	0
317bbCL/	0	0
317iiCL/	0	0
317ffCL/	0	0
804sgCL/cm	0	0
804sfCL/cm	391	0
804fgCL/cm	0	0
804ffCL/cm	0	0
1005jCL/cm	0	0
1005bCL/cm	0	0
1108s3CL/cm	0	0
1108f10CL/cm	0	0
1129s6CL/cm	0	0
1129f9CL/cm	0	0
1219s3CL/cm	0	0
1219f10CL/cm	0	0
105f1CL/cm	0	0
105f5CL/cm	0	0
105s3CL/cm	0	0
105s7CL/cm	0	0