

TRENDS IN BENTHIC ALGAL COMMUNITY RESPONSE TO A SMALL-SCALE
GRADIENT OF CURRENT VELOCITIES ALONG A STREAMBED TRANSECT

Xiaozhao Song

A Thesis

Submitted to the Graduate College of Bowling Green
State University in partial fulfillment of
the requirements for the degree of

MASTER OF SCIENCE

August 2007

Committee:

Rex L. Lowe, Advisor

Paul A. Moore

Daniel M. Pavuk

ABSTRACT

Rex L. Lowe, Advisor

Current has been found to be one of the controlling factors that account for the patchiness of the periphyton community. This study determined how the benthic algal communities were distributed naturally along a streambed transect, along which a gradient of current velocities from low to high were observed and measured. It also determined whether similar variations in benthic algal community patterns would be recreated when such a natural gradient of currents were duplicated in the experimental flumes. Results indicated that the gradient of currents functioned as a determinant in modulating the benthic algal communities indirectly by affecting the distribution of the different types of substrata, such as fine organic mats, pebbles, and sandstones, from the margin to the center of the streambed. Variations in benthic algal community patterns, in terms of relative abundance of cell numbers and relative abundance of algal biovolume, were quantitatively tested to be a function of the patterns of substrata along the gradient of current velocities from low to high. Large-celled long filamentous *Mougeotia* dominated in near-shore slow flowing stream zones where fine organic sediments were present. With the sloughing of *Mougeotia* towards the center of the streambed transect, small chain-forming diatoms displayed an increase in relative abundance of algal biovolume along the same transect.

To my grandmother Jinnan Mei, who believed and loved me.....

ACKNOWLEDGMENTS

The most special gratitude goes to my advisor Dr. Rex Lowe. Rex, you are such a wonderful advisor and friend who has supported and inspired me throughout the past two years. Special thanks also go to my other committee members, Dr. Paul Moore and Dr. Daniel Pavuk. Paul, thank you for all your help at the Stream Research Facility, and your inspiration given to the project. Dan, thank you for your teaching in the statistics class and your suggestions on my thesis writing.

I would also like to say thank you to my lovely labmates, Paula Furey, Meg Woller, Jennifer Ress, and Evan Thomas. Thank you all for your emotional support, writing/statistic assistance, and timely get-togethers for the completion of this thesis project.

Thank you to Kandice Fero and Jenn Bergner for your assistance in the field experiments, as well as thank you all at University of Michigan Biological Station for your research help and support.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS.....	5
Study Site	5
Experimental Design.....	5
Sample Collection.....	7
Sample Processing and Analysis	7
Community and Statistical Analysis.....	8
RESULTS	11
Condition of Stream and Artificial Flumes	11
Species Composition	11
Community Structure	13
DISCUSSION.....	15
Condition of Stream and Artificial Flumes	15
Communities Structure	15
Conclusion	19
LITERATURE CITED.....	20
APPENDIX OF FIGURES AND TABLES	23

LIST OF FIGURES

Figure	Page
1	Map of Michigan Showing the Location of the Maple River and Map of the Maple River, Emmet County, Michigan, Showing the East Branch, the West Branch, and the Main Branch of the Maple River..... 27
2	Relative Abundance of Cell Numbers for Each Algal Division from the Streambed Communities in Response to the Gradient of Current Velocities..... 28
3	Relative Abundance of Cell Biovolume for Each Algal Division from the Streambed Communities in Response to the Gradient of Current Velocities..... 28
4	Relative Abundance of Cell Numbers for Each Algal Division from the Artificial Flume Communities in Response to the Gradient of Current Velocities..... 29
5	Relative Abundance of Cell Biovolume for Each Algal Division from the Artificial Flume Communities in Response to the Gradient of Current Velocities..... 29
6	Relative Abundance of Cell Biovolume for Each Physiognomic Algal Group from the Artificial Flume Communities in Response to the Gradient of Current Velocities... 30
7	Relative Abundance of Cell Biovolume for Each Physiognomic Algal Group from the Streambed Communities in Response to the Gradient of Current Velocities..... 30
8a	Summary Statistic for the Physiognomic Group MA and Results of Post-hoc Tukey's Test of Streambed Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed) 31
8b	Summary Statistic for the Physiognomic Group MA and Results of Post-hoc Tukey's Test of Artificial Flume Algal Responses Over the Gradient of Current Velocities in

	Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	
	31
9a	Summary Statistic for the Physiognomic Group BM and Results of Post-hoc Tukey's Test of Streambed Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	32
9b	Summary Statistic for the Physiognomic Group BM and Results of Post-hoc Tukey's Test of Artificial Flume Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	
	32
10a	Summary Statistic for the Physiognomic Group TY and Results of Post-hoc Tukey's Test of Streambed Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	33
10b	Summary Statistic for the Physiognomic Group TY and Results of Post-hoc Tukey's Test of Artificial Flume Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	33
11a	Summary Statistic for the Physiognomic Group EM and Results of Post-hoc Tukey's Test of Streambed Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	34
11b	Summary Statistic for the Physiognomic Group EM and Results of Post-hoc Tukey's Test of Artificial Flume Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	34

12a	Summary Statistic for the Physiognomic Group LF and Results of Post-hoc Tukey's Test of Streambed Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	35
12b	Summary Statistic for the Physiognomic Group LF and Results of Post-hoc Tukey's Test of Artificial Flume Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	35
13a	Summary Statistic for the Physiognomic Group BC and Results of Post-hoc Tukey's Test of Streambed Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	36
13b	Summary Statistic for the Physiognomic Group BC and Results of Post-hoc Tukey's Test of Artificial Flume Algal Responses Over the Gradient of Current Velocities in Terms of Relative Abundance of Algal Biovolume (Arcsine Square Root Transformed)	36
14	<i>Mougeotia</i> Dominantly Floating above the Fine Sediments along the Margin of the Streambed	37

LIST OF TABLES

Table		Page
1	Species List with Categorization and Average Biovolume Per Counting Unit	23
2	P-values of the Two-factor Analysis of Variance Showing No Significant Difference in Algal Response to Current Velocity between Field Observation Sites and Artificial Flume Sites, as well as No Interaction of Site Settings and Category on Algal Response to Current Velocity, in terms of Relative Abundance of Cell Numbers	26
3	P-values of the Two-factor Analysis of Variance Showing No Difference in Algal Response to Current Velocity between Field Observation Sites and Artificial Flume Sites, as well as No Interaction of Site Settings and Category on Algal Response to Current Velocity, in terms of Relative Abundance of Algal Biovolume	26

INTRODUCTION

Benthic algal communities are composed of all the algal taxa associated with substrata at the bottom of stream ecosystems and are key communities in driving the whole stream ecosystems in terms of providing food resources for other organisms through carbon fixation. Benthic algal communities often display spatial and temporal variations in biomass and community structure in response to a variety of biotic and abiotic environmental variables to which those communities are subjected. Several studies have been conducted to determine the mechanisms under which biotic and abiotic environmental variables modulate the structure and function of benthic algal communities. Some common target environmental variables potentially regulating benthic algal communities include nutrients (Biggs and Lowe 1994, Gaiser et al. 2006), substrata (Miller et al. 1987, Vadeboncoeur et al. 2006), and grazers (Steinman 1991, Tuchman and Stevenson 1991).

However, none of these environmental variables (also including those that were not mentioned above) exert impacts on benthic algal communities alone. In natural settings, the structure and function of benthic algal communities are driven by a combination of many environmental variables simultaneously and the interactions between these variables often complicate investigations of the relationships between benthic algal communities and their surrounding environments. For instance, a study on benthic algal biomass dynamics in nine gravel bedded rivers by Biggs and Close (1989) found that variations in benthic algal biomass were the result of both current velocity and nutrient concentrations and were not just a function of nutrient availability. Another study in a second order stream in eastern Tennessee demonstrated that grazers and nutrients simultaneously limited algal biomass (Hill et al. 1992).

Wellnitz and Poff (2006) showed how longer grazing duration and lower current velocity could collectively accelerate benthic algal regrowth.

Among a number of different environmental variables that modulate benthic algal communities, current velocity has received considerable attention (Jones 1951, Ghosh and Gaur 1991, Biggs et al. 1998). The direct effects of current on benthic algal community structure can be categorized into two contrasting aspects. On one hand, an increase in current can positively affect the benthic algal community by increasing the turbulent flux and thus the transport of nutrients that can be absorbed by individual benthic algal cells, and the efflux of waste products. This can stimulate the metabolism (photosynthesis, respiration, and specific growth rates) of each individual benthic alga (Lock and John 1979, Borchardt 1996, Biggs and Stokseth 1996). Conversely, an increase in current velocity can negatively affect the benthic algal communities by decreasing immigration rates and increasing the drag on algal attachment to the substrata on which they grow. As a result, colonization of benthic algae is reduced and sloughing of algal growth increases (Stevenson 1983, Biggs and Thomsen 1995).

In addition to these direct effects of current on the benthic algal community, current indirectly modulates benthic algal community structure by interacting with both the biotic and abiotic controlling factors described previously (Nielson 1950, Poff and Ward 1992, etc). In general, current has indirect effects on benthic algal community structure by modulating habitat conditions, such as the type, size, and stability of substratum or by altering the taxonomy, distribution, and quantity of invertebrate grazers and fish that feed on or disturb benthic algal communities. For example, larger substrata are usually associated with faster flow and are more available for benthic macroalgae to grow on (Power and Stewart 1987, Dodds 1991). The density of the benthic algal mat is likely to be lower in fast-current zones where herbivorous

invertebrates (such as caddis flies and beetles) dominate in community dynamics and benthic algal immigration rates are low (Merritt and Cummins 1984).

Although, previous studies have examined the influences of current velocity, along with other environmental variables, upon the structure and function of benthic algal communities, little work has been done investigating the trend of the structure of benthic algal communities in response to small-scale gradient of current velocities. In this study, the effect of small-scale gradient of current velocities was made possible by investigating benthic algal structure along a streambed transect with current velocity increasing from the margin to the middle of that transect, compared to benthic algal communities created in experimental flumes in responses to a similar gradient of current velocities.

The objectives of this study were: 1) to determine how the benthic algal communities were distributed naturally along a streambed transect that had a small-scale gradient of current velocities, which were also associated with different patterns of substrata. 2) to determine whether similar variations in benthic algal community patterns would be recreated when such a natural gradient of currents was duplicated in the experimental flumes.

Assuming that all other parameters regulating benthic algal communities were constant in this study, I hypothesized that the gradient of currents functions as a determinant in modulating the benthic algal communities indirectly by affecting the distribution of the substrata, such as fine organic mats, pebbles, and sandstones, from the margin to the center of the streambed. Variations in benthic algal community patterns, in terms of relative abundance of cell numbers and relative abundance of algal biovolume, were quantitatively tested to be a function of the patterns of substrata along the gradient of current from low to high. Specifically, I hypothesized that filamentous macroalgal taxa such as *Ulothrix* and *Mougeotia* would be abundantly floating

in slow-flowing stream zones where fine sediments predominated. Conversely, off-shore zones settled by stable substrata (pebbles) would be more likely colonized by attached algal taxa, such as some monoraphid diatoms *Achnantheidium* and *Cocconeis* and some stalked diatoms (i.e., *Cymbella*) that produced mucilage for their association with substrata.

Conducted in a stream in the Great Lakes region of North America, the goal of this study was to contribute to the data base that can help predict benthic algal community patterns in other aquatic systems with similar habitat conditions.

MATERIALS AND METHODS

Study Site

There is a greater possibility to observe variations in the structure and function of a benthic algal community when streambed sediments are relatively stable, and light, water temperatures, and nutrient concentrations are relatively high and invariant (Power and Stewart 1987, Scarsbrook and Townsend 1993). Thus, in this study I chose to conduct the following field observations and manipulated experiments during the summer in the Maple River, Michigan, when and where such ideal habitat conditions are well met (Pan 1993).

The East Branch of the Maple River (EBMR) is a typical boreal stream which originates from Douglas Lake and flows into Burt Lake. Both of the lakes are alkaline glacial lakes in northern Michigan (Fig. 1). One riffle area in the EBMR, one-half mile upstream from the Stream Research Facility (SRF), University of Michigan Biological Station (UMBS), was chosen as the field observation site. EBMR is pristine and located in a remote surrounding, making the disturbance level and eutrophic state that are usually caused by human activities, such as boating, sewage effluent, and agricultural activities, weak and constant in this study. In addition, EBMR is shallow with its riparian vegetation in the form of shrubs (relatively low in height), allowing the stream to receive relatively evenly distributed amount of light throughout the water surface in summer.

Experimental Design

Field Observations

In the chosen riffle area, a gradient of currents comprising 0, 10.0 ± 0.5 , 20.0 ± 1.0 , 30.0 ± 1.5 , and 46.0 ± 2.3 cm/s was obtained by an Acoustic Doppler Velocimeter (ADV) measuring current velocities of potential sampling sites with distinguishable patterns of substrata

along a transect of the streambed. As a result, five sample collecting sites were selected and spread along the transect running from the margin to the center of the streambed. The patterns of substrata on which the on-site periphyton communities colonized included fine layers of organic detritus, median-sized pebbles, large pebbles, and fine sand grains. Three replicate samples were collected from each site.

Manipulative Experiments

Manipulative experiments were conducted at the SRF, UMBS. Water was pumped from the stream via an intake at SRF, dispensed throughout the experimental station by polyvinyl chloride gutters, and controlled by valves. Fifteen U-type vinyl flumes, 13 cm wide and 250 cm long, were used as artificial flumes to simulate the microhabitats that were subjected to the same gradient of current velocities observed at the field site. In other words, a gradient of current velocities of 0, 10.0 ± 0.5 , 20.0 ± 1.0 , 30.0 ± 1.5 , and 46.0 ± 2.3 cm/s was constructed and applied to the artificial flumes. The measurements of current velocities in the artificial flumes were conducted by collecting flowing water with a 2-liter graduated cylinder at the open end of each flume over a short period of time recorded by a stop watch. The value of each current velocity was achieved via volume of water being divided by the size of vertical surface area of the flowing water in each flume and then divided by the time that was used to collect that amount of water with the graduated cylinder. Treatment of each current velocity was repeated three times in a set of three vinyl flumes. Square ceramic tiles, 35 cm² in surface area, were lined up in each flume as artificial substrata for the algal colonization. The colonization was allowed to occur between July 24th and August 9th, 2006 for a total period of sixteen days. The flumes were unshaded and protected from exterior disturbance (i.e., rain, wind, and storm) by a cover of

transparent plastic membranes. The water depth of the flumes was generally very shallow (<4cm deep).

Sample Collection

For both the field observation and manipulative experiments, a total number of 105 periphyton samples (with 15 from field and 90 from SRF, respectively) were collected quantitatively using a metal ring of 3.2 cm² in surface area. For the field observations, epipellic and epipsammic samples were collected using plastic pipettes with the end obliquely cut. The obliquely cut plastic pipettes allowed a complete collection, which might otherwise have been lost due to the ambient flowing water. Epilithic samples were collected by firstly retrieving pebbles from the sites and then scraping (by a blade) an area of 3.2 cm² using the same metal ring. For the manipulative experiments, both plastic pipettes and blades were used to remove algal samples from the ceramic tiles. Three tiles were randomly picked for algal sampling in each vinyl flume, with each selected tile being scraped at the center and the margin of the surface area separately.

All samples were stored in individual screw-topped vinyl bottles with approximately 20 ml of the ambient stream water. Samples were then taken back to laboratory within six hours and preserved with glutaraldehyde to the final concentration of 3% for future species identification and enumeration.

Water samples were taken from water columns at both field and experimental sites and then transported back to the laboratory at UMBS for generation of chemical data (pH, Total Phosphate, Total Nitrogen, SiO₂, etc.).

Sample Processing and Analysis

Algal density was estimated initially by enumerating algal units within each subsample in a Palmer-Maloney nanoplankton counting chamber under a light microscope (Olympus BX51) at 400× magnification. A minimum of 300 algal units were counted and identified to species level (Komarek 2003) for each subsample, with the exception of diatoms, which were only enumerated without species identification at this point. An area of 10 μm×10 μm of the growth colony of blue-green algae was considered to be one counting unit. For small blue green filamentous algae (such as *Anabaena*), 10 μm in length was counted as a unit, while one cell as one unit for large green filamentous algae (such as *Mougeotia*). For other soft algae and diatoms, each individual cell represented a counting unit.

Another algal subsample was used to make permanent diatom slides. Diatom slides were prepared by boiling a portion of the subsample with the same volume of nitric acid to the subsample's original volume (Patrick and Reimer 1966). The suspension was then diluted with distilled water and allowed to settle for 8 hours, after which the sample was decanted. This process was repeated until the pH of the suspension became neutral. The cleaned samples were then air dried onto coverslips and mounted in Naphrax[®]. Diatoms were identified to species level (Patrick and Reimer 1966, Krammer and Lange-Bertalot 1986, 1991) using the same light microscope at 1000× magnification under oil immersion.

Algal biomass was estimated by calculating algal biovolume based on the geometric shapes of each algal species (Hillebrand et al. 1999). An average algal biovolume was established by measuring at least 15 counting units for a dominant species and five for a rare species.

Community and Statistical Analysis

In order to investigate the community structure of the periphyton subjected to the gradient of current velocities, algal taxa were categorized into six groups based on the morphological and ecological characteristics of each species present. The six physiognomic groups of algal taxa were: 1) benthic cells forming long or small chains as colonies (BC); 2) biraphid benthic cells free to move (motile) and loosely lying on the substratum (BM); 3) benthic cells attached erectly to substratum via mucilage stalks (EM); 4) large cylindrical cells forming long filaments (LF); 5) monoraphid benthic cells lying flat and attached to substrata via mucilage pads (MA); 6) Cells originated from plankton in upper water, also called tychoplankton (TY). Relative abundance of cell numbers and relative abundance based on total algal biovolume of each physiognomic group were statistically tested along the gradient of current velocities in both the field and experimental flume samples.

All statistical analyses were conducted via the MINITAB[®] Release 14 and Microsoft[®] Office Excel 2003. Two-factor Analysis of Variance (ANOVA) was run to determine the algal responses to the gradient of current velocities between field observations and manipulative experiments, among ecological and morphological categories, as well as the effect of interaction of site settings and categories ($\alpha=0.05$). The relative abundance of cell numbers and relative abundance of algal biovolume were both transformed with arcsine square root for the two-factor ANOVA analyses and the post-hoc Tukey's tests.

Percent Stacked Area Charts were produced to compare the trend of percentage each algal division contributed in terms of both relative abundance of cell numbers and relative abundance of algal biovolume over the gradient of current velocities in both field and experimental settings. Post-hoc Tukey's tests were used to reveal how each algal physiognomic

group responded to the gradient of current velocities differentially in terms of relative abundance of algal biovolume at both site settings.

RESULTS

Condition of Stream and Artificial Flumes

Water temperatures were relatively constant at an average of $28 \pm 2^\circ$ C over the experimental period. All the sampling sites were neutral to slightly alkaline (pH level averaged at 7.68). There were no significant differences in nutrient levels between the natural and experimental sampling sites, except that the streambed water had an average of $12 \mu\text{gN/L}$ of $\text{NH}_4\text{-N}$ and $9.5 \mu\text{gN/L}$ of $\text{NO}_3\text{-N}$, compared to $16 \mu\text{gN/L}$ of $\text{NH}_4\text{-N}$ and $6 \mu\text{gN/L}$ of $\text{NO}_3\text{-N}$ for water flowing through the artificial flumes. The averages of other assays of water chemistry in both the field and experimental settings were as follows: $2 \mu\text{gP/L}$ of $\text{PO}_4\text{-P}$, $11.5 \mu\text{gP/L}$ of Total Phosphorus, 0.3 mg N/L of Total Nitrogen. The results of ADV data analysis turned out that the correlation coefficients were around 0% for all the five different field sampling sites, suggesting that the dynamic readings from ADV not be used in this study. Nevertheless, the mean current velocity measurements were still capable of indicating that the gradient of current velocities from low to high (0 , 10.0 ± 0.5 , 20.0 ± 1.0 , 30.0 ± 1.5 , and $46.0 \pm 2.3 \text{ cm/s}$) was found at the sampling sites along the streambed transect.

Species Composition

From the 45 samples examined in this study, 34 genera and 70 species of diatoms (Bacillariophyta), 8 species of blue green algae (Cyanobacteria), 9 species of green algae (Chlorophyta), and 1 species of Euglenophytes were identified and enumerated using light microscopy. Since the algae colonizing the artificial flumes were originally from the stream water pumped one-half mile downstream of the streambed sampling sites, biovolume for algae from the natural and artificial settings were considered to be similar for each species. The algal

biovolume per cell ranged from 19 to 36,022 μm^3 for the diatoms, 1 to 269 μm^3 for the cyanobacteria, 67 to 196,220 μm^3 for the greens, and 103 μm^3 for the only species (*Euglena* sp.) found in Euglenophytes. The genus *Mougeotia* significantly dominated periphyton biovolume in the samples obtained from slow current sites in both natural and artificial settings. However, diatom species dominated species numbers in all sampling sites, including both field and flumes sites.

Of the samples obtained from the streambed sites, the percentages of diatom cells counted slightly varied and averaged at 82.5%. Diatoms averaged at 57.9% of total algal biovolume (Fig. 2). The most abundant algal division was Chlorophyta, in terms of algal biovolume, from samples obtained from streambed sites with slow current velocity (87.4% at 0 cm/s and 80.7% at 10.0 ± 0.5 cm/s). However, for samples obtained from sites with high current velocity, diatoms dominated total algal biovolume: 69.1% at 20.0 ± 1.0 cm/s, 95.4% at 30.0 ± 1.5 cm/s, and 93.3% at 46.0 ± 2.3 cm/s (Fig. 3).

Of samples from artificial flumes, diatoms averaged at 81.2% in species numbers (Fig. 4), and averaged at 50.2% in relative abundance of total algal biovolume. The same trend for the relative abundance of diatoms (it increased as current velocity increased) also occurred in samples from the artificial flumes: 19.6% at 0 cm/s, 21.2% at 10.0 ± 0.5 cm/s, 43.9% at 20.0 ± 1.0 cm/s, 72.6% at 30.0 ± 1.5 cm/s, and 93.5% at 46.0 ± 2.3 cm/s (Fig. 5).

The dominant diatom genera in terms of cell number counted in periphyton communities from both natural and artificial settings were *Achnanthydium* (averaged at 14.3% for field and 12.5% for manipulative experiments, respectively) and *Staurosira* (averaged at 31.9% for field and 37.6% for manipulative experiments, respectively). *Achnanthydium* was a small (its biovolume averaged at 103 μm^3) monoraphid genus prostrately attached to hard substrata and

Staurosira was also small-celled (with $163 \mu\text{m}^3$ as its average biovolume) that formed long chains in this study. The genus *Mougeotia* allowed the division of Chlorophyta to become the most abundant in terms of total algal biovolume in samples from sites that were subjected to slow current velocity. Three species of *Mougeotia* were present in large long filaments in this study, with an average of $73,827 \mu\text{m}^3$ in biovolume per cell.

Community Structure

There was no significant difference in algal response to current velocity=0 cm/s with respect to the algal cell numbers counted between samples from streambed sites and artificial flumes (ANOVA, $P=0.678$, $DF=1$), as well as no significant effects of interaction of site settings where samples were obtained and physiognomic categories on the algal response in terms of cell density to $V=0$ cm/s (ANOVA, $P=0.934$, $DF=5$). However, the six morphological and ecological groups of algae responded to $V=0$ cm/s significantly differently in terms of algal cell density (ANOVA, $P=0.000$, $DF=5$). The same phenomenon (no significant effects of site settings, no significant effects of interaction of site settings and categories, but significant effect of categories on algal response in terms of cell density to current velocity) occurred in algal communities responding to other current velocities that were chosen in this study (Table 2).

Similarly, in terms of relative abundance of algal biovolume, there was no significant difference in algal response to current velocity=0 cm/s between samples from streambed sites and artificial flumes (ANOVA, $P=0.799$, $DF=1$), as well as no significant effects of interaction of site settings and physiognomic categories on the algal response to $V=0$ cm/s (ANOVA, $P=0.995$, $DF=5$). However, the six morphological and ecological groups of algae responded to $V=0$ cm/s significantly differently as far as relative abundance of algal biovolume was concerned (ANOVA, $P=0.000$, $DF=5$). This same phenomenon (no significant effects of site settings, no

significant effects of interaction of site settings and categories, but significant effects of categories on algal response in terms of relative abundance of algal biovolume to current velocity) occurred in algal communities responding to other current velocities (Table 3).

The six physiognomic groups of algal taxa responded to current velocity differentially in terms of relative abundance of algal biovolume for the periphyton communities from both natural and artificial settings (Fig. 6 and Fig. 7, respectively). The trend for each physiognomic group in terms of relative abundance of algal biovolume over the gradient of current velocities were illustrated via the post-hoc Tukey's tests (Fig. 8a through Fig. 13b). The relative abundance of long filamentous algae stayed constant when current velocity increased from 0 cm/s to 10.0 ± 0.5 cm/s, and then experienced a great significant decrease as current velocity continued to increase. Biraphid, motile diatoms reached the highest relative abundance of algal biovolume at the second highest ($V=30.0 \pm 1.5$ cm/s) rather than the highest (46.0 ± 2.3 cm/s) current velocity. The same trend also applied to tycho plankton. Compared to long filamentous algae, benthic chain-forming diatoms displayed an opposite trend in terms of relative abundance of algal biovolume: a positive increase in relative abundance accompanying the increasing current velocity. There were no significant trends in terms of relative abundance of algal biovolume for the two other minor algal groups, stalked diatoms and adnate diatoms with single raphes.

DISCUSSION

Condition of Stream and Artificial Flumes

Physical parameters, including water temperature, light regime, concentration of nutrients, were relatively invariant along the streambed transect and between the field sites and experimental flumes. The invariance of stream and artificial flumes condition made it possible for this study to focus on the effects of the gradient of current velocities on the benthic algal communities under both site settings. The attempts to measure the turbulent dynamics of each field sampling sites by ADV were stopped by the low signal-to-noise ratio, which resulted in the near zero percentages (far below the satisfactory limit 40% for using ADV data) of correlation coefficients for each sampling site.

Community Structure

As expected, algal community structure was significantly different from the margin to the center of the streambed (associated with an increasing gradient of current velocities). Further manipulative experiments in the SRF supported the observation that current velocity contributed greatly in structuring the algal communities in the same respect. More specifically, a shift from dominance by large-celled upright filamentous taxa at low velocities to more small chain-forming taxa at higher velocities occurred in algal communities in both the natural and artificial settings.

Theoretically, current velocity provides a mass transfer subsidy of nutrients, as well as shear stress for periphyton communities (Borchardt 1996). The above counteracting processes simultaneously exert influences on periphyton communities, with one or another being the dominant factor in modulating the structure and function of periphyton communities under specific conditions. In this study, current velocity indirectly played an important role in

engendering the patchy distribution of the periphyton communities by determining the patterns of substrata on which the periphyton colonized.

Mats of fine organic detritus were sloughed by the increasing current velocity along the transect of the streambed, which precipitated a shift of substrata for periphyton from fine sediments to hard substrata that were more resistant to the form drag and surface friction of shear stress. With still or low current velocities water, fine organic sediments served as both rich nutrient resource and stable substrata for periphyton communities to maintain a high species diversity and biomass. Conversely, higher current velocities excluded some algal taxa (large-celled long filamentous algae in this study) that preferred slow current with fine sediments as their substrata.

The genus *Mougeotia*, one of the large-celled long filamentous algae present in the algal communities, displayed the greatest shift in relative abundance in response to the small-scaled gradient of current velocities from the margin to the center of the streambed. *Mougeotia* accounted for more than 96% of the total algal biovolume of the division Chlorophyta and made the division the most dominant in the algal communities that were subjected to low current velocities (0 cm/s and 10.0 ± 0.5 cm/s). However, the percentage of cell numbers of *Mougeotia* was quite low (less than 10%). *Mougeotia* was observed in the growth form of tangled filaments growing into a dense blanket along the margin of the streambed in this study (Fig 14). The marginal zone of the streambed was characterized by relatively low current water flowing above the layers of fine detrital organic sediments. The dense *Mougeotia* present on the marginal sediment tended to slow down water flow with the resultant increase in the accumulation of organic detritus from the surrounding environment. The formation of such layers of organic detritus provided habitat for epipelton, and the dense blanket of *Mougeotia* provided substrata for

epiphytic algae. Epipelagic algae growing on organic sediments developed into dense mat-like communities. Since most epipelagic and epiphytic algal taxa belong to the Bacillariophyta division, this may explain why the cell numbers of diatoms in the marginal zones was not significantly less than in the fast current zones associated with more diatoms attached to hard substratum (pebbles and sand grains). The growth form of *Mougeotia* as filamentous masses into dense blanket in slow current water was also recorded by Whitton (1971) and Ilmavirta et al. (1977). Additionally, the dominance of total algal biovolume by *Mougeotia* at low current velocities was exaggerated in this study because the measurements of algal biovolume were only based on the geometric dimensions of the preserved species, whose cavities were mostly saturated and enlarged by water.

With the sloughing of long filamentous algae towards the center of the streambed transect, the group of chain-forming diatoms experienced an increase in the relative abundance of algal biovolume along that transect with the increasing gradient of current velocities. It may be an important strategy for some diatom species to form chains in colonies to adapt to the increasing current flow, since layers of fine detritus on which the individuals tended to colonize were washed out with an increasing current velocity. Those chain-forming diatoms present in this study were represented by the three subspecies of *Staurosira construens*, which has been recorded as a frequent chain-forming diatom species accustomed to fast water flow by Morales (2005).

It was unsurprising to have motile biraphid diatoms, as well as tychoplankton, reach the maximum relative abundance of algal biovolume at median current velocities. Tychoplanktonic algal taxa arrived at their biovolume crest at $V=20.0\pm 1.0$ cm/s, which was lower than the one ($V=30.0\pm 1.5$ cm/s) for the motile biraphid diatoms to arrive at theirs. Species of motile biraphid

diatoms and tychoplankton only loosely, rather than tightly, attached to substrata, so their relative abundance was potentially more subjected to the counteracting effects (nutrient subsidy and shear stress) of current velocity upon the whole algal communities. The trade-off between the two counteracting processes possibly explained why those groups of algae maintained the peak relative abundance of algal biovolume at the median current velocities, rather than the ends of the velocity gradient.

There was no significant change of relative abundance of algal biovolume in stalked diatoms and adnate diatoms with single raphes in response to the gradient of current velocities along the streambed transect in this study. This was contrary to the findings of Biggs et al. (1998) who concluded that stalked communities displayed a unimodal distribution in biomass with both subsidy and stress processes dominating different ends of the velocity gradient. Their result corroborated the classic “subsidy-stress” model (Odum et al. 1979), which stated that small scale perturbations involving usable nutrients would stimulate ecosystem function while continued perturbation would be negative to the community equilibrium and functioning. The lack of responses of the stalked and adnate diatoms to the gradient of current velocity along the streambed transect might be due to the inconsistent sizes and stability of the substrata off which those whole algal communities were scraped. All the field sampling sites were chosen based only on the current velocities to which those algal communities were subjected and the types of substrata on which the algal communities colonized. Little effort was taken to investigate and incorporate the substratum size and stability, which may have had considerable impacts on the distribution of herbivores (Denicola and McIntire 1991, Robson and Barmuta 1998), which, in turn, could directly exert influences upon algal abundance and species composition by grazing at certain levels (Hill and Knight 1988, Steinman 1996). The reason why there were also no

stronger results for the manipulative experiments in terms of adnate and stalked diatoms distribution in the SRF could potentially be a function of the rareness of those two physiognomic groups compared to other more abundant ones.

Additionally, regardless of the morphological and ecological categories of the algal taxa, there were more diatom species recorded in terms of relative abundance of algal biovolume in periphyton communities towards the center the streambed, where higher current velocities were measured. However, several species, such as *Achnathidium exigua* and *Gomphonema parvulum* (Goldsborough 1994, Cremer et al. 2004), that have been recorded as taxa only associated with sediments were also found in the center stream zones that were characterized by being embedded with median-sized and large pebbles. The overlap of species that were expected to be found at separate sites of the streambed transect occurred probably for the reason that some algal taxa of the upstream algal communities might be sloughed downstream and trapped in the final field algal samples.

Conclusion

This study investigated how algal communities responded to the gradient of current velocities along a streambed transect, which intrinsically required the incorporation of substratum types into this study. In conclusion, the small-scaled gradient of current velocities functioned as a robust abiotic factor, complementary with substratum types, in regulating the periphyton community structure. This resulted in near-shore communities being dominated by large-celled long filamentous algae with increasing small chain-forming diatoms toward the stream center.

LITERATURE CITED

- Biggs, B. J. F. & M. E. Close. 1989. Periphyton biomass dynamics in gravel bed rivers-the relative effects of flows and nutrients. *Freshwat. Biol.* 22(2): 209-231.
- Biggs, B. J. F. & R. L. Lowe. 1994. Responses of 2 trophic levels to patch enrichment along a New Zealand stream continuum. *N.Z. J. Mar. Freshwat. Res.* 28(2): 119-134
- Biggs, B. J. F. & H. A. Thomsen. 1995. Disturbance in stream periphyton by perturbations in shear stress: time to structural failure and differences in community resistance. *J. Phycol.* 31:233-41.
- Biggs, B. J. F. & S. Stokseth. 1996. Hydraulic habitat preferences for periphyton in rivers. *Regul. Riv.* 12:251-61.
- Biggs, B. J. F., Goring, D. G. & V. I. Nikora. 1998. Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *J. Phycol.* 34: 598-9.
- Borchardt, M. A., Hoffmann, J. P. & P. W. Cook. 1994. Phosphorus uptake kinetics of *Spirogyra fluviatilis* (Charophyceae) in flowing water. *J. Phycol.* 30:403-17.
- Borchardt, M. A. 1996. Nutrients. In Steveson, R. J., Bothwell, M. L. & R. L. Lowe. [Eds.] *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, San Diego, pp. 183-227.
- Denicola, D. M. & C. D. Mcintire. 1991. Effects of hydraulic refuge and irradiance on grazer-periphyton interactions in laboratory streams. *J. North Am. Benthol. Soc.* 10(3): 251-262.
- Dodds, W. K. 1991. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. *Water Res.* 25:1325-7.
- Fogg, C. E. 2001. Algal adaptation to stress. In Rai L. C., J. P. Gaur (eds), *Algal Adaptation to Environmental Stresses*. Springer, Verlag Berlin Heidelberg New York: 3-8.
- Gaiser, E. E., Childers, D. L., Jones, R. D., Richards, J. H., Scinto L. J. & J. C. Trexler. 2006. Periphyton responses to eutrophication in the Florida Everglades: Cross-system patterns of structural and compositional change. *Limnol. Oceanogr.* 51(1):617-630.
- Ghosh, M. & J. P. Gaur. 1991. Regulatory influence of water current on algal colonization in an unshaded stream at Shillong (Meghalaya, India). *Aquat. Bot.* 40: 37-46.
- Hill, W. R. & A. W. Knight. 1988. Concurrent grazing effects of two stream insects on periphyton. *Limnol. Oceanogr.* 33:15-26
- Hill, W. R., Boston, H. L. & A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. *Can. J. Fish. Aquat. Sci.* 49: 504-512.

- Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollinger, U. & T. Zohary. 1999. Biovolume calculation for pelagic and benthic microalgae. *J. Phycol.* 35: 403-424.
- Ilmavirta, V., Jones, R. J. & T. Kairesalo. 1977. The structure and photosynthetic activity of pelagial and littoral plankton communities in Lake Pääjärvi, southern Finland. *Ann. Bot. Fenn.* 14:7-16.
- Jones, J. R. E. 1951. The ecological study of the River Towy. *J. Anim. Ecol.* 20:68-8.
- Komarek, J. 2003. Coccoid and colonial cyanobacteria. Filamentous cyanobacteria. *Freshwater Algae of North America*. J. D. Weber and R. G. Smith (editors). 59-196.
- Krammer, K. & H. Lange-Bertalot. 1986. Bacillariophyceae. 1. Teil: Naviculaceae. Süßwasserflora von Mitteleuropa. H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer (editors). Band 2. Gustav Fischer, Stuttgart.
- Krammer, K. & H. Lange-Bertalot. 1986. Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. Süßwasserflora von Mitteleuropa. H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer (editors). Band 2. Gustav Fischer, Stuttgart.
- Krammer, K. & H. Lange-Bertalot. 1986. Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. Süßwasserflora von Mitteleuropa. H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer (editors). Band 2. Gustav Fischer, Stuttgart.
- Krammer, K. & H. Lange-Bertalot. 1991. Bacillariophyceae. 4. Teil: Achnanthaceae. Kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema. Süßwasserflora von Mitteleuropa. Band 2. Gustav Fischer, Stuttgart.
- Lock, M. A. & P. John. 1979. The effect of flow patterns on uptake of phosphorus on river periphyton. *Limnol. Oecnaogr.* 24:376-83.
- Merritt, R. W. & K. W. Cummins. 1984. "An introduction to the Aquatic Insects of North America," 2nd ed. Kendall/Hunt, Dubuque, IA.
- Miller, A. R., Lowe, R. L. & J. T. Rotenberry. 1987. Succession of diatom communities on sand grains. *J. Ecol.* 75:693-709.
- Morales, E. A. 2005. Observations of the morphology of some known and new fragilarioid diatoms (Bacillariophyceae) from rivers in the USA. *Phycol. Res.* 53(2): 113-133.
- Nielson, A. 1950. The torrential invertebrate fauna. *Oikos* 2:177-19.
- Pan Y.D. 1993. The effects of nutrient on periphyton. Dissertation for doctor of philosophy. Bowling Green State University, Bowling Green, OH.

- Patrick, R. and C. W. Reimer. 1966. The diatoms of the United States: Exclusive of Alaska and Hawaii. Volume 1. Monographs of the Academy of Natural Sciences of Philadelphia, Philadelphia.
- Poff, N. L. & J. V. Ward. 1992. Heterogeneous currents and algal resources mediate *in situ* foraging activity of a mobile stream grazer. *Oikos* 65:465-13.
- Power, M. E. & A. J. Stewart. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *Am. Midl. Nat.* 117:333-12.
- Robson, B. J. & L. A. Barmuta. 1998. The effect of two scales of habitat architecture on benthic grazing in a river. *Freshwat. Biol.* 39 (2): 207-220
- Scarsbrook, M. R. & C. R. Townsend. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwat. Biol.* 29:395-15.
- Steinman, A. D. 1991. Effects of herbivore size and hunger level on periphyton communities. *J. Phycol.* 27:54-59.
- Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. *Algal Ecology: Freshwater Benthic Ecosystems*. J. R. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). Academic Press, San Diego, California, USA. 341-373.
- Stevenson, R. J. 1983. Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration. *Ecology* 64:1514-24.
- Tuchman, N. C. & R. J. Stevenson. 1991. Effects of selective grazing by snails on benthic algal communities. *J. North Am. Benthol. Soc.* 10:430-443.
- Vadeboncoeur, Y., Kalff, J., Christoffersen, K. & E. Jeppesen. 2006. Substratum as a driver of variation in periphyton chlorophyll and productivity in lakes. *J. North Am. Benthol. Soc.* 25(2): 379-392.
- Wellnitz, T. & N. L. Poff. 2006. Herbivory, current velocity and algal regrowth: how dose periphyton grow when the grazers have gone? *Freshwat. Biol.* 51(11):2114-2123.
- Whitton, B. A. 1971. Filamentous algae as weeds. In 3rd *European Weed Res. Council Symp.*, Oxford. 249-263.

APPENDIX
TABLES AND FIGURES

Table 1. Species List with Categorization and Average Biovolume Per Counting Unit. BC represents benthic valves forming long or small chains, BM represents biraphid, loosely lying on substratum (motile), EM represents attached erectly to substratum (in mucilage), LF represents long filament, MA represents monoraphid, adnate, and TY represents tychoplankton.

Bacillariophyta	Biovolume (μm^3)	Grouping
<i>Achnantheidium affine</i> (Grunow) Czarnecki	39	MA
<i>Achnantheidium clevei</i> (Grunow) Czarnecki	243	MA
<i>Achnantheidium exigua</i> Grunow	71	MA
<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki	59	MA
<i>Amphipleura pellucida</i> (Kützing) Kützing	1460	BM
<i>Amphora pediculus</i> (Kützing) Grunow	19	BM
<i>Aulacoseira ambigua</i> (Grunow) Simonsen	296	TY
<i>Cocconeis neodiminuta</i> Krammer	624	MA
<i>Cocconeis pediculus</i> Ehrenberg	419	MA
<i>Cocconeis placentula</i> Ehrenberg	38	MA
<i>Cyclotella michiganiana</i> Skvortzow	824	TY
<i>Cyclotella ocellata</i> Pantocsek	1411	TY
<i>Cyclotella striata</i> (Kützing) Grunow	584	TY
<i>Cymbella affinis</i> Kützing	410	EM
<i>Cymbella amphicephala</i> Nägeli	249	EM
<i>Cymbella hybrida</i> Grunow	68	EM
<i>Cymbella microcephala</i> Grunow	1465	EM
<i>Diploneis oblongella</i> (Nägeli) Cleve	338	BM
<i>Epithemia turgida</i> (Ehrenberg) Kützing	8357	BM
<i>Eucocconeis flexella</i> (Kützing) Cleve	1743	MA
<i>Fistulifera saprophila</i> (Lange-Bertalot & Bonik) Lange-Bertalot	39	BM
<i>Fragilaria acus</i> Kützing	305	TY
<i>Fragilaria capucina</i> var. <i>mesolepta</i> (Rabenhorst) Rabenhorst	283	TY
<i>Fragilaria intermedia</i> Grunow	562	TY
<i>Gomphonema angustatum</i> (Kützing) Rabenhorst	396	BM
<i>Gomphonema gracile</i> Ehrenberg	1698	BM
<i>Gomphonema minutum</i> (Agardh) Agardh	979	BM
<i>Gomphonema parvulum</i> (Kützing) Kützing	357	BM
<i>Gomphonema sphaerophorum</i> Ehrenberg	479	BM
<i>Gomphonema truncatum</i> Ehrenberg	1322	BM
<i>Hippodonta capitata</i> (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski	423	BM
<i>Hippodonta hungarica</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski	291	BM
<i>Kolbesia ploenensis</i> (Hustedt) Round & Bukhtiyarova	59	MA
<i>Martyana martyi</i> (Héribaud) Round	295	EM
<i>Melosira varians</i> Agardh	1990	BC
<i>Meridion circulare</i> (Greville) Agardh	252	EM

<i>Navicula cryptocephala</i> Kützing	510	BM
<i>Navicula gastrum</i> (Ehrenberg) Kützing	4210	BM
<i>Navicula oblonga</i> Kützing	3063	BM
<i>Navicula praeterita</i> Hustedt	1185	BM
<i>Navicula pseudoscutiformis</i> Hustedt	160	BM
<i>Navicula radiosa</i> Kützing	2728	BM
<i>Navicula salinarum</i> Grunow	2476	BM
<i>Navicula shadei</i> Krasske	106	BM
<i>Neidium ampliatum</i> (Ehrenberg) Krammer	4011	BM
<i>Nitzschia amphibia</i> Grunow	278	BM
<i>Nitzschia laccum</i> Lange-Bertalot	924	BM
<i>Nitzschia linearis</i> (Agardh) W. Smith	68	BM
<i>Nitzschia palea</i> (Kützing) W. Smith	579	BM
<i>Pinnularia gentiles</i> (Donkin) Cleve	34419	BM
<i>Pinnularia viridis</i> (Nitzsch) Ehrenberg	36022	BM
<i>Planothidium lanceolatum</i> (Brébisson) Round & Bukhtiyarova	178	MA
<i>Planothidium Oestrupii</i> (Cleve) Round & Bukhtiyarova	75	MA
<i>Planothidium pseudotanense</i> (Cleve) Lange-Bertalot	106	MA
<i>Pseudostaurosira brevistriata</i> (Grunow) Williams & Round	133	BC
<i>Reimeria sinuata</i> (Gregory) Kociolek & Stoermer	298	BM
<i>Rhopalodia gibba</i> (Ehrenberg) O. Müller	15372	BM
<i>Sellaphora pupula</i> (Kützing) Mereschk	571	BM
<i>Stauroforma exiguiiformis</i> (Lange-Bertalot) Flower	94	BC
<i>Stauroneis smithii</i> Grunow	131	BM
<i>Staurosira construens f. binodis</i> (Ehrenberg) Hustedt	260	BC
<i>Staurosira construens f. construens</i> (Ehrenberg) Grunow	95	BC
<i>Staurosira construens f. venter</i> (Ehrenberg) Hustedt	133	BC
<i>Staurosirella ansata</i> (Hohn & Hellerman) Kingston	255	BC
<i>Staurosirella leptostauron</i> (Ehrenberg) Williams & Round	286	BC
<i>Staurosirella pinnata</i> (Ehrenberg) Williams & Round	186	BC
<i>Stephanodiscus binderanus</i> (Kützing) Krieger	148	TY
<i>Surirella tenera</i> Gregory	18707	BM
<i>Synedra rumpens</i> Kützing	1437	BC
<i>Synedra ulna</i> (Nitzsch) Ehrenberg	6104	BC
Cyanophyta		
<i>Anabaena</i> sp.1	81	TY
<i>Aphanocapsa</i> sp.1	102	TY
<i>Chroococcus turgidus</i> (Kützing) Nägeli	269	TY
<i>Coelosphaerium</i> sp.1	78	TY
<i>Merismopedia major</i> (W. Smith) Geitler	5	TY
<i>Microcystis</i> sp.1	1	TY
<i>Oscillatoria limosa</i> (Agardh) Gomont	189	LF
<i>Phormidium</i> sp.1	11	LF
Chlorophyta		
<i>Closterium acutum</i> Brébisson	377	TY
<i>Cosmarium caelatum</i> Ralfs	8773	TY

<i>Dimorphococcus</i> sp.1	67	TY
<i>Mougeotia</i> sp.1	2057	LF
<i>Mougeotia</i> sp.2	23205	LF
<i>Mougeotia</i> sp.3	196220	LF
<i>Oocystis</i> sp.1	375	TY
<i>Pediastrum tetras</i> (Ehrenberg) Ralfs	789	TY
<i>Scenedesmus</i> sp.1	123	TY
<i>Sphaerocystis</i> sp.1	524	TY
<i>Staurastrum</i> sp.1	893	TY
Euglenophytes		
<i>Euglena</i> sp.1	103	TY

Current Velocity	0 cm/s	10.0±0.5 cm/s	20.0±1.0 cm/s	30.0±1.5 cm/s	46.0±2.3 cm/s
Site Settings	0.678 (1)	0.706 (1)	0.992 (1)	0.553 (1)	0.964 (1)
Category	0.000 (5)	0.000 (5)	0.000 (5)	0.000 (5)	0.000 (5)
Site settings ×Category	0.934 (5)	0.939 (5)	0.929 (5)	0.629 (5)	0.804 (5)

Table 2. P-values (Degrees of Freedom) of the Two-factor Analysis of Variance showing no difference in algal response to current velocity between field sites and artificial flume sites, as well as no interaction of site settings and categorization on algal response to current velocity, in terms of relative abundance of cell numbers.

Current Velocity	0 cm/s	10.0±0.5 cm/s	20.0±1.0 cm/s	30.0±1.5 cm/s	46.0±2.3 cm/s
Site Settings	0.799 (1)	0.884 (1)	0.719 (1)	0.216 (1)	0.895 (1)
Category	0.000 (5)	0.000 (5)	0.000 (5)	0.011 (5)	0.001 (5)
Site settings ×Category	0.995 (5)	0.964 (5)	0.870 (5)	0.279 (5)	0.919 (5)

Table 3. P-values (Degrees of Freedom) of the Two-factor Analysis of Variance showing no difference in algal response to current velocity between field observation sites and artificial flume sites, as well as no interaction of site settings and categorization on algal response to current velocity, in terms of relative abundance of algal biovolume.

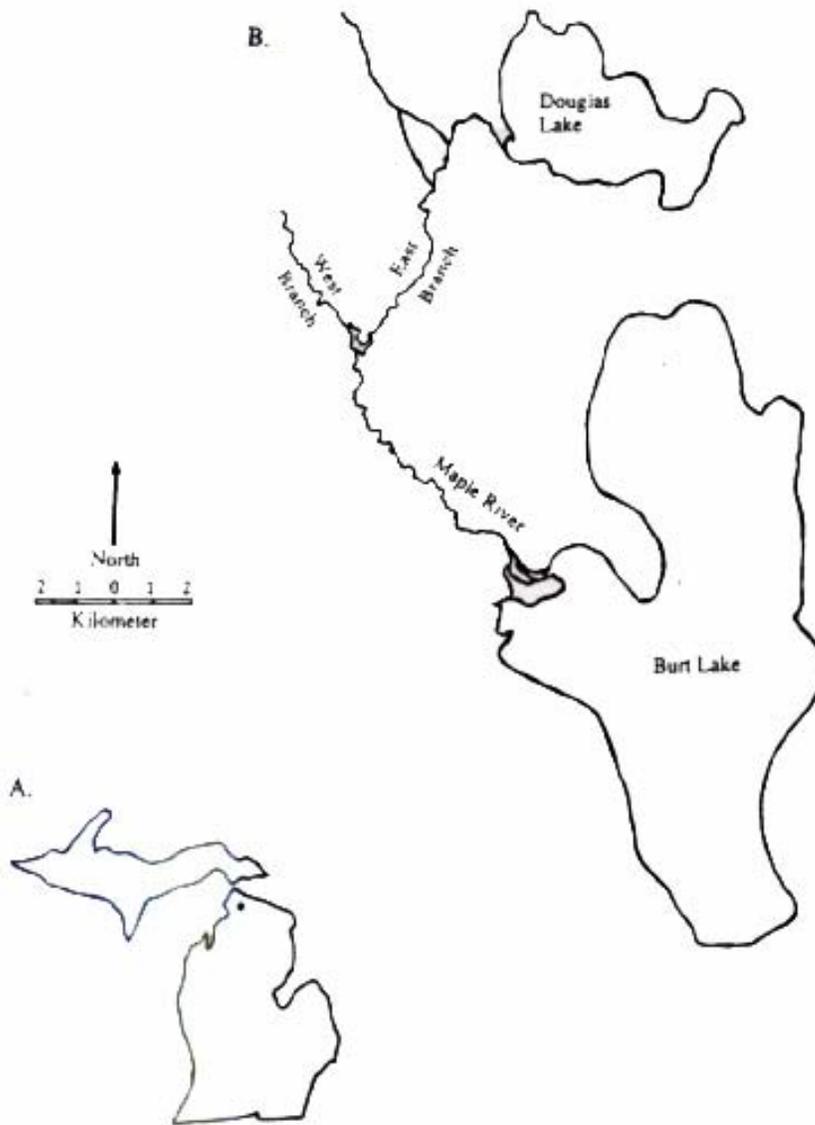


Fig 1 A. Map of Michigan showing the location of the Maple River.

B. Map of the Maple River, Emmet County, Michigan, showing the East Branch, the West Branch, and the Main Branch of the Maple River.

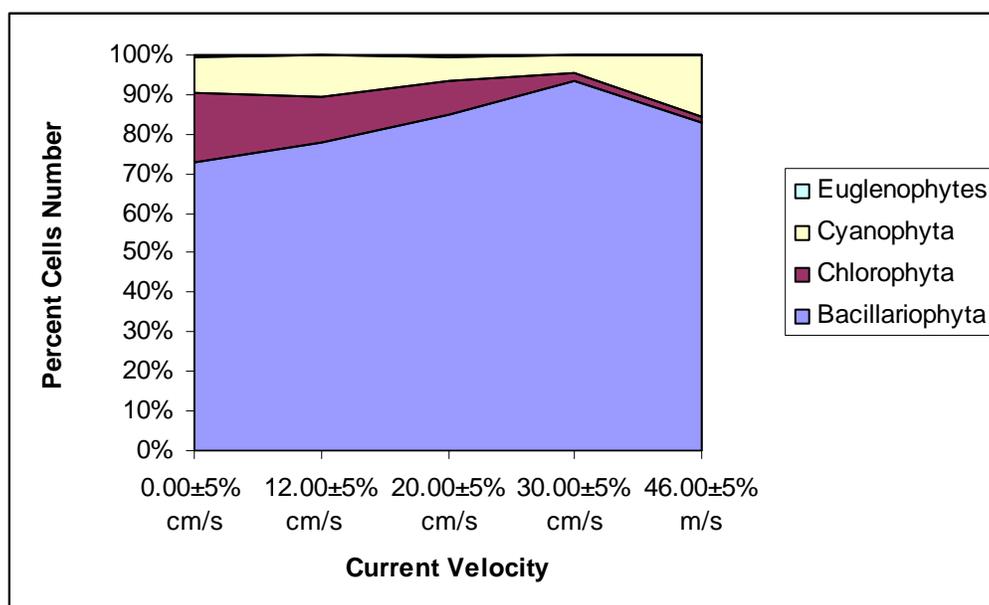


Figure 2. Relative abundance of cell numbers for each algal division from the streambed communities in response to the gradient of current velocities.

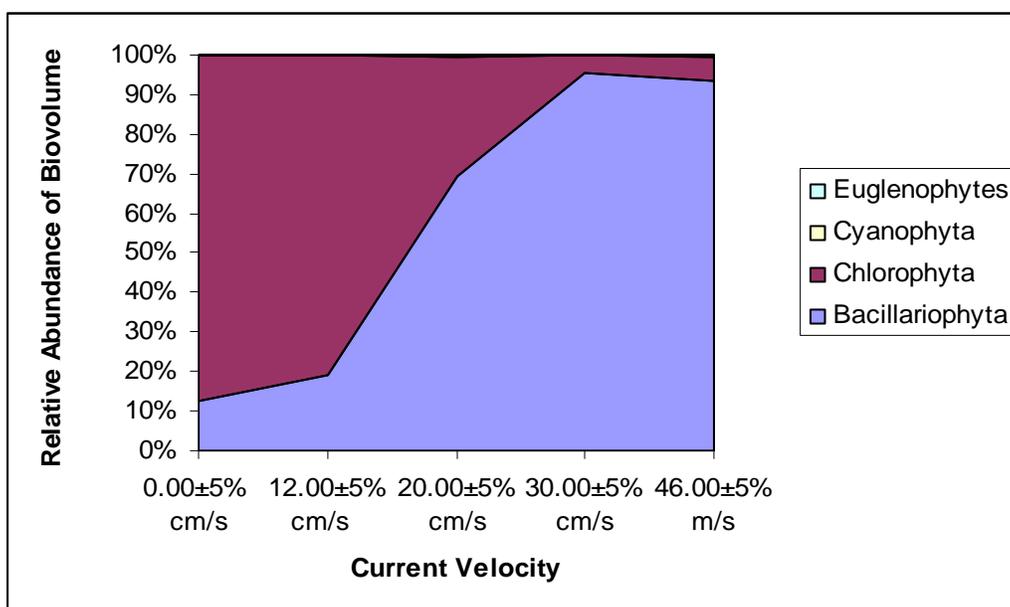


Figure 3. Relative abundance of algal biovolume for each algal division from the streambed communities in response to the gradient of current velocities.

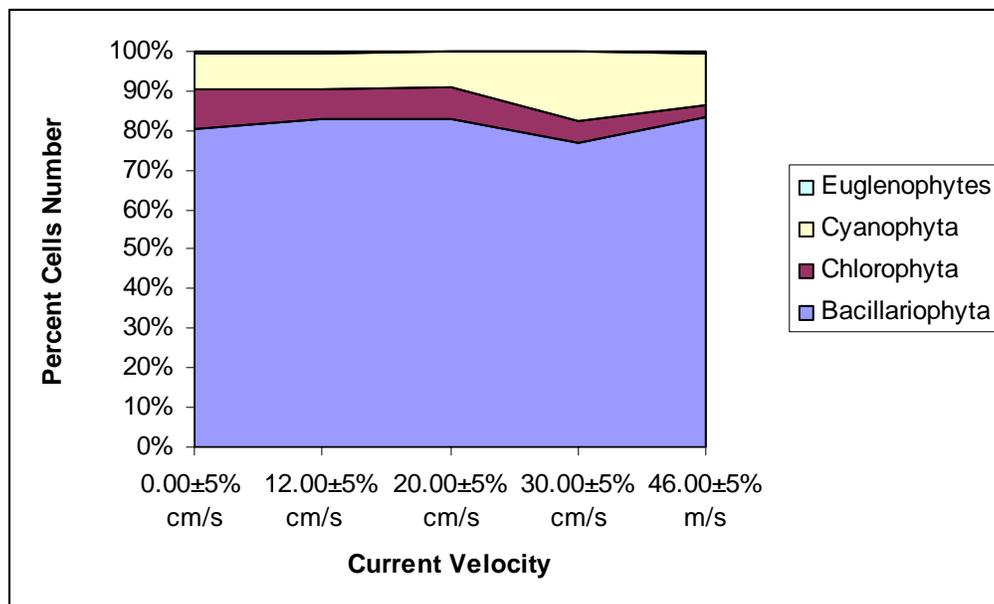


Figure 4. Relative abundance of cell numbers for each algal division from the artificial flume communities in response to the gradient of current velocities.

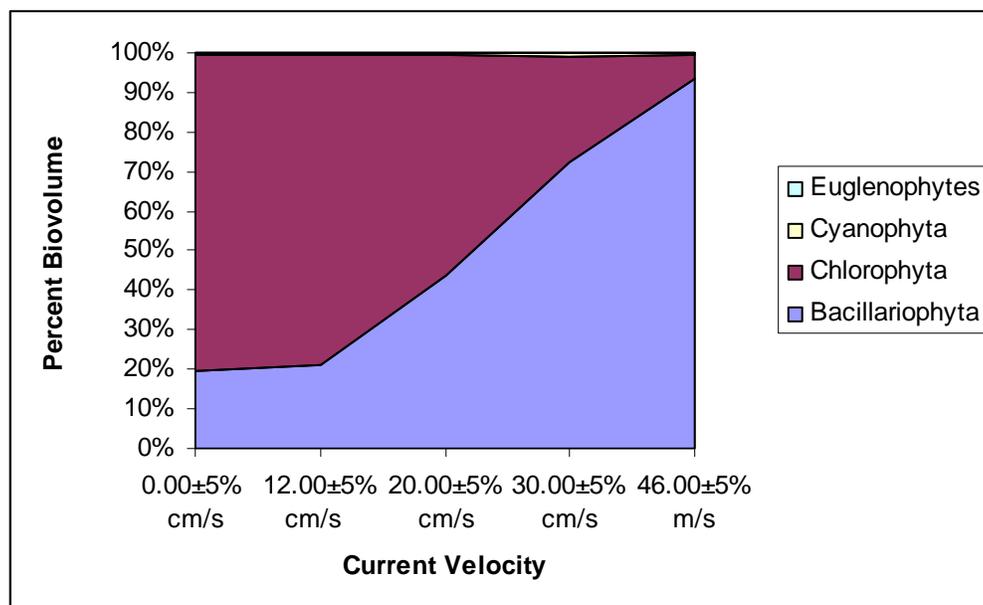


Figure 5. Relative abundance of algal biovolume for each algal division from the artificial flume communities in response to the gradient of current velocities.

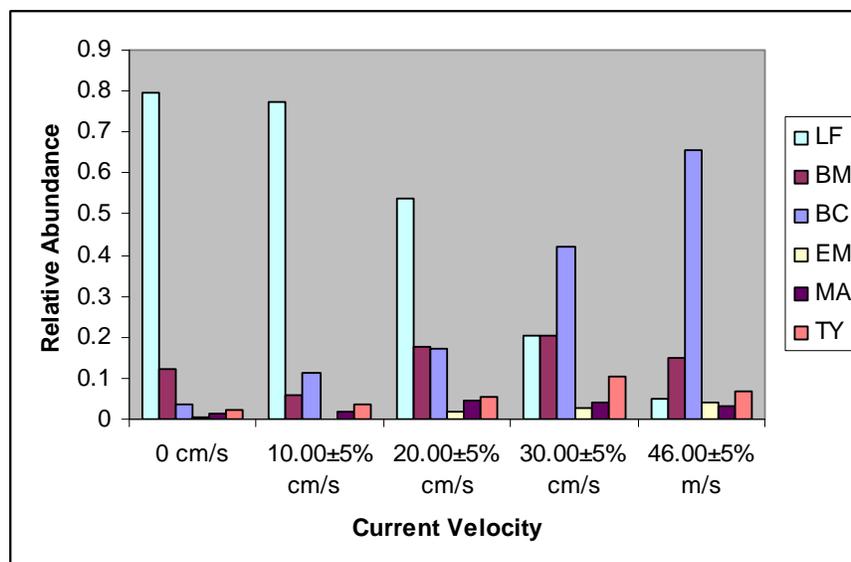


Figure 6: Relative abundance of algal biovolume for each physiognomic algal group from the artificial flume communities in response to the gradient of current velocities. BC represents benthic diatoms forming long or small chains, BM represents biraphid, loosely lying on substratum (motile), EM represents attached erectly to substratum (in mucilage), LF represents long filament, MA represents monoraphid, adnate, and TY represents tychoplankton.

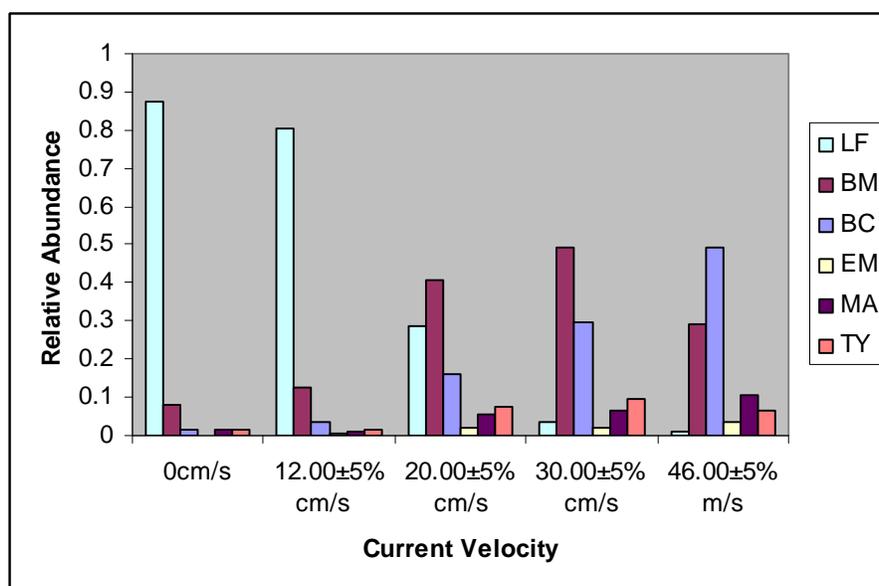


Figure 7: Relative abundance of algal biovolume for each physiognomic algal group from the streambed communities in response to the gradient of current velocities. BC represents benthic valves forming long or small chains, BM represents biraphid, loosely lying on substratum (motile), EM represents attached erectly to substratum (in mucilage), LF represents long filament, MA represents monoraphid, adnate, and TY represents tychoplankton.

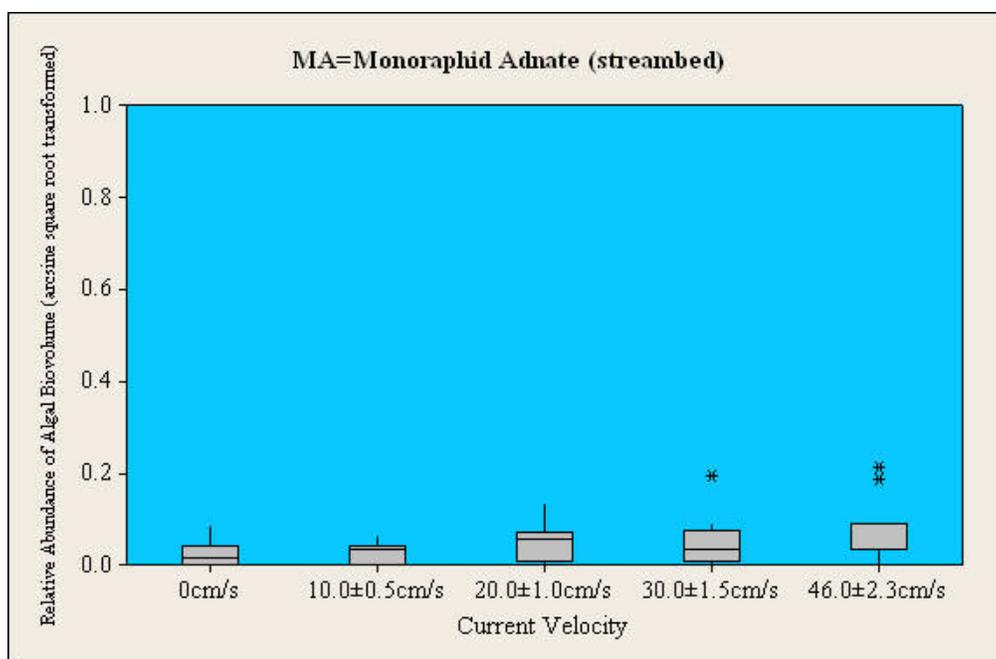


Figure 8a. Summary statistic for the physiognomic group MA and results of post-hoc Tukey's test of streambed algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

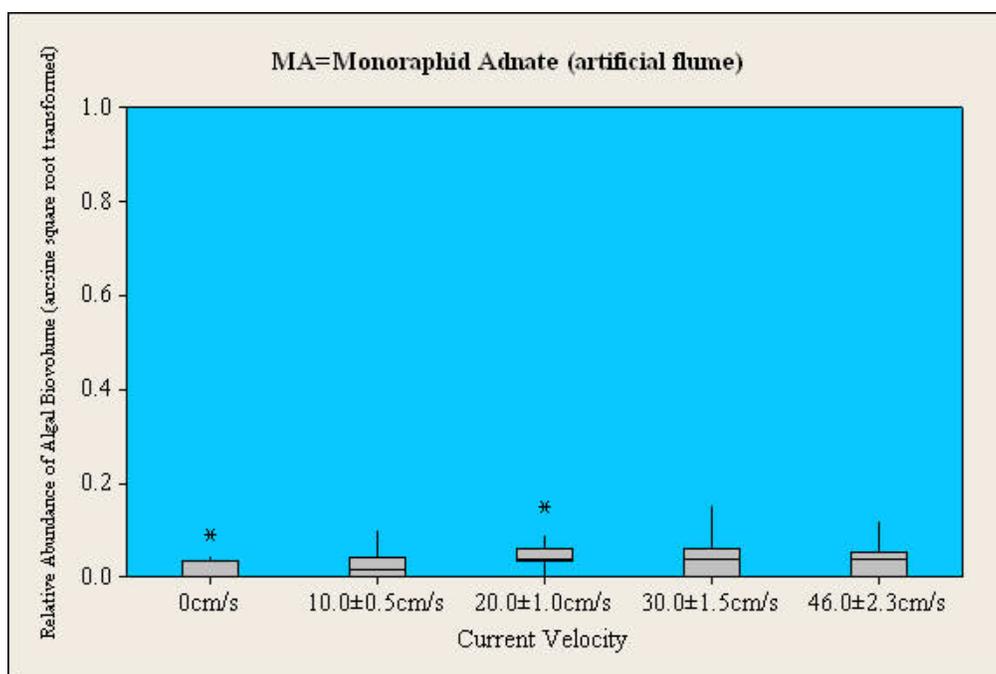


Figure 8b. Summary statistic for the physiognomic group MA and results of post-hoc Tukey's test of artificial flume algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

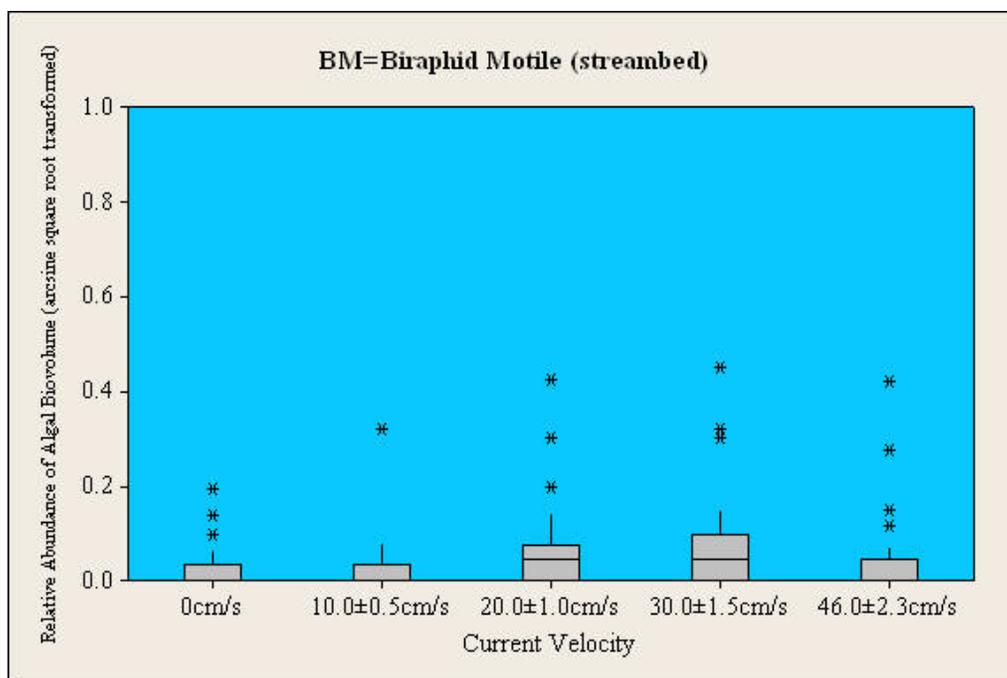


Figure 9a. Summary statistic for the physiognomic group BM and results of post-hoc Tukey's test of streambed algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

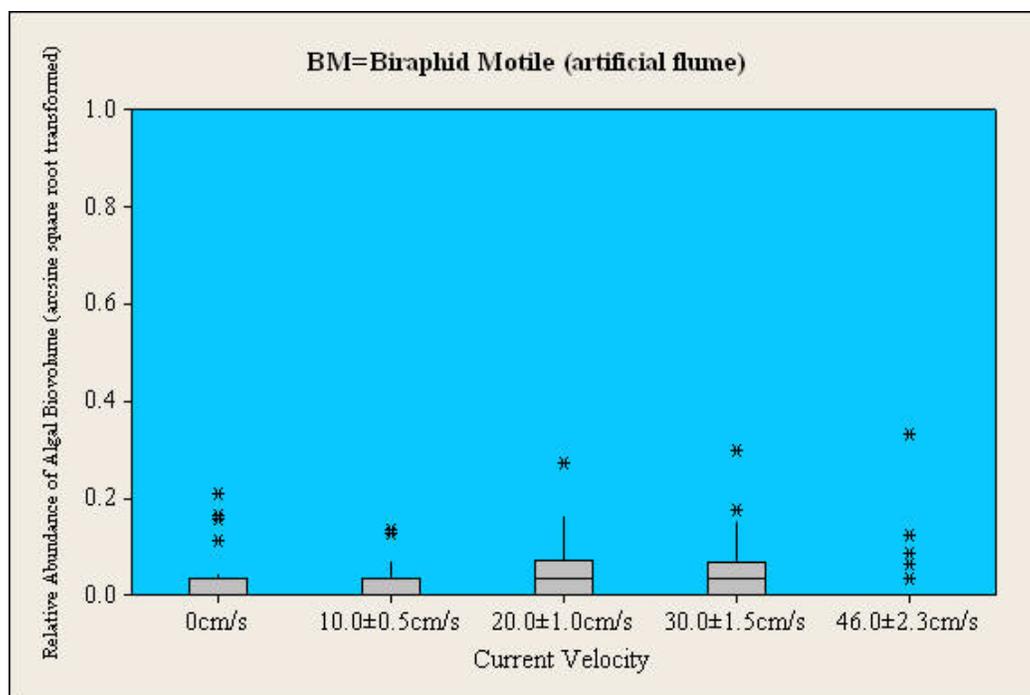


Figure 9b. Summary statistic for the physiognomic group BM and results of post-hoc Tukey's test of artificial flume algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

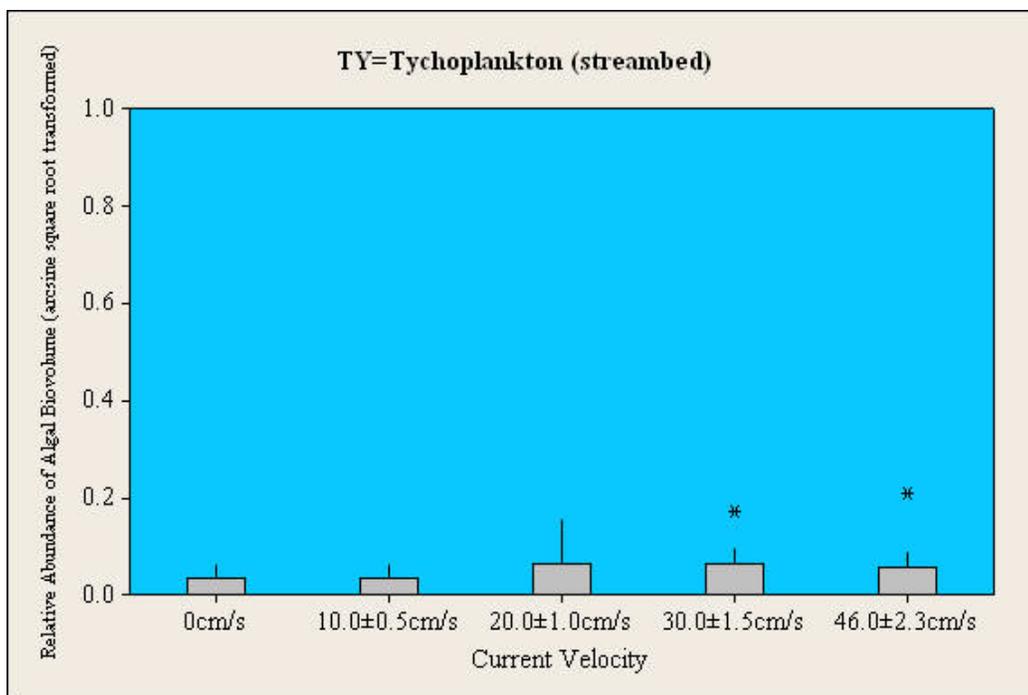


Figure 10a. Summary statistic for the physiognomic group TY and results of post-hoc Tukey's test of streambed algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

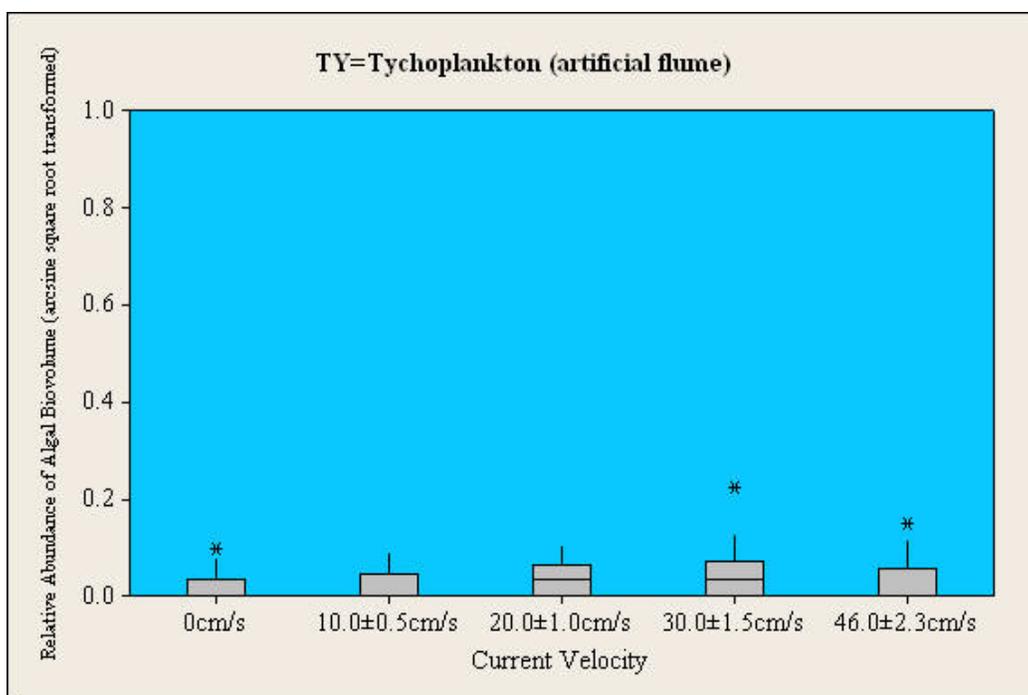


Figure 10b. Summary statistic for the physiognomic group TY and results of post-hoc Tukey's test of algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

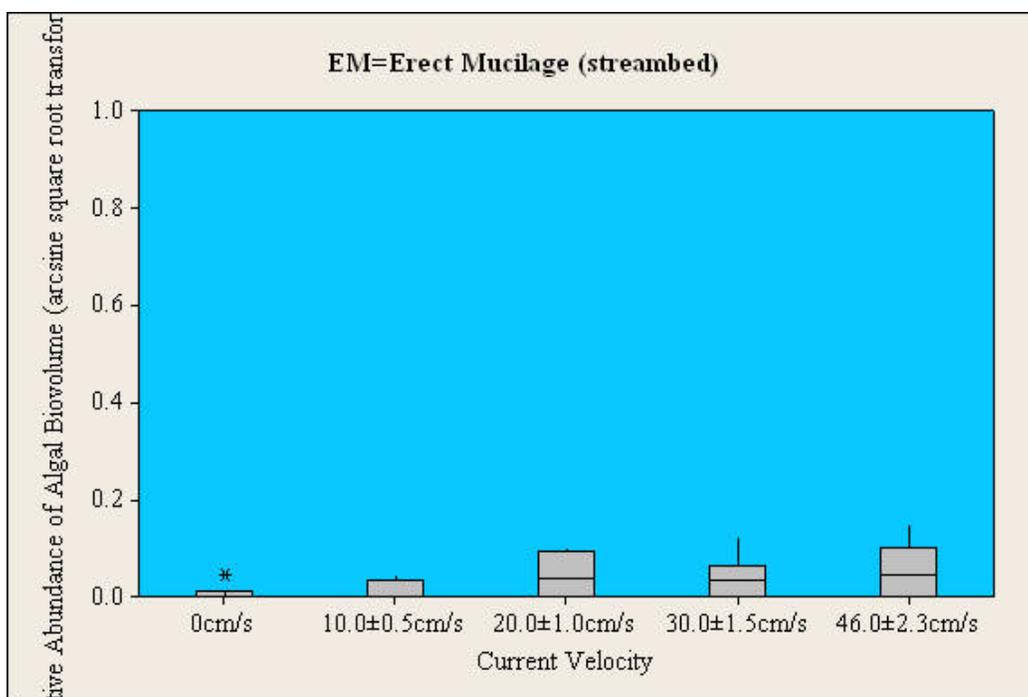


Figure 11a. Summary statistic for the physiognomic group EM and results of post-hoc Tukey's test of streambed algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

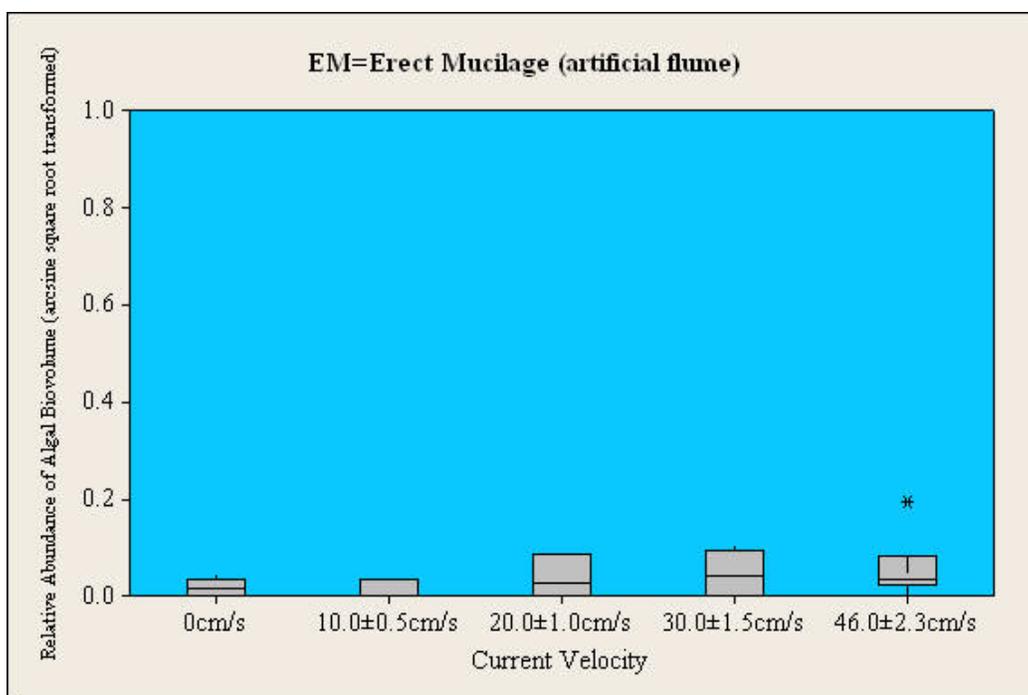


Figure 11b. Summary statistic for the physiognomic group EM and results of post-hoc Tukey's test of artificial flume algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

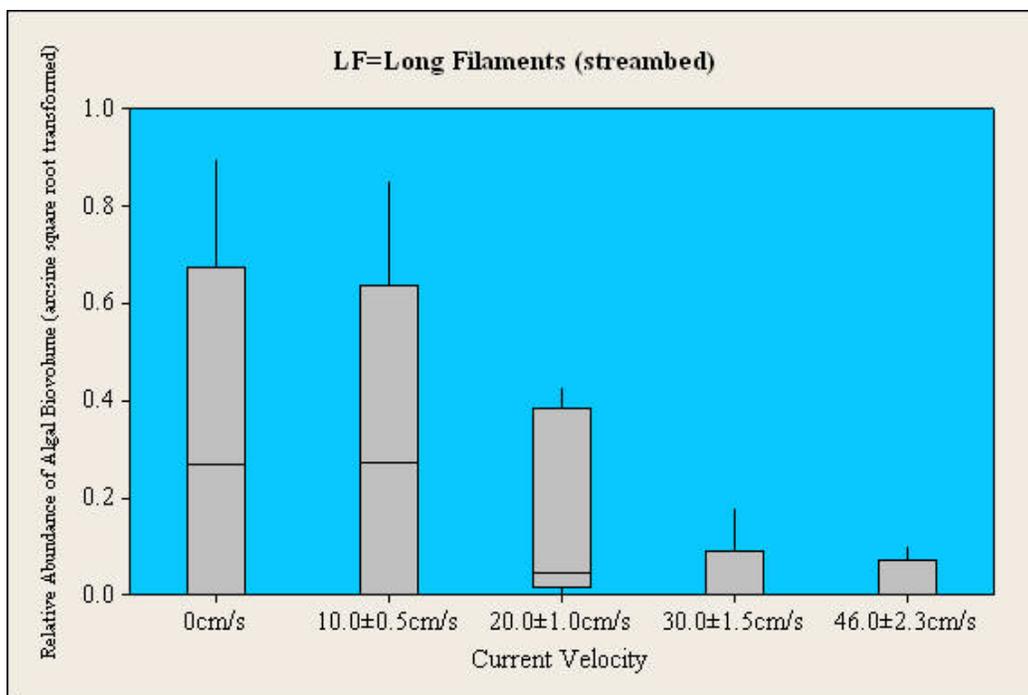


Figure 12a. Summary statistic for the physiognomic group LF and results of post-hoc Tukey's test of streambed algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

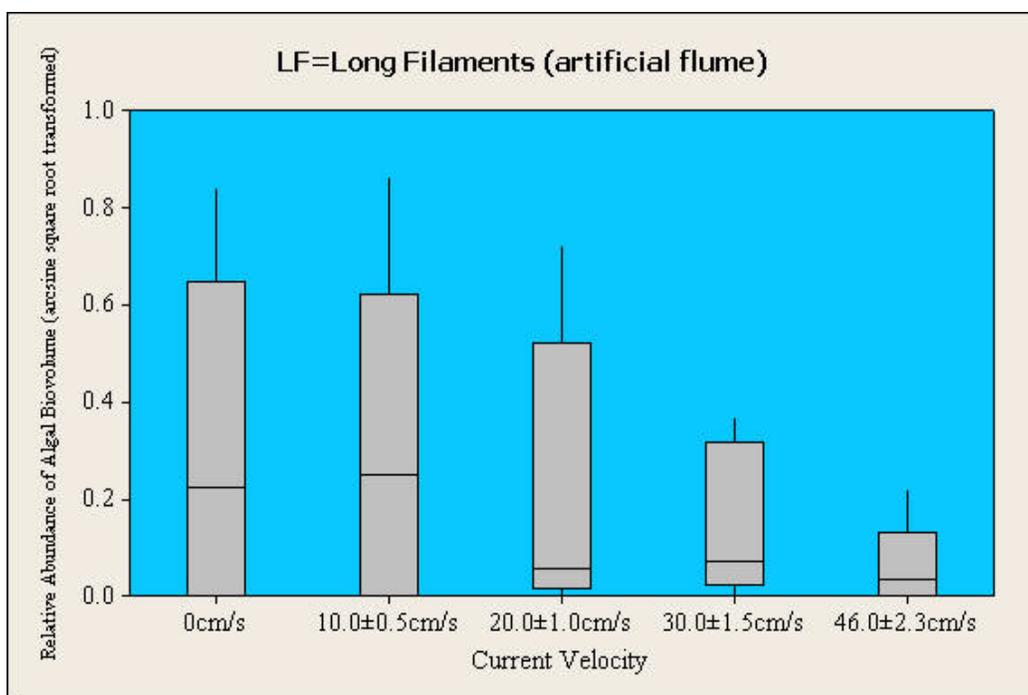


Figure 12b. Summary statistic for the physiognomic group LF and results of post-hoc Tukey's test of artificial flume algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

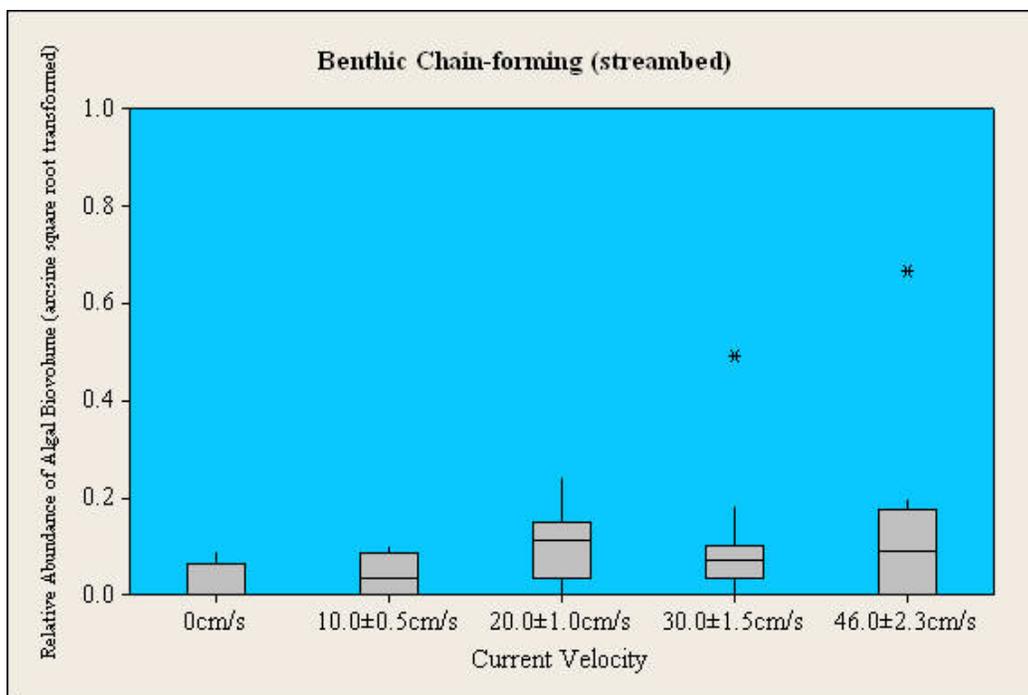


Figure 13a. Summary statistic for the physiognomic group BC and results of post-hoc Tukey's test of streambed algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)

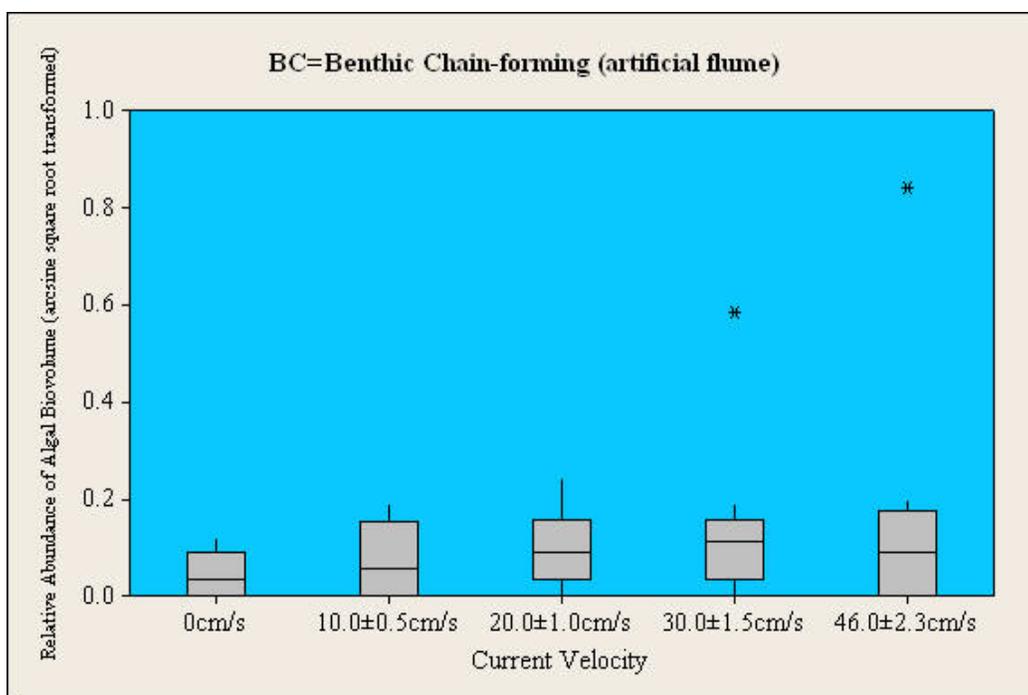


Figure 13b. Summary statistic for the physiognomic group BC and results of post-hoc Tukey's test of artificial flume algal responses over the gradient of current velocities in terms of relative abundance of algal biovolume (arcsine square root transformed). (Physiognomic group abbreviation was explained in Table 1)



Figure 14. *Mougeotia* dominantly floating above the fine sediments along the margin of the streambed.