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Characterization of the autotrophic component in periphyton upon *Typha angustifolia* detritus in a freshwater wetland

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CHARACTERIZATION OF THE AUTOTROPHIC COMPONENT IN PERIPHYTON UPON *TYPHA ANGUSTIFOLIA* DETRITUS IN A FRESHWATER WETLAND

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APPROVAL

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ABSTRACT

The autotrophic component of periphyton on *Typha angustifolia* detritus was characterized in a freshwater wetland during a single growing season. 58 genera of algae and cyanobacteria, representing six divisions, were observed throughout the study period. Although the combined algae-cyanobacteria density from within and outside the *Typha* stands were significantly affected by both sample date and the combination of date and location, no significant differences occurred in biovolume. Similarly, no clear evidence of successional patterns was observed.

Although few significant interactions were observed, *Typha* detritus provided a substratum for vast numbers and biomass of periphyton. A combined density for the observed taxa within the *Typha* stand averaged 134,588 cells cm^{-2}, while the density outside the stand averaged 108,853 cells cm^{-2}. The average total biovolume for the taxa within the *Typha* stand was $245 \times 10^6 \pm 23 \times 10^6$ and $136 \times 10^3 \pm 314 \times 10^6$ μm^3 cm^{-2} outside.

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INTRODUCTION

Many studies have examined the biomass and productivity of heterotrophs (bacteria and fungi) associated with wetland plant detritus (Haines *et al.* 1987, Neely 1994, Mann and Wetzel 1996, Neely and Wetzel 1997, Dilly and Irmler 1998, Komínková *et. al.* 2000, Newel 2001), but few have focused upon the detrital autotrophs (attached algae and cyanobacteria). Autotrophic constituents of periphyton are important contributors to the primary productivity within freshwater systems (Allen 1971, Cattaneo and Kalff 1980, Kairesalo 1983, Wetzel 1983, Burkholder and Wetzel 1989a, Burkholder and Wetzel 1989b, Scalles and Shure 1989, McCormick *et al.* 1998). In some cases, this contribution may reach 90% of the annual total primary production (Wetzel 1983). In addition to potential high productivity, detrital autotrophs may affect nutrient cycling and trophic level support by increasing organic matter decay (Neely 1994), and by enhancing water quality through uptake and accumulation of contaminants, such as phosphorus (Cronk and Mitch 1994) and heavy metals (Lakatos *et al.* 1998).

Microbial communities supported by wetland plants affect nutrient transformation and flux, total organic carbon pools, and energetic pathways within wetland systems (Wetzel 1993). The microbial community associated with decaying wetland plants is certainly dominated by bacteria and fungi, but algae may also be important (Neely 1994). Väätänen and Sundquist (1977), and Polunin (1994) suggested that algae may interfere with decomposers through the competition of nutrients and space necessary for cellulolytic activities. Findlay *et al.* (1993), however, found no relationship between periphytic algae and bacteria. In contrast, Wetzel (1990) suggested a strong possibility for organic compound coupling between algae and bacteria. In fact, Neely and Wetzel

(1995) indicated that, within periphyton layers, productivity of bacteria was coupled directly to photosynthetic and metabolic activities of algae and cyanobacteria. Additionally, other studies in pelagic zones have suggested that the presence of algae may accelerate or stimulate growth of heterotrophic bacteria (Cole 1982, Fingerhut and Soeder 1984). In littoral zones, detrital algae may enhance plant senescence (Rogers and Breen 1983, Burkholder and Wetzel 1989b, Wetzel 1996). Furthermore, Kühl *et al.* (1996) determined that a coupling of photosynthesis and respiration occurred between cyanobacteria and bacteria in biofilms. Neely (1994) provided evidence that epiphytic algal presence increased plant decay. And, Neely and Wetzel (1997) suggested that heterotrophic activity, facilitated by DOC release during algal senescence, increased decomposition of *Typha latifolia* L.

Most studies of epiphyton have focused exclusively on living plant tissues (Burkholder and Wetzel 1989a, 1989b, Findlay *et al.* 1990, Grimshaw *et al.* 1997, Hopson *et al.* 1998, McCormick *et al.* 1998). Furthermore, other studies have compared periphytic communities on living plants with periphyton on artificial plants (Allen 1971, Stock and Ward 1989, Burkholder and Wetzel 1989a, Kaur and Mehra 1998, Pickney and Micheli 1998). There are, however, many other types of substrata within wetlands upon which periphyton may attach. Dead plant tissues, for example, function as effective substrata, in the form of submerged and floating litter, on which periphyton may develop (Wetzel 1993). The significance of detrital autotrophs seems overlooked in many studies of wetland plant decomposition. Although some researchers have examined the periphyton on dead emergent plant tissues (Meulemans and Roos 1985, Müller 1994, Neely and Wetzel 1997), no studies have described the community structure of periphytic

autotrophs attached to plant litter. Thus, the objective of this study was to characterize the autotrophic component in epiphyton on toppled *Typha angustifolia* litter in a freshwater wetland during a single growing season. Community structure attributes were defined as taxonomic composition, community architecture, species diversity, species dominance, species density and species biovolume.

Light is an important determinant of autotroph community structure in epiphyton (Müller 1994), and because light intensity is conversely proportional to the thickness of the periphytic layer, the algal community may be affected (Meulemans and Roos 1985). Murkin *et al.* (1992) determined that light was limiting to epiphytic algal production, despite high nutrient availability, in Delta Marsh. Furthermore, Harrison and Hildrew (1998) suggested that light was a limiting factor to periphytic algal abundance. Wellnitz and Ward (1998) determined that light, in combination with algal grazers, affected periphytic algal species composition and standing crop. Given the effect of light on periphyton communities, a second objective of this study was to compare detrital autotrophic communities between periphyton-colonized litter in a well-lighted zone outside a *Typha angustifolia* stand and the periphyton developing in dense, shaded areas within the *Typha* stand.

LITERATURE REVIEW

Introduction

Periphyton is defined as an association of aquatic organisms that grow upon submerged substrates (Weitzel 1979, Wetzel 1983). Submerged substrates include rock (epilithic), sediment (epilipelic), animals (epizoic), sand (episammic), wood (epidendric) and plants (epiphytic). These organisms include both autotrophs and heterotrophs. The autotrophs include the cyanobacteria (blue-green algae) and many eukaryotic algae such as the chlorophytes (Green algae) and bacillariophytes (Diatoms). The heterotrophic components include fungi, protozoa, small invertebrates and some types of bacteria. Epiphyton typically consists of two components: an adnate component with the main cell axis in direct contact with the macrophyte and the loosely attached component that develops away from the macrophyte. These organisms not only contribute to the overall quality of the aquatic system, but may act as a precursor, in addition to bacteria, to the successional sequence of other epiphytes and organisms.

Algae are fundamental to many processes that occur within the aquatic ecosystem, particularly with regard to the nutrient cycles and trophic level support. Periphyton also enhance water quality and function as pollution indicators. Lakato *el al.* (1998) determined that the efficiency of contaminant elimination, filtration and accumulation within a reed belt was increased by periphyton, which improved the surrounding water quality. And, Cronk and Mitsch (1994) found that periphyton contributed to nutrient uptake and waterborne solid removal in constructed freshwater wetlands.

The autotrophic component of periphyton contributes significantly to overall production within freshwater systems. Allen (1971) determined that epiphytic algae

contributed 21.4% of the total annual production in a temperate lake and 31.3% of the total littoral production in the same lake. Cattaneo and Kalff (1980) and Kairesalo (1983) found that epiphytes attached to macrophytes can play an important role in total primary production, by fixing carbon in greater amounts than surrounding macrophytes, even though periphyton biomass was significantly lower than that of the macrophytes. In many lakes, periphyton contribute as much as 90% of the annual total primary production (Wetzel 1983). Burkholder and Wetzel (1989a) estimated that epiphytic algae were significant contributors to the primary production in a hard water lake. Furthermore, Schalles and Shure (1989) determined that algae in the littoral zone of a shallow wetland in the Carolina Bays contributed as much as one-third of the net primary production within that wetland. In addition, McCormick *et al.* (1998) also found that the majority of the productivity in the sloughs of the Everglades was accounted for by periphyton.

In wetlands, epiphytic algae on emergent plant litter have the potential to affect nutrient and energy pathways by increasing decay of detritus and utilization of dissolved organic matter by microbes (Neely 1994). This is an important consideration because the production and decomposition of plant material are dominant processes of wetlands, and many wetland ecosystem attributes are regulated by the metabolism of microbes supported by emergent plants (Wetzel 1993). Such attributes include nutrient accumulation and storage, organic carbon availability and energetic pathways. Periphyton also regulate nutrient dynamics (Wetzel 1990, 1993) by the release and immobilization of nutrients during decomposition, thereby affecting the chemistry of the surrounding waters (Neely and Baker 1989).

Development of Periphyton on Submersed, Living Leaves

Although the roles of autotrophs in periphyton are many, examination of community structure, colonization, and changes through time are critical to understanding the contribution of algae and cyanobacteria to wetland functions. Hoagland *et al.* (1982) described the dynamics of diatom communities upon suspended artificial substrates as being similar to higher plant succession. However, because Korte and Blinn (1982) reported development of an organic biofilm within 2 hours upon artificial surfaces in a stream, periphyton communities potentially develop substantially faster than do communities of higher plants. The well-developed organic biofilm may modify the surface charge and serve as a prerequisite of bacterial attachment. Bacteria were attached to the coated substrata by use of mucilaginous strands and, although the bacteria did not seem to be a prerequisite for specific algal assembles, opportunistic diatoms began to attach after the bacteria. These diatoms included taxa that have mucilaginous coats or produce short stalks, *e.g.* species of *Gomphonema* and *Navicula*. As parts of these genera began to develop, other diatoms colonized, such as *Fragilaria* and *Nitzschia.* These predominately adnate diatoms were then followed by long-stalked diatoms (other species of *Gomphonema*), large rosettes of diatoms including species of *Nitzschia* and *Synedra* and finally the filamentous green alga *Stigeoclonium*. In addition, Muelemans and Roos (1985) described a particular architecture of three distinct layers growing upon dead stems of *Phragmites australis* (Cav.) Trin. ex Steudel. The organisms that occurred during original colonization represented the basal and intermediate layers, and a later-developing layer was called the uppermost layer. The basal layer can be directly influenced by the shading of the uppermost layer, which may cause the basal layer to

deteriorate and separate from the substratum. In addition, microtopographic features of the substrata may influence the activity of the basal layer (Stock and Ward 1989).

Periphyton also occurs on submersed and emergent living plant structures (epiphyton). Periphyton (epiphyton) development on submersed living leaves has been closely examined. In fact, most studies of periphyton consider exclusively living plant structures (Burkholder and Wetzel 1989a, Burkholder and Wetzel 1989b, Grimshaw *et al*. 1997, Findlay *et al.* 1990, McCormick *et al.* 1998, Hopson *et al.* 1998). In one study, Burkholder and Wetzel (1990) examined the epiphytic colonization of the submersed macrophyte *Scirpus subterminalis* in a Michigan lake. The study considered specifically an epiphytic community of 102 taxa located on the oldest leaves. Almost 43% of the community was comprised of diatoms and 26% were Cyanobacteria. Common diatom taxa were *Cyclotella, Cymbella, Navicula, Achnanthes minutissima,* and *Synedra*. Common Cyanobacteria taxa included *Aphanocapsa, Aphanothece, Gleocapsa, Pelogloea,* and *Synechococcus*. Diatoms were present in a greater proportion of the total cell count during November-April, while the Cyanobacteria represented the majority during July. The study also demonstrated that different diatom cell types were present at different times during the growing season. From May to mid-June, pennate diatom species represented 48% of the total diatom biovolume and from mid-June through the rest of the growing season, pinnate taxa represented approximately 91% of the diatom biovolume. *Cyclotella,* a centric diatom, contributed 7% on average of the total diatom cells and 28% of the total diatom biovolume during May-October. Furthermore, *Cyclotella* represented 25% of the total algal biovolume in June and 32% in April. On

average, only 12% of the biovolume consisted of vyanophytes. Other taxa were observed, but only contributed 4% of the total algal biovolume during May-October.

Romo and Galanti (1998) examined the distribution and composition of epiphyton on *Trapa natans* over a four-month period (June-September) in a shallow eutrophic lake. The total algal biomass was positively correlated with the seasonal growth of *T. natans*. Algal succession was initiated by colonization of adnate forms, followed by basally-attached forms, and subsequently leading to the loosely-attached forms (*i.e.* stalk-formers) and finally colonized with filamentous forms. The lamina and petiole of *T. natans* had a higher mean algal biomass and abundance than the stem and roots. Algal density, biomass and epiphytic abundance declined vertically from the petiole to the lowest root segment. Abundance of cyanobacteria was greatest on the lamina, whereas green algae were most abundant on the petiole and diatoms dominated the stem and root sections. Algal assemblages on the lamina and petiole were distinctly different than on the stems and roots. Early in the growing season (June), the upper portions of *T. natans* were colonized by *Gleocystis* cf. *gigas, Cocconeis placentula, Achnanthes minitissima*, *Scenedesmus lunatus*, and *Tetraedron minimum*. The latter two taxa were present at lower densities than the former taxa. *Gleocystis* cf. *gigas* contributed 40-72% of the total abundance in June. By the beginning of July, the lamina and petiole were dominated by *Achnanthes minutissima, Gomphonema parvulum,* and *Spondylosium planum*. In mid-late July, *Achnanthes minutissima* and *Podohedra falcata* dominated the petiole; whole *G. parvulum*, *Nostoc spongiaeforme* and *Anabaena anomala* were subdominant. The Cyanobacteria were not as dominant on the petiole as were *G. parvulum, Euastrum*

denticulatum and *P. falcata.* The stem was dominated by *A. minutissima*, whereas the upper roots were dominated by *Cymbella cesatii* and a species of *Heteroleiblenia* sp.

During the first half of August, *Nostoc spongiaeforme* and *Anabaena anomala* dominated the petiole (34%). The upper stem and root were dominated by *Achnanthes minutissima, C. cesatii,* and *Cyclotella ocellata.* The lower roots were dominated by different taxa consisting of *Heteroleiblenia* sp. and *Oocystis* sp. In late August, the Cyanobacteria upon the lamina declined, communities upon the petiole remained unchanged and the stem and root assemblages were similar, consisting of *Heteroleiblenia* sp., *Oocystis* sp., *Scenedesmus ecornis, Tetraedron minimum, Cyclotella ocellata* and *Cymbella cesatii.*

By the end of the growing season and at the onset of *Trapa* senescence, new alga taxa appeared on the lamina and petiole. Some examples included *Merismopedia punctata, Cosmarium* sp., *Desmidium swartzii, Synedra acus,* and *S. ulna.*

In another study, Hopsen *et al.* (1998) examined the abundance and community composition of epiphyton on various plant taxa, including species of *Najas* and *Hydrilla*, occurring in Lake Okeechobee, Florida, a shallow, sub-tropical lake. This study was conducted during a 13-month period, beginning in December 1990. Diatoms were found to represent the greatest percentage of every sample site examined. Furthermore, diatoms were the dominant taxa found upon each host plant type.

Living vs. Artificial Leaf Surfaces

Artificial surfaces have long been a popular means for study of periphyton (Cattaneo and Amireault 1992). And, in fact, many studies make direct comparisons of periphyton colonization upon artificial and natural substrates (Allen 1971, Stock and

Ward 1989, Burkholder and Wetzel 1989a, Kaur and Mehra 1998, Pickney and Micheli 1998). Some periphyton studies used artificial substrates exclusively (Hoagland *et al.* 1982, Korte and Blinn 1983, Bothwell *et al.* 1993, Francoeur and Lowe 1998, Wellinitz and Ward 1998).

Over a 14-week study period (June-September), Burkholder and Wetzel (1989) compared periphyton colonization on natural and artificial *Potamogeton illinoensis* in a phosphorus-limited hard water lake. Early in the growing season, algal cell number was approximately 15-fold greater on the artificial plants. In addition, algal biovolume on the artificial *Potamogeton* was approximately 17-fold greater than on the live plants. As the growing season continued (8 weeks), biovolume and cell counts were only two-fold greater on the artificial plants. By the end of the growing season, (14 weeks), comparable biovolumes and cell counts occurred on the two substrata.

Throughout the growing season, the loosely attached periphyton composition differed between the two substrates. Diatom contribution to total algal biovolume on the artificial leaves was greatest early in the growing season. The most abundant diatoms were species of *Gomphonema*, contributing 30% of the total algal biovolume in July (8 weeks). By the end of the growing season, *Gomphonema* spp. had declined to 15% of the total biovolume while *Cymbella* spp.and *Cyclotella* spp. increased to 21% and 15%, respectively. During week 8 (July) of the study, maximum cyanobacteria biovolume occurred and both the cyanobacteria and chlorophyta contributed equally to total algal biomass. Cyanobacteria biovolume increased to 30% of total algal biovolume by week 14 (September) as green algae decreased to insignificant numbers. Early in the growing season, *Stichogloea deoderleinii* accounted for 25% of the loosely attached algal

biovolume upon the natural *Potamogeton.* Later in the growing season, (late July), diatoms represented 85% of the total biovolume. During that time, the dominant diatom genus was *Cymbella,* which comprised about 24% of the total biovolume. By the latter part of the growing season, (mid-September), loosely attached cyanobacteria increased to 50% of the total algal biomass.

The Burkholder and Wetzel (1989) study also examined the adnate portion of the epiphytic community on *P. illinoensis*. On both artificial and natural substrates, bacteria were the initial colonizers. On young natural leaves, bacterial cell numbers were 1000-fold greater than artificial leaves. Although adnate algae were rarely found on young and artificially simulated young leaves, some colonization did occur. However, adnate cell numbers were insignificant on both types of substrata when compared to the loosely attached component of the periphyton. The adnate diatom taxa were *Achnanthes minutissima, Cocconeis placentula, Cymbella minuta, Eunotia arcus, Gomphonema* spp., *Navicula microcephala,* and *Synedra* spp. The adnate Cyanobacteria component consisted primarily of *Anabaena* spp., which contributed to a higher percentage of the population on the artificial leaves.

Kaur and Mehra (1998) compared periphyton colonization on natural and artificial *Eichhornia crassipes.* The study was conducted in laboratory conditions over a 3-week period. Both artificial and natural substrates displayed similar colonization and successional patterns. Species, found on both substrate types, included *Cyclotella meneghiniana, Cymatopluera solea, Fragilaria capucina, Navicula palea, Synedra ulna, Oscillatoria formosa, Euglena deses,* and *Closterium acerosum.* Diatoms comprised the major portion of the algal assemblages on both substrates. Species composition and

density differences did, however, occur. Species found only on natural substrates included *Eudorina elegans* and *Dinobryon sertularia*. *Neidium productum, Navicula rhyncocephala* and *Cyclotella meneghiniana* were observed on living plants before the artificial plants.

Development of Periphyton on Dead, Emergent Plant Tissues

In freshwater wetlands, high productivity of vegetation, coupled with low herbivory, results in large amounts of detrital biomass. Similar to submersed living plant tissues, dead emergent plant tissues provide substrata for development of periphyton. The standing-dead biomass, as well as detrital litter, provides potentially a large surface area for periphyton development (Wetzel 1993). Relative to periphyton upon submerged plants, algae upon dead emergent plant tissues and detrital litter has been poorly studied.

Meulemans and Roos (1985), however, described the periphytic community structure upon dead *Phragmites australis* stems in an oligo-mesotrophic lake. Clear seasonal differences occurred with maximum diatom cell numbers in winter and minimum diatoms in summer. During the summer months, green and red algae contributed to more than 50% of total chlorophyll. The diatom community occurred as three main layers. The lowest layer, or basal layer, consisted of species of *Achnanthes, Amphora, Cocconeis, Eunotia,* and *Synedra.* The intermediate layer was comprised of species of *Cymbella, Gomphonema,* and *Rhoicospaenia.* The top-most layer included species of *Diatoma, Fragilaria, Melosira* and *Tabellaria*. Although *Gomphonema* increased in autumn, the cell numbers in the intermediate layer was relatively constant. In January, *Achnanthes* and *Fragilaria* density increased in the basal and upper-most

layers, respectively. From January through May, a six-fold increase in diatom density was mainly comprised of those species located in the uppermost layer. Furthermore, increases in cell volume were proportionally greater than cell density. Cell volume increased by 30-fold during late winter and early spring, relative to summer and fall. Red algae, including *Batrachospermum* and *Auduoinella*, were present in small numbers on *Phragmites* throughout the year. However, from June to September, *Batrachospermum* reached numbers that produced macroscopic cultures. The green algae *Oedogonium*, *Bulbochaete* and *Mougeotia* were present from June to the end of the year.

A more recent study investigated the development of periphyton on *Phragmites australis* in a eutrophic lake over a three-year period (Müller 1994). Epiphytic biomass, determined by chlorophyll concentrations, averaged approximately 22.76 *u*g chlorophyll-a cm^{-2}, and reached a maximum in April. A second short-lived maximum, after a marked decrease in biomass, occurred in late spring. A chlorophyll-a minimum occurred in July or August, averaging approximately 1.29 *u*g cm^{-2}. Diatoms were the most abundant algal group, contributing to approximately 80% of the total biomass in autumn and winter, and over 95% during the spring maximum. Green algae dominated in early April and exhibited a second maximum in June and July. The Cyanobacteria were most abundant during June and July, but accounted for no more than 22% of the total biomass.

Diatom biovolume during the spring peak was 3.310 mm^3 cm^{-2} in 1989, 1.480 mm^3 cm^{-2} in 1990 and 1.780 mm^3 cm^{-2} in 1991. Diatom biovolume, however, declined rapidly after the spring maximum to less than 0.250 mm^3 cm^{-2} and never recovered. The most abundant diatom taxa during the spring maximum consisted of those that were

loosely attached in intermediate and upper-most layers. Taxa within these two layers included *Cymbella lanceolata, C. cymbiformis, C. prostrata, Fragilaria capucina* var. *vaucheriae, F. ulna* var. *acus, Gomphonema acuminatum* and *G. olicium.* Adnate or basal species increased during later summer and dominated during the autumn and winter months. This layer was mainly composed of diatom taxa such as *Epithemia adnata, E. sorex, E. turgida, Achnanthes minutissima, Navicula tripunctata, Navicula* spp., and *Rhoicosphenia abbreviata.* During late summer, *Gomphonema acuminatum* and *G. gracile* were the dominant diatom species, while *Cocconeis plancentula, Epithemia* spp., and *Rhopalodia gibba* dominated the autumn and winter months.

The green algae were the highest in May and June. For those months, the average biovolume was 0.298 mm^3 cm^{-2} in 1989, 0.151 mm^3 cm^{-2} in 1990, and 0.492 mm^3 cm^{-2} in 1991. *Oedogonium* cf. *irregulare* var. *condensatum,* was the most abundant, but *Mougeotia* sp., and *Spirogyra* sp. were the dominant taxa, when considering biovolume. Cyanobacteria were present throughout the year, but only in small numbers. Maximum abundance occurred during May and July with biovolumes of 0.036 mm^3 cm^{-2} in 1989, 0.038 mm^3 cm^{-2} in 1990, and 0.039 mm^3 cm^{-2} in 1991. The predominant species included *Lyngbya* spp., *Phromidium* spp., and *Plectonema* spp.

Combined, the aforementioned studies of periphyton suggest a consistent scheme of colonization and architectural development upon both natural and artificial substrata. Although detritus potentially provides a significant substratum for periphyton development, the natural substrates examined in the studies have been confined to living and senescing organisms (mostly plants). Thus, critical questions remain about algal colonization on toppled emergent plant litter and other types of detritus.

Role of Epiphytic Algae in the Degradation of Organic Matter

Many studies have focused on the effects of heterotrophic bacteria and fungi associated with decaying plants (Haines *et al.* 1987, Neely 1994, Mann and Wetzel 1996, Neely and Wetzel 1997, Dilly and Irmler 1998), but few studies have explored the role attached autotrophs might play in decomposition. Given known roles of periphyton and heterotroph-algal couplings in pelagic systems, this seems to be an important oversight. A complete understanding of periphyton function on decaying emergent plants seems critical to developing a more complete model of plant decay within wetlands.

Some researchers have suggested that algae interfere with decomposers by competing for space and nutrients; however, this avenue needs further investigation (Väätänen and Sundquist 1977, Polunin 1984). Studies of stream periphyton have suggested that interactions between periphytic bacteria and algae do not exist, or are negligible (Findlay *et al.* 1993). Wetzel (1996), on the other hand, suggested that more often, heterotrophs seem to benefit by the presence of autotrophic communities. These benefits may be provided by the couplings of organic compounds between the autotrophic and heterotrophic organisms within the periphytic community. For example, autotrophs provide dissolved organic carbon (DOC) and oxygen required by some heterotrophs for metabolic processes. In addition, Wetzel (1990) suggested that the probability of couplings of organic compounds between bacteria and algae are as likely as those between the macrophytes and attached epiphytes, organisms with well-documented interactions. Neely (1994) provided evidence suggesting that epiphytic algae are major contributors to the decay of *Typha latifolia* and observed that higher algal

densities increased the rate of plant decay. Kühl *et al.* (1996) reported a coupling of photosynthesis and respiration in biofilms between Cyanobacteria and heterotrophic bacteria. Furthermore, Neely and Wetzel (1997*)* suggested that *T. angustifolia* decomposition varies with solar radiation, and perhaps algal photosynthesis. Epiphytic algae may stimulate decay through releases of DOC, oxygen or other means, which may facilitate heterotrophic activity.

The many roles of periphyton in freshwater wetlands are becoming increasingly appreciated. These organisms contribute to nutrient availability, water quality, and may provide substances that are important to the overall quality of the freshwater system. Also, Wetzel (1984) suggested that the stability of the overall aquatic system depends on the energy stored within the detrital organic matter. Because decomposition of organic matter is important to the energy and nutrient flux in aquatic systems, understanding such interactions involving decomposers and algae should substantially advance our knowledge of fundamental wetland processes.

METHODS

Study Site Description

The study was conducted in Willow Pond, located at the University of Michigan Matthaei Botanical Gardens (Washtenaw County, Superior Township, Sec. 24, T2S, R6E, approximately 0.18 miles east of Dixboro Road, 17' 57.51" N, 39' 42.82" W). Willow Pond is a small lacustrine system with dense beds of *Chara* sp. in the deeper areas and dense clones of *Typha angustifolia* L. bordering the edge. The pond, which is approximately 55 meters wide and 185 meters long, is fed by Parker Brook from the north side and has a small outlet on the east end. The general depth of the pond within the sampling area is approximately 3 feet.

Sampling

Detritus sampling began in May 1998 and continued biweekly though November 1998. On every sampling date, four samples were randomly collected from each of two different locations within Willow Pond, for a total of eight samples per sampling date. The sample locations within Willow Pond consisted of an area inside the *T. angustifolia* stand and another area located exterior to the stand toward the center of the pond. Overall, a total of 112 samples were collected throughout the 14 sampling dates. Size, condition, and age of the leaf litter were not considered during collection. Each sample consisted of three 5 mm plugs, removed through use of a cork borer, from a single piece of toppled *T. angustifolia* leaf litter floating in Willow Pond. The three plugs were then placed into a single Falcon tube containing 5 ml of preservative and labeled. The preservative consisted of either 2.5% glutaraldehyde or diluted 6:3:1 solution. The 6:3:1

solution consisted of 6 parts H_2O, 3 parts ethanol and 1 part formalin; this solution was then diluted to 33% (Prescott 1979).

Additionally, light intensity (at water surface), water temperature, and dissolved oxygen content were measured at both sample locations (inside and outside of the *T. angustifolia* stand) on every sampling date. Light intensity was measured with a LyCor Radiometer light photometer and measured approximately 1 cm above the water surface at each of the sampling locations. Sampling time was not consistent throughout the study period. Dissolved oxygen content and water temperature were assessed at each sample location with an YSI model 57 combined temperature-oxygen meter.

On October 29, 1998 a 30-meter transect was established along the fringe of Willow Pond through the *T. angustifolia* stand in order to collect cattail data. Along the 30-meter transect, a 0.25 m^2 hoop was randomly dropped every 2 meters and the cattails inside the hoop were counted to estimate density of *T. angustifolia* at Willow Pond. Cattails from both the 1997 and 1998 growing seasons were counted. Additionally, twenty-five cattail stalks, including leaves, were randomly collected along the 30 meter transect to facilitate determining the approximate surface area available for periphyton community establishment. Surface area of the collected cattails was measured through use of a caliper and ruler.

Identification and Enumeration of Epiphytic Algae and Cyanobacteria

For every sample date, two of the four collected samples from each of the two locations were examined (two samples collected inside the cattail stand and two collected outside the cattail stand). Prior to microscopic analysis, each sample tube was shaken,

using a Vortex mixer, for approximately 10 seconds to assist in the detachment of the epiphyton from the three collected plugs. Each of the three litter plugs were then removed from the sample tube and both sides were scraped with a razor blade to detach any periphyton remaining on the plug. The scraped material was then rinsed off the razor blade and back into the sample tube using the preservative from the corresponding sample tube. To ensure homogeneity, the sample tube was shaken again with the Vortex mixer for 10 seconds. Immediately following the second mixing, an aliquot of the material was removed from the sample tube, placed on a Palmer depressed counting slide, and covered with a glass cover slip. This aliquot was examined and represented the sample from which it was removed.

Each sample was examined by use of a Leica DMRB light microscope at 200X total magnification. Cell counts were performed using a horizontal transect, in some cases multiple transects, along the Palmer slide, until 300 cells were counted. Length and width of algal cells were recorded, and each counted algal cell was identified to genus (Patrick and Reimer 1967, Prescott 1979, Krammer and Lange-Bertalot 1986). Cell counts included algal fragments observed within each transect. These fragments typically consisted of damaged cells and/or diatom frustules. The number of algal cells per transect was used to calculate algal density for each genus. Calculations for densities were conducted by using the following formulae:

- *Area of Palmer depression / area of transect(s) =* $\boldsymbol{A}$
- *Genus cell density* $*\boldsymbol{A}$ *= density of cells in Palmer slide*
- *Density of cells in Palmer slide / 0.1 ml* $*$*(5 ml) = density of genus in sample tube*
- *Density of cells in sample / surface area on litter* (cm^2) *= density* ($cells\ cm^{-2}$)

Subsequent to density calculations, biovolumes of each genus per sample were determined using the following representative formulae from cell dimensions (Wetzel and Likens 1991, Hillerbrand *et al.* 1999):

- 2 cones (*i.e. Navicula, Eunotia, Closterium*, etc.) $\pi LW^2/12$
- Box/square (*i.e. Synedra, Nitzschia,* etc.) LWT
- Ellipsoid cone (*i.e. Gomphonema*) $\pi W^2(L=W/2)/12$
- Cylinder (*i.e. Anabaena, Mougeotia,* etc.) $\pi R^2L/4$
- Ellipsoid (*i.e. Rhopalodia, Scenedesmus,* etc.) $\pi LW^2/6$
- Sphere (*i.e. Cosmarium, Chroococcus,* etc.) $\pi R^3/6$
- Prolate spheroid (*i.e. Pandorina, Dinobyron*, etc.) $\pi/6W^2L$
- Elliptic prism (*Achnanthes*) $\pi/4LWT$
- ½ Elliptic prism (*Cymbella*) $\pi/4LWT$

Average biovolumes per cell were determined for each genus and used to calculate the total biovolume per cm^2 upon the *Typha* litter surface area by using the following formula:

- *Total biovolume(μm^3 cm^{-2}) = density(cells cm^{-2}) * average biovolume(μm^3 cm^{-2})*

Analysis of variance (ANOVA) was used to determine whether differences in biovolume and/or density occurred between the two sample sites, sample dates and the combination of sample date and sample site for each genus. All analyses were conducted using the Statistical Analysis System (SAS 1985)

RESULTS

General Habitat Description

The emergent vegetation forming the cattail stand consisted primarily of *Typha angustifolia*. Also present in and near the stand were culms of *T. latifolia* as well as *Lythrum salicaria*. However, the latter two species were not found within the sampling area. Average water temperature during the study period inside and outside of the cattail stand was 19.5º C and 19.7º C, respectively. Average dissolved oxygen content inside of the cattail stand was 7.38 ± 0.79 (SE) mg l^{-2}, compared with 11.35 ± 0.73 mg l^{-2} outside the stand. During the growing season, light intensity was approximately four times higher over the open water relative to within the *T. angustifolia* stand.

Composition of Periphyton Community

During the study period, 58 genera, representing 6 divisions (Table 1) of algae and cyanobacteria were identified on *T. angustifolia* litter. Approximately 39% of the taxa were diatoms (Bacillariophyta), 31% were green algae (Chlorophyta), and 24% were cyanobacteria (Cyanophyta). Within these divisions, 16 genera occurred frequently and were considered dominant taxa (defined as present on ≥ 50% of the sample dates). Frequent diatom genera included *Achnanthes, Cymbella, Fragilaria, Gomphonema, Mastogloia, Navicula, Nitzschia, Rhopalodia,* and *Synedra.* The most frequent green algae were *Cosmarium, Mougeotia, Oedogonium,* and *Spirogyra.* The most frequently occurring cyanobacteria consisted of *Chroococcus* and *Oscillatoria.*

Figure 1 depicts the total density, average biovolume and the total biovolume for all algal and cyanobacteria taxa observed during the study period of May-November.

Table 1. Algal taxa observed on the surface of *Typha angustifolia* detritus from May to November 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor MI.

Division Bacillariophyta	
Achnanthes *	*Pediastrum*
Amphora	*Pleurotaenium*
Caloneis	*Scenedesmus* *
Cocconeis	*Spirogyra* *
Cymbella *	*Staurastrum*
Denticula	*Stigeoclonium*
Diatoma	*Zygnema*
Diploneis	
Encyonema	Division Chysophyta
Epithemia	*Dinobryon*
Eucocconeis	*Ophiocytium*
Eunotia	
Fragilaria *	Division Cyanophyta
Gomphonema *	*Anabaena*
Mastogloia *	*Chroococcus* *
Navicula *	*Cylindrospermum*
Nitzschia *	*Gloeothrichia*
Pinnularia	*Gloeocapsa*
Rhopalodia *	*Gloeothece*
Stauroneis	*Gomphosphaeria*
Synedra *	*Lyngbya*
	Merismopedia
Division Chlorophyta	*Microchaete*
Bulbocheate	*Nostoc*
Cheatophora	*Oscillatoria* *
Chlamydomonas	*Scytonema*
Closterium	*Tolypothrix*
Cosmarium *	
Euastrum	Division Euglenophyta
Eudorina	*Phacus*
Microsterias	*Trachelomonas*
Mougeotia *	
Oedogonium *	Division Pyrrhopyta
Pandorina	*Peridinium*

* Frequently occurring taxa (defined as present ≥ 50% of the sample dates).

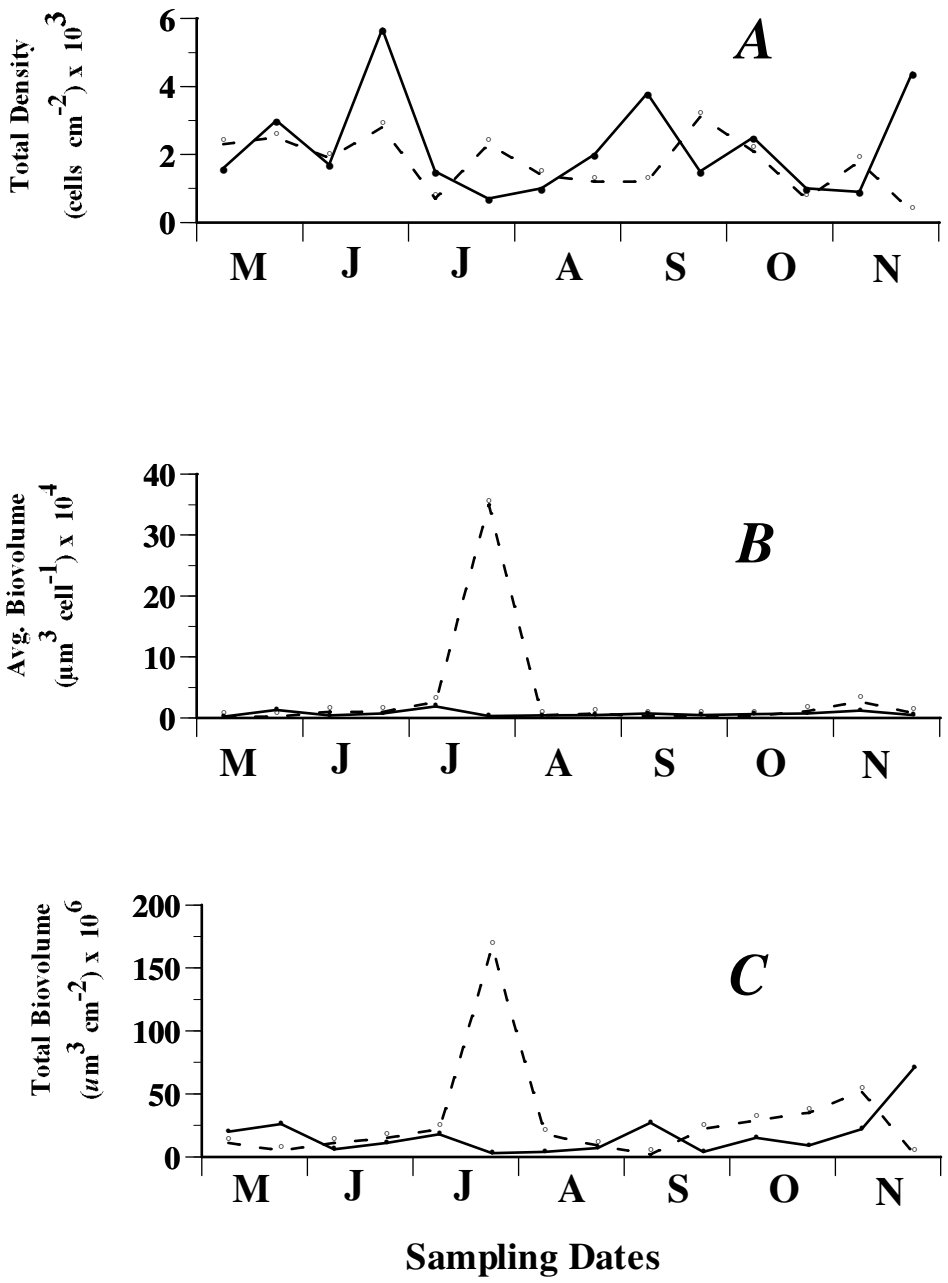

Figure 1. The total density (***A***), the average biovolume (***B***), and total biovolume (***C***) for all the algal taxa observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI. Samples were collected within (-) and outside (--) the *T. angustifolia* stands.

The average density for taxa comprising the aforementioned divisions inside the *Typha* stand averaged 134,588 cells ± 62,946 (SE) cm^{-2} over the course of the growing season. Similarly, mean density outside *Typha* stands was 108,853 cells ± 47,705 cm^{-2}. The combined algae-cyanobacteria density (both inside and outside) was significantly affected by the sampling date (p=0.03), as well as the interaction of date and location (p=0.05). Location, however, did not have a significant effect on total algae-cyanobacteria density; *i.e*., inside and outside locations were not significantly different. The average algae-cyanobacteria cell biovolume was 6,865 ± 32,119 and 33 x 10^3 ± 697 x 10^3 $u m^3$ $cell^{-1}$ inside and outside the *Typha* stands, respectively. The average total biovolume for the community within the *Typha* stand was 245 x 10^6 ± 251 x 10^6 and 136 x 10^3 ± 3,435 x 10^6 $u m^3$ cm^{-2} outside. In no instances were differences significant for either the total or average biovolume between the interior and exterior samples. The Shannon-Weiner Index of species diversity was 1.014 within the stand and 1.022 exterior to the stand.

Bacillariophyta

Throughout the study period, the diatoms dominated the detrital periphyton community. Three diatoms, *Achnanthes, Gomphonema,* and *Rhopalodia* dominated the Bacillariophyta. During the study period, the mean density of diatoms located inside the cattail stand was 116 x 10^3 cells ± 82.3 x 10^3 cm^{-2}, while the mean outside was 84 x 10^3 ± 40.6 x 10^3 cm^{-2} (Figure 2). Average cell biovolume was 2,546 ± 42,016 $u m^3$ $cell^{-1}$ inside the stand and 1,380 ± 8,327 $u m^3$ $cell^{-1}$ outside the stand. The average total biovolume for the diatoms was 590 x 10^6 ± 1,593 x 10^6 $u m^3$ cm^{-2} and 150 x 10^6 ± 98.3 x 10^6 $u m^3$ cm^{-2} inside and outside

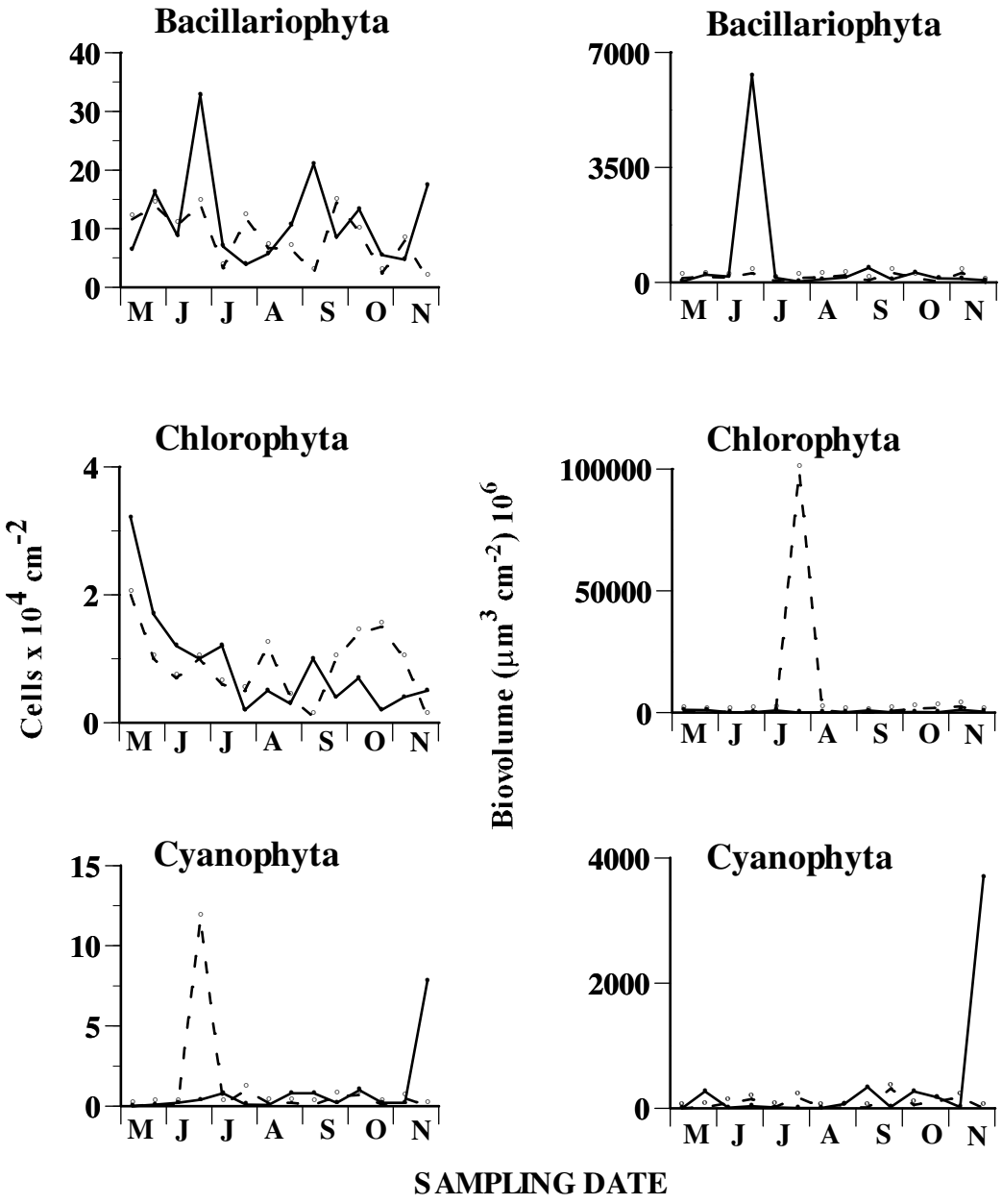

Figure 2. Mean density and total biovolume of the dominant algae-cyanobacteria divisions observed on the surface of *Typha angustifolia*. Samples were collected inside (-) and outside (--) of *T. angustifolia* stands from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

the *Typha* stands, respectively (Table 2). Differences between the outside and inside diatoms were not significant (Table 3).

Maximum diatom density and biovolume occurred on June 24 inside of the *Typha* stand. The mean density was 32,800 cells ± 263,083, the average cell biovolume was 13,684 ± 56,855 $u m^3$ $cell^{-1}$, and the total biovolume was 6,292 x 10^6 ± 5,768 x 10^6 $u m^3$ cm^{-2} (Figure1). Outside the stand, however, maximum diatom density and total biovolume occurred on September 16, (14.4 x 10^4 ± 53,473 and 290 x 10^6 ± 193.6 x 10^6, respectively), and the maximum average cell biovolume of 2,141 ± 5,038 $u m^3$ cm^{-2} occurred on July 27.

Achnanthes was the most abundant diatom taxon both inside and outside of the cattail stand with mean densities of 36,943 cells ± 33,309 and 25,289 cells ± 17,746, respectively, over the season (Figure 3). *Fragilaria*, on the other hand, was the least abundant dominant diatom within and outside of the cattail stand with a mean density of 1,036 cells ± 780 and 1,399 cells ± 808, respectively (Figure 3). The mean density of *Achnanthes* reached a maximum on June 24 inside (137 x 10^3 cells ± 110 x 10^3) and on June 10 outside (59 x 10^3 cells ± 26,880) of the cattail stand. Although *Achnanthes* was the most abundant diatom in both locations, its small size resulted in low measures of biovolume (Figure 4). In fact, at both locations, the presence of *Achnanthes* resulted in both the lowest average cell biovolume and total biovolume, accounting for < 1% of the Bacillariophyta. Within the *Typha* stand, average cell biovolume for *Achnanthes* was 18 ± 2.08 $u m^3$ $cell^{-1}$, and the total biovolume was 624 x 10^3 ± 509 x 10^3 $u m^3$ cm^{-2}. Outside of the stand, the average cell biovolume of *Achnanthes* was 18.4 ± 2.2 $u m^3$ $cell^{-1}$, and total biovolume was 457 x 10^3 ± 328 x 10^3 $u m^3$ cm^{-2}.

Table 2. Average density and total biovolume (± SE) for all algal taxa in their divisions observed on the surface of *Typha angustifolia* detritus from May to November 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

Division	Average Density (cells cm^{-2}) 10^3		Total Biovolume (μm^3 cm^{-2}) 10^6	
	Inside	Outside	Inside	Outside
Bacillariophyta	116 (± 31.1)	84 (± 15.3)	590 (± 602)	150 (± 37.2)
Chlorophyta	8.9 (± 2.75)	9.2 (± 1.92)	520 (± 163)	7913 (± 10012)
Chrysophyta	0.13 (± 0.11)	0.21 (± 0.21)	2 (± 2.41)	0.77 (± 0.84)
Cyanophyta	9.1 (± 7.65)	11 (± 11.6)	352 (± 372)	81 (± 33.8)
Euglenophyta	0.9 (± 0.79)	6.2 (± 5.1)	2.3 (± 1.73)	4.1 (± 2.93)
Pyrrhophyta	0.07 (± 0.04)	0.23 (± 0.21)	0.5 (± 0.35)	1.6 (± 1.27)

Table 3. ANOVA of sample date and sample location (±SE) on densities and total biovolumes of the algae-cyanobacteria divisions observed on the surface of *Typha angustifolia* detritus from May to November 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI. (* = $p \leq 0.05$)

	Density			Total Biovolume		
Bacillariophyta		(r^2=0.57)			(r^2=0.061)	
	d.f	MS	F	d.f	MS	F
Day	13	7.4 x 10^3	1.45	13	29 x 10^8	1.93
Location	1	105 x 10^3	2.05	1	2.5 x 10^8	1.57
Day x Location	13	65 x 10^3	1.27	13	26.7 x 10^8	1.32
Chlorophyta		(r^2=0.63)			(r^2=0.49)	
	d.f	MS	F	d.f	MS	F
Day	13	137 x10^3	2.12*	13	30.2 x 10^8	0.88
Location	1	0.9 x 10^3	0.17	1	51.2 x 10^8	1.49
Day x Location	13	96 x 10^3	1.49	13	36.4 x 10^8	1.06
Chrysophyta		(r^2=0.44)			(r^2=0.45)	
	d.f	MS	F	d.f	MS	F
Day	13	861	1.32	13	16.2 x 10^5	1.13
Location	1	33.9	0.05	1	3.2 x 10^5	0.23
Day x Location	13	219	0.34	13	8.7 x 10^5	0.61
Cyanophyta		(r^2=0.50)			(r^2=0.46)	
	d.f	MS	F	d.f	MS	F
Day	13	25 x 10^3	0.99	13	11 x 10^7	0.66
Location	1	0.9 x 10^3	0.04	1	9.5 x 10^7	0.57
Day x Location	13	29 x 10^3	1.17	13	18.6 x 10^7	1.11
Euglenophyta		(r^2=0.43)			(r^2=0.43)	
	d.f	MS	F	d.f	MS	F
Day	13	9.8 x 10^3	0.71	13	23 x 10^5	0.7
Location	1	25.1 x 10^3	1.81	1	15 x 10^5	0.49
Day x Location	13	11 x 10^3	0.78	13	26 x 10^5	0.84
Pyrrhopyta		(r^2=0.72)				
	d.f	MS	F	d.f	MS	F
Day	13	763	2.75*	13	-	-
Location	1	326	1.18	1	-	-
Day x Location	13	758	2.73*	13	-	-

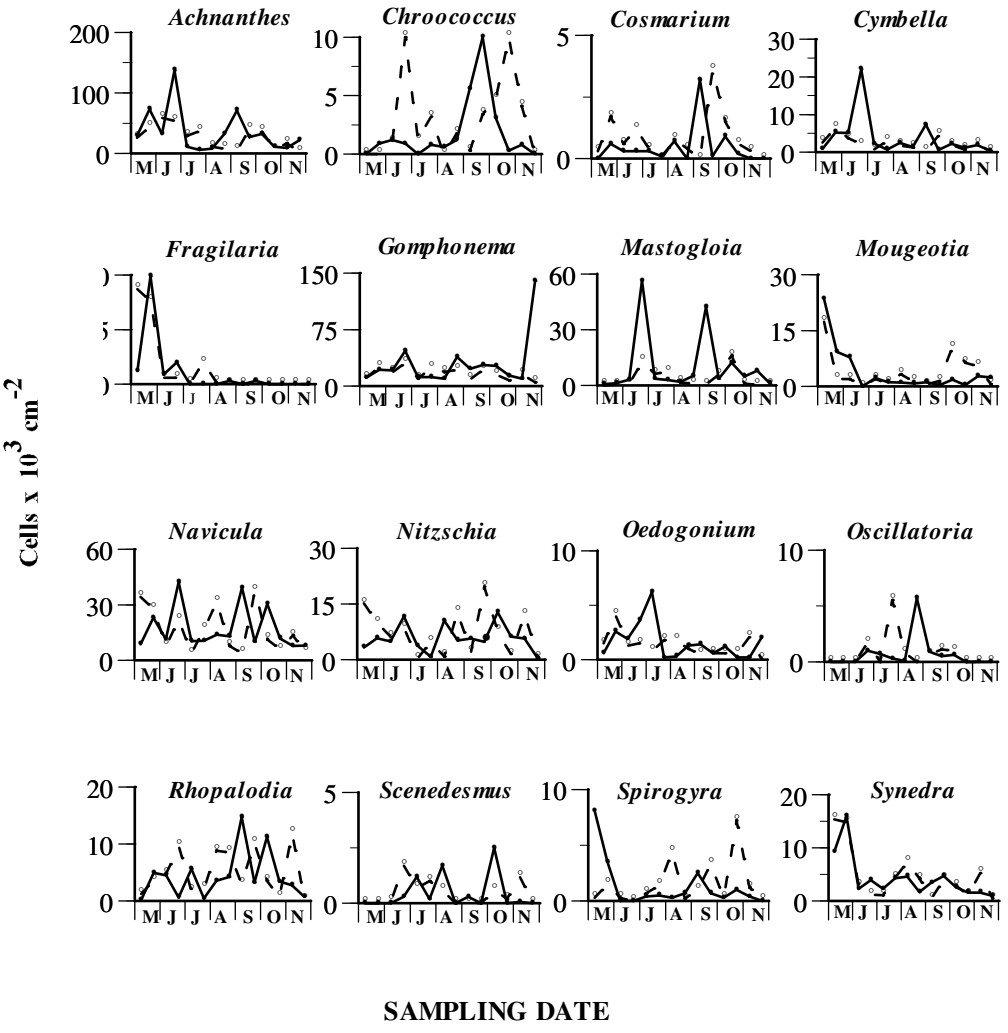

Figure 3. Mean density of the dominant algae-cyanobacteria taxa observed on the surface of *Typha angustifolia*. Samples were collected inside (-) and outside (--) the *T. angustifolia* stands from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

The dominant diatom (cellular and total biovolume) was *Gomphonema* with both the highest average cell biovolume and total biovolume inside the cattail stand of 20,065 ± 72,638 $u m^3$ cell $^{-1}$ and 443,323 x 10^3 ± 1,604,386 x 10^3 $u m^3$ cm^{-2}, respectively. Although *Gomphonema* had the greatest cellular and total biovolume inside of the cattail stand, *Rhopalodia* dominated outside of the stand, with a mean cell biovolume of 19,162 ± 3,784 $u m^3$ cell $^{-1}$and a total biovolume, 99,542 x 10^3 ± 90,435 x 10^3 $u m^3$ cm^{-2} (Figure 4). On June 24, the average cell biovolume and total biovolume of *Gomphonema* reached maxima of 272 x 10^3 ± 273 x 10^3 $u m^3$ cell $^{-1}$ and 6,027,456 x 10^3 ± 5,992,520 x 10^3 $u m^3$ cm^{-2}, respectively. The maximum average cell biovolume for *Rhopalodia* of 24,307 ± 697 $u m^3$ cell $^{-1}$ was reached on May 27 within the stand, while the maximum mean total biovolume of 236,220 x 10^3 ± 227,254 x 10^3 $u m^3$ cm^{-2} was reached outside on October 29.

Although the densities of the smaller diatom *Achnanthes* were many times that of the larger diatoms, the larger diatoms accounted for much more biovolume. Throughout the study period, the largest size class of diatoms (≥ 2001 um^3 cm^{-2}) typically accounted for more than 30% of the diatom biovolume (Figure 5), and the percentage of the smallest size class (1-100) remained nearly constant at approximately 10%.

Although no significant differences were found for the diatoms examined as a division, two significant differences were found when the diatom genera were examined separately (Table 4). The sampling date significantly affected ($p \geq 0.05$) the density and total biovolume of *Fragilaria* and *Synedra*. The interaction of date and location significantly affected *Navicula*.

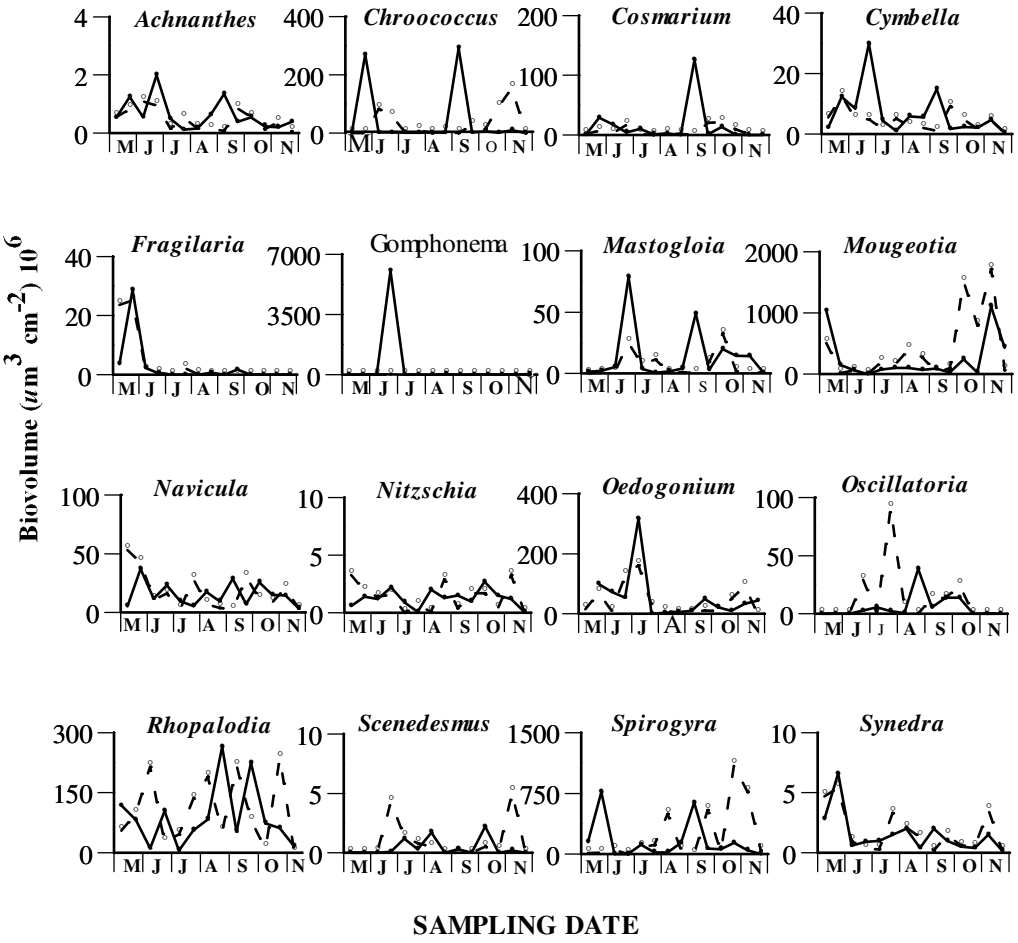

Figure 4. Total biovolume of dominant algae and cyanobacteria observed on the surface of *Typha angustifolia*. Samples were collected inside (-) and outside (--) of *T. angustifolia* stands from May to November, 1998 in Willow Pond, Matthai Botanical Gardens, Ann Arbor, MI.

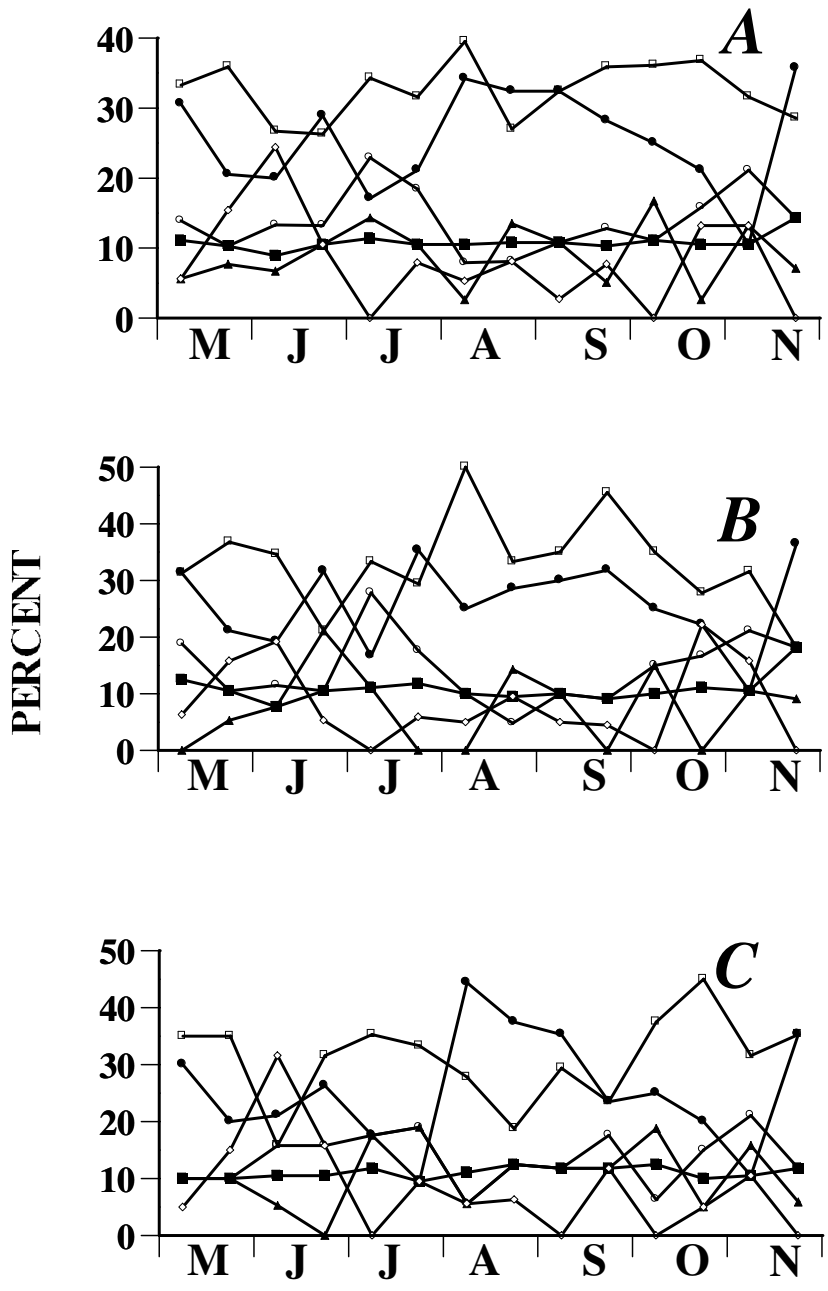

Figure 5. Percentage of total biovolume represented by six cell size classes ($u m^3 cm^{-2}$) in the Bacillariophyta; 1-100 (■), 101-500 (●), 501-1000 (○), 1001-1500 (▲), 1501-2000 (◊), and ≥ 2001 (□),observed on the surface of *Typha angustifolia*. The total diatoms (**A**), diatoms collected inside (**B**), and diatoms collected outside (**C**) of *T. angustifolia* stands were sampled from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

Chlorophyta

Although the Chlorophytes were not as abundant as the diatoms, both average cell biovolume and mean total biovolume were greater. Although there were no statistically significant differences, the Chlorophytes outside of the cattail stand were both greater in mean cell biovolume and total biovolume than inside the stand. Inside the *Typha* stand, the mean density for the growing season was 8,869 cells ± 7,268 cm^{-2}, while outside the mean density was 9,225 ± 5,078 cm^{-2} (Table 2). Within the stand, the average cell biovolume was 15,519 ± 47,014 μm^3 $cell^{-1}$ and the total biovolume was 520 x 10^6 ± 431 x 10^6 μm^3 cm^{-2}. Outside of the stand, the average cell biovolume was 105,471 ± 1,272,130 μm^3 $cell^{-1}$ and the total biovolume was 7,913 x 10^6 ± 26,490 x 10^6 μm^3 cm^{-2}.

Chlorophyta density ranged from 2,006-32,259 cells cm^{-2} inside and 1,033-19,762 cells cm^{-2} outside, reaching a maximum for both locations on May 13 (Figure 2). Maximum average cell biovolume (59,295 ± 137,875 μm^3 $cell^{-1}$) of the Chlorophytes occurred on July 8 inside the cattail stand. The maximum total biovolume inside was reached on October 29 (1,206 x 10^6 ± 258 x 10^6 μm^3 cm^{-2}). On July 27, both the maximum average cell biovolume (1,150 x 10^6 ± 4.8 x 10^6 μm^3 $cell^{-1}$) and the maximum total biovolume (99,644 x 10^6 ± 99,300 x 10^6 μm^3 cm^{-2}) (Figure 2) for the outside community was reached. Although the density of the Chlorophyta varied significantly among sampling dates, no other significant differences occurred between the Chlorophytes inside and outside the *Typha* stand (Table 3).

Mougeotia was the most abundant green alga in the Chlorophyta for the growing season, accounting for 44% and 42% of all Chlorophytes inside and outside the *T. angustifolia* stand, respectively. The average density for *Mougeotia* inside the cattail

stand was 3,897 cells ± 5,129, while outside the density was 3,852 ± 4,265 cells cm^{-2}. Although mean density for *Mougeotia* was similar both outside and inside the cattail stand, the maximum density occurred within the stand (23,540 ± 11,333 cells cm^{-2}) on May 13 (Figure 3). The maximum average cell biovolume and total biovolume (Figure 4) within the stand was reached on October 29 (306,302 ± 117,291 $u m^3$ cell $^{-1}$ and 1,105 x 10^6 ± 1050 x 10^6 $u m^3$ cm^{-2}, respectively).

The maximum mean density for *Mougeotia* outside of the stand (17,437 cells cm^{-2} ± 6,393) occurred on May 13 (Figure 3). On October 29, the mean biovolume and total biovolume reached maxima of 609 x 10^3 ± 328 x 10^3 $u m^3$ cell $^{-1}$ and 1,716 x 10^6 ± 1,171 x 10^6, $u m^3$ cm^{-2}, respectively.

Inside the cattail stand, *Oedogonium* had the second greatest mean density and biovolume after *Mougeotia*, and was followed by *Spirogyra* and *Cosmarium*, respectively (Figures 3 & 4). Outside of the stand, *Spirogyra* had the second greatest mean density (Figure 3), average biovolume and total biovolume (Figure 3) followed by *Oedogonium*. *Cosmarium* had the lowest numbers of the four dominant Chlorophytes.

Interestingly, while *Cosmarium* was the least abundant green alga in density and biovolume, it was the only Chlorophyta where both the sampling date, as well as the interaction between the sample date and location, had a significant effect on the density (Table 4). However, this significant interaction can be explained by the observation that *Cosmarium,* within the cattail stand, reached a maximum total biovolume on September 2 (Figure 4) that was at least 5 times greater than any other time or location during the study period. *Mougeotia* density also varied among the sampling dates.

Throughout the study period, no single size class dominated the Chlorophyta (Figure 6). Although the third largest size (10,001-50,000 $u m^3$ cm^{-2}) dominated early, the size class began to taper in dominance through the rest of the study period.

Cyanophyta

The mean density of the Cyanobacteria collected inside the *T. angustifolia* stand was 9,060 ± 20,238 cells cm^{-2}, and the mean density outside the stand was 11,022 ± 30,787 cells cm^{-2} (Figure 2). The average cell biovolume for cyanobacteria was similar inside and outside the stand (4,680 ± 33,162 and 4,817 ± 16,604 $u m^3$ cell $^{-1}$, respectively). However, total biovolume differed according to location collected. Inside, the biovolume was 352 x 10^6 ± 934 x 10^6 $u m^3$ cm^{-2}, while outside the biovolume was 81 x 10^6 ± 89.4 x 10^6 $u m^3$ cm^{-2} (Table 2).

The Cyanophyta were most abundant on the last collection date, November 14, with a mean density of 38,846 ± 53,892 (Figure 2). Also on the last date, a maximum total biovolume of 1,851 x 10^6 ± 988 x 10^6 $u m^3$ cm^{-2} was reached. However, the average biovolume reached a maximum on May 27 of 18 x 10^3 ± 85 x 10^3 $u m^3$ cell $^{-1}$.

Of the three dominant Cyanophyta, *Chroococcus* occurred in the greatest abundance both inside and outside the *Typha* stand (1,241 ± 1,305, 2,116 ± 2,737 cells cm^{-2}, respectively) (Figure 3). For *Chroococcus* collected inside the cattail stand, the mean density was greatest (5,572 cells ± 2,565) on September 2. On the other hand, *Chroococcus* collected outside reached a maximum of 9,881 cells ± 9,299 on June 24 (Figure 3). As with the Bacillariophyta, no significant differences between the interior and exterior

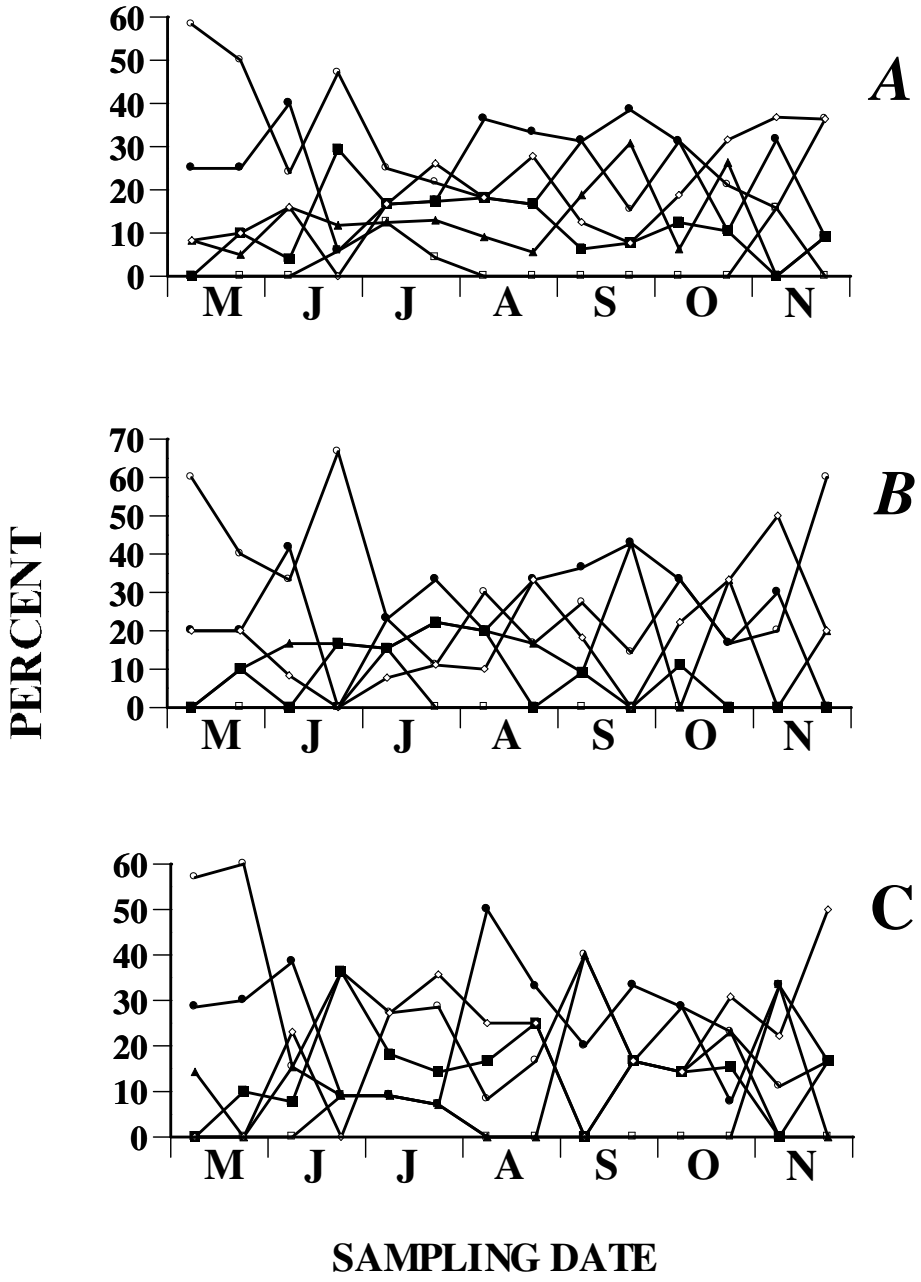

Figure 6. Percentage of total biovolume represented by six cell size classes ($u m^3 cm^{-2}$) in the Chlorophyta; 1-2000 (■), 2001-10000 (●), 10001-50000 (○), 50001-100000 (▲), 100001-500000 (◊), and ≥ 500001 (□),observed on the surface of *Typha angustifolia*. The total chlorophytes (**A**), those collected inside (**B**), and those collected outside (**C**) of *T. angustifolia* stands were sampled from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

samples occurred. No significant differences were found between the interior and exterior samples for any genus of Cyanophyta.

In addition to being the most abundant cyanobacterium, *Chroococcus* was also the largest (Figure 4). Inside the *Typha* stand, the average biovolume of *Chroococcus* was $3.7 \times 10^3 \pm 122 \times 10^3$ $u m^3$ cell $^{-1}$, while the total biovolume was $42.2 \times 10^6 \pm 101 \times 10^6$ $u m^3$ cm^{-2}. Outside the stand, the average biovolume of *Chroococcus* was 17,776 ± 35,253 $u m^3$ cell $^{-1}$, while the total biovolume was $322 \times 10^6 \pm 43.8 \times 10^6$ $u m^3$ cm^{-2}. On May 27, the average biovolume of Cyanophyta reached a maximum, as did the average biovolume for *Chroococcus* collected inside the stand ($45.8 \times 10^4 \pm 45 \times 10^4$ $u m^3$ cell $^{-1}$) (Figure 4). And, similar to mean density, total biovolume for the *Chroococcus* collected within the *Typha* stand reached a maximum ($292 \times 10^6 \pm 275 \times 10^6$ $u m^3$ cm^{-2}) on September 2. Exterior to the *Typha* stand, the average *Chroococcus* biovolume reached a maximum of $118 \times 10^3 \pm 117 \times 10^3$ $u m^3$ cell $^{-1}$ on October 15. Similar to the Cyanophyta, total biovolume for *Chroococcus* collected outside reached a maximum of $156 \times 10^6 \pm 55.2 \times 10^6$ $u m^3$ cm^{-2} on October 29 (Figure 4).

Although *Chroococcus* was present on all but one sampling date, *Oscillatoria* was observed on only eight sampling dates (Figure 3). The mean densities for *Oscillatoria* were 697 ± 1,406 and 770 ± 1,295 inside and outside the *Typha* stand, respectively.

In a manner similar to the diatoms, the largest cell size class (≥ 8,001 $u m^3$ cm^{-2}) dominated the Cyanophyta throughout the study period (Figure 7). When separated according to collection site, the largest and second largest (4,001-8,000 $u m^3$ cm^{-2}) size

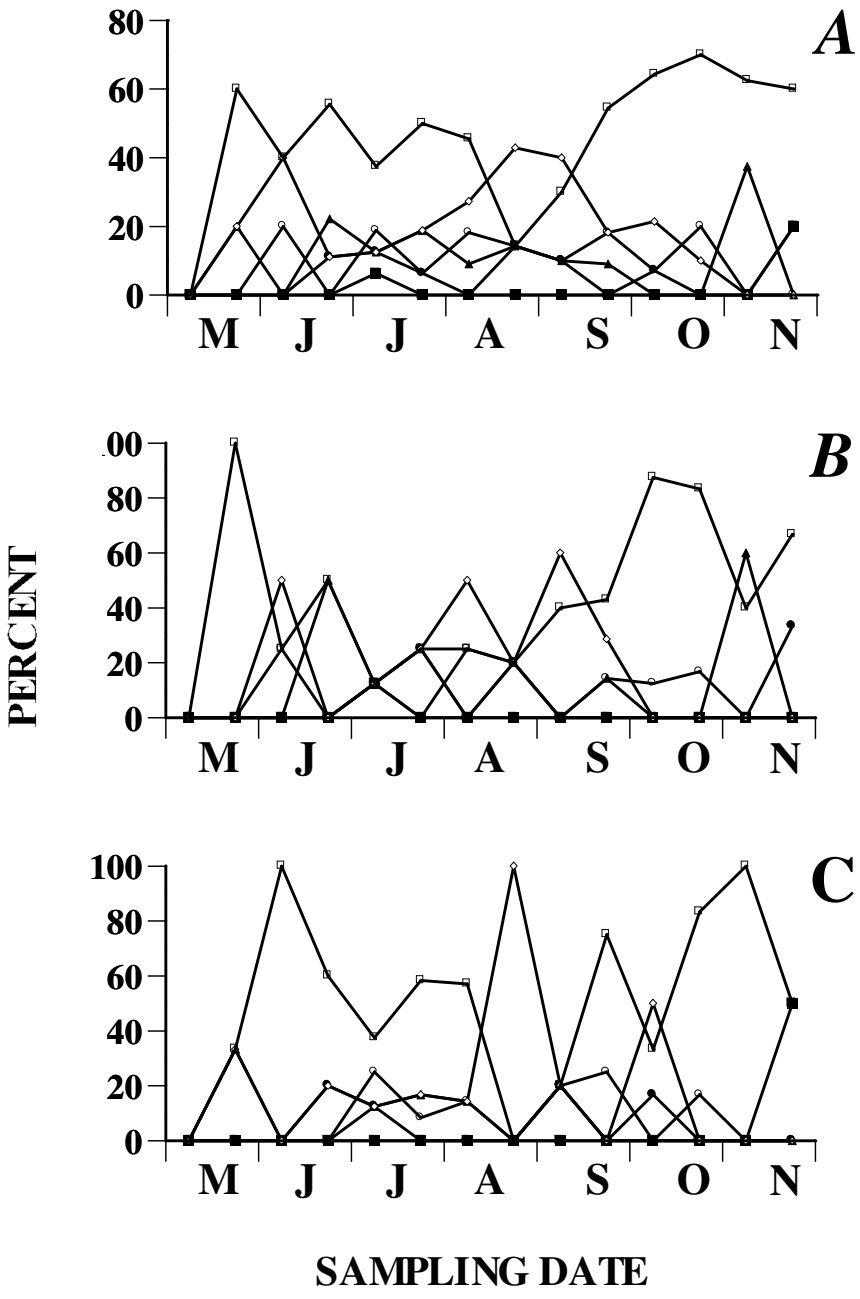

Figure 7. Percentage of total biovolume represented by six cell size classes ($\mu m^3 cm^{-2}$) in the Cyanophyta; 1-500 (■), 501-1000 (●), 1001-2000 (○), 2001-4000 (▲), 4001-8000 (◊), and ≥ 8001 (□),observed on the surface of *Typha angustifolia*. The total blue-greens (**A**), those collected inside (**B**), and those collected outside (**C**) of *T. angustifolia* stands were sampled from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

classes dominated over the smaller sizes. In fact, the proportion of cyanobacteria small size classes (1- 500 $u m^3$ cm^{-2}) was negligible. However, toward the end of the study period, the second size class diminished dramatically and disappeared on the last sampling date (November 14).

Cattail Stand Characteristics

Along a 30-meter transect within the study area, the average density of *Typha spp*. was 55.25 plants m^{-2} in 1998 and 97.25 plants m^{-2} in 1997. The average surface area of *T. angustifolia* (leaves & stems) observed at the study site was 2,507.85 cm^2 $plant^{-1}$. The potential surface area for periphyton attachment in 1998 (combining plants from both 1997 and 1998) was 381,193 cm^2 m^{-2} of the marsh. Algal densities calculated for the entire cattail stand are approximate and based on the assumption that the observed densities were representative of the study area. For example, using the observed densities for Willow Pond, the potential density of *Achnanthes*, the most abundant alga observed, would have been approximately 1.41 x 10^{10} m^{-2} on cattail tissue only,(*i.e.*, not including epipelic algae). The overall study site total biovolume of *Gomphonema*, the largest diatom observed inside the stand, would have been approximately 1.69 x 10^{14} $u m^3$ m^{-2} (Table 5). And, taken as a whole, the potential mean algae-cyanobacteria density within the stand was approximately 5.03 x 10^{10} cm^2 m^{-2} and the total algae-cyanobacteria biovolume was approximately 5.58 x 10^{14} $u m^3$ m^{-2} inside the cattail stand (Table 5).

Table 5. Potential densities and biovolumes of dominant algal/cyanobacteria genera and for the *Typha spp.* stand as observed from May to November 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI. In addition, potential totals for all observed algal divisions are shown.

	Density (cells m^{-2}) x 10^8		Biovolume (μm^3 m^{-2}) x 10^{12}	
	Inside	Outside	Inside	Outside
Bacillariophyta	442	320	225	57.2
Achnanthes	141	96.4	0.24	1.74
Cymbella	14.47	8.6	2.59	1.66
Fragilaria	3.95	5.33	1.02	1.43
Gomphonema	114	63.7	169	3.98
Mastogloia	39.78	14.7	5.4	2.52
Navicula	65.62	62.1	5.82	6.6
Nitzschia	2.22	27.7	0.482	0.62
Rhopalodia	16.3	19	31.5	37.94
Synedra	16.2	17.9	0.583	0.676
Chlorophyta	33.8	35	198	3020
Cosmarium	1.79	3.07	4.85	2.31
Mougeotia	14.9	14.7	95.45	158
Oedogonium	6.09	4.94	19.39	16.03
Scenedesmus	1.7	2.06	0.162	0.394
Spirogyra	4.97	5.7	58.69	90.1
Cyanophyta	23	42	134	31
Chroococcus	4.73	8.07	16.11	12.28
Oscillatoria	2.66	2.94	2.27	4.87
Total (All observed divisions)	503	421	558	3110

DISCUSSION

The many functions of periphyton in freshwater ecosystems have been well established, including the significant roles they play in primary production, the filtration of contaminants, and food chain support. Dead biomass and detrital litter have been recognized as a potentially large substratum for periphyton development (Wetzel 1993), although very few studies have examined periphyton upon detritus. Therefore, the purpose of this study was to characterize the epiphytic autotroph community living upon a detrital substratum (*Typha angustifolia*) in a freshwater wetland system. Characterization included calculating the magnitude of the autotrophic component of the epiphyton upon the detritus and the determination of the effects of season and sample location.

Although only a few studies of detrital periphyton exist, the development of periphyton upon living and artificial leaves has been closely examined. In one study, for example, Burkholder and Wetzel (1989b) observed epiphytic algae upon living *Scirpus subterminalis*. The epiphytic community they observed consisted of over 100 taxa and represented 7 divisions. In other studies, Hoagland *et al*. (1982) observed 93 taxa representing 23 genera of diatoms, Kaur and Mehra (1998) observed 50 taxa representing 7 divisions in a study comparing periphyton upon natural and artificial substrates, and a total of 104 algal species representing 5 main algal groups were observed by Romo and Galanti (1998) during their study of *Trapa natans*. *Typha angustifolia* detritus examined from Willow Pond provided substrata for 58 genera of algae and cyanobacteria representing 6 divisions (Table 1). In their study, Burkholder and Wetzel (1989b) observed that diatoms made up 43% of the community and the Cyanobacteria made up

26%. Comparable to the aforementioned study, the detrital community observed from Willow Pond consisted of 39% diatoms, 24% cyanobacteria and 31% green algae. The most common genera observed in this study, including *Achnanthes*, *Oedogonium*, and *Chlorococcus*, were observed in other similar studies of living, artificial and dead substrata (Meulemans and Roos 1985, Burkholder and Wetzel 1989b, Burkholder and Wetzel 1990, Kaur and Mehra 1998, Romo and Galanti 1998). Similar to other studies, the diatoms observed in this study represented the most abundant of the six taxonomic divisions observed. For example, throughout their 13-month study of epiphytic communities upon submersed macrophytes, Hopsen *et al.* (1998) observed that diatoms represented the greatest percentage of every sample site. During this study, the seasonal average densities of the diatoms observed constituted approximately 87% of the algae observed upon detritus outside the *Typha* stand and approximately 77% of those observed within the stand. Chlorophyta or Cyanophyta were the 2nd and 3rd most dominant divisions, respectively. Densities of these divisions were similar as observed outside and within the cattail stand (Table 2).

The dominance of the diatoms observed in this study may be explained by first reviewing the development of periphyton upon other substrata (*e.g.* artificial and living plants). The development of the periphyton community upon solid substrata has been the subject of much study (Hoagland *et al.* 1982, Korte and Blinn 1982, Meulemans and Roos 1985, Burkholder and Wetzel 1989a, 1989b, Romo and Galanti 1998). Meulemans and Roos (1985) described the epiphyton community as structured into three distinct layers: the basal, the intermediate, and the uppermost layer. Hoagland *et al.* (1982) described typical cell types within the three layers. Opportunistic algal cells within the

basal layer were adnate and having mucilaginous coats or producing short stalks. The intermediate layer was comprised mostly of long-stalked diatoms and large rosettes of diatoms, and the uppermost layer consisted primarily of filamentous green algae. Therefore, because each of the layers of the community has the potential to be occupied by diatoms, the diatoms would potentially be the most abundant. For example, during this study, one of the dominant diatom genera observed was *Navicula.* Species of *Navicula* are known to form mucilaginous coats (*e.g. N. menisculus* var. *upsaliensis*) thereby attaching adnate to the substrate and likely found within the basal layer of periphytic communities. Another dominant diatom genus observed in this study, *Gomphonema,* includes species which produce both short and long stalks and, in doing so, may be included in both the basal and intermediate layers. Three other dominant diatom genera observed in this study, *Fragilaria, Nitzschia,* and *Synedra* produce mucilaginous pads by which they form apical rosettes. The shorter rosettes of *Fragilaria* and *Nitzschia* would be observed in the upper basal and lower intermediate layers, while the lengthy rosettes of *Synedra* would be observed in the upper intermediate and lower uppermost layers.

Although other studies observed distinct differences in the taxonomic makeup of different substrata over time (Meulemans and Roos 1985, Burkholder and Wetzel 1990, Burkholder and Wetzel 1989b, Kaur and Mehra 1998), no distinct successional patterns were observed during this study. One explanation for the absence of distinct successional patterns during this study is the method by which the study was conducted. Specifically, while other studies have sampled periphyton using a controlled environment, artificial substrates and living plants or other immobile substrata, this study used toppled leaves of

Typha angustifolia floating in Willow Pond without consideration of the age of the litter collected. Therefore, because community development over time was not considered, successional patterns for the entire detrital periphyton community of Willow Pond could not be clearly distinguished and were not found in this study.

However, some of the algae and cyanobacteria observed in this study demonstrated typical periphyton successional behaviors. For example, similar to other studies, *Fragilaria*, which is considered to be an early opportunistic diatom (Korte and Blinn 1982), was more abundant during the beginning of the study period (Figure 3). *Cosmarium,* noted as a late successional alga (Romo and Galanti 1998), was observed in greater abundance later in the growing season (Figure 3). In addition, although *Synedra*, a genus usually observed toward the latter portions of community development (Korte and Blinn 1982), was observed to be more abundant, as well as larger, during the beginning of the study period (Figures 3 and 4), Meulemans and Roos (1985) observed that the uppermost layer reached maximum development in May, which is the same month *Synedra* was most abundant. Meulemans and Roos (1985), observed filamentous green algae maxima during the month of May, which coincides with the abundance of *Mougeotia, Oedogonium,* and *Spirogyra* at Willow Pond.

Although no distinct successional patterns were observed during this study, the total algae-cyanobacteria density varied significantly over time as well as the interaction of sample date and location. However, sample date only significantly affected the densities of 2 of the 6 taxonomic divisions (Chlorophyta and Pyrrhopyta) and had no significant affect on the total biovolume (Table 3). Nevertheless, when each dominant genus was examined, sample date had a significant effect on the densities of *Cosmarium,*

Fragilaria, Mougeotia, and *Synedra* as well as the total biovolumes of *Fragilaria* and *Synedra* (Table 4).

During the study period, light intensity was approximately four times higher outside the *Typha* stand than within the stand. Although light is often limiting to periphytic abundance and is an important contributor to the composition of the periphyton community (Müller 1994, Meulemans and Roos 1985, Harrison and Hildrew 1998, Wellnitz and Ward 1998), no significant differences in density or biovolume occurred between the locations for any dominant taxonomic division or genus observed during this study. The different effects of light intensity on algal biomass, abundance, species composition, and community structure may explain the lack of significant differences between the two locations may be. For example, Meulemans and Heinis (1981) observed that, although light intensity was higher outside a reed stand, periphyton biomass was low. Furthermore, Meulemans (1988) described that the photosynthetic capacity of epiphytic algae is strongly reduced during the summer and suggests that high light intensities may inhibit algae during the spring months. And, Meulemans and Roos (1985) observed that that self-shading by the uppermost layer of the periphyton has a detrimental effect on the basal layer. Many studies suggest that ultraviolet radiation penetrating the earth's atmosphere can have a detrimental effect on periphyton productivity, cause photoinhibition or alter the DNA structure of algae (Bothwell *et al.* 1993, Moeller 1994, Vinebrooke and Leavitt 1996, Buma *et al*. 1997). Kairesalo (1983) found that in the spring, periphyton biomass declines due to the shading of macrophytic growth. However, some algae are low-light adapted and may not be affected by shading (Garcia and Purdie 1992, Veldhuis and Kraay 1993). Although light has been suggested

to affect periphytic algae species composition (Wellnitz and Ward 1998, Romo and Galanti 1998), the Shannon-Weiner Index of species diversity for samples observed inside and outside the *T. angustifolia* stand did not significantly differ (1.014 and 1.022, respectively). Therefore, algal shade adaptation within the cattail stand, in combination with possible photoinhibition effects outside of the stand, may have been enough to suppress any significant differences in algal density or biovolume.

Similar to light, other environmental factors, specifically temperature and oxygen, contribute to autotroph abundance in periphyton. Slight changes in temperature and light intensity affect the availability of important elements such as oxygen and carbon and temperature is the most important environmental factor that regulates oxygen concentrations (Horne and Goldman 1994). Oxygen limitation alone may directly influence both herbivore distribution and herbivory intensity. During our study, only slight differences in temperature and dissolved oxygen were observed between the two sample locations. Although herbivory was not quantified in this study, the observed similar environmental conditions, in association with the lack of significant differences between the locations, suggest that herbivory as well as temperature and oxygen had little or no effect on the communities observed.

In freshwater wetlands, low herbivory, together with high productivity of vegetation, results in large amounts of detrital biomass. Wetzel (1993) observed that the standing-dead biomass, including detrital litter, potentially provides a very large surface area of substrata where periphyton may flourish. Moreover, Wetzel and Neely (1997) found that emergent plant litter provides surface area upon which complex microbiota communities may develop and produce intense autotrophic activity. The is study is no

exception to the aforementioned observations. The average surface area of *T. angustifolia* at the study area, for instance, was 2,507.85 cm^{-2} per plant. And, similar to the observations of Burkholder and Wetzel (1989b) and Romo and Galanti (1998) of periphyton on living leaves, this study demonstrated that detritus provides an ample substratum for an enormous amount of periphyton. For example, considering the surface area of the average *T. angustifolia* observed during this study and using only the diatom densities observed within the cattail stand, the potential number of diatoms per plant would be nearly 3 billion. Furthermore, the potential diatom density would be over 76 billion cells m^{-2} upon the total surface area of *T. angustifolia* for periphyton at the study area.

In summary, *T. angustifolia* detritus was observed to provide ample substratum for an enormous amount of periphytic algae and cyanobacteria. Although algal-cyanobacteria density was significantly affected by location and sample date, two factors considered to be of importance, algal-cyanobacteria biovolume was not significantly affected. In addition, observations in this study provided no clear evidence to demonstrate periphyton community development. However, while other studies of periphyton community development utilized static substrata (both natural and artificial), this study sampled litter in a natural dynamic environment. Furthermore, timing of litter deposition was not considered in this study. Therefore, the lack of significant evidence to demonstrate periphyton community development suggests that the age (time of deposition) and state (static vs. dynamic) of the litter (or substrate) may be important considerations in studies of the autotrophic component in periphyton.

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Appendix 2. Mean density and total biovolume of the dominant algal-cyanobacteria divisions observed upon the surface of *Typha angustifolia* from May to November, 1998 at Willow Pond, Matthaei Botanical Gardens.

	Mean Density (cells x 10^4)					
	Bacillariophyta		Chlorophyta		Cyanophyta	
	Inside	Outside	Inside	Outside	Inside	Outside
13-May	6.4	11.6	3.2	2	0	0
27-May	16.2	13.9	1.7	1	0.09	0.1
10-Jun	8.8	10.5	1.2	0.7	0.2	0.1
24-Jun	32.8	14.3	1	1	0.4	11.7
8-Jul	7	3.3	1.2	0.6	0.8	0.1
27-Jul	3.9	11.8	0.2	0.5	0.1	1
5-Aug	5.7	6.7	0.5	1.2	0.08	0.2
29-Aug	10.6	6.6	0.3	0.4	0.8	0.2
2-Sep	21	2.4	1	0.1	0.8	0.1
16-Sep	8.5	14.4	0.4	1	0.2	0.6
29-Sep	13.3	9.5	0.7	1.4	1	0.7
15-Oct	5.5	2.4	0.2	1.5	0.2	0.1
29-Oct	4.7	7.9	0.4	1	0.2	0.5
14-Nov	17.3	1.5	0.5	0.1	7.8	0.01
	Total Biovolume (um^3 cm^{-2}) 10^6					
	Bacillariophyta		Chlorophyta		Cyanophyta	
	Inside	Outside	Inside	Outside	Inside	Outside
13-May	26	133	1183	552	0	0
27-May	227	168	1071	123	269	17.6
10-Jun	180	145	184	428	7.6	82.9
24-Jun	6292	281	204	465	34.2	144
8-Jul	136	45.9	932	1255	14.7	19.3
27-Jul	28.6	131	121	99694	3.9	174
5-Aug	97.2	157	138	927	3	13
29-Aug	146	212	220	336	67.3	7.6
2-Sep	436	62.9	875	31	338	14.4
16-Sep	96.8	290	141	670	19.3	313
29-Sep	303	143	336	1566	271	52.6
15-Oct	120	32.7	189	1975	178	112
29-Oct	107	287	1206	2650	20.81	178
14-Nov	67.6	0.02	484	115	3699	2.9

Appendix 3. Mean density of dominant algae and cyanobacteria observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

	Mean Density (cells x 10^3 cm^{-2})							
	Achnanthes		*Chroococcus*		*Cosmarium*		*Cymbella*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	29	26	0	0	0	0.3	0.9	2.6
27-May	73	43	0.9	0	0.6	1.7	5.2	6.4
10-Jun	32	59	1.2	1	0.3	0.6	5.1	3.8
24-Jun	137	54	0.9	10	0.3	1.2	22	2
8-Jul	11	29	0	1.2	0.3	0.4	2.3	0.7
27-Jul	6	37	0.8	3.2	0.1	0	0.7	3
5-Aug	8	11	0.6	0	0.7	0.8	2.5	1.8
29-Aug	32	8	1.2	1.8	0	0.4	1.4	1.3
2-Sep	71	5	5.6	0.3	3.2	0	7.3	0.2
16-Sep	27	40	10	3.4	0.1	3.6	0.6	4.5
29-Sep	32	37	3.1	4.7	0.9	1.5	2.2	2
15-Oct	11	6	0.3	10	0.2	0.6	1.2	0.7
29-Oct	9	17	0.8	4.1	0	0.3	1.9	2.3
14-Nov	22	3	0	0.02	0	0	0.4	0.2
	Frgilaria		*Gomphonema*		*Mastigloia*		*Mougeotia*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	1.2	8.7	11	11	0.7	0	23.5	17.4
27-May	9.9	7.6	22	25	1.2	0.3	9.3	2
10-Jun	0.9	0.6	21	18	3.1	0.7	7.8	2
24-Jun	2	0.6	47	31	56.3	13	0	0
8-Jul	0	0.07	12	9.8	3.5	6.2	2.2	2
27-Jul	0	2	12	24	2.9	7.4	1.1	0.9
5-Aug	0	0.2	10	19	1.8	1.6	1	3.3
29-Aug	0.3	0	39	22	5.1	0.9	0.8	1.3
2-Sep	0	0	23	9.3	42.2	0.4	1.1	0.5
16-Sep	0.3	0	28	22	3.5	5.8	0.4	1.5
29-Sep	0	0	27	15	12.2	16	1.8	10.5
15-Oct	0	0	14	7.7	4.8	0.9	0.4	6.4
29-Oct	0	0	10	16	7.9	0.3	2.7	5.4
14-Nov	0	0	140	5.1	1	0.4	2.4	0.6

Appendix 3 (con't). Mean density of dominant algae and cyanobacteria observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

	Navicula		*Nitzschia*		*Oedogonium*		*Oscillatoria*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	8.6	34.3	3.3	15.1	0.6	1.5	0	0
27-May	23	27.9	5.8	9.9	2.6	4.1	0	0
10-Jun	11.5	7.8	4.9	6.2	1.9	1.3	0	0
24-Jun	42.3	22.1	11.6	8.7	3.6	1.5	1	1.7
8-Jul	10.5	3.6	3.8	0.2	6.2	0.8	0.7	0
27-Jul	10.6	16.7	0.8	4.9	0.2	1.8	0.3	5.5
5-Aug	14	31.6	10.5	0.9	0.3	1.8	0.08	0.8
29-Aug	13	7.9	5.2	12.8	1.3	1	5.7	0
2-Sep	39.3	3.9	5.7	2	1.4	0.5	0.9	0.6
16-Sep	10.1	37.3	4.8	19.6	0.6	0.6	0.5	1.1
29-Sep	30.5	11.3	12.7	7.6	1.2	0.6	0.6	1
15-Oct	11.9	5.9	6.2	1.3	0.2	0.6	0	0
29-Oct	7.8	13.5	5.7	12.1	0.2	2.1	0	0
14-Nov	8	4.3	0.3	0.6	2	0.1	0	0
	Rhopalodia		*Scenedesmus*		*Spirogyra*		*Synedra*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	0.1	1.2	0	0	8.1	0.3	9.3	15.4
27-May	4.9	3.5	0	0	3.5	1.5	16	14.8
10-Jun	4.5	4.8	0	0.1	0	0.3	2.3	2.9
24-Jun	0.6	9.6	0.3	1.7	0	0	3.9	1.2
8-Jul	5.6	1.7	1.2	0.7	0.4	0.7	2.3	1.1
27-Jul	0.4	2.2	0.2	1	0.5	1.4	4.3	4.4
5-Aug	3.5	8.8	1.7	0.6	0.3	4.4	4.6	7.4
29-Aug	4.2	8.5	0	0	0.7	0.2	1.7	4.2
2-Sep	14.7	3	0.3	0	2.5	1	3.5	0.5
16-Sep	3.2	10.2	0	0	0.7	3.3	4.7	4.2
29-Sep	11.2	3.5	2.5	0.6	0.3	0.3	2.6	2.9
15-Oct	3.4	0.6	0	0.2	1	7.2	1.6	1.1
29-Oct	2.7	11.9	0.07	1.2	0.4	1.2	1.6	5.3
14-Nov	0.7	0.2	0	0	0	0.1	1	0.5

Appendix 4. Total biovolume of dominant algae and cyanobacteria observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

Total Biovolume (um^3 cm^{-2}) 10^6								
	Achnanthes		*Chroococcus*		*Cosmarium*		*Cymbella*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	0.525	0.544	0	0	0	1.218	2.08	5.418
27-May	1.24	0.826	270	0	28.592	6.677	12.22	12.7
10-Jun	0.544	1.088	2.216	82.857	17.53	2.663	8.42	5.067
24-Jun	1.992	0.945	2.587	59.81	4.109	16.436	29.86	4.807
8-Jul	0.495	0.155	1.218	1.027	9.74	1.154	4.43	1.735
27-Jul	0.113	0.522	1.595	11.647	0.962	0	0.971	5.042
5-Aug	0.149	0.162	2.435	0	2.221	3.253	5.8265	2.75
29-Aug	0.618	0.138	0.97	7.646	0	1.326	5.49	1.99
2-Sep	1.338	0.066	292	0.214	125.928	0	14.791	1.036
16-Sep	0.384	0.844	2.207	26.767	0.792	19.909	1.676	9.14
29-Sep	0.535	0.555	6.159	14.289	13.45	21.112	2.286	4.729
15-Oct	0.231	0.127	0.932	91.364	0.69	9.69	2.0347	1.734
29-Oct	0.197	0.369	10.198	155.452	0	1.218	4.59	4.402
14-Nov	0.376	0.054	0	0.0014	0	0	0.404	0.498
	Frgilaria		*Gomphonema*		*Mastigloia*		*Mougeotia*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	3.57	23.59	5.8	6.9	1.5	0	1029	505
27-May	28.67	25.076	12.7	18.9	2.1	0.6	153	17.9
10-Jun	2.31	1.14	13.2	15.4	5.4	1.3	62.2	56.3
24-Jun	0.493	0.643	6027	16	78.4	24.9	0	0
8-Jul	0	0	7.5	7	3.7	6.9	71.6	199
27-Jul	0	2.211	9.1	9.5	0.7	11.4	98.4	148
5-Aug	0	0.135	5.9	8.3	1.7	0.5	103	412
29-Aug	0.643	0	26.5	11.2	4.1	1	66.5	269
2-Sep	0	0	7.1	3.1	48.7	0.4	90.2	21.8
16-Sep	1.71	0	9.7	16.7	3	9.5	24.6	95.6
29-Sep	0	0	14.8	9.8	19.8	32.6	239	1510
15-Oct	0	0	11.4	6.2	14.4	2	28.3	796
29-Oct	0	0	9.1	15	14.2	0.5	1105	1716
14-Nov	0	0	46.2	2.4	0.8	0.8	436	64.2

Appendix 4 (con't.). Total biovolume of dominant algae and cyanobacteria observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

	Navicula		*Nitzschia*		*Oedogonium*		*Oscillatoria*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	5.3	53.2	0.6	3.3		14.9	0	0
27-May	37.1	42.7	1.4	1.9	100	69.5	0	0
10-Jun	11.6	10.6	1.2	1.4	73	8.6	0	0
24-Jun	23.3	16	2.2	1.6	53.4	128	2.7	29.1
8-Jul	9.5	3	0.9	0.03	316	161	5.6	0
27-Jul	5.4	28.7	0.1	0.7	0.7	27.8	2.3	90.9
5-Aug	17.6	7.1	2	0.1	3	9.7	0.5	6.8
29-Aug	9.6	3.9	1.3	2.9	5.6	4.3	38.7	0
2-Sep	28.6	2.3	1.5	0.4	9.8	3.9	5.7	13.4
16-Sep	7.1	30.5	1	1.7	49.3	10.8	13.8	13.6
29-Sep	25.7	11.5	2.7	1.7	21.5	9.6	14	25
15-Oct	15	8.8	1.5	0.3	9.4	49.3	0	0
29-Oct	14.4	20.6	1.2	3.3	33.6	91.1	0	0
14-Nov	3.5	3.3	0.1	0.1	43.6	0.3	0	0
	Rhopalodia		*Scenedesmus*		*Spirogyra*		*Synedra*	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
13-May	3.8	30.4	0	0	146	13.6	2.8	4.7
27-May	118	55.5	0	0	767	17.3	6.6	5.4
10-Jun	82.3	97.4	0	0.1	0	52	0.6	1
24-Jun	11	214	0.08	4.3	0	0	0.9	0.3
8-Jul	104	26	1.2	1.3	114	82.4	1	0.3
27-Jul	5.7	45.9	0.3	0.8	20.3	113	1.5	3.3
5-Aug	56.3	135	1.7	0.5	22	495	2	2.1
29-Aug	83.1	189	0	0	139	46.9	0.4	1.3
2-Sep	264	54.2	0.3	0	636	5.6	2	0.2
16-Sep	53	216	0	0	67.2	542	1	1.5
29-Sep	225	80.5	2.2	0.5	58.2	22.2	0.5	0.6
15-Oct	73.3	11.3	0	0.2	139	1102	0.4	0.5
29-Oct	61.4	236	0.2	5.1	47.8	771	1.5	3.6
14-Nov	16.1	2.2	0	0	0	45.8	0.2	0.2

Appendix 5. Percentage of the Bacillariophyta, represented by 6 size classes, observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthai Botanical Gardens, Ann Arbor, MI.

All diatoms observed							
u m^3 cm^{-2}	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
1-100	11.1	10.3	8.9	10.5	11.4	10.5	10.5
101-500	30.6	20.5	20	28.9	17.1	21.1	34.2
501-1000	13.9	10.3	13.3	13.2	22.9	18.4	7.9
1001-1500	5.6	7.7	6.7	10.5	14.3	10.5	2.6
1501-2000	5.6	15.4	24.4	10.5	0	7.9	5.3
≥ 2000	33.3	35.9	26.7	26.3	34.3	31.6	39.5
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
1-100	10.8	10.8	10.3	11.1	10.5	10.5	14.3
101-500	32.4	32.4	28.2	25	21.1	10.5	35.7
501-1000	8.1	10.8	12.8	11.1	15.8	21.1	14.3
1001-1500	13.5	10.8	5.1	16.7	2.6	13.2	7.1
1501-2000	8.1	2.7	7.7	0	13.2	13.2	0
≥ 2000	27	32.4	35.9	36.1	36.8	31.6	28.6
Diatoms observed inside *Typha* stand							
u m^3 cm^{-2}	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
1-100	12.5	10.5	7.7	10.5	11.1	11.8	10
101-500	31.3	21.1	19.2	31.6	16.7	35.3	25
501-1000	18.8	10.5	11.5	10.5	27.8	17.6	10
1001-1500	0	5.3	7.7	21.1	11.1	0	0
1501-2000	6.3	15.8	19.2	5.3	0	5.9	5
≥ 2000	31.3	36.8	34.6	21.1	33.3	29.4	50
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
1-100	9.5	10	9.1	10	11.1	10.5	18.2
101-500	28.6	30	31.8	25	22.2	10.5	36.4
501-1000	4.8	10	9.1	15	16.7	21.1	18.2
1001-1500	14.3	10	0	15	0	10.5	9.1
1501-2000	9.5	5	4.5	0	22.2	15.8	0
≥ 2000	33.3	35	45.5	35	27.8	31.6	18.2
Diatoms observed outside *Typha* stand							
u m^3 cm^{-2}	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
1-100	10	10	10.5	10.5	11.8	9.5	11.1
101-500	30	20	21.1	26.3	17.6	9.5	44.4
501-1000	10	10	15.8	15.8	17.6	19	5.6
1001-1500	10	10	5.3	0	17.6	19	5.6
1501-2000	5	15	31.6	15.8	0	9.5	5.6
≥ 2000	35	35	15.8	31.6	35.3	33.3	27.8
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
1-100	12.5	11.8	11.8	12.5	10	10.5	11.8
101-500	37.5	35.3	23.5	25	20	10.5	35.3
501-1000	12.5	11.8	17.6	6.3	15	21.1	11.8
1001-1500	12.5	11.8	11.8	18.8	5	15.8	5.9
1501-2000	6.3	0	11.8	0	5	10.5	0
≥ 2000	18.8	29.4	23.5	37.5	45	31.6	35.3

Appendix 6. Percentage of the Chlorophyta, represented by 6 size classes, observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthai Botanical Gardens, Ann Arbor, MI.

All green algae observed							
$u\,m^3\,cm^{-2}$	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
< 2000	0	10	4	29.4	16.7	17.4	18.2
2001-10000	25	25	40	5.9	16.7	17.4	36.4
10001-50000	58.3	50	24	47.1	25	21.7	18.2
50001-100000	8.3	5	16	11.8	12.5	13	9.1
100001-500000	8.3	10	16	0	16.7	26.1	18.2
≥ 500000	0	0	0	5.9	12.5	4.3	0
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
< 2000	16.7	6.3	7.7	12.5	10.5	0	9.1
2001-10000	33.3	31.3	38.5	31.1	10.5	31.6	9.1
10001-50000	16.7	31.3	15.4	31.3	21.1	15.8	36.4
50001-100000	5.6	18.8	30.8	6.3	26.3	0	9.1
100001-500000	27.8	12.5	7.7	18.8	31.6	36.8	36.4
≥ 500000	0	0	0	0	0	15.8	0
Green algae observed inside *Typha* stand							
$u\,m^3\,cm^{-2}$	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
< 2000	0	10	0	16.7	15.4	22.2	20
2001-10000	20	20	41.7	0	23.1	33.3	20
10001-50000	60	40	33.3	66.7	23.1	11.1	30
50001-100000	0	10	16.7	16.7	15.4	22.2	20
100001-500000	20	20	8.3	0	7.7	11.1	10
≥ 500000	0	0	0	0	15.4	0	0
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
< 2000	0	9.1	0	11.1	0	0	0
2001-10000	33.3	36.4	42.9	33.3	16.7	30	0
10001-50000	16.7	27.3	14.3	33.3	16.7	20	60
50001-100000	16.7	9.1	42.9	0	33.3	0	20
100001-500000	33.3	18.2	0	22.2	33.3	50	20
≥ 500000	0	0	0	0	0	0	0
Green algae observed outside *Typha* stand							
$u\,m^3\,cm^{-2}$	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
< 2000	0	10	7.7	36.4	18.2	14.3	16.7
2001-10000	28.6	30	38.5	9.1	9.1	7.1	50
10001-50000	57.1	60	15.4	36.4	27.3	28.6	8.3
50001-100000	14.3	0	15.4	9.1	9.1	7.1	0
100001-500000	0	0	23.1	0	27.3	35.7	25
≥ 500000	0	0	0	9.1	9.1	7.1	0
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
< 2000	25	0	16.7	14.3	15.4	0	16.7
2001-10000	33	20	33.3	28.6	7.7	33.3	16.7
10001-50000	16.7	40	16.7	28.6	23.1	11.1	16.7
50001-100000	0	40	16.7	14.3	23.1	0	0
100001-500000	25	0	16.7	14.3	30.8	22.2	50
≥ 500000	0	0	0	0	0	33.3	0

Appendix 7. Percentage of the Cyanophyta, represented by 6 size classes, observed on the surface of *Typha angustifolia* from May to November, 1998 in Willow Pond, Matthai Botanical Gardens, Ann Arbor, MI.

All Cyanophytes observed							
u m^3 cm^{-2}	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
1-500	0	0	0	0	6.3	0	0
501-1000	0	0	0	11.1	12.5	6.3	0
1001-2000	0	0	20	0	18.8	6.3	18.2
2001-4000	0	20	0	22.2	12.5	18.8	9.1
4001-8000	0	20	40	11.1	12.5	18.8	27.3
≥ 8000	0	60	40	55.6	37.5	50	45.5
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
1-500	0	0	0	0	0	0	20
501-1000	14.3	10	0	7.1	0	0	20
1001-2000	14.3	10	18.2	7.1	20	0	0
2001-4000	14.3	10	9.1	0	0	37.5	0
4001-8000	42.9	40	18.2	21.4	10	0	0
≥ 8000	14.3	30	54.5	64.3	70	62.5	60
Cyanophytes observed inside *Typha* stand							
u m^3 cm^{-2}	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
1-500	0	0	0	0	12.5	0	0
501-1000	0	0	0	0	12.5	25	0
1001-2000	0	0	25	0	12.5	0	25
2001-4000	0	0	0	50	12.5	25	0
4001-8000	0	0	50	0	12.5	25	50
≥ 8000	0	100	25	50	12.5	25	25
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
1-500	0	0	0	0	0	0	0
501-1000	20	0	0	0	0	0	33.3
1001-2000	20	0	14.3	12.5	16.7	0	0
2001-4000	20	0	14.3	0	0	60	0
4001-8000	20	60	28.6	0	0	0	0
≥ 8000	20	40	42.9	87.5	83.3	40	66.7
Cyanophytes observed outside *Typha* stand							
u m^3 cm^{-2}	13-May	27-May	10-Jun	24-Jun	8-Jul	27-Jul	5-Aug
1-500	0	0	0	0	0	0	0
501-1000	0	0	0	20	12.5	0	0
1001-2000	0	0	0	0	25	8.3	14.3
2001-4000	0	33.3	0	0	12.5	16.7	14.3
4001-8000	0	33.3	0	20	12.5	16.7	14.3
≥ 8000	0	33.3	100	60	37.5	58.3	57.1
	29-Aug	2-Sep	16-Sep	29-Sep	15-Oct	29-Oct	14-Nov
1-500	0	0	0	0	0	0	50
501-1000	0	20	0	16.7	0	0	0
1001-2000	0	20	25	0	16.7	0	0
2001-4000	0	20	0	0	0	0	0
4001-8000	100	20	0	50	0	0	0
≥ 8000	0	20	75	33.3	83.3	100	50

Table 4. ANOVA of sample date and sample location (±SE) on densities and total biovolumes of the algae-cyanobacteria genera observed on the surface of *Typha angustifolia* detritus from May to November 1998 in Willow Pond, Matthaei Botanical Gardens, Ann Arbor, MI.

DENSITY																
	Achnanthes		*Chroococcus*		*Cosmarium*		*Cymbella*		*Fragilaria*		*Gomphonema*		*Mastogloia*		*Mougeotia*	
EFFECT	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**
Day	13	0.95	13	1.17	13	2.89**b**	13	1.26	13	9.09**a**	13	0.71	13	1.6	13	3.92**a**
Location	1	1.54	1	1.25	1	3.17	1	1.24	1	0.66	1	1.57	1	2.52	1	0
Day x Location	13	0.96	13	1.13	13	3.78**b**	13	1.23	13	1.83	13	0.86	13	1.01	13	0.72
	Navicula		*Nitzchia*		*Oedogonium*		*Oscillatoria*		*Rhopalodia*		*Scenedesmus*		*Spyrogyra*		*Synedra*	
	d.f.	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**
Day	13	1.48	13	1.08	13	1.45	13	1.36	13	0.95	13	0.87	13	0.72	13	11.92**a**
Location	1	0.07	1	0.63	1	0.48	1	0.03	1	0.23	1	0.1	1	0.05	1	0.5
Day x Location	13	1.78	13	1.03	13	1.42	13	1.6	13	1.2	13	0.7	13	0.92	13	1.06
TOTAL BIOVOLUME																
	Achnanthes		*Chroococcus*		*Cosmarium*		*Cymbella*		*Fragilaria*		*Gomphonema*		*Mastogloia*		*Mougeotia*	
EFFECT	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**
Day	13	1.71	13	0.85	13	1.56	13	0.29	13	6.49**a**	13	1.01	13	1.66	13	1.87
Location	1	1.22	1	0.12	1	0.93	1	0.26	1	0.47	1	1.02	1	1.6	1	1.06
Day x Location	13	0.88	13	1.29	13	1.84	13	0.43	13	0.86	13	1	13	0.78	13	0.6
	Navicula		*Nitzchia*		*Oedogonium*		*Oscillatoria*		*Rhopalodia*		*Scenedesmus*		*Spyrogyra*		*Synedra*	
	d.f.	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**	**d.f.**	**F**
Day	13	2.91**b**	13	1.13	13	1.45	13	1.01	13	0.85	13	0.81	13	0.66	13	9.45**a**
Location	1	0.47	1	0.75	1	0.1	1	0.94	1	0.31	1	1.36	1	0.44	1	0.75
Day x Location	13	2.84**b**	13	1.17	13	0.3	13	1.08	13	1.15	13	0.9	13	1	13	1.18

a= $p \leq 0.001$; **b**= $p \leq 0.01$