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Response of the Epiphytic Algal Communities to Experimentally Elevated Nutrient Levels in Intertidal Salt Marsh Habitats

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RESPONSE OF THE EPIPHYTIC ALGAL COMMUNITIES TO EXPERIMENTALLY ELEVATED NUTRIENT LEVELS IN INTERTIDAL SALT MARSH HABITATS

By

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Abstract

Epiphytes are organisms attached to plants and are responsible for the majority of primary productivity in many aquatic systems. While epiphytes serve as a valuable food resource to herbivores, they may prove deleterious to the host plant by competing for light and nutrients, as well as increasing sheer stress. This study evaluated the impacts of nutrient additions, nitrogen and phosphorus, on the epiphytic algal community on *Spartina alterniflora* over the course of two growing seasons. Three nutrient treatments (N, P, and N+P) and one control treatment were placed in a salt marsh in the Tolomato River during the growing seasons of 2011 and 2012. To assess community development, we examined biomass, ash-free dry mass (AFDM), chlorophyll-*a* levels, cell counts, and community diversity by algal division. The nutrient additions did not significantly alter any of the measured parameters in either sampling year. However, the sampling month did have a significant ($p<0.05$) effect on biomass, chlorophyll-*a*, and community composition. A total of 155 infrageneric taxa were identified. Biomass tended to be dominated by diatoms and red algae, while cyanobacteria were most abundant. In both years, biomass was highest in the spring with a second smaller pulse in the fall. Conversely, chlorophyll-*a* levels varied between the years and did not show the same

monthly patterns as AFDM. A laboratory study subjecting *S. alterniflora* to the same nutrient additions also found no significant effects of increased nutrients, but did observe temporal changes in biomass and chlorophyll-*a* levels. Overall, epiphytic growth was not influenced by nutrient additions in this study suggesting that this and other similar salt marsh systems may be resilient to anthropogenic eutrophication. Instead, other factors, such as light and herbivory, likely played a key role in determining epiphytic algal growth and community composition.

Introduction

Eutrophication of aquatic systems from anthropogenic sources has increased over the past decades primarily from fertilizer runoff, human waste, and agricultural runoff (Lin *et at.,* 1996; Valiela *et al.,* 1997; Gil *et al.*, 2006; Kebede-Westhead *et al.*, 2006). Fertilizers, whether chemically manufactured or created from animal excrement, are typically applied to soils, and when applied in excess leach through the soil into the ground water or directly enter nearby watersheds via surface runoff (Balata *et al.*, 2008). Human waste from failing septic tanks or from inadequate waste treatment facilities also enters the water system creating elevated levels of nutrients (Edmondson *et al.,* 1956; Malueg *et al.,* 1973). Increases in nutrient levels, particularly nitrogen and phosphorus, have negatively impacted estuarine, freshwater, and marine systems around the world (Howarth *et al.*, 2000; Cardoso *et al.,* 2004).

Increased eutrophic conditions in aquatic environments may alter natural algal biomass and community composition (Fairchild *et al.,* 1985; Armitage *et al.,* 2006). These conditions may lead to upward cascading effects on grazers and macrophytes (Cattaneo *et al.*, 1998; Garcia *et al.*, 1999), result in anoxic conditions (Heck *et al.*, 2006), and reduce macrophyte growth (Sand-Jensen, 1990; Ozimek *et al.*, 1991; Valiela *et al.*, 1997; Cardoso *et al.*, 2004). Algal blooms are episodic in nature and typically occur when high nutrient levels allow for rapid growth of microalgal species. While many algal blooms are short lived, harmful effects may have long lasting impacts on communities in aquatic environments. Valiela *et al.* (1997) showed that blooms have the capacity to displace native macrophytes, corals, and algae due to direct

harmful chemical effects and anoxic conditions from bacterial decomposition. The common thread of these impacts is the increased growth of algae, which rapidly uptake nutrients, in turn leading to a high rate of reproduction. Many studies have assessed the interactions between algal growth, macrophytes, and food web dynamics (e.g., Karez *et al.*, 2000; Chase and Knight, 2006), however, few studies have addressed the impacts of increased nutrient levels on epiphytic algal community composition.

Aquatic algae exhibit numerous growth forms and habitat preferences. Planktonic algae drift or swim through the water column, where they provide a food source to many larger organisms such as crustaceans and fish (McCormick *et al.*, 1998). As important as phytoplankton are to aquatic systems, other assemblages exist which provide many similar benefits to the aquatic environment. These assemblages include benthic (periphyton) algae, epilithic (rock-living) algae, epipelic (sediment-living) and episammic (sand-living) algae, and epiphytic (plant-living) algae. The different terms given to algal assemblages are derived from the substrate on which the algae are associated. Some algal species are not confined to a single assemblage community, but utilize different substrates depending on life history strategies, environmental conditions, or spatial and temporal variability (Anesio *et al.*, 2003).

Benthic algae is a broad term that refers to algae attached to or associated with bottom substratum. Some benthic algae attach to the benthos while others remain motile to move along the substratum. Epipelic and episammic algae assemblages are specifically those colonizing sediments and sand, respectively. Epilithic algae colonize hard substrate such as rocks, boulders, and bedrock (Wehr and Sheath, 2003). These three assemblages fall under the umbrella term of benthic algae. The remaining assemblage is algae living on or using vegetation as a substrate known as epiphytes (Frankovich and Fourqurean, 1997).

Macrophytes are important to aquatic system for primary and secondary production (Twilley *et al.* 1985) and macrophytes have extensive underground root and rhizome structures which aid in sediment retention (Orth and Moore, 1984). Their roots and rhizomes also contain large stores of nutrients such as phosphorus and nitrogen which provide essential nutrients to the plant when ambient levels in the water are low or assimilation through leaf blades is limited (Cornelisen and Thomas, 2004). As the plants die or senesce leaves and stems, the nutrients and plant material that settle on the benthos may enter the sediments through bacterial biodegradation or sedimentation (Haack and McFeters, 1982; Moeller *et al.*, 1988). The sediments contain essential phosphorus which can efflux back into the water column at the sediment-water interface under anoxic conditions (Frevert, 1979; Bostrom *et al.*, 1982; Carlton and Wetzel, 1988). Phosphorus can also cycle back into the water column by benthic organisms reworking the sediment through bioturbation or by directly consuming organic material with phosphorus attached to it (Zicker *et al.*, 1965; Nalepa *et al.*, 1983; Barbiero and Welch, 1992).

Algae, much like macrophytes, are a vital component to aquatic systems, whether in temperate lakes or tropical estuaries, providing structural habitat for marine organisms (macroalgae), producing oxygen, nutrient cycling, and serving as a primary food source to many invertebrate species (Eppley and Peterson, 1979; Bronmark, 1985; Caraco *et al.*, 1992; Moncreiff *et al.*, 1992; Williams and Ruckelshaus, 1993; Tiffany and Lange, 2002). Epiphytic communities are exceedingly diverse and important primary producers, with species variability depending on host specifications including: temperature, spatial and temporal influences, and water chemistry (McIntire, 1968; Lowe and Pan, 1996). Communities can range from filamentous green algae to silicaceous diatoms to blue-green algae (Stowe, 1982; Moncreiff *et al.*, 1992; Chung and Lee, 2008). Some of these epiphytes (e.g., diatoms) attach directly to the

submerged aquatic vegetative substrate, while others (e.g., cyanobacteria) are in loose association with the aquatic vegetation.

All aquatic algal groups require nutrients within the water column, benthos, or host organism. Aquatic environments are extremely heterogeneous, likely making the availability of required nutrients temporally and spatially variable. Nitrogen and phosphorus are commonly viewed as the most important and typically most limiting nutrients for algal growth (Havens *et al*., 2001). The importance of these nutrients is based on necessary cellular functions. Nitrogen is essential for the production of amino acids, chlorophyll, and other nitrogen containing compounds. Phosphorus is essential for DNA synthesis, generation of ATP, and proteins. Aquatic systems with low nitrogen and phosphorus levels limit algal cell's ability to perform essential cellular functions and expend energy to reproduce.

Nitrogen is seen as the most limiting factor for algal growth in coastal marine environments (Howarth, 1988; Vitousek *et al*., 1997). Most nitrogen absorbed by plants and algae is in the biologically available forms of ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-). Ammonium and nitrates originate from organic material including urea, excreted amino acids, or bacterial decomposition. However, the main source of nitrate in aquatic systems comes from terrestrial runoff and human activities (sewage, fertilizers, and industrial waste). Usage of these different nitrogen species varies by algal and plant species and soil conditions (e.g. pH). While atmospheric nitrogen (N_2) is biologically unavailable, cyanobacteria are able to fix N_2 into cellular nitrogen and NH_4^+ making it available to other organisms (Graham *et al*., 2009). Fixing nitrogen is energetically expensive and observed as an inducible physiological activity. Therefore, fixation will only occur when ambient nitrogen levels fall below biological demands (Wolk, 1973; Graham *et al.*, 2009).

Phosphorus is typically the limiting factor for algal growth in freshwater environments (Frankovich and Fourqurean, 1997). Phosphorus is typically supplied to aquatic systems as dissolved inorganic orthophosphates from terrestrial sources similar to those of nitrogen (i.e. sewage, fertilizers, industrial waste) or from rock weathering. Phosphate $(PO_4)^{3-}$ has a strong affinity to bind to metal cations or organic molecules causing it to precipitate out of the water column. The phosphate may remain in the sediment until benthic organisms consume it or water currents resuspend the material (e.g. spring and fall turnover). Phosphorus is able to continually cycle through the aquatic environment via uptake by organisms and sedimentation of organic material.

When epiphytic algae attach to vegetation, mobility is restricted and the ability to capture nutrients from the water column is limited. These algae possess physical and chemical adaptions for nutrient acquisition such as enzymatic production of alkaline phosphatase, ability for heterotrophic energy production, luxury consumption and storage capabilities in times of plenty (Pringle, 1990; Rugenski, 2008). For example, phosphatase is secreted by algal cells in periods of low phosphorus concentrations to cleave phosphates from organic molecules to make them available to the algae (Wehr and Sheath, 2003). Further, macrophytes may provide epiphytes with dual the benefits of substrate and a nutrient source. Phosphorus from the macrophyte leaches into the water where it is readily absorbed by the attached epiphyte (Rogers and Breen, 1981).

Aquatic systems are commonly influenced by allochthonous sources of nutrients. Anthropogenic eutrophication manifests itself through algal blooms which have detrimental impacts on the macrophyte community (Short *et al.*, 1993). Epiphytic algal buildup on macrophytes reduces photosynthetic available radiation (PAR) for submerged macrophytes from

biogenic turbidity and leaf loading (Sand-Jensen, 1990; Gross *et al.*, 2003). Increased epiphytic algae may reduce the diffusion of nutrients from the water column to the macrophyte leading to reduced host plant growth and biomass (Twilley *et al.*, 1985; Coleman and Burkholder, 1994; Hauxwell *et al.*, 1998; Nelson and Lee, 2001; Fourqurean, 2010). In high water velocity or turbulent aquatic systems, macrophytes have adapted leaf structures to reduce drag from water movement. Large colonies of epiphytes increase surface area and friction on the macrophyte leaf surface resulting in potential tearing or damage of the vegetation (Littler and Littler, 1999).

Epiphytes do not always have detrimental effects on the host (Gacia *et al.*, 1999). Epiphytes and macrophytes can co-exist when waters have nutrient level ranges within natural limits. While epiphytic algae benefit from the macrophyte as a substrate and a source of secreted nutrients (Irlandi *et al.*, 2004), macrophytes may benefit from the reduced grazing pressure by herbivores (e.g. Karez *et al.*, 2000; Gil *et al.*, 2006; Fonseca and de Mattos Bicudo, 2010). This relationship relies on a healthy ecosystem to provide positive feedback involving herbivores consuming epiphytes from the surface of macrophyte leaves, large quantities of nutrients being absorbed by macrophytes, and water clarity allowing for adequate light penetration (Valiela *et al.*, 1997).

Nutrient concentrations in the water influence algal growth rates. Larger classes of green algae and cyanobacteria are found to have lower growth rates, but are able to absorb and store a greater amount of nutrients for steady growth regardless of ambient water nutrient content (Nielsen, 2006; Graham *et al.*, 2009). One morphological adaptation that small algal cells have obtained is simple geometric shapes with high surface area:volume (SA/V) ratios. Smaller algal cells with higher SA/V ratios are able to have rapid nutrient consumption and rapid growth rates.

These smaller algal cells, typically phytoplankton, increase in abundance during nutrient pulses, but are usually limited to periods of excess nutrient availability (Graham *et al.*., 2009).

Changes in epiphytic communities can quickly shift from slow-growing macroalgal species to microalgae with exponential growth rates (Smith *et al*., 1999; Havens *et al.*, 2001). Small cyanobacteria and phytoplankton exhibit faster growth rates than larger macroalgae (Reynolds, 2006). Phytoplankton and cyanobacteria have growth rates that exceed benthic diatoms and filamentous green algae, suggesting community shifts may occur with additional levels of nitrogen and phosphorous in the water (Coleman and Burkholder, 1994; Pedersen and Borum, 1997; Armitage *et al*., 2006). However, natural nutrient concentrations fluctuate seasonally creating temporal limits for microalgae growth. Larger algal species or those with slower growth rates are able to persist perennially while cyanbacteria have seasonal fluctuations in abundance (Greenwood and Rosemond, 2005).

The southeastern United States has numerous river systems that flow into the Atlantic Ocean and the Gulf of Mexico, where they form estuaries (Frazel, 2009). These coastal lowlands are ideal for creating salt marsh estuaries at the mouth of the rivers where tidal influences are important. Intertidal salt marshes in the southeastern US are dominated by one macrophytic plant species, *Spartina alterniflora* (McLusky, 1981). These salt marshes are extremely productive ecosystems and have been referred to as the "nurseries of the sea" (US EPA, 2011). Natural tidal influences allow for marine organisms to enter the transitional zone of freshwater systems. Estuaries provide natal habitat for marine mammals, nesting habitat for bird species, and food sources and protection for many fish species, and saline levels appropriate for oysters and mollusks (Coen *et al*., 2007; Barnes *et al*., 2007).

Many studies have been conducted to determine the impacts to the phytoplankton and epiphytic algal growth, while few studies have addressed the implications to the epiphytic community composition (Cattaneo and Kalff, 1980; Moss, 1981; Borum, 1985). Epiphytic algal biomass has been shown to increase from nutrient enrichment leading to negative impacts on the host vascular plants such as increased drag and decreased sunlight attenuation. As algae are a key component of estuarine energetics, alterations to this energy base may play a pivotal role in the health and productivity of the aquatic ecosystem.

The purpose of the study is to evaluate the response of the intertidal salt marsh epiphytic algal community to elevated nutrient levels. Nutrient levels were experimentally raised to reflect potential anthropogenic enrichment levels. Using both field and laboratory experiments, several metrics were examined to determine the response of the epiphytic algal community. Changes will be evaluated based on biomass measured by community composition, biomass, and chlorophyll-*a* over the course of two growing seasons. Also, within these metrics, the specific *Spartina* island will be evaluated to determine if the location within the study site and month influences algal growth. This information will provide scientific information on a community where currently little is known, and can increase knowledge of the impacts to coastal systems as anthropogenic impacts increase.

Materials and Methods

Study System

The Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR) is a protected estuarine reserve located in northeast Florida, and is one of 27 research reserves within

the National Atmospheric Administration's (NOAA) network of United States National Estuarine Research Reserve System. The name of the reserve stems from the three river systems producing the estuary, the Guana, Tolomato, and Matanzas. The Guana and Tolomato Rivers converge south of Pine Island and flow into the Atlanta Ocean through the St. Augustine Inlet.

Nine creek systems flow into the Tolomato River, six flowing east into the river and three flowing west. The drainage basin of the river encompasses a total of approximately 84 square miles. Much of the drainage basin is outside of the Reserve, granting the management of the upland and wetland habitats to the private sector. As part of the intracoastal waterway, the main channel of the Tolomato River is dredged to maintain a navigable water way. The basis of this research occurred within the smooth cordgrass (*Spartina alterniflora*) salt marshes of the Tolomato River. The substrate that these salt marsh plants persist on is primarily intertidal sand and mud flats (Frazel, 2009). Some areas within the mud flats have hard substrate comprised of oyster beds.

Field study

Nutrient additions manipulations were performed at three different salt marsh islands located at a single intertidal site along the Tolomato River in the northern portion of the GTM estuary located on the Atlantic coast of northeast Florida (Figure 1). To accommodate all required nutrient treatments, three small islands (i.e., 10-20 m circumference) were randomly selected from a group of islands that had monospecific stands of *S. alterniflora*, experienced regular tidal inundation, and had limited external environmental alterations (e.g., undisturbed salt marsh with no shoreline development). The three salt marsh islands were located off of the main river channel, generally had mixed open mud and oyster reef substrates, and were within 10-20

m proximity of each other (thus similar environmental conditions). Experimental 1 m^2 plots were established around the perimeter of each of the *S. alterniflora* islands. At each sample plot, one of four nutrient treatments was randomly assigned: non-enriched control (C), nitrogen enrichment (N), phosphorus enrichment (P), and a combined nitrogen + phosphorus enrichment (N+P); with each treatment delivered in nutrient-diffusing agar in a 125 mL clay pot. Each treatment was replicated eight times (thus n = 32 plots total) and distributed around the three islands (n = 10 treatments on two of the islands and 12 on the third). Individual sample plot treatments were identified by placing pin flags labeled with the treatment (C, N, P, N+P) and number (1-8) in the substrate.

Elevated levels of nutrients were made to mimic eutrophic conditions created by heavy inputs of nutrients from anthropogenic or natural sources using previously established levels (Fairchild *et al.*, 1985; Corkum, 1996). To produce the desired experimental nutrient manipulations within the clay pots the following 1 L solutions were made: control – 20 g of agar, nitrogen – 50 g of agar and 82 g of calcium nitrate ($Ca(NO_3)_2$), phosphorous – 50 g of agar and 87.5 g of potassium phosphate ($KH_2(PO_4)$), and combined N+P – 80 g agar, 82 g of calcium nitrate and 87 g of potassium phosphate. The agar concentrations varied from 2% in the control treatment, 5% in the individual N and P treatments, and to 8% in the N+P treatment. An increased agar concentration was required for the combined N+P to solidify (Fairchild *et al.*, 1985, Corkum, 1996). The varying concentrations of agar were not seen to impact the diffusion rate of the nutrients, and therefore, not anticipated to influence algal responses (Rugenski *et al.*, 2008). Nitrogen, phosphorus, and combined N+P concentrations were each applied at 0.5M.

Sample processing

Plot establishment and baseline data occurred just before the 2011 growing season (March 2011-October 2011). Monthly sampling continued during the 2012 growing season (April-October 2012). Over the course of the two field seasons, 480 total samples were collected (2011: 32 samples/month * 8 month; 2012: 32 samples/month * 7 months). During monthly sampling, each plot was examined for the following metrics: epiphytic algal community composition, total epiphytic algal biomass, and chlorophyll-*a* levels. One *S. alterniflora* stem was haphazardly selected and removed from within 0.25 m of each clay pot. The stem was cut at a length of 10-20 cm and placed in a collection bottle to be processed upon returning to the laboratory. The length of each stem was recorded to determine the surface area from which the algae were attached. Epiphytic algae were removed from the stem utilizing a modified technique of Fairchild et al. (1985) by gently scraping off all growth. Algae were returned to the collection bottle where 10 mL of 2.5% gluteraldahyde and 40 mL of water was added for sample preservation. Due to the sensitivity of chlorophyll-*a* todegrade to phaeophytin, immediate chlorophyll-*a* readings were taken utilizing a Turner Model 7200 fluorometer (Turner Biosystems, Sunnyvale, CA). The chlorophyll-*a* levels were then calculated to account for the stem area and expressed as μ/cm^{-2}. Homogenized samples were further examined for algal community species composition and biomass. Bio-assay samples (10 mL) were pipetted into scintillation vials for species identification. The remaining sample was filtered using Whatman glass fiber filters (GFIF) to obtain biomass. The GFIF filters provided a carbon-free filter paper able to withstand the combustion of samples.

Biomass from each of the 32 samples was determined by obtaining the ash-free dry mass (AFDM). After filtration, the samples were placed in a drying oven at 80°C for a period of 24

hours. Once dried, they were placed in a desiccator to cool to room temperature and were then weighed to the nearest ten-thousandth grams. Ashed masses were obtained by combusting the samples at 500°C for a period of 90 minutes, cooling, and then weighing each sample.

The 10mL bio-assay samples were examined via microscope for species identification and enumeration using a 0.1 mL aliquot placed on a slide. A minimum of 400 cells were counted in each sample and biovolumes calculated using previously published geometric shapes (Wetzel and Likens, 1991). Three methods of algae biovolume estimation and species identification were used: 1) 400 cell count, 2) three sweep scans, and 3) three half slide scans. Each organism observed was identified to the lowest level possible using taxonomical keys (e.g. Schneider and Searles, 1991; Cox, 1996; Komárek and Anagnostidis, 1999; Hindák, 2008).

Because of the close proximity of the three marsh islands at the study site, water quality parameters (i.e. salinity, temperature) were collected using a YSI 85 handheld meter (YSI, Yellow Springs, Ohio). In addition, continuous water quality and monthly nutrient data were collected at the nearby GTMNERR Pine Island station (30.050615, -81.367922; approx. 5 km south) and made available through the NOAA NERR Centralized Data Management Office (CDMO) website (http://cdmo.baruch.sc.edu/).

Lab study

To assess epiphytic alagal community biomass and chlorophyll-a shifts in a controlled environment, a laboratory study was conducted under ambient conditions in a nearby greenhouse facility (located on the roof of the UNF Biological Sciences building). Whole *S. alterniflora* plants (e.g. root mass and aboveground plant material) were collected from the salt marsh

approximately 100 m from the *in situ* nutrient manipulation site along the Tolomato River. Three living plants were placed into one of 24 individual 5-gal buckets, and a nutrient treatment (n = 6 for each treatment) was randomly assigned to each bucket following similar nutrient concentrations outlined above. An electronic air pump was installed to circulate the water in each bucket for the duration of the experiment. Salinity levels were maintained between 29-40 ppt, the typical range in which the salt marsh fluctuated during field collections. Lab experiments began in October 2012 and ran for a period of 28 days.

Three sampling events occurred over the 28 day experiment: day 0, day 14, and day 28. One *S. alterniflora* stem was clipped at a length of approximately 15 cm and placed in a collection bottle to be immediately processed. The metrics of ash-fee dry mass, chlorophyll-*a*, and community composition were obtained following the same procedure performed for samples collected in the field study.

Data analysis

Biotic Data

The epiphytic algal growth represented by chlorophyll-*a* and AFDM served as an indicator for responses to eutrophic water conditions. Biomass and chlorophyll-*a* were compared for each treatment (C, N, P, N+P) over the course of the two sampling years and between the three islands to determine if there was a significant effect ($p<0.05$) from nutrient addition to epiphytic algae using a mixed-model-repeated-measures Analysis of Variance (ANOVA) using the program SAS 9.2 (SAS, Cary, North Carolina).

Epiphytic algal community-level response variables recorded included species abundance (# of cells), density (cells/cm^2), and biovolume ($\mu m^3/cm^2$). Species abundance was based on cell counts and species density was calculated by dividing the species cell counts by the stem area. Biovolumes for each organism were estimated from work conducted by Hillebrand *et al.* (1999) and was calculated as the volume of each cell in relation to the total epiphytic algal colonization on the *Spartina*.

To determine how species grouped together with respect to nutrient treatment, community composition of the different treatments and time periods were analyzed using the Non-metric Multidimensional Scaling (NMDS) technique within SAS 9.2. Differences in community diversity (species richness and relative abundance) were determined by calculating values from the Shannon-Wiener Index (H′) (Shannon-Weaver, 1949):

$$H' = -\Sigma(P_i * \ln P_i)$$

where P_i equals the proportion of individuals observed in each sample to the total number of individuals in each sample.

Values for the Shannon-Wiener Index can range from 0 to rarely above 5 indicating the biodiversity of a system, however, biological values typically range from 0 to 4.0 (Magurran, 2004). An Index value of 0 would indicate only one species present in the system and increasing values indicate greater species richness and even relative abundances. Determination of significance of diversity ($p<0.05$) from each treatment was analyzed using the mixed-model-repeated-measures ANOVA in SAS 9.2.

From calculations of H′, community evenness (E) was determined to allow for comparisons of relative abundances between the communities. Pielou's evenness calculations were made using the following equation:

$$E = H' / \ln(S)$$

where S equals the total number of species in the community

Values can range between 0 – 1. Zero values indicate that the majority of species are rare and the community has a few species that are very abundant. Values of 1 indicate species are equally abundant (Smith and Wilson, 1996). Community diversity indices will be analyzed using the mixed model repeated measures ANOVA in SAS 9.2.

Results

Field study results

Data collected during the two sampling seasons provided details on how the epiphytic algal community may respond to nutrient additions. Below, the data is presented by the three metrics, community composition, algal biomass, and chlorophyll-*a* levels. Within each metric, the sampling years were separated to determine if similar trends occurred over the course of two years. Background environmental characterists and study site analysis was also presented to determine if the site influenced the results.

Sampling occurred monthly to collect *Spartina* stems. Even with the efforts to collect samples from every plot each month, some samples were unobtainable due to field difficulties. A list of missing sampling data is presented in Table 1.

Environmental Characteristics

Water temperature, salinity, and dissolved oxygen were collected from the field site during each monthly sampling event (Table 2). In 2011, data collected at the study site ranged from a low 29.2 ppt in September to a high of 42 ppt in August. Rainfall data collected from St. Johns River Water Management District (SJRWMD) archived hydrological data indicated that no rainfall occurred within 5 days of the monthly salinity readings that would have flushed large quantities of freshwater into the river system thereby reducing salinity levels. Water temperatures increased as spring and summer progressed and then decreased during the fall months. Temperatures ranged from 19.2 ºC in October to 30.4 ºC in August. The average dissolved oxygen levels was 4.84 mg/L and ranged from 3.10 to 6.40 mg/L.

In 2012, salinity levels varied throughout the sampling season with a general trend of decreased concentrations in the summer months. Levels ranged from 10.5 ppt in August to 37.9 ppt in May. Precipitation data was collected from the SJRWMD archived hydrological data. Precipitation measurements showed rainfall totals of over 28.2 mm in the 3-5 prior days from sample collection events in June and August, the two months with the lowest salinity levels. Water temperatures, as expected, were coolest in the early spring and late fall months with a steady increase throughout the summer months. Temperatures ranged from 16.7 ºC in October to 32.0 ºC in August. The average dissolved oxygen levels was 5.62 mg/L and ranged from 2.98 to 6.92 mg/L.

Nutrient data for 2011 and 2012 showed varying levels of phosphate (PO_4), ammonium (NH_4) nitrite (NO_2) and nitrate (NO_3) throughout the growing season (Table 2).

Island Effects

In this study, data was collected from three separate, but closely located *Spartina* islands. Biomass (mg/cm^2) and chlorophyll-*a* (µg/cm^2) were not significantly ($p=0.2371$) influenced by the specific island in which data were collected. Islands showed significant ($p<0.001$) monthly change in biomass for the three islands with a spring maximum (March-May) with a second lesser fall maximum occurring in August and September (Figure 2). Island 1, 2, and 3 had a spring maximum of 0.34 mg/cm^2, 0.38 mg/cm^2, 0.40 mg/cm^2 respectively in March and an apparent outlying spike of 0.45 mg/cm^2 at Island 3 in May. Summer low biomass values for Island 1 was 0.05 mg/cm^2 in May, 0.14 mg/cm^2 for Island 2 in July, and 0.13 mg/cm^2 for Island 3 in June. The secondary fall maximum ranged from 0.29 mg/cm^2 at Island 2 in September to 0.18 mg/cm^2 at Island 3 in August.

Chlorophyll-*a* also showed a significant ($p<0.001$) monthly fluctuation at each of the islands (Figure 3). Chlorophyll-*a* levels remained relatively stable from March to August, varying at the most by 0.89 µg/cm^2 (1.27-2.16 µg/cm^2) at Island 3 during that time period. March chlorophyll-*a* levels were 1.11 µg/cm^2, 1.27 µg/cm^2, and 1.27 µg/cm^2 at Islands 1, 2, and 3, respectively. September and October levels increased significantly at each island reaching a maximum of 5.33 µg/cm^2 at Island 2 in October.

Based on non-significant differences between islands in biomass and chlorophyll-*a* measurements, it was deemed that the islands had no influence on the treatments. Therefore, the biomass and chlorophyll-*a* data were combined from each island were grouped together as one site for all further analysis.

Epiphytic algal community composition

2011

Abundance

Algal cell counts were grouped together by division within each nutrient treatment (Bacillariophyta (diatoms), Chlorophyta (green algae), Cyanobacteria (blue-green algae), and Rhodophyta (red algae)). Cyanobacteria were the most abundant in each nutrient treatment for each month. The greatest abundance of cyanobacteria was present in August within the nitrogen treatment totaling 19,248 cells (89%) of the total nitrogen epiphytic abundance (Figure 4A and Figure 4B). Green algae consistently had the lowest total abundance within each nutrient treatment, reaching the highest proportion of total community abundance (5%, 108 total cells) in March within the control treatment and the lowest proportion (0%, 21 total cells) in July within the nitrogen treatment. Diatoms and red algae were found in moderate abundances each month with reds frequently observed second in total abundance to cyanobacteria. The overall proportion of the community that comprised of diatoms and reds were 9% (3-20%) and 13% (2-28%), respectively. Four samples, control-March, nitrogen-September, nitrogen+phosphorous-September, and nitrogen+phosphorous-October, were the only data sets that showed diatoms to be more abundant than red algae (Table 3).

Nutrient treatments had no significant effect on the abundance of epiphytic algae in any of the four divisions. However, monthly variations in abundance of overall epiphytic growth were present. Total abundance was lowest in March with a total of 10,064 cells, however, care must be taken into account due to a sample size of n=22 resulting from the agar solidification failure. Total abundance of the community increased from March through August where the

maximum epiphytic abundance reached 75,032 cells followed by a decline through October (38,771 cells) (Figure 5).

Each algal division saw a significant effect of month affecting the abundance of those species (Figure 6). Cyanobacteria had a highly significant ($p<0.0001$, $df=28$) monthly abundance patterns that followed that of the total epiphytic abundance pattern. Green algae abundances showed significant ($p=0.0012$, $df=28$) monthly variation. Greatest abundance of green algae was observed in the spring and fall months with the lowest abundance occurring in July with a total of 84 cells (Table 4). Monthly diatom abundance was highly significant ($p<0.0001$, $df=28$). Monthly changes showed a slow increase over the course of the growing season from a low abundance (1,113 cells) in March to a high (5,170 cells) in October. Red algal abundance had a significant ($p=0.0162$) monthly change in abundance that showed a less distinct trend. Abundances gradually increased from March (1,165 cells) until a maximum was reached in July (7,577 cells). The abundance decreased in August, but resumed the gradual increase through October.

Density

The density of epiphytic algal growth provided information on colonization that incorporates the *Spartina* stem area. Nutrient treatments had no significant effect on the density of epiphytic algae in any of the four divisions cyanobacteria ($p=0.0608$, $df=28$), green algae ($p=0.5387$, $df=28$), diatoms ($p=0.1362$, $df=28$), and red algae ($p=0.6129$, $df=28$). Total algal densities increased from minimum of 20,422 cells/cm^2 in March to a maximum of 218,822 cells/cm^2 in August after which the density decreased through October to 57,472 cells/cm^2 (Figure 7).

Epiphytic algal density exhibited significant time effect for all four divisions, cyanobacteria ($p<0.0001$, df=28), green algae ($p=0.0008$, df=28), diatoms ($p<0.0001$, df=28), and red algae ($p=0.0003$, df=28). Cyanobacteria had the greatest cell density each month of sampling (Figure 8). Monthly changes in cyanobacterial density were evident by gradual increases from 14,921 cells/cm^2 in March to 193,889 cells/cm^2 in August followed by a density decrease through October which totaled 33,863 cells/cm^2 (Table 5). Green algae consistently had the lowest cell densities observed of the four divisions. The monthly densities were greatest in early spring and late fall - March with 781 cells/cm^2 and October with 591 cells/cm^2 - with declining densities towards the summer months with a minimum density in July of 95 cells/cm^2. Diatom densities had an overall increase from March (1,936 cells/cm^2) through October (10,215 cells/cm^2). April and June had slight density decreases at which time increasing trend continued. Red algal densities fluctuated in a similar pattern as cyanobacteria throughout the months. Densities increased from a minimum in March (2,784 cells/cm^2) until a maximum density was reached in July (16,903 cells/cm^2) and then declined through October (12,803 cells/cm^2).

Biovolume

Another method to quantify epiphytic communities is based on the volume of each cell (biovolume). Monthly trends for biovolume showed a minimum in spring with March and April having a biovolumes of 5,056 cm^3/cm^2 and 4,150 cm^3/cm^2, respectively. Epiphytic biovolume greatly increased in May to 10,320 cm^3/cm^2 and maintained a consistent biovolume through July. Another increase in biovolume occurred in August (14,135 cm^3/cm^2) and continued through October with a monthly maximum of 16,251 cm^3/cm^2 (Figure 9).

Nutrient enrichment did not significantly affect the biovolume of any of the four divisions of algae, cyanobacteria ($p=0.1213$, $df=28$), green algae ($p=0.0606$, $df=28$), diatoms ($p=0.1040$, $df=28$), and red algae ($p=0.5494$, $df=28$). However, there was a significant effect of time on total epiphytic algal biovolumes in the four divisions, cyanobacteria ($p=0.0001$, $df=28$), green algae ($p=0.0006$, $df=28$), diatoms ($p<0.0001$, $df=28$), and red algae ($p=0.0058$, $df=28$). The greatest algal division biovolume during the sampling season occurred in October within the diatom division measuring 10,092 cm^3/cm^2 (Figure 10).

Cyanobacteria biovolumes increased from a low in March accounting for 262 cm^3/cm^2 to a high in August accounting for 2,182 cm^3/cm^2. Biovolume then declined through October to 444 cm^3/cm^2 (Table 6). Green algae had the lowest biovolume each month of sampling. Biovolumes ranged from 25 cm^3/cm^2 in July to 110 cm^3/cm^2 in March. Green algal biovolumes increased and decreased with no clear monthly trend. Diatom biovolume was the greatest for six of the eight sampling events, with red algae exceeding diatom biovolume the other two sampling events in June and July. Diatom biovolumes increased from April until June. From July through October, the biovolumes alternately increased and decreased. A minimum diatom biovolume occurred in April measuring 1,973 cm^3/cm^2. Red algal biovolumes increased from a spring minimum in March of 1,286 cm^3/cm^2 to a summer maximum in August of 6,060 cm^3/cm^2 and then declined slightly in the fall to 5,636 cm^3/cm^2 in October.

Community Diversity

A total of 137 infra-generic taxa were identified (Table 7) and represented four algal divisions: Bacillariophyta (diatoms), Chlorophyta (green algae), Cyanobacteria (blue-green algae), and Rhodophyta (red algae). Diatoms had a total of 72 taxa identified within 56 genera

and two groups of diatoms identified only to shape (centric and pennate). Green algae had a total of 16 taxa identified within 14 genera including one unknown species. Cyanobacteria had a total of 44 taxa identified within 19 genera, and red algae had a total of 5 taxa identified within 4 genera.

The dominant genus observed in any of the algal divisions was *Leptolyngbya* sp. (Table 7). The most abundant division was cyanobacteria with a total of 238,494 cells observed. The other three divisions had substantially fewer total cells observed. Green algae had a total of 2,265 cells with the dominant taxa of *Ulothrix* sp. with 680 cells observed. Diatoms had a total of 21,332 cells with the dominant taxa of *Melosira* sp. consisting of two taxa *Melosira* sp. (4,306 cells) and *Melosira moniliformis* (2,748 cells) observed. Red algae had a total of 35,315 cells with the dominant taxa of *Polysiphonia* sp. consisting of two species *Polysiphonia subtilissima* (16,153 cells) and *Polysiphonia atlantica* (3,412 cells) observed.

Species richness for the nutrient treatments varied from a mean of 25 species in the control treatment to 28 species within the nitrogen+phosphorus treatment (Table 8). A NMDS analysis of the species and nutrient treatments revealed no significant effect on the species community due to nutrient treatment. Thus, species richness was pooled to reflect monthly community changes. The number of species observed each month increased from the fewest species in March with 56 to a high of 87 in August (Table 9).

Biodiversity (H′) varied little between each nutrient treatment ranging from a mean of 1.75 in the nitrogen treatment to 1.83 in the nitrogent+phosphorus treatment. Community evenness (E) for the treatments ranged from a mean of 0.538 in the nitrogen treatments to a mean of 0.573 in the control treatments. No significance of nutrient treatment ($p=0.6648$, $df=28$) was present on H′. A significant ($p=0.0087$, $df=28$) effect of month on biodiversity was present.

Due to non-significant treatment effects, Shannon-Wiener Index values were calculated for each month. The diversity index increased through the sampling season with the minimum diversity observed in March with a mean of 2.15 and the greatest diversity observed in October with a mean of 3.00. Community evenness followed the same monthly increase with a minimum evenness in March and the greatest evenness in October (Table 9). Evenness was not significantly affected by nutrient or time ($p=0.2921$, $p=0.2599$, respectively), but there was a significant interaction between nutrient and time ($p=0.0236$, $df=28$). Using a one-way ANOVA, the nitrogen treatment was the only nutrient treatment that was significantly affected by month ($p=0.0095$, $df=40$).

2012

Abundance

Algal cell counts were grouped together by division within each nutrient treatment (Bacillariophyta (diatoms), Chlorophyta (green algae), Cyanobacteria (blue-green algae), and Rhodophyta (red algae)). Cyanobacteria were the most abundant in each nutrient treatment every month. The greatest abundance of cyanobacteria was present in April within the nitrogen treatment totaling 18,724 cells (91%) of the total nitrogen epiphytic abundance (Figure 11). Green algae consistently had the lowest total abundance within each nutrient treatment reaching the highest proportion of community abundance (3%, 261 total cells) in April within the control treatment (Table 10). Diatoms and red algae were found in moderate abundances each month with reds observed second in total abundance to cyanobacteria. The overall proportion of the community that comprised of diatoms and reds were 8% (1-17%) and 18% (4.55-31%), respectively.

Nutrient treatments had no significant effect on the abundance of epiphytic algae in any of the four divisions, cyanobacteria ($p=0.1365$, $df=28$), green ($p=0.0740$, $df=28$), diatoms ($p=0.7273$, $df=28$). However, monthly changes in abundance of epiphytic growth were present. Total cell abundance was greatest in May with a total of 59,139 cells and lowest in October with a total of 22,465 cells. Total abundance of the community had an overall decrease from April (49,080 cells) through October. May and September had increases in abundance from the previous month (Figure 12).

Three of the four algal divisions saw a significant effect of month on the abundance of those species, cyanobacteria ($p<0.0001$, $df=28$), green algae ($p=0.0001$, $df=28$), and diatoms ($p<0.0001$, $df=28$). The dominance of cyanobacterial cell abundance was the driving force of the total epiphytic abundance pattern (Figure 13). Cyanobacterial abundance was greatest in May with a total of 49,546 cells and lowest in October with 15,725 cells (Table 11). Greatest abundance of green algae was observed in April with 878 cells and declined over the course of the sampling season. No green algal cells were observed in the month of September which was followed by 19 cells observed in October. Over the sampling season, diatom abundances gradually increased from a minimum in April of 1,494 cells through October with 2,457 cells. Two population spikes occurred in June and August with 3,190 and 3,287 cells, respectively. Red algal abundances were not significantly ($p=0.3475$, $df=28$) affected by month. Abundances varied slightly from April to June ranging from 7,413 to 8,011 and then gradually decreased through October.

Density

Nutrient treatments had no significant effect on the density of epiphytic algae in any of the four divisions. Total algal densities were greatest in spring and early summer (April through July) and lowest in late summer through the fall (August through October). The densities ranged from a maximum of 94,569 cells/cm^2 in May to a monthly minimum in October with 29,694 cells/cm^2 (Figure 14).

Epiphytic algal density had significant monthly effects in all four divisions, cyanobacteria ($p<0.0001$, df=28), green algae ($p<0.0001$, df=28), diatoms ($p=0.0152$, df=28), and red algae ($p=0.0082$, df=28). Cyanobacteria had the greatest cell density each month of sampling (Figure 15). Monthly cyanobacterial densities were highest in May with 74,986 cells/cm^2 and lowest in August which totaled 16,680 cells/cm^2 (Table 12). Cyanobacteria had a monthly trend with greater densities from April through July and significantly lower densities in August through October. Green algae had the lowest cell densities observed of the four divisions each month. The monthly densities were greatest in early spring totaling 1,044 cells/cm^2 in April and decreased through the sampling season reaching a low in September when no green algal cells were observed. Green algae were again observed in October with a density of 50 cells/cm^2. Monthly diatom densities remained relatively consistent throughout the sampling season to range from a low of 2,453 cells/cm^2 in September to a high of 3,217 cells/cm^2 in October. Two density spikes occurred in June and August with 5,489 and 5,805 cells/cm^2, respectively. Red algal densities were greatest in the spring and early summer, April through June, and decreased through the fall. The maximum density occurred in April with 19,763 cells/ cm^2 with a minimum density of 7,202 cm^2 in September.

Biovolume

Monthly trends showed increasing epiphytic biovolume from April to August ranging from 9,232 cm^3/cm^2 to 11,884 cm^3/cm^2 (Figure 16). A substantial decrease in biovolume occurred in the fall to a monthly minimum of 3,828 cm^3/cm^2 in September.

Nutrient enrichment did not significantly affect the biovolume of any of the four divisions of algae cyanobacteria ($p=0.4144$, $df=28$), green algae ($p=0.3867$, $df=28$), diatoms ($p=0.5200$, $df=28$), and red algae ($p=0.2913$, $df=28$). However, the month of sampling significantly affected total epiphytic algal biovolumes in the four divisions, cyanobacteria ($p=0.0001$, $df=28$), green algae ($p<0.0001$, $df=28$), diatoms ($p=0.0003$, $df=28$), and red algae ($p<0.0001$, $df=28$). The greatest algal division biovolume during the sampling season occurred in June within the red algal division measuring 6,475 cm^3/cm^2 (Figure 17).

Cyanobacteria biovolumes had two monthly patterns, greater biovolumes from April through July and lower biovolumes from August through October (Table 13). The maximum biovolume was measured in May (896 cm^3/cm^2) and the minimum biovolume was measured in August (194 cm^3/cm^2). Green algae had the lowest biovolume each month of sampling. The green algal biovolumes decreased throughout the sampling season. Biovolumes ranged from 0 cm^3/cm^2 in September to 85 cm^3/cm^2 in April. The diatom division had the second greatest biovolume throughout the sampling season. A minimum diatom biovolume occurred in September measuring 1,532 cm^3/cm^2 and a maximum biovolume in August measuring 5,054 cm^3/cm^2. Red algal biovolumes were greatest in the spring through late summer (April through August). Maximum biovolume occurred in June with 6,475 cm^3/cm^2. Biovolumes decreased gradually from the maximum until August when the biovolume decreased by approximately 60% in September.

Diatom biovolume had a significant interaction between month and nutrient (p=0.0243, df=28). Using a one-way ANOVA, the nutrient treatments of nitrogen (p=0.0016, df=28) and the control (p=0.0122, df=28) showed a significant effect of time on the diatom biovolume. No other division had a significant interaction between month and nutrient treatment.

Community Diversity

A total of 118 infra-generic taxa were identified (Table 14) and represented four algal divisions: Bacillariophyta (diatoms), Chlorophyta (green algae), Cyanobacteria (blue-green algae), and Rhodophyta (red algae). Diatoms had a total of 59 taxa identified within 49 genera including two groups of diatoms identified only to shape (centric and pennate). Green algae had a total of 10 taxa identified within nine genera including one unknown species. Cyanobacteria had a total of 43 taxa identified within 20 genera including one unknown species. Red algae had a total of six taxa identified within five genera.

The most dominant genus observed in any of the algal divisions was *Leptolyngbya* sp. (Table 14). The most abundant division was cyanobacteria with a total of 195,318 cells observed. The other three divisions had substantially fewer total cells observed. Green algae had a total of 2,089 cells, the dominant taxa being *Ulothrix* sp. with 813 cells observed. Diatoms had a total of 16,266 cells with the dominant genus of *Melosira* sp. consisting of two taxa *Melosira* sp. (3,243 cells) and *Melosira moniliformis* (864 cells). Red algae had a total of 42,557 cells with the dominant taxa of *Polysiphonia* sp. consisting of two species *Polysiphonia subtilissima* (18,682 cells) and *Polysiphonia atlantica* (3,822 cells).

Species richness for the nutrient treatments varied from a mean of 25 species in the control treatment to 23 species in the nitrogen and nitrogen+phosphorus nutrient treatment

groups (Table 15). The species richness for each nutrient treatment was pooled monthly to determine the overall community compositional changes. The number of species decreased through the season from April with a maximum species richness of 90 species to 64 species in October.

The biodiversity (H′) of the epiphytic algal community was determined using the Shannon-Wiener Index. H′ varied slightly between each of the nutrient treatments over the course of the sampling season, ranging from a mean of 1.54 in the nitrogen+phosphorus treatment to 1.70 in the phosphorus treatment. The evenness of the communities for the treatments ranged from a mean of 0.50 in the nitrogen+phosphorus treatment to 0.54 in the phosphorus treatment (Table 15). Biodiversity calculations were tested for significance by performing a repeated measures mixed model ANOVA, for each nutrient treatment and month. No significant effect of nutrient treatment ($p=0.2602$, $df=28$) was present on H′. A significant ($p<0.0001$, $df=28$) effect of month on biodiversity was present.

Due to non-significant treatment effects and significant monthly effects, Shannon-Wiener Index values were calculated for each month. Epiphytic algal community H′ ranged from a mean of 2.24 in September to a mean of 2.86 in April-June (Table 16). When the biodiversity was calculated per month, there was a significant interaction between nutrients and month ($p=0.0033$, $df=28$). Using a one-way ANOVA, each nutrient treatment, control ($p=0.0176$, $df=28$), nitrogen ($p=0.0020$, $df=28$), nitrogen+phosphorus ($p=0.0003$, $df=28$), phosphorus ($p=0.0007$, $df=28$), was significantly affected by month. Community evenness (E) over the sampling season ranged from a mean of 0.53 to a mean of 0.66. Nutrient treatments did not have a significant effect on the community evenness ($p=0.3292$, $df=28$). Evenness of the community was significantly affected by time ($p<0.0001$, $df=28$) and the interaction of the nutrient with time ($p=0.0007$, $df=28$).

Nutrients and time showed significant interactions within the nitrogen+phosphorus ($p=0.0024$, $df=28$) and phosphorus ($p=0.0015$, $df=28$) treatments.

Epiphytic algal biomass

2011

Nutrient manipulations simulating eutrophication were applied throughout the growing season (March-October) in 2011. N+P treatments were not placed in the salt marsh until April due to unexpected failure of agar solidification. Mean algal biomass for the treatments ranged from 0.176 mg/cm^2 to 0.223 mg/cm^2. The effects of each nutrient treatment, control, nitrogen, phosphorous, and the combination did not significantly influence the growth of epiphytic algae ($p=0.2804$, $df=28$). Algal biomass had the highest mean value of 0.412 mg/cm^2 at the initiation of the study (March) within the nitrogen treatment plots (Figure 18). The lowest mean value measured was 0.0551 mg/cm^2 within the control treatment plots at the end of the study (October) (Table 17). Control treatment biomass ranged from a mean of 0.0551 mg/cm^2 to 0.197 mg/cm^2. Nitrogen treatment biomass ranged from a mean of 0.0647 mg/cm^2 to 0.412 mg/cm^2. Phosphorous treatment biomass ranged from a mean of 0.0975 mg/cm^2 to 0.360 mg/cm^2. The combined treatment biomass ranged from a mean of 0.0610 mg/cm^2 to 0.277 mg/cm^2.

Although nutrient treatments failed to show significant effects on algal growth, monthly changes in biomass were significant ($p<0.001$, $df=28$) for all nutrient treatments. Biomasses for each nutrient treatment were pooled into singular monthly biomasses to further elucidate the monthly changes in epiphytic biomass. The pooled results revealed a spring maximum followed by a summer minimum and a second fall maximum. Growth of epiphytes on *Spartina* was greatest in March with a mean biomass of 0.297 mg/cm^2. Biomass declined through June at

which point it increased to 0.172 mg/cm^2 in September. A final decline in biomass was present at the end of the growing season with a low of 0.0696 mg/cm^2 (Figure 19).

2012

Nutrient manipulations simulating eutrophication were applied throughout the growing season in 2012 (April-October). The mean biomass for each treatment ranged from 0.0839 mg/cm^2 to 0.131 mg/cm^2 (Figure 20). Effects of each nutrient treatment, control, nitrogen, phosphorous, and the combination did not significantly influence the growth of epiphytic algae ($p=0.5355$, $df=28$). Algal biomass had the highest mean value of 0.3397 mg/cm^2 during the first sampling event in April within the nitrogen treatment plots (Figure 21). The lowest mean value measured was 0.0206 mg/cm^2 within the nitrogen treatment plots in July. Mean control treatment biomass ranged from 0.0394 mg/cm^2 to 0.133 mg/cm^2 (Table 18). Mean nitrogen treatment biomass ranged from 0.0206 mg/cm^2 to 0.340 mg/cm^2. Mean phosphorous treatment biomass ranged from 0.0212 mg/cm^2 to 0.241 mg/cm^2. The mean of the combined treatment biomass ranged from 0.0270 mg/cm^2 to 0.197 mg/cm^2.

Nutrient treatments failed to show significant effects on algal growth, although monthly changes in biomass were significant ($p<0.001$, $df=28$) for all nutrient treatments. Biomasses for each nutrient treatment were pooled into singular monthly values for the seasonal changes in epiphytic biomass (Figure 22). The pooled results revealed a spring maximum followed by a summer minimum and a small fall increase. Growth of epiphytes on *Spartina* was greatest in March with a mass of 0.2105 mg/cm^2 and declined through August to a monthly low of 0.0469 mg/cm^2. There was a slight increase to 0.0523 mg/cm^2 at the end of the growing season.

Epiphytic algal chlorophyll-*a*

2011

Chlorophyll-*a* (µg/cm^2) levels did not follow the trends of biomass when exposed to elevated nutrient treatments. Instead of having a spring and fall maximum as in biomass, chlorophyll-*a* remained at low levels from March through August for all nutrient treatments, ranging from 0.912 µg/cm^2 in March within the phosphorous treatment to 2.26 µg/cm^2 in August within the combination treatment, and had rapid increases through October to a high of 5.78 µg/cm^2 within the phosphorous treatment (Figure 23). The mean chlorophyll-*a* levels ranged from 2.18 µg/cm^2 to 2.45 µg/cm^2 with the highest mean level in the control treatment (Table 19). Chlorophyll-*a* was not significantly ($p=0.7521$, $df=28$) affected by the nutrient treatments. Therefore, the nutrient treatments were combined in each month to give an average chlorophyll-*a* level.

Again monthly changes in chlorophyll-*a* were statistically significant ($p<0.001$, $df=28$). The chlorophyll-*a* levels fluctuated slightly from March through August, ranging from a low of 1.22 µg/cm^2 in March to a high of 1.91 µg/cm^2 in August (Figure 24). The end-of-growing-season increased significantly in September and October yielding a maximum chlorophyll-*a* level of 5.04 µg/cm^2.

2012

Chlorophyll-*a* levels for each nutrient treatment exhibited a similar trend with low levels in April and May followed by a summer maximum in June with a decline through October (Figure 25). The highest mean monthly chlorophyll-*a* level occurred in June within the phosphorus treatment plots (3.355 µg/cm^2) (Table 20). The lowest mean monthly chlorophyll-*a*

level occurred in October within the nitrogen treatment plots (0.5882 µg/cm^2). Mean chlorophyll-*a* levels for the treatments ranged from 1.367 µg/cm^2 to 1.737 µg/cm^2 (Figure 26). Chlorophyll-*a* was not significantly ($p=.4432$, $df=28$) affected by the nutrient treatments. Monthly changes in chlorophyll-*a* were statistically significant ($p<0.001$, $df=28$). Therefore, the nutrient treatments were combined in each month to give an average chlorophyll-*a* level. Average monthly chlorophyll-*a* levels had low April and May levels and experienced a spike in June of 3.029 µg/cm^2 followed by a precipitous decline through October to a low of 0.9350 µg/cm^2 (Figure 27).

Annual and Combined Monthly Patterns

Monthly changes in biomass and chlorophyll-*a* was compared to show the relationship between the two commonly used parameters of assessing algal growth in 2011. The two measurements showed an inverse relationship. Biomass had the highest values in March when chlorophyll-*a* was at a minimum (Figure 28). Conversely, chlorophyll-*a* had the highest values in October when biomass was at a minimum. July and August showed similar trends with decreasing values in each in July and slight increases in each in August.

In 2012, the two growth parameters showed an overall decrease from initial values in April to final measurements in October. However, biomass consistently decreased over the sampling season, while chlorophyll-*a* had a seasonal spike occurring in June (Figure 29).

Over the course of the two sampling seasons, biomass had two different trends. Similar trends existed from April through June in which both years experienced decreases from a spring maximum (Figure 30). The two years diverged in biomass trends in July when 2011 experienced a secondary fall maximum and 2012 had a continued decline until August when biomasses

increased slightly. Using the repeated measures mixed model ANOVA, biomass was significantly affected by year ($p<0.0001$, $df=7$) and the interaction of year and month ($p<0.0001$, $df=42$).

Chlorophyll-*a* levels observed in the two sampling seasons varied greatly between the two years. The two years and the interaction of the year and month were significantly different each with a $p<0.0001$. In 2011, chlorophyll-*a* experienced slight increases from March until August with a significant increase in September and October (Figure 31). In 2012, chlorophyll-*a* levels were low in spring and fall and experienced a summer maximum in June.

Yearly total abundances and densities did not show similar trends from 2011 to 2012, and as density is a related parameter to abundance, the patterns for density followed that of abundance (Figure 32 and Figure 33). The trends for each metric, cell abundance and density, were not similar from year to year and they were not significantly different from 2011 to 2012 ($p=0.895$, $df=227$; $p=0.110$, $df=226$, respectively). The abundance and density of epiphytes in 2011 increased from a minimum in March until a maximum in August and then declined through October. In 2012, abundance and density were greatest in April and May and then declined throughout the remainder of the sampling season.

Abundances of the different algal divisions responded differently to the sampling year and month of sampling. When the different algal divisions were analyzed, only diatoms showed a significant yearly effect ($p=0.0113$, $df=7$). The other algal division abundances were not significantly different from the sampling in 2011 and 2012. However, each of the four algal divisions did show a significant interaction ($p<0.0001$, $df=42$) between year and month of sampling. Density showed similar statistical results with diatoms and cyanobacteria having significant yearly effects ($p=0.0003$ and $p=0.0018$, $df=7$, respectively). Interactions with the

year and month was significant for diatoms ($p<0.0001$, df=42), greens ($p=0.0005$, df=42), and cyanobacteria ($p<0.0001$, df=42). Red algae did not show any significant differences in densities from year to year.

Biovolumes of the epiphytes over the two sampling seasons did not have similar trends, however, the years did not a significant different in total biovolume ($p=0.317$, df=226). The 2011 biovolumes increased throughout the sampling season with the maximum biovolume recorded in October and 2012 had decreasing biovolumes after a seasonal maximum occurring in June (Figure 34). Diatoms had the greatest overall biovolume for the two sampling seasons followed by red algae. Similar to the abundance analysis for the two sampling seasons, diatoms and cyanobacteria were the only algal divisions significantly affected by the sampling year ($p=0.0006$ and $p=0.0022$, df=7) and each had an interaction between year and month ($p<0.0001$ and $p<0.0001$, df=42).

The epiphytic algal community composition was fairly stable over the two years of sampling with 137 infrageneric taxa identified in 2011 and 118 infrageneric taxa identified in 2012. Not all taxa overlapped between the two years. There were a total of 155 infrageneric taxa identified over the two years of sampling (Table 21). Of the 155 taxa, 77 were diatoms within 62 genera and two groups of diatoms were identified only to shape (centric and pennate). Green algae had a total of 17 taxa identified within 14 genera including one unknown species. Cyanobacteria had a total of 54 taxa identified within 23 genera including one unknown species. Red algae had a total of 7 taxa identified within 6 genera.

As the community composition was fairly stable over the two years, the overall epiphytic algal cell abundance was also fairly stable. Total epiphytic cell abundance in 2011 with 297,421 cells was slightly greater than the abundance in 2012 with 256,230 cells, and had a combined

sampling total of 553,651 cells. Over the two sampling seasons, the dominant algal division remained cyanobacteria with a total of 433,812 cells (2011: 238,494 and 2012: 195,318) and the dominant genus remained *Leptolyngbya* sp. with a total of 115,229 (2011: 55,237 and 2012: 59,992) cells in three separate infrageneric taxa (Table 21).

Species richness over the two years of sampling resulted in two opposing trends of when the years had the greatest species richness. In 2011, species richness increased throughout the sampling season to a high of 87 species in August while species richness in 2012 decreased throughout the sampling season from a high of 90 species in April (Table 22). Biodiversity (H´) followed the same seasonal trends as the species richness with increasing values through the 2011 season from 2.15 in March to 3.00 in October and decreasing values through the 2012 season from 2.86 in April to 2.58 in October (Table 22).

Lab study results

Epiphytic algal growth

Biomass

Mean biomass for the treatments ranged from 0.00544 mg/cm^2 to 0.0457 mg/cm^2 (Table 23). Using a repeated measures, mixed model ANOVA, the effects of each nutrient treatment, nitrogen, phosphorous, and the combination did not significantly influence the growth of epiphytic algae ($p=0.2251$, $df=20$). Algal biomass increased from Day 0 to Day 14 when nutrient additions were introduced to the treatment buckets (Figure 35). The control treatments experienced a decrease in biomass throughout the experiment. Nitrogen had the greatest increase in biomass increasing from 0.0104 mg/cm^2 to 0.0457 mg/cm^2 at Day 14. It also had the greatest

decrease in biomass by Day 18 to 0.00688 mg/cm^2. Phosphorus and nitrogen+phosphorus had very similar increases and decreases throughout the experiment.

Just as nutrient treatments failed to show significant effects on algal growth, time, also, did not significantly influence biomass (p=0.0697, df=20) for the nutrient treatments. Biomasses for each nutrient treatment were pooled into singular weekly biomasses to observe changes in epiphytic biomass. The pooled results showed maximum epiphytic growth on the *Spartina* stems at Day 14 with 0.0235 mg/cm^2 and minimum growth at Day 28 with 0.00989 mg/cm^2 (Figure 36).

Chlorophyll-*a*

Chlorophyll-*a* levels increased in the first 14 days of the lab study in all four treatments (Figure 37). The greatest increase in chlorophyll-*a* levels occurred in the phosphorus treatment with an increase from a mean of 2.95 µg/cm^2 at Day 0 to 11.65 µg/cm^2 at Day 14. There was only a slight increase in the control treatment from a mean of 2.95 µg/cm^2 to 3.84 µg/cm^2 at Day 14. All four treatments had a decrease in chlorophyll-*a* levels from Day 14 through Day 28. The mean chlorophyll-*a* levels ranged from 1.30 µg/cm^2 to 11.65 µg/cm^2 with the highest mean level in the phosphorus treatment (Table 24). Chlorophyll-*a* was not significantly (p=0.1295, df=20) affected by the nutrient treatments. Therefore, the nutrient treatments were combined each week to give an average chlorophyll-*a* level.

Weekly changes in chlorophyll-*a* were statistically significant (p=0.001, df=20). The chlorophyll-*a* levels increased from a minimum at Day 0 with a level of 2.95 µg/cm^2 to a maximum at Day 14 with a level of 8.48 µg/cm^2 and falling again at Day 28 to 2.98 µg/cm^2 (Figure 38).

Discussion

Field study

Research into algal epiphytes includes examining inputs to the aquatic food web, contributions to nutrient cycling between the host macrophytes and the water column, and decreased light attenuation for the host plant with concurrent epiphytic algal growth (Karez *et al.*, 2000; Moncreiff and Sullivan, 2001; Gross *et al.*, 2003). These studies have been vital in understanding the relationships between different trophic groups, energy transfers, and how stable aquatic ecosystem is maintained. In this study, manipulations to water chemistry via nutrient additions were used to determine the impacts on epiphytic algal growth and species composition on *Spartina alterniflora* in an estuarine environment. These results were also compared with a laboratory mesocosm study. An extensive literature search was conducted to elucidate other research pertaining to nutrient enrichment salt marsh dwelling on epiphytic algae. While numerous studies of nutrient enrichment and epiphytic algae on submerged seagrasses have been conducted, only a handful of studies have addressed salt marsh dominated *Spartina* habitats.

Nutrients play a key role in algal growth (Wetzel, 2001; Graham *et al*., 2009). Phosphate and total nitrogen (ammonium, nitrate, and nitrite) nutrient levels recorded from the datasonde in 2011 and 2012 at the Pine Island water monitoring station in the Tolomato River do not exceed that of the nutrient manipulation level of 0.5M concentrations. Therefore, ambient water conditions are not at eutrophic levels. Likewise, Phlips *et al.* (2004) indicated that the site could

not be considerend eutrophic with a Nutrient Loading Index value of 1 (low load) ranging from 1-4.

Nutrient levels can be highly variable from year to year based on terrestrial land use changes. However, according to county land use records, the Tolomato River watershed has seen minimal impacts from 2004 to 2011 (www.co.st-johns.fl.us). Vitousek *et al.* (1997) noted that marine waters are typically limited by nitrogen availability. Valiela *et al.* (1997) propose that nitrogen typically controls maximum algal growth rates in estuarine systems. Epiphytes living on eelgrass (*Zostera marina*) responded with significant biomass increases as ambient nitrogen concentrations increased within Roskilde Fjord, Denmark (Borum, 1985). Elevated nutrient concentrations deployed during this study were able to achieve eutrophic levels and epiphytic algae were expected to show growth responses found in numerous previous nutrient manipulation studies.

Influences on epiphytic growth are not limited only to water nutrient loading. Spatial heterogeneity, the density and diversity of herbivores, epiphyte host plants, seasonal changes in sunlight, temporal variability of algal growth, and taxonomic composition of the epiphytes influence overall growth (Foy *et al.*, 1976; Pedersen and Borum, 1996; Cattaneo *et al.*, 1998; Jackson *et al.* 2006). A great deal of the spatial heterogeneity may be attributed to different substrates on which organisms attach and the environmental in which they inhabit (Armitage, 2006). Three different *Spartina* islands were utilized for the nutrient manipulations and control plots in this study. Each of these islands was in close proximately to one another and showed no statistically significant differences in biomass or chlorophyll-*a* when exposed to elevated nutrient levels. As this study addressed one host macrophytes (*Spartina*) and collection of epiphytes from a consistent location on the *Spartina* stem, efforts were successful to reduce variability in

environmental conditions, and that possible site heterogeneity will not impact the study. Similar results were found by Fourqurean *et al.* (2010) hat spatial variability of water column nutrient concentrations did not affect the epiphyte loads on seagrasses in the Florida Keys.

Throughout the two year study, nutrient additions did not show significant impacts on epiphytic algal growth. Average biomass each year was at a maximum at the initial season collection date (March, 2011 and April 2012). The average biomass of both years decreased through the summer months and saw a second, yet weaker maximum in the fall months. Biomass levels in 2012 had a less dramatic fall maximum than in 2011. For each growth parameter (biomass and chlorophyll-*a*), seasonal changes were statistically significant. There are many possible factors that contribute to the bimodal biomass maximas including increased herbivory during the summer months, the growth of the host macrophytes, and sub-optimal sunlight radiance levels. Significant seasonal biomass changes by other researchers in many different aquatic habitats. Borum (1985) found a similar bimodal seasonal influence on epiphytes in a Danish estuary. Gordon *et al.* (2008) studied the effects of salinity on epiphytic algal growth in the St. Lucia estuary in South Africa and found similar bimodal biomass peaks in the spring and fall months.

Chlorophyll-*a* patterns from the two sampling years did not show similar patterns. The vast majority of algae possess chlorophyll-*a* as a primary photopigment (Graham *et al.*, 2009). Thus, increased levels of chlorophyll-*a* are often used as a surrogate for algal growth (Stevenson *et al.*, 1996). In 2011, chlorophyll-*a* exhibited a spring minimum with only a slight increase through August after which levels significantly increased until the end of sampling in October. The pattern exhibited in 2012 showed spring and fall minimums with a summer maximum peaking in June. These results reflect similar patterns presented by Jackson *et al.* (2006).

Interestingly, algal biomass measurements taken in June 2012 represent the beginning of the summer minimum. Variability in chlorophyll-*a* patterns from year to year may be dependent on the algal community composition and other environmental factors and not from elevated nutrient levels.

Epiphytic algae are a nutrient rich and vital food source for many aquatic organisms (Pinckney and Micheli, 1997). Insects and aquatic invertebrates consume large quantities of algae from submerged and emergent macrophytes (Moncreiff and Sullivan, 2001). Resident and transient herbivores associated with estuarine macrophytes include copepods, amphipods, polychaetes, snails, shrimp, crabs, and small fish and emergent insects such as caddisflies and stoneflies (Morgan and Kitting, 1984; Kitting *et al.*, 1984; Brönmark, 1985; Moncreiff *et al.*, 1992; Kneib, 1997; Williams and Williams, 1998; Sotka and Hay, 2006). Most herbivores show seasonal changes in abundance and densities (Minello and Zimmerman, 1992; Gacia *et al.*, 1999). Gacia *et al.* (1999) noted that small fish such as pinfish (*Lagodon rhomboides*) and black mullet (*Mugil cephalus*), consumers of epiphytic algae, exhibited maximum grazing pressures in the summer months. Increases in algal biomass can thus provide increased food sources for herbivores. This rapid herbivory may mask algal growth, perhaps leading to erroneous interpretations of lack of algae growth following nutrient additions (Williams and Ruckelshaus, 1993; Gil *et al.*, 2006; Sotka and Hay, 2006). The observed seasonal summer decrease in algal biomass may be, in part, due to increased levels herbivory.

Spartina alterniflora and seagrasses experience increased seasonal growth during the late spring and throughout the summer months (Borum, 1985). During periods of rapid growth, older leaf blades and stems that are colonized by epiphytic algae are replaced with new growth with low epiphytic algal loads. Macrophytes that undergo blade abandonment when dense epiphytic

colonization occurs or sloughing off old leaves as new leaf grow are able to regulate epiphytic loads and minimize negative shading and leaf drag that may damage the plant (Sand-Jensen, 1990; Littler and Littler, 1999). Other natural defenses that macrophytes possess are a waxy coating to inhibit algal attachment (Jackson *et al.*, 2006). Sloughing off of epiphytes via new growth or waxy coatings may have reduced the impacts of nutrient enrichment on the *S. alterniflora*.

The project site was located within the Tolomato River which is influenced by tidal currents. Epiphytes maintain their position on their host plant by different methods of attachment mucilaginous pads, colony stalks, tubes, and slime layers (Fletcher and Callow, 1992; Holland *et al.*, 2004). Most of the epiphytic algal divisions identified during the study contained organisms that produced holdfasts directly implanted onto the *Spartina* stem. Other individuals were loosely attached to the surface. Epiphytic algae that were able to colonize the *Spartina* stems had to contend with fast moving tidal currents, surface current generated from wind, and river flow rates. Tidal and wind currents in Tolomato River produced a strong impact to the estuarine environment (Phlips *et al.*, 2004). Nutrient enrichment may have allowed for greater algal growth, but algae that were not able to adequately attach to the *Spartina* were not recovered during sample collection.

Other physical processes may play a role in masking significant results of nutrient enrichment. Estuaries typically have turbid water from the sediment movement from terrestrial sources entering the freshwater and incoming tidal water movements (Dardeau *et al.*, 1992; Dauer *et al.*, 2000). Reduced water clarity will reduce light penetration resulting in inhibited growth of photosynthetic algae (Philips *et al.*, 1996). Reduced light penetration limited the epiphytic algal during times of high tide and lower portions of the *S. alterniflora* was submerged.

During low tide, the epiphytic algae had to cope with full UV sun exposure. Few algal groups and species are capable of handling periods of low light levels followed by periods of extreme UV radiation (Dor, 1984). Another compounding effect that may limit epiphytic algal growth is exposure to desiccating conditions during low tide (Mann and Steinke, 1988). The combination of highly variable light levels and desiccating conditions pose a challenge to many epiphytic algal species when nutrient levels are not the limiting factor (Philips *et al.*, 1996).

Algal community species richness appeared to be rather diverse both years of data collection with 137 infrageneric taxa in 2011 and 118 in 2012 and a total of 155 different infrageneric taxa identified. Diatoms made up the majority (50%) of the taxa with 77 infrageneric taxa, followed by 54 infrageneric cyanobacteria taxa at 35%. Green algal and red algae taxa were represented by 17 taxa and 7 taxa, respectively for a total of 16% of the identified taxa. Greater levels of diatom species richness followed results found in previous studies (e.g. Stowe, 1982, Armitage *et al.*, 2006; Jackson *et al.*, 2006) which analyzed epiphytic algal communities on *Spartina*. These studies, however, also found diatoms to be the most abundant algal division. Diatoms are also considered excellent colonizers which results in increased species richness as evident in this study and high abundances in other studies (Azim and Asaeda, 2005).

The high degree of species richness can be attributed to a few different environmental and biological factors including host plant surface heterogeneity and nutrient concentrations (Pringle, 1990; Cattaneo *et al.*, 1998; Tiffany and Lange, 2002; Hinogosa-Garro *et al.*, 2010). *Spartina* stem and leaf blade surfaces provide attachment sites to algae. Greater surface complexity increases the surface area and microhabitats providing for greater epiphyte richness (Pringle, 1990; Hinogosa-Garro *et al.*, 2010). Surface complexity does not only equate to the

macrophyte host, but also to the epiphyte community already attached. Also, early colonizers of the epiphytic community identified on *Spartina* stems provided additional surface structure for further community development and species richness (Tiffany and Lange, 2002).

Nutrient concentrations have shown to reduce algae species richness in aquatic environments as a few species are able to out-compete others for nutrients and exhibit faster growth rates (Tilman, 1982). However, in this study and studies by Bolata *et al.* (2008) and Pringle (1990), nutrient treatments did not significantly affect the species richness. A connection may exist between the *Spartina* microniches and community complexity of epiphytes which shelter the community from experiencing decreased richness with increased nutrient enrichment.

Species richness is often coupled with a diversity calculation. The Shannon-Wiener Biodiverity Index was used to determine if nutrient treatments affected the diversity of the algal community assemblages. Shannon-Wiener Index values were not significantly affected by nutrient treatment, but showed the sampling month significantly affected the community diversity in both sampling years. Algal community diversity was greatest in both sampling years when the species richness was the greatest. This occurred in the latter half of 2011 and the beginning of 2012. Diversity readings ranged from 2.15 to 3.00. Typical ecological diversity levels do not exceed 4 (Magurran, 2004). Thus, the algal community is viewed having a heterogeneous species composition due to habitat complexity on the *Spartina* stems and leaf blades.

A second measure of diversity was used beyond the Shannon-Wiener Index. Species evenness, measured on a scale of 0-1, was assessed to determine how close in abundance the species were. Nutrient enrichment did not significantly affect the evenness of the community in either 2011 or 2012 with mean values ranging from 0.57 to 0.50. Sampling month did

significantly affect the evenness of the community both years. The mean evenness values per month ranged from 0.68 to 0.53. Evenness increased through the sampling season in 2011 in conjunction with the increased species richness and diversity. Evenness in 2012 increased in the summer months, but did not increase with species richness or diversity as in 2011. The algae community had a moderate evenness of species abundance in part due to the great abundance of cyanobacteria.

The epiphytic algal community identified during this study revealed an overwhelming dominance of cyanobacteria. Over the two years of sample collection, over 78% of the total algal cells consisted of cyanobacteria. Cyanobacteria are capable of rapid growth under favorable environmental conditions such as adequate light and nutrient levels (Foy *et al.*, 1976). Epiphytic cyanobacteria are also tolerant to emergence from water for periods of time making intertidal saltmarshes suitable habitat. Philips *et al.* (1996) observed cyanobacteria genera including the nitrogen fixing genus *Calothrix* colonizing the upper vertical zone of mangrove pneumatophores. The second most abundant algal division was red algae with approximately 14% of the epiphytic algal abundance. Some red algae, including the observed *Caloglossa leprieurii*, are typically found on lower vertical portions of macrophytes where exposure to high sunlight and desiccation can be minimized (Philips *et al.*, 1996). Diatoms were the third most abundant algal division comprising of approximately 7% of the epiphytic algal community. Green algae were the least abundant algal division making up approximately 1% of the community. Each sampling season followed these divisional proportions of algal abundance. These results contradict other studies which have reported diatoms and green algae to be the abundant epiphytic algal divisions (e.g. Stowe, 1982; Dardeau *et al.*, 1992; Jackson *et al.*, 2006).

As discussed earlier, herbivory plays an important role in epiphytic algal biomass and therefore abundance. Diatoms and green algae provide a nutrient rich food source to grazing herbivores, which may have caused the overall low abundance of these two divisions (Kupferberg, 2003). Red algae and cyanobacteria have different, but effective anti-herbivory mechanisms which may have contributed to their prevalence (Valiela *et al.*, 1997). Red algae are known to produce secondary compounds that reduce palatability for herbivores. Also, large cell size and tough cell structure restricts consumption to larger herbivores (Graham *et al.* 2007). Cyanobacteria anti-herbivory methods include toxin production and mucilaginous sheaths (Pennings *et al.*, 1997; Pajdak-Stós, 2001). Both of these defense mechanisms allow cyanobacteria to have limited losses to herbivory.

This study looked at nutrient enrichment to identify possible epiphytic algal community responses. However, no significant responses were identified based on nutrient treatments for any of the algal divisions. Epiphytic algal abundance and density on the *Spartina* showed significant seasonal changes at both the algal division and community level for each year. The month of sampling significantly influenced the abundance and density of all algal divisions in both sampling seasons. Total algal abundances and densities were greater in 2011 than in 2012; however, the differences were not significant. With yearly comparisons by division, diatoms were the only division that had significantly different abundances from year to year. Each of the algal divisions showed significant yearly and monthly differences. This may to be due to the highly dynamic and variable conditions that impact estuaries and algal communities.

Light levels greatly influence algal growth and abundance, with green algae have increased abundance in spring and summer, red algae in the fall, and diatoms in the winter and spring partially as a result of differential photo-pigment adaptations (Stowe, 1982; Davis and

Lee, 1983). Diatoms and red algae have greater tolerances and/or preference to low light levels than green algae which fare better under higher light intensities (Hill, 1996; Hynes, 2001; Philips *et al.*, 1996; Graham, 2009). However, monthly cell abundances for diatoms and red algae did not follow the abundance trends set forth by Davis and Lee (1983) and Stowe (1982) which found greatest diatom abundances in the winter and spring and red algae in the fall. In 2011, reds had greater abundances in summer and diatoms increased in abundance from spring through fall. Data from 2012 showed reds with the greatest abundance in spring and diatom abundances fluctuated with no distinct changes throughout the sampling season (Figure 6 and Figure 13).

Biovolume is a metric of algal growth which takes into account the vast disparity between small and much larger cells (e.g. diatoms may be orders of magnitude larger than cyanobacteria) (Reynolds, 1986). Total algal community biovolume has great implications for macrophytes, as increased biomass leads to increased drag, less light attenuation, and more cells competing for nutrients that are colonized with epiphytes. Epiphytic loads of small cells may allow for greater abundances to persist on the host plant prior to damage due to shading or drag (Wetzel, 2001). In this study, cyanobacteria was the dominant division of epiphytes, yet had lower biovolumes every month than diatoms and red algae. Biovolumes were not significantly affected by nutrient treatments through the course of the study. Seasonal changes in biovolume were significant in all of the algal divisions in all sampling months in 2011 and 2012.

A physiological factor that may have reduced the impacts of nutrients on the community composition is that some algal species are capable of luxury consumption of nutrients (Pedersen and Borum, 1996). Luxury consumption allows algae to absorb greater quantities of nitrogen and phosphorus than necessary for growth, maintenance, and reproduction (Pringle, 1990). Larger cells are able to absorb greater amounts of nutrients for storage which is a beneficial

function for large diatoms green algae, and red algae. Large cyanobacteria have polyphosphate bodies and cyanophicin granules for luxury nutrient storage. Storage of excess nutrients provides the cells with limiting nutrients during times of low nutrient availability (Pedersen and Borum, 1996). Smaller cells, though not capable of absorbing greater amounts of nutrients typically have a greater surface area to volume ratio that allows for rapid uptake of nutrients which may be beneficial to small cyanobacteria and green algae (Pringle, 1990; Graham, 2009). The epiphytic algal community may have been able to obtain maximum nutrients for growth and luxury consumption so that the biomass, chlorophyll-*a*, abundance, density, and biovolumes were not significantly affected by nutrient enrichment.

Lab study

The three different nutrient treatments (nitrogen, phosphorus, and nitrogen+phosphorus) did not significantly vary from the control treatment when measuring biomass or chlorophyll-*a*. Significant effects on biomass and chlorophyll-*a* were present in regards to the date sampled. Over the 28 days, the biomass and chlorophyll-*a* levels increased from the baseline values to spike at day 14 and drop again at day 28.

Biomass and chlorophyll-*a* tracked similar result patterns over the 28 day experiment. This differs greatly from the field results for both parameters. In neither year did the biomass and chlorophyll-*a* values show similar trends over the course of data collection. Under the controlled settings of the greenhouse, environmental conditions were static. Ambient temperature, salinity, and water movement in the mesocosms were not subject to natural/environmental fluctuations. As discussed earlier, environmental factors such as water movements, light attenuation, herbivory can influence biomass and chlorophyll-*a* were largely

removed from the mesocosm study. Therefore, it is not surprising that biomass and chlorophyll-*a* had similar responses during the study.

Although nutrient treatments did not cause statistically significant increases in biomass or chlorophyll-*a*, the control treatments had the lowest mean values at day 14 and day 28. The nutrients may have had some effect on algal growth causing a short-term bloom. The bloom was followed by a crash in biomass and chlorophyll-*a* by day 28. Eutrophic conditions in the first 14 days caused sharp increases in algal growth; however, once the excess nutrients were depleted, the algae experienced a crash by day 28. In the mesocosm study, nutrients were the limiting factor for growth. Had more sampling been conducted over the 28 day period, a more detailed depiction of nutrient cycling through the system would be shown. Also, if the study would have been conducted for a longer period of time, a more definitive pattern may have emerged.

Conclusions

In an effort to examine the impacts of anthropogenic eutrophication, it was found that over two years of sample collection growth epiphytic algal and community composition were not affected by elevated nutrient levels. Mimicking eutrophic conditions did not result in increased biomass or shifts in community composition. Conversely to anthropogenic impacts, it appears that natural environmental factors (i.e. herbivory, light availability, seasonality, water movements, and species interactions) were driving forces behind the observed changes. These natural fluctuations may change from year to year causing the different community relative to the specific limiting factor at play.

This study addressed epiphytic algae communities attached to *Spartina alterniflora* in a saltmarsh. Numerous studies have addressed the impacts in other aquatic environments, particularly seagrasses and freshwater lakes and rivers. Results have shown a mixed response to eutrophic conditions in the natural environment, with some showing increased biomass and decreased community richness and diversity while others have shown no response in algal growth or changes in the community. Complementing the field study was the mesocosm lab study. The lab study followed published research illustrating how eutrophication increases algal biomass. It appears that there are many factors that influence how the algae community will respond to changes in the environment. Algae have many different pressures that limit growth including herbivory, light conditions, spatial and temporal heterogeneity, and nutrients. Aquatic systems are very dynamic and limiting factors may change from year to year or site to site. Blanket statements concluding one factor is the most important in determining algae community impacts would be an over simplification leading to erroneous conclusions.

The paucity of studies conducted on epiphytic algae of *Spartina*, and more generally on algal studies in northeast Florida saltmarshes made this thesis an invaluable addition to estuarine and algae science. Northeast Florida represents a geographic location void of marine and estuarine algal studies. It is the goal that this study can provide a baseline dataset of the epiphytic algae community and factors that may influence how it responses to environmental perturbations.

Figure 1. Location of the *in situ* nutrient manipulation study site within the Tolomato River, GTMNERR, Ponte Vedre, Florida.

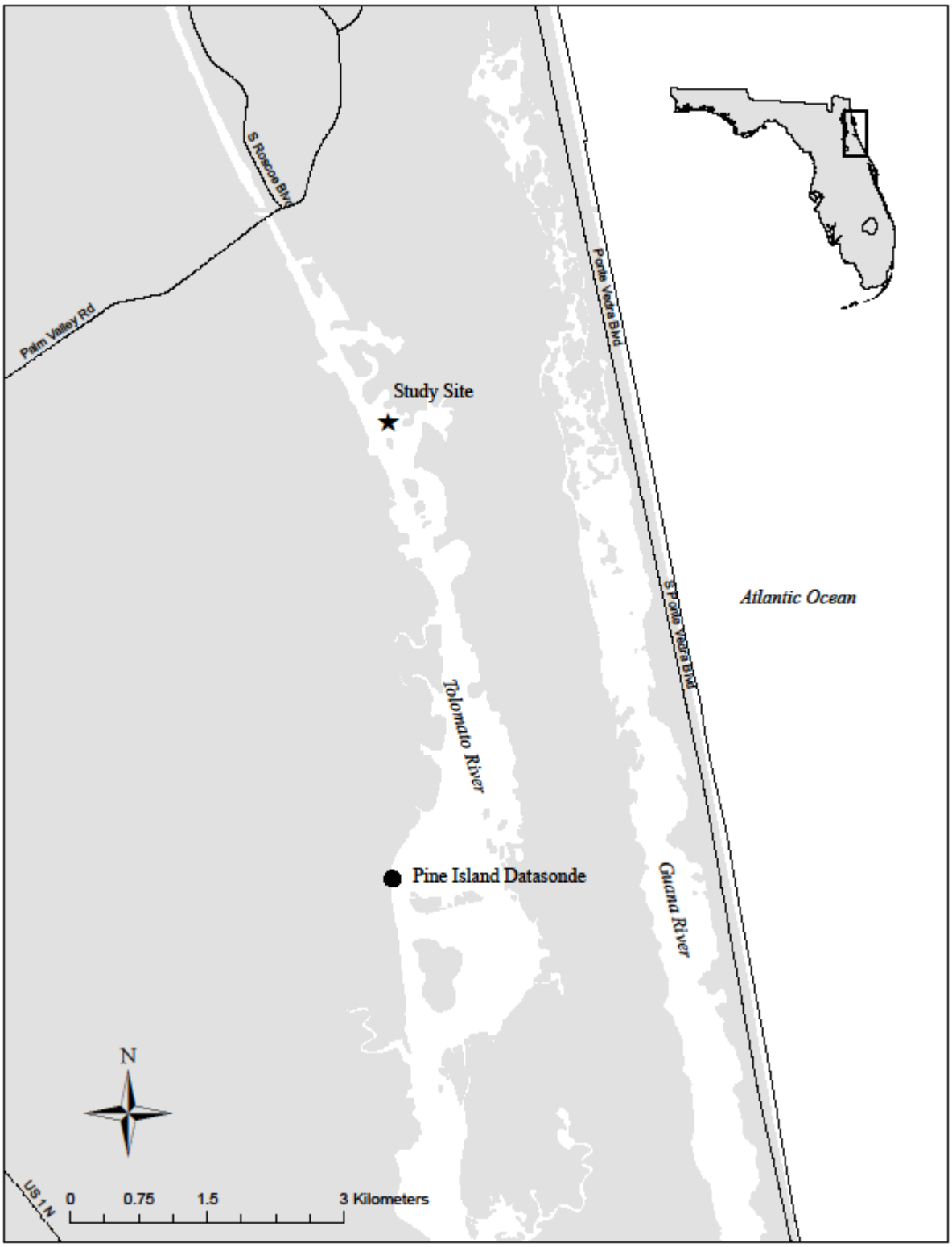

Figure 2. Average biomass (mg/cm^2) (±1 SD) of the epiphytic algae of each island for the sampling period of March through October 2011. Standard deviations are represented by the error bars.

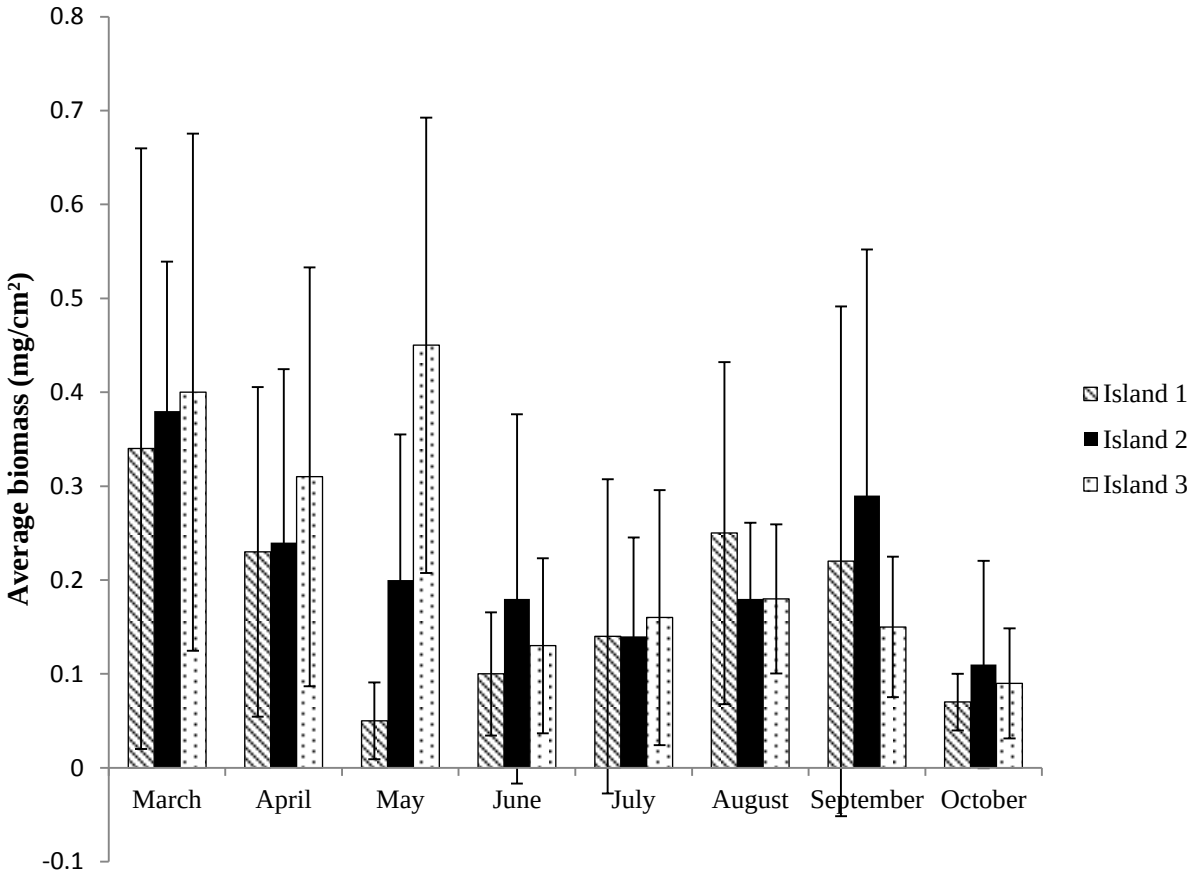

Figure 3. Average chlorophyll-*a* (µg/cm^2) (±1 SD) of the epiphytic algae of each island for the sampling period of March through October 2011.

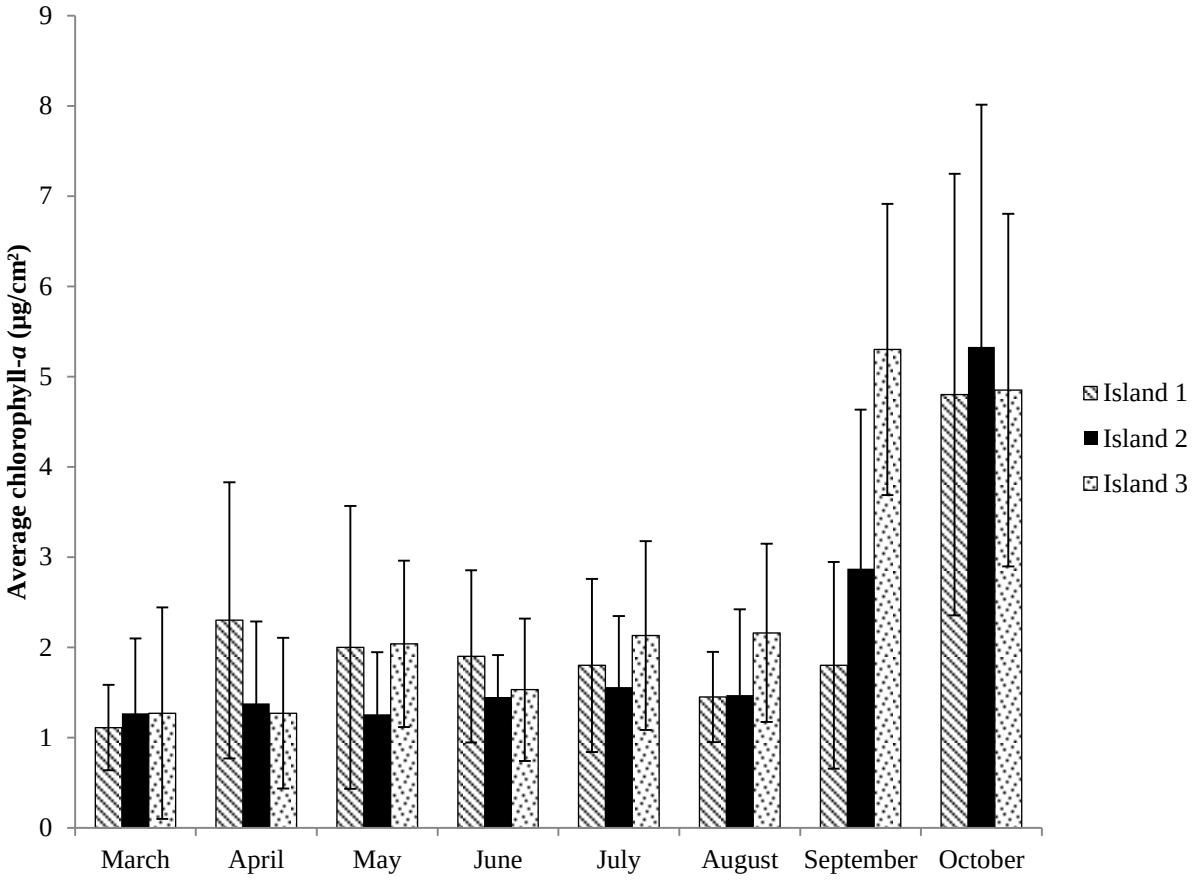

Figure 4A. Algal cell abundance (number of cells) by division of the total epiphytic algal community for each nutrient treatment for the sampling period of March through October 2011. Order of nutrient treatments depicted by each bar per month: Control, Nitrogen, Phosphorus, and Nitrogen+Phosphorus

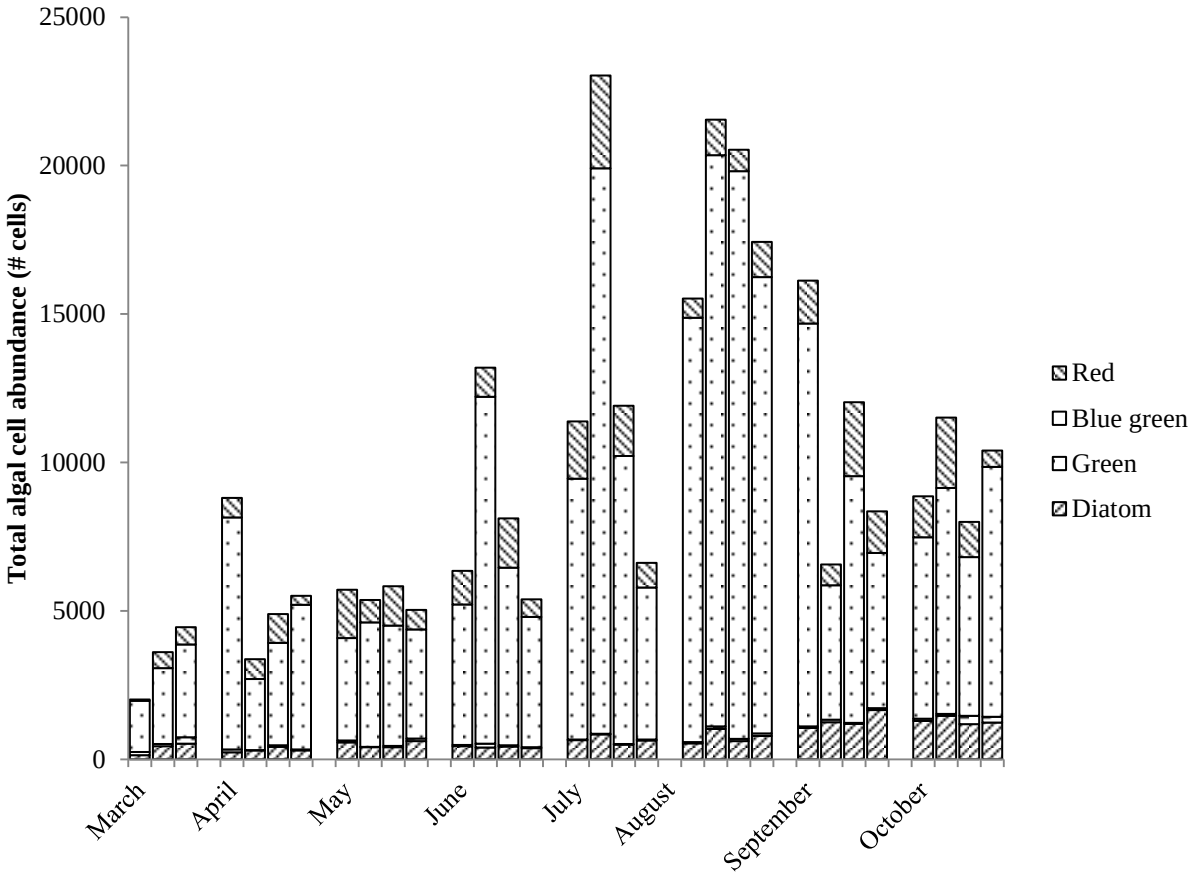

Figure 4B. Algal percent (%) abundance (number of cells) by division of the total epiphytic algal community for each nutrient treatment for the sampling period of March through October 2011. Order of nutrient treatments depicted by each bar per month: Control, Nitrogen, Phosphorus, and Nitrogen+Phosphorus.

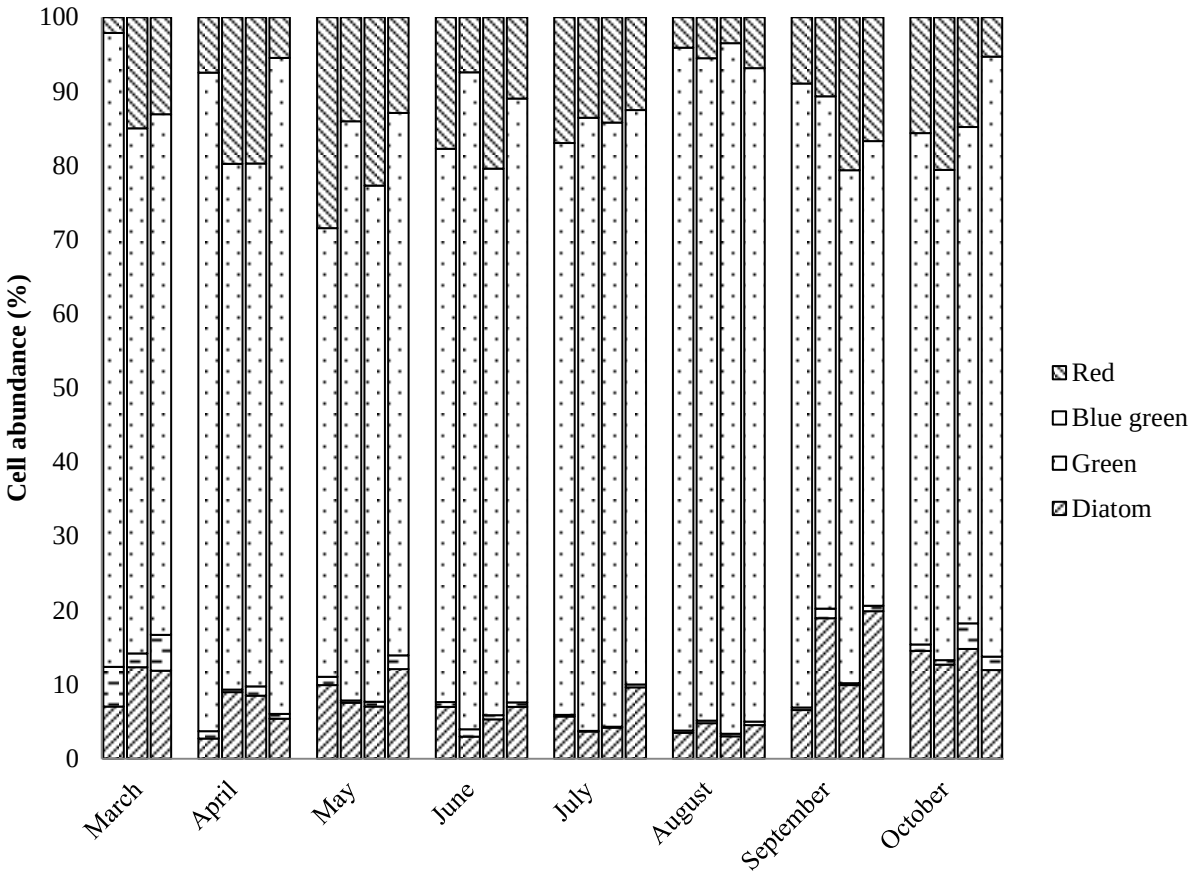

Figure 5. Total epiphytic algal abundance (number of cells) collected from all treatments for the sampling period of March through October 2011.

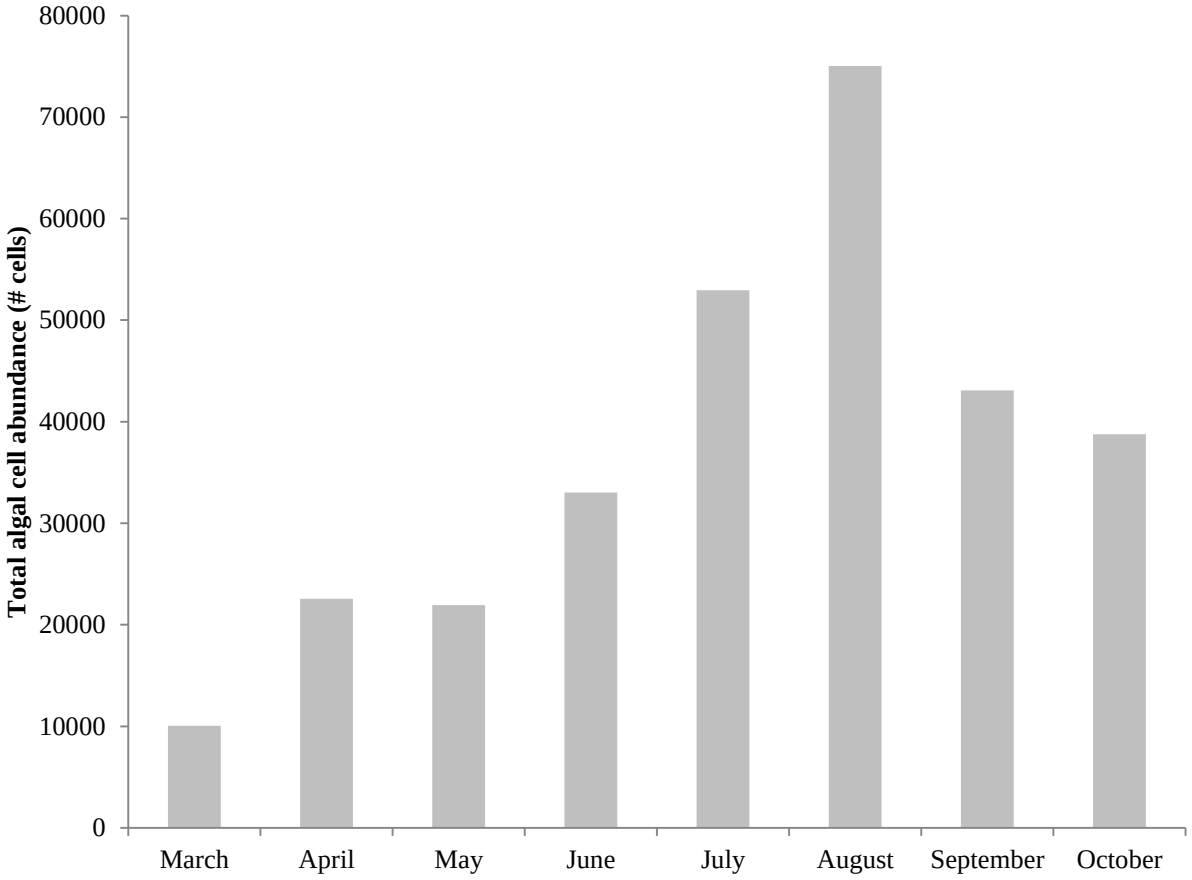

Figure 6. Total epiphytic algal abundance (number of cells) by division collected from all treatments for the sampling period of March through October 2011.

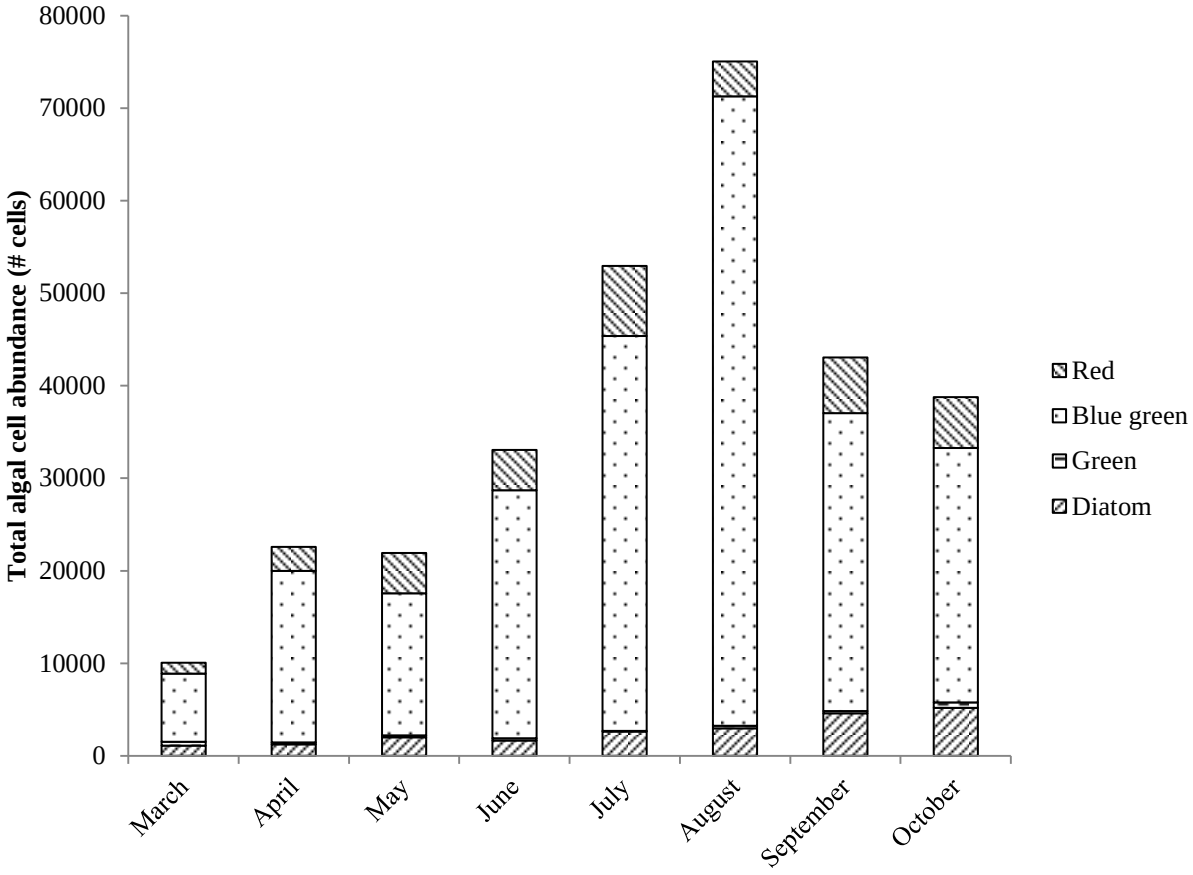

Figure 7. Total epiphytic algal density (cells/cm^2) collected from all treatments for the sampling period of March through October 2011.

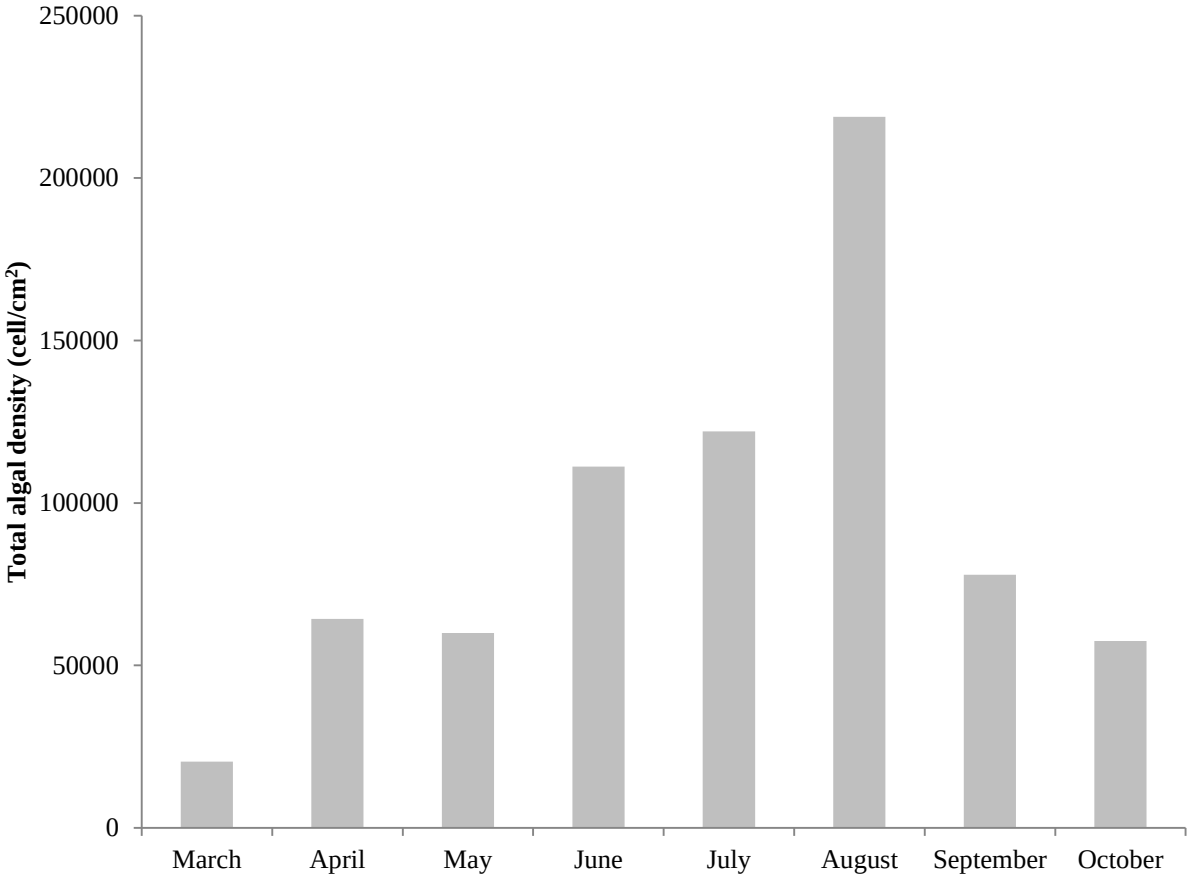

Figure 8. Total epiphytic algal density (cells/cm^2) by division collected from all treatments for the sampling period of March through October 2011.

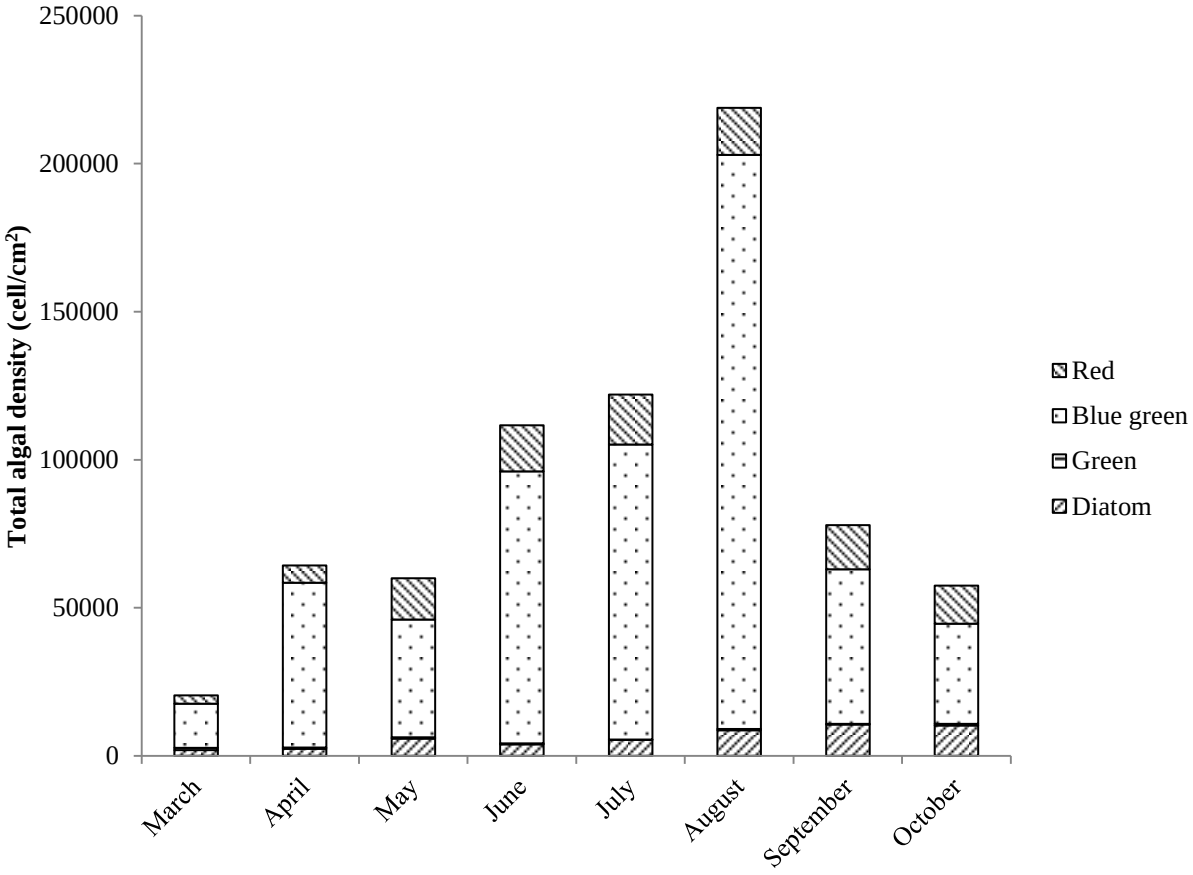

Figure 9. Total epiphytic algal biovolume (cm^3/cm^2) collected from all treatments for the sampling period of March through October 2011.

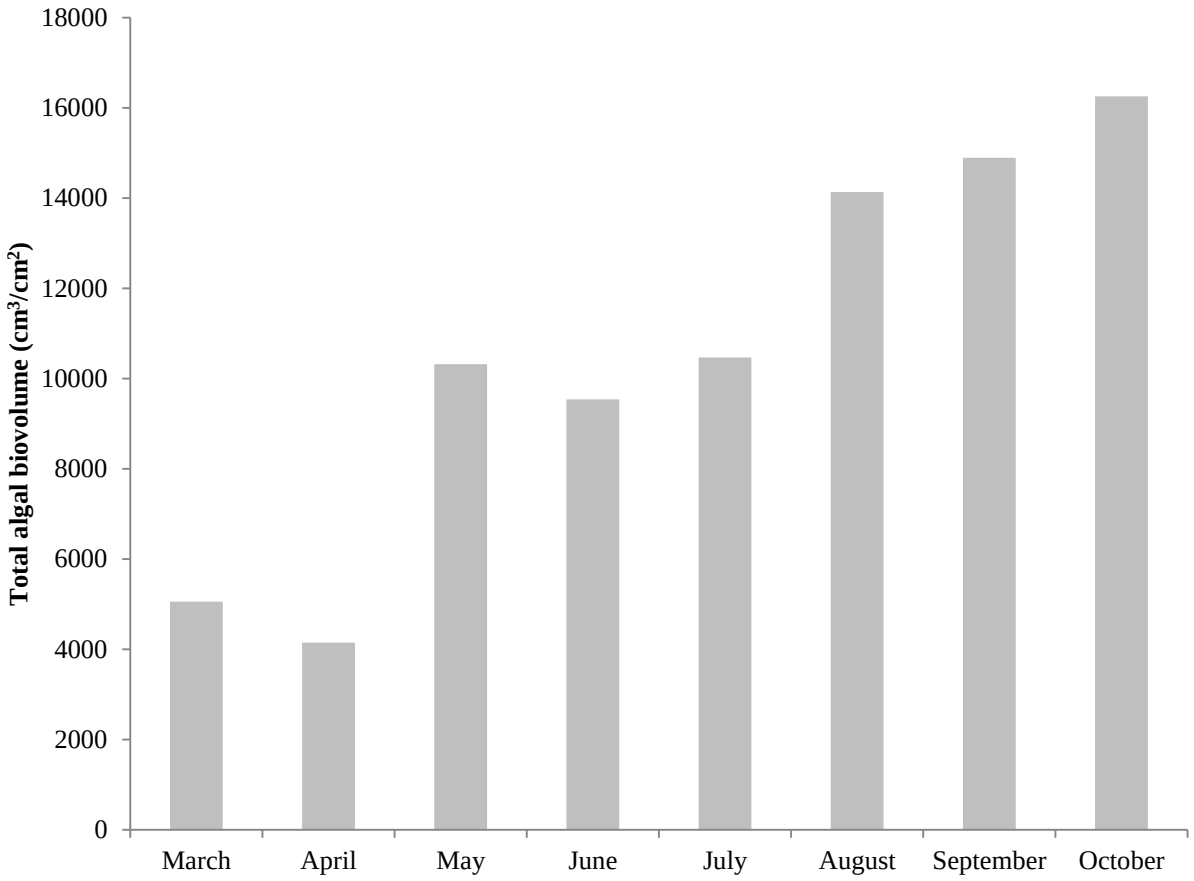

Figure 10. Total epiphytic algal biovolume (cm^3/cm^2) by division collected from all treatments for the sampling period of March through October 2011.

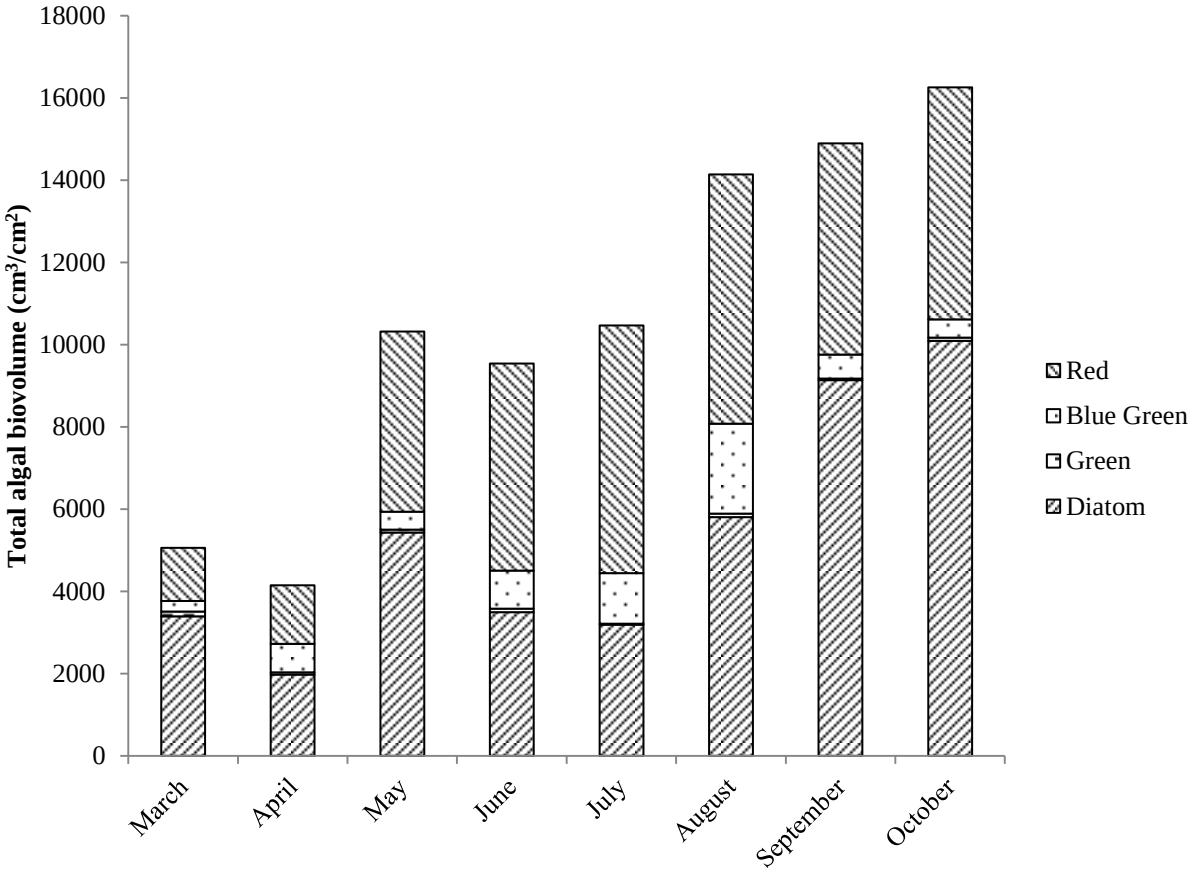

Figure 11. Algal percent (%) abundance (number of cells) by division of the total epiphytic algal community for each nutrient treatment for the sampling period of April through October 2012. Order of nutrient treatments depicted by each bar per month: Control, Nitrogen, Phosphorus, and Nitrogen+Phosphorus.

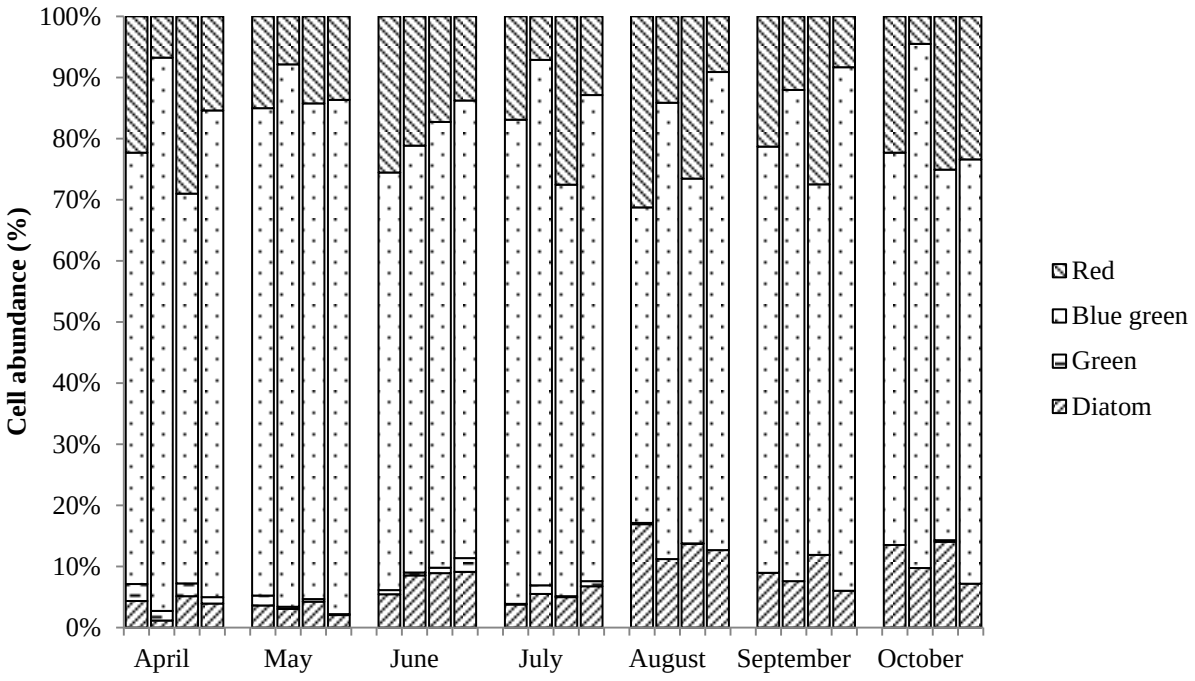

Figure 12. Total epiphytic algal abundance (number of cells) collected from all treatments for the sampling period of April through October 2012.

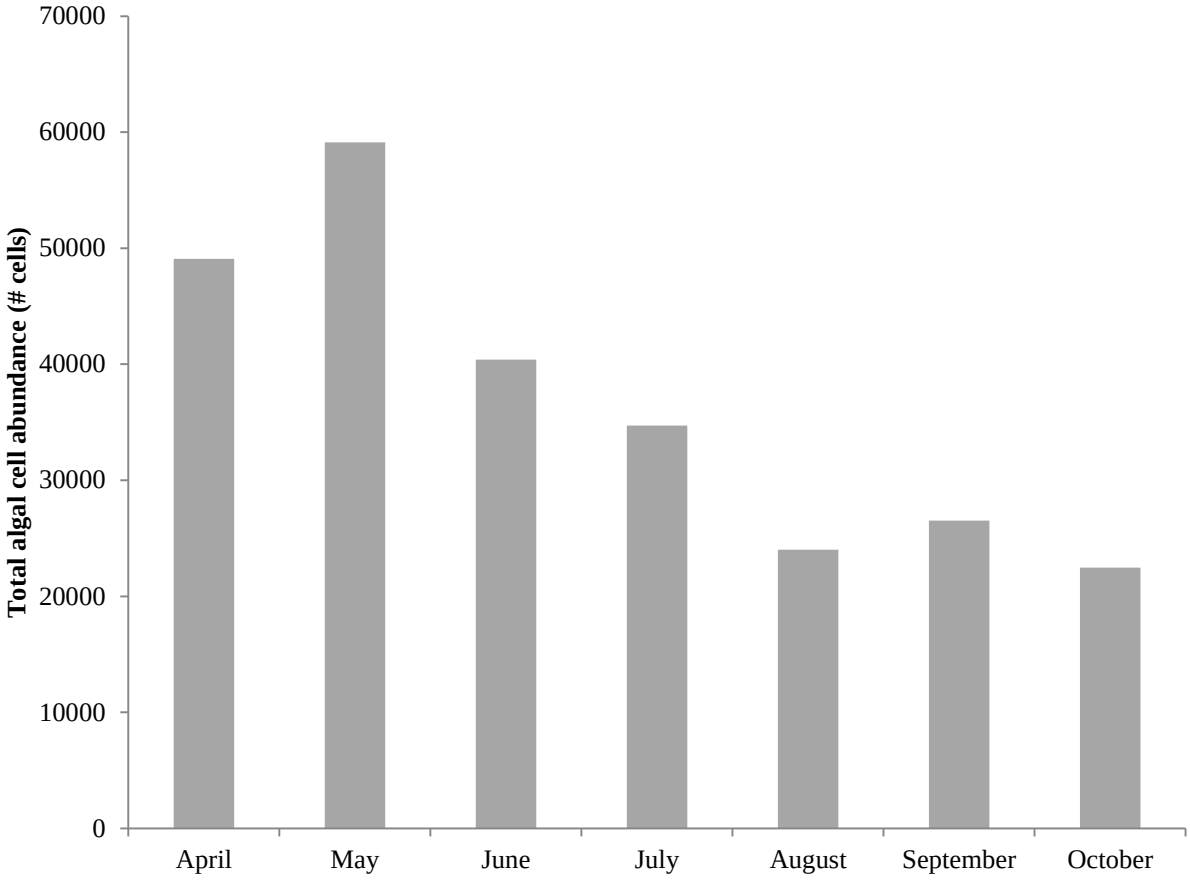

Figure 13. Total epiphytic algal abundance (number of cells) by division collected from all treatments for the sampling period of April through October 2012.

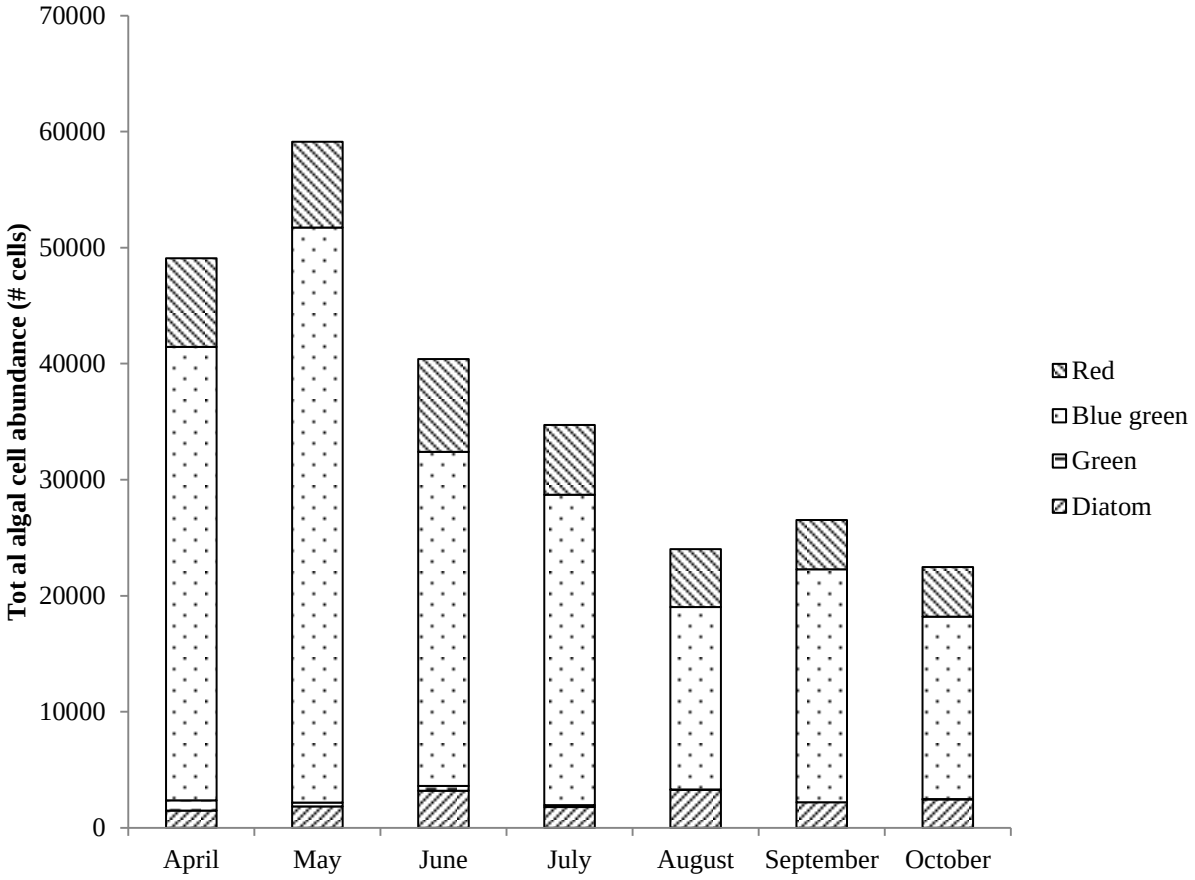

Figure 14. Total epiphytic algal density (cells/cm^2) collected from all treatments for the sampling period of April through October 2012.

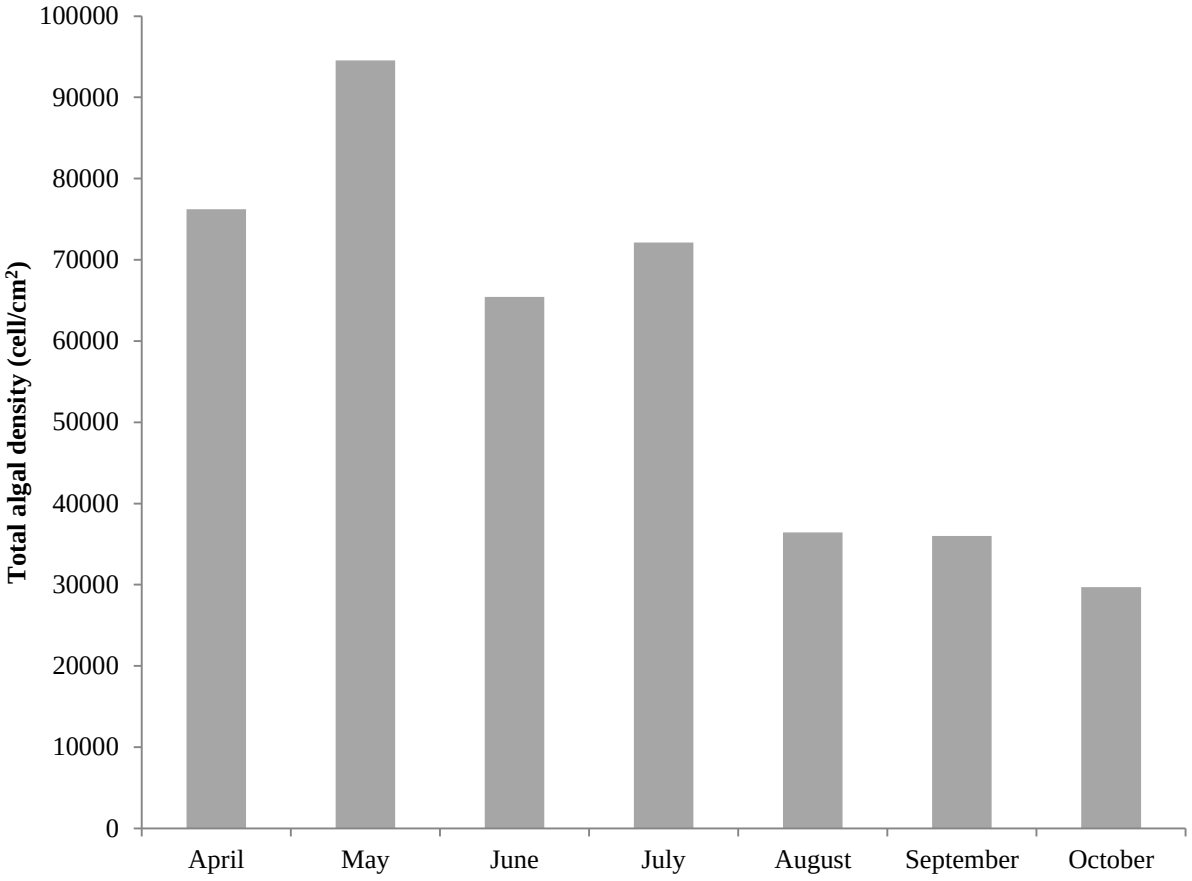

Figure 15. Total epiphytic algal density (cells/cm^2) by division collected from all treatments for the sampling period of April through October 2012.

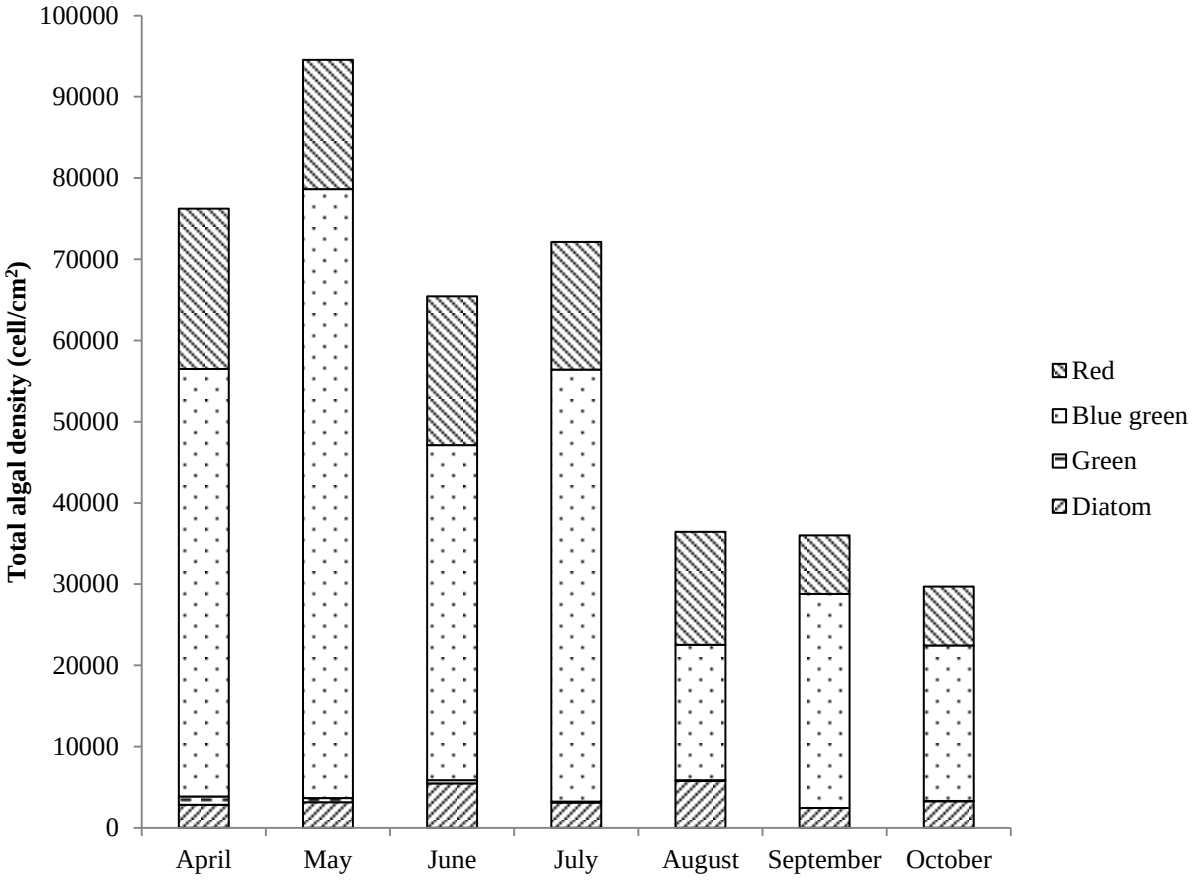

Figure 16. Total epiphytic algal biovolume (cm^3/cm^2) collected from all treatments for the sampling period of April through October 2012.

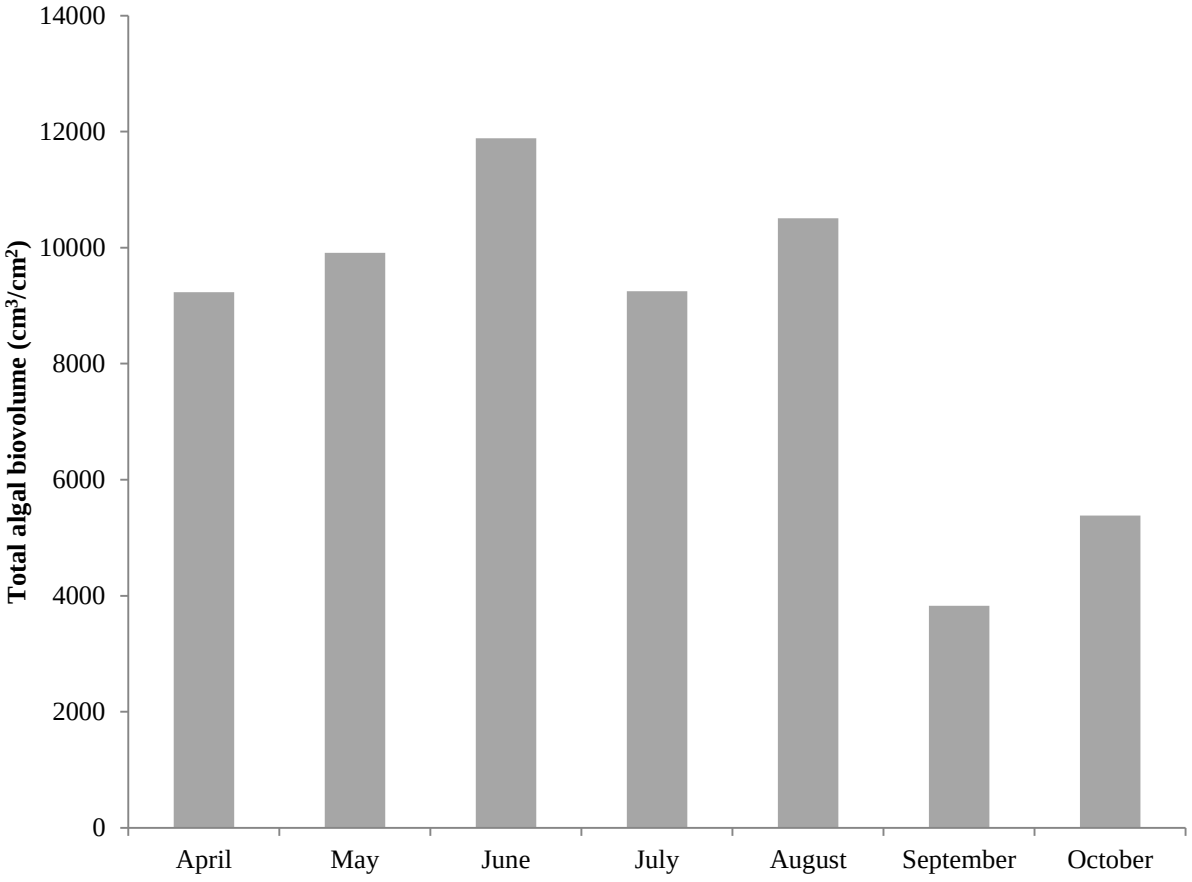

Figure 17. Total epiphytic algal biovolume (cm^3/cm^2) by division collected from all treatments for the sampling period of April through October 2012.

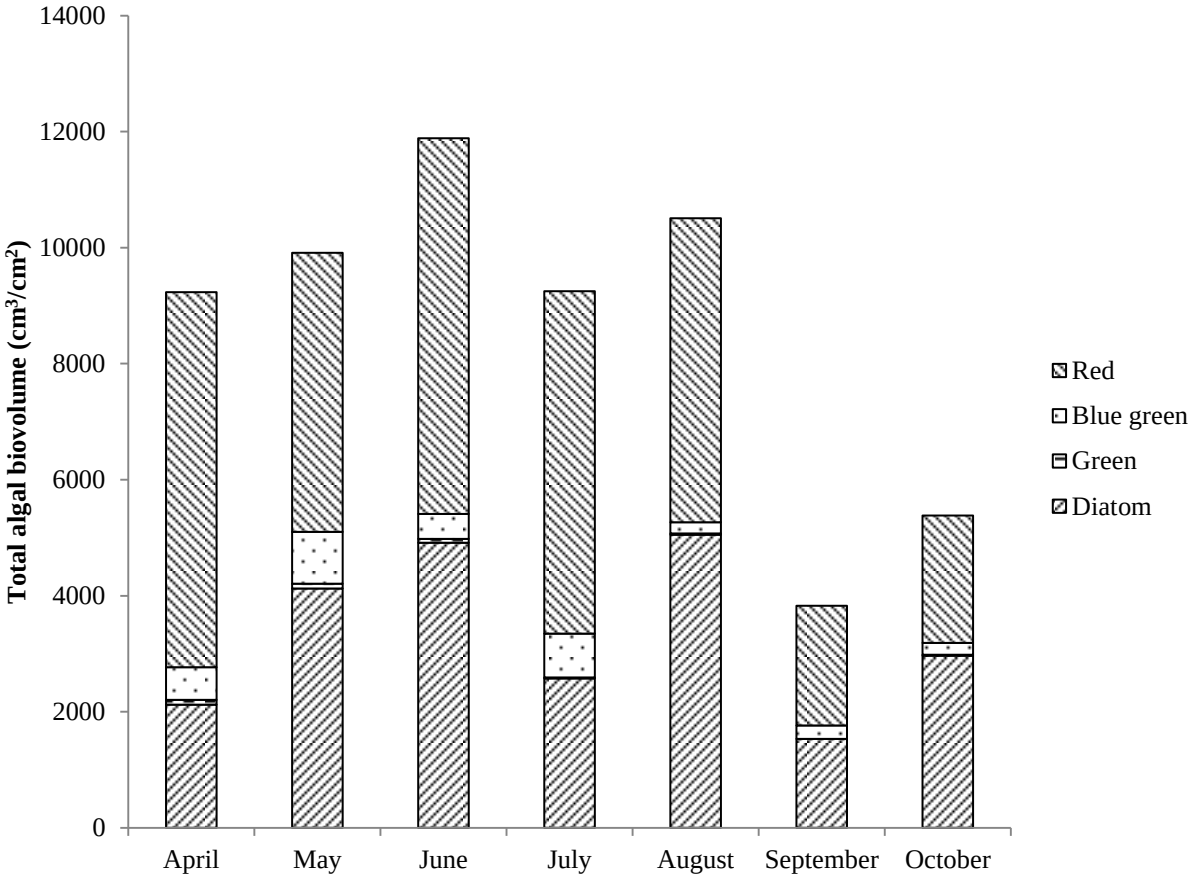

Figure 18. Average biomass (mg/cm^2) (±1 SD) of epiphytic algae per treatment for the sampling period of March through October 2011.

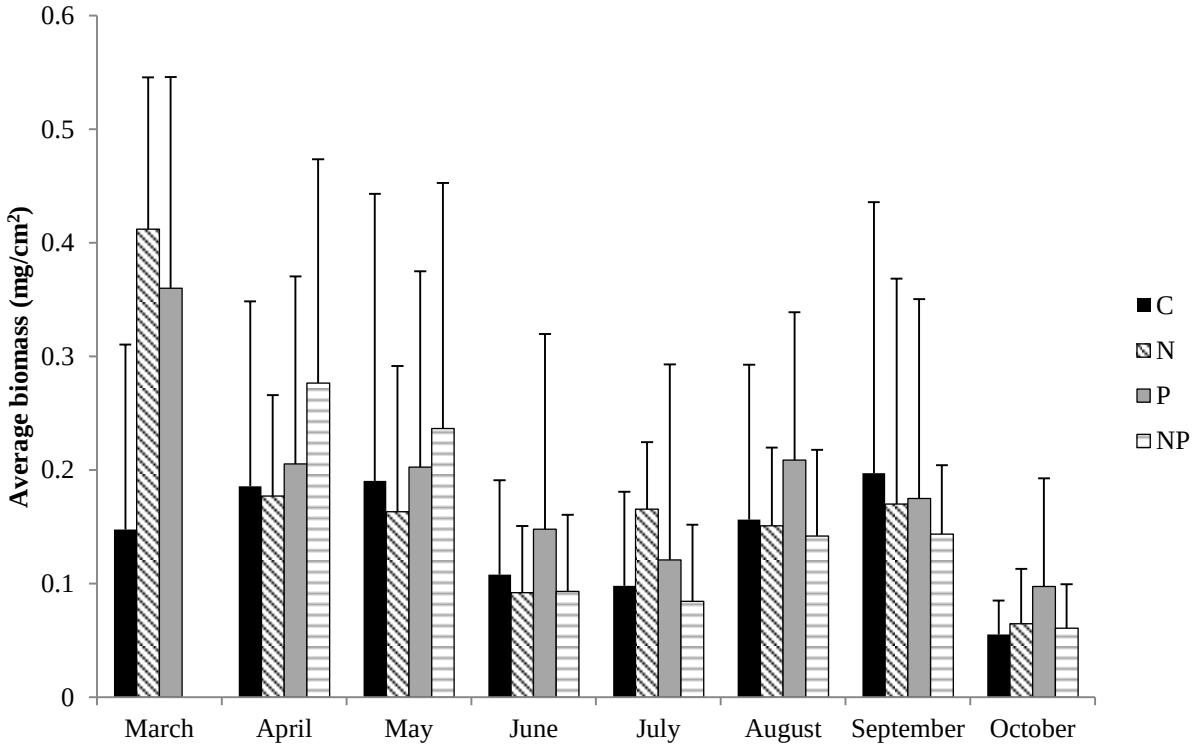

Figure 19. Total average biomass (mg/cm^2) (±1 SD) of epiphytic algae collected from all treatments for the sampling period of March through October 2011.

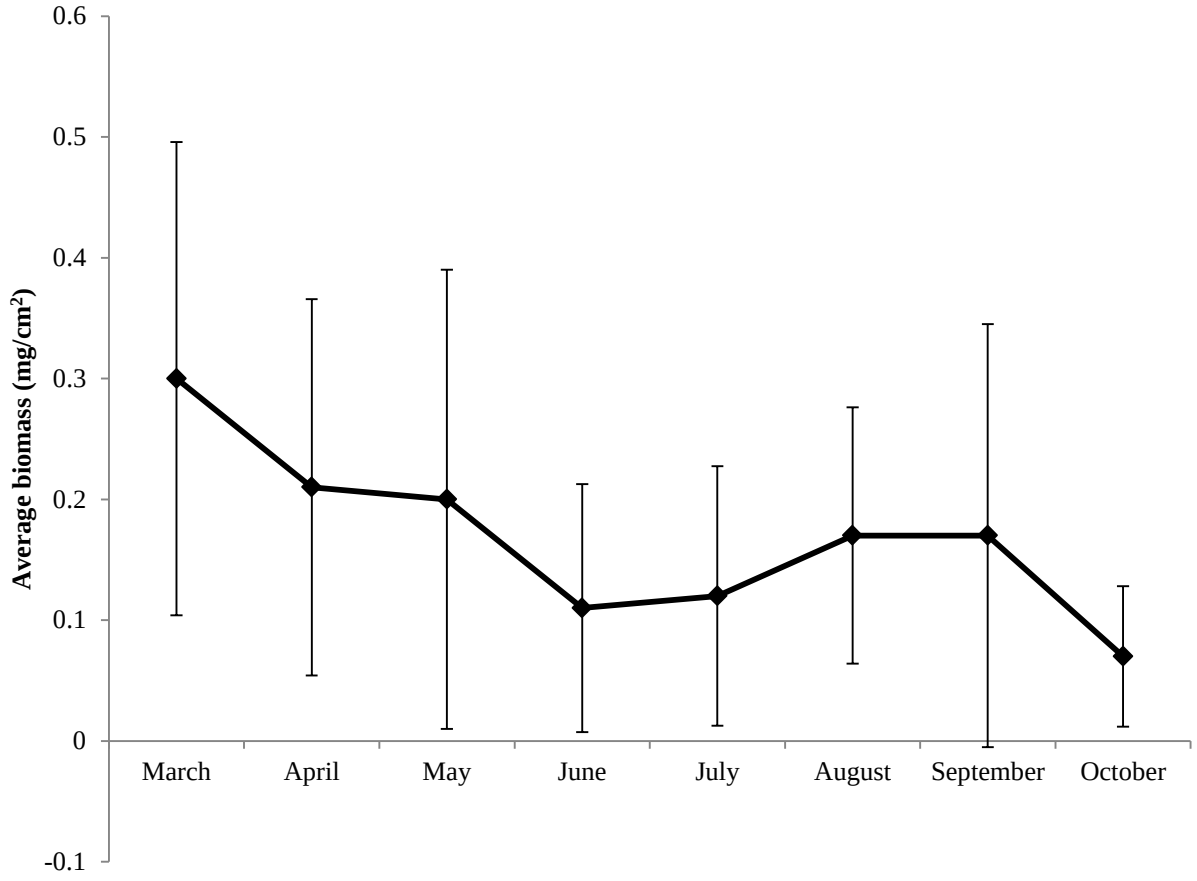

Figure 20. Average biomass (mg/cm^2) (±1 SD) of epiphytic algae for the control and nutrient treatments combined over the sampling period of April through October 2012. C=control, N=nitrogen, NP=nitrogen+phosphorus, and P=phosphorus.

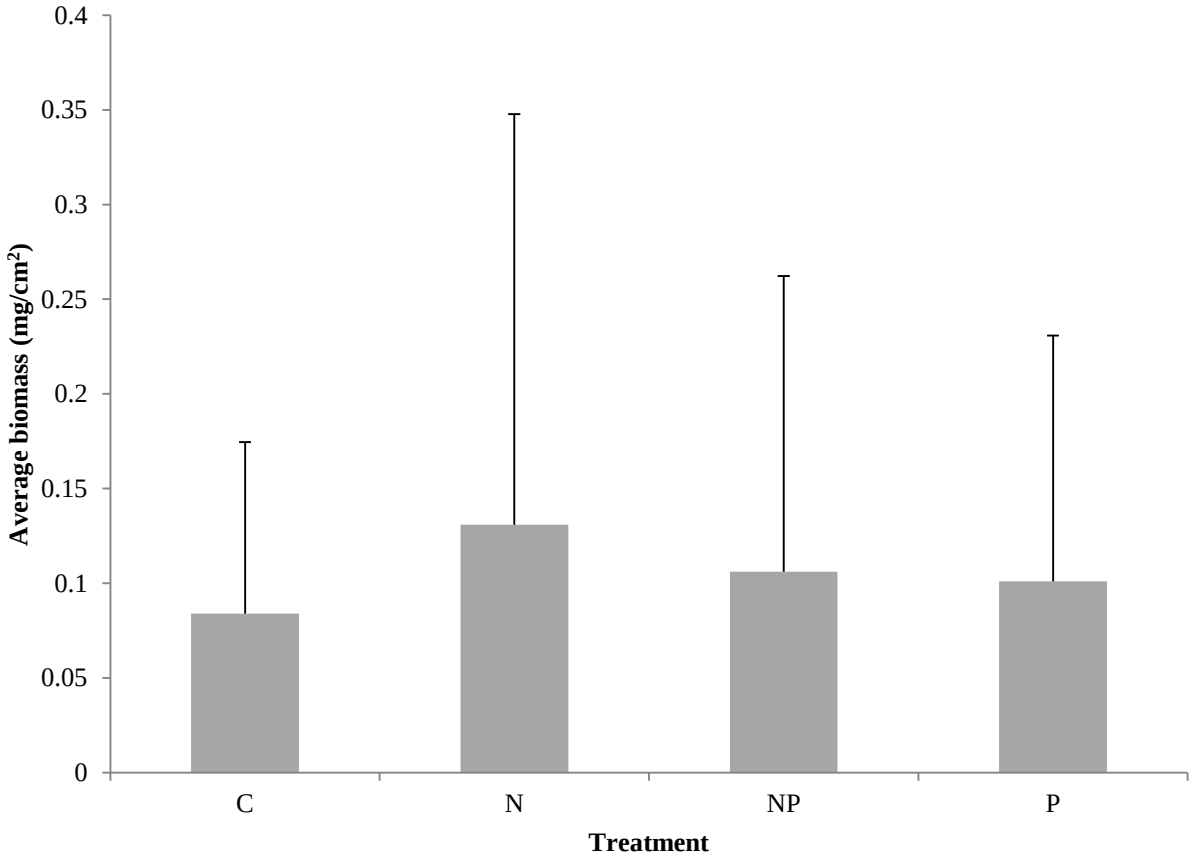

Figure 21. Average biomass (mg/cm^2) (±1 SD) of epiphytic algae per treatment for the sampling period of April through October 2012.

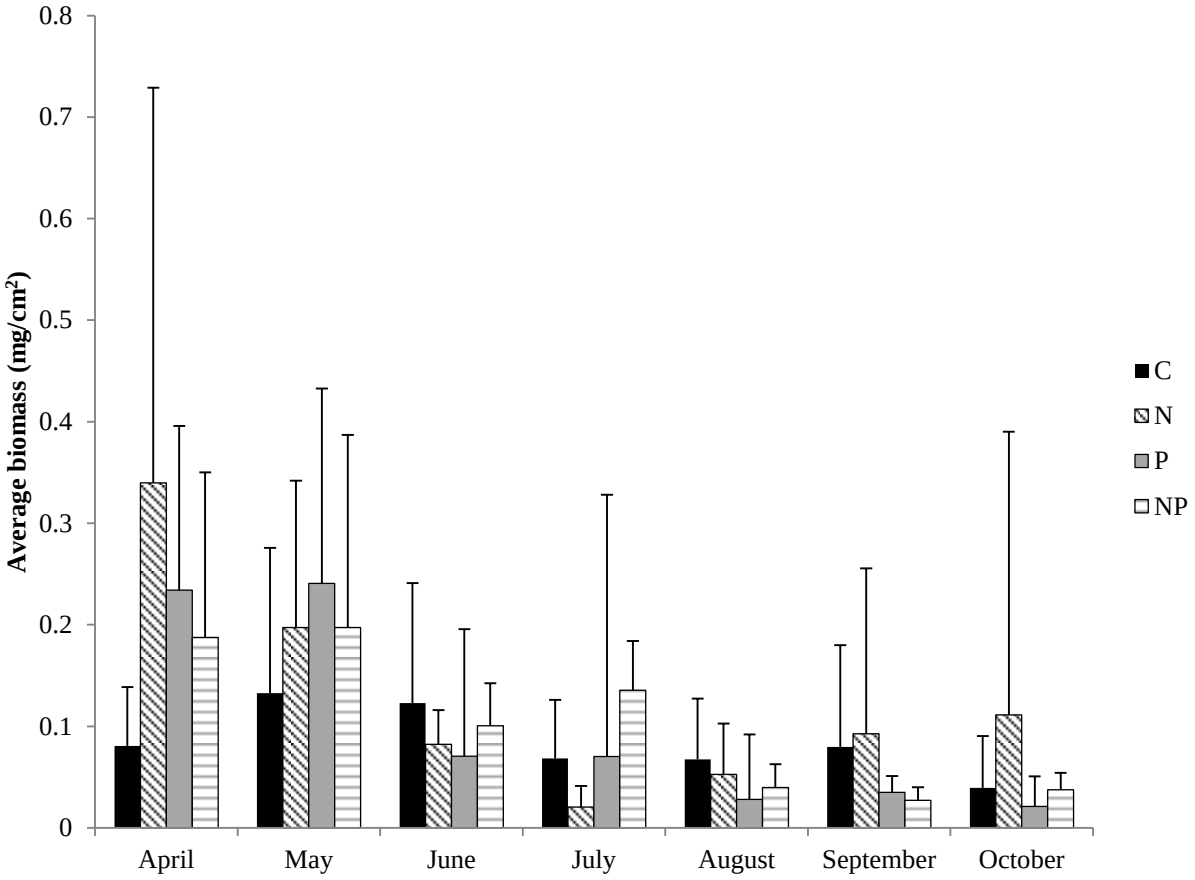

Figure 22. Total average biomass (mg/cm^2) (±1 SD) of epiphytic algae collected from all treatments for the sampling period of April through October 2012.

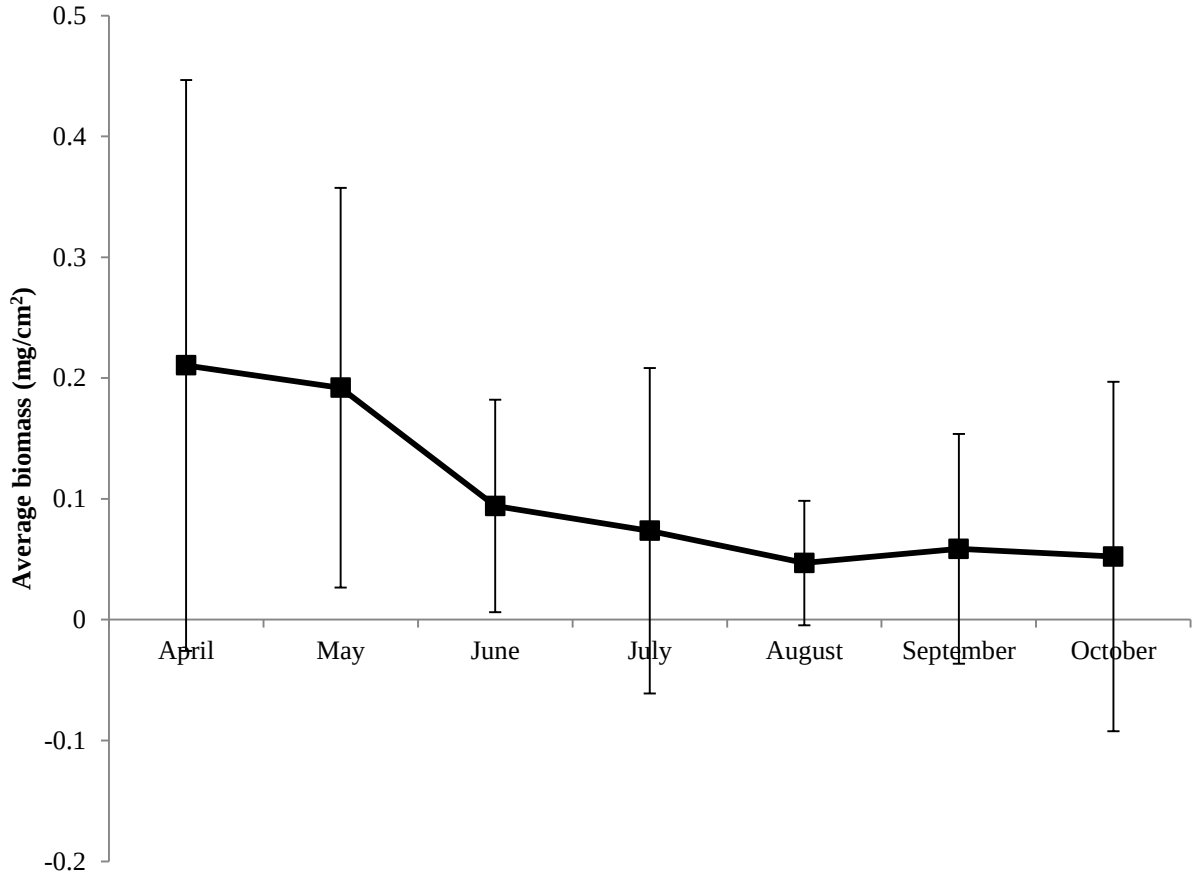

Figure 23. Average chlorophyll-*a* (µg/cm^2) (±1 SD) of epiphytic algae per treatment for the sampling period of March through October 2011.

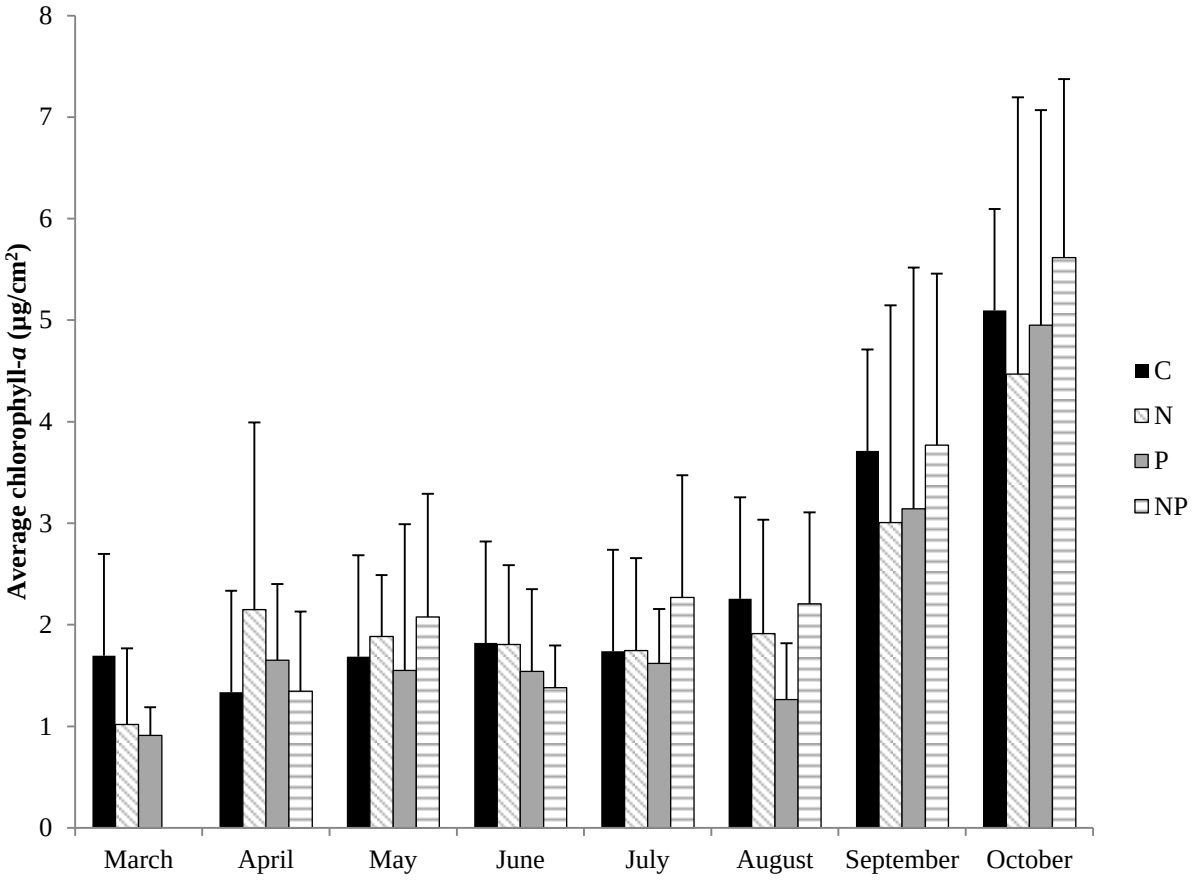

Figure 24. Total average chlorophyll-*a* (µg/cm^2) (±1 SD) of epiphytic algae collected from all treatments for the sampling period of March through October 2011.

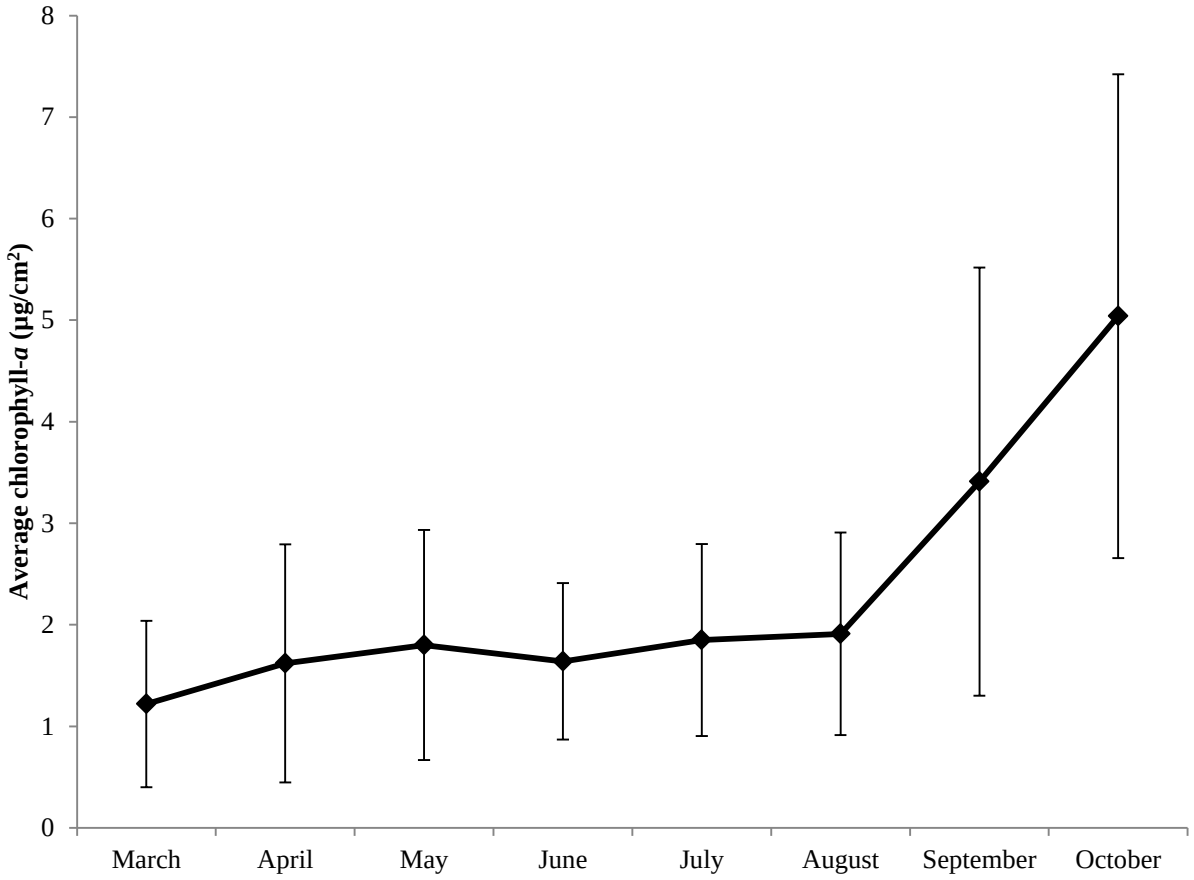

Figure 25. Average chlorophyll-*a* (µg/cm^2) (±1 SD) of epiphytic algae per treatment for the sampling period of April through October 2012.

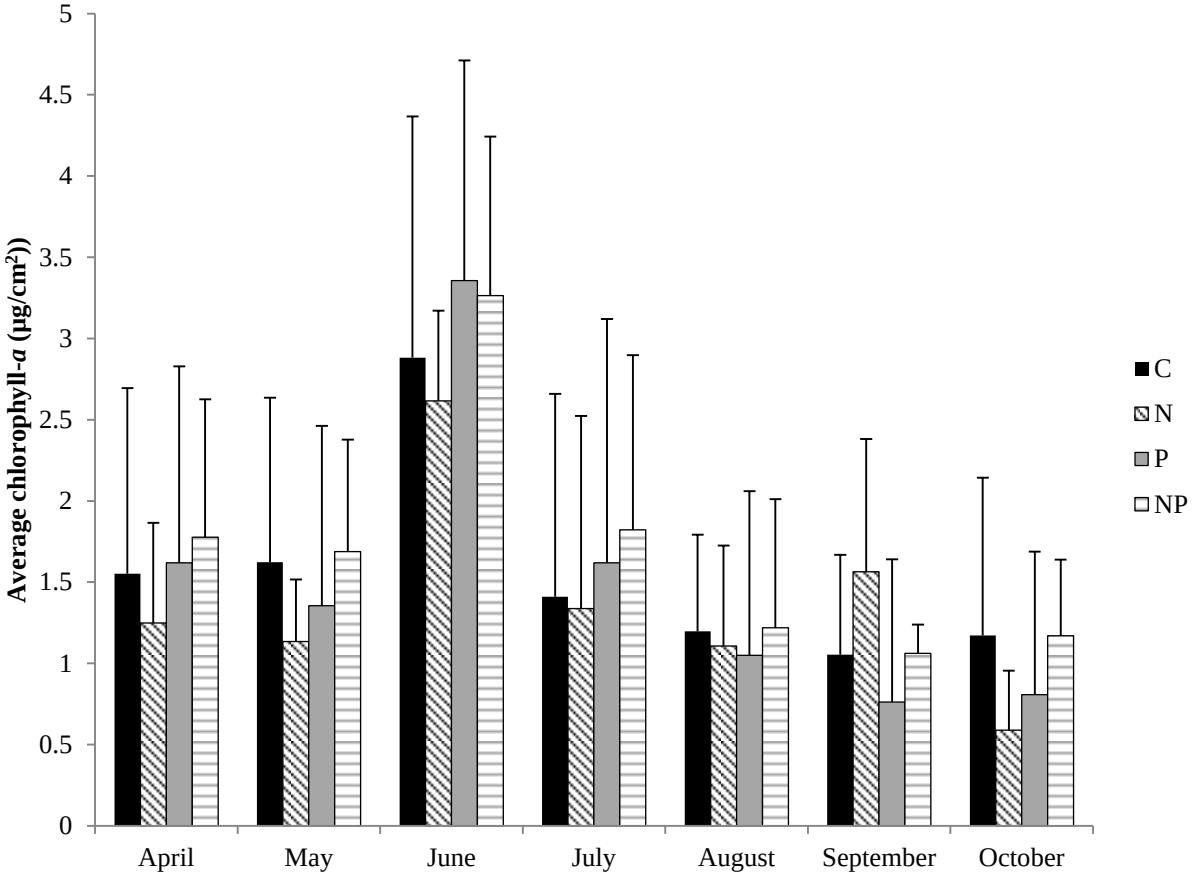

Figure 26. Average chlorophyll-*a* (µg/cm^2) (±1 SD) for the control and nutrient treatments combined over the sampling period of April through October 2012. C=control, N=nitrogen, NP=nitrogen+phosphorus, and P=phosphorus.

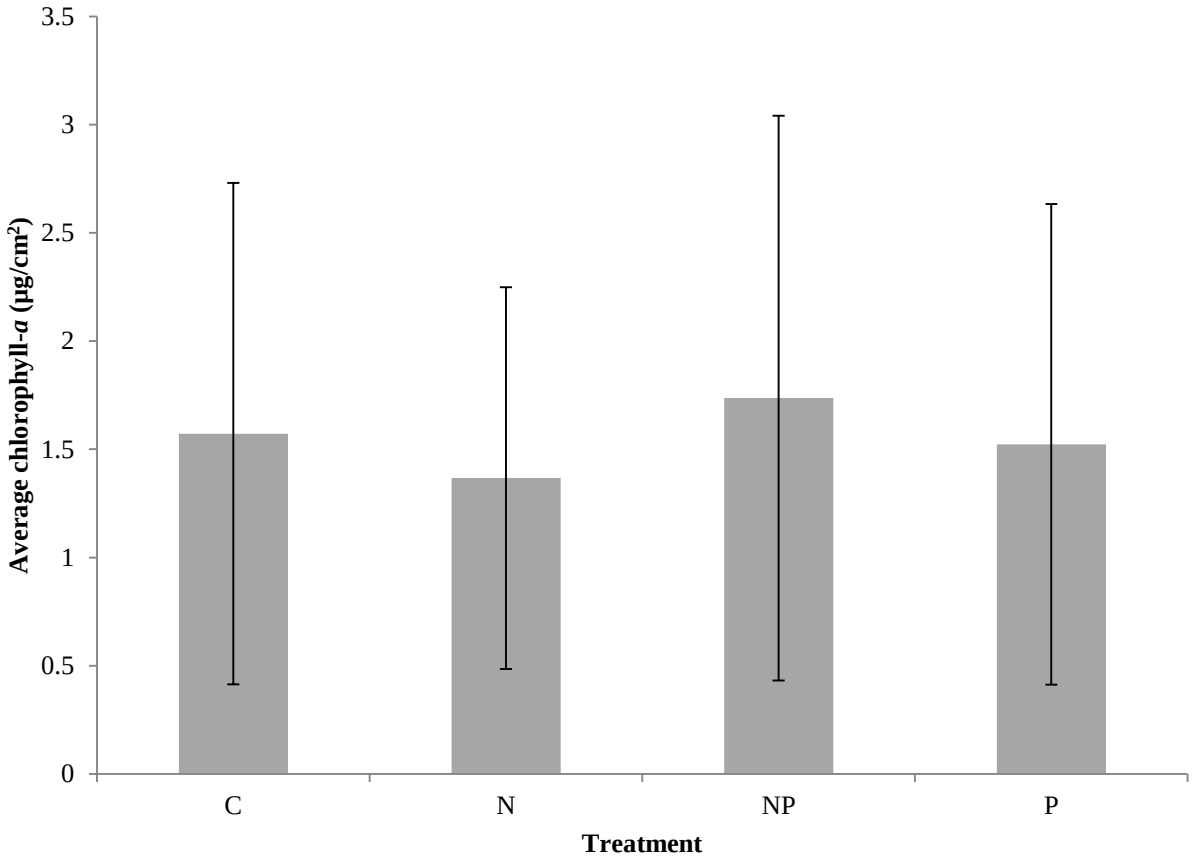

Figure 27. Total average chlorophyll-*a* (µg/cm^2) (±1 SD) of epiphytic algae collected from all treatments for the sampling period of April through October 2012.

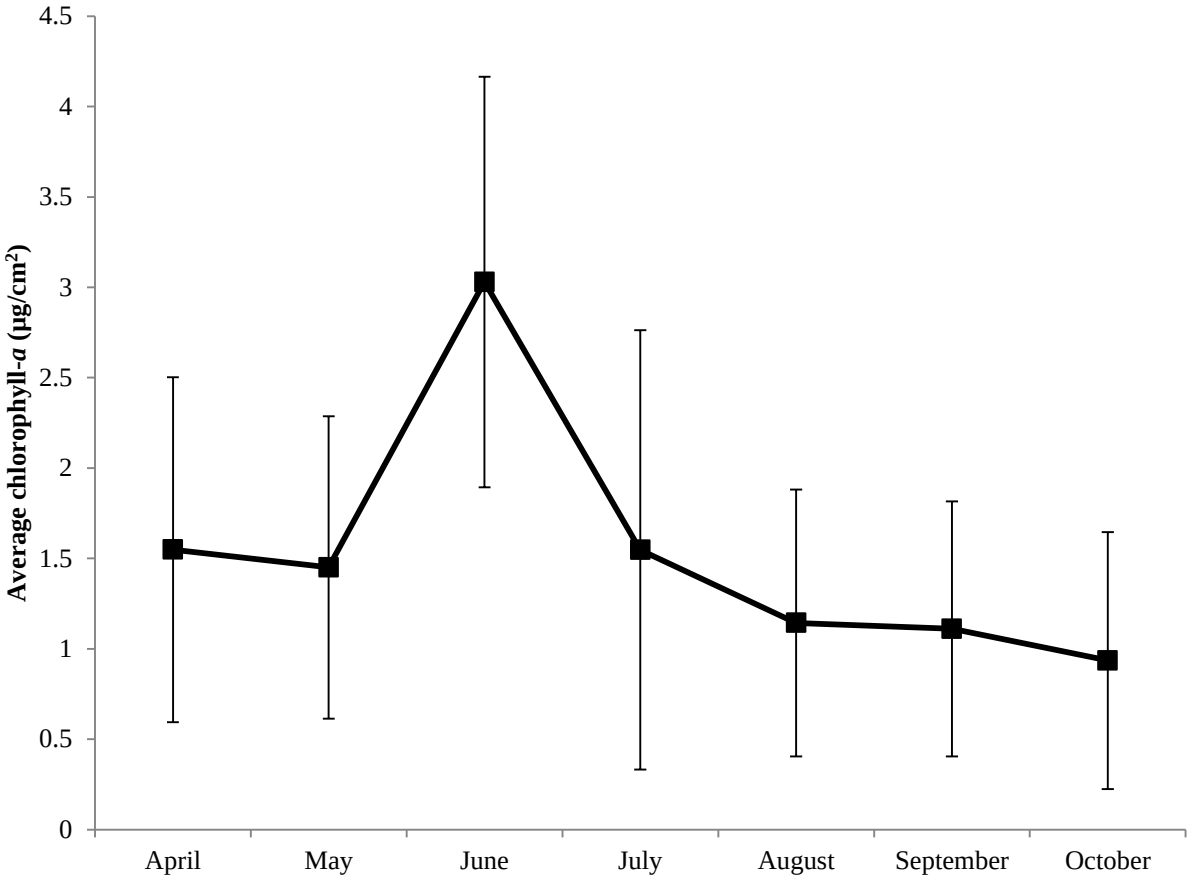

Figure 28. Average biomass (mg/cm^2) and chlorophyll-a (µg/cm^2) (±1 SD) of epiphytic algae collected from all treatments for the sampling period of March through October 2011.

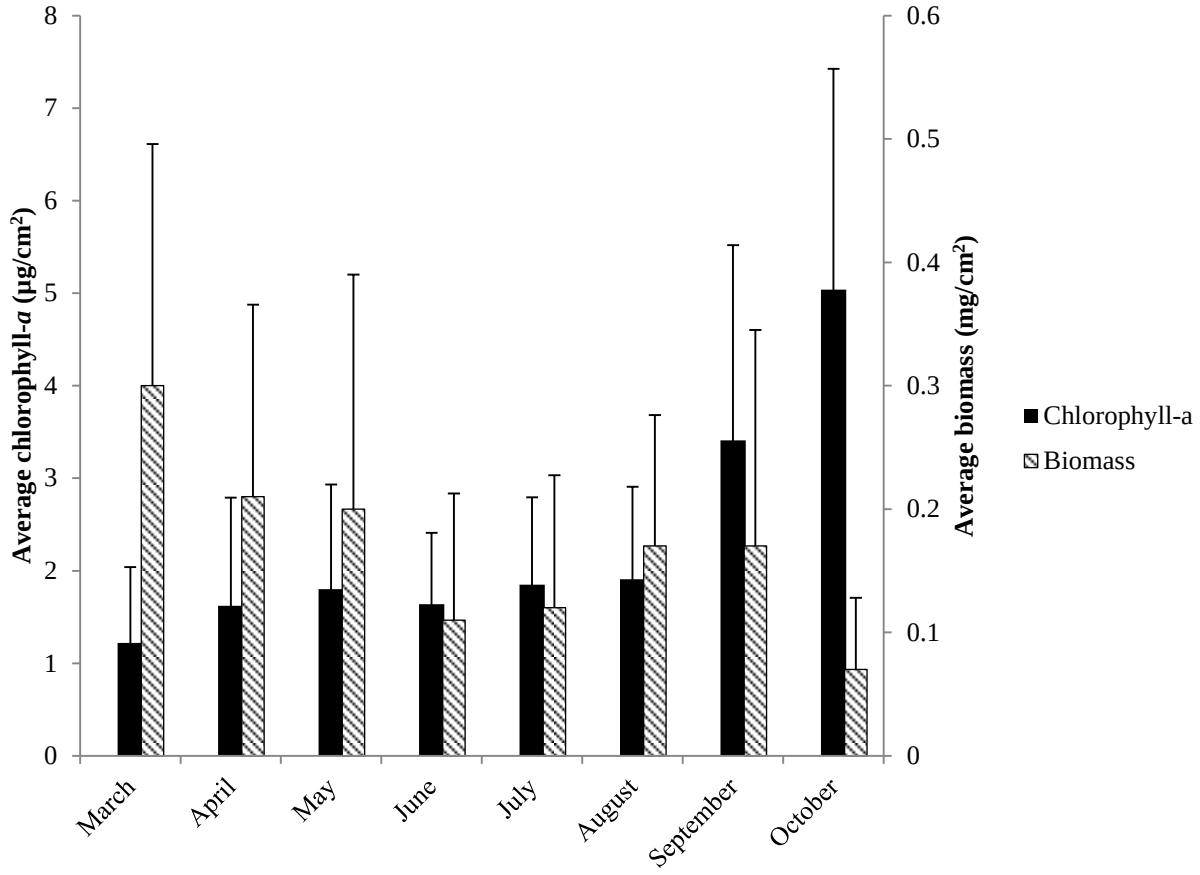

Figure 29. Average biomass (mg/cm^2) and chlorophyll-*a* (µg/cm^2) (±1 SD) of epiphytic algae collected from all treatments for the sampling period of April through October 2012.

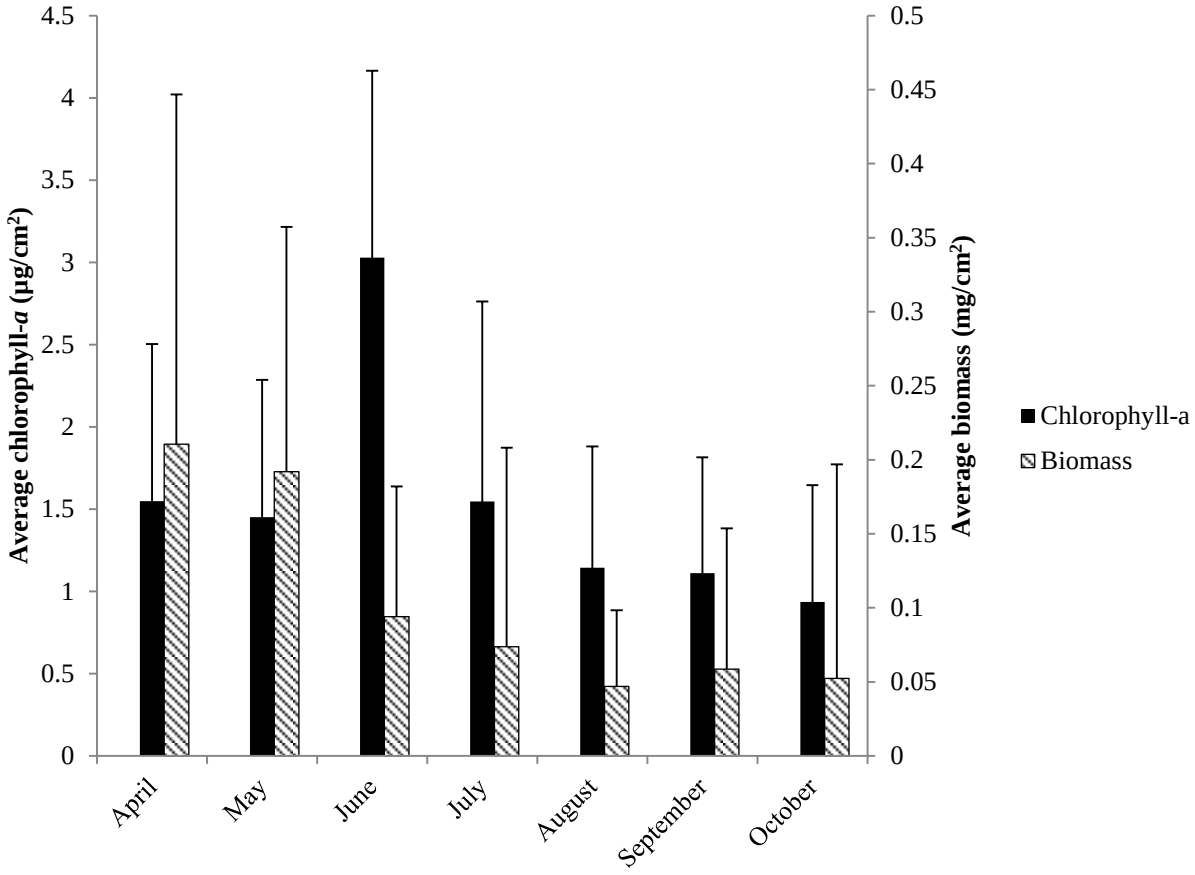

Figure 30. Comparison of average biomass (mg/cm^2) (±1 SD) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

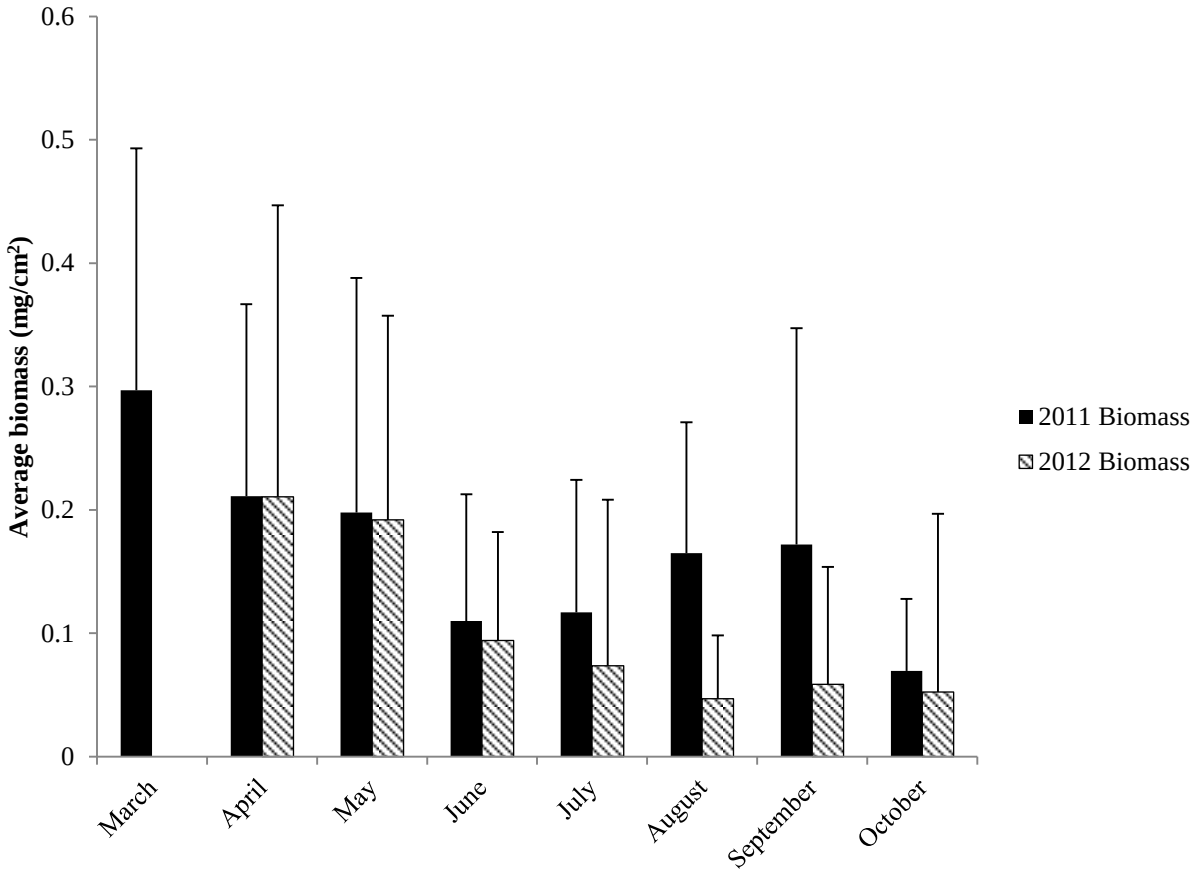

Figure 31. Comparison of average chlorophyll-*a* (µg/cm^2) (±1 SD) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

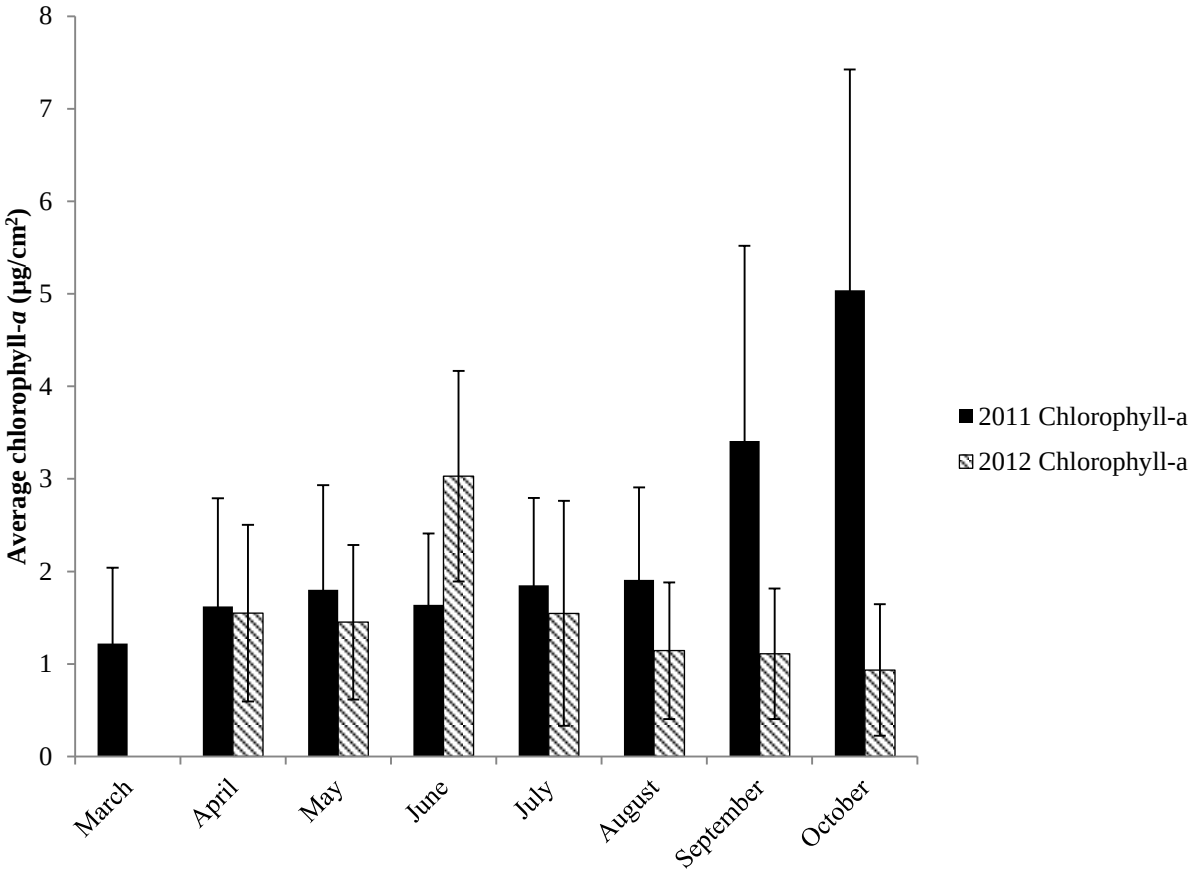

Figure 32. Comparison of total epiphytic algal abundance (number of cells) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

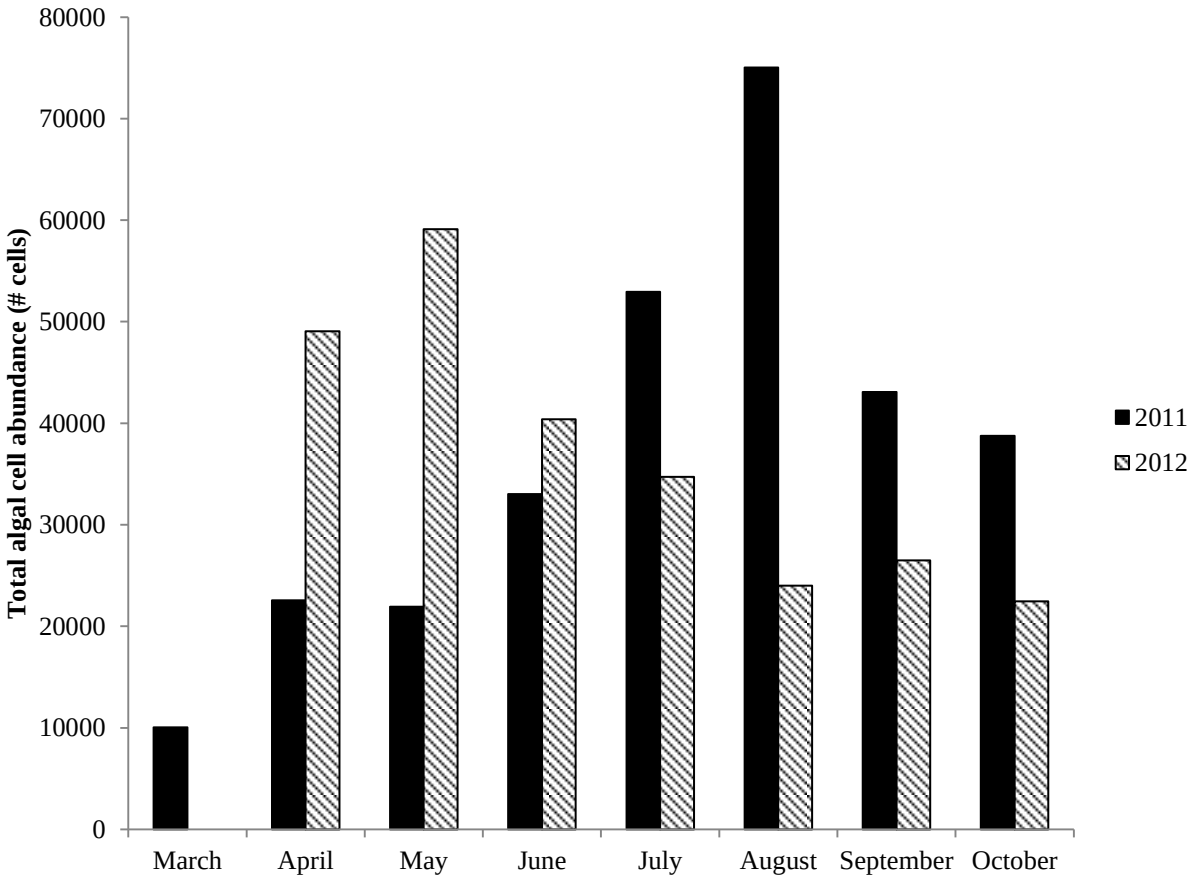

Figure 33. Comparison of total epiphytic algal density (cells/cm^2) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

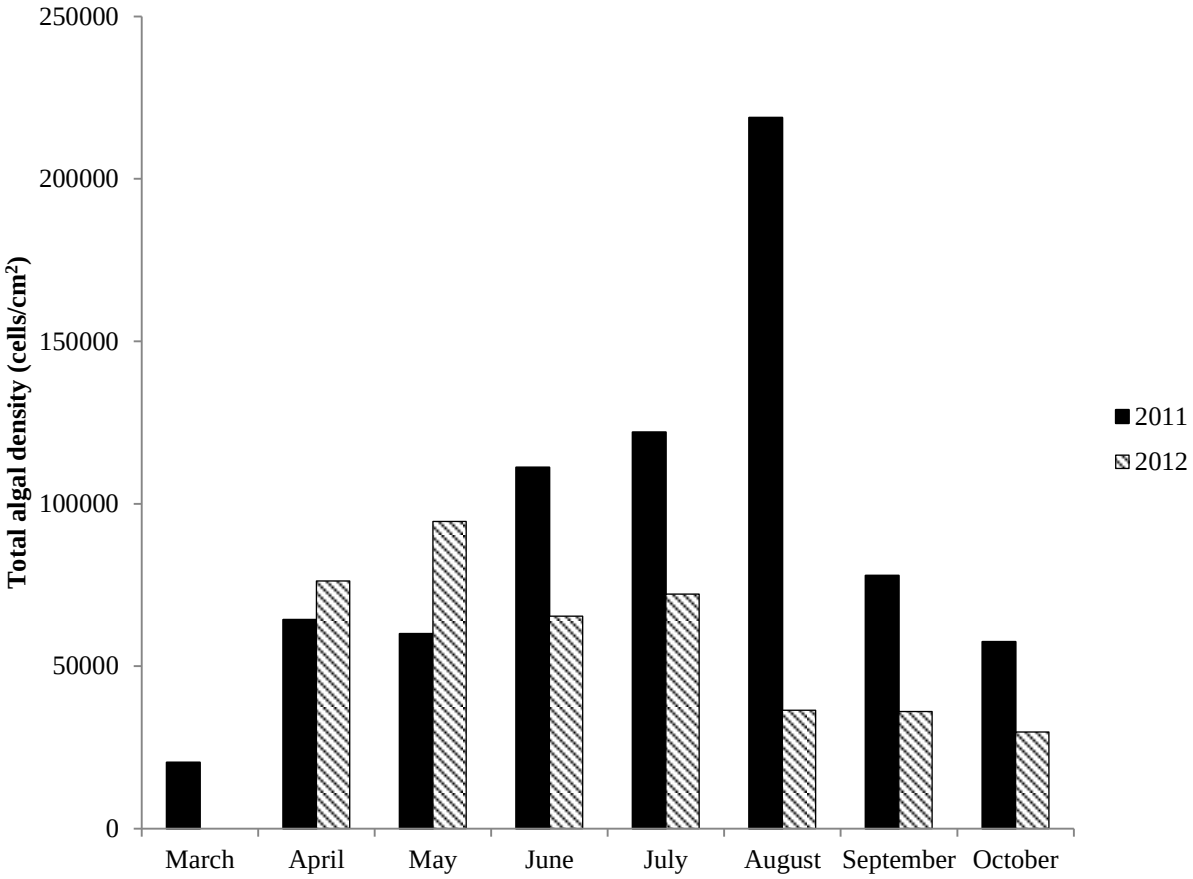

Figure 34. Comparison of total epiphytic algal biovolume (cm^3/cm^2) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

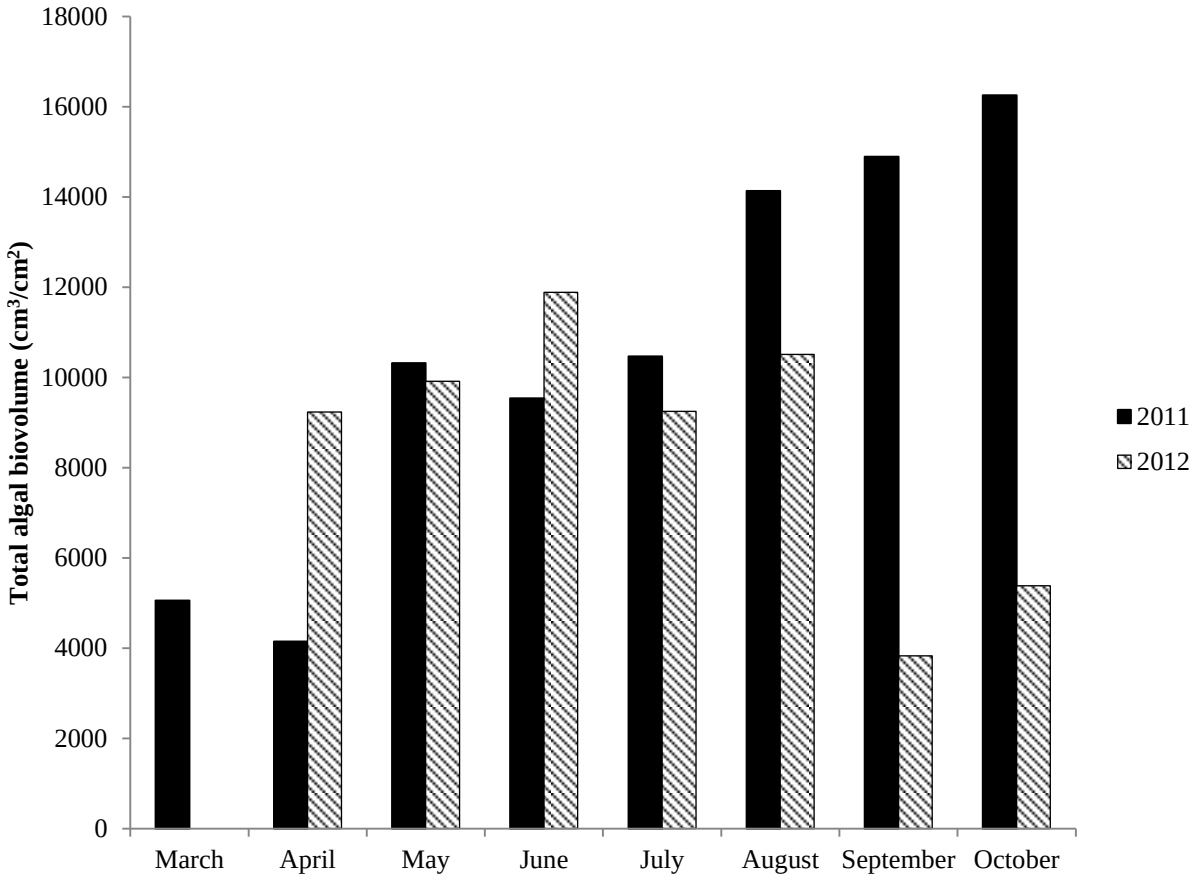

Figure 35. Average biomass (mg/cm^2) (±1 SD) of epiphytic algae per treatment collected during the 28-day lab nutrient manipulation study.

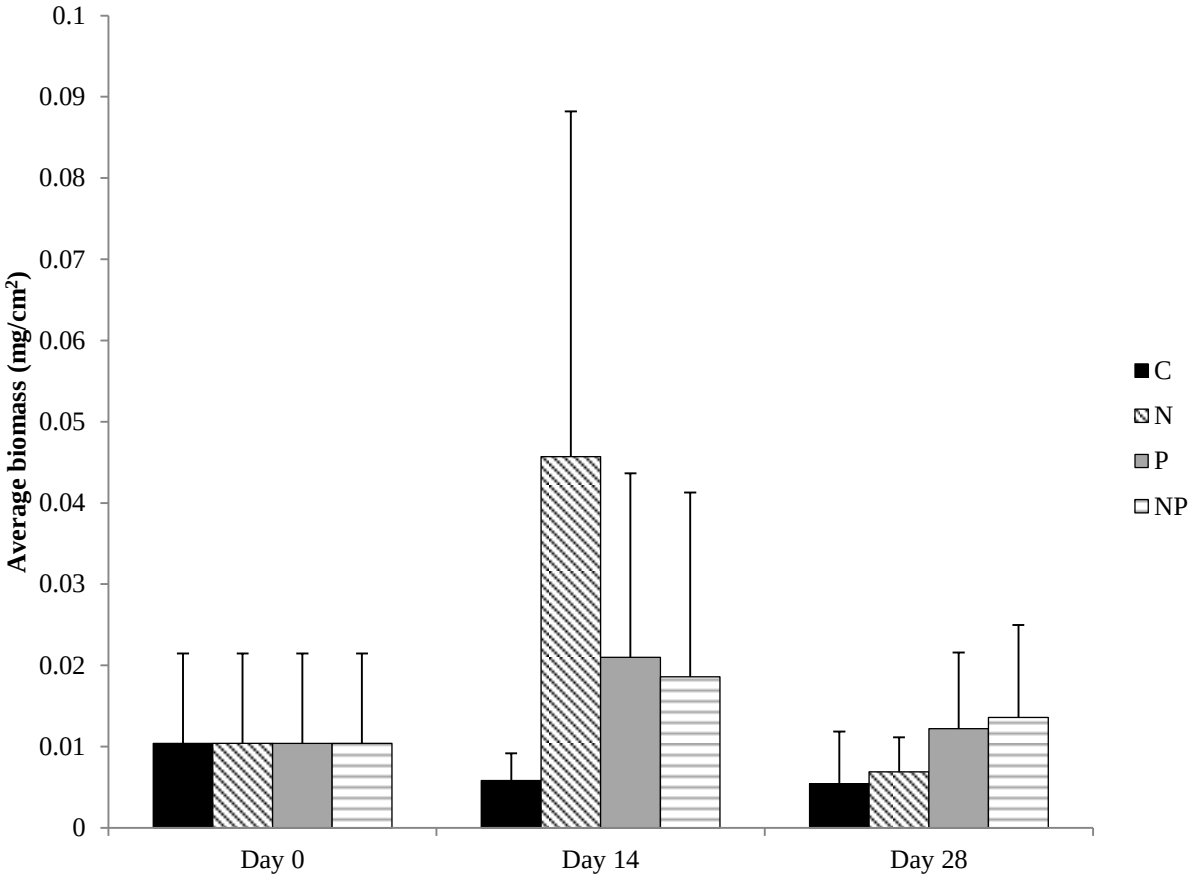

Figure 36. Combined average biomass (mg/cm^2) (±1 SD) across all treatments of epiphytic algae collected during the 28-day lab nutrient manipulation study.

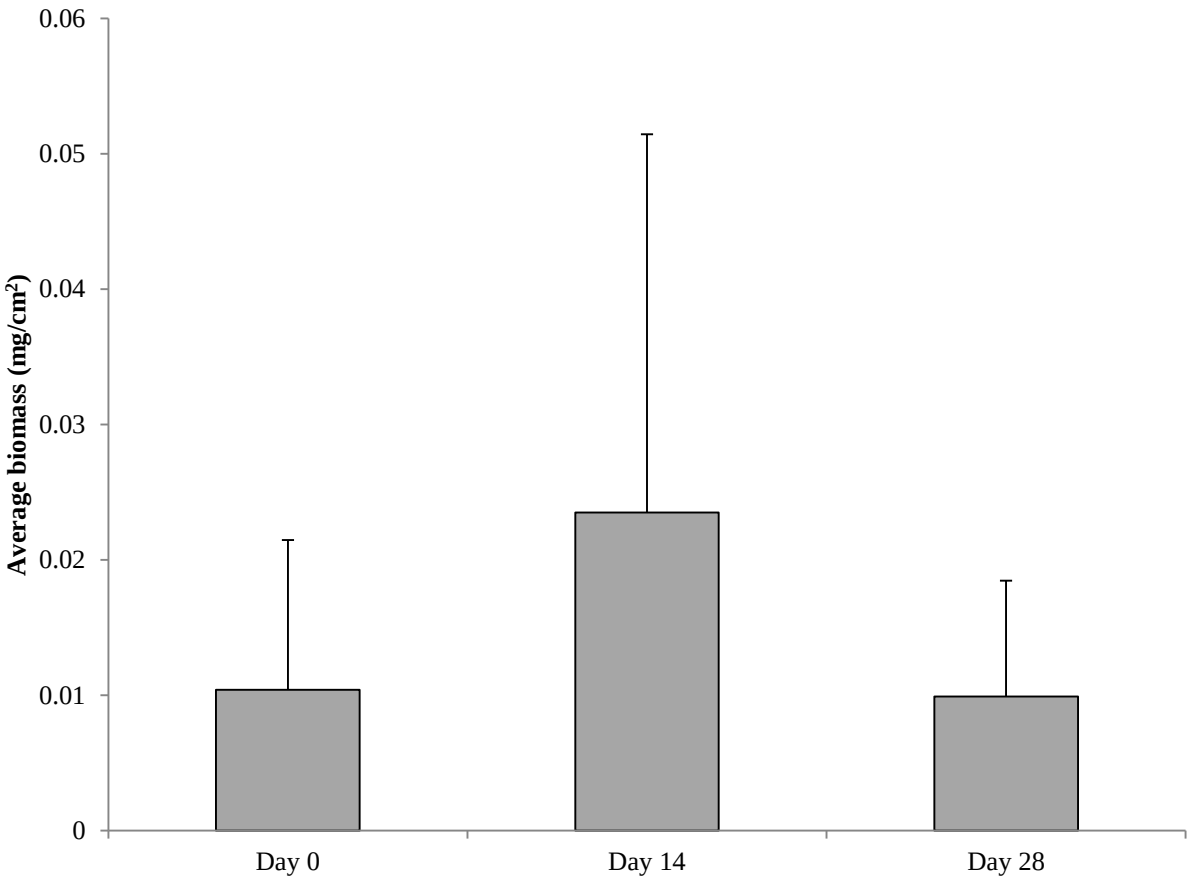

Figure 37. Average chlorophyll-*a* (µg/cm^2) (±1 SD) of epiphytic algae per treatment collected during the 28-day lab nutrient manipulation study.

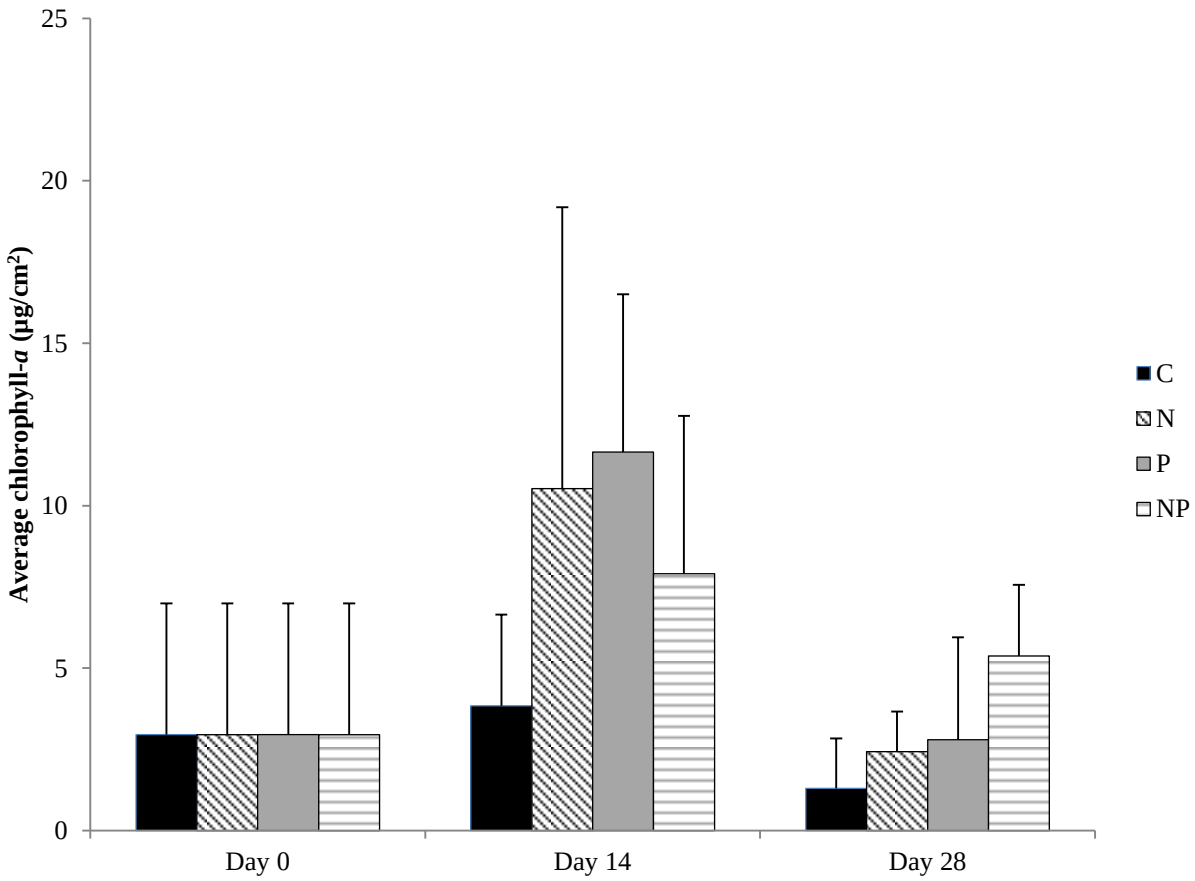

Figure 38. Combined average chlorophyll-*a* (µg/cm^2) (±1 SD) across all treatments of epiphytic algae collected during the 28-day lab nutrient manipulation study.

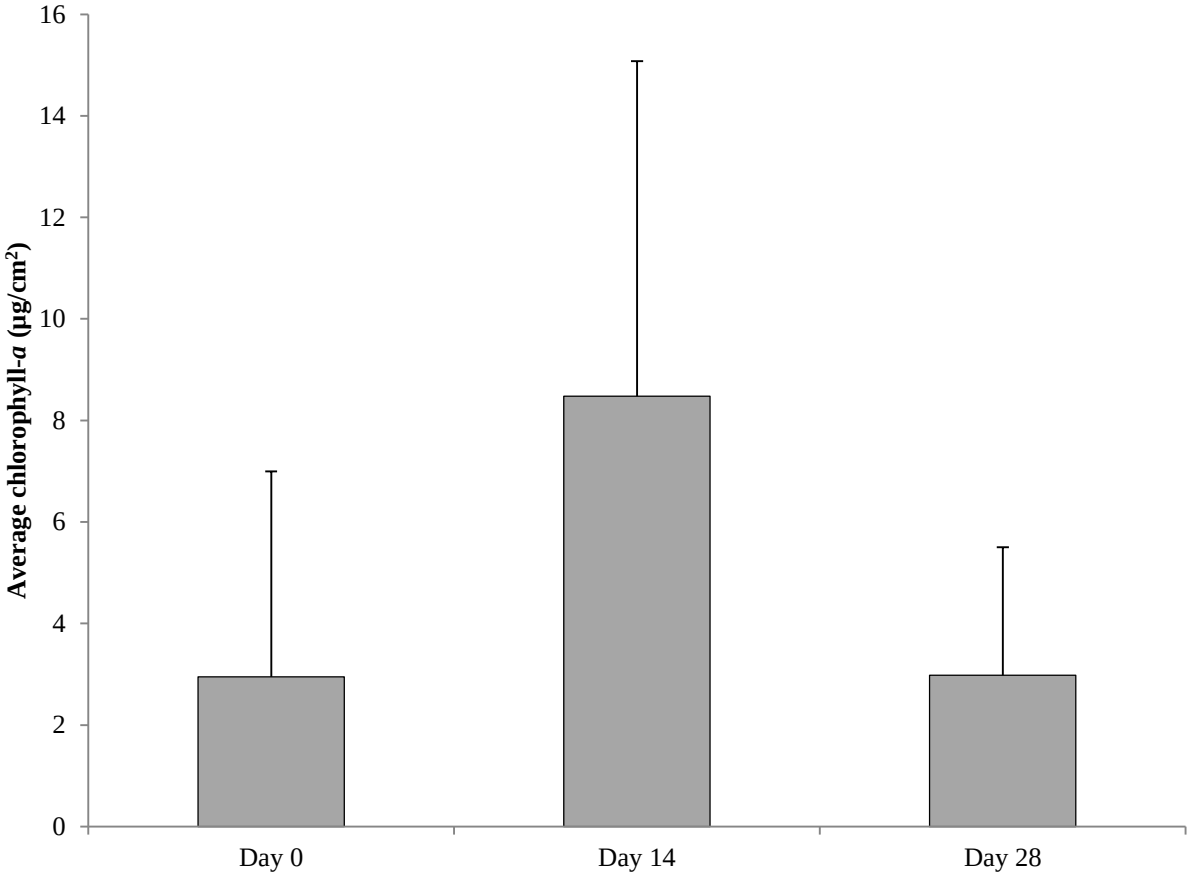

Table 1. Missing data points. ('X' denotes unobtained data.)

Date	Sample	Parameter				
		Chlorophyll-*a*	AFDM	Abundance	Density	Biovolume
			2011			
March	N7		X	X	X	X
March	N8	X	X	X	X	X
March	NP1-NP8	X	X	X	X	X
April	N6			X	X	X
August	NP5	X	X	X	X	X
September	NP6	X	X	X	X	X
			2012			
April	P6			X	X	X
September	C4	X	X	X	X	X
September	N5	X	X	X	X	X
September	NP2	X	X	X	X	X
September	P8	X	X	X	X	X
October	C1			X	X	X
October	C8	X	X	X	X	X
October	NP2	X	X	X	X	X

Table 2. Site physical and chemical parameters measured for the 2011 and 2012 sampling seasons. Nutrient data was obtained from the NOAA NERR Centralized Data Management Office.

Date	Water Temperature °C	Salinity ppt	Dissolved Oxygen mg/L	PO_4 mg/L	NH_4 mg/L	NO_2 mg/L	NO_3 mg/L
				2011			
March	20.9	34.8	6.00	0.0010 ± .005	0.019 ± .001	0.00	0.0049 ± .0003
April	25.1	42.0	3.10	0.011 ± 0.0	0.051 ± .004	0.0030 ± .0002	0.0074 ± .0006
May	28.5	38.9	4.80	0.070 ± .001	0.038 ± .001	0.00	0.0041 ± .001
June	28.1	41.1	4.80	0.016 ± 0.0	0.034 ± 0.0	0.00	0.0054 ± .0002
July	29.8	38.0	4.80	0.023 ± .005	0.11 ± .004	0.0040 ± 0.0	0.0099 ± .0007
August	30.4	39.2	3.70	0.018 ± 0.0	0.047 ± .002	0.0024 ± .0001	0.0029 ± .0004
September	24.2	29.2	5.10	0.020 ± .005	0.076 ± .008	0.0048 ± .0001	0.018 ± .0008
October	19.2	33.2	6.40	0.014 ± .001	0.060 ± .005	0.013 ± .0005	0.033 ± .001
				2012			
April	23.7	35.7	6.04	0.0090 ± .001	0.046 ± .005	0.0044 ± .003	0.041 ± 0.0
May	24.6	37.9	6.31	0.012 ± .01	0.028 ± .003	0.016 ± 0.0	0.018 ± .0006
June	27.0	16.4	6.16	0.0070 ± .0005	0.020 ± .002	0.0025 ± .001	0.0099 ± .002
July	31.7	18.3	6.20	0.014 ± 0.0	0.31 ± .001	0.0021 ± .003	0.0046 ± .0007
August	32.0	10.5	2.98	0.017 ± .005	0.068 ± .005	0.043± .005	0.012 ± 0.0
September	28.0	26.8	4.70	0.024 ± 0.0	0.14 ± .01	0.11 ± 0.0	0.025 ± 0.0
October	16.7	26.0	6.92	0.009 ± .001	0.063 ± .002	0.0038 ± .0001	0.015 ± 0.0

Table 3. 2011 algal cell abundance (# cells) by division including percent (%) of total community for each nutrient treatment.

	Control				Nitrogen			
	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta
March	141 (7%)	108 (5%)	1718 (86%)	43 (2%)	444 (12%)	68 (2%)	2553 (71%)	540 (15%)
April	237 (3%)	89 (1%)	7822 (89%)	660 (7%)	302 (9%)	11 (0%)	2389 (71%)	666 (20%)
May	566 (10%)	64 (1%)	3455 (61%)	1624 (28%)	405 (8%)	16 (0%)	4190 (78%)	754 (14%)
June	444 (7%)	39 (1%)	4736 (74%)	1128 (18%)	391 (3%)	132 (1%)	11693 (89%)	981 (7%)
July	646 (6%)	24 (0.2%)	8776 (77%)	1934 (17%)	839 (4%)	21 (0%)	19046 (83%)	3124 (13%)
August	541 (3%)	43 (1%)	14292 (92%)	641 (4%)	1026 (5%)	80 (0%)	19248 (89%)	1189 (6%)
September	1055 (6%)	56 (1%)	13573 (84%)	1444 (9%)	1243 (19%)	86 (1%)	4535 (69%)	702 (11%)
October	1287 (14%)	77 (1%)	6112 (69%)	1384 (16%)	1460 (13%)	70 (1%)	7610 (66%)	2373 (20%)

	Phosphorus				Nitrogen+Phosphorus			
	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta
March	528 (12%)	215 (5%)	3124 (70%)	582 (13%)	-	-	-	-
April	415 (8%)	61 (1%)	3447 (71%)	966 (20%)	297 (5%)	35 (1%)	4871 (88%)	303 (7%)
May	409 (7%)	38 (1%)	4054 (69%)	1324 (23%)	607 (12%)	93 (2%)	3679 (73%)	649 (13%)
June	429 (5%)	46 (1%)	5981 (74%)	1658 (20%)	375 (7%)	33 (1%)	4385 (81%)	592 (11%)
July	498 (4%)	12 (0%)	9712 (82%)	1691 (14%)	635 (10%)	27 (0%)	5121 (77%)	828 (13%)
August	616 (3%)	76 (0%)	19123 (93%)	723 (4%)	785 (5%)	83 (0%)	15370 (63%)	1196 (7%)
September	1192 (10%)	29 (0%)	8320 (69%)	2485 (21%)	1661 (20%)	59 (0%)	5235 (63%)	1395 (17%)
October	1182 (15%)	276 (3%)	5353 (67%)	1184 (15%)	1241 (12%)	190 (2%)	8418 (81%)	554 (%)

Table 4. 2011 total algal cell abundance (number of cells) by division.

	Division			
Month	Cyanobacteria	Chlorophyta	Bacillariophyta	Rhodophyta
March	7,395	391	1,113	1,165
April	18,529	196	1,251	2,595
May	15,378	212	1,987	4,350
June	26,795	250	1,639	4,359
July	42,670	84	2,612	7,577
August	68,033	282	2,968	3,749
September	32,205	230	4,609	6,026
October	27,493	613	5,170	5,495
Total	238,498	2,258	21,349	35,316

Table 5. 2011 total algal cell density (cells/cm^2) by division.

	Division			
Month	Cyanobacteria	Chlorophyta	Bacillariophyta	Rhodophyta
March	14,921	781	1,936	2,785
April	55,608	430	2,388	5,888
May	39,753	447	5,860	13,912
June	91,822	334	3,886	15,176
July	99,682	95	5,370	16,902
August	193,890	437	8,609	15,885
September	52,498	160	10,378	14,836
October	33,863	591	10,215	12,804
Total	582,037	3,275	48,642	98,186

Table 6. 2011 total algal biovolume (cm^3/cm^2) by division.

	Division			
Month	Cyanobacteria	Chlorophyta	Bacillariophyta	Rhodophyta
March	262	110	3,395	1,289
April	692	55	1,973	1,430
May	434	70	5,429	4,387
June	928	87	3,492	5,032
July	1,235	25	3,186	6,020
August	2,182	88	5,805	6,060
September	578	42	9,135	5,138
October	444	80	10,092	5,636
Total	6,755	557	42,507	34,992

Table 7. Algal taxa identified and abundance (# cells) from all plots for the sampling period of March through October 2011. A total of 137 infra-generic taxa were identified.

Species	Division	Abundance
Achnanthes inflata	Bacillariophyta	961
Achnanthes sp.	Bacillariophyta	106
Achnanthidium sp.	Bacillariophyta	380
Actinella sp.	Bacillariophyta	4
Actinocyclus sp.	Bacillariophyta	426
Amphipleura sp.	Bacillariophyta	5
Amphiprora sp.	Bacillariophyta	114
Amphora sp.	Bacillariophyta	414
Asterionella sp.	Bacillariophyta	1
Aulacoseira sp.	Bacillariophyta	597
Biddulphia sp.	Bacillariophyta	34
Brachysira sp.	Bacillariophyta	10
Caloneis sp.	Bacillariophyta	2
Cavinula sp.	Bacillariophyta	4
Climacodium fraunenfeldianum	Bacillariophyta	63
Cocconeis sp.	Bacillariophyta	281
Coscinodiscus sp.	Bacillariophyta	131
Cyclostephanus sp.	Bacillariophyta	1
Cyclotella sp.	Bacillariophyta	49
Cymatopleura sp.	Bacillariophyta	24
Cymbella sp.	Bacillariophyta	364
Diademis sp.	Bacillariophyta	2
Diatoma sp.	Bacillariophyta	7
Diatomeis sp.	Bacillariophyta	1
Diploneis bombus	Bacillariophyta	50
Diploneis chersonensis var. *apiformis*	Bacillariophyta	86
Diploneis crabro	Bacillariophyta	1
Diploneis didyma	Bacillariophyta	74
Diploneis pupula	Bacillariophyta	2
Diploneis sp.	Bacillariophyta	144
Diploneis sp.2	Bacillariophyta	1
Encyonema sp.	Bacillariophyta	5
Epithemia sp.	Bacillariophyta	110
Eunotia sp.	Bacillariophyta	170
Fragilaria sp.	Bacillariophyta	917
Frustulia sp.	Bacillariophyta	274
Gomphonema sp.	Bacillariophyta	46

Species	Division	Abundance
Gyrosigma fasciola	Bacillariophyta	34
Gyrosigma sp.	Bacillariophyta	1,175
Hantzschia sp.	Bacillariophyta	11
Hydrosera sp.	Bacillariophyta	13
Luticola sp.	Bacillariophyta	4
Mastagloia sp.	Bacillariophyta	77
Melosira moniliformis	Bacillariophyta	2,748
Melosira sp.	Bacillariophyta	4,306
Meridion sp.	Bacillariophyta	1
Navicula sp.	Bacillariophyta	753
Nedium sp.	Bacillariophyta	2
Nitzschia acicularis	Bacillariophyta	3
Nitzschia longissima	Bacillariophyta	37
Nitzschia setaceum	Bacillariophyta	4
Nitzschia sp.	Bacillariophyta	1,481
Opephora sp.	Bacillariophyta	19
Pinnularia sp.	Bacillariophyta	266
Placoneis sp.	Bacillariophyta	6
Pleurosigma sp.	Bacillariophyta	103
Rhopalodia sp.	Bacillariophyta	3
Sellaphora sp.	Bacillariophyta	38
Stauroneis sp.	Bacillariophyta	2
Staurosira sp.	Bacillariophyta	10
Staurosirella sp.	Bacillariophyta	1
Stephanocyclus sp.	Bacillariophyta	2
Stephanodiscus sp.	Bacillariophyta	227
Surirella sp.	Bacillariophyta	68
Synedra spp.	Bacillariophyta	1,120
Synedra ulna	Bacillariophyta	1
Terpinsoe sp.	Bacillariophyta	165
Thallassiosira sp.	Bacillariophyta	72
Tryblionella granulata	Bacillariophyta	57
Tryblionella sp.	Bacillariophyta	124
centric diat	Bacillariophyta	600
pennate diat	Bacillariophyta	1,938
TOTAL		21,332
Actinotaenium sp.	Chlorophyta	1
Cladophora sp.	Chlorophyta	384
Closterium kutzingii	Chlorophyta	1
Closterium spp.	Chlorophyta	204
Cosmarium sp.	Chlorophyta	136
Cylindrocystis sp.	Chlorophyta	1

Species	Division	Abundance
Enteromorpha sp.	Chlorophyta	46
Geminella sp.	Chlorophyta	255
Gonatozygon sp.	Chlorophyta	2
Mougeotia spp.	Chlorophyta	412
Netrium sp.	Chlorophyta	1
Pleurotaenium sp.	Chlorophyta	8
Spirotaenia sp.	Chlorophyta	3
Staurastrum spp.	Chlorophyta	1
Ulothrix sp.	Chlorophyta	680
Unknown green algae	Chlorophyta	130
TOTAL		2,265
Anabaena spp.	Cyanobacteria	346
Calothrix sp.	Cyanobacteria	249
Chamaesiphon sp.	Cyanobacteria	373
Chroococcus sp.	Cyanobacteria	72
Coleofasculatus sp.	Cyanobacteria	30,629
Geitlerinema sp.	Cyanobacteria	2,103
Johannesbaptista sp.	Cyanobacteria	72
Komvophoron sp.	Cyanobacteria	11
Leptolyngbya halophila	Cyanobacteria	112
Leptolyngbya sp.	Cyanobacteria	55,125
Lyngbya cf. martensiana	Cyanobacteria	3,650
Lyngbya confervoides	Cyanobacteria	1,023
Lyngbya meneghiniana	Cyanobacteria	1,030
Lyngbya salina	Cyanobacteria	1,327
Lyngbya semiplena	Cyanobacteria	2,649
Lyngbya sordida	Cyanobacteria	58
Lyngbya sp.	Cyanobacteria	15,731
Lyngbya sp.2	Cyanobacteria	308
Lyngbya sp.3	Cyanobacteria	29
Merismopedia spp.	Cyanobacteria	1,547
Microcoleus sp.	Cyanobacteria	49,234
Microcoleus sp.2	Cyanobacteria	5,631
Microcoleus vaginatus	Cyanobacteria	625
Oscillatoria cf. curviceps	Cyanobacteria	212
Oscillatoria cf. limosa	Cyanobacteria	119
Oscillatoria cf. lutea	Cyanobacteria	45
Oscillatoria cf. princeps	Cyanobacteria	125
Oscillatoria cf. subbrevis	Cyanobacteria	191
Oscillatoria cf. tenuis	Cyanobacteria	4,371
Oscillatoria lloydiana	Cyanobacteria	4,065
Oscillatoria margaritifera	Cyanobacteria	502

Species	Division	Abundance
Oscillatoria minata	Cyanobacteria	437
Oscillatoria nigro-viridis	Cyanobacteria	9,556
Oscillatoria simplicissima	Cyanobacteria	241
Oscillatoria spp.	Cyanobacteria	13,631
Phormidium spp.	Cyanobacteria	23,949
Phormidium spp.1	Cyanobacteria	37
Phormidium spp.2	Cyanobacteria	564
Pseudanabaena spp.	Cyanobacteria	2,905
Spirulina labyrinthiformis	Cyanobacteria	1,623
Spirulina sp.	Cyanobacteria	1,906
Stigonema sp.	Cyanobacteria	2,041
Synechococcus sp.	Cyanobacteria	20
Tolypothrix spp.	Cyanobacteria	20
TOTAL		238,494
Caloglossa leprieurii	Rhodophyta	14,816
Murrayella sp.	Rhodophyta	945
Polysiphonia subtilissima	Rhodophyta	16,153
Polysiphonia atlantica	Rhodophyta	3,412
Rhodella sp.	Rhodophyta	4
TOTAL		35,330

Table 8. 2011 species richness (min/max) from each sample plot, Shannon-Wiener Diversity (H´), and Evenness (E) of the epiphytic algal community for each nutrient treatment.

	C			N			P			NP		
Month	Richness	H´	E	Richness	H´	E	Richness	H´	E	Richness	H´	E
March	10 (9-13)	1.50	0.647	21 (17-29)	1.71	0.557	20 (16-24)	1.76	0.584	-	-	-
April	16 (12-22)	1.48	0.542	19 (13-25)	1.76	0.600	17 (12-21)	1.51	0.536	21 (15-23)	1.68	0.559
May	27 (18-36)	1.83	0.560	25 (22-28)	1.86	0.580	28 (19-34)	1.85	0.555	27 (25-30)	1.98	0.599
June	26 (18-32)	1.81	0.556	28 (21-34)	1.58	0.471	25 (19-27)	1.80	0.564	25 (23-31)	1.77	0.552
July	29 (25-37)	1.85	0.550	30 (22-34)	1.63	0.482	29 (25-36)	1.76	0.523	34 (23-47)	2.12	0.604
August	29 (19-37)	2.04	0.609	33 (22-44)	1.71	0.492	29 (22-35)	1.71	0.510	31 (24-37)	1.74	0.507
September	31 (24-35)	1.87	0.548	30 (18-35)	2.09	0.625	33 (21-37)	1.96	0.568	32 (27-40)	1.86	0.538
October	27 (18-33)	2.00	0.610	26 (19-37)	1.63	0.507	32 (22-38)	1.83	0.530	28 (18-40)	1.70	0.512
Mean	25	1.82	0.57	27	1.75	0.54	27	1.77	0.55	28	1.83	0.55

Table 9. 2011 combined species richness from all sampling plots, Shannon-Wiener Diversity (H´), and Evenness (E) of the epiphytic algal community.

Month	Species Richness	H´	E
March	56	2.15	0.53
April	61	2.25	0.55
May	72	2.62	0.61
June	66	2.30	0.55
July	79	2.56	0.59
August	87	2.81	0.63
September	84	2.96	0.67
October	80	3.00	0.68

Table 10. 2012 algal cell abundance (# cells) by division including percent (%) of total community for each nutrient treatment.

	Control				Nitrogen			
	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta
April	408 (4%)	261 (3%)	6608 (71%)	2090 (22%)	235 (1%)	324 (2%)	18724 (90%)	1403 (7%)
May	427 (4%)	192 (2%)	9394 (80%)	1774 (15%)	476 (3%)	55 (0%)	13954 (89%)	1235 (8%)
June	595 (5%)	79 (1%)	7504 (68%)	2807 (26%)	1007 (9%)	52 (0%)	8240 (70%)	2499 (21%)
July	388 (4%)	9 (0%)	8119 (79%)	1734 (17%)	333 (6%)	85 (1%)	5218.5 (86%)	432 (7%)
August	1094 (17%)	13 (0%)	3336 (52%)	2022 (31%)	722 (11%)	0 (0%)	4809 (75%)	913 (14%)
September	510 (9%)	0 (0%)	3969 (70%)	1214 (21%)	708 (8%)	0 (0%)	7485 (80%)	1121 (12%)
October	494 (14%)	0 (0%)	2343 (64%)	815 (22%)	554 (10%)	0 (0%)	4864 (86%)	258 (4%)

	Phosphorus				Nitrogen+Phosphorus			
	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta	Bacillariophyta	Chlorophyta	Cyanobacteria	Rhodophyta
April	451 (5%)	184 (2%)	5628 (64%)	2558 (29%)	400 (4%)	109 (1%)	8123 (80%)	1574 (15%)
May	578 (4%)	55 (0%)	11010 (81%)	1935 (15%)	369 (2%)	28 (0%)	15187 (84%)	2469 (14%)
June	696 (9%)	69 (1%)	5687 (73%)	1349 (17%)	892 (9%)	223 (2%)	7350 (75%)	1356 (14%)
July	500 (5%)	13 (0%)	6739 (67%)	2761 (28%)	568 (7%)	66 (1%)	6665 (79%)	1083 (13%)
August	818 (14%)	1 (0%)	3557 (60%)	1581 (26%)	653 (13%)	0 (0%)	4034 (78%)	472 (9%)
September	589 (12%)	0 (0%)	3011 (61%)	1365 (27%)	394 (6%)	0 (0%)	5602 (86%)	546 (8%)
October	954 (14%)	19 (0%)	4126 (61%)	1707 (25%)	455 (7%)	0 (0%)	4392 (69%)	1484 (24%)

Table 11. 2012 total algal cell abundance (number of cells) by division.

	Division			
Month	Cyanobacteria	Chlorophyta	Bacillariophyta	Rhodophyta
April	39,083	878	1,494	7,625
May	49,546	330	1,850	7,413
June	28,781	423	3,190	8,011
July	26,742	173	1,789	6,010
August	15,736	14	3,287	4,988
September	20,067	0	2,201	4,246
October	15,725	19	2,457	4,264
Total	195,679	1,837	16,268	42,557

Table 12. 2012 total algal density (# cells/cm^2) by division.

	Division			
Month	Cyanobacteria	Chlorophyta	Bacillariophyta	Rhodophyta
April	52,601	1,044	2,832	19,763
May	74,986	502	3,138	15,943
June	41,243	383	5,489	18,305
July	53,171	105	3,118	15,756
August	16,680	50	5,805	13,899
September	26,357	0	2,453	7,202
October	19,139	50	3,271	7,233
Total	284,177	2,134	26,106	98,101

Table 13. 2012 total algal biovolume (cm^3/cm^2) by division.

	Division			
Month	Cyanobacteria	Chlorophyta	Bacillariophyta	Rhodophyta
April	563	85	2,121	6,463
May	896	83	4,124	4,810
June	428	65	4,915	6,475
July	755	15	2,576	5,901
August	194	18	5,054	5,241
September	233	0	1,532	2,062
October	202	17	2,968	2,194
Total	3,272	282	23,291	33,147

Table 14. Algal taxa identified and abundance (# cells) from all plots for the sampling period of April through October 2012. A total of 118 infra-generic taxa were identified.

Species	Division	Abundance
Achnanthes inflata	Bacillariophyta	805
Achnanthes sp.	Bacillariophyta	1,509
Achnanthidium spp.	Bacillariophyta	272
Actinella sp.	Bacillariophyta	2
Actinocyclus sp.	Bacillariophyta	202
Actinoptchus sp.	Bacillariophyta	2
Amphipleura sp.	Bacillariophyta	3
Amphiprora sp.	Bacillariophyta	64
Amphora sp.	Bacillariophyta	196
Aulacoseira sp.	Bacillariophyta	367
Bacillaria sp.	Bacillariophyta	5
Bellarochia sp.	Bacillariophyta	30
Biddulphia sp.	Bacillariophyta	37
Brachysira sp.	Bacillariophyta	32
Caloneis sp.	Bacillariophyta	139
Cavinula sp.	Bacillariophyta	106
Climacodium fraunenfeldianum	Bacillariophyta	10
Cocconeis sp.	Bacillariophyta	231
Coscinodiscus sp.	Bacillariophyta	155
Craticula sp.	Bacillariophyta	2
Cyclotella sp.	Bacillariophyta	127
Cymatopleura sp.	Bacillariophyta	2
Cymbella sp.	Bacillariophyta	164
Diadesmis sp.	Bacillariophyta	3
Diploneis bombus	Bacillariophyta	54
Diploneis chersonensis var. *apiformis*	Bacillariophyta	80
Diploneis didyma	Bacillariophyta	64
Diploneis sp.	Bacillariophyta	115
Epithemia sp.	Bacillariophyta	52
Eunotia sp.	Bacillariophyta	43
Fragilaria sp.	Bacillariophyta	334
Frustulia sp.	Bacillariophyta	238
Gomphonema sp.	Bacillariophyta	35
Gyrosigma fasciola	Bacillariophyta	12
Gyrosigma sp.	Bacillariophyta	1,359

Species	Division	Abundance
Hydrosera sp.	Bacillariophyta	2
Luticola sp.	Bacillariophyta	159
Martyana sp.	Bacillariophyta	1
Mastagloia sp.	Bacillariophyta	29
Melosira sp.	Bacillariophyta	3,243
Melosira moniliformis	Bacillariophyta	864
Navicula sp.	Bacillariophyta	284
Neidium sp.	Bacillariophyta	3
Nitzschia longissima	Bacillariophyta	29
Nitzschia sp.	Bacillariophyta	888
Opephora sp.	Bacillariophyta	11
Pinnularia sp.	Bacillariophyta	188
Pleurosigma sp.	Bacillariophyta	81
Sellaphora sp.	Bacillariophyta	83
Stauroneis sp.	Bacillariophyta	3
Stephanodiscus sp.	Bacillariophyta	122
Surirella sp.	Bacillariophyta	64
Synedra spp.	Bacillariophyta	579
Terpsinoe sp.	Bacillariophyta	326
Thallassiosira sp.	Bacillariophyta	60
Tryblionella sp.	Bacillariophyta	50
Tryblionella granulata	Bacillariophyta	51
Centric diat	Bacillariophyta	717
Pennate diat	Bacillariophyta	1,580
TOTAL		16,268
Cladophora sp.	Chlorophyta	202
Closterium kutzingii	Chlorophyta	3
Closterium spp.	Chlorophyta	25
Cosmarium sp.	Chlorophyta	1
Enteromorpha sp.	Chlorophyta	210
Geminella sp.	Chlorophyta	252
Mougeotia spp.	Chlorophyta	537
Oedogonium sp.	Chlorophyta	3
Ulothrix sp.	Chlorophyta	813
Unknown green	Chlorophyta	43
TOTAL		2,089
Anabaena spp.	Cyanobacteria	521
Blennothrix lyngbyacea	Cyanobacteria	576
Blennothrix majus	Cyanobacteria	846

Species	Division	Abundance
Blennothrix sp.	Cyanobacteria	57
Calothrix sp.	Cyanobacteria	2,735
Chamaesiphon sp.	Cyanobacteria	117
Chroococcus sp.	Cyanobacteria	135
Coleofasculatus sp.	Cyanobacteria	14,468
Geitlerinema sp.	Cyanobacteria	517
Johannesbaptista sp.	Cyanobacteria	1,434
Komvophoron sp.	Cyanobacteria	166
Leptolyngbya sp.	Cyanobacteria	59,874
Leptolyngbya sp.2	Cyanobacteria	118
Lyngbya aestuarii	Cyanobacteria	1,156
Lyngbya cf. martensiana	Cyanobacteria	1,945
Lyngbya confervoides	Cyanobacteria	262
Lyngbya meneghiana	Cyanobacteria	162
Lyngbya salina	Cyanobacteria	571
Lyngbya semiplena	Cyanobacteria	6,853
Lyngbya sp.	Cyanobacteria	16,618
Lyngbya sp.2	Cyanobacteria	1,025
Merismopedia spp.	Cyanobacteria	1,212
Microcoleus sp.	Cyanobacteria	38,494
Microcoleus sp.2	Cyanobacteria	2,541
Nodularia sp.	Cyanobacteria	863
Oscillatoria cf. limosa	Cyanobacteria	62
Oscillatoria cf. lutea	Cyanobacteria	83
Oscillatoria cf. tenuis	Cyanobacteria	182
Oscillatoria lloydiana	Cyanobacteria	1,522
Oscillatoria margaritifera	Cyanobacteria	1,276
Oscillatoria mengehiana	Cyanobacteria	54
Oscillatoria nigro-viridis	Cyanobacteria	4,334
Oscillatoria simplicissima	Cyanobacteria	726
Oscillatoria spp.	Cyanobacteria	4,464
Phormidium holdenii	Cyanobacteria	1,052
Phormidium spp.	Cyanobacteria	16,829
Phormidium spp.2	Cyanobacteria	2,503
Pseudanabaena spp.	Cyanobacteria	4,236
Spirulina labyrinthiformis	Cyanobacteria	428
Spirulina sp.	Cyanobacteria	3,670
Stichosiphon sp.	Cyanobacteria	50
Stigonema sp.	Cyanobacteria	481
Unknown blue-green	Cyanobacteria	100

TOTAL		195,318
Species	Division	Abundance
Bostrychia sp.	Rhodophyta	4,598
Caloglossa sp.	Rhodophyta	14,721
Dipterosiphonia reversa	Rhodophyta	215
Murrayella sp.	Rhodophyta	519
Polysiphonia subtilissima	Rhodophyta	18,682
Polysiphonia atlantica	Rhodophyta	3,822
TOTAL		42,557

Table 15. 2012 species richness (min/max) from each sample plot, Shannon-Wiener Diversity (H´), and Evenness (E) of the epiphytic algal community for each nutrient treatment.

	C			N			P			NP		
Month	Richness	H´	E	Richness	H´	E	Richness	H´	E	Richness	H´	E
April	27 (12-40)	1.76	0.54	25 (19-31)	1.62	0.51	29 (13-46)	2.01	0.61	29 (19-44)	1.85	0.55
May	25 (11-39)	1.63	0.51	31 (22-42)	2.08	0.61	30 (27-38)	1.86	0.55	30 (24-43)	1.76	0.52
June	31 (24-39)	2.05	0.60	31 (26-36)	1.88	0.55	27 (21-32)	1.89	0.57	32 (13-40)	1.99	0.59
July	24 (16-30)	1.79	0.57	18 (10-26)	1.29	0.45	23 (10-35)	1.78	0.58	21 (6-36)	1.54	0.52
August	23 (14-34)	1.75	0.56	21 (14-29)	1.54	0.50	17 (4-28)	1.33	0.50	16 (3-30)	1.35	0.51
September	20 (13-30)	1.24	0.42	19 (14-26)	1.38	0.47	24 (19-30)	1.60	0.51	16 (8-23)	0.945	0.33
October	20 (11-26)	1.39	0.48	19 (13-28)	1.63	0.56	20 (11-37)	1.42	0.48	20 (17-24)	1.36	0.46
Mean	25	1.66	0.52	23	1.63	0.52	24	1.70	0.54	23	1.54	0.50

Table 16. 2012 combined total species richness from all sampling plots, Shannon-Wiener Diversity (H´), and Evenness (E) of the epiphytic algal community.

Month	Species Richness	H´	E
April	90	2.86	0.63
May	87	2.86	0.64
June	78	2.86	0.66
July	76	2.77	0.64
August	67	2.67	0.64
September	66	2.24	0.53
October	64	2.58	0.62

Table 17. 2011 mean (with range) algal biomass (mg/cm^2) by treatment.

	Control	n=	Nitrogen	n=	Phosphorus	n=	Nitrogen+Phosphorus	n=
March	0.185 (0.0372-0.541)	8	0.515 (0.183-0.595)	6	0.450 (0.0506-0.575)	8	-	0
April	0.232 (0.0327-0.521)	8	0.221 (0.113-0.391)	8	0.346 (0.0917-0.549)	8	0.296 (0.0989-0.246)	8
May	0.238 (0.0115-0.737)	8	0.204 (0.0427-0.453)	8	0.296 (0.00418-0.464)	8	0.165 (0.00955-0.525)	8
June	0.135 (0.0208-0.240)	8	0.115 (0.0305-0.197)	8	0.116 (0.0268-0.173)	8	0.216 (0.0184-0.211)	8
July	0.122 (0.0118-0.117)	8	0.207 (0.033-0.448)	8	0.106 (0.0238-0.280)	8	0.153 (0.0220-0.249)	8
August	0.181 (0.0281-0.460)	8	0.189 (0.0742-0.274)	8	0.222 (0.0388-0.364)	8	0.220 (0.0551-0.267)	7
September	0.246 (0.0286-0.158)	8	0.213 (0.00647-0.183)	8	0.169 (0.0185-0.544)	8	0.250 (0.0346-0.208)	7
October	0.0688 (0.0206-0.0894)	8	0.0809 (0.0190-0.150)	8	0.0762 (0.0394-0.328)	8	0.0737 (0.0164-0.120)	8

Table 18. 2012 mean (with range) algal biomass (mg/cm^2) by treatment.

	Control	n=	Nitrogen	n=	Phosphorus	n=	Nitrogen+Phosphorus	n=
April	0.0807 (0.0149-0.122)	8	0.340 (0.0658-1.27)	8	0.234 (0.0101-0.451)	8	0.187 (0.0260-0.553)	8
May	0.133 (0.00667-0.341)	8	0.197 (0.0185-0.461)	8	0.241 (0.0487-0.289)	8	0.187 (0.0561-0.556)	8
June	0.123 (0.0260-0.346)	8	0.0822 (0.0423-0.119)	8	0.0705 (0.0401-0.161)	8	0.101 (0.0253-0.0837)	8
July	0.0683 (0.0185-0.190)	8	0.0206 (0.00654-0.0688)	8	0.0701 (0.00724-0.120)	8	0.136 (0.00527-0.766)	8
August	0.0673 (0.0121-0.133)	8	0.0527 (0.00955-0.165)	8	0.0279 (0.00597-0.0670)	8	0.0396 (0.00451-0.194)	8
September	0.0798 (0.0195-0.300)	7	0.0926 (0.0197-0.462)	7	0.0351 (0.00962-0.0472)	7	0.0270 (0.00395-0.0501)	7
October	0.0394 (0.00801-0.147)	7	0.111 (0.00279-0.801)	8	0.0212 (0.00816-0.0546)	8	0.0375 (0.0128-0.0916)	7

Table 19. 2011 mean (with range) chlorophyll-a (µg/cm^2) by treatment.

	Control	n=	Nitrogen	n=	Phosphorus	n=	Nitrogen+Phosphorus	n=
March	1.70 (0.446-3.85)	8	1.02 (0.605-2.69)	7	0.912 (0.506-1.28)	8	-	0
April	1.34 (0.697-3.61)	8	2.15 (0.687-5.92)	8	1.65 (0.594-2.87)	8	1.35 (0.521-2.71)	8
May	1.69 (0.144-3.95)	8	1.88 (0.875-2.84)	8	1.55 (0.0879-4.83)	8	2.08 (0.468-3.38)	8
June	1.82 (0.987-3.75)	8	1.81 (0.635-2.74)	8	1.54 (0.299-2.88)	8	1.38 (0.646-1.98)	8
July	1.74 (0.475-3.94)	8	1.75 (0.517-2.95)	8	1.62 (0.759-2.31)	8	2.27 (0.608-4.14)	8
August	2.26 (0.427-3.78)	8	1.91 (0.982-4.52)	8	1.26 (0.635-2.04)	8	2.21 (0.921-3.59)	7
September	3.71 (0.398-7.08)	8	3.01 (0.799-7.18)	8	3.14 (0.287-6.24)	8	3.79 (1.26-6.04)	7
October	5.10 (2.56-9.92)	8	4.47 (1.14-8.14)	8	4.95 (0.945-7.44)	8	5.62 (2.07-7.24)	8

Table 20. 2012 mean (with range) algal chlorophyll-a (µg/cm^2) by treatment.

	Control	n=	Nitrogen	n=	Phosphorus	n=	Nitrogen+Phosphorus	n=
April	1.55 (0.370-2.19)	8	1.25 (0.650-2.38)	8	1.62 (0.576-3.05)	8	1.78 (0.635-4.27)	8
May	2.88 (0.373-3.31)	8	1.14 (0.524-1.49)	8	1.35 (0.245-2.18)	8	1.69 (0.257-3.58)	8
June	2.88 (0.977-4.94)	8	2.62 (1.52-3.20)	8	3.36 (1.97-5.42)	8	3.26 (1.43-5.78)	8
July	1.41 (0.541-4.20)	8	1.34 (0.302-3.63)	8	1.62 (0.162-2.17)	8	1.82 (0.209-4.78)	8
August	1.98 (0.412-1.76)	8	1.06 (0.437-1.53)	8	1.05 (0.0686-2.01)	8	1.22 (0.130-3.35)	8
September	1.05 (0.278-1.76)	7	1.57 (0.754-3.06)	7	0.762 (0.502-1.03)	7	1.06 (0.180-2.35)	7
October	1.17 (0.410-2.91)	7	0.588 (0.203-1.274	8	0.808 (0.356-1.80)	8	1.17 (0.204-2.27)	7

Table 21. Comparison of total epiphytic algal taxa identified and abundance (number of cells) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

		2011	2012
Species	Division	Abundance	Abundance
Achnanthes inflata	Bacillariophyta	961	805
Achnanthes sp.	Bacillariophyta	106	1,509
Achnanthidium sp.	Bacillariophyta	380	272
Actinella sp.	Bacillariophyta	4	2
Actinoptchus sp.	Bacillariophyta	-	2
Actinocyclus sp.	Bacillariophyta	426	202
Amphipleura sp.	Bacillariophyta	5	3
Amphiprora sp.	Bacillariophyta	114	64
Amphora sp.	Bacillariophyta	414	196
Asterionella sp.	Bacillariophyta	1	-
Aulacoseira sp.	Bacillariophyta	597	367
Bacillaria sp.	Bacillariophyta	-	5
Bellarochia sp.	Bacillariophyta	-	30
Biddulphia sp.	Bacillariophyta	34	37
Brachysira sp.	Bacillariophyta	10	32
Caloneis sp.	Bacillariophyta	2	139
Cavinula sp.	Bacillariophyta	4	106
Climacodium fraunenfeldianum	Bacillariophyta	63	10
Cocconeis sp.	Bacillariophyta	281	231
Coscinodiscus sp.	Bacillariophyta	131	155
Craticula sp.	Bacillariophyta	-	2
Cyclostephanus sp.	Bacillariophyta	1	-
Cyclotella sp.	Bacillariophyta	49	127
Cymatopleura sp.	Bacillariophyta	24	2
Cymbella sp.	Bacillariophyta	364	164
Diadesmis sp.	Bacillariophyta	2	3
Diatoma sp.	Bacillariophyta	7	-
Diatomeis sp.	Bacillariophyta	1	-
Diploneis bombus	Bacillariophyta	50	54
Diploneis chersonensis var. *apiformis*	Bacillariophyta	86	80
Diploneis crabro	Bacillariophyta	1	-
Diploneis didyma	Bacillariophyta	74	64
Diploneis pupula	Bacillariophyta	2	-
Diploneis sp.	Bacillariophyta	144	115
Diploneis sp.2	Bacillariophyta	1	-

Encyonema sp.	Bacillariophyta	5	-
Epithemia sp.	Bacillariophyta	110	52
Eunotia sp.	Bacillariophyta	170	43
Fragilaria sp.	Bacillariophyta	917	334
Frustulia sp.	Bacillariophyta	274	238
Gomphonema sp.	Bacillariophyta	46	35
Gyrosigma fasciola	Bacillariophyta	34	12
Gyrosigma sp.	Bacillariophyta	1,175	1,359
Hantzschia sp.	Bacillariophyta	11	-
Hydrosera sp.	Bacillariophyta	13	2
Luticola sp.	Bacillariophyta	4	159
Martyana sp.	Bacillariophyta	-	1
Mastagloia sp.	Bacillariophyta	77	29
Melosira moniliformis	Bacillariophyta	2,748	864
Melosira sp.	Bacillariophyta	4,306	3,243
Meridion sp.	Bacillariophyta	1	-
Navicula sp.	Bacillariophyta	753	284
Neidium sp.	Bacillariophyta	2	3
Nitzschia acicularis	Bacillariophyta	3	-
Nitzschia longissima	Bacillariophyta	37	29
Nitzschia setaceum	Bacillariophyta	4	-
Nitzschia sp.	Bacillariophyta	1,481	888
Opephora sp.	Bacillariophyta	19	11
Pinnularia sp.	Bacillariophyta	266	188
Placoneis sp.	Bacillariophyta	6	-
Pleurosigma sp.	Bacillariophyta	103	81
Rhopalodia sp.	Bacillariophyta	3	-
Sellaphora sp.	Bacillariophyta	38	83
Stauroneis sp.	Bacillariophyta	2	3
Staurosira sp.	Bacillariophyta	10	-
Staurosirella sp.	Bacillariophyta	1	-
Stephanocyclus sp.	Bacillariophyta	2	-
Stephanodiscus sp.	Bacillariophyta	227	122
Surirella sp.	Bacillariophyta	68	64
Synedra spp.	Bacillariophyta	1,120	579
Synedra ulna	Bacillariophyta	1	-
Terpinsoe sp.	Bacillariophyta	165	326
Thallassiosira sp.	Bacillariophyta	72	60
Tryblionella granulata	Bacillariophyta	57	51
Tryblionella sp.	Bacillariophyta	124	50
Centric diatom	Bacillariophyta	600	717
Pennate diatom	Bacillariophyta	1,938	1,580
TOTAL		21,332	16,266

Actinotaenium sp.	Chlorophyta	1	-
Cladophora sp.	Chlorophyta	384	202
Closterium kutzingii	Chlorophyta	1	3
Closterium spp.	Chlorophyta	204	25
Cosmarium sp.	Chlorophyta	136	1
Cylindrocystis sp.	Chlorophyta	1	-
Enteromorpha sp.	Chlorophyta	46	210
Geminella sp.	Chlorophyta	255	252
Gonatozygon sp.	Chlorophyta	2	-
Mougeotia spp.	Chlorophyta	412	537
Netrium sp.	Chlorophyta	1	-
Oedigonium sp.	Chlorophyta	-	3
Pleurotaenium sp.	Chlorophyta	8	-
Spirotaenia sp.	Chlorophyta	3	-
Staurastrum spp.	Chlorophyta	1	-
Ulothrix sp.	Chlorophyta	680	813
Unknown green algae	Chlorophyta	130	43
TOTAL		2,265	2,089
Anabaena spp.	Cyanobacteria	346	521
Blennothrix lyngbyacea	Cyanobacteria	-	576
Blennothrix majus	Cyanobacteria	-	846
Blennothrix sp.	Cyanobacteria	-	57
Calothrix sp.	Cyanobacteria	249	2,735
Chamaesiphon sp.	Cyanobacteria	373	117
Chroococcus sp.	Cyanobacteria	72	135
Coleofasciculatus sp.	Cyanobacteria	30,629	14,468
Geitlerinema sp.	Cyanobacteria	2,103	517
Johanesbaptista sp.	Cyanobacteria	72	1,434
Komvophoron sp.	Cyanobacteria	11	166
Leptolyngbya halophila	Cyanobacteria	112	-
Leptolyngbya sp.	Cyanobacteria	55,125	59,874
Leptolyngbya sp.2	Cyanobacteria	-	118
Lyngbya aestuarii	Cyanobacteria	-	1,156
Lyngbya cf. martensiana	Cyanobacteria	3,650	1,945
Lyngbya confervoides	Cyanobacteria	1,023	262
Lyngbya meneghiniana	Cyanobacteria	1,030	162
Lyngbya salina	Cyanobacteria	1,327	571
Lyngbya semiplena	Cyanobacteria	2,649	6,853
Lyngbya sordida	Cyanobacteria	58	-
Lyngbya sp.	Cyanobacteria	15,731	16,618
Lyngbya sp.2	Cyanobacteria	308	1,025

Lyngbya sp.3	Cyanobacteria	29	-
Merismopedia spp.	Cyanobacteria	1,547	1,212
Microcoleus sp.	Cyanobacteria	49,234	38,494
Microcoleus sp.2	Cyanobacteria	5,631	2,541
Microcoleus vaginatus	Cyanobacteria	625	-
Nodularia sp.	Cyanobacteria	-	863
Oscillatoria cf. curviceps	Cyanobacteria	212	-
Oscillatoria cf. limosa	Cyanobacteria	119	62
Oscillatoria cf. lutea	Cyanobacteria	45	83
Oscillatoria cf. princeps	Cyanobacteria	125	-
Oscillatoria cf. subbrevis	Cyanobacteria	191	-
Oscillatoria cf. tenuis	Cyanobacteria	4,371	182
Oscillatoria lloydiana	Cyanobacteria	4,065	1,522
Oscillatoria margaritifera	Cyanobacteria	502	1,276
Oscillatoria mengehiana	Cyanobacteria	-	54
Oscillatoria minata	Cyanobacteria	437	-
Oscillatoria nigro-viridis	Cyanobacteria	9,556	4,334
Oscillatoria simplicissima	Cyanobacteria	241	726
Oscillatoria spp.	Cyanobacteria	13,631	4,464
Phormidium holdenii	Cyanobacteria	-	1,052
Phormidium spp.	Cyanobacteria	23,949	16,829
Phormidium spp.1	Cyanobacteria	37	-
Phormidium spp.2	Cyanobacteria	564	2,503
Pseudanabaena spp.	Cyanobacteria	2,905	4,236
Spirulina labyrinthiformis	Cyanobacteria	1,623	428
Spirulina sp.	Cyanobacteria	1,906	3,670
Stichosiphon sp.	Cyanobacteria	-	50
Stigonema sp.	Cyanobacteria	2,041	481
Synechococcus sp.	Cyanobacteria	20	-
Tolypothrix spp.	Cyanobacteria	20	-
Unknown blue-green	Cyanobacteria	-	100
TOTAL		238,494	195,318
Bostrychia sp.	Rhodophyta	-	4,598
Caloglossa leprieurii	Rhodophyta	14,816	14,721
Dipterosiphonia reversa	Rhodophyta	-	215
Murrayella sp.	Rhodophyta	945	519
Polysiphonia atlantica	Rhodophyta	3,412	3,822
Polysiphonia subtilissima	Rhodophyta	16,153	18,682
Rhodella sp.	Rhodophyta	4	-
TOTAL		35,330	42,557
GRAND TOTAL		297,421	256,230

Table 22. Comparison of total epiphytic algal species richness. Shannon-Weiner Diversity (H´), and evenness (E) collected from all treatments over the course of the two sampling seasons, March through October 2011 and April through October 2012.

	2011			2012		
Month	Species Richness	H´	E	Species Richness	H´	E
March	56	2.15	0.53	-	-	-
April	61	2.25	0.55	90	2.86	0.63
May	72	2.62	0.61	87	2.86	0.64
June	66	2.30	0.55	78	2.86	0.66
July	79	2.56	0.59	76	2.77	0.64
August	87	2.81	0.63	67	2.67	0.64
September	84	2.96	0.67	66	2.24	0.53
October	80	3.00	0.68	64	2.58	0.62

Table 23. Mean biomass (mg/cm^2) with range of values from each mesocosm of epiphytic algae per treatment for the 28 day lab study.

	Control	Nitrogen	Phosphorus	Nitrogen+Phosphorus
Day 0	0.0104 (0.00314-0.0325)	0.0104 (0.00314-0.0325)	0.0104 (0.00314-0.0325)	0.0104 (0.00314-0.0325)
Day 14	0.00583 (0.00328-0.0112)	0.0457 (0.00379-0.121)	0.0210 (0.00308-0.0356)	0.0186 (0.00131-0.0592)
Day 28	0.00544 (0.000848-0.0180)	0.00688 (0.00110-0.0104)	0.0122 (0.00327-0.0262)	0.0136 (0.00388-0.0336)

Table 24. Mean chlorophyll-a ($\mu g/cm^2$) with range of values from each mesocosm of epiphytic algae per treatment for the 28 day lab study.

	Control	Nitrogen	Phosphorus	Nitrogen+Phosphorus
Day 0	2.95 (0.420-11.0)	2.95 (0.420-011.0)	2.95 (0.420-11.0)	2.95 (0.420-11.0)
Day 14	3.84 (1.21-9.14)	10.5 (1.11-24.3)	11.7 (0.53-20.9)	7.91 (1.72-12.3)
Day 28	1.30 (0.63-4.41)	2.43 (0.580-3.96)	2.8 (0.500-6.42)	5.38 (1.62-8.59)

Literature Cited

American Public Health (APHA). (1992). Standard Methods for the evaluation of water and wastewater. 18th ed. APHA, Washington, DC.

Anesio, A.M., P.C. Abreu, and B.A. Biddanda. (2003). The role of free and attached microogranisms in the decomposition of estuarine macrophyte detritus. *Estuarine, Coastal Shelf Science*, 56:197-202.

Armitage, A. R., T.A. Frankovich, and J. W. Fourqurean. (2006). Variable responses within epiphytic and benthic microalgal communities to nutrient enrichment. *Hydrobiologia*, 569:423-435.

Azim, M.E. and T. Asaeda. (2005). Periphyton structure, diversity and colonization. *In* M.E. Azim, M.C.J Verdegem, A.A. van Dam, and M.C.M. Beveridge eds. "Periphyton: ecology, exploitation, and management". CABI Publishing, MA. pp. 15-29.

Balata, D., I Bertocci, L. Piazzi, and U. Nesti. (2008). Comparison between epiphyte assemblages of leaves and rhizomes of the seagrass *Posidonia oceanica* subjected to different levels of anthropogenic eutrophication. *Estuarine, Coastal and Shelf Science,* 79:533-540.

Barbiero, R.P. and E.B. Welch. (1992). Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. *Freshwater Biology*, 27:249-260.

Barko, J.W. and R.M. Smart. (1986). Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecological Society of America*, 67:1328-1340.

Barnes, T.K., A.K. Volety, K. Chartier, F.J. Mazzotti, and L. Pearlstine. (2007). A habitat Suitability Index Model for the Eastern Oyster (*Crassostrea virginica*), a tool for restoration of the Caloosahatchee Estuary, Florida. *Journal of Shellfish Research*, 26:949-959.

Borum, J. (1985). Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology*, 87:211-218.

Bostrom, B., M. Jansson, and C. Forsberg. (1982). Phosphorus release from lake sediments. *Hydrobiologia Beih. Ergebn. Limnology*, 18:5-59.

Brönmark, C. (1985). Interactions between macrophytes, epiphytes and herbivores: An experimental approach. *Oikos*, 45:26-30.

Caraco, N.F., J.J. Cole, and G.E. Likens. (1992). New and recycled primary production in an oligotrophic lake: Insights for summer phosphorus dynamics. *Limnology and Oceanography*, 37:590-602.

Cardoso, P.G., M.A Pardal, A.I Lillebø, S.M. Ferreira, D. Raffaelli, and J.C. Marques. (2004). Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology,* 302:233-248.

Carlton, R.E. and R.G. Wetzel. (1988). Phosphorus flux from lake sediments: Effects of epipelic algal oxygen production. *Limnology and Oceanography,* 33:562-570.

Cattaneo, A., G. Galanti, S.Gentinetta, and S. Romo. (1998). Epiphytic algae and macro invertebrates on submerged and floating-leaved macrophytes in an Italian lake. *Freshwater Biology,* 39:725-740.

Cattaneo, A. and J. Kalff. (1980). The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography,* 25:280-289.

Chase, J. M. and T. M. Knight. (2006). Effects of eutrophication and snails on Eurasian watermilfoil (*Myriophyllum spicatum*) invasion. *Biological Invasions,* 8:1643-1649.

Chung, M.H., and K.S. Lee. (2008). Species composition of the epiphytic diatoms of the leaf tissues of three *Zostera* species distributed on the southern coast of Korea. *Algae*, 23:75-81.

Coen, L.D., R.D. Brumbaugh, D. Bushek, R. Grizzle, M.K. Luckenbach, M.H. Posey, S.P. Powers, and S.G. Tolley. (2007). Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*, 341:303-307.

Coleman, V.L. and J.M. Burkholder. (1994). Community structure and productivity of epiphytic microalgae on eelgrass (*Zostera marina* L.) under water-column nitrate enrichment. *Journal of Experimental Marine Biology and Ecology*, 179:29-48.

Corkum, L. D. (1996). Patterns of nutrient release from nutrient diffusing substrates in flowing water. *Hydrobiologia,* 333:37-43.

Cox, E.J. (1996). Identification of Freshwater Diatoms from Live Material. Chapman & Hall, New York. 156 pp.

Currin, C.A., S.Y. Newell, and H.W. Paerl. (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in saltmarsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series,* 121:99-116.

Dardeau, M.R., R.F. Modlin, W.W. Schroeder, and J.P Stout. (1992). Estuaries. *In* C.T. Hackney, M.M. Adams, and W.H. Martin, eds. "Biodiversity of the Southeastern U.S.: Aquatic communities." John Wiley & Sons, Inc., New York. pp. 614-744.

Dauer, D.M., J.A. Ranasinghe, and S.B. Weisberg. (2000). Relationships between benthic community condition, water quality, sediment quality, nutrient loads, and land use patterns in Chesapeake Bay. *Estuaries,* 23:80-96.

Dor, I. (1984). Epiphytic blue-green algae (cyanobacteria) of the Sinai mangal: considerations in vertical zonation and morphological adaptations. *In:* F. D. For and I.Dor, eds. "Hydrobiology of the Mangal - the Ecosystem of the Mangrove Forests." L Developments in Hydrobiology. Dr W. Junk Publishers, The Hague, pp. 35—54.

Edmondson, W.T., G.C. Anderson, and D.R. Peterson. (1956). Artificial eutrophication of Lake Washington. *Limnology and Oceanography*. 1:47-53.

Eppley, R.W. and B.J. Peterson. (1979). Particulate organic matter flux and planktonic new production in the deep ocean. *Nature (London)*, 282:677-680.

Fairchild, G. W., R. L. Lowe, W.B. Richardson. (1985). Algal periphyton growth on nutrient-diffusing substrates: An in situ bioassay. *Ecology*, 66:465-472.

Fazel, D. (2009). Site profile of the Guana Tolomato Matanzas National Estuarine Research Reserve. Ponte Vedra, FL. 151 pp.

Fletcher, R.L. and M.E. Callow. (1992). The settlement, attachment, and establishment of marine algal spores. *British Phycological Journal*, 27:303-329.

Fonseca, B.M. and C.E. de Mattos Bicudo. (2010). How important can the presence/absence of macrophytes be in determining phytoplankton strategies in two different tropical shallow reservoirs with different trophic status? *Journal of Plankton Research*, 32:31-46.

Frankovich and Fourqurean. (1997). Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Press Series*, 159:37-50.

Frevert, T. (1979). The pE redox concept in natural sediment-water systems; its role in controlling phosphorus release from lake sediments. *Hydrobiologia*, 55:278-297.

Garcia, E., M.M. Littler, and D.S. Littler. (1999). An experimental test of the capacity of food web interactions (fish-epiphytes-seagrasses) to offset the negative consequences of eutrophication on seagrass communities. *Estuarine, Coastal and Shelf Science*, 48:757-766.

Gil, M., A.R. Armitage, J.W. Fourqurean. (2006). Nutrient impacts on epifaunal density and species composition in a subtropical seagrass bed. *Hydrobiologia*, 569:437-447.

Graham, L.E., M. Graham, and L.W. Wilcox. (2009). Algae. Prentice-Hall, Inc., Upper Saddle River, New Jersey. 616 pp.

Haack, T.K. and G.A. McFeters. (1982). Nutritional relationships among microoganisms in an epilithic biofilm community. *Microbiology Ecology*, 8:115-126.

Hauxwell, J., J. Cebrian, C. Furlong, and I. Valiela. (2001). Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology*, 82:1007-1022.

Havens, K.E., J. Hauxwell, A.C. Tyler, S. Thomas, K.J. McGlathery, J. Cebrian, I. Valiela, A.D. Steinman, and S. Hwang. (2001). Complex interactions between autotrophs in shallow marine and freshwater ecosystems: implications for community responses to nutrient stress. *Environmental Pollution*, 113:95-107.

Heck, K.L., J.F. Valentine, J.R. Pennock, G. Chaplin, and P.M. Spitzer. (2006). Effects of nutrient enrichment and grazing on shoalgrass *Halodule wrightii* and its epiphytes: results of a field experiment. *Marine Ecology Progress Series*, 326:145-156.

Hill, W. (1996). Effects of light. *In* (R.J. Stevenson, M.L. Bothwell, and R.L. Lowe, eds.) "Algal Ecology". Academic Press, New York. pp 121-148.

Hillebrand, H., C. Durselen, D. Kirschtel, U. Pollingher, and T. Zohary. (1999). Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, 35:403-424.

Hindák, F. (2008). Colour Atlas of Cyanophytes. VEDA, Bratislava. 253 pp.

Hinojosa-Garro D., C.F. Mason, and G.J.C. Underwood. (2010). Influence of macrophyte spatial architecture on periphyton and macroinvertebrate community in shallow water bodies under contrasting management. *Fundamentals of Applied Limnology*, 177:19-37.

Holland, R., T.M. Dugdale, R. Wetherbee, A.B. Brennan, J.A. Finlay, J.A. Callow, and M.E. Callow. (2004). Adhesion and motility of fouling diatoms on a silicone elastomer. *Biofouling*, 20:323-329.

Howarth, R.W. (1988). Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecological and Systematics*, 19:89-110.

Howarth, R.W. (2000). Nutrient pollution of coastal rivers, bays, and seas. *Issues in Ecology*, 7:1-15.

Hynes, H.B.N. (2001). "The Ecology of Running Waters." Blackburn Press, New Jersey. 588 pp.

Irlandi, E.A., B.A. Orlando, and P.D. Biber. (2004). Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. *Marine Ecology Progress Series*, 279:81-91.

Karez, R., S. Engelbert, and U. Sommer. (2000). 'Co-consumption' and 'protective coating': two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte-host interactions. *Marine Ecology Progress Series*, 205:85-93.

Kebede-Westhead, E., C. Pizarro, and W.W. Mulbry. (2006). Treatment of swine manure effluent using freshwater algae: Production, nutrient recovery, and elemental composition of algal biomass at four effluent loading rates. *Journal of Applied Phycology*, 18:41-46.

Kitting, C.L., B. Fry, and M.D. Morgan. (1984). Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecolgia*, 62:145-149.

Kupferberg, S. (2003). Facilitation of periphyton production by tadpole grazing: functional differences between species. *Freshwater Biology*, 37:427-439.

Lin, H.-J., S.W. Nixon, D.I. Taylor, S.L. Granger, and B.A. Buckley. (1996). Responses of epiphytes on eelgrass, *Zostera marina* L., to separate and combined nitrogen and phosphorus enrichment. *Aquatic Botany*, 52:243-258.

Malueg, K.W., R.M Brice, D.W. Schults, and D.P. Larsen. (1973). The Shagawa Lake project-Lake restoration by nutrient removal from wastewater effluent. Publ. EPA-R3-73-026, National Environmental Research Center, Corvallis, Oregon.

Magurran, A.E. (2004). Measuring Biological Diversity. Blackwell Publishing, Massachusetts. pp.106-108.

Mann, F.D. and T.D. Steinke. (1988). Photosynthetic and respiratory responses of mangrove-associated red algae *Bostrychia radicans* and *Caloglossa leprieurii*. *South African Journal of Botany*, 54:203-207.

McCormick, P.V., R.E. Shuford III, J.G. Backus, and W.C. Kennedy. (1998). Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A.. *Hydrobiologia*, 362:185-208.

Minello, T.J. and R.J. Zimmerman. (1992). Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. *Marine Ecology Progress Series*, 90: 273-285.

Moeller, R.E., R.G. Wetzel, and C.W. Osenberg. (1988). Concordance of phosphorus limitation in lakes: Bacterioplankton, phytoplankton, epiphyte-snail consumers, and rooted macrophytes. *In* E. Jeppersen, Ma. Sondergaard, Mo., Sondergaard, and K. Christoffersen, eds. The Structuring Role of Submerged Macrophytes in Lakes. Springer-Verlag, New York. pp. 318-325.

Moncreiff, C.A. and M.J. Sullivan. (2001). Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series*, 215:93-106.

Moncreiff, C.A., M.J. Sullivan, A.E. Daehnick. (1992). Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Marine Ecology Progress Series*, 87:161-171.

Moore, R.H. (1992). Low salinity backbays and lagoons. *In* "Biodiversity of the Southeastern United States: Aquatic Communities" (C.T. Hackney, M.M. Adams and W.H. Martin, eds.). John Wiley & Sons, New York. pp 541-613.

Morgan, M.D. and C.L. Kitting. (1984). Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnology and Oceanography*, 29:1066-1076.

McLusky, D. (1981). Primary Producers. *In* "The Estuarine Ecosystems". Halstead Press, New York. pp. 37-52.

Nalepa, T.F., W.S. Gardner, and J.M. Malczyk. (1983). Phosphorus release by three kinds of benthic invertebrates: Effect of substrate and water medium. *Canadian Journal of Fisheries and Aquatic Sciences*, 40:810-813

Nelson, T.A. and A. Lee. (2001). A manipulative expermiment demonstrates that blooms of the macroalgal *Ulvaria obscura* can reduce eelgrass shoot density. *Aquatic Botany*, 71:149-154.

Nielsen, K.J., C.A. Blanchette, B.A. Menge, and J. Lubchenco. (2006) Physiological snapshots reflect ecological performance of the sea palm *Postelsia palmaeformis* (Phaeophyceae) across intertidal elevation and exposure gradients. *Journal of Phycology*, 42:548-559.

Ozimek, T., E. Pieczynska, and A. Hankiewicz. (1991). Effects of filamentous algae on submerged macrophyte growth: A laboratory experiment. *Aquatic Botany,* 41, 309-315.

Pajdak-Stós, E. Fialkowska, and J. Fyda. (2001). *Phormidiium autumnale* (Cyanobacteria) defense against three ciliate grazer species. *Aquatic microbial ecology*, 23:237-244.

Pederson, M.F. and J. Borum. (1996). Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Marine Ecology Progress Series*, 142:261-272.

Pederson, M.F. and J. Borum. (1997). Nutrient control of estuarine macroaglae: growth strategy and the balance between nitrogen requirements and uptake. *Marine Ecology Progress Series*, 161:155-163.

Pennings, S.C., S.R. Pablo, and V.J. Paul. (1997). Chemical defenses of the tropical, benthic marine cyanobacterium *Hormothannion entermophoides*: Diverse consumers and synergisms. *Limnology and Oceanography*, 42:911-917.

Pinckney, J.L. and F. Micheli. (1997). Microalgae on seasgrass mimics: Does epiphyte community structure differ from live seagrasses?

Philips, A. G.Lambert, J.E. Granger, and T.D. Steinke. (1996). Vertical zonation of epiphytic alge associated with *Avicennia marina* (Forssk.) Vierh. Pneumatophores at Beachwood Mangroves Nature Reserve, Durban, South Africa. *Botanica Marina*, 39:137-175.

Pringle, C. (1990). Nutrient spatial heterogeneity: effects on community structure, physiognomy, and diversity of stream algae. *Ecology*, 71:905-920.

Reynolds, C.S. (2006). Ecology of Phytoplankton. Cambridge University Press, Cambridge, UK. 384 pp.

Rogers, K.H. and C.M. Breen. (1981). Effects of epiphyton on *Potamogeton crispus* L. leaves. *Microbiology Ecology*, 9:351-363.

Rugenski, A.T., A.M. Marcarelli, H.A. Bechtold, and R.S. Inouye. (2008). Effects of temperature and concentration on nutrient release rates from nutrient diffusing substrates. *Journal of the North American Benthological Society*, 27:52-57.

Sand-Jensen, K. (1990). Epiphyte shading: Its role in resulting depth distribution of submerged aquatic macrophytes. *Folia Geobotanica and Phytotaxonomica*, 25:315-320.

Schneider, C.W. and R.B. Searles. (1991). Seaweeds of the Southeastern United States: Cape Hatteras and Cape Canaveral. Duke University Press, Durham, North Carolina. 553 pp.

Smith, B. and J.B Wilson. (1996). A consumer's guide to evenness indices. *OIKOS*, 76: 70-82.

Smith, V.H., J.D. Tilman, and J.C. Nekola. (1999). Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution*, 100:179-196.

Sotka, E.E. and M.E. Hay. (2009). Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. *Coral Reefs*, 28:555-568.

Stowe, W. C. (1982). Diatoms epiphytic on the emergent grass spartina alterniflora in a louisiana salt marsh. *Transactions of the American Microscopical Society*, 101:162-173.

Tiffany, M.A. and C.B. Lange. (2002). Diatoms provide attachment sites for other diatoms: a natural history of epiphytism from southern California. *Phycologia*, 41:116-124.

Tilman, D. (1982). Resource competition and community structure. *Monographs in Population Biology*, 17. 279 pp.

Twilley, R.R., W.M. Kemp, K.W. Staver, J.C. Stevenson, and W.R. Boynton. (1985). Nutrient enrichment of estuarine submerged vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series*, 23:179-191.

Valiela, I., J. McClelland, J. Hauxwell, P.J. Behr, D. Hersh, and K. Foreman. (1997). Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography*, 42:1105-1118.

Vitousek, P.M., J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger, and D.G. Tilman. (1997). Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications*, 71:737-750.

Wehr, J.D. and R.G. Sheath. (2003). Freshwater Habitats of Algae. *In* J.D. Wehr and R.G. Sheath, eds "Freshwater Algae of North America: Ecology and Classification". Academic Press, New York, pp. 11-57.

Wetzel, R.G. (2001). Limnology. Academic Press, New York, 1006 pp.

Wetzel, R.G. and G.E. Linkens. (1991). Limnological Analyses. Springer-Verlag, New York. 391 pp.

Williams, D.D. and N.E. Williams. (1998). Aquatic insects in an estuarine environment: densities, distribution and salinity tolerance. *Freshwater Biology*, 39: 411-421.

Williams, S. L. and M.H. Ruckelshaus. (1993). Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology*, 74:904-918.

Zicker, E.L., K.C. Berger, and A.D. Hasler. (1956). Phosphorus release from bog lake muds. *Limnology and Oceanography*, 1:296-303.

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