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The Influence of Phosphorus on Periphyton Mats from the Everglades and Three Tropical Karstic Wetlands

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THE INFLUENCE OF PHOSPHORUS ON PERIPHYTON MATS FROM THE EVERGLADES AND THREE TROPICAL KARSTIC WETLANDS

A dissertation submitted in partial fulfilment of the

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in

BIOLOGY

by

Josette Marie La Hée

2010

To: Dean Kenneth G. Furton
College of Arts and Sciences

This dissertation, written by Josette Marie La Hée, and entitled The Influence of Phosphorus on Periphyton Mats from the Everglades and Three Tropical Karstic Wetlands, having been approved with respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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Jennifer Richards

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James Fourqurean

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Evelyn Gaiser, Major Professor

Date of Defense: June 4, 2010

The dissertation of Josette Marie La Hée is approved.

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Interim Dean Kevin O'Shea
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Florida International University, 2010

DEDICATION

This dissertation is dedicated to my parents, Franklyn A. La Hée and Sonia M. Brown La Hée, who convinced me that I could do anything my heart desired and then stood by my side as I tried. This accomplishment is as much yours as it is mine. Thank you.

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ABSTRACT OF THE DISSERTATION

THE INFLUENCE OF PHOSPHORUS ON PERIPHYTON MATS FROM THE EVERGLADES AND THREE TROPICAL KARSTIC WETLANDS

by

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Professor Evelyn Elaine Gaiser, Major Professor

The distinctive karstic, freshwater wetlands of the northern Caribbean and Central American region support the prolific growth of calcite-rich periphyton mats. Aside from the Everglades, very little research has been conducted in these karstic wetlands, which are increasingly threatened by eutrophication. This study sought to (i) test the hypothesis that water depth and periphyton total phosphorus (TP) content are both drivers of periphyton biomass in karstic wetland habitats in Belize, Mexico and Jamaica, (ii) provide a taxonomic inventory of the periphytic diatom species in these wetlands and (iii) examine the relationship between periphyton mat TP concentration and diatom assemblage at Everglades and Caribbean locations.

Periphyton biomass, nutrient and diatom assemblage data were generated from periphyton mat samples collected from shallow, marl-based wetlands in Belize, Mexico and Jamaica. These data were compared to a larger dataset collected from comparable sites within Everglades National Park. A diatom taxonomic inventory was conducted on the Caribbean samples and a combination of ordination and weighted-averaging modeling techniques were used to compare relationships between periphyton TP

concentration, periphyton biomass and diatom assemblage composition among the locations.

Within the Everglades, periphyton biomass showed a negative correlation with water depth and mat TP, while periphyton mat percent organic content was positively correlated with these two variables. These patterns were also exhibited within the Belize, Mexico and Jamaica locations, suggesting that water depth and periphyton TP content are both drivers of periphyton biomass in karstic wetland systems within the northern Caribbean region.

A total of 146 diatom species representing 39 genera were recorded from the three Caribbean locations, including a distinct core group of species that may be endemic to this habitat type. Weighted averaging models were produced that effectively predicted mat TP concentration from diatom assemblages for both Everglades (R^2=0.56) and Caribbean (R^2=0.85) locations. There were, however, significant differences among Everglades and Caribbean locations with respect to species TP optima and indicator species. This suggests that although diatoms are effective indicators of water quality in these wetlands, differences in species response to water quality changes can reduce the predictive power of these indices when applied across systems.

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CHAPTER I

General Introduction

Karstic wetlands can be found throughout the world and collectively comprise a distinctive set of habitats that are all defined by the dominance of limestone in the underlying bedrock. Within the Caribbean and Central American region, freshwater karstic wetlands occur as expanses of inundated coastal and inland plains, underlain by ancient limestone bedrock. Topographical and hydrological variation greatly influence vegetation assemblages across these wetland landscapes, producing a patchwork of habitat types that range from elevated pine rockland forests to deep-water sloughs. Included among these varied habitat types are extensive areas of shallow, marl-based marshes, which are characterized by low water phosphorus (P) concentration (<10 $\mu g\ L^{-1}$), a distinctive macrophyte community and the prolific growth of calcitic, cyanobacterial mats known as periphyton mats (Browder *et al*., 1994; Cooper *et al*., 1999; Gunderson, 1994; Rejmánková and Komárková, 2000; Novelo and Tavera, 2003; Gaiser *et al*., 2006).

Although the presence of these mats has been confirmed from multiple areas within the Caribbean and Central American region (Rejmánková *et al*., 2004), most of the taxonomical and ecological research has been conducted in the southern Florida Everglades, one of the most intensely studied wetland ecosystems in the western hemisphere. The historic Everglades wetland ecosystem once covered an expanse of approximately 10,000 km^2, however, industrial and agricultural developments and the resultant alterations in the spatial expanse, water quality and natural flow regime, have

led to the reduction of "natural" wetland area to just over half its original size (Willard *et al*., 2001; Winkler *et al*., 2001). The system still remains the largest contiguous wetland system in North America and one of the largest freshwater wetlands in the world (Mitsch and Gosselink, 2000).

Periphyton mats within this system were first described in 1928 by Dachnowski-Stokes as part of a study on coastal subsidence and subsequent work has served to characterize the composition and structure of these mats, as well as document the variations in mat types across habitat types (e.g. Loveless, 1959, Brock, 1970; Van Meter-Kasanof, 1973; Wilson, 1974; Wood and Maynard, 1974; Gleason and Spackman, 1974; Browder, 1982; Raschke, 1993). More recently, in light of concerted efforts towards the development of monitoring and restoration strategies within the Everglades, periphyton studies have focused on the potential use of periphyton mats as indicators of environmental stress and recovery (McCormick and Stevenson1998; Noe and Childers, 2007; Gaiser *et al*., 2004).

Calcitic periphyton mats are structurally dominated by filamentous cyanobacteria (primarily *Schizothrix* spp. and *Scytonema* spp.), which form an interwoven network in which diatoms, green algae, desmids, heterotrophic bacteria and fungi grow amid polysaccharide mucilage strands and interstitial deposits of calcium carbonate (Van Meter-Kasanof, 1973; Swift and Nicholas, 1987; Donar *et al*., 2004; Stal, 2000; Rejmánková and Komárková, 2000). Diatoms are a particularly important periphyton mat component, contributing to both mat form and function. Taxonomic studies have identified a distinctive assemblage of diatom species (including *Brachysira neoexilis, Encyonema evergladianum, Encyonema* spp*., Fragilaria syngrotesca, Mastogloia smithii*

var. *lacustris, Mastogloia smithii, Navicula cryptotenella, Nitzschia palaea* and *Nitzschia serpentiraphe*) which has not been reported from other habitat types and is possibly endemic to subtropical/tropical freshwater karstic wetlands (Slate and Stevenson, 2000 and 2007; Gaiser *et al*. 2006). The organic matrix of mucopolysaccharide threads produced by certain species of attached and motile diatoms (e.g. *Gomphonema* spp. and *Mastogloia smithii*) encourages periphyton mat cohesion and, along with cyanobacterial mucilage sheaths, aid in resistance to mat desiccation (Azim and Asaeda, 2005; Donar *et al*., 2004; Thomas *et al*., 2006; Gaiser *et al*., 2010). The copious production of glycocalyx also serves as an extracellular organic reservoir of nutrients that may sustain microbial activity under oligotrophic conditions and stimulate microbial heterotrophic activity following extended periods of desiccation (Gaiser *et al*., 2010; Hagerthey *et al*., in press).

Everglades periphyton mats are among the most productive in the world, with reported annual net primary production rates of greater 10,000 g C m^{-2} $year^{-1}$, which in some areas, exceed production rates of macrophytic vegetation (Browder *et al*., 1994; Goldsborough and Robinson, 1996; Ewe *et al*., 2006). The various algal, bacterial and detrital components of these mats comprise a significant food source for microinvertebrates, macroinvertebrates and fish, and the intricate structural architecture of these mats provides microhabitats for these organisms, many of which are able to persist during dry periods by using the moist mat layers as a refuge (Williams and Trexler, 2006; Liston *et al*., 2008). Periphyton mats are also important biogeochemical regulators, which facilitate the deposition of calcium carbonate throughout the system, influence the production of detrital floc (Neto *et al*., 2006) and are responsible for diurnal and annual fluctuations in water chemistry (McCormick *et al*., 2001; Munyon, in prep.).

Within this system, spatial and temporal patterns of hydrological change are manifest as changes in water depth, duration of inundation and duration of dry down, all of which are important ecological drivers (Gottlieb *et al*., 2006). Periphyton mats are specifically influenced by changes in water depth and duration of dry down. Mat inorganic content declines significantly in response to increasing water depth, resulting in a predominance of mats with high organic content in deeper areas and mats with high calcite content in shallower areas (Gottlieb *et al*., 2006; Gaiser *et al*., 2004). Under extended dry conditions, periphyton mats can become desiccated but have been shown to be capable of rapid recovery and growth upon re-wetting (Thomas *et al*., 2006; Gottlieb *et al*., 2006).

Because the Everglades is an extremely oligotrophic system in which phosphorus (P) is the main limiting nutrient (Noe *et al*., 2001), the rapid uptake and assimilation of P by periphyton mats is also of particular importance (McCormick and Scinto, 1999; Scinto and Reddy, 2003). Except under conditions of extreme and/or prolonged eutrophication, periphyton TP uptake efficiently removes TP from the water column, such that water TP concentration tends to remain low even with increased inputs of TP to the system (Gaiser *et al*., 2006). Periphyton mats can, however, show physiological, physical and compositional changes in response to low levels of TP enrichment within a matter of hours or days (McCormick and O'Dell, 1996; McCormick *et al*., 2001; Gaiser *et al*., 2005; Iwaniec *et al*., 2006; Munyon, in prep.) and therefore, elevated periphyton mat TP concentrations serve as a more reliable metric of TP inputs to the system than water column TP (Gaiser *et al*., 2005).

In addition to rapidly removing TP from the water column, periphyton mats also exhibit marked responses to increases in TP, the most obvious being an anomalous decrease in overall mass and increase in organic content (Pan *et al*., 2000; McCormick *et al*., 2001; Gaiser *et al*., 2006). This response is also echoed in the diatom assemblage, which is dominated by species that exhibit a low tolerance for nutrient enrichment (McCormick *et al*., 1996; Cooper *et al*., 1999; Slate and Stevenson, 2007), but under enriched conditions, this assemblage shifts from an one of endemic mat species to one dominated by 'weedy' benthic taxa (Swift and Nicholas, 1987; Grimshaw *et al*., 1993; McCormick and O'Dell, 1996; Pan *et al*., 2000). The established relationship between periphytic diatom assemblage and TP has been used to develop diatom based calibration models to infer water (Slate and Stevenson, 2007), soil (Cooper *et al*., 1999) and periphyton mat (Gaiser *et al*., 2006) TP concentrations within the Everglades, as well as to indicate past environmental conditions and identify anthropogenically driven changes to the system using paleoecological techniques (Slate and Stevenson, 2000).

The aforementioned body of work has served to show that within the Everglades wetland system both hydrology and water quality (primarily phosphorus concentrations) are significant in determining the form and function of periphyton mats. It also highlights that pweriphyton mat diatom assemblages are particularly useful indicators of water quality.

Within the Caribbean and Central American region there exist karstic wetlands that are very similar to those found within the Everglades. These wetlands resemble the Everglades with respect to climate, geology, vegetation, water quality, and the presence of calcite-rich periphyton mats (Rejmánková, 2001; Rejmánková and Komárková, 2000;

Novelo and Tavera, 2003; Novelo *et al*., 2007). The existence of such similar systems provides a venue for examining relationships between periphyton and environmental conditions in multiple tropical karstic wetlands, and facilitates a test of the validity of generalizing relationships observed in the Everglades to represent what may occur in tropical, freshwater karstic wetlands as a whole. Also, portions of these wetlands have been subjected to agricultural and industrial activities, which have led to changes in water quality and concomitant ecosystem degradation (Rejmánková and Komárková, 2005). Although the use of biological indicators would be valuable in the management of these wetlands, the pervasive lack of environmental and species data across much of the region precludes the development of site-specific diatom inference models.

The main objectives of this study therefore seek to (i) examine relationships between periphyton mat attributes and water quality in karstic wetland habitats in Belize, Mexico and Jamaica, compare these relationships to those found within similar Everglades wetland habitats and test the hypothesis that water depth and periphyton TP content are both drivers of periphyton biomass in tropical karstic wetland systems (Chapter II), (ii) provide a taxonomic inventory of the diatom species of periphyton mats from wetlands in Belize, Mexico, Jamaica (Chapter III) and (iv) examine and compare the relationship between periphyton mat TP concentrations and diatom assemblage at the Everglades and Caribbean locations and determine the feasibility of employing models relating diatom assemblage to water quality in the Everglades to similar systems within the wider Caribbean (Chapter IV).

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CHAPTER II

Phosphorus and hydrology as drivers of periphyton mat biomass in the Everglades and three tropical karstic wetlands

ABSTRACT

Hydrology and water quality greatly influence periphyton mat production in the Everglades, where increases in water depth and periphyton mat total phosphorus (TP) concentrations result in an anomalous decline in periphyton mat biomass. This study was conducted to determine whether these responses are unique to the Everglades or are symptomatic of tropical karstic wetland systems within the northern Caribbean region. Periphyton mat samples and water quality data were collected at sites in shallow, marl-based wetlands in Belize, Mexico and Jamaica. These data were compared to a larger dataset collected from comparable sites within the Everglades National Park. Periphyton mat biomass was negatively correlated with TP and water depth at Everglades ($p<0.0001$) and Caribbean ($p<0.05$) locations. Percent organic content was positively correlated with TP within the Everglades ($R^2=0.44$, $p<0.0001$), and water depth at both Everglades ($R^2=0.23$, $p<0.0001$) and Caribbean locations ($R^2=0.35$, $p<0.001$). Principle Component Analysis showed that at Everglades and Caribbean locations, periphyton mats with higher TP were found at deeper sites and had lower biomass and higher organic content. These results strongly suggest that water depth and, to a greater extent, periphyton mat TP, are both drivers of periphyton mat dynamics in tropical karstic wetland systems.

INTRODUCTION

Karstic wetlands occur throughout the world and collectively comprise a distinctive set of habitats that exist as an expanse of shallow marsh or swampland overlying limestone bedrock. While the constituent flora and fauna may vary considerably among these wetlands, one biological component that tends to be a common feature is the cyanobacteria-dominated communities that occur as thick, multilayered calcium carbonate (calcite)-rich mats (Stal, 2000). As is the case with periphyton mats in other aquatic systems, these mats serve multiple ecological roles and are greatly influenced by changes in environmental conditions (McCormick and Scinto, 1999; Gaiser, 2009). The relationships between periphyton mat ecology and various environmental conditions have been most intensely studied within the Everglades wetland system in southern Florida, U.S.A. This expansive karstic wetland system has been subjected to the effects of decades of anthropogenic alterations, prompting investigations of the use of periphyton mats as indicators of environmental stress and recovery (McCormick and Stevenson1998; Noe and Childers, 2007; Gaiser *et al*., 2004).

Throughout much of the Everglades, periphyton occurs as epipelic, epiphytic or free floating masses of thick mat, the various forms of which may be distinguished primarily by their dominant taxonomic group and the relative contribution of the inorganic (calcite) component to overall periphyton mat mass (Van-Meter Kasanof, 1973; Browder, 1982). Mats range from those dominated by filamentous cyanobacteria, (primarily *Schizothrix* spp. and *Scytonema* spp.) and diatoms, with a major calcite component, to those dominated by desmids and filamentous green algae, with a minor

calcite component. The various photosynthetic components of these mats tend to display a high microbial taxonomic diversity and the complement of taxa forming the dominant group varies considerably depending on mat type (Van-Meter Kasanof, 1973; Swift and Nicholas, 1987; Slate and Stevenson, 2007; Gaiser, 2009).

Calcitic mats can constitute the most productive biological component of Everglades wetlands, displaying cross-system biomass values which, in many areas, exceed that of standing macrophytic vegetation (Ewe *et al*., 2006; Gaiser, 2009; Richardson, 2009). As the base of the algal food web, the edible portions of these mats are a significant food source for microinvertebrates, macroinvertebrates and fish, and their structural architecture provides microhabitats for these organisms, many of which use the moist mat layers as a refuge during dry periods (Williams and Trexler, 2006; Liston *et al*., 2008). Periphyton mats are also important biogeochemical regulators within the Everglades wetland system, where they significantly influence diurnal and annual changes in water chemistry and facilitate the deposition of calcite, which is the dominant soil type in shallow, short-hydroperiod marshes (i.e. marshes which remain flooded for 3 to 8 months out of the year) (McCormick and Scinto, 1999; Scinto and Reddy, 2003).

The results of multiple studies conducted across a variety of Everglades habitats have shown that periphyton mat form and function varies predictably in relation to hydroperiod and water chemistry (McCormick and O'Dell, 1996; Childers *et al*., 2001; Noe *et al*., 2002; Gaiser *et al*., 2004; Iwaniec *et al*., 2006). Many of these studies have also revealed specific relationships and processes, the controlling mechanisms of which are still not fully understood.

Both water depth and the period of inundation change across the wetland landscape in response to topographical variability. The inorganic content of periphyton mats, which is dominated by calcite, declines significantly as water depth increases, resulting in a predominance of mats with high organic content in deeper areas and mats with high calcite content in shallower areas (Gottlieb *et al*., 2006; Gaiser *et al*., 2004). Under extended dry conditions, periphyton mats can become desiccated, but have been shown to be capable of rapid recovery and growth upon re-wetting (Thomas *et al*., 2006; Gottlieb *et al*., 2006). A paradoxical negative relationship between periphyton mat total phosphorus (TP) concentration and biomass has also been identified. As periphyton mat TP concentrations exceed 250 μg P g^{-1} dry weight, mats begin to display significantly reduced biomass and may disintegrate entirely after continued exposure to elevated phosphorus levels (Pan *et al*., 2000; McCormick *et al*., 2001). This response to enrichment is in opposition to the general pattern observed in aquatic systems, where an increase in limiting nutrients results in a concomitant increase in algal growth rates and total biomass (McCormick *et al*., 2001). This body of work suggests that both hydrology and water quality (primarily phosphorus levels) are significant in determining the form and function of periphyton mats within the Everglades wetland system. However, it is currently unknown whether the importance of these factors as drivers of periphyton mat ecology is unique to the Everglades, or if the observed patterns are characteristic of tropical, freshwater karstic wetlands in general.

Recent studies conducted in karstic wetlands within Mexico, Belize and Jamaica have identified areas with similar climate, geology and vegetation that support habitats and periphyton mat communities comparable to those found in the Everglades

(Rejmánková, 2001; Rejmánková and Komárková, 2000; Novelo and Tavera, 2003; Novelo *et al*., 2007). The existence of such similar systems provides a venue for examining relationships between periphyton mats and environmental conditions in multiple tropical karstic wetlands and facilitates a test of the validity of generalizing relationships observed in the Everglades to represent what may occur in tropical, freshwater karstic wetlands. The main objectives of this study therefore seek to (i) examine relationships between periphyton mat attributes and water quality in karstic wetland habitats in Belize, Mexico and Jamaica, (ii) compare these relationships to those found within similar Everglades wetland habitats and (iii) test the hypothesis that water depth and periphyton mat TP content are both drivers of periphyton mat biomass in tropical karstic wetland systems.

SITE DESCRIPTION

Sampling was conducted in three wetland systems, similar with respect to geology, climate, hydrology and vegetation and located within the northern Caribbean Basin: the Sian Ka'an Biosphere Reserve (and areas to the south) in Quintana Roo, Mexico; the New River Lagoon in Orange Walk, Belize; and the Broad River in the Black River Morass, St. Elizabeth, Jamaica (Figure 2-1, Table 2-1).

The Sian Ka'an Biosphere Reserve and the wetlands extending beyond its boundary to the south, encompass a 6500 km^2 area along the south eastern coast of the Yucatan Peninsula in Quintana Roo, Mexico (Cairns *et al*., 2005). The Yucatan peninsula is an uplifted marine platform which extends from the greater Yucatan platform and

serves as a divide between the Gulf of Mexico and the Caribbean Sea. The geological formation is a 2 to 3 km thick sequence dominated by limestone, with intermittent layers of dolomite, anhydrite and gypsum (Weidie, 1985). The karstic wetland marshes located within the Yucatan region are dominated by low phosphorus, inland freshwater, marl-based habitats and coastal mesohaline habitats. The most common freshwater macrophytic species include *Cladium jamaicense* (sawgrass)*, Eleocharis* spp. (spikerush) and *Typha domingensis* (southern cattail), each of which tends to become dominant at low, intermediate and high water depths, respectively (Rejmánková *et al*., 1996). Dwarf populations of *Rhizophora mangle* (red mangrove) become more abundant as salinity levels increase, and form the dominant tree species in the coastal brackish water marshes. Calcitic periphyton mats are abundant in both freshwater and brackish water habitats with marl substrates (Rejmánková *et al*., 1996). Inland sampling sites were confined to freshwater, *Eleocharis* spp. marshes, and closer to the coast, brackish water sites dominated by dwarf *Rhizophora mangle* were sampled.

The New River Lagoon, located in the district of Orange Walk in northern Belize, is an approximately 23 km long and 750 m wide stretch of the New River, which is the longest river contained entirely within Belize (Meerman, 2006). The area lies just to the southeast of the basal portion of the Yucatan peninsula and exhibits geological features similar to the adjacent landmass (Weidie, 1985). The New River Lagoon is flanked by extensive marshes dominated mainly by *Cladium jamaicense, Eleocharis cellulosa* and *Eleocharis interstincta*, with intermittent deeper pools supporting dense assemblages of *Nymphea ampla* (dotleaf waterlilly). Sampling sites in this area were again confined to *Eleocharis* spp. marshes adjacent to the lagoon.

The Black River Morass encompasses the largest wetland and river system within the Greater and Lesser Antillean archipelago (Davis *et al*., 1998; Massa and Haynes-Sutton, 1998). It lies within the Black River Basin, which occupies an area of approximately 1,488 km^2 in the south-western region of Jamaica. The area is divided into two main sections: the Upper and Lower Morass. The Upper Morass is approximately 97 km^2 (Cronberg, 1983) and is composed of a mass of swampy lowlands with limestone bedrock covered by peat deposits. The Lower Morass which is approximately 57 km^2 (Enell, 1984), exists as an area of down-faulted, poorly karstified limestone, overlain by a relatively thin clay and peat sequence. Inland marsh areas display mixed vegetation dominated by *Cladium jamaicense* and *Eleocharis* spp., with large stands of *Typha domingensis* being present in some areas (Azan and Webber, 2007). Closer to the coast, assemblages dominated by *Rhizophora mangle* are prevalent and these trees can also be found bordering the main waterways as they meander through the wetland system. Sampling sites were located within *Cladium jamaicense* and *Eleocharis* spp. marshes bordering the Broad River, a major tributary of the Black River.

Data collected from these wetlands were compared to a larger dataset collected from a total of 110 sites within the Everglades National Park, in southern Florida, U.S.A (Figure 2-1, Table 2-1). The Everglades freshwater wetland system encompasses an area of approximately 5,000 km^2, and is one of the largest contiguous wetland systems in North America (McCormick *et al*., 1998; Childers *et al*., 2001). The system is geologically young, having formed less than 5,000 years ago as a result of extended hydroperiod regimes that encouraged the deposition of peat and marl in the midst of a limestone depression (Gleason and Stone, 1994). The vegetation structure of the

Everglades marsh habitats is similar to that of the previously described sites, with *Cladium jamaicense* and *Eleocharis* spp. marshes being common and *Nymphaea odorata* (American white waterlilly)*, Nymphaea aquatica* (water shield) and *Nuphar advena* (spatterdock) characterizing deeper slough areas (Gunderson, 1994; Richardson, 2009). For this study, the data utilized were drawn from a large dataset derived from multiple seasonal sampling events conducted throughout the Everglades as part of the Periphyton component of the Comprehensive Everglades Restoration Plan (see CERP, 2005; Gaiser, 2009).

METHODS

Each of the Caribbean study locations was visited on two occasions; once during a wet period and once during a dry period. Due to abnormal seasonal rainfall patterns during the course of the study, wet and dry *periods* did not necessarily coincide with the typical regional wet and dry *seasons*. "Wet" and "dry" designations were therefore applied based on rainfall levels at each location during the sampling period, relative to typical wet and dry seasonal rainfall levels. The Everglades samples were collected during October to December, 2005 (wet period) and September to December, 2006 (dry period) as part of the periphyton mat component of the CERP seasonal sampling regime. The sites in Mexico were visited in December 2006 (wet period) and March 2008 (dry period), the Belize sites in May 2007 (dry period) and November 2007 (wet period), and the Jamaica sites in May 2008 (dry period). Samples were collected during the wet period at Jamaica sites, however, these were qualitative grab samples, which precluded any

quantitative analyses and so were not included in this study. Efforts were made to conduct sampling at as many sites as possible within each location, however during dry periods the number of sites sampled varied according to the ability to locate sites that sustained water levels greater than 5cm. During wet periods, sampling efforts were contingent on the ability to gain access to sites and were then limited to sites that did not exceed water depths of 1m.

At each location, sampling sites were limited to marshes dominated by *Eleocharis* spp., however, at some sites *Nymphaea* spp., *Cladium jamaicense* and dwarf *Rhizophora mangle* were also present. At each site, GPS coordinates were recorded and sampling was then conducted using a 1-m^2 throw trap to delineate a 1-m^2 area which was treated as a sample plot (Kushlan, 1981). Four plots were sampled at each site. For each plot a photograph was first taken of the surface view of the quadrat and then soil type (e.g., marl, peat, clay, sand), periphyton mat type (e.g., benthic, floating, epiphytic) and water depth were recorded.

Periphyton mat cover was recorded as separate *in situ* estimates of the percent of the plot covered by benthic, epiphytic and floating periphyton mat. All periphyton material was then cleared from the plot by hand, placed onto a bar seine net and coarsely sorted to remove animals and any attached marl. Live submerged aquatic vegetation (SAV) often becomes intricately incorporated into the periphyton mat structure, especially in situations where a very close association has developed between the algal mat and its plant substrate (Browder *et al*., 1994). This is most often seen in mats associated with species such as *Utricularia purpurea* (floating mats), *Eleocharis cellulosa*, *Cladium jamaicensis* (epiphytic mats) and *Chara* sp. (benthic mats). To

account for these associations two estimates of periphyton mat biovolume were recorded in the field. For the first, all plant material was removed from the collected periphyton mats and "periphyton only" material was measured using a perforated 2,000 ml graduated cylinder that allowed water to drain, permitting periphyton mat biovolume to be recorded. Next, the removed plant material was measured in the graduated cylinder, and this biovolume was added to the first to produce a periphyton + SAV total biovolume. The first of these estimates of biomass is henceforth referred to as periphyton mat biovolume (BV), while the latter is considered total periphyton mat biovolume (TBV). A subsample of 120 ml was removed from the "periphyton only" mat material, placed in a sterile sample bag and stored in a cooler with ice for transport to the lab. When no observable calcitic periphyton mats were present, epipelon was sampled from the benthos and epiphytic films were scraped from any macrophytes present.

In the laboratory, each sample was weighed to obtain a wet weight, and then transferred to a clean 500-ml beaker to which an additional 20 ml of distilled water was added to facilitate homogenizing. From the homogenized total volume, a 50-ml subsample was poured into a pre-weighed aluminum pan, dried in an oven at 80ºC for 48 hrs and later removed and weighed to estimate periphyton mat dry mass (DM). The dried sample was placed in a muffle furnace at 500ºC for 3 hrs and again weighed to produce an ash weight, which is the inorganic portion of the sample. The difference between these two values was calculated as the ash-free dry mass (AFDM), which represents the organic portion of the periphyton mat sample. Another 50-ml subsample was removed from the homogenized total sample, poured into a labeled 120-ml sample cup and placed in a drying oven at 80°C until completely dry. The dried contents were then ground

using a mortar and pestle and analyzed for TP following the methods of Solórzano and Sharp (1980). A final 1-ml subsample was removed and filtered through a GFF filter, which was later analyzed for chlorophyll *a*, following acetone extraction (Welschmeyer, 1994).

A total of 9 variables were recorded and analyzed: periphyton mat + SAV total biovolume (TBV ml m^{-2}), periphyton mat biovolume (BV ml m^{-2}), periphyton mat dry mass (DM g m^{-2}), periphyton mat ash-free dry mass (AFDM g m^{-2}), periphyton mat percent organic content (ORG = ((AFDM/DM) x 100), periphyton mat total phosphorus (TP µg P g^{-1} dry mass), periphyton mat chlorophyll *a* biomass (CH µg m^{-2}), periphyton mat chlorophyll *a* concentration (CHC µg g^{-1} dry mass) and water depth (WD cm). Prior to statistical analysis, each dataset was first transformed to meet the assumption of normality: TBV, BV and WD were square root transformed, DM and AFDM were 4^{th} root transformed, ORG, TP, CH and CHC were log10 transformed, with log10(x+1) being used for CH and CHC values to ensure log values were positive.

Statistical analyses were conducted to determine (i) differences among locations, (ii) differences between wet and dry periods, and (iii) relationships between and among measured variables. For these analyses, five sets of data were used: Everglades samples, Belize samples, Mexico samples, Jamaica samples and a composite of all the Belize, Mexico and Jamaica sites, collectively referred to as the Caribbean samples. Differences among locations were analyzed using analysis of variance (ANOVA) followed by Tukey's test (analyses were done using PASW Statistics 18). The results reported for the analyses of differences among sites, therefore, indicate which location (if any) was significantly different to *all* other locations. Differences between sampling occasions for

each location (wet vs dry) were analyzed using Student's T-test. Regression analysis and Pearson's correlation (done using the statistical program R) were used to test for significant linear relationships between pairs of variables. PCORD 5 (McCune and Grace, 2002) was used to perform a Principal Component Analysis (PCA) examining differences among sites for all locations based on the 9 measured variables. The PCA was performed twice, first using Everglades sites only and second using Caribbean sites only. These two results allowed comparisons to be made between patterns in the Everglades and the Caribbean locations. Joint plots were used to show the direction and strength of the relationships among these measured variables.

RESULTS

Site comparisons

Habitat characteristics among the sampled locations overlapped, with most sites being dominated by *Eleocharis* spp. growing in shallow (<1m) marl based soils, inundated by circumneutral waters. Among all four locations, average pH ranged from 7.2 to 9.2 and average conductivity ranged from 441.8 to 15,047.7 $\mu S\ cm^{-1}$ (Table 2-2). Some sampling sites within the Mexico location (Mahahual and Marisma) were closer to the coast and supported a macrophytic assemblage dominated by *Rhizophora mangle* and *Eleocharis* spp. At these sites average pH and conductivity levels were greater than all other sites (Table 2-2), which is a result of the influx of brackish-water at these sites. During the dry period sampling period at the Belize location, the interior marsh areas were completely dry and inaccessible. Sampling was therefore limited to *Eleocharis* spp.

marshes bordering the New River Lagoon, where, prior to the dry season, lagoonal waters with elevated TP would have advanced into these peripheral marshes.

Water depth levels at sampling sites ranged from 5 to 105 cm among the four locations. Belize sites had a significantly greater mean water depth than Mexico sites during the wet period ($p = 0.025$) and Jamaica sites had a significantly lower mean water depth than the Everglades sites during the dry period ($p = 0.001$) (Figure 2-2a). Periphyton mat TP values were between 25 and 786 $\mu g\ g^{-1}$ among all locations. During the dry period, the Belize location had mats with a significantly higher mean TP compared to Mexico and the Everglades ($p = 0.018$ and $p < 0.0001$ respectively) and during the wet period Belize periphyton mat TP concentrations were significantly higher than at the Everglades location ($p = 0.036$) (Figure 2-2b).

TBV and BV ranged from 0 to 13,933 ml m^{-2} and 0 to 11,000 ml m^{-2} respectively, while mat DM and AFDM ranged from 0 to 2,079 g m^{-2} and 0 to 590 g m^{-2} respectively. Belize had significantly lower TBV and BV than Mexico and Everglades locations ($p < 0.001$) and significantly lower mean DM and AFDM when compared to all locations ($p < 0.022$), with the disparity being most pronounced during the dry period (Figure 2-2c, d, e and f).

Periphyton mat ORG ranged from 9.3 to 89.9% among all locations, with no significant differences among the locations (Figure 2-2g). CH biomass and CHC ranged from 0 to 362,088 $\mu g\ m^{-2}$ and 0 to 1,217 $\mu g\ g^{-1}$ respectively. Belize showed significantly lower values for CH compared to all other locations, ($p < 0.0001$) during both wet and dry periods. CHC was lower at the Belize location than at the Everglades ($p < 0.0001$) and Mexico location ($p = 0.007$), but only during the wet period (Figure 2-2h and i).

Wet period to dry period comparisons

Across all locations, water depth showed temporal variation, having greater values during the wet periods than during the dry periods, with the difference being significant for Everglades ($p = 0.001$) and Belize ($p < 0.0001$) (Figure 2-2a). Periphyton mat TP concentration showed no significant difference between wet and dry periods at any location (Figure 2-2b).

TBV, BV and DM measures showed no differences between wet and dry periods at any location. However, Belize AFDM was higher during the wet period ($p = 0.01$) (Figure 2-2c, d, e, f).

Periphyton mat ORG was higher during the wet period for Belize ($p = 0.002$), but no significant differences were seen between periods for the Everglades and Mexico (Figure 2-2g). CH was only different between wet and dry periods for Belize, where values were greater ($p = 0.002$) during the wet period (Figure 2-2h). CHC was consistently higher during the dry period across all locations, with the difference being significant at the Belize location ($p < 0.0001$) (Figure 2-2i).

Relationships between all variables and water depth

TBV, BV, DM, AFDM and CH all tended to decline in relation to water depth (Figure 2-3a, b, c, d, e), and while the negative relationships were all significant for the Everglades ($p<0.0001$), only BV and CH showed a significant trend for Caribbean sites ($p=0.037$ and $p=0.023$). The relationship between CHC and water depth differed between the Everglades and the Caribbean sites (Figure 2-3f), with the former showing a significant positive relationship ($R^2=0.35$, $p<0.0001$) and the latter showing a significant

negative relationship (R^2=0.34, p<0.001). Periphyton mat ORG showed a strong and significant positive relationship with water depth for both Everglades (R^2=0.23, p<0.0001) and Caribbean sites (R^2=0.35, p<0.001) (Figure 2-3g).

Relationships between all variables and TP

Periphyton mat biomass, measured as TBV, BV, DM, AFDM and CH biomass showed a strong and significant negative relationship with TP at both Everglades (p<0.0001) and Caribbean (p<0.01) sites (Figure 2-4a, b, c, d, e). Periphyton mat ORG tended to increase with TP at both Everglades and Caribbean sites, but the relationship was only significant for the Everglades (R^2=0.44, p<0.0001) (Figure 2-4f). CHC also increased with TP, and this relationship was significant at both Everglades (R^2=0.60, p<0.0001) and Caribbean sites (R^2=0.18, p=0.009) (Figure 2-4g).

There was a significant positive relationship between water depth and TP for the Everglades (R^2=0.18, p<0.0001), however this pattern was not seen for the Caribbean sites (Figure 2-4h).

Relationships among all variables

For the Everglades PCA (Figure 2-5a), axes 1, 2 and 3 explained 91.2% of the variation (73.3%, 11.0% and 6.8% respectively). TBV, BV, DM, AFDM and CH were all strongly positively correlated with axis 1 (R^2 =0.74, R^2 =0.89, R^2 =0.97, R^2 =0.94, R^2 =0.68, respectively; p<0.0001), while CHC, ORG, mat TP and water depth were negatively correlated with this axis (R^2 =0.74, R^2 =0.62, R^2 =0.63, R^2 =0.39, respectively; p<0.0001). This suggests that periphyton mats with higher TP concentrations tended to

have lower biomass, higher ORG and were found at deeper sites, while mats with lower TP concentrations tended to have higher biomass, lower ORG and were found at shallower sites. Water depth also showed a positive correlation with axis 3 (R^2 =0.42, p<0.0001), possibly reflecting the difference between sites sampled during the wet period and those sampled during the dry period.

For the Caribbean PCA (Figure 2-5b), axes 1, 2 and 3 explained 92.0% of the variation (57.9%, 21.4% and 12.7% respectively). TBV, BV, DM, AFDM and CH were all strongly positively correlated with axis 1 (R^2 =0.93, R^2 =0.94, R^2 =0.95, R^2 =0.92, R^2 =0.66, respectively; p<0.0001), while mat TP was negatively correlated with this axis (R^2 =0.56; p<0.0001). This again suggests that as in the Everglades, sites that displayed higher mat TP concentrations also had mats of lower biomass. Unlike the Everglades PCA, however, Caribbean CHC and water depth showed positive and negative correlations with axis 2 respectively (R^2 =0.79, R^2 =0.69; p<0.0001). This reflects the negative relationship between these two variables, in which deeper sites tended to have periphyton mats with lower CHC. Periphyton mat ORG alone was correlated with axis 3 (R^2 =0.64; p<0.0001), which likely reflects the influence of both water depth and mat TP.

DISCUSSION

Within the Everglades wetland system, periphyton mats are noted for their large standing crop and productivity (Goldsborough and Robinson, 1996; Ewe *et al*., 2006; Gaiser, 2009), as well as their response to changes in hydrology and water quality (Gottlieb *et al*., 2006; McCormick *et al*., 2001; Gaiser *et al*., 2005 and 2006). In this

study, very strong significant relationships between water depth, phosphorus and periphyton mat biomass were observed within the Everglades wetland system and these trends, though less robust, were also evident at karstic wetland sites within three widely separated Caribbean locations.

Water depth effects on periphyton mats were evaluated by examining a range of sites that showed natural spatial variation in water depth, as well as temporal differences associated with the wet and dry periods. Within the Everglades, periphyton mat mass, measured as TBV (which includes organic and inorganic matter and associated aquatic vegetation), BV and DM (which include only organic and inorganic matter) and AFDM and CH (which include only organic matter), decreased as water depth increased. However, the ORG and CHC showed the opposite trend of increasing in response to increased water depth. Thus, while absolute values for both organic and inorganic mass decreased with increasing water depth, the relative contributions of these components to overall mat biomass did not respond in the same way. As water depth increased, the proportion of periphyton mat algal content increased, while there was a concomitant decrease in the percent of inorganic mass.

Considering that the ORG within these mats was very high in shallower sites, accounting for up to ~91% of total mat biomass, the significant reduction in inorganic mass with increased water depth is clearly responsible for the reduction in total periphyton mat biomass with increased water depth. This result demonstrates a pattern that has been described in other studies. Gottlieb and others (2006), in a study comparing periphyton mats from long and short-hydroperiod marshes within the Everglades, found that although short hydroperiod sites had, on average, greater than 5 times the biomass

found at long-hydroperiod sites, the ORG in short-hydroperiod marsh periphyton mats averaged only 37%, while that of long-hydroperiod marsh periphyton mats averaged 53%. Differences among sites may arise because in short-hydroperiod marshes periphyton mats grow in close association with the marl substrate and incorporate more calcium carbonate into its biomass than the floating periphyton mats common in long-hydroperiod areas. The reduction of mat biomass as water depth increases can also be a result of associated changes in water chemistry. In deeper, peat-based areas, there is generally a reduction in ambient pH levels and calcite saturation levels, both of which influence calcium carbonate deposition within periphyton mats (Gleason and Spackman, 1974; McCormick and Scinto, 1999; Pentecost and Whitton, 2000). The inhibition of calcium carbonate precipitation results in the development of floating and epiphytic periphyton mats with reduced calcite content, reduced total biomass, and elevated ORG. In more shallow habitats, ambient conditions support calcium carbonate deposition, lending to the production of mostly benthic and epiphytic periphyton mats with a high calcite content, high total biomass and low ORG.

The lower pH levels associated with deep-water habitats could have an additional effect on periphyton mats. Calcium carbonate has been shown to bind phosphorus, making it unavailable for biological uptake (Otsuki and Wetzel, 1972). However, as pH levels decline, phosphorus becomes liberated from calcium carbonate and remains available within the water column (McCormick and Scinto, 1999). Under these conditions, periphyton mats rapidly take up and utilize available phosphorus, and this leads to increased mat TP concentrations (Grimshaw *et al*., 1993; Thomas *et al*., 2002).

This effectively explains the strong positive relationship between water depth and periphyton TP that was observed at the Everglades sites.

Analysis of the data from the Caribbean karstic wetland sites also showed a decrease in periphyton mat biomass and increase in organic matter as water depth increased. Unlike the Everglades results, however, these relationships were not always significant. The reduced strength of these relationships is most likely a result of some of the Belize sample sites, which were located along the border of a river lagoon and did not extend all the way in to the adjacent *Eleocharis* spp. marshes (which were completely dry and inaccessible during the dry period visit). These Belize sample sites were therefore taken from typical long-hydroperiod marshes; however, this was not reflected by their water depths, which were at the time fairly low as a result of severe drought. This led to the collection of non-calcitic, low biovolume, unconsolidated, detrital samples, with elevated TP content from sites of low to moderate water depth. If this interpretation is correct, their inclusion would have reduced the strength of the relationships between water depth and biovolume and mat TP content across Caribbean sites.

The Belize wet-period samples also influenced the relationship between water depth and CHC. Many of these samples had high ORG consisting of dead organic matter, but very little live algae. This resulted in a significant positive linear relationship between water depth and periphyton mat ORG, but a negative correlation between water depth and CHC. It is likely that if the number of sites sampled was greater, these few samples would have had less of an impact on the overall pattern of the data.

The influence of TP on periphyton mats has been well documented within the Everglades. Multiple studies have been conducted in the Water Conservation Areas in

the northern part of the Everglades, where inflows of nutrient enriched water drained from agricultural areas to the north have created a north to south water quality gradient (Smith and McCormick, 1999; McCormick and Laing, 2003). McCormick *et al.* (1998) compared water quality and periphyton mat biomass at phosphorus enriched and un-enriched sites within this area and found periphyton mat ash-free dry weight to be much lower in phosphorus enriched sites (ranging from 3 to 68 g AFDM m^{-2}) when compared to un-enriched sites (ranging from 100 to 1600 g AFDM m^{-2}). Two separate mesocosm studies conducted in the same area showed that periphyton mat biomass, measured as both AFDM and ash weight, decreased as mat TP increased (Pan *et al*., 2000) and that at high mat TP concentrations (>250 μg P g^{-1} dry mass), mat biomass declined significantly, resulting in the elimination of metaphyton (floating periphyton mats) and complete disintegration of periphyton mats (McCormick *et al*., 2001).

In a 5-year dosing experiment conducted by Gaiser *et al.* (2004, 2005 and 2006), protracted low-level phosphorus addition demonstrated that periphyton mats were efficient at rapidly sequestering phosphorus from the water column, resulting in elevated mat TP concentrations (>150 μg P g^{-1} dry mass). They also found that mat DM and AFDM declined as mat TP increased, while ORG was positively correlated with mat phosphorus concentrations.

These studies illustrate that there exists a negative linear relationship between periphyton mat TP and biomass, and a positive linear relationship between periphyton mat TP and the proportion of organic matter within the mat. These two relationships were evident at both Everglades and Caribbean sites in the results of this study, where all but one of these relationships were significant; the exception being between ORG and

mat TP content at the Caribbean sites, arguably the result of small sample size or inclusion of an anomalous sampling event from Belize.

The similarity in the nature of the influence of water depth and mat TP concentrations on mat biomass and ORG indicate that both are important in determining mat biomass. There is, however, a notable difference in the strength of these relationships. The relationship between mat TP and all the variables tested was consistently stronger than that between water depth and the tested variables. This suggests that phosphorus availability is the main driver of periphyton mat biomass, with water depth and the related changes in water chemistry (primarily pH levels and CO_2 partial pressure), acting as enabling factors that regulate phosphorus availability within the water column (Scinto and Reddy, 2003).

As a major component of the tropical karstic wetland ecological structure, periphyton mats contribute to the physical architecture of the system, influence food web structure and regulate multiple biogeochemical processes. It is therefore reasonable to expect that any changes in the environmental conditions of the habitats where these mats are found could have profound effects on the functioning of the mats, and by extension, the wider wetland ecosystem. It is for this reason that efforts must be made to understand how environmental factors affect periphyton mat function, as this will allow us to better predict how anticipated climate change and environmental management decisions may impact these unique systems. In an effort to enhance our knowledge of periphyton mat ecology in tropical karstic wetlands and its impact on the ecology of the overall wetland system, it is also desirable to obtain information from as wide a range of such wetlands as is possible.

Furthermore, the Everglades has been characterized as 'unique' by some authors (e.g., Noe *et al*. 2001), unintentionally questioning the generality of work done there. This study helps to establish a more general framework for understanding the ecology of the Everglades, while expanding the potential application of work done there to less well-studied regions.

Future work will endeavor to incorporate more karstic wetlands from the Caribbean region, as well as increase the range of habitat types and number of sites sampled within these wetlands. In addition, studies conducted in the Everglades suggest that hydrology and water quality greatly influence other ecosystem components, such as food web structure (Liston *et al*., 2008; Chick *et al*., 2008) and diatom community composition (Gaiser *et al*., 2006; Slate and Stevenson, 2007). To enhance our understanding of these relationships, future work should seek to examine these relationships in a broader context within the Caribbean region.

CONCLUSIONS

The results of this study have served to clarify the distinct relationships between (i) water depth and mat ORG and (ii) periphyton mat TP concentrations and biomass in Everglades and Caribbean marshes and provide evidence to support the idea that the observed relationships are indeed characteristic of tropical karstic wetlands and not unique to the Everglades system. Results also show that water depth and periphyton mat TP content are both correlated with periphyton mat biomass in tropical karstic wetland systems, suggesting that they are drivers for periphyton mat dynamics in these systems.

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Table 2-1. Location of Caribbean sampling sites, presented as latitudinal and longitudinal bounding GPS coordinates of sampling sites within each location.

Bounding GPS coordinates of sampling sites	Sian Ka'an National Park, Quintana Roo, Mexico	New River Lagoon, Indian Church, Belize	Slipe River, Black River Morass, St. Elizabeth, Jamaica
EAST	087º30.585	88º37.958'	78 ˚ 46.972
WEST	087º57.579	88º39.212'	77 ˚ 48.874
NORTH	19º52.342	17º47.111'	18 ˚ 03.182
SOUTH	18º47.223	17 ˚ 37.166	18 ˚ 01.524

Table 2-2. Number of sites sampled (N), water characteristics and periphyton attributes for each location during wet and dry periods. Average values are given along with standard deviation values in brackets. Missing data are indicated with a dash (−).

SITE	N	pH	COND (µS cm^{-1})	WD (cm)	TBV (ml m^{-2})	BV (ml m^{-2})	TP (µg P g^{-1} DM)	DM (g m^{-2})	ORG (%)	AFDM (g m^{-2})	CH (µg m^{-2})	CHC (µg g^{-1} DM)
Belize-Wet	12	7.3 (0.5)	441.8 (208.6)	73.2 (8.5)	876.0 (1474.8)	857.1 (1486.4)	239.7 (106.7)	77.1 (133.4)	67.8 (19.1)	30.1 (48.2)	140.2 (132.7)	48.3 (52.5)
Belize-Dry	9	8.3 (0.2)	690.3 (104.0)	31.6 (11.8)	101.6 (264.6)	101.6 (264.6)	543.1 (187.9)	3.2 (6.7)	37.4 (17.9)	1.5 (3.0)	1288.5 (2602.0)	260.6 (175.0)
Jamaica-Dry	5	8.4 (0.5)	447.6 (137.3)	11.6 (12.7)	2251.3 (1712.6)	2251.3 (1712.6)	200.3 (16.5)	156.0 (104.8)	28.7 (7.2)	39.4 (25.5)	29693.0 (19940.6)	222.5 (83.1)
Mexico-Wet	6	-	1259.0 (952.5)	37.9 (10.3)	7460.7 (3043.8)	6772.6 (2957.6)	212.5 (93.7)	365.0 (195.5)	37.9 (7.4)	121.4 (49.5)	37195.4 (12261.7)	129.7 (51.5)
Mexico-Dry	4	9.2 (0.4)	15047.7 (16670.5)	30.3 (23.4)	4564.3 (2568.5)	4144.6 (2720)	193.7 (210.9)	317.4 (233.9)	42.5 (15.5)	109.4 (76.5)	133456.4 (153012.9)	465.3 (257.1)
Everglades-Wet	55	7.2 (0.3)	496.1 (525.3)	54.5 (20.5)	3993.8 (2950.7)	3352.5 (3003.0)	146.0 (111.1)	303.4 (371.5)	49.9 (19.0)	96.9 (95.9)	12995.2 (10945.1)	143.5 (131.4)
Everglades-Dry	55	7.4 (0.3)	445.9 (261.7)	39.4 (21.1)	4784.8 (3149.9)	3756.8 (2980.6)	157.1 (104.1)	333.1 (433.2)	46.6 (16.8)	109.6 (117.9)	17114.8 (11727.4)	159.1 (201.1)

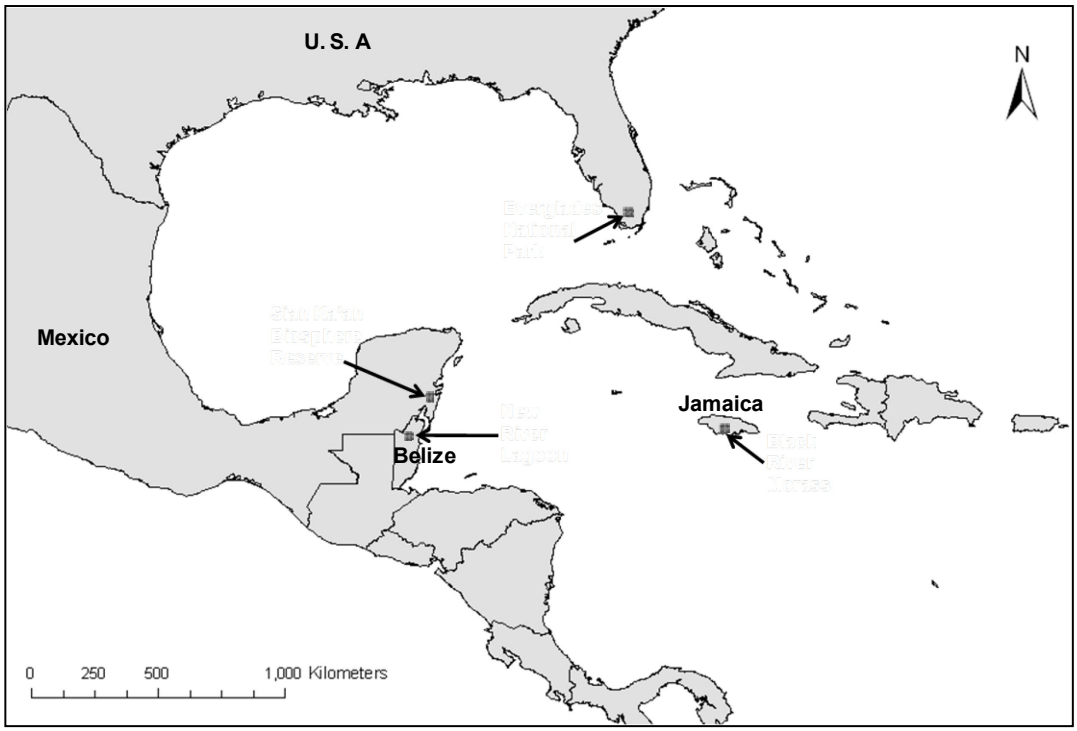

Figure 2-1. Map of northern Caribbean region showing the four sampling locations for this study.

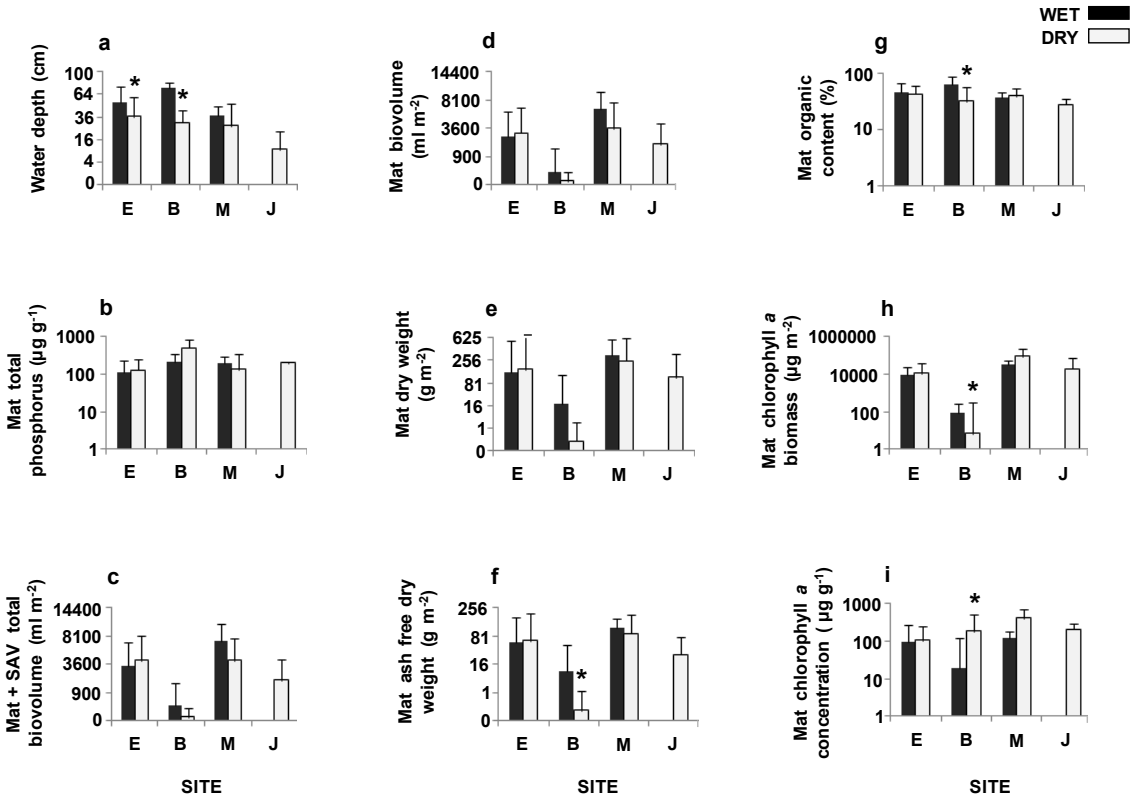

Figure 2-2. Bar graphs showing average values for all measured variables during wet and dry sampling periods at Everglades (E), Belize (B), Mexico (M) and Jamaica (J) sites. Graphs were created using transformed values for each variable and X and Y axes are scaled to facilitate transformed values. Error bars represent one standard deviation. Columns marked with an asterisk indicate a significant difference (ANOVA and Tukey's test, $p<0.05$) between average values during the wet and dry period.

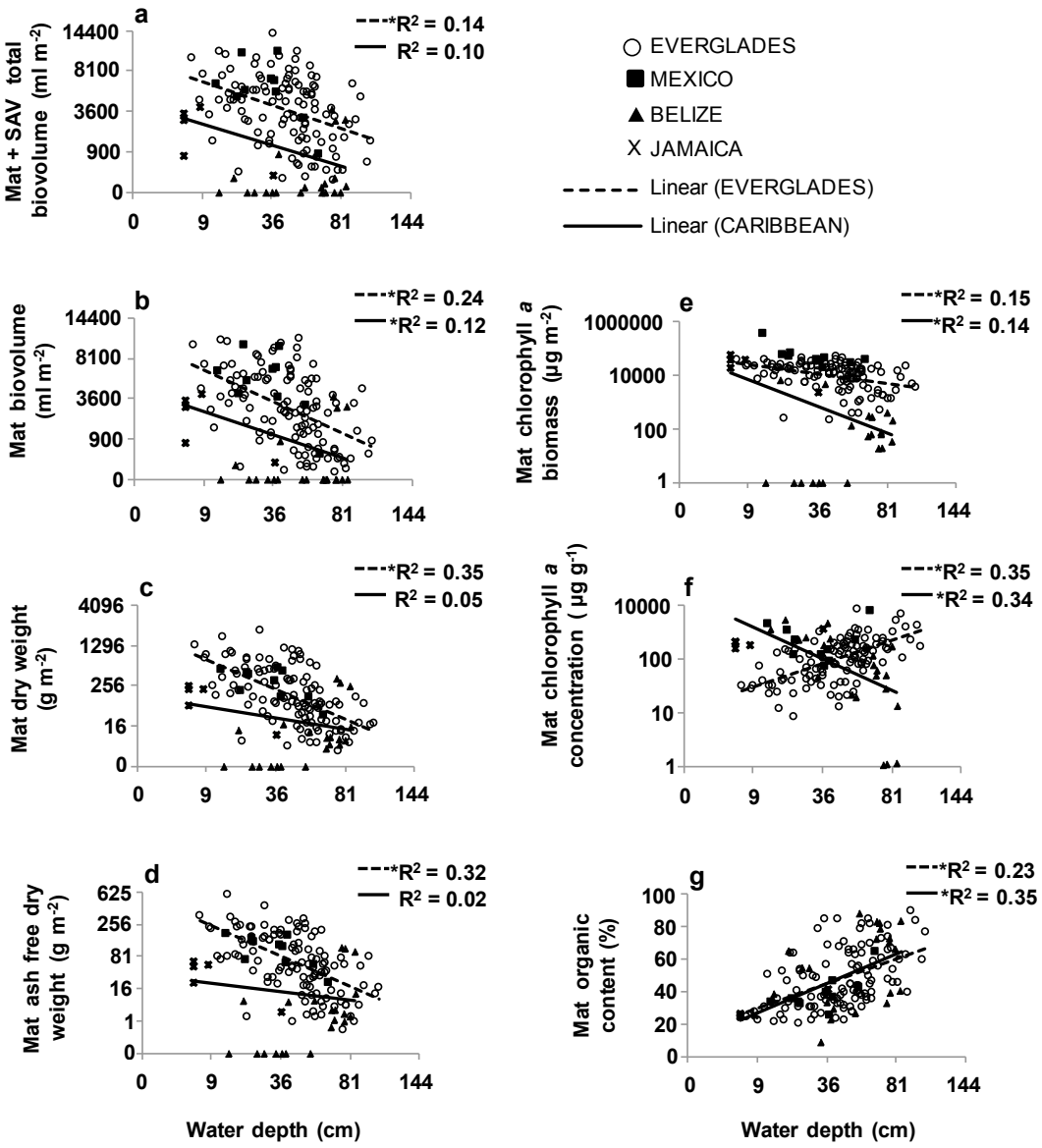

Figure 2-3. Scatterplots showing relationships between water depth and all other measured variables at each site. Graphs were created using transformed values for each variable. X and Y axes were scaled to facilitate transformed values. Two sets of regression lines and R^2 values are shown. The dashed line describes data from all the Everglades sites and the solid line describes the combined dataset from the Caribbean sites. R^2 values marked with an asterisk indicate a significant correlation between the variables ($p<0.01$).

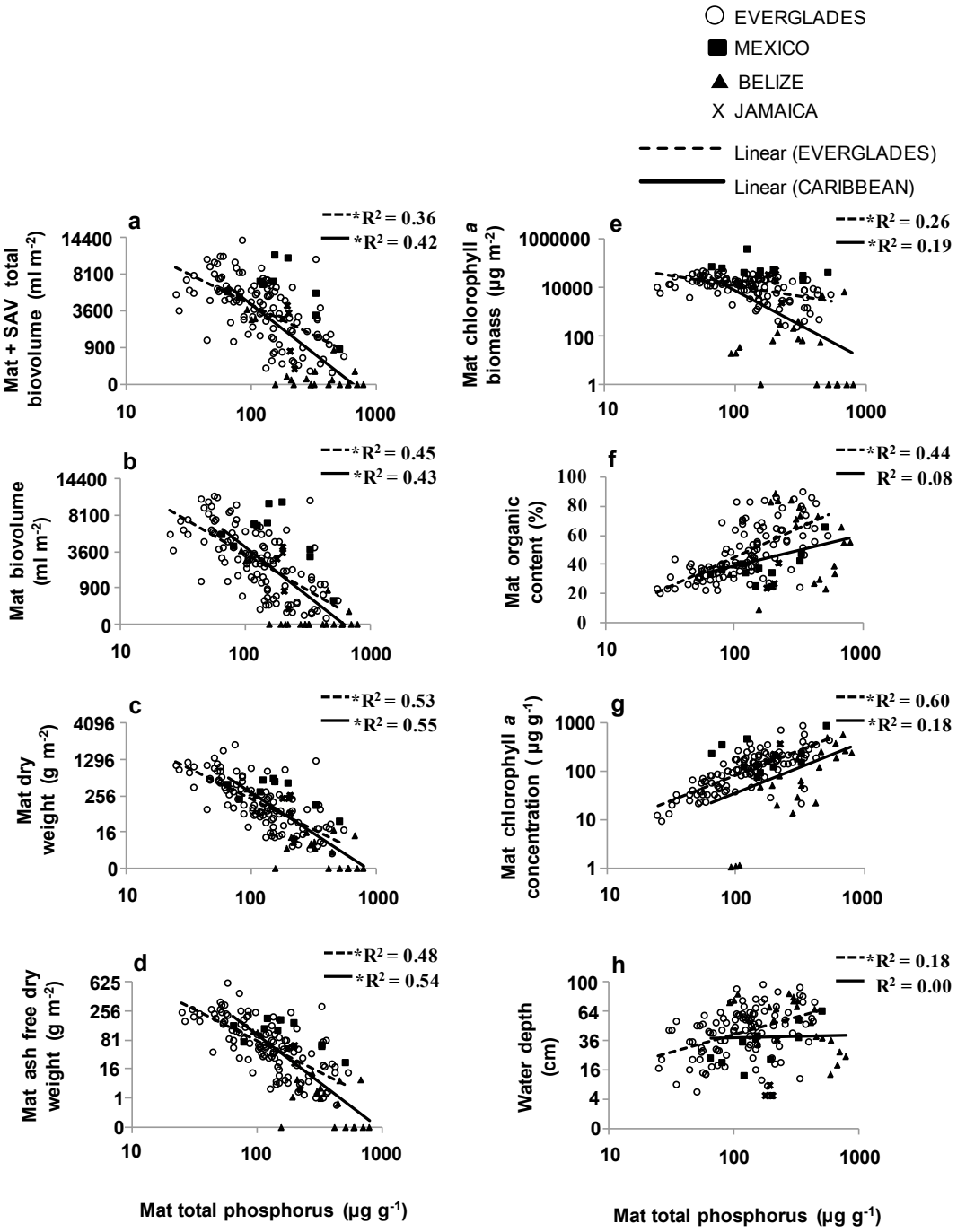

Figure 2-4. Scatterplots showing relationships between periphyton TP and all other measured variables at all sites. Graphs were created using transformed values for each variable. X and Y axes were scaled to facilitate transformed values. Two sets of regression lines, equations and R^2 values are shown. The dashed line describes data from all the Everglades sites and the solid line describes the combined dataset from the Caribbean sites. R^2 values marked with an asterisk indicate a significant correlation between the variables ($p<0.001$).

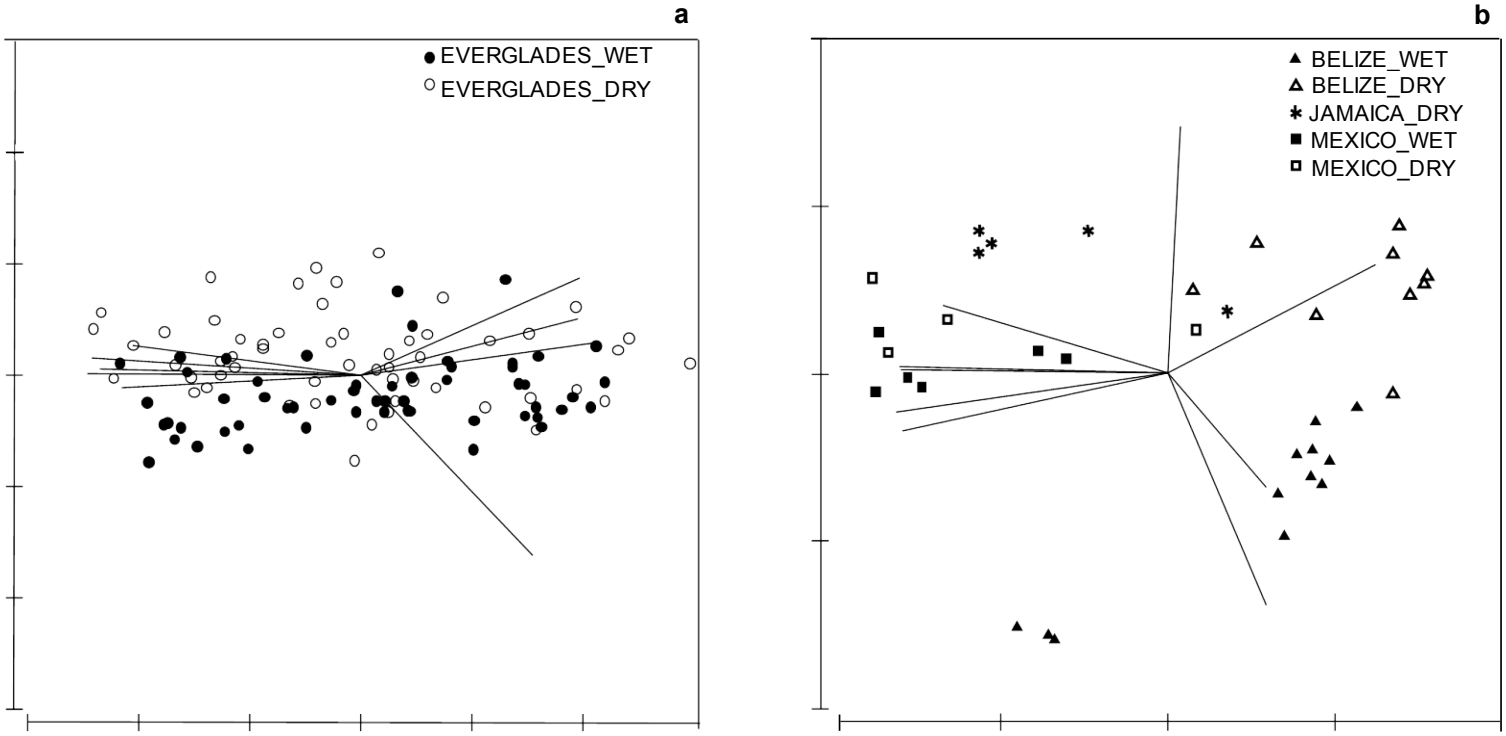

Figure 2-5. Principle component analysis joint plots of Everglades sites (a) and Caribbean sites (including M, B, J data) (b). Vectors on each plot represent the direction and strength of the relationship among environmental variables and periphyton attributes.

CHAPTER III

Diatom species of calcitic periphyton mats from karstic wetland habitats in Belize, Mexico and Jamaica

ABSTRACT

The diatom assemblage associated with calcitic periphyton mats from karstic wetlands in the Everglades is distinct and includes a core group of species that may be considered endemic to this type of habitat. Little is known about the diatom assemblage from similar karstic wetlands throughout the Caribbean and Central American region. This study was therefore conducted to produce a taxonomic inventory of the diatom species of periphyton mats from multiple karstic wetlands within the region.

Diatoms were identified from periphyton mats collected during wet and dry periods from similar shallow, karstic freshwater wetland habitats in Belize, Mexico and Jamaica. A comprehensive species list was produced, along with photomicrographs, morphological descriptions and autecological information for each species.

A total of 146 diatom species representing 39 genera were recorded from the three locations. Twenty eight of these species were found to be present at all three locations and the most common among these (with average abundances greater than 1% at all locations) included *Brachysira neoexilis, Encyonema evergladianum, Encyonema* spp., *Fragilaria syngrotesca, Mastogloia smithii* var. *lacustris, Mastogloia smithii, Navicula cryptotenella, Nitzschia palaea* and *Nitzschia serpentiraphe*.

INTRODUCTION

Throughout the Caribbean and Central American region, freshwater karstic wetlands occur as expanses of inundated coastal and inland plains, underlain by ancient limestone bedrock. The natural variation in topography and hydrology across these wetland landscapes produces a patchwork of habitat types, including extensive shallow, marl-based marshes, which are characterized by low water phosphorus (P) concentrations (<10 μg L^{-1}), a distinctive macrophyte community and the prolific growth of calcitic, cyanobacterial mats (Browder *et al*., 1994; Gunderson, 1994; Rejmánková and Komárková, 2000; Novelo and Tavera, 2003; Gaiser *et al*., 2006).

These consolidated mats are referred to as "periphyton mats" because of their tendency to grow as attached masses on benthic substrates, as well as submerged and floating vegetation (Van-Meter Kasanof, 1973; Browder, 1982; Figure 3-1). Filamentous cyanobacteria (primarily *Schizothrix* spp. and *Scytonema* spp.) dominate the periphyton mat assemblage, forming an interwoven structure in which diatoms, green algae, desmids, heterotrophic bacteria and fungi grow amid polysaccharide mucilage strands and interstitial deposits of calcium carbonate (Van Meter-Kasanof, 1973; Swift and Nicholas, 1987; Donar *et al*., 2004; Stal, 2000; Rejmánková and Komárková, 2000).

Periphyton mat ecology has been most intensely studied in the southern Florida Everglades, an approximately 5,000 km^2 karstic wetland system in which anthropogenic alterations to hydrological regimes and water quality have prompted investigations into the use of periphyton mats as indicators of environmental stress and recovery (McCormick and Stevenson1998; Noe and Childers, 2007; Gaiser *et al*., 2004). Within

this system, periphyton mats have been noted for their large standing crop and high productivity (Browder *et al*., 1994; Goldsborough and Robinson, 1996; Ewe *et al*., 2006; Gaiser, 2009), as well as their importance as a food source for microinvertebrates, macroinvertebrates and fish, (Williams and Trexler, 2006; Liston *et al*., 2008). As biogeochemical regulators, periphyton mats also facilitate the deposition of calcium carbonate throughout the system, influence the production of detrital floc (Neto *et al*., 2006) and are responsible for diurnal and annual changes in water chemistry (McCormick *et al*., 2001; Munyon, in prep.). Because the Everglades is an extremely oligotrophic system in which phosphorus (P) is the main limiting nutrient (Noe *et al*., 2001), the rapid uptake and assimilation of P by periphyton mats is also of particular importance (McCormick and Scinto, 1999; Scinto and Reddy, 2003). In the Everglades elevated periphyton mat TP concentrations serve as a reliable metric of TP inputs to the system (Gaiser *et al*., 2005) and anomalous decreases in overall periphyton mat mass and increases in organic content in response to elevated TP concentrations, serve as early indicators of nutrient enrichment (Pan *et al*., 2000; McCormick *et al*., 2001; Gaiser *et al*., 2006).

Within the Everglades, diatoms have been identified as being a particularly important periphyton mat component, contributing to both mat form and function. The organic matrix of mucopolysaccharide threads produced by certain species of attached and motile diatoms (e.g. *Gomphonema* spp. and *Mastogloia smithii*) encourages periphyton mat cohesion and, along with cyanobacterial mucilage sheaths, aid in resistance to mat desiccation (Azim and Asaeda, 2005; Donar *et al*., 2004; Thomas *et al*., 2004; Gaiser *et al*., 2010). The copious production of glycocalyx also serves as an

extracellular organic reservoir of nutrients that may sustain microbial activity under oligotrophic conditions and stimulate microbial heterotrophic activity following extended periods of desiccation (Gaiser *et al*., 2010; Hagerthey *et al*., in press).

Taxonomic studies have identified a distinctive assemblage of Everglades diatom species (including *Brachysira neoexilis, Encyonema evergladianum, Encyonema* spp., *Fragilaria syngrotesca, Mastogloia smithii* var. *lacustris, Mastogloia smithii, Navicula cryptotenella, Nitzschia palaea* and *Nitzschia serpentiraphe*) that has not been reported from other habitat types and is possibly endemic to subtropical/tropical freshwater karstic wetlands (Slate and Stevenson, 2000 and 2007; Gaiser *et al*., 2006). Many of these species exhibit a low tolerance for nutrient enrichment (McCormick *et al*., 1996; Cooper *et al*., 1999; Slate and Stevenson, 2007) and under enriched conditions, the endemic diatom assemblage is replaced by one dominated by 'weedy' benthic taxa (Swift and Nicholas, 1987; Grimshaw *et al*., 1993; McCormick and O'Dell, 1996; Pan *et al*., 2000). The established relationship between periphytic diatom assemblage and TP has been used to develop diatom based calibration models to infer water (Slate and Stevenson, 2007), soil (Cooper *et al*., 1999) and periphyton mat (Gaiser *et al*., 2006) TP concentrations within the Everglades, as well as indicate past environmental conditions and identify anthropogenically driven changes to the system using paleoecological techniques (Slate and Stevenson, 2000).

Very little work has been conducted on periphyton mats from other karstic wetland habitats within the region. However, from the few studies which have been done, it is known that in these systems, patterns of P uptake by periphyton mats (Rejmánková and Komárková, 2005) and changes in mat biomass in response to P

enrichment (La Hée *et al*., in prep.) are consistent with patterns identified in the Everglades. In addition, one survey of diatom assemblages from periphyton mats in the El Eden Ecological Reserve in Quintana Roo, Mexico, (Novelo *et al*., 2007; Ibarra *et al*., 2009) has identified diatom species representative of the distinctive core assemblage characteristic of Everglades periphyton mats. These findings confirm the similarity among these systems and help to further characterize the anomalous relationship between periphyton mat attributes and eutrophication, which though previously thought to be unique to the Everglades, now seems to be typical of tropical/sub-tropical karstic wetland systems in this region. Furthermore, these studies provide information which suggests that diatom-based inference models, such as those developed within the Everglades, may be a useful tool for tracking environmental changes within these systems.

The development of useful inference models is contingent on the availability of taxonomic and ecological information for the region of interest. At present, however, there is a pervasive lack of such information throughout much of the Caribbean and Central American region. The main aim of this study is therefore to supplement the body of information currently available for this region by providing a taxonomic inventory of the diatom species of periphyton mats from wetlands in Belize, Mexico, Jamaica. A comprehensive species list for three Caribben karstic wetlands is herein presented, along with photomicrographs, morphological descriptions and autecological information for each species. This information may be used in future studies as a basis for developing site-specific, diatom-based environmental inference models.

SITE DESCRIPTION

Sampling was conducted in three wetland systems, similar with respect to geology, climate, hydrology and vegetation, located within the northern Caribbean Basin: the Sian Ka'an Biosphere Reserve (and areas to the south), in Quintana Roo, Mexico; the New River Lagoon in Orange Walk, Belize; and the Broad River, in the Black River Morass, St. Elizabeth, Jamaica (Figure 3-2, Table 3-1).

The Sian Ka'an Biosphere Reserve and the wetlands extending beyond its boundary to the south, encompass a 6500 km^2 area along the south eastern coast of the Yucatan Peninsula in Quintana Roo, Mexico (Cairns *et al*., 2005). The Yucatan peninsula is an uplifted marine platform which extends from the greater Yucatan platform and serves as a divide between the Gulf of Mexico and the Caribbean Sea. The geological formation is a 2 to 3 km thick sequence dominated by limestone, with intermittent layers of dolomite, anhydrite and gypsum (Weidie, 1985). The karstic wetland marshes located within the Yucatan region are dominated by low phosphorus, inland freshwater, marl based habitats and coastal mesohaline habitats. The most common freshwater macrophytic species include *Cladium jamaicense* (sawgrass)*, Eleocharis* spp. (spikerush) and *Typha domingensis* (southern cattail), each of which tends to become dominant at low, intermediate and high water depths, respectively (Rejmánková *et al*., 1996). Dwarfed populations of *Rhizophora mangle* (red mangrove) become more abundant as salinity levels increase, and form the dominant tree species in the coastal brackish water marshes. Calcitic periphyton mats are abundant in both freshwater and brackish water habitats with marl substrates (Rejmánková *et al*., 1996). Inland sampling sites were

confined to freshwater, *Eleocharis* spp. Marshes, and closer to the coast, brackish water sites dominated by dwarf *Rhizophora mangle* were sampled.

The New River Lagoon, located in the district of Orange Walk to the north of Belize, is an approximately 23 km long and 750 m wide stretch of the New River, which is the longest river contained entirely within Belize (Meerman, 2006). The area lies just to the southeast of the basal portion of the Yucatan peninsula and exhibits geological features similar to the adjacent landmass (Weidie, 1985). The New River Lagoon is flanked by marshes dominated mainly by *Cladium jamaicense, Eleocharis cellulosa* and *Eleocharis interstincta*, with intermittent deeper pools supporting dense assemblages of *Nymphea ampla* (dotleaf waterlilly). Sampling sites in this area were again confined to *Eleocharis* spp. marshes adjacent to the lagoon.

The Black River Morass encompasses the largest wetland and river system within the Greater and Lesser Antillean archipelago (Davis *et al*., 1998; Massa and Haynes-Sutton, 1998). It lies within the Black River Basin, which occupies an area of approximately 1,488 km^2 in the south-western region of Jamaica. The area is divided into two main sections: the Upper and Lower Morass. The Upper Morass is approximately 97 km^2 (Cronberg, 1983) and is composed of a mass of swampy lowlands with limestone bedrock covered by peat deposits. The Lower Morass which is approximately 57 km^2 (Enell, 1984), exists as an area of down-faulted, poorly karstified limestone, overlain by a relatively thin clay and peat sequence. Inland marsh areas display mixed vegetation dominated by *Cladium jamaicense* and *Eleocharis* spp., with large stands of *Typha domingensis* being present in some areas (Azan and Webber, 2007). Closer to the coast, assemblages dominated by *Rhizophora mangle* are prevalent

and these trees can also be found bordering the main waterways as they meander through the wetland system. Sampling sites were located within *Cladium jamaicense* and *Eleocharis* marshes bordering the Broad River, a major tributary of the Black River.

METHODS

Sample collection

Each of the Caribbean study locations was visited on two occasions; once during a wet period and once during a dry period. As a result of abnormal seasonal rainfall patterns during the study period, wet and dry *periods* did not necessarily coincide with the typical regional wet and dry *seasons*. "Wet" and "dry" designations were therefore applied on the basis of rainfall levels at each location during the sampling period, relative to typical wet and dry seasonal rainfall levels. The Everglades samples were collected during October to December, 2005 (Wet period) and September to December, 2006 (Dry period) as part of the periphyton component of the CERP seasonal sampling regime. The Mexico sites were visited in December 2006 (Wet period) and March 2008 (Dry period), the Belize sites in May 2007 (Dry period) and November 2007 (Wet period), and the Jamaica sites in December, 2007 (Wet period) and May 2008 (Dry period). Efforts were made to conduct sampling at as many sites as possible, however during dry periods the number of sites sampled varied according to the ability to locate areas that sustained water levels greater than 5cm. During wet periods, sampling efforts were contingent on the ability to gain access to sites, and were then limited to sites that did not exceed water depths of approximately 1m.

At each location, sampling sites were limited to three main types of wetland areas: (i) marshes dominated by *Eleocharis* spp. and/or *Nymphaea* spp., (ii) marshes dominated by *Cladium jamaicense* and (iii) swamps dominated by dwarf *Rhizophora mangle*. At each site, GPS coordinates were recorded and sampling was then conducted using a 1-m^2 throw trap to delineate a 1-m^2 area which was treated as a sample plot (Kushlan, 1981). Periphyton mat samples were collected from four plots at each site. At each plot a photograph was taken to record the surface view, and water depth, pH and conductivity were recorded. Periphyton mat material was then collected by hand, placed onto a seine net and coarsely sorted to remove animals, plant material and marl. A subsample of 120 ml was removed from the periphyton material, placed in a sterile sample bag and stored in a cooler with ice for transport to the lab. When no observable calcitic periphyton mats were present, epipelon was sampled from the benthos and epiphytic films were scraped from any macrophytes present.

Sample processing

In the laboratory, each sample was transferred to a clean 500-ml beaker to which an additional 20 ml of distilled water was added to facilitate homogenizing. From the homogenized total volume, a 50-ml sub-sample was removed, poured into a labelled 120-ml sample cup and placed in a drying oven at 80°C until completely dry. The dried contents were then ground using a mortar and pestle and analyzed for TP following the methods of Solórzano and Sharp (1980). An additional 10-ml sub-sample was removed and processed for quantitative diatom analysis, using the sulphuric acid oxidation method of Hasle and Fryxell (1970). A measured amount of cleaned/processed material was then

pipetted unto a glass coverslip and permanently fixed to a glass slide using Naphrax ® mounting medium.

Taxonomic identification

A minimum of 500 diatom valves were counted along random transects on each slide at a magnification of X 1000, using a Nikon Eclipse E600 ® compound light microscope. Diatom species identification was done using standard available taxonomic reference sources, as well as reference materials archived at the Ruth Patrick Centre at the Philadelphia Academy of Sciences, Pennsylvania, U.S.A.

Environmental information and community analyses

Maximum, minimum and average values for water depth, pH and conductivity were calculated separately for wet and dry periods for each location. Prior to statistical analysis, periphyton mat TP (TP μg P g^{-1} dry mass) data were log10 transformed and diatom percentage abundance data were fourth root transformed to satisfy assumptions of normality (Clarke and Gorley, 2001).

Average per-site species richness and Shannon-Weiner diversity were calculated for each location, and differences within and among locations were tested for using ANOVA, followed by Tukey's test, using the SPSS ® statistical package. The program C2 (Juggins, 2003) was used to determine TP optima and tolerance levels for diatom species present at all three locations and Indicator species analysis (done using the program PCORD 5 ®; McCune and Grace, 2002) was conducted to identify species that effectively indicated either "high" or "low" TP concentrations.

RESULTS AND DISCUSSION

Habitat characterization

Habitat characteristics among the sampled locations overlapped, with most sites being dominated by *Eleocharis* spp. growing in shallow (<1m) marl based soils, inundated by circumneutral waters. Among all three locations, average pH ranged from 7.2 to 9.2 and average conductivity ranged from 441.8 to 15,047.7 $\mu S\ cm^{-1}$ (Table 3-2). Some sites within two areas at the Mexico location (Mahahual and Marisma) were closer to the coast and supported a macrophytic assemblage dominated by *Rhizophora mangle* and *Eleocharis* spp. At these sites average pH and conductivity levels were greater than all other sites (Table 3-2), which is a result of the influx of brackish-water at these sites. During the dry period sampling session at the Belize location, the interior marsh areas were completely dry and inaccessible. Sampling was therefore limited to *Eleocharis* spp. marshes bordering the New River Lagoon, where, prior to the dry season, lagoonal waters with elevated TP could have advanced into these peripheral marshes.

Diatom community analyses

A total of 148 diatom species representing 39 genera were recorded from the three locations. Twenty eight of these species were found to be present at all three locations and the most common among these (with average abundances greater than 1% at all locations) included *Brachysira neoexilis, Encyonema evergladianum, Encyonema* spp., *Fragilaria syngrotesca, Mastogloia smithii* var. *lacustris, Mastogloia smithii, Navicula cryptotenella, Nitzschia palaea* and *Nitzschia serpentiraphe* (Table 3-3).

Average, per-sample species richness at the Belize, Mexico and Jamaica locations was 18.5, 18.7 and 21.9 respectively, and the average per-sample species diversity at these locations was 1.66, 2.00 and 2.01 respectively (Table 3-4). The TP optima and tolerance levels were determined for the 28 species common to all locations and using the combined Caribbean dataset, 12 indicator species were identified, 3 of which were indicative of low mat TP concentrations (*Encyonema evergladianum, Amphora sulcata* and *Nitzschia tubicola*) and 9 of which indicated high mat TP concentrations (*Achnanthidium neomicrocephalum, Eunotia flexuosa, Gomphonema* cf. *vibriodes, Eunotia camelus, Eunotia* cf. *karenae, Achnanthidium* sp. 2*, Achnanthidium exiguum, Synedra acus* var. *angustissima* and *Nitzschia scalaris*) (Table 3-3).

Annotated list of diatom taxa from Belize, Mexico and Jamaica sites

Taxonomic information for each diatom identified in this study includes the genus and species name, as well as variety or form if known, and the recognized author. Published reference literature used for the identification of each taxon is provided, along with any taxonomic synonyms used in the reference material. Taxa for which no adequate reference could be found are described using diatom valve length, width and striae count of cells observed in the current study. Information regarding the average abundance of taxa at each location is given in Table 3-3, where designations of rare (<1%), uncommon (1 to <5%), common (5 to <20%) and abundant (>20%) are given. All photomicrographs presented in the following plates were taken at 1000X and the scale bar in the lower right corner of each plate represents 10 μm. Photomicrographs of very large diatoms were sized independent of the other photomicrographs on the same

plate and a separate scale bar was included directly below the photomicrograph, again representing 10 μm.

Achnanthidium exiguum (Grunow) Czarnecki (Plate: 1 Figure: 5)

Synonyms: *Achnanthes exigua* Grunow var. *exigua.*

Literature: Krammer and Lange-Bertalot (2004), pp. 295 [Plate: 23; Figure: 6-7]; Novelo *et al*., (2007), pp. 97 [Plate: 4; Figure 3a –b].

Remarks: This species was identified as an indicator of high periphyton mat TP concentration.

Achnanthidium inflatum (Kützing) Hutton (Plate: 1 Figure: 1)

Synonyms: Achnanthes inflata (Kützing) Grunow

Literature: Krammer & Lange-Bertalot (1991) pp. 253 [Plate: 2; Figure: 9 – 10]; Podzorski (1985) pp. 97 [Plate 4; Figure: 13 – 15]

Achnanthidium neomicrocephalum H. Lange-Bertalot & F. Staab (Plate: 1 Figure: 2)

Synonyms: Achnanthidium minutissimum (Kützing) Czarneki; Achnanthidium minutissimum var. gracillima (Meister) Lange- Bertalot; Achnanthes minutissima Kützing; Achnanthes microcephala (Kützing) Grunow

Literature: Krammer and Lange-Bertalot (2004), pp. 450 [Plate: 89; Figure: 1-10]; Novelo *et al*., (2007), pp. 97 [Plate: 4; Figure 4a –b, 5a-c]; Podzorski (1985) pp. 99 [Plate 5; Figure: 1 – 6]

Remarks: This species exhibited a TP optimum and tolerance of 442 µg P g^{-1} dry mass and 33 µg P g^{-1} dry mass respectively and was identified as an indicator of high periphyton mat TP concentration.

Achnanthidium sp.1 (Plate: 1 Figure: 3)

Synonyms: *Achnanthes marginulata* Grunow

Literature: Podzorski (1985) pp. 97 [Plate 4; Figure: 19 – 21]

Remarks: Length: 10-17 µm Width: 2-4 µm Striae: 36/10 µm.

Actinocyclus normanii (Gregory ex Greville) Hustedt (Plate: 12 Figure: 5)

Literature: Krammer & Lange-Bertalot (1991) pp. 395 [Plate 82; Figure: 1]

Remarks: Width: 46-80 µm Punctae: 8-9/10 µm Extended rimoportulae: 10-14

Amphora cymbifera var. *heritierarum* Wachnicka & Gaiser (Plate: 17 Figure: 10)

Literature: Wachnicka and Gasier, (2007) pp. 395 [Figure 7-8]

Amphora sulcata (Brébisson) Cleve (Plate: 17 Figure: 11)

Literature: Wachnicka and Gaiser (2007) pp. 420 [Figure 113 – 115]

Remarks: This species was identified as an indicator of low periphyton mat TP concentration.

Amphora sp.2 (Plate: 17 Figure: 3)

Remarks: Length: 70 µm Width: 10 µm Striae: 12/10 µm.

Amphora sp.3 (Plate: 17 Figure: 4)

Remarks: Length: 70 µm Width: 20 µm Striae: 9/10 µm.

Amphora copulata (Kützing) Schoeman & Archibald (Plate: 17 Figure: 8)

Literature: Wachnicka & Gaiser (2007) pp. 434 [Figure 172 - 173]

Amphora corpulenta var. *capitata* Tempere et Peragallo (Plate: 17 Figure: 9)

Literature: Wachnicka & Gaiser (2007) pp. 409 [Figure 63]

Amphora pseudoproteus Wachnicka & Gaiser (Plate: 17 Figure: 1, 2 and 7)

Literature: Wachnicka & Gaiser (2007) pp. 434 [Figure 180 - 182]

Anomoneis sphaerophora (Ehrenberg) Pfitzer (Plate: 13 Figure: 1-2)

Literature: Metzeltin & Lange-Bertalot (2007) pp.626 [Plate 178A; Figure: 2, 4]; Krammer & Lange-Bertalot (1997) pp. 625 [Figure: 92: 1 – 2]; Podzorski (1985) pp. 97 [Plate 8; Figure: 3]

Aulacoseira ambigua (Grunow) Simonsen (Plate: 1 Figure: 17)

Literature: Krammer & Lange-Bertalot (1991) pp. 273 [Plate 21: Figure 8 – 11]

Aulacoseira granulata (Ehrenberg) Simonsen (Plate: 1 Figure: 18)

Literature: Krammer & Lange-Bertalot (1991) pp. 265 [Plate 17: Figure 4]

Brachysira estonarium Witkowski, Lange-Bertalot & Metzeltin (Plate: 1 Figure: 10)

Literature: Witkowski, Lange-Bertalot & Metzeltin (2000) pp 711 [Plate: 134 Figure 1 – 3]

Remarks: Length: 21-34.5 μm Width: 4.5-5.5 μm, Striae not discernable

Brachysira brebissonii Ross (Plate: 1 Figure: 9)

Literature: Lange-Bertalot & Moser (1994) pp. 185 [Figure 1 – 18]

Brachysira cf. *hofmanniae* Lange-Bertalot (Plate: 2 Figure: 1)

Literature: Lange-Bertalot & Moser (1994) pp. 119 [Figure 1 - 6]

Remarks: Length: 27-56 μm Width: 7.5-8.5 μm, Striae not discernable

Brachysira neoexilis Lange-Bertalot (Plate: 1 Figure: 8)

Synonyms: Anomoeoneis vitrea (Grunow) Ross

Literature: Lange-Bertalot & Moser (1994) pp. 117 [Figure 1 – 7]; pp. 119 [Figure 19 – 22]; Podzorski (1985) pp. 105 [Plate 8; Figure: 4 – 6]

Remarks: The occurrence of this species overlapped with that of *Brachysira procera* and *Brachysira pumila* at multiple sites. The gradation in the range of sizes and froms led to the consideration of these three taxa as morphs of the same species. They were therefore lumped during analyses and together displayed a TP optimum and tolerance of 273 μg P g^{-1} dry mass and 32 μg P g^{-1} dry mass respectively.

Brachysira procera Lange-Bertalot & Moser (Plate: 2 Figure: 2)

Literature: Lange-Bertalot & Moser (1994) pp. 117 [Figure 8 – 12; 20 – 24]

Remarks: The occurrence of this species overlapped with that of *Brachysira neoexilis* and *Brachysira pumila* at multiple sites. The gradation in the range of sizes and froms led to the consideration of these three taxa as morphs of the same species. They were therefore lumped during analyses and together displayed a TP optimum and tolerance of 273 µg P g^{-1} dry mass and 32 µg P g^{-1} dry mass respectively.

Brachysira pumila Metzeltin & Lange-Bertalot (Plate: 1 Figure: 11)

Literature: Metzeltin & Lange-Bertalot (1998) pp. 439 [Plate 102; Figure 13-17]

Remarks: The occurrence of this species overlapped with that of *Brachysira procera* and *Brachysira neoexilis* at multiple sites. The gradation in the range of sizes and froms led to the consideration of these three taxa as morphs of the same species. They were therefore lumped during analyses and together displayed a TP optimum and tolerance of 273 µg P g^{-1} dry mass and 32 µg P g^{-1} dry mass respectively.

Caloneis sp.1 (Plate: 4 Figure: 8)

Synonyms: *Caloneis bacillum* (Grunow) Cleve

Literature: Podzorski (1985) pp113 [Plate 12; Figure: 14]

Remarks: Length: 27-45 µm Width: 6-9 µm Striae: 28/10 µm

Caloneis sp.2 (Plate: 4 Figure: 10)

Synonyms: *Caloneis bacillum* (Grunow) Cleve

Literature: Podzorski (1985) pp113 [Plate 12; Figure: 15]

Remarks: Length: 39 µm Width: 9 µm Striae: 22/10 µm

Caloneis sp.3 (Plate: 4 Figure: 11)

Synonyms: *Caloneis bacillum* (Grunow) Cleve

Literature: Podzorski (1985) pp113 [Plate 12; Figure: 16]

Remarks: Length: 32 µm Width: 8.5 µm Striae: 21/10 µm

Caponea caribbea Podzorski (Plate: 4 Figure: 7)

Literature: Podzorski (1985) pp113 [Plate 12; Figure: 5 – 7]

Cocconeis placentula Ehrenberg

Literature: Podzorski (1985) pp 97 [Plate 4; Figure: 1 – 3]

Craticula cuspidata (Kützing) Mann (Plate: 11 Figure: 3)

Literature: Metzeltin & Lange-Bertalot (1998) pp. 427 [Plate 96; Figure 3]

Craticula sp.1 (Plate: 12 Figure: 2)

Remarks: Length: 225-228 µm Width: 50-51 µm Striae: 12-14/10 µm

Cyclotella meneghiniana Kützing (Plate: 2 Figure: 4)

Literature: Tanaka (2007) pp 121 [Figure 1a – 7b]

Remarks: This species displayed a TP optimum and tolerance of 289 µg P g^{-1} dry mass and 29 µg P g^{-1} dry mass respectively.

Cyclotella litoralis Lange & Syvertsen (Plate: 2 Figure: 3)

Literature: Tanaka (2007) pp 111 [Figure 1a – 4b]

Remarks: Width: 23.5-31 µm Striae: 9/10 µm Punctae: 6-8

Cyclotella cf. *atomus* var. *gracilis* Genkil & Kiss (Plate: 2 Figure: 5)

Literature: Tanaka (2007) pp 83 [Figure 1a – 3b]

Cyclotella sp.1 (Plate: 2 Figure: 6)

Remarks: Width: 4-5 µm Striae: 14/5 µm

Cymbella aspera (Ehrenberg) Cleve (Plate: 10 Figure: 3)

Synonyms: *Cymbella aspera* (Ehrenberg) Peragallo

Literature: Krammer & Lange-Bertalot (1997) pp. 705 [Figure 131: 2 -3]

Diploneis oblongella (Naegeli ex Kuetzing) Ross (Plate: 7 Figure: 6)

Literature: Krammer & Lange-Bertalot (1997) pp. 658 [Figure 108: 9 - 10]

Remarks: Length: 19-23 µm Width: 8 µm Striae: 20/10 µm.

This species displayed a TP optimum and tolerance of 225 µg P g^{-1} dry mass and 27 µg P g^{-1} dry mass respectively.

Diploneis parma Cleve (Plate: 7 Figure: 2 and 5)

Remarks: Length: 24-42.5 µm Width: 17-21 µm Striae: 12-14/10 µm Areolae: 16-18/10 µm. This species exhibited a TP optimum and tolerance of 235 µg P g^{-1} dry mass and 30 µg P g^{-1} dry mass respectively.

Diploneis cf. *elliptica* var. *tropica* Frenguelli (Plate: 7 Figure: 1)

Literature: Metzeltin, D., H. Lange-Bertalot, and F. García Rodríguez (2005) pp. 471 [Plate 113; Figure 5 - 8]

Diploneis elliptica (Plate: 5 Figure: 6)

Literature: Krammer (1997) pp. 659 [Plate: 108; Figure: 14 – 15]

Remarks: Length: 37-65 µm Width: 24-29.5 µm Striae: 10-12/10 µm Areolae: 16/10

Diploneis sp.2 (Plate: 5 Figure: 7)

Diploneis sp.5 (Plate: 7 Figure: 3)

Remarks: Length: 43-46 µm Width: 19-22 µm Striae: 13-14/10 µm Areolae: 8-9/10

Diploneis sp.6 (Plate: 7 Figure: 4)

Remarks: Length: 28-48 µm Width: 17-23 µm Striae: 11-12/10 µm

Diploneis cf. *finnica* (Plate: 16 Figure: 5)

Literature: Krammer & Lange-Bertalot (1997) pp. 663 [Figure 110: 1 - 2]; Hustedt (1959) pp. 561 [Figure: 1064]

Remarks: Length: 70-75 µm Width: 41-44 µm Striae: 8-9/10 µm Areolae: 16/10

Encyonema evergladianum Krammer (Plate: 4 Figure: 3)

Literature: Krammer (1997) pp. 333 [Plate: 142; Figure: 1 – 7]

Remarks: Length: 12-30 µm Width: 4-5 µm Striae: 20-24/10 µm. This species exhibited a TP optimum and tolerance of 229 µg P g^{-1} dry mass and 28 µg P g^{-1} dry mass respectively and was indicative of low periphyton mat TP concentration.

Encyonema jemtlandicum var. *venezolanum* Krammer (Plate: 14 Figure: 3-4)

Literature: Krammer (1997) pp. 208; pl. 14, fig. 1 – 3

Encyonema silesiacum (Bleisch) Mann (Plate: 14 Figure: 2)

Literature: Krammer (1997) pp. 189 [Plate: 4; Figure: 11 – 18]

Encyonema sp.1 (Plate: 14 Figure: 5)

Encyonema sp.2 (Plate: 14 Figure: 6)

Remarks: The occurrence of this species overlapped with that of *Encyonema* sp. 3 at multiple sites. The gradation in the range of sizes and froms led to the consideration of these two taxa as morphs of the same species. They were therefore lumped during analyses and together displayed a TP optimum and tolerance of 230 µg P g^{-1} dry mass and 27 µg P g^{-1} dry mass respectively.

Encyonema sp.3 (Plate: 14 Figure: 7)

Remarks: The occurrence of this species overlapped with that of *Encyonema* sp. 3 at multiple sites. The gradation in the range of sizes and froms led to the consideration of these two taxa as morphs of the same species. They were therefore lumped during analyses and together displayed a TP optimum and tolerance of 230 µg P g^{-1} dry mass and 27 µg P g^{-1} dry mass respectively.

Encyonema vulgare var. *vulgare* Krammer (Plate: 14 Figure: 1)

Literature: Krammer (1997) pp. 259 [Plate: 39; Figure: 3 – 4]

Encyonopsis microcephala (Grunow) Krammer (Plate: 4 Figure: 5)

Literature: Krammer (1997) pp. 335 [Plate: 143; Figure: 14 – 18]

Remarks: Length: 15.5-22 µm Width: 4-4.5 µm Striae: 26-32/10 µm. This species exhibited a TP optimum and tolerance of 334 µg P g^{-1} dry mass and 25 µg P g^{-1} dry mass respectively.

Encyonopsis subminuta Krammer et Reichardt (Plate: 4 Figure: 14)

Literature: Krammer (1997) pp. 339 [Plate: 144; Figure: 6 – 9]

Remarks: Length: 27 μm Width: 4 μm Striae: 26/10 μm.

Epithemia sp.1 (Plate: 16 Figure: 4)

Eunotia camelus Ehrenberg (Plate: 15 Figure: 9)

Literature: Metzeltin & Lange-Bertalot (1998) pp.293 [Plate: 29; Figure: 1 – 11]

Remarks: This species was identified as an indicator of high periphyton mat TP concentration.

Eunotia cf. *karenae* Metzeltin & Lange-Bertalot (Plate: 15 Figure: 2)

Literature: Metzeltin & Lange-Bertalot (2007) pp. 105 [Plate: 48; Figure: 1 – 4]

Remarks: Length: 121-192 μm Width: 6-7 μm Striae: 10-12/10 μm Areolae: 28/10 μm. This species was indicative of high periphyton mat TP concentration.

Eunotia cf. *yberai* Frenguelli (Plate: 15 Figure: 12)

Literature: Metzeltin, Lange-Bertalot & García Rodríguez (2005) pp.289 [Plate: 22; Figure 1 – 4]

Eunotia flexuosa (Brébisson) Kützing (Plate: 15 Figure: 5)

Literature: Krammer & Lange-Bertalot (1991) pp. 511 [Plate: 140; Figure: 9]

Remarks: This species exhibited a TP optimum and tolerance of 368 µg P g^{-1} dry mass and 25 µg P g^{-1} dry mass respectively and was indicative of high periphyton mat TP concentration.

Eunotia implicata Nörpel, Lange-Bertalot & Alles (Plate: 15 Figure: 7)

Literature: Krammer & Lange-Bertalot (1991) pp. 517 [Plate: 143; Figure: 1 – 9]

Eunotia cf. *monodon* Ehrenberg (Plate: 15 Figure: 3)

Literature: Metzeltin, Lange-Bertalot & García Rodríguez (2005) pp.291 [Plate: 23; Figure 4 – 5]; Krammer & Lange-Bertalot (1991) pp. 547 [Plate: 158; Figure: 2]

Eunotia naegelii Migula (Plate: 15 Figure: 4)

Literature: Krammer & Lange-Bertalot (1991) pp. 511 [Plate: 140; Figure: 1 – 3]

Eunotia rabenhorstiana var. *elongata* (Patrick) Metzeltin & Lange-Bertalot (Plate: 15 Figure: 1)

Literature: Metzeltin & Lange-Bertalot (1998) pp. 363 [Plate: 64; Figure: 11]

Eunotia botuliformis Wild, Norpel & Lange-Bertalot (Plate: 15 Figure: 11)

Literature: Lange-Bertalot (1993) pp. 230 [Plate: 33; Figure: 2 – 4; 11 – 15]

Eunotia sp.1 (Plate: 15 Figure: 6)

Eunotia sp.2 (Plate: 15 Figure: 8)

Eunotia sp.3 (Plate: 15 Figure: 10)

Fallacia pygmaea (Kützing) Stickle & Mann (Plate: 8 Figure: 5)

Synonyms: *Navicula pygmaea*

Literature: Metzeltin & Lange-Bertalot (1998) pp. 419 [Plate: 92; Figure: 9 - 11]; Podzorski (1985) pp107 [Plate 9; Figure: 6]

Fragilaria (?) sp.1 cf. *famelica* (Kützing) Lange-Bertalot (Plate: 5 Figure: 3)

Literature: Lange-Bertalot (1993) pp. 189 [Plate: 12; Figure: 13]; Krammer & Lange-Bertalot (1991) pp. 453 [Plate: 111; Figure: 6]

Remarks: Length: 44-71 µm Width: 2-2.5 µm Striae: 15-20/10 µm. This species exhibited a TP optimum and tolerance of 263 µg P g^{-1} dry mass and 29 µg P g^{-1} dry mass respectively.

Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot (Plate: 5 Figure: 4)

Literature: Krammer & Lange-Bertalot (1991) pp. 447 [Plate: 108; Figure: 10 - 15]

Fragilaria synegrotesca Lange-Bertalot (Plate: 5 Figure: 2)

Synonyms: *Fragilaria vaucheriae* (Kützing) Petersen

Literature: Lange-Bertalot (1993) pp. 189 [Plate: 12; Figure: 3 – 7]; Podzorski (1985) pp. 91 [Plate: 1; Figure: 13]

Remarks: This species exhibited a TP optimum and tolerance of 266 µg P g^{-1} dry mass and 29 µg P g^{-1} dry mass respectively.

Fragilaria cf. *ulna* (Nitzsch) Lange-Bertalot (Plate: 16 Figure: 2)

Remarks: Length: 180 µm Width: 4 µm Striae: 10/10 µm

Fragilaria ulna var. *ulna* (Nitzsch) Lange-Bertalot (Plate: 16 Figure: 1)

Literature: Krammer & Lange-Bertalot (1991) pp. 475 [Plate: 122; Figure: 1]

Remarks: This species exhibited a TP optimum and tolerance of 281 µg P g^{-1} dry mass and 31 µg P g^{-1} dry mass respectively.

Frustulia rhomboides var. *crassinervia* (Brebisson ex. W. Smith) Ross (Plate: 3 Figure: 3)

Literature: Krammer & Lange-Bertalot (1997) pp. 631 [Figure: 6 - 7]

Gomphonema affine Kützing (Plate: 8 Figure: 4)

Literature: Tobias & Gaiser (2006) pp. 390 [Figure: 10 – 14]

Gomphonema gracile Ehrenberg (Plate: 8 Figure: 3)

Literature: Tobias & Gaiser (2006) pp. 396 [Figure: 48 – 50]

Gomphonema intricatum var. *vibrio* (Ehrenberg) Cleve (Plate: 8 Figure: 2)

Synonyms: *Gomphonema intricatum* var. *vibrio* Ehrenberg sensu Fricke

Literature: Tobias & Gaiser (2006) pp. 396 [Figure: 51 – 62]

Remarks: This species exhibited a TP optimum and tolerance of 329 µg P g^{-1} dry mass and 32 µg P g^{-1} dry mass respectively.

Gomphonema parvulum (Kützing) Grunow (Plate: 8 Figure: 10)

Literature: Tobias & Gaiser (2006) pp. 400 [Figure: 67 – 68]

Gomphonema cf. *vibriodes* Reichardt & Lange-Bertalot (Plate: 8 Figure: 1)

Literature: Tobias & Gaiser (2006) pp. 392 [Figure: 38 – 42]

Remarks: This species exhibited a TP optimum and tolerance of 406 µg P g^{-1} dry mass and 32 µg P g^{-1} dry mass respectively and was indicative of high periphyton mat TP concentration.

Hantzschia cf. *elongata* (Hantzsch) Grunow (Plate: 10 Figure: 2)

Literature: Hustedt (1959) pp. 848 [Figure: 751]; Lange-Bertalot (1993) pp. 385 [Plate: 109; Figure: 1 - 3]; Krammer & Lange-Bertalot (1997) pp. 395 [Plate: 89; Figure: 1 - 2]

Hantzschia spectabilis (Ehrenberg) Hustedt (Plate: 10 Figure: 5)

Literature: Krammer & Lange-Bertalot (1997) pp. 399 [Plate: 91; Figure: 1 - 3]

Hantzschia cf. *vivacior* Lange-Bertalot (Plate: 10 Figure: 4)

Literature: Lange-Bertalot (1993) pp. 374 [Plate: 104; Figure: 1 – 6]

Mastogloia braunii Grunow (Plate: 13 Figure: 4 and 7)

Literature: Krammer & Lange-Bertalot (1997) pp. 845 [Figure: 200:1 - 3]

Mastogloia cf. *smithii* Thwaites ex. W. Smith (Plate: 8 Figure: 9)

Literature: Literature: Krammer & Lange-Bertalot (1997) pp. 847 [Figure: 201: 3 - 5]

Remarks: This species exhibited a TP optimum and tolerance of 240 µg P g^{-1} dry mass and 29 µg P g^{-1} dry mass respectively.

Mastogloia smithii var. *lacustris* Grunow (Plate: 8 Figure: 8)

Literature: Literature: Krammer & Lange-Bertalot (1997) pp. 847 [Figure: 201:1]

Remarks: This species exhibited a TP optimum and tolerance of 239 µg P g^{-1} dry mass and 26 µg P g^{-1} dry mass respectively and was indicative of low periphyton mat TP concentration.

Mastogloia lanceolata Thwaites ex. Smith (Plate: 13 Figure: 6)

Literature: Podzorski (1985) pp. 99 [Plate: 5; Figure: 19 - 20]

Mastogloia elliptica (Agardh) Cleve (Plate: 13 Figure: 9)

Literature: Krammer & Lange-Bertalot (1997) pp. 847 [Figure: 201: 10 – 13]

Mastogloia elliptica var. *dansei* (Thwaites) Cleve (Plate: 13 Figure: 5)

Literature: Krammer & Lange-Bertalot (1997) pp. 849 [Figure: 202: 1 – 2]

Navicella pusilla (Grunow) Krammer (Plate: 3 Figure: 2)

Synonym: *Cymbella pusilla* Grunow

Literature: Krammer & Lange-Bertalot (1997) pp. 738 [Figure: 148: 1 – 9]

Navicula brasiliana (Cleve) Cleve (Plate: 13 Figure: 3)

Synonym: *Naviculadicta brasiliana* (Cleve) Lange-Bertalot

Literature: Krammer & Lange-Bertalot (1997) pp. 545 [Figure: 52: 1 – 2]; Metzeltin & Lange-Bertalot (1998) pp. 421 [Plate: 93; Figure: 6 - 7]

Navicula cf. *radiosa* Kützing (Plate: 3 Figure: 1)

Synonyms: *Navicula lanceolata* (Agardh)

Literature: Krammer & Lange-Bertalot (1997) pp. 499 [Figure: 29: 1 - 2]; Podzorski (1985) pp. 115 [Plate: 13; Figure: 19]; Podzorski (1985) pp. 115 [Plate: 13; Figure: 13]

Remarks: Length: 46-71 μm Width: 7-9 μm Striae: 14/10 μm. This species exhibited a TP optimum and tolerance of 282 μg P g^{-1} dry mass and 35 μg P g^{-1} dry mass respectively and was indicative of low periphyton mat TP concentration.

Navicula constans Hustedt (Plate: 4 Figure: 12)

Literature: Krammer & Lange-Bertalot (1997) pp. 536 [Figure: 48: 10 – 11]

Navicula cryptotenella Lange-Bertalot (Plate: 3 Figure: 4)

Literature: Krammer & Lange-Bertalot (1997) pp. 507 [Figure: 33: 9 - 11]

Remarks: This species exhibited a TP optimum and tolerance of 332 µg P g^{-1} dry mass and 30 µg P g^{-1} dry mass respectively and was indicative of low periphyton mat TP concentration.

Navicula palestinae Gerloff, Natour & Rivera (Plate: 8 Figure: 7)

Navicula pseudocrassirostris Hustedt (Plate: 8 Figure: 6)

Navicula stroemii Hustedt (Plate: 1 Figure: 14)

Literature: Krammer & Lange-Bertalot (1997) pp. 579 [Figure: 69: 1 – 3]

Navicula subtilissima Cleve (Plate: 4 Figure: 13)

Literature: Krammer & Lange-Bertalot (1997) pp. 599 [Figure: 79: 22]

Remarks: This species exhibited a TP optimum and tolerance of 291 µg P g^{-1} dry mass and 35 µg P g^{-1} dry mass respectively and was indicative of low periphyton mat TP concentration.

Neidium ampliatum (Ehrenberg) Krammer (Plate: 4 Figure: 1-2)

Literature: Krammer & Lange-Bertalot (1997) pp. 653 [Figure: 105: 5]

Nitzschia acicularis (Plate: 10 Figure: 6)

Literature: Krammer & Lange-Bertalot (1997) pp. 386 [Plate: 85; Figure: 1 - 3]

Nitzschia amphibia (Grunow) Lange-Bertalot (Plate: 6 Figure: 11)

Literature: Krammer & Lange-Bertalot (1997) pp. 372 [Plate: 78; Figure: 15]

Nitzschia denticula Grunow (Plate: 6 Figure: 9)

Synonyms: *Denticula kuetzingii* Grunow

Literature: Lange-Bertalot (1993) pp. 407 [Plate: 120; Figure: 1 - 2]

Nitzschia lacunarum Hustedt (Plate: 10 Figure: 7)

Literature: Krammer & Lange-Bertalot (1997) pp. 324 [Plate: 54; Figure: 4]

Nitzschia microcephala Grunow (Plate: 6 Figure: 7)

Literature: Krammer & Lange-Bertalot (1997) pp. 382 [Plate: 83; Figure: 16]

Remarks: Length: 13.5-16.5 µm Width: 3-4 µm Striae: 13-14/10 µm.

Nitzschia nana Grunow (Plate: 10 Figure: 9)

Literature: Krammer & Lange-Bertalot (1997) pp. 250 [Plate: 17; Figure: 5,7]

Nitzschia palaea (Kutzing) Smith (Plate: 6 Figure: 5-6)

Literature: Krammer & Lange-Bertalot (1997) pp. 334 [Plate: 59; Figure: 3]

Remarks: This species exhibited a TP optimum and tolerance of 222 µg P g^{-1} dry mass and 24 µg P g^{-1} dry mass respectively.

Nitzschia scalaris (Ehrenberg) Smith (Plate: 6 Figure: 1)

Literature: Krammer & Lange-Bertalot (1997) pp. 266 [Plate: 25; Figure: 1 - 4]

Remarks: This species was indicative of high periphyton mat TP concentration.

Nitzschia semirobusta Lange-Bertalot (Plate: 6 Figure: 10)

Literature: Lange-Bertalot (1993) pp. 407 [Plate: 120; Figure: 3 - 19]

Nitzschia serpentiraphe Lange-Bertalot (Plate: 6 Figure: 2)

Literature: Lange-Bertalot (1993) pp. 419 [Plate: 126; Figure: 1-7]

Remarks: This species exhibited a TP optimum and tolerance of 180 µg P g^{-1} dry mass and 18 µg P g^{-1} dry mass respectively and was indicative of low periphyton mat TP concentration.

Nitzschia sp.1 (Plate: 6 Figure: 8)

Remarks: Length: 21µm Width: 2 µm Striae: 13/5 µm

Nitzschia thermalis var. *minor* Hilse (Plate: 10 Figure: 10)

Literature: Hustedt (1959) pp. 857 [Figure: 772]

Nitzschia obtusa var. *kurzii* Rabenhorst ex Cleve & Moller (Plate: 17 Figure: 6)

Synonym: *Nitzschia obtusa* var. *lata* Hagelstein

Literature: Krammer & Lange-Bertalot (1997) pp. 251 [Plate: 17; Figure: 3]; Podzorski (1985) pp 137 [Plate 24; Figure: 1]

Nitzschia linearis var. *subtilis* (Grunow) Hustedt (Plate: 6 Figure: 3-4)

Synonym: *Nitzschia subtilis* Grunow

Literature: Krammer & Lange-Bertalot (1997) pp. 327 [Plate: 55; Figure: 8]; Podzorski (1985) pp 138 [Plate 25; Figure: 15]

Remarks: This species was indicative of low periphyton mat TP concentration.

Parlibellus sp.1 (Plate: 12 Figure: 2)

Pinnularia acrosphaeria (Brébisson) W. Smith (Plate: 9 Figure: 10)

Literature: Krammer & Lange-Bertalot (1997) pp. 807 [Figure: 181:3]

Pinnularia cf. *neomajor* var. *inflata* Krammer (Plate: 9 Figure: 1)

Literature: Metzeltin & Lange-Bertalot (2007) pp. 721 [Plate: 225; Figure: 4]; Krammer (2000) pp 602 [Plate 171; Figure: 2]

Remarks: Length: 181 µm Width: 27 µm Striae: 8/10 µm

Pinnularia sp.1 (Plate: 9 Figure: 3)

Remarks: Length: 121µm Width: 16 µm Striae: 8/10 µm

Pinnularia sp.2 (Plate: 9 Figure: 5)

Remarks: Length: 117 µm Width: 26 µm Striae: 9/10 µm

Pinnularia sp.4 (Plate: 9 Figure: 2)

Literature: Metzeltin & Lange-Bertalot (2007) pp. 721 [Plate: 225; Figure: 4]; Krammer (2000) pp 602 [Plate 171; Figure: 2]

Remarks: Length: 131 µm Width: 24 µm Striae: 8/10 µm

Pinnularia sp.5 (Plate: 9 Figure: 9)

Remarks: Length: 70 µm Width: 9 µm Striae: 10/10 µm

Pinnularia sp.7 (Plate: 9 Figure: 12)

Remarks: Length: 70-98 µm Width: 13-15 µm Striae: 8-9/10 µm

Pinnularia tropica Hustedt (Plate: 9 Figure: 4)

Literature: Foged (1984) pp.145 [Plate: 11; Figure: 2]

Remarks: Length: 109 µm Width: 20 µm Striae: 7/10 µm

Pinnularia divergens Smith (Plate: 9 Figure: 7)

Literature: Krammer & Lange-Bertalot (1997) pp. 803 [Figure:179: 4]

Remarks: Length: 85 µm Width: 12 µm Striae: 10/10 µm

Pinnularia microstauron (Ehrenberg) Cleve (Plate: 9 Figure: 8)

Literature: Metzeltin & Lange-Bertalot (2007) pp. 797 [Plate: 263; Figure: 10, Plate: 264; Figure: 8-9]

Remarks: Length: 72-80 µm Width: 10-12 µm Striae: 8/10 µm

Pinnularia stoermeri Metzeltin & Lange-Bertalot (Plate: 9 Figure: 11, 6)

Literature: Metzeltin & Lange-Bertalot (2007) pp. 753 [Plate: 241; Figure: 2-3]

Remarks: Length: 80-118 µm Width: 18-24 µm Striae: 7/10 µm

Pinnularia pisciculus var. *angusta* Metzeltin & Krammer (Plate: 9 Figure: 13)

Synonyms: *Pinnularia braunii* Metzeltin & Krammer

Literature: Krammer & Lange-Bertalot (1997) pp. 819 [Figure: 187: 3]; Metzeltin & Lange-Bertalot (2007) pp. 817 [Plate: 273; Figure: 8]

Remarks: Length: 43 µm Width: 8 µm Striae: 10/10 µm

Plagiotropis sp.1 (Plate: 12 Figure: 1)

Remarks: Length: 142-153 µm Width: 21-23 µm, Striae: 17/10 µm.

Planothidium frequentisimum (Plate: 1 Figure: 7)

Synonyms: *Achnanthes lanceolata* var. *dubia* Grunow

Literature: Podzorski (1985) pp. 97 [Plate 4; Figure: 16 – 17]

Pleurosigma sp.1 (Plate: 11 Figure: 1)

Proschkinia sp.1 (Plate: 4 Figure: 6)

Remarks: Length: 25-26 µm Width: 3.5-5 µm, Striae not discernable

Rhopalodia gibba (Ehrenberg) Muller (Plate: 12 Figure: 4)

Literature: Krammer & Lange-Bertalot (1997) pp. 439 [Plate: 111; Figure: 2,6]; Podzorski (1985) pp 131 [Plate 21; Figure: 11]

Sellaphora laevissima (Kützing) Krammer (Plate: 1 Figure: 13)

Synonyms: *Navicula laevissima* (Kützing)

Literature: Krammer & Lange-Bertalot (1997) pp. 575 [Figure: 67: 8 -10]

Remarks: This species exhibited a TP optimum and tolerance of 321 µg P g^{-1} dry mass and 33 µg P g^{-1} dry mass respectively.

Sellaphora pupula (Kützing) Mereschkowsky (Plate: 13 Figure: 8)

Synonyms: *Navicula pupula* (Kützing)

Literature: Krammer & Lange-Bertalot (1997) pp. 575 [Figure: 67: 1 - 2]

Sellaphora rioplatensis Metzeltin, Lange-Bertalot & García-Rodríguez (Plate: 1 Figure: 16)

Sellaphora sp.1 (Plate: 1 Figure: 15)

Remarks: Length: 12-16 µm Width: 5-6 µm Striae: 12-14/5 µm

Seminavis eulensteinii (Grunow) Danielidis, Ford & Kennett (Plate: 17 Figure: 5)

Literature: Wachnicka and Gaiser (2007) pp.437 [Figure. 191-192, 195-197].

Stauroneis pachycephala Cleve (Plate: 4 Figure: 4)

Literature: Metzeltin & Lange-Bertalot (2007) pp. 547 [Plate: 139; Figure: 44 – 45]; Podzorski (1985) pp. 105 [Plate: 8; Figure: 2]

Stauroneis phoenicentron (Nitzsch) Ehrenberg (Plate: 11 Figure: 3)

Literature: Podzorski (1985) pp. 97 [Plate 7; Figure: 4]

Remarks: Length: 212-242 µm Width: 39-45 µm Striae: 11/10 µm Areolae: 16/10 µm.

Stauroneis cf. *smithii* var. *incisa* Pantocsek (Plate: 1 Figure: 12)

Literature: Siver, Hamilton, Stachura-Suchoples & Kociolek (2005) pp.385 [Plate 68; Figure: 3]

Remarks: Length: 22-27 µm Width: 7-8 µm Striae: 24/10 µm. Similar to *S. smithii* var. *incisa*, but striae density is lower; 24/10 µm instead of 28-31/ µm.

Staurosira construens Ehrenberg (Plate: 5 Figure: 5)

Synonyms: *Fragilaria construens* Ehrenberg

Literature: Krammer & Lange-Bertalot (1997) pp. 489 [Plate: 129; Figure: 22 - 23]

Staurosirella pinnata var. *pinnata* (Ehrenberg) Williams & Round

Stenopterobia curvula (Smith) Krammer (Plate: 10 Figure: 8)

Literature: Krammer & Lange-Bertalot (1997) pp. 563 [Plate: 171; Figure: 6,7]

Surrirella elegans f. *elongata* Skvortzow (Plate: 10 Figure: 1)

Literature: Krammer & Lange-Bertalot (1997) pp. 545 [Plate: 162; Figure: 6]

Synedra acus var. *angustissima* (Grunow) Van Heurck (Plate: 16 Figure: 3)

Literature: Krammer & Lange-Bertalot (1991) pp. 459 [Plate: 114; Figure: 21];
Siver, Hamilton, Stachura-Suchoples & Kociolek (2005) pp. 287 [Plate: 20; Figure: 5]

Remarks: This species was identified as an indicator of low periphyton mat TP concentration.

Tabularia tabulata (Agardh) Snoeijs (Plate: 5 Figure: 1)

Synonyms: *Fragilaria fasciculata* (Agardh) Lange-Bertalot; *Synedra fasciculata* var. *truncata* (Greville) Patrick

Literature: Krammer & Lange-Bertalot (1991) pp. 501 [Plate: 135; Figure: 5]; Podzorski (1985) pp. 91 [Plate: 1; Figure: 17]

Unknown sp.1 (Plate: 1 Figure: 4)

Remarks: Length: 27 µm Width: 5.5 µm Striae: 33/10 µm

Unknown sp.2 (Plate: 1 Figure: 6)

Remarks: Length: 10 µm Width: 5.5 µm Striae: 13/5 µm

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Table 3-1. Location of Caribbean sampling sites, presented as latitudinal and longitudinal bounding GPS coordinates of sampling sites within each location.

	Sian Ka'an National Park, Quintana Roo, Mexico	New River Lagoon, Indian Church, Belize	Slipe River, Black River Morass, St. Elizabeth, Jamaica
EAST	087º30.585	88º37.958'	78 ˚ 46.972
WEST	087º57.579	88º39.212'	77 ˚ 48.874
NORTH	19º52.342	17º47.111'	18 ˚ 03.182
SOUTH	18º47.223	17 ˚ 37.166	18 ˚ 01.524

Table 3-2. Number of sites sampled (N), water characteristics and periphyton attributes for each location during wet and dry periods. Average values are given along with standard deviation values in brackets. Missing data are indicated with a dash (−).

SITE	N	pH	Conductivity ($\mu S\ cm^{-1}$)	Water depth (cm)	Total Biovolume ($ml\ m^{-2}$)	Biovolume ($ml\ m^{-2}$)	TP ($\mu g\ P\ g^{-1}$ DM)	Dry Mass ($g\ m^{-2}$)	Organic content (%)	Ash Free Dry Mass ($g\ m^{-2}$)	Chlorophyll ($\mu g\ m^{-2}$)	Chlorophyll concentration ($\mu g\ g^{-1}$ DM)
Belize Wet	12	7.3 (0.5)	441.8 (208.6)	73.2 (8.5)	876.0 (1474.8)	857.1 (1486.4)	239.7 (106.7)	77.1 (133.4)	67.8 (19.1)	30.1 (48.2)	140.2 (132.7)	48.3 (52.5)
Belize Dry	9	8.3 (0.2)	690.3 (104.0)	31.6 (11.8)	101.6 (264.6)	101.6 (264.6)	543.1 (187.9)	3.2 (6.7)	37.4 (17.9)	1.5 (3.0)	1288.5 (2602.0)	260.6 (175.0)
Jamaica Wet	5	7.9 (0.2)	522.6 (62.4)	9.6 (3.6)	-	-	405.2 (158.3)	-	-	-	-	-
Jamaica Dry	5	8.4 (0.5)	447.6 (137.3)	11.6 (12.7)	2251.3 (1712.6)	2251.3 (1712.6)	200.3 (16.5)	156.0 (104.8)	28.7 (7.2)	39.4 (25.5)	29693.0 (19940.6)	222.5 (83.1)
Mexico Wet	6	-	1259.0 (952.5)	37.9 (10.3)	7460.7 (3043.8)	6772.6 (2957.6)	212.5 (93.7)	365.0 (195.5)	37.9 (7.4)	121.4 (49.5)	37195.4 (12261.7)	129.7 (51.5)
Mexico Dry	4	9.2 (0.4)	15047.7 (16670.5)	30.3 (23.4)	4564.3 (2568.5)	4144.6 (2720)	193.7 (210.9)	317.4 (233.9)	42.5 (15.5)	109.4 (76.5)	133456.4 (153012.9)	465.3 (257.1)

Table 3-3. List of non-rare species showing the number of locations (N) at which each species was found, along with an indicator of average percentage abundance at each location: Belize (B), Mexico (M) and Jamaica (J). Rare (<1%): *; Uncommon (1 to <5%): **; Common (5 to <20%): ***; Abundant (>20%): ****. Species absence from a location is indicated with a dash (−).

	N		Avg. Per. Abun.	
		B	M	J
Achnanthidium neomicrocephalum H. Lange-Bertalot & F. Staab	3	****	*	**
Brachysira neoexilis Lange-Bertalot	3	****	***	***
Brachysira procera Lange-Bertalot & Moser	3	****	***	***
Caponea caribbea Podzorski	3	*	*	*
Cyclotella meneghiniana Kützing	3	*	**	*
Diploneis oblongella (Naegeli ex Kuetzing) Ross	3	*	*	**
Diploneis parma Cleve	3	*	*	**
Encyonema evergladianum Krammer	3	***	****	****
Encyonema sp.2	3	**	***	**
Encyonema sp.3	3	*	*	*
Encyonopsis microcephala (Grunow) Krammer	3	*	**	***
Encyonopsis subminuta Krammer et Reichardt	3	*	**	**
Eunotia flexuosa (Brébisson) Kützing	3	*	*	*
Fragilaria (?) sp.1 cf. *famelica* (Kützing) Lange-Bertalot	3	**	**	**
Fragilaria synegrotesca Lange-Bertalot	3	***	***	***
Fragilaria ulna var. *ulna* (Nitzsch) Lange-Bertalot	3	**	*	*
Gomphonema intricatum var. *vibrio* (Ehrenberg) Cleve	3	**	*	*

Table 3-3. C'ntd.

	N		Avg. Per. Abun.	
Gomphonema cf. *vibriodes* Reichardt & Lange-Bertalot	3	**	**	*
Mastogloia cf. *smithii* Thwaites ex. W. Smith	3	***	****	***
Mastogloia smithii var. *lacustris* Grunow	3	**	**	*
Navicula cf. *radiosa* Kützing	3	**	**	**
Navicula cryptotenella Lange-Bertalot	3	**	**	**
Navicula subtilissima Cleve	3	**	*	**
Nitzschia lacunarum Hustedt	3	*	*	*
Nitzschia palaea (Kutzing) Smith	3	**	***	***
Nitzschia semirobusta Lange-Bertalot	3	**	***	***
Nitzschia serpentiraphe Lange-Bertalot	3	**	**	**
Sellaphora laevissima (Kützing) Krammer	3	*	*	*
Anomoneis sphaerophora (Ehrenberg) Pfitzer	2	*	*	-
Encyonema silesiacum (Bleisch) Mann	2	*	*	-
Eunotia camelus Ehrenberg	2	***	*	-
Eunotia cf. *karenae* Metzeltin & Lange-Bertalot	2	**	*	-
Navicella pusilla (Grunow) Krammer	2	*	***	-
Nitzschia denticula Grunow	2	***	***	-
Nitzschia microcephala Grunow	2	*	**	-
Pinnularia sp.1	2	*	*	-

Table 3-3. C'ntd.

	N		Avg. Per. Abun.	
Plagiotropis sp.1	2	**	*	-
Amphora sulcata (Brébisson) Cleve	2	-	**	**
Gomphonema affine Kützing	2	-	*	*
Mastogloia braunii Grunow	2	-	**	*
Nitzschia linearis var. *subtilis* (Grunow) Hustedt	2	-	***	**
Rhopalodia gibba (Ehrenberg) Muller	2	-	*	**
Achnanthidium exiguum (Grunow) Czarnecki	2	**	-	*
Achnanthidium sp.1	2	**	-	*
Amphora copulata (Kützing) Schoeman & Archibald	2	*	-	*
Caloneis sp.1	2	*	-	*
Cocconeis placentula Ehrenberg	2	*	-	*
Eunotia cf. *yberai* Frenguelli	2	*	-	*
Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot	2	*	-	*
Gomphonema gracile Ehrenberg	2	*	-	*
Mastogloia elliptica (Agardh) Cleve	2	**	-	**
Navicula stroemii Hustedt	2	*	-	*
Neidium ampliatum (Ehrenberg) Krammer	2	*	-	*
Nitzschia nana Grunow	2	*	-	*
Pinnularia microstauron (Ehrenberg) Cleve	2	*	-	*

Table 3-3. C'ntd.

	N		Avg. Per. Abun.	
Sellaphora pupula (Kützing) Mereschkowsky	2	*	-	*
Staurosira construens Ehrenberg	2	**	-	*
Staurosirella pinnata var. *pinnata* (Ehrenberg) Williams & Round	2	**	-	*
Synedra acus var. *angustissima* (Grunow) Van Heurck	2	*	-	*
Aulacoseira ambigua (Grunow) Simonsen	1	**	-	-
Aulacoseira granulata (Ehrenberg) Simonsen	1	**	-	-
Brachysira brebissonii Ross	1	****	-	-
Brachysira pumila Metzeltin & Lange-Bertalot	1	***	-	-
Craticula cuspidata (Kützing) Mann	1	*	-	-
Craticula sp.1	1	*	-	-
Cymbella aspera (Ehrenberg) Cleve	1	*	-	-
Diploneis sp.5	1	*	-	-
Diploneis sp.6	1	*	-	-
Epithemia sp.1	1	*	-	-
Eunotia botuliformis Wild, Norpel & Lange-Bertalot	1	*	-	-
Eunotia cf. *monodon* Ehrenberg	1	**	-	-
Eunotia implicata Nörpel, Lange-Bertalot & Alles	1	*	-	-

Table 3-3. C'ntd.

	N		Avg. Per. Abun.	
Eunotia naegelii Migula	1	*	-	-
Eunotia rabenhorstiana var. *elongata* (Patrick) Metzeltin & Lange-Bertalot	1	*	-	-
Eunotia sp.1	1	*	-	-
Eunotia sp.2	1	*	-	-
Eunotia sp.3	1	*	-	-
Fallacia pygmaea (Kützing) Stickle & Mann	1	**	-	-
Frustulia rhomboides var. *crassinervia* (Brebisson ex. W. Smith) Ross	1	*	-	-
Gomphonema parvulum (Kützing) Grunow	1	*	-	-
Hantzschia cf. *elongata* (Hantzsch) Grunow	1	*	-	-
Hantzschia spectabilis (Ehrenberg) Hustedt	1	*	-	-
Mastogloia elliptica var. *dansei* (Thwaites) Cleve	1	*	-	-
Navicula brasiliana (Cleve) Cleve	1	*	-	-
Navicula constans Hustedt	1	*	-	-
Nitzschia amphibia (Grunow) Lange-Bertalot	1	***	-	-
Nitzschia scalaris (Ehrenberg) Smith	1	*	-	-
Nitzschia thermalis var. *minor* Hilse	1	*	-	-

Table 3-3. C'ntd.

	N		Avg. Per. Abun.	
Pinnularia acrosphaeria (Brébisson) W. Smith	1	*	-	-
Pinnularia cf. *neomajor* var. *inflata* Krammer	1	*	-	-
Pinnularia sp.2	1	*	-	-
Pinnularia sp.4	1	*	-	-
Pinnularia sp.5	1	*	-	-
Pinnularia sp.7	1	*	-	-
Pinnularia stoermeri Metzeltin & Lange-Bertalot	1	*	-	-
Pinnularia tropica Hustedt	1	*	-	-
Stauroneis cf. *smithii* var. *incisa* Pantocsek	1	*	-	-
Stauroneis pachycephala Cleve	1	*	-	-
Stauroneis phoenicentron (Nitzsch) Ehrenberg	1	*	-	-
Stenopterobia curvula (Smith) Krammer	1	*	-	-
Surrirella elegans f. *elongata* Skvortzow	1	*	-	-
Unknown sp.1	1	*	-	-
Unknown sp.2	1	*	-	-

Table 3-3. C'ntd.

	N		Avg. Per. Abun.	
Amphora cymbifera var. *heritierarum* Wachnicka & Gaiser	1	-	*	-
Amphora sp.2	1	-	*	-
Amphora sp.3	1	-	*	-
Amphora corpulenta var. *capitata* Tempere et Peragallo	1	-	*	-
Amphora pseudoproteus Wachnicka & Gaiser	1	-	*	-
Brachysira estonarium Witkowski, Lange-Bertalot & Metzeltin	1	-	*	-
Brachysira cf. *hofmanniae* Lange-Bertalot	1	-	**	-
Cyclotella litoralis Lange & Syvertsen	1	-	*	-
Cyclotella cf. *atomus* var. *gracilis* Genkil & Kiss	1	-	*	-
Cyclotella sp.1	1	-	*	-
Diploneis cf. *elliptica* var. *tropica* Frenguelli	1	-	*	-
Hantzschia cf. *vivacior* Lange-Bertalot	1	-	*	-
Mastogloia lanceolata Thwaites ex. Smith	1	-	***	-
Navicula palestinae Gerloff, Natour & Rivera	1	-	**	-
Navicula pseudocrassirostris Hustedt	1	-	**	-
Nitzschia acicularis	1	-	**	-
Nitzschia sp.1	1	-	**	-
Nitzschia sp.2	1	-	**	-
Parlibellus sp.1	1	-	**	-

Table 3-3. C'ntd.

Pinnularia divergens Smith	1	-	*	-
Pleurosigma sp.1	1	-	*	-
Proschkinia sp.1	1	-	**	-
Seminavis eulensteinii (Grunow) Danielidis, Ford & Kennett	1	-	*	-
Achnanthidium inflatum (Kützing) Hutton	1	-	-	*
Actinocyclus normanii (Gregory ex Greville) Hustedt	1	-	-	*
Caloneis sp.2	1	-	-	*
Caloneis sp.3	1	-	-	*
Diploneis elliptica	1	-	-	*
Diploneis cf. *finnica*	1	-	-	*
Diploneis sp.2	1	-	-	*
Encyonema jemtlandicum var. *venezolanum* Krammer	1	-	-	**
Encyonema sp.1	1	-	-	*
Encyonema vulgare var. *vulgare* Krammer	1	-	-	**
Fragilaria cf. *ulna* (Nitzsch) Lange-Bertalot	1	-	-	*
Nitzschia obtusa var. *kurzii* Rabenhorst ex Cleve & Moller	1	-	-	*
Tabularia tabulata (Agardh) Snoeijs	1	-	-	*
Pinnularia pisciculus var. angusta Metzeltin & Krammer	1	-	-	*
Planothidium frequentisimum	1	-	-	*
Sellaphora rioplatensis Metzeltin, Lange-Bertalot & García-Rodríguez	1	-	-	*
Sellaphora sp.1	1	-	-	*

Table 3-4. Average per-site species richness (S) and diversity (H) for all locations. Standard deviations are indicated in parentheses.

Site	No. of samples	Total no. of species	S	H
BELIZE	21	113	18.48 (6.51)	1.67 (0.49)
MEXICO	10	84	18.70 (4.45)	2.00 (0.33)
JAMAICA	10	87	21.90 (4.41)	2.01 (0.22)

Figure 3-1. Benthic (a) and epiphytic (b) periphyton mat specimens collected from karstic marsh habitats.

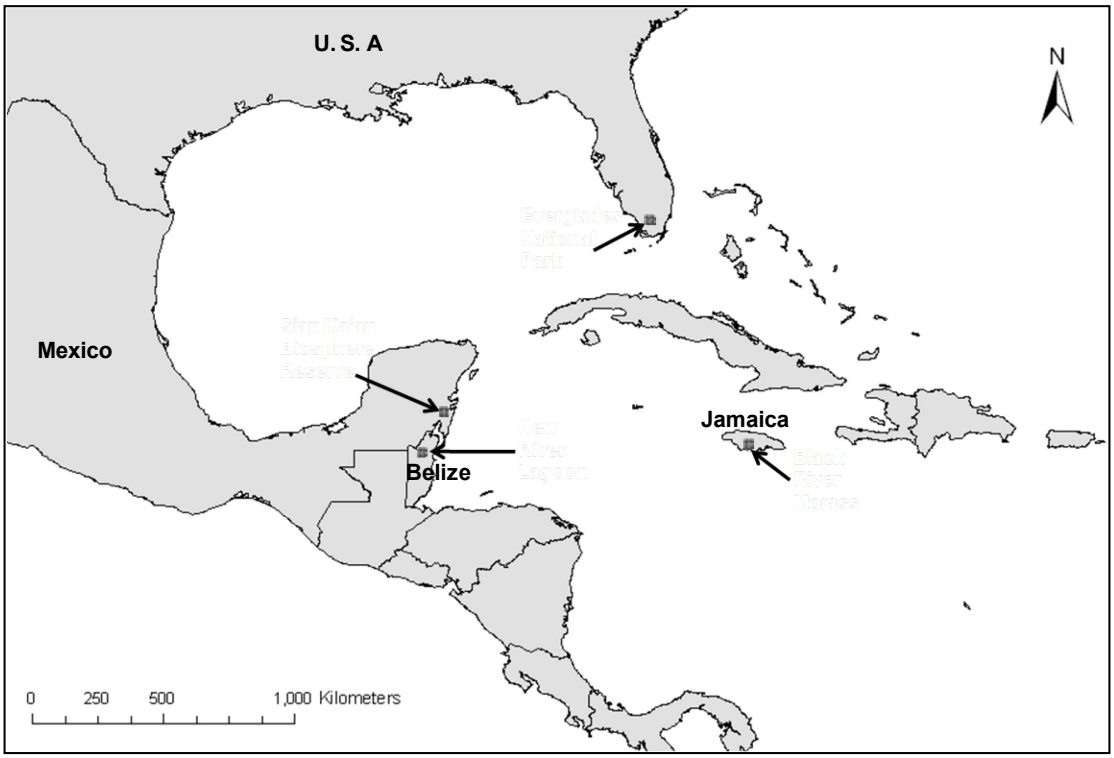

Figure 3- 2. Map of northern Caribbean region showing the three sampling locations for this study. The Everglades location is included for comparison.

Plate 1. Figures 1-1 through 1-18

Figure 1-1. *Achnanthidium inflatum*

Figure 1-2. *Achnanthidium neomicrocephalum*

Figure 1-3. *Achnanthidium* sp.1

Figure 1-4. Unknown species 1

Figure 1-5. *Achnanthidium exiguum*

Figure 1-6. Unknown species 2

Figure 1-7. *Planothidium frequentisimum*

Figure 1-8. *Brachysira neoexilis*

Figure 1-9. *Brachysira brebissonii*

Figure 1-10. *Brachysira estonarium*

Figure 1-11. *Brachysira pumila*

Figure 1-12. *Stauroneis* cf. *smithii* var. *incisa*

Figure 1-13. *Sellaphora laevissima*

Figure 1-14. *Navicula stroemii*

Figure 1-15. *Sellaphora* sp.1

Figure 1-16. *Sellaphora rioplatensis*

Figure 1-17. *Aulacoseira ambigua*

Figure 1-18. *Aulacoseira granulata*

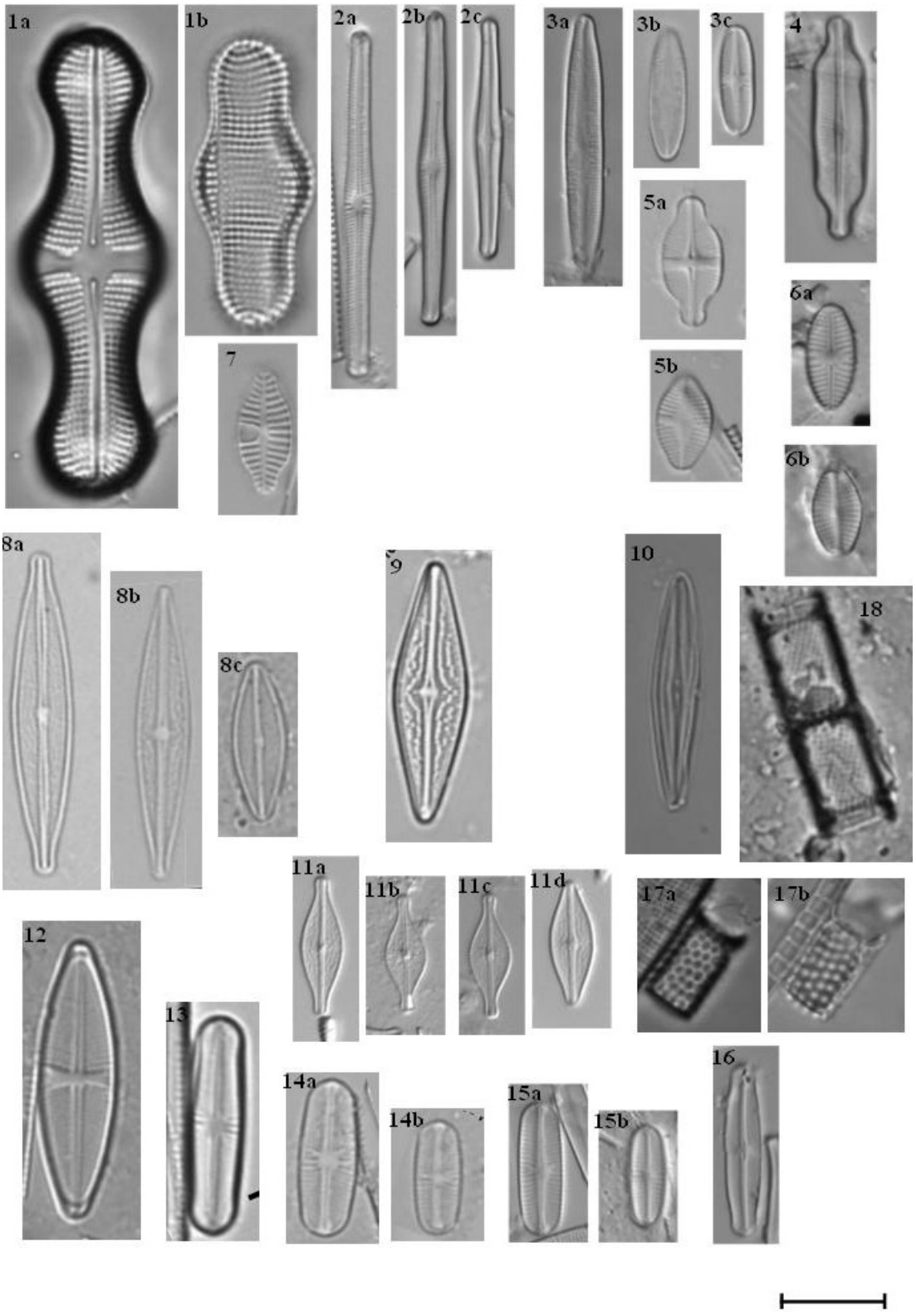
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Plate 2. Figures 2-1 through 2-7

Figure 2-1. *Brachysira* cf. *hofmanniae*

Figure 2-2. *Brachysira procera*

Figure 2-3. *Cyclotella litoralis*

Figure 2-4. *Cyclotella meneghiniana*

Figure 2-5. *Cyclotella* cf. *atomus* var. *gracilis*

Figure 2-6. *Cyclotella* sp.1.

Figure 2-7. *Diploneis puella*

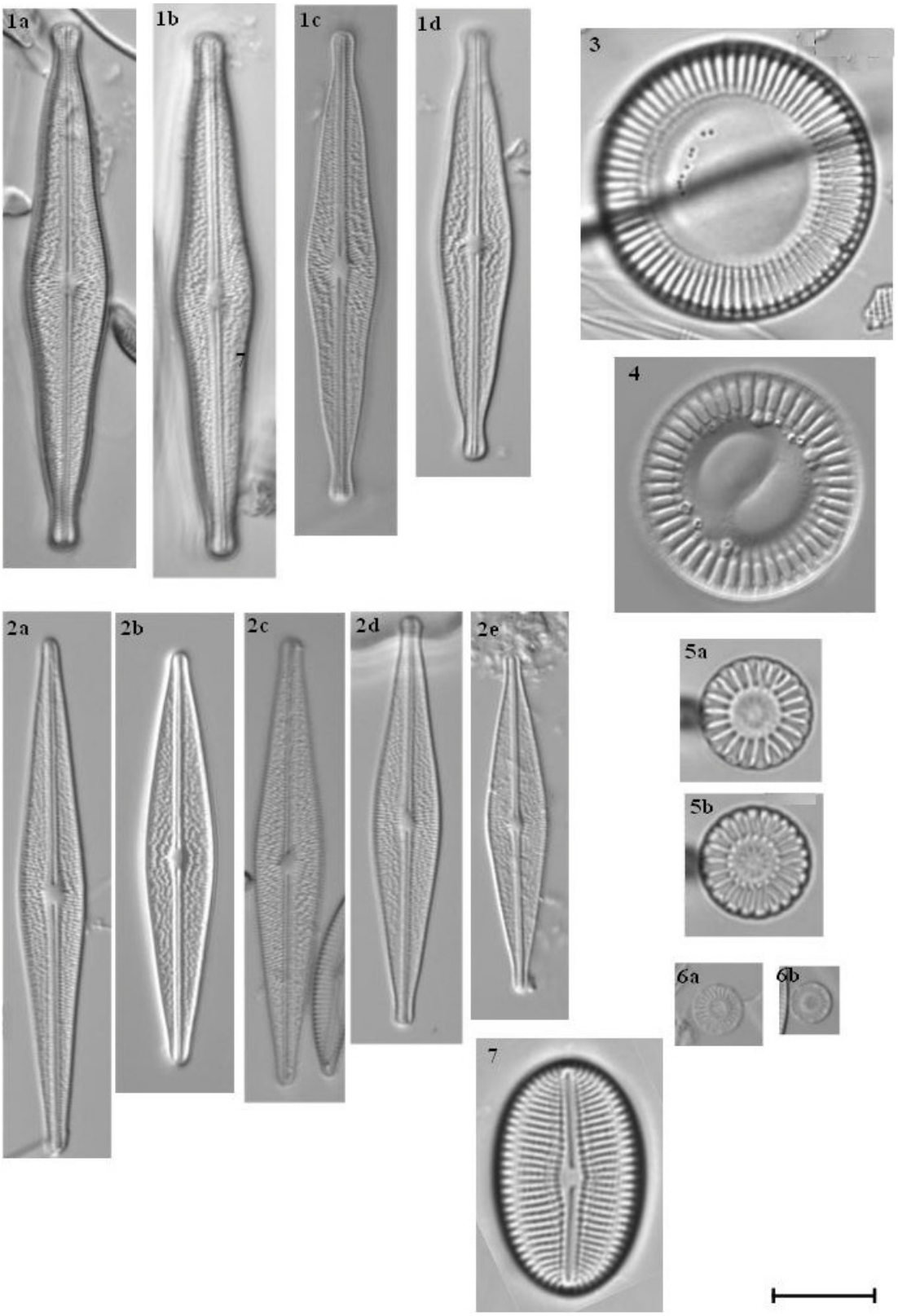
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Plate 3. Figures 3-1 through 3-4

Figure 3-1. *Navicula* cf. *radiosa*

Figure 3-2. *Navicella pusilla*

Figure 3-3. *Frustulia rhomboides* var. *crassinervia*.

Figure 3-4. *Navicula cryptotenella*

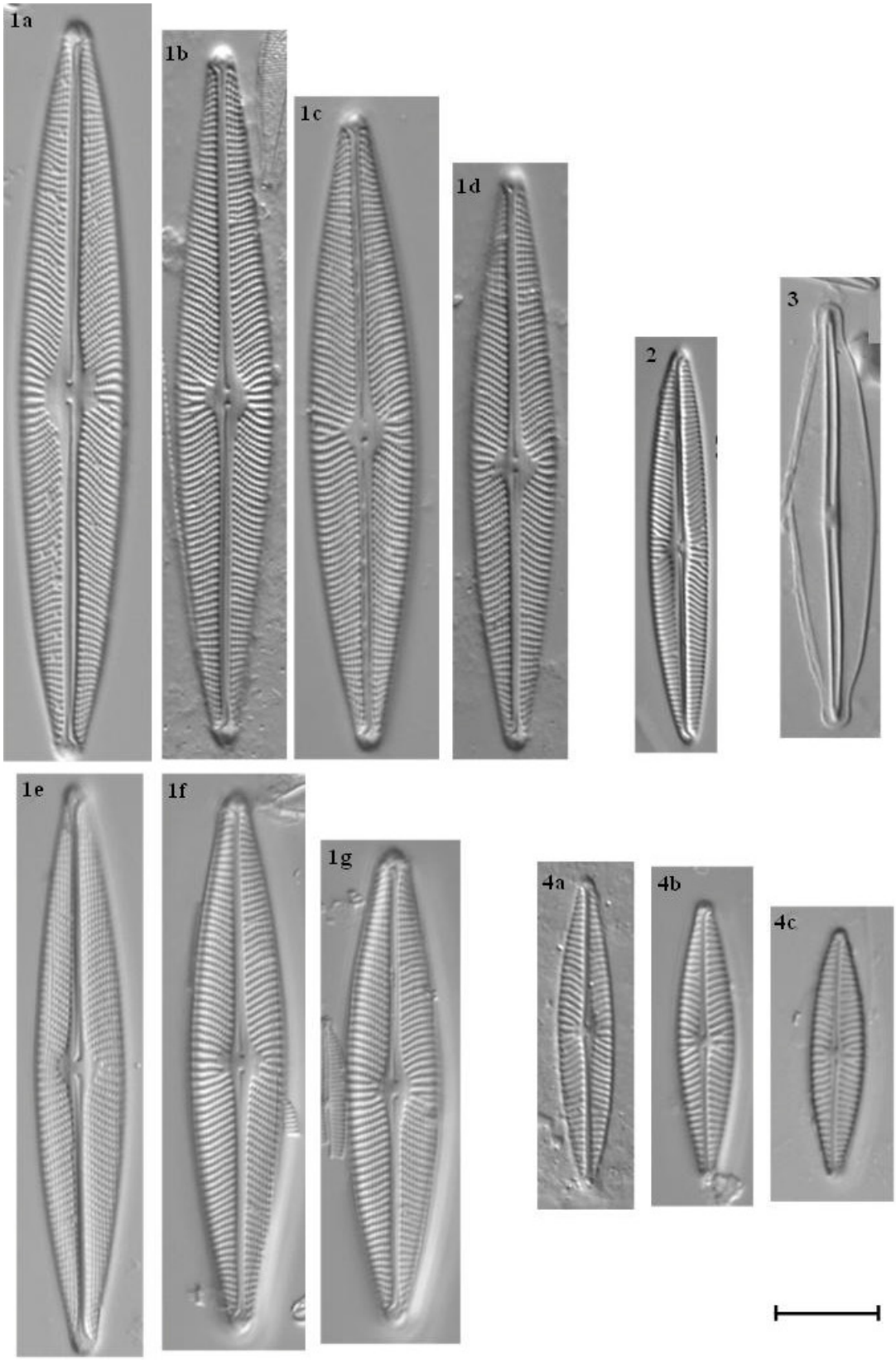
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Plate 4. Figures 4-1 through 4-14

Figure 4-1. *Neidium ampliatum*

Figure 4-2. *Neidium ampliatum*

Figure 4-3. *Encyonema evergladianum*

Figure 4-4. *Stauroneis pachycephala*

Figure 4-5. *Encyonopsis microcephala*

Figure 4-6. *Proschkinia* sp.1

Figure 4-7. *Caponea caribbea*

Figure 4-8. *Caloneis* sp.1

Figure 4-9. *Caloneis* sp.1

Figure 4-10. *Caloneis* sp.2

Figure 4-11. *Caloneis* sp.3

Figure 4-12. *Navicula constans*

Figure 4-13. *Navicula subtilissima*

Figure 4-14. *Encyonopsis subminuta*

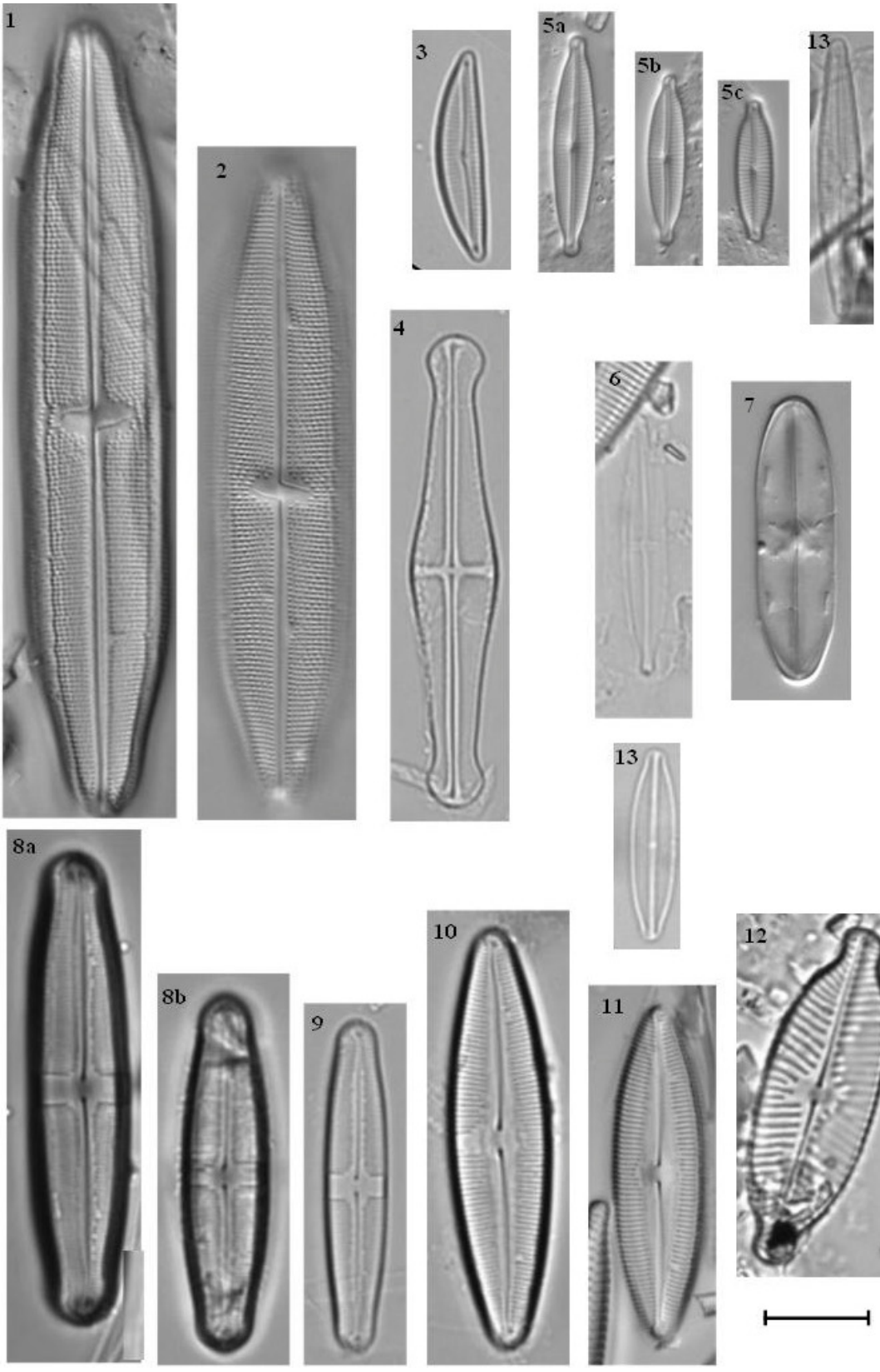
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Plate 5. Figures 5-1 through 5-7

Figure 5-1. *Tabularia tabulata*

Figure 5-2. *Fragilaria synegrotesca*

Figure 5-3. *Fragilaria (?)* sp.1 cf. *famelica*

Figure 5-4. *Fragilaria capucina* var. *vaucheriae*

Figure 5-5. *Staurosira construens*

Figure 5-6. *Diploneis* sp.1

Figure 5-7. *Diploneis* sp.2

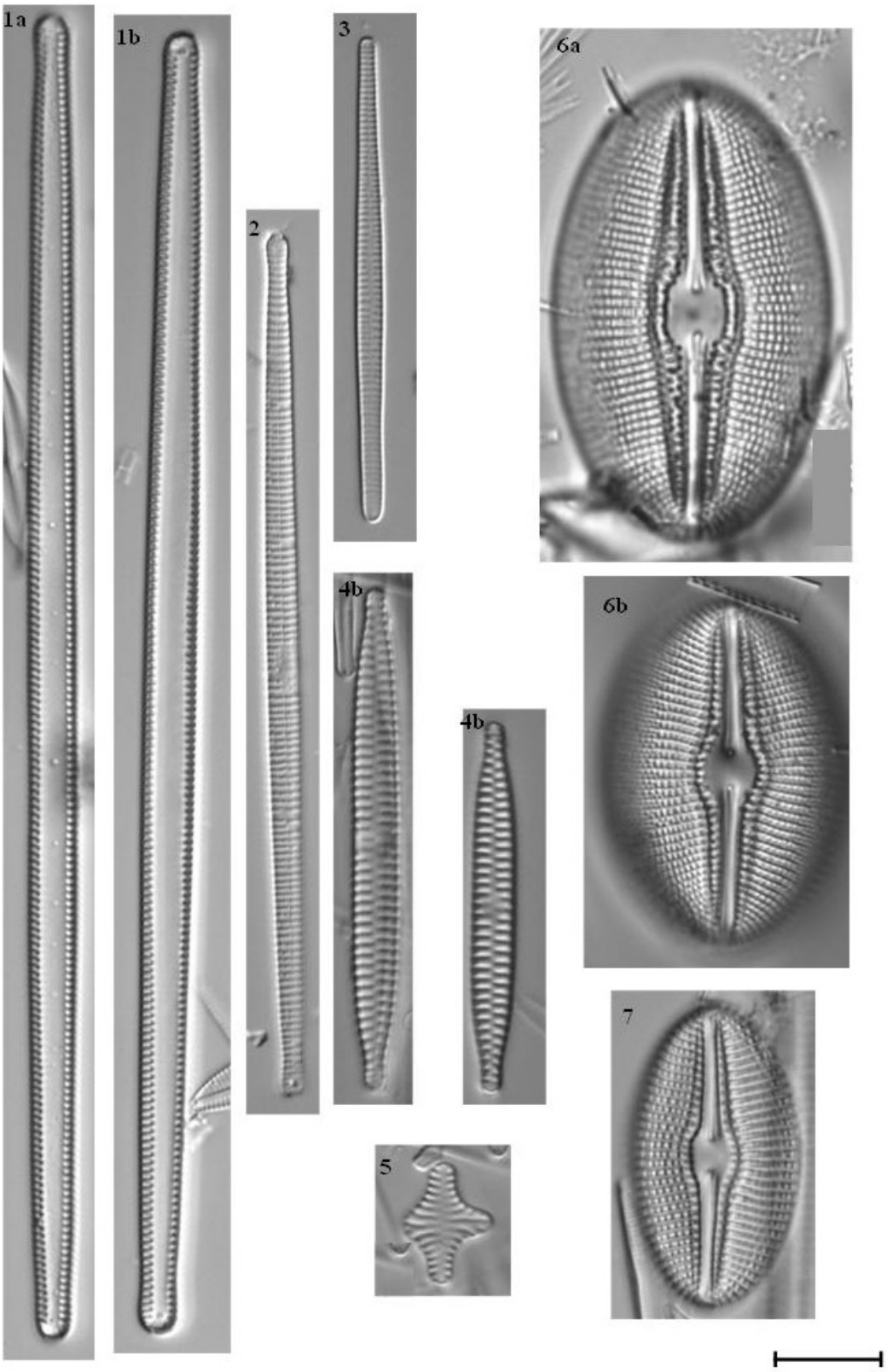
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Plate 6. Figures 6-1 through 6-11

Figure 6-1. *Nitzschia scalaris*

Figure 6-2. *Nitzschia serpentiraphe*

Figure 6-3. *Nitzschia linearis* var. *subtilis*

Figure 6-4. *Nitzschia linearis* var. *subtilis*

Figure 6-5. *Nitzschia palaea*

Figure 6-6. *Nitzschia palaea*

Figure 6-7. *Nitzschia microcephala*

Figure 6-8. *Nitzschia* sp.1

Figure 6-9. *Nitzschia denticula*

Figure 6-10. *Nitzschia semirobusta*

Figure 6-11. *Nitzschia amphibia*

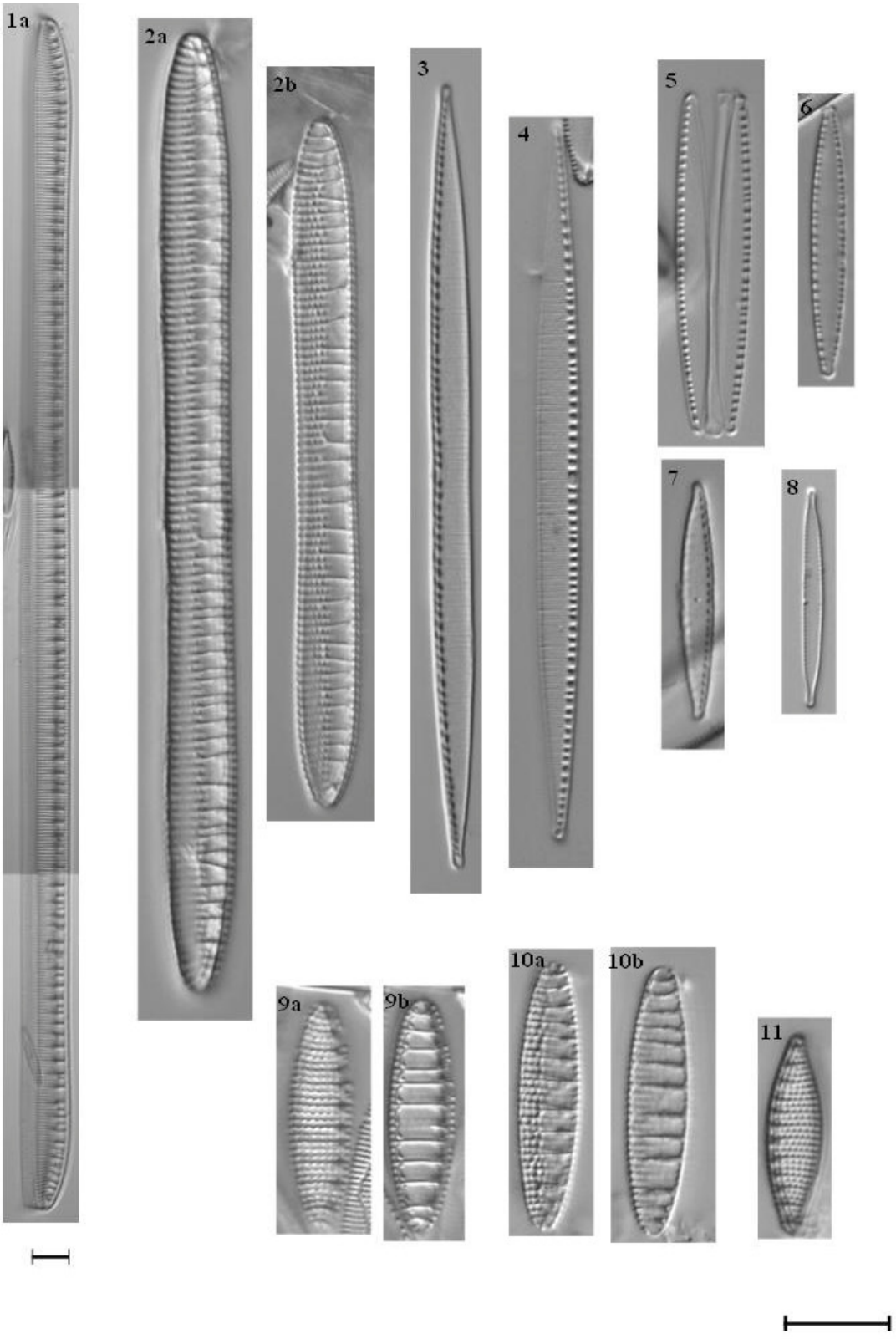
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Plate 7. Figures 7-1 through 7-6

Figure 7-1. *Diploneis* cf. *elliptica* var. *tropica*

Figure 7-2. *Diploneis parma*

Figure 7-3. *Diploneis* sp.5

Figure 7-4. *Diploneis* sp.6

Figure 7-5. *Diploneis ovalis*

Figure 7-6. *Diploneis oblongella*

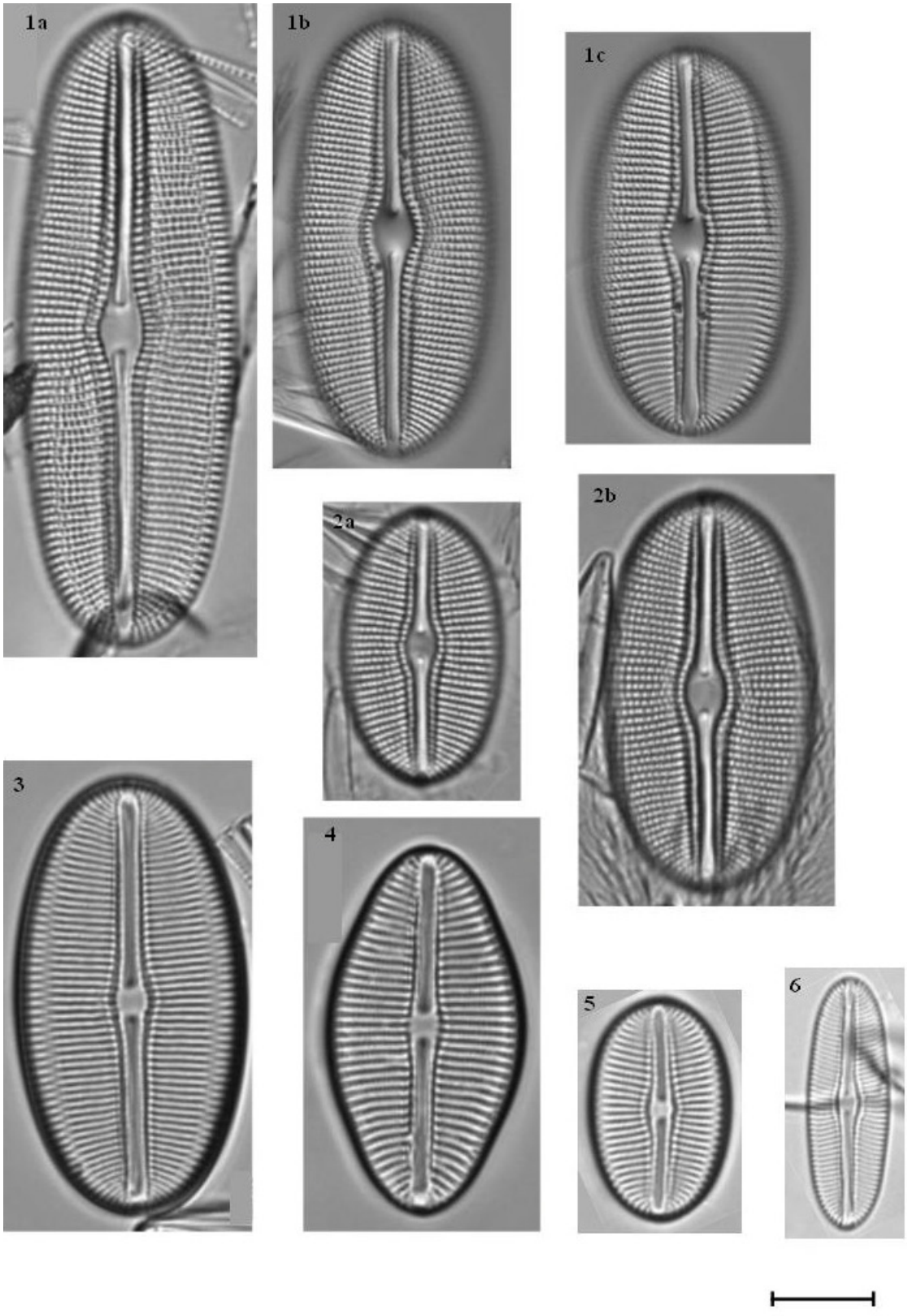
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Plate 8. Figures 8-1 through 8-10

Figure 8-1. *Gomphonema* cf. *vibriodes*

Figure 8-2. *Gomphonema intricatum* var. *vibrio*

Figure 8-3. *Gomphonema gracile*

Figure 8-4. *Gomphonema affine*

Figure 8-5. *Fallacia pygmaea*

Figure 8-6. *Navicula pseudocressirostris*

Figure 8-7. *Navicula palistinae*

Figure 8-8. *Mastogloia smithii* var. *lacustris*

Figure 8-9. *Mastogloia smithii*

Figure 8-10. *Gomphonema parvulum*

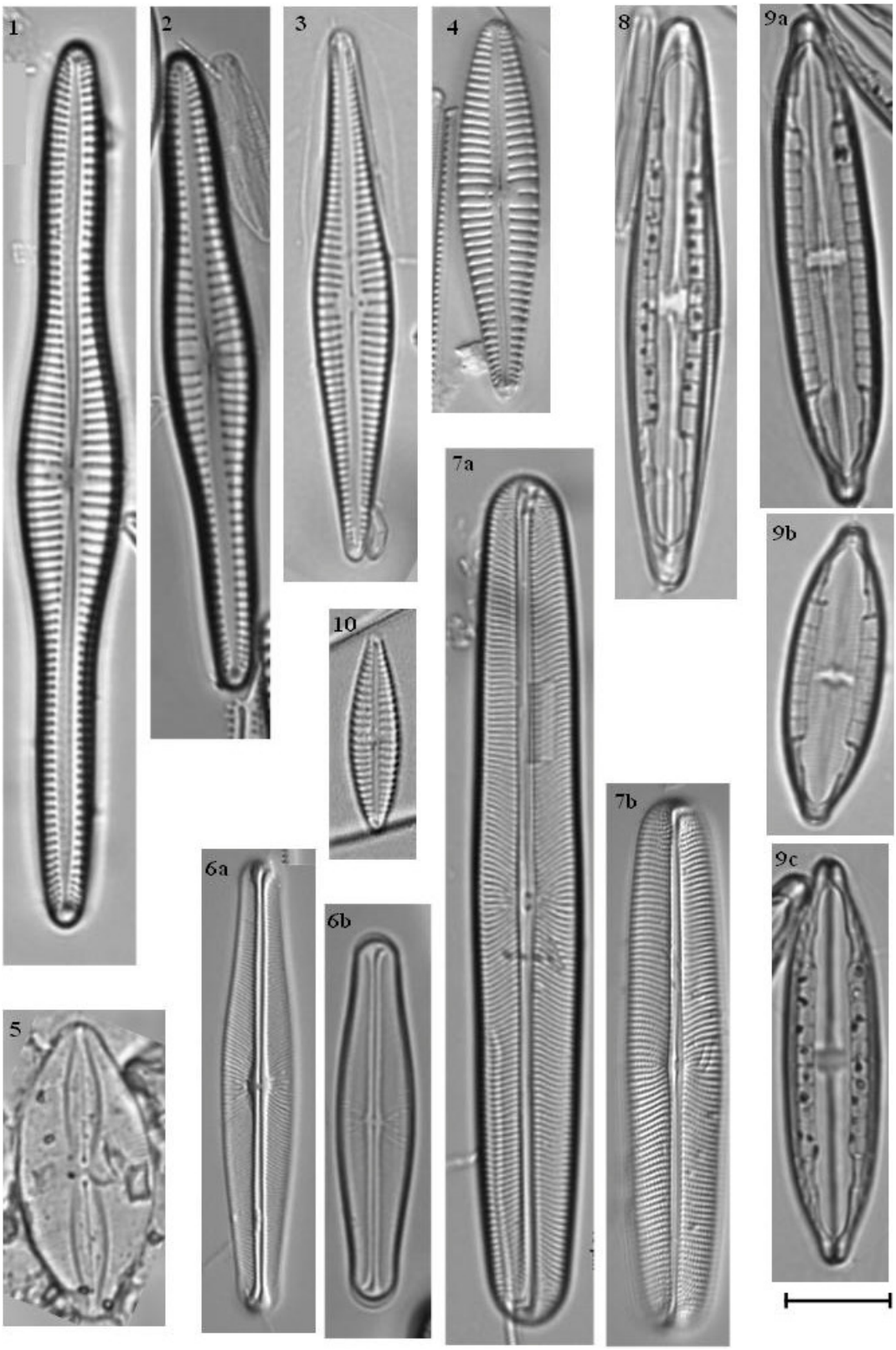
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Plate 9. Figures 9-1 through 9-13

Figure 9-1. *Pinnularia* cf. *neomajor* var. *inflata*

Figure 9-2. *Pinnularia* sp.4

Figure 9-3. *Pinnularia* sp.1

Figure 9-4. *Pinnularia tropica*

Figure 9-5. *Pinnularia* sp.2

Figure 9-6. *Pinnularia stoermeri*

Figure 9-7. *Pinnularia divergens*

Figure 9-8. *Pinnularia microstauron*

Figure 9-9. *Pinnularia* sp.5

Figure 9-10. *Pinnularia acrosphaeria*

Figure 9-11. *Pinnularia stoermeri*

Figure 9-12. *Pinnularia* sp.7

Figure 9-13. *Pinnularia pisciculus* var. *angusta*

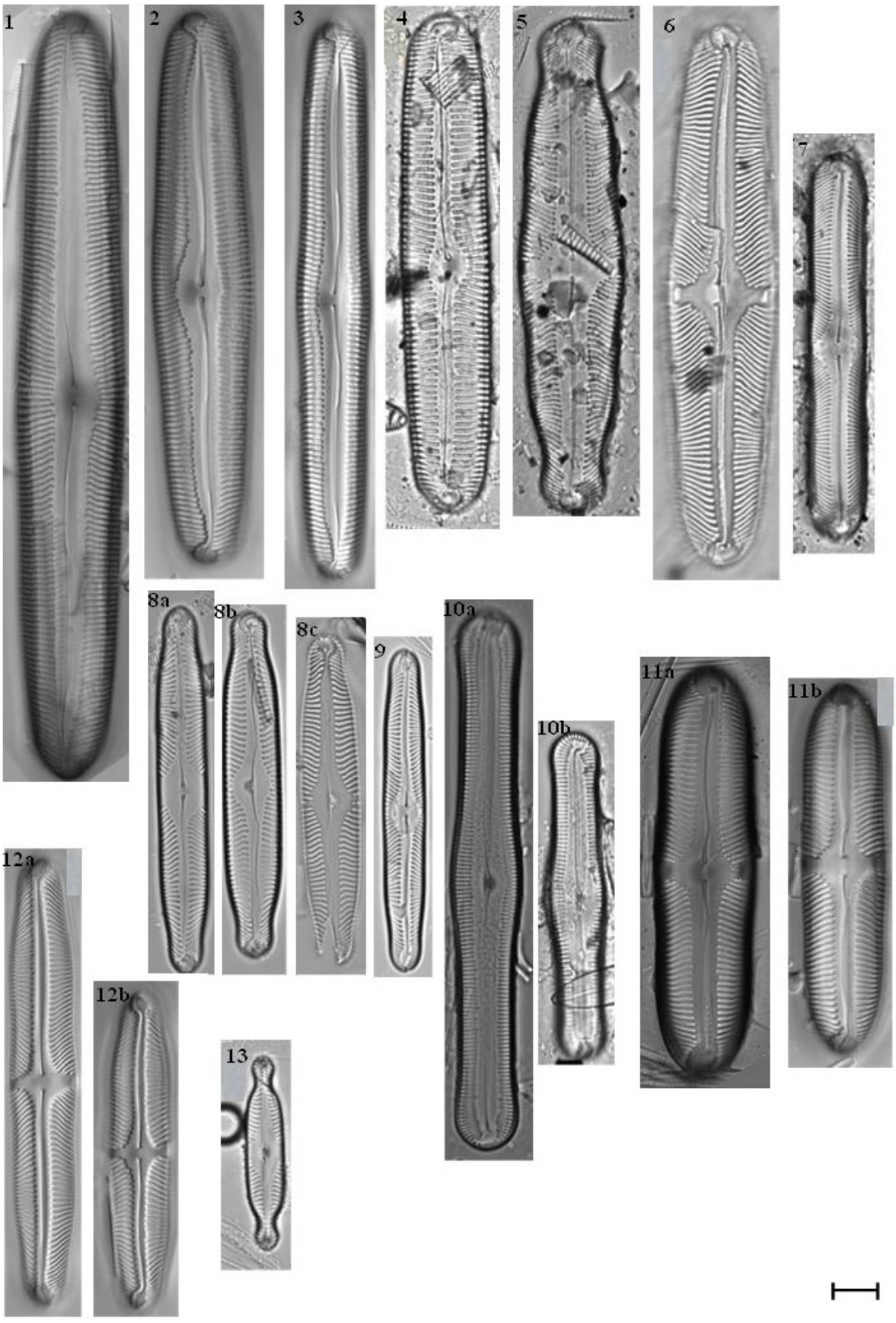
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Plate 10. Figures 10-1 through 10-10

Figure 10-1. *Surrirella elegans* f. *elongata*

Figure 10-2. *Hantzschia* cf. *elongata*

Figure 10-3. *Cymbella aspera*

Figure 10-4. *Hantzschia* cf. *vivacior*

Figure 10-5. *Hantzschia spectabilis*

Figure 10-6. *Nitzschia acicularis*

Figure 10-7. *Nitzschia lacunarum*

Figure 10-8. *Stenopterobia curvula*

Figure 10-9. *Nitzschia nana*

Figure 10-10. *Nitzschia thermalis* var. *minor*

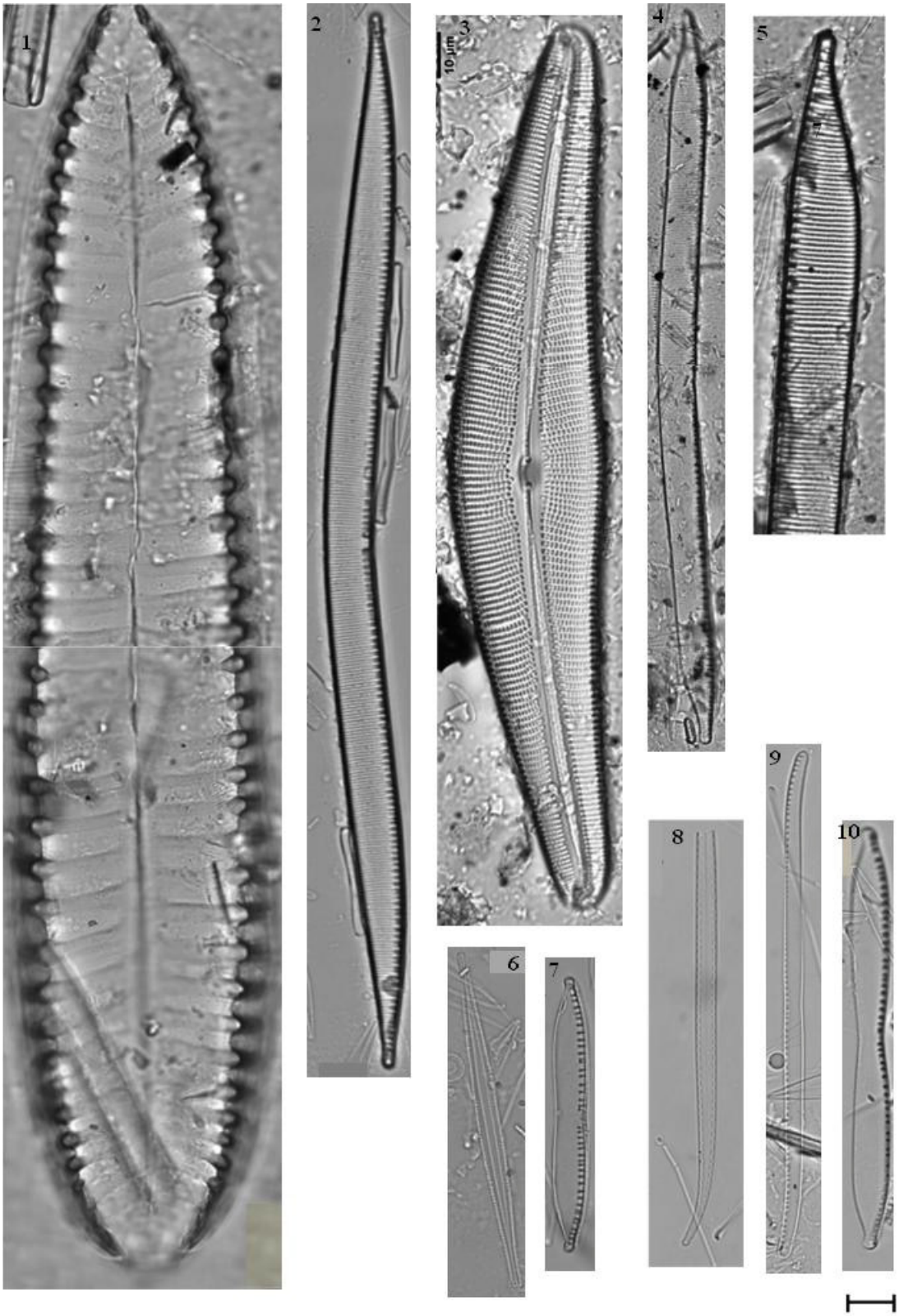
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Plate 11. Figures 11-1 through 11-3

Figure 11-1. *Pleurosigma* sp.1

Figure 11-2. *Craticula cuspidata*

Figure 11-3. *Stauroneis phoenicentron*

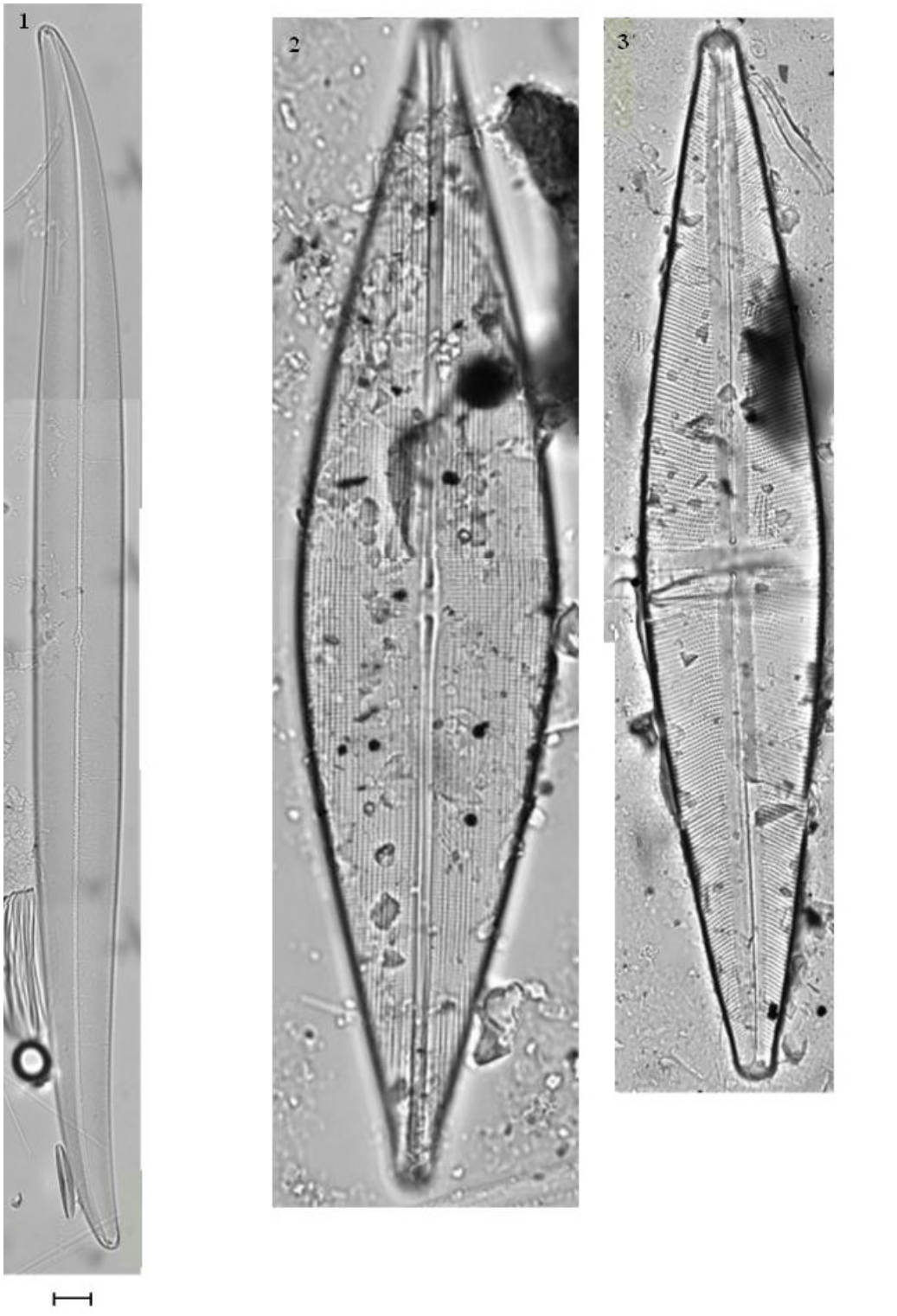
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Plate 12. Figures 12-1 through 12-5

Figure 12-1. *Plagiotropis* sp.1

Figure 12-2. *Parlibellus* sp.1

Figure 12-3. *Craticula* sp.1

Figure 12-4. *Rhopalodia gibba*

Figure 12-5. *Actinocyclus normanii*

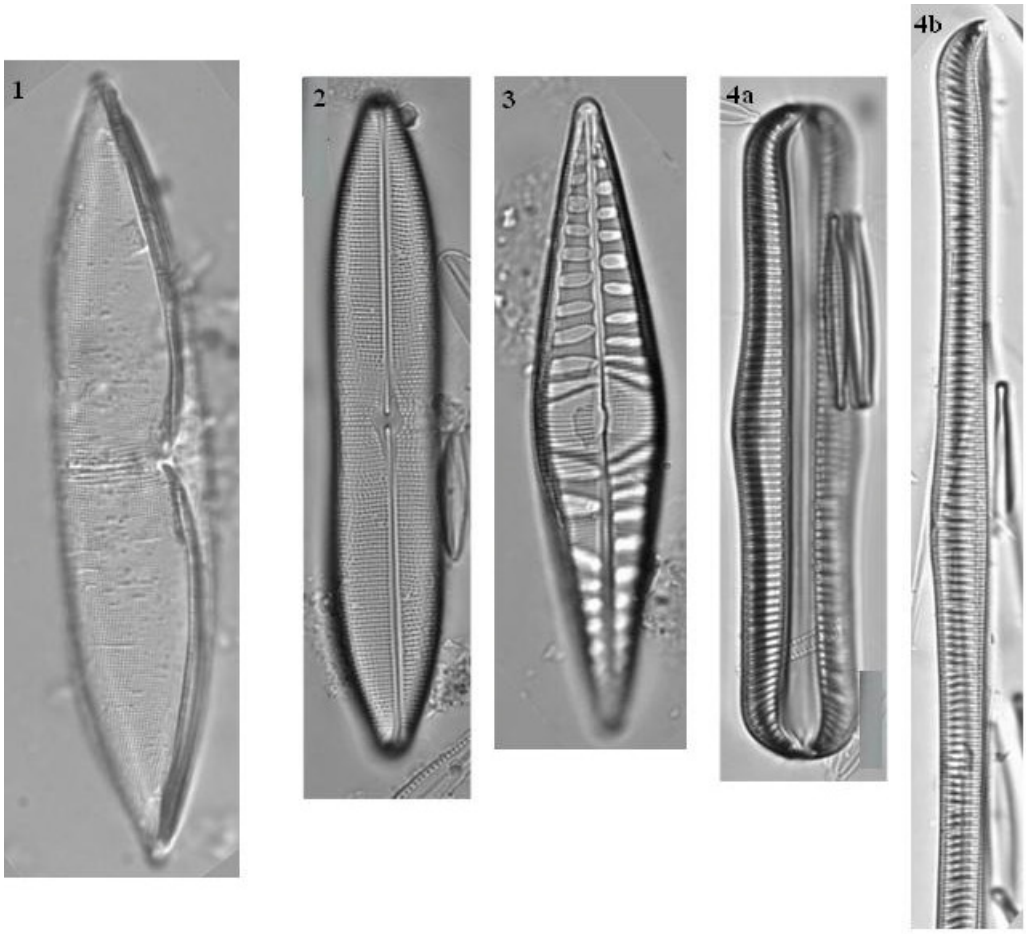
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Plate 13. Figures 13-1 through 13-9

Figure 13-1. *Anomoneis sphaerophora*

Figure 13-2. *Anomoneis sphaerophora forma ?*

Figure 13-3. *Navicula brasiliana*

Figure 13-4. *Mastogloia braunii*

Figure 13-5. *Mastogloia elliptica* var. *dansei*

Figure 13-6. *Mastogloia lanceolata*

Figure 13-7. *Mastogloia braunii*

Figure 13-8. *Sellaphora pupula*

Figure 13-9. *Mastogloia elliptica*

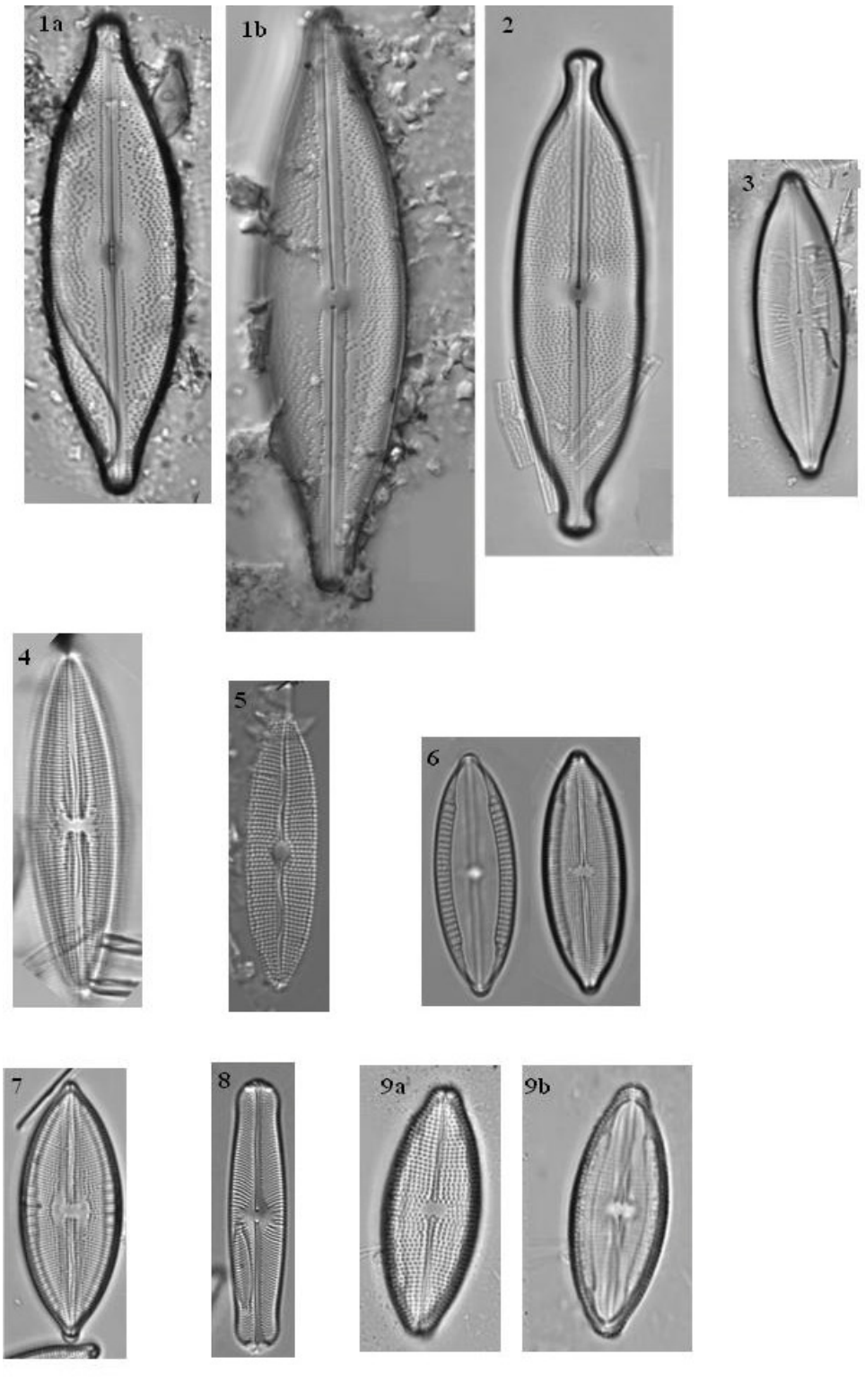
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Plate 14. Figures 14-1 through 14-7

Figure 14-1. *Encyonema vulgare* var. *vulgare*

Figure 14-2. *Encyonema silesiacum*

Figure 14-3. *Encyonema jemtlandicum* var. *venezolanum*

Figure 14-4. *Encyonema jemtlandicum* var. *venezolanum*

Figure 14-5. *Encyonema* sp.1

Figure 14-6. *Encyonema* sp.2

Figure 14-7. *Encyonema* sp.3

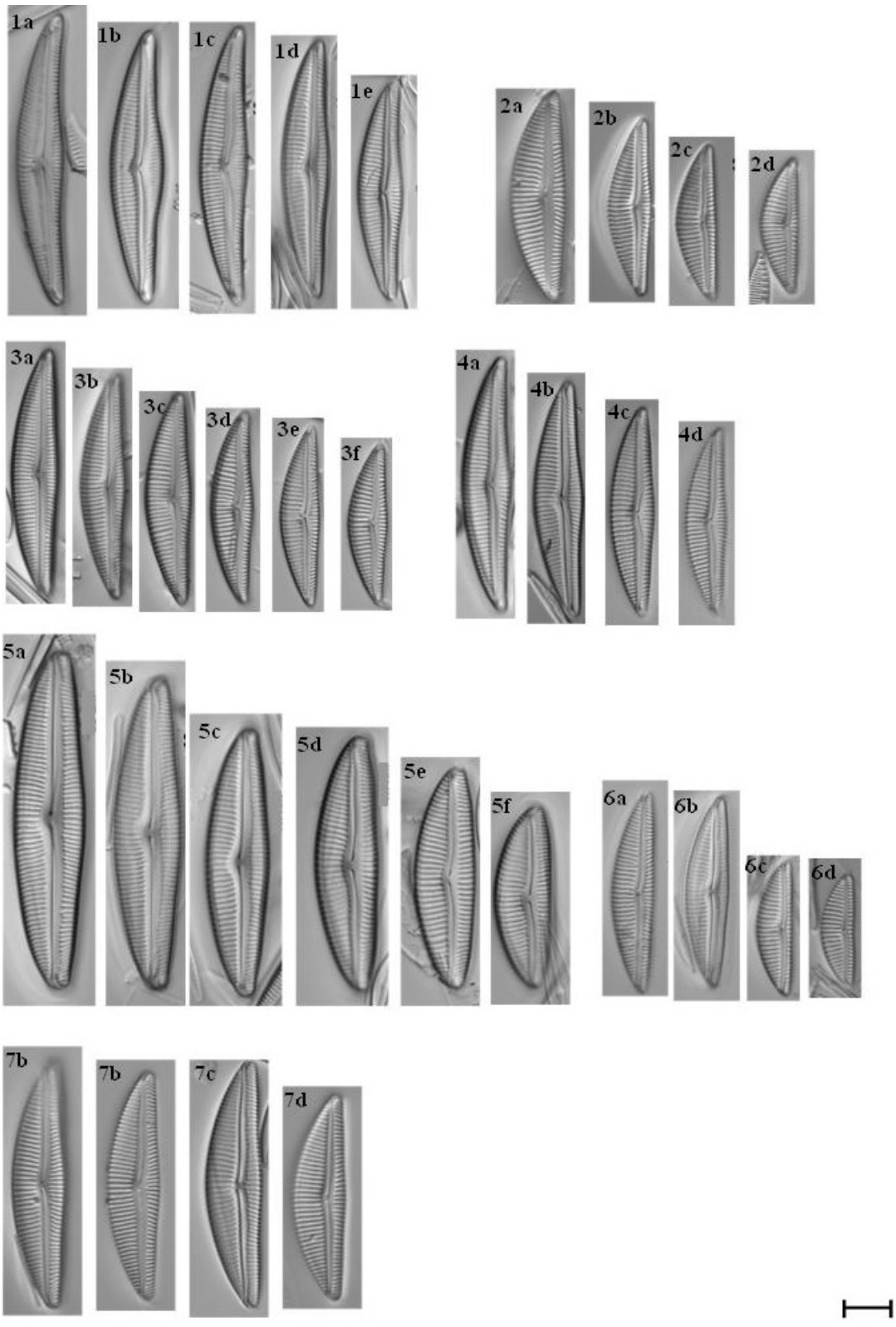
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Plate 15. Figures 15-1 through 15-12

Figure 15-1. *Eunotia rabenhorstiana* var. *elongata*

Figure 15-2. *Eunotia* cf. *karenae*

Figure 15-3. *Eunotia* cf. *monodon*

Figure 15-4. *Eunotia naegelii*

Figure 15-5. *Eunotia flexuosa*

Figure 15-6. *Eunotia* sp.1

Figure 15-7. *Eunotia implicata*

Figure 15-8. *Eunotia* sp.2

Figure 15-9. *Eunotia camelus*

Figure 15-10. *Eunotia* sp.3

Figure 15-11. *Eunotia botuliformis*

Figure 15-12. *Eunotia* cf. *yberai*

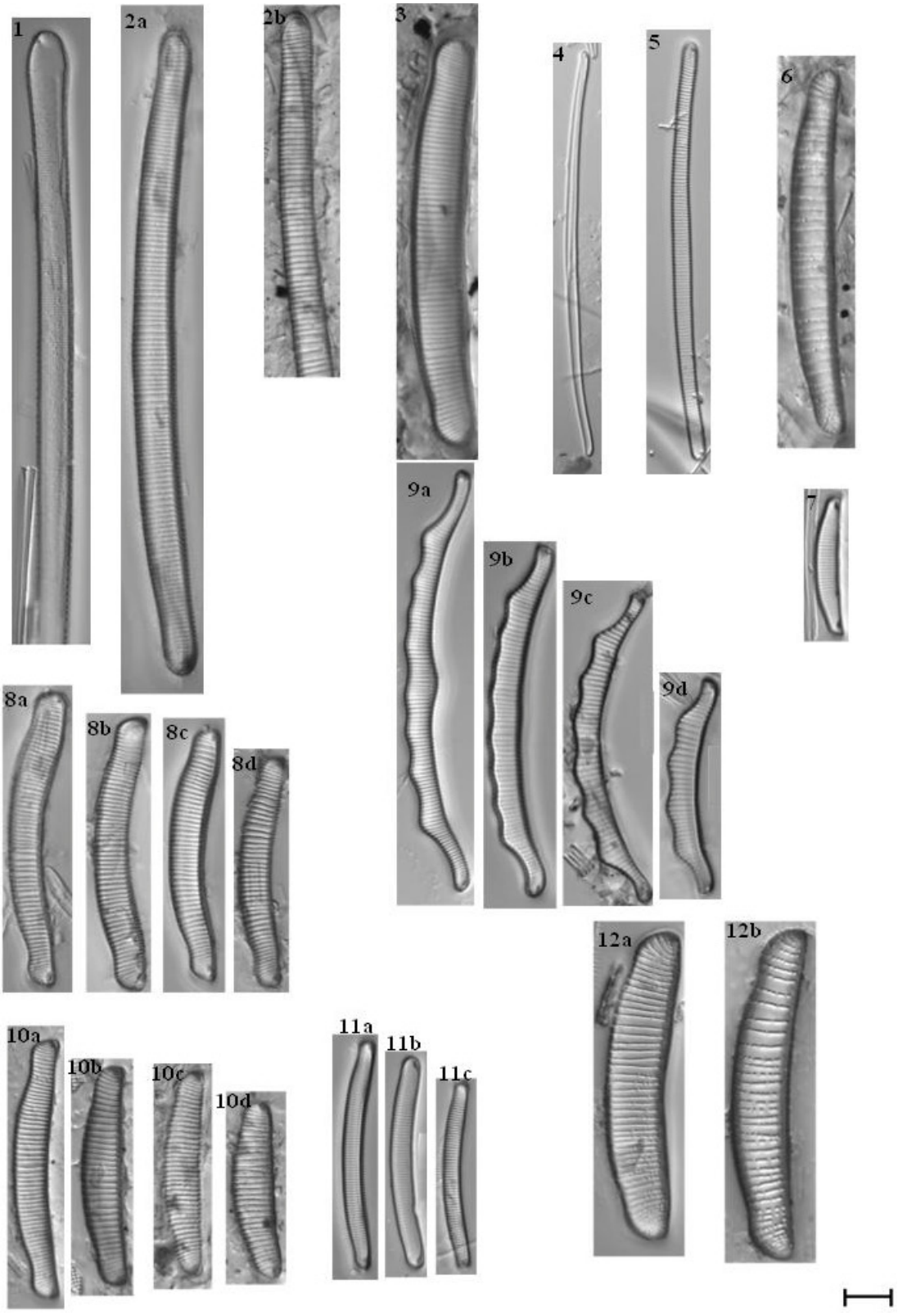
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Plate 16. Figures 16-1 through 16-5

Figure 16-1. *Fragilaria ulna* var. *ulna*

Figure 16-2. *Fragilaria* cf. *ulna*

Figure 16-3. *Synedra acus* var. *angustissima*

Figure 16-4. *Epithemia* sp.1

Figure 16-5. *Diploneis* sp.7

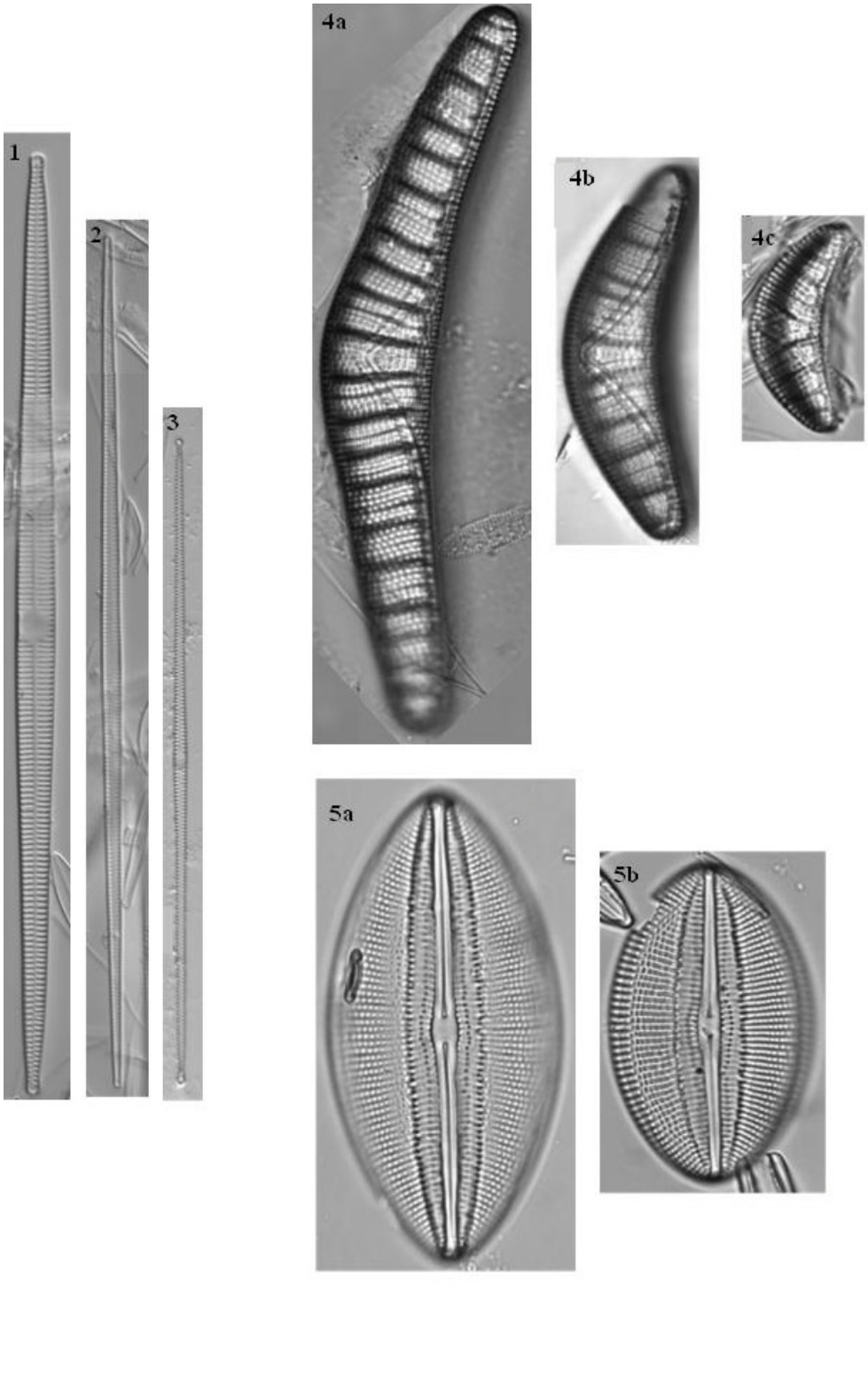
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Plate 17. Figures 17-1 through 17-11

Figure 17-1. *Amphora pseudoproteus*

Figure 17-2. *Amphora* sp.1

Figure 17-3. *Amphora* sp.2

Figure 17-4. *Amphora* sp.3

Figure 17-5. *Seminavis eulensteinii*

Figure 17-6. *Nitzschia obtusa* var. *kurzii*

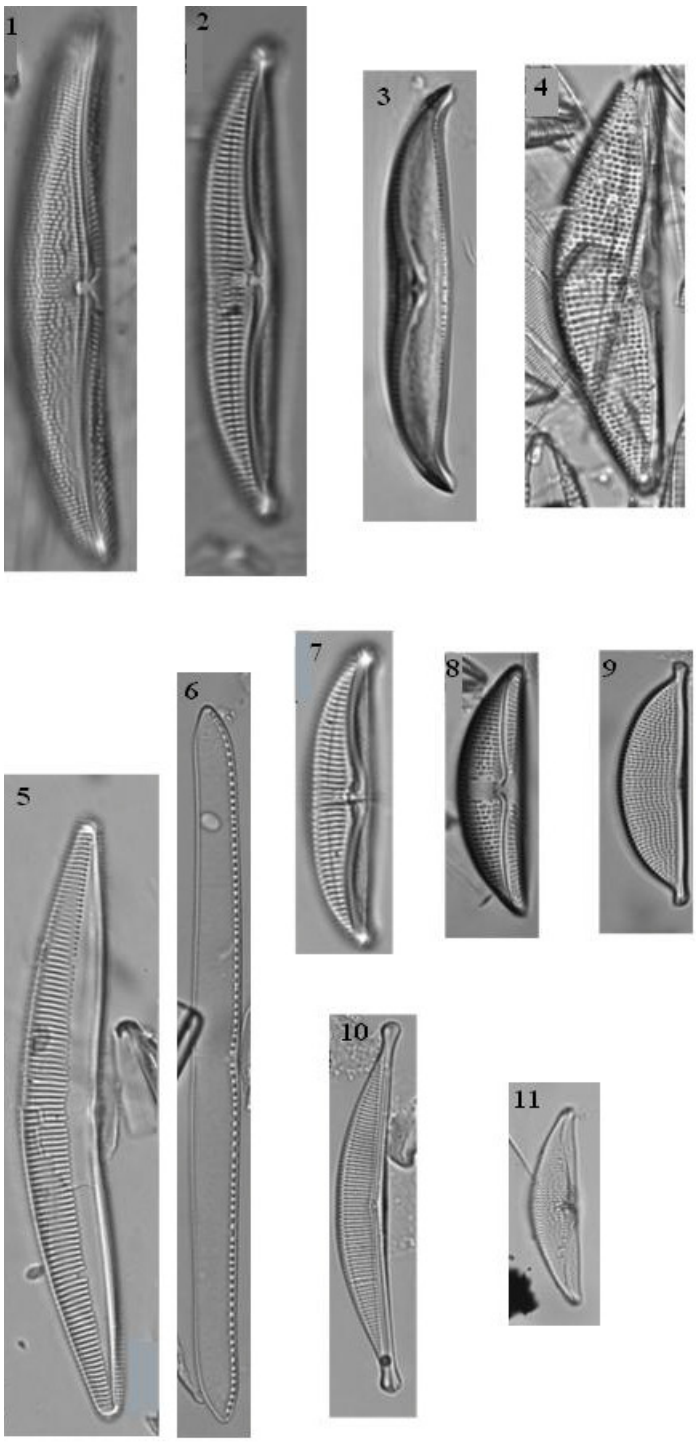
Figure 17-7. *Amphora* sp.4

Figure 17-8. *Amphora copulata*

Figure 17-9. *Amphora corpulenta* var. *capitata*

Figure 17-10. *Amphora cymbifera* var. *heritierarum*

Figure 17-11. *Amphora sulcata*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CHAPTER IV

Periphytic diatom assemblages as indicators of water quality in the Everglades and three tropical karstic wetlands

ABSTRACT

Within the Everglades, periphyton mat total phosphorus (TP) is the best metric for detecting phosphorus (P) enrichment and periphytic diatom assemblages are effective indicators of water quality change. In this study, relationships between diatom assemblages and water quality were investigated in three Caribbean karstic wetlands and cross system diatom inference models were assessed. Periphyton mat TP and diatom assemblage data were generated from samples collected in karstic wetland habitats in Belize, Mexico and Jamaica. Ordination and weighted-averaging modeling techniques were used to examine relationships between periphyton mat TP concentrations and diatom assemblages among the locations. Diatom assemblages changed in relation to periphyton mat TP concentrations, such that "low" and "high" TP assemblages could be identified. Species TP optima and indicator species differed between Everglades and Caribbean locations, however weighted averaging models effectively predicted mat TP concentrations from diatom assemblages for both Everglades (R^2=0.56) and Caribbean (R^2=0.85) locations. This study demonstrates the effectiveness of diatoms as indicators of water quality in Caribbean karstic wetlands. However, the cross system application of diatom based inference models should be employed with caution, as variations in the response of species to water quality reduces the accuracy of model based predictions.

INTRODUCTION

Much of the Caribbean and Central American region is underlain by ancient limestone bedrock (Eocene karst), which, where elevated from the ocean can contain isolated, riverine or tidal freshwater depression wetlands. These wetlands are characterized by low concentrations of water column nutrients and a distinctive biological community, particularly an abundance of thick, calcareous benthic periphyton mats (Rejmánková and Komárková, 2000; Novelo and Tavera, 2003; Gaiser *et al*., 2006; La Hée *et al*., in prep). Because these wetlands are naturally depleted in nutrients, enhanced supplies coming from surface water runoff from agricultural and industrial activities and altered groundwater interactions have long-lasting cascading ecosystem effects (Hagerthey *et al*., 2009) that begin with the microbial community (Gaiser *et al*., 2005). Tools providing an early warning of these changes are valuable, as remediation practices can be established prior to a new hysteretic state is reached (Hagerthey *et al*., 2009). Water column concentration of dissolved or total nutrients is not a useful metric of enrichment history due to high rates of abiotic adsorption and biotic assimilation, even as communities are irrevocably altered when exposed to even low-level increases in nutrient load (Gaiser *et al*., 2005).

Most science on nutrient-induced state changes in karstic wetlands has taken place in the Florida Everglades, an expansive 5,000 km^2 subtropical wetland that has been exposed to decades of enrichment resulting mainly from agricultural development and runoff in the upstream drainage (Willard *et al*., 2001; Winkler *et al*., 2001). Experiments and observations along enrichment gradients developed downstream of

canal inflows have demonstrated that plant productivity is limited by phosphorus (McCormick and O'Dell; McCormick *et al*., 1996), and that very low supplies (<5 ug L^{-1} above ambient) can initiate a state change (Gaiser *et al*., 2005). Excess phosphorus added to natural ecosystems is removed within hours or days by microbial communities existing in periphyton, detritus and sediments (Noe *et al*., 2001), and together with adsorption to associated calcium carbonate (Scinto and Reddy, 2001), these communities maintain water column concentrations below 5-6 ug L-*1* (Thomas *et al*., 2006), except in locations with a long history of enrichment (McCormick *et al*., 1996). Although P is efficiently removed by microbes it drives marked physiological, physical and compositional changes (McCormick and O'Dell, 1996; McCormick *et al*., 2001; Gaiser *et al*., 2005; Iwaniec *et al*., 2006; Munyon, 2010), and persistent increases later lead to changes in soil respiration, macrophyte growth and composition and consumer function (DeBusk *et al*., 2001; Reddy *et al*., 1993; Smith *et al*., 2009).

Native Everglades wetlands are noted for the presence of an abundance of benthic periphyton, referred to as "mats" due to their tendency to grow as attached masses on benthic, submerged and floating substrates (Van-Meter Kasanof, 1973; Browder, 1982; Figure 4-1). These mats can reach extreme standing crops and productivity within this system (Browder *et al*., 1994; Goldsborough and Robinson, 1996; Ewe *et al*., 2006; Gaiser, 2009), that regulates the production of detritus (Neto *et al*., 2006), supports the community of aquatic consumers (Williams and Trexler, 2006; Liston *et al*., 2008), contribute to gas flux (Munyon, 2010, McCormick *et al*., 1996, 1997) and influences soil quality through deposition of calcium carbonate throughout the system. Filamentous cyanobacteria (primarily *Schizothrix* spp. and *Scytonema* spp.) dominate the periphyton

mat assemblage, forming an interwoven structure in which diatoms, green algae, desmids and heterotrophic bacteria grow amid polysaccharide mucilage strands and interstitial deposits of calcium carbonate (Van Meter-Kasanof, 1973; Swift and Nicholas, 1987; Donar *et al*., 2004; Stal, 2000). In addition to rapidly removing TP from the water column, periphyton mats also exhibit marked responses to increases in TP, the most obvious being an anomalous decrease in overall mass and increase in organic content (Pan *et al*., 2000; McCormick *et al*., 2001; Gaiser *et al*., 2006). The response to increased TP is also echoed in the algal assemblage, with a loss of carbonate-precipitating cyanobacteria and a switch from an endemic diatom assemblage to one dominated by 'weedy' benthic taxa (Swift and Nicholas, 1987; Grimshaw *et al*., 1993; McCormick *et al*., 1996; McCormick and O'Dell, 1996; Pan *et al*., 2000). Because the diatom assemblage is particularly diverse and responsive to P, diatom-based P inference models have been developed to infer water (Slate and Stevenson, 2007), soil (Cooper *et al*., 1999) and periphyton mat (Gaiser *et al*., 2006) TP levels, providing a more integrated understanding of P load history than these measurements do directly. Therefore, within the Everglades wetland system, periphytic diatom assemblages have proven to be a highly effective tool for monitoring water quality changes.

Recent studies have identified karstic wetlands within the Caribbean region, with marsh habitats and periphyton mats comparable to those found within the Everglades (Rejmánková, 2001; Novelo *et al*., 2007). In these wetlands, periphyton mat biomass is extremely high and shows a paradoxical negative relationship in response to P enrichment, a pattern which parallels that identified in the Everglades (La Hée *et al*., in prep). These wetlands have a less extensive history of enrichment compared to the

Everglades, however, areas that have been subjected to agricultural and industrial activities exhibit significant changes in water quality and concomitant ecosystem degradation (Rejmánková and Komárková, 2005). The use of diatoms as bioindicators would be valuable in the management of these wetlands. The lack of environmental and species data across much of the region, however, precludes the development of site specific diatom inference models. (Rejmánková, 2001).

Under these circumstances, diatom TP inference models developed within the Everglades may be used to predict environmental changes within Caribbean wetlands. The cross-system application of calibration models has been used in other systems (Weilhoefer and Pan, 2006; Charles *et al*., 2006), as well as in palaeoecological work in which the response of modern diatom flora to present environmental conditions is used to infer past environmental conditions (Battarbee, 1986; Smol *et al*., 1986; Dixit *et al*., 1992b; Fritz *et al*., 1999). The use of cross system models is, however, contingent on the systems being environmentally similar, with an overlapping species assemblage that exhibits a parallel response to water quality change. It is currently not known whether the diatom community within these wetlands are the same as those within the Everglades or if they respond similarly to P.

The main objectives of this study therefore aim to (i) examine periphytic diatom assemblages from karstic wetland habitats in Belize, Mexico and Jamaica, compare these to those found within similar wetland habitats in the Everglades and examine the relationship between periphyton mat TP levels and diatom assemblage at these locations, (ii) determine the feasibility of employing models relating diatom assemblage to water quality in the Everglades to similar systems within the wider Caribbean.

SITE DESCRIPTION

Sampling was conducted in three wetland systems, similar with respect to geology, climate, hydrology and vegetation, located within the northern Caribbean Basin: the Sian Ka'an Biosphere Reserve (and areas to the south), in Quintana Roo, Mexico; the New River Lagoon in Orange Walk, Belize; and the Broad River, in the Black River Morass, St. Elizabeth, Jamaica (Figure 4-2, Table 4-1).

The Sian Ka'an Biosphere Reserve and the wetlands extending beyond its boundary to the south, encompass a 6500 km^2 area along the south eastern coast of the Yucatan Peninsula in Quintana Roo, Mexico (Cairns *et al*., 2005). The Yucatan peninsula is an uplifted marine platform which extends from the greater Yucatan platform and serves as a divide between the Gulf of Mexico and the Caribbean Sea. The geological formation is a 2 to 3 km thick sequence dominated by limestone, with intermittent layers of dolomite, anhydrite and gypsum (Weidie, 1985). The karstic wetland marshes located within the Yucatan region are dominated by low phosphorus, inland freshwater, marl based habitats and coastal mesohaline habitats. The most common freshwater macrophytic species include *Cladium jamaicense* (sawgrass)*, Eleocharis* spp. (spikerush) and *Typha domingensis* (southern cattail), each of which tends to become dominant at low, intermediate and high water depths, respectively (Rejmánková *et al*., 1996). Dwarfed populations of *Rhizophora mangle* (red mangrove) become more abundant as salinity levels increase, and form the dominant tree species in the coastal brackish water marshes. Calcitic periphyton mats are abundant in both freshwater and brackish water habitats with marl substrates (Rejmánková *et al*., 1996). Inland sampling sites were

confined to freshwater, *Eleocharis* spp. Marshes, and closer to the coast, brackish water sites dominated by dwarf *Rhizophora mangle* were sampled.

The New River Lagoon, located in the district of Orange Walk to the north of Belize, is an approximately 23 km long and 750 m wide stretch of the New River, which is the longest river contained entirely within Belize (Meerman, 2006). The area lies just to the southeast of the basal portion of the Yucatan peninsula and exhibits geological features similar to the adjacent landmass (Weidie, 1985). The New River Lagoon is flanked by marshes dominated mainly by *Cladium jamaicense, Eleocharis cellulosa* and *Eleocharis interstincta*, with intermittent deeper pools supporting dense assemblages of *Nymphea ampla* (dotleaf waterlilly). Sampling sites in this area were again confined to *Eleocharis* spp. marshes adjacent to the lagoon.

The Black River Morass encompasses the largest wetland and river system within the Greater and Lesser Antillean archipelago (Davis *et al*., 1998; Massa and Haynes-Sutton, 1998). It lies within the Black River Basin, which occupies an area of approximately 1,488 km^2 in the south-western region of Jamaica. The area is divided into two main sections: the Upper and Lower Morass. The Upper Morass is approximately 97 km^2 (Cronberg, 1983) and is composed of a mass of swampy lowlands with limestone bedrock covered by peat deposits. The Lower Morass which is approximately 57 km^2 (Enell, 1984), exists as an area of down-faulted, poorly karstified limestone, overlain by a relatively thin clay and peat sequence. Inland marsh areas display mixed vegetation dominated by *Cladium jamaicense* and *Eleocharis* spp., with large stands of *Typha domingensis* being present in some areas (Azan and Webber, 2007). Closer to the coast, assemblages dominated by *Rhizophora mangle* are prevalent

and these trees can also be found bordering the main waterways as they meander through the wetland system. Sampling sites were located within *Cladium jamaicense* and *Eleocharis* marshes bordering the Broad River, a major tributary of the Black River.

Data collected from these wetlands were then compared to a larger dataset collected from a total of 134 sites within the Everglades National Park, in southern Florida, U.S.A. The Everglades freshwater wetland system encompasses an area covering approximately 5,000 km^2, and is one of the largest contiguous wetland systems in the North America (McCormick *et al*., 1998; Childers *et al*., 2001). The system is geologically young, having formed less than 5,000 years ago as a result of extended hydroperiod regimes that encouraged the deposition of peat and marl in the midst of a limestone depression (Gleason and Stone, 1994). The vegetation structure of the Everglades marsh habitats is similar to that of the previously described sites, with *Cladium jamaicense* and *Eleocharis* spp. marshes being common and *Nymphaea odorata* (American white waterlilly)*, Nymphaea aquatica* (water shield) and *Nuphar advena* (spatterdock) characterizing deeper slough areas (Gunderson, 1994; Richardson, 2009). For this study, the data utilized were drawn from a large dataset derived from multiple seasonal sampling events conducted throughout the Everglades as part of the Comprehensive Everglades Restoration Plan (CERP, 2005; Gaiser, 2009).

METHODS

Each of the Caribbean study locations was visited on two occasions; once during a wet period and once during a dry period. As a result of abnormal seasonal rainfall

patterns during the study period, wet and dry *periods* did not necessarily coincide with the typical regional wet and dry *seasons*. "Wet" and "dry" designations were therefore applied based on rainfall levels at each location during the sampling period, relative to typical wet and dry seasonal rainfall levels. The Everglades samples were collected during October to December, 2005 (Wet period) and September to December, 2006 (Dry period) as part of the periphyton component of the CERP seasonal sampling regime. The Mexico sites were visited in December 2006 (Wet period) and March 2008 (Dry period), the Belize sites in May 2007 (Dry period) and November 2007 (Wet period), and the Jamaica sites in December, 2007 (Wet period) and May 2008 (Dry period). Efforts were made to conduct sampling at as many sites as possible, however during dry periods the number of sites sampled varied according to the ability to locate areas that sustained water levels greater than 5cm. During wet periods, sampling efforts were contingent on the ability to gain access to sites, and were then limited to sites that did not exceed water depths of approximately 1m.

At each location, sampling sites were limited to three main types of wetland areas: (i) marshes dominated by *Eleocharis* spp. and/or *Nymphaea* spp., (ii) marshes dominated by *Cladium jamaicense* and (iii) swamps dominated by dwarf *Rhizophora mangle*. At each site, GPS coordinates were recorded and sampling was then conducted using a 1-m^2 throw trap to delineate a 1-m^2 area which was treated as a sample plot (Kushlan, 1981). Periphyton mat samples were collected from four plots at each site. At each plot a photograph was taken to record the surface view, and water depth, pH and conductivity were recorded. Periphyton mat material was then collected by hand, placed onto a seine net and coarsely sorted to remove animals, plant material and marl. A subsample of 120

ml was removed from the periphyton material, placed in a sterile sample bag and stored in a cooler with ice for transport to the lab. When no observable calcitic periphyton mats were present, epipelon was sampled from the benthos and epiphytic films were scraped from any macrophytes present.

In the laboratory, each sample was transferred to a clean 500-ml beaker to which an additional 20 ml of distilled water was added to facilitate homogenizing. From the homogenized total volume, a 50-ml sub-sample was removed, poured into a labelled 120-ml sample cup and placed in a drying oven at 80°C until completely dry. The dried contents were then ground using a mortar and pestle and analyzed for TP following the methods of Solórzano and Sharp (1980). An additional 10-ml sub-sample was removed and processed for quantitative diatom analysis, using the sulphuric acid oxidation method of Hasle and Fryxell (1970). A measured amount of cleaned/processed material was then pipetted unto a glass coverslip and permanently fixed to a glass slide using Naphrax ® mounting medium. Diatom species were identified using standard available taxonomic reference sources (See Dissertation Chapter 3) and a minimum of 500 diatom valves were counted along random transects on each slide at a magnification of X 1000, using a Nikon Eclipse E600 ® compound light microscope.

Maximum, minimum and average values for water depth, pH and conductivity were calculated separately for wet and dry periods for each location. No conductivity and pH values were available for the Everglades sites for the period during which samples were collected. The values herein presented were instead derived from data recorded from the same sites during the CERP 2008 wet and dry season sampling episodes, and serve primarily to characterize the physico-chemical features of these sites.

Prior to statistical analysis, periphyton mat TP (TP µg P g^{-1} dry mass) data were log10 transformed and diatom percentage abundance data were fourth root transformed to satisfy assumptions of normality (Clarke and Gorley, 2001). Rare species are often excluded from assemblage analyses because their presence can create a greater amount of "noise" in the data and often reduces the clarity of underlying patterns (McCune and Grace, 2002). Species that occurred in less than 1% of samples *and* at abundances of less than 5% were therefore considered rare and removed from the dataset prior to analyses.

Sampling effort was not the same at all locations, however, provided that samples are collected in a similar manner, from similar habitats and overlap with respect to species composition, the bias of unequal sampling effort can be circumvented by employing rarefaction curves (Tipper, 1979). A rarefaction curve represents an accumulation curve derived from averaging the species richness values observed in a number of randomly selected smaller sub-samples of a fixed size (n), pulled from the larger sample (N) (Siegel and German, 1982). These curves can then be compared among locations to determine whether or not differences in species-area distributions are evident. The shape of each curve reveals information regarding how well the assemblage was sampled relative to its overall richness. Curve shape is generally influenced by both the total number of species present within the sampled assemblage and the evenness of their distribution across sample sites (Hughes *et al*., 2001). Situations in which few species are present and/or species are distributed evenly across sample sites, result in curves which tend more towards a convex shape (i.e., steep initial incline, which begins to level off quickly). When species richness is relatively high and/or species are less evenly distributed across the sampled landscape, the likelihood of finding new species with each

successive sampling event is increased, and this is reflected in the shape of the curve which tends towards a linear form (Hughes *et al*., 2001). The same shape may also occur as a result of small sample size.

Rarefaction curves were generated for each of the four locations and for the combined Caribbean sites using the program EstimateS, Version 8.2.0 ® (Colwell, 2010; see http://viceroy.eeb.uconn.edu/estimates). Both the number of sampling sites and the number of species observed were relativized to their respective totals in order to compare the relationship between sampling effort and number of species observed (i.e., the shape of the curves) across all locations (Hughes *et al*., 2001).

Average per-site species richness and Shannon-Weiner diversity were also calculated for each location, and differences within and among locations were tested for using ANOVA, followed by Tukey's test, using the SPSS ® statistical package. Relationships between richness, diversity and periphyton mat TP at each location were then examined using Pearson's correlation.

Diatom assemblage analyses were conducted using six sets of data: Everglades samples (E), Belize samples (B), Mexico samples (M), Jamaica samples (J), a composite of all the Belize, Mexico and Jamaica sites, collectively referred to as the Caribbean samples (C) and a composite of all sites from all locations (T). An initial analysis was done on the T dataset using Non-metric Multidimensional Scaling (NMDS) (done using the program PCORD 5 ®; McCune and Grace, 2002) and Analysis of Similarity (ANOSIM) (done using the program PRIMER ® version 6; Clarke and Gorley, 2001) to examine differences among sites and locations, based on diatom assemblage. The stress value for the NMDS analysis was reported, along with the global R and significance

values for the ANOSIM analysis. Subsequent ANOSIM pairwise comparative tests were used to evaluate significant differences in diatom assemblage between pairs of sites. The resultant R statistic and significance level were reported. The vector representing the direction and strength of the relationship between periphyton mat TP and diatom assemblage dissimilarity was applied to the NMDS plot and the R^2 reported.

To determine whether or not the diatom assemblage at each site was influenced by sampling period, sites were categorized into wet and dry period samples and NMDS and ANOSIM analyses were then conducted on E, B, M, J and C datasets, using the categorized data to examine differences among the diatom assemblages of "wet" and "dry" TP sites at each location.

To evaluate the relationship between diatom assemblage and TP at each location, sites were first categorized as having either "high" or "low" TP periphyton mats. These designations were derived by first averaging the periphyton mat TP concentrations within a given location and then expressing the TP concentration for any given assemblage at a site within this location, as the deviation away from the local average, as shown below:

$$C = (OTP - ATP)/STP$$

Where C = the designated TP category, OTP = Observed periphyton mat TP concentration at the *site*, ATP = Average periphyton mat TP for the *location* and STP = Standard deviation of periphyton mat TP for *location*. This calculation produces the following categories:

$C < 0$: Site mat TP concentration < Average for location ➔ Designated "Low" TP

$C \geq 0$: Site mat TP concentration ≥ Average for location ➔ Designated "High" TP

The NMDS and ANOSIM analyses were then conducted on E, B, M, J and C datasets, using the categorized data, to examine differences among the diatom assemblages of "high" and "low" TP sites at each location. For each location, regression analysis and Pearson's correlation were used to test for significant linear relationships between the generated NMDS ordination scores and periphyton mat TP. Results are reported for all locations, however NMDS plots are shown for only the E and C datasets. The vector representing the direction and strength of the relationship between periphyton mat TP and diatom assemblage dissimilarity was again applied to each NMDS plot.

The program C2 (Juggins, 2003) was used to determine TP optima and tolerance levels for diatom species and subsequently create weighted averaging models based on the relative abundances of the various diatom species at different periphyton mat TP concentrations. This analysis was initially done for each of the four locations (E, B, M, J), however, the fewer the number of sites included in the analyses, the shorter the length of the TP gradient over which averages can be calculated for each species, and the greater the variation around the calculated average. Relatively small datasets therefore tend to produce less reliable models with elevated prediction errors. For this reason, the Belize, Mexico and Jamaica datasets, which contained 21, 10 and 10 sites respectively, were combined to form a single Caribbean dataset of 41 sites that was analyzed. Only the results for the Everglades and combined Caribbean sites are reported.

For the Everglades and combined Caribbean sites, observed periphyton mat TP was regressed against diatom inferred periphyton mat TP, and the predictive power (R^2) and the bootstrapped root mean square error of prediction (RSME expressed as μg P g^{-1} periphyton mat dry weight) were calculated. Species common to all four locations were

identified, and the TP optima calculated for combined Caribbean sites were regressed against the optima values for the same species at the Everglades sites.

Indicator species analysis (done using PCORD) was conducted to identify species that effectively indicated either "high" or "low" TP concentrations. This analysis again requires a minimum of data points to produce effective estimates and for this reason these analyses were only conducted with the Everglades dataset and the combined Caribbean dataset.

RESULTS

Habitat characteristics among the sampled locations overlapped, with most sites being dominated by *Eleocharis* spp. growing in shallow (<1m) marl based soils, inundated by circumneutral waters. Among all four locations, average pH ranged from 7.2 to 9.2 and average conductivity ranged from 441.8 to 15,047.7 $\mu S\ cm^{-1}$ (Table 4-2). Some sites within two areas at the Mexico location (Mahahual and Marisma) were closer to the coast and supported a macrophytic assemblage dominated by *Rhizophora mangle* and *Eleocharis* spp. At these sites average pH and conductivity levels were greater than all other sites (Table 4-2), which is a result of the influx of brackish-water at these sites.

A total of 187 diatom species representing 45 genera were recorded from the four locations (Table 4-3). Ninety-four of these species were included in diatom assemblage analyses following the removal of rare species. Of these 94 species, 22 were found to be present at all four locations and the most common among these (with average abundances greater than 1% at all locations) were *Brachysira neoexilis, Encyonema evergladianum,*

Encyonema spp., *Fragilaria syngrotesca, Mastogloia smithii* var. *lacustris, Mastogloia smithii, Navicula cryptotenella, Nitzschia palaea* and *Nitzschia serpentiraphe*.

Five rarefaction curves were generated, one for each of the four locations, and an additional curve based on the combined data from the three Caribbean locations (Figure 4-3). The shape of the Everglades curve shows that a large proportion of the species present was captured in a relatively small proportion of the samples collected. This suggests that the assemblage was adequately sampled. The curves generated for the Belize, Mexico, Jamaica and combined Caribbean sites all have practically the same shape, which implies that these assemblages were all sampled with equal effort relative to their overall richness. The actual shape of each of these curves, which tended toward a linear form, suggests that these locations had greater rates of species accumulation, greater diversity and required a greater sampling effort to capture the complement of species present.

Average, per-sample species richness at Everglades sites (14.9) was significantly lower ($p < 0.001$) than Belize, Mexico and Jamaica sites (18.5, 18.7, 21.9 respectively) and the average per-sample species diversity for Everglades and Belize sites (1.59 and 1.66 respectively) were both significantly lower ($p < 0.001$) than Mexico and Jamaica sites (2.00 and 2.01 respectively) (Table 4-4). Species diversity (H) did not show a significant relationship with TP at any of the locations. However, species richness was correlated with TP at the Belize sites ($R^2 = 0.36$, $p < 0.01$).

The NMDS analysis of the diatom assemblages from the four locations showed compositional overlap. There was however some separation of sites, with the Belize dry period assemblages being most distinct (Stress = 0.17; Figure 4-4). The ANOSIM

analysis confirmed the general NMDS pattern, revealing significant differences in diatom assemblages among Everglades and Caribbean sites (global $R = 0.417$; $p < 0.001$). Subsequent pairwise-comparison tests detected significant differences between all pairs of assemblages (All pairwise values for Global $R > 0.36$; $p < 0.02$), except for those from Jamaica wet and Mexico dry (Global $R < 0.27$; $p > 0.09$). The assemblages from the Belize dry period samples were the most different compared to all other assemblages (All pairwise values for Global $R > 0.63$; $p < 0.003$). Compositional dissimilarity among diatom assemblages was correlated with periphyton mat TP (Vector $R^2 = 0.41$) and the Belize dry period assemblages clustered out at the high end of the TP range (Figure 4-4).

The NMDS and ANOSIM analyses conducted on assemblages categorized according to sample period showed an overlapping of "wet" and "dry" period assemblages, with no distinct separation between the groups, except for the clustering out of the Belize dry period sites (ANOSIM Global $R = 0.018$ and $p = 0.011$).

The NMDS analyses of assemblage data categorized according to periphyton mat TP concentrations (i.e., "high" or "low" TP assemblages), showed a separation of high and low TP assemblages within Belize (NMDS stress = 0.14; ANOSIM Global $R = 0.431$ and $p < 0.001$), Mexico (NMDS stress = 0.05; ANOSIM Global $R = 0.516$ and $p < 0.017$), Jamaica (NMDS stress = 0.11; ANOSIM Global $R = 0.321$ and $p < 0.033$), Everglades (Stress = 0.19; ANOSIM Global $R = 0.228$ and $p < 0.001$) (Figure 4-5a), and combined Caribbean sites (Stress = 0.12; ANOSIM Global $R = 0.197$ and $p < 0.001$) (Figure 4-5b). In each of the NMDS plots, diatom assemblage dissimilarity was correlated with periphyton mat TP (Belize: Vector $R^2 = 0.44$; Mexico: Vector $R^2 = 0.46$;

Everglades: Vector $R^2 = 0.436$; Caribbean: Vector $R^2 = 0.564$; $p < 0.05$), except for the Jamaica plot (Vector $R^2 = 0.17$; $p = 0.24$).

Two weighted averaging models were developed on the basis of the relative abundances of the various diatom species at different periphyton mat TP concentrations in the Everglades and for the combined Caribbean sites. Observed periphyton mat TP was regressed against diatom species inferred periphyton mat TP for the Caribbean and Everglades assemblages, respectively (Figure 4-6), and for both models, diatom inferred periphyton mat TP effectively predicted observed periphyton mat TP (Caribbean: $R^2 = 0.85$, RMSE = 66.1 μg TP g^{-1}; Everglades: $R^2 = 0.56$, RMSE = 113.4 μg TP g^{-1})

The TP optima and tolerance levels for all species are presented in Table 4-2. An examination of the 22 species common to all four locations showed that the TP optimum for each of these species was generally lower at the Everglades sites than at the combined Caribbean sites ($p < 0.0001$). Further examination revealed a positive relationship between the Everglades species optima and the Caribbean species optima ($R^2 = 0.53$, $p < 0.001$; Figure 4-7a). When the same 22 species were ranked according to their TP optima at Everglades and Caribbean sites respectively, there was also a positive relationship between the two sets of ranks ($R^2 = 0.50$, $p < 0.001$; Figure 4-7b).

Indicator species analysis identified 17 Everglades species and 11 Caribbean species that indicated either “high” or “low” periphyton mat TP concentrations (Table 4-2). Only one indicator species (*Eunotia flexuosa*) was shared by both Everglades and Caribbean sites, and this species indicated “high” TP concentrations at both locations.

DISCUSSION

This study identified a core diatom assemblage of relatively common species that occurred across all Caribbean locations, which comprised a group of taxa previously documented as common in Everglades marshes. This assemblage, which includes *Brachysira neoexilis, Encyonema evergladianum*, *Encyonema* spp., *Fragilaria syngrotesca*, *Mastogloia smithii* var. *lacustris*, *Mastogloia smithii*, *Navicula cryptotenella*, *Nitzschia palaea* and *Nitzschia serpentiraphe,* is distinctive of, and possibly endemic to, subtropical and tropical freshwater karstic wetlands (Slate and Stevenson, 2000 and 2007; Gaiser *et al* 2006).

Some of these species have been previously recorded in freshwater habitats in Cuba (Foged, 1984) and Jamaica (Podzorski, 1985), and a survey of diatom assemblages from periphyton mats in the El Eden Ecological Reserve in Quintana Roo, Mexico, (Novelo *et al*., 2007; Ibarra *et al*., 2009). The current study is, however, the first to describe this distinctive core assemblage from periphyton mats in Belize and Jamaica.

Despite the ubiquitous presence of this core assemblage among the locations, there were some compositional differences among the four locations and among sites within each location. This variation is often seen as a result of natural habitat heterogeneity and microhabitat variability (Weilhoefer and Pan, 2006), but may also be due, in part, to the influence of environmental variables other than TP that were not evaluated in this particular study. The greatest disparity in assemblages among the locations involved the separation of the Belize dry period samples from all other

assemblages. These samples were collected during an intense drought period from *Eleocharis* spp. marshes located adjacent to a river lagoon and are likely influenced by periodic, inland excursions of lagoon water. Periphyton samples at these sites were non-calcitic, unconsolidated and had elevated phosphorus levels, which is symptomatic of the form of periphyton present under conditions of deep water, with elevated phosphorus concentrations (McCormick and O'Dell, 1996). As such mat types were rare at other sites in this study, these samples were recognized as different in the community analyses.

Differences in sampling effort among locations could influence derived diversity and richness estimates owing to the possibility of an underestimation of diversity at under-sampled sites (Hughes *et al*., 2001). However, differences in the shapes of the Everglades, Belize, Mexico, Jamaica and combined Caribbean rarefaction curves showed that even though fewer sites were sampled at each of the Caribbean locations, periphyton mats from those locations supported a greater number of diatom species than those from the Everglades. This result, which was reinforced by the examination of average per-site richness and diversity, suggests that the Everglades diatom flora has a lower diversity than the compared Caribbean karstic wetland flora, however, the underlying reason for this is unclear.

The level of species diversity within a given locale is determined by a combination of factors. These include, but are not limited to: the distance between the locale and possible species source locations, the availability and efficiency of transport mechanisms, the frequency of immigration and emigration events, competitive interactions, habitat heterogeneity, evolutionary processes of speciation, stochastic disturbances and the length of time over which these factors are allowed to exert their

various influences (Rosenzweig, 1997; Kristiansen, 1996; Hubbell, 2001; Charalambidou and Santamaria, 2002; Figuerola and Green 2002). The geographically isolated position of the Everglades and its relatively young geological age (ca. 5,000 years old) support the assumption that diatom assemblages may have developed following a process of species introductions from older regional wetlands (Slate and Stevenson, 2007). This would explain why the locations all share a core diatom assemblage, which under this scenario would have first developed in the older wetlands and subsequently been introduced to the Everglades following a series of dispersal events. This could also help to explain the lower diversity exhibited by the Everglades sites compared to the Caribbean sites. First, the Everglades system would be dependent on continuous introductions from the older systems to enhance the number of species present and it is reasonable to assume that the younger system (sink) would consistently have lower numbers of species than the older systems (source pools) until an equilibrium level is attained (Ricklefs, 1979). Second, in addition to species numbers increasing due to introductions, species numbers may also increase as a result of local speciation events. Again, it is expected that older systems would have a longer period over which such events could occur, compared to younger systems (Ricklefs, 1979). Both of these ideas suggest that the younger Everglades would have had less time to develop a more diverse flora than the older Caribbean sites.

The latitudinal diversity gradient, which is evidenced by the reduction in species richness with distance from the tropics, has been best documented in plant and animal communities from terrestrial and marine systems (Willig *et al*., 2003). The pattern of change in diversity has not been sufficiently examined as a forcing factor in freshwater, microbial communities (Leighton, 2005; Hillebrand, 2004), but could potentially

influence diatom diversity patterns, such that subtropical systems such as the Everglades would have lower diversity than the more tropical Caribbean locations. It is also possible that the diversity of diatom species in the Everglades is restricted by particular features of the subtropical climate that are not experienced in the more tropical Caribbean locations. Foremost among these climatic features is temperature, which exhibits greater extremes in the sub-tropical Everglades wetland than in the tropical Caribbean wetlands. Under these conditions, species diversity in the Everglades may be limited to those that can tolerate the fluctuations in temperatures, whereas the more moderate tropical climate would support a wider range of species.

The influence of season on diatom assemblages was examined to rule out the possibility of seasonal effects masking or enhancing the influence of TP on diatom assemblages. Seasonal variability in light and temperature in the subtropics and tropics are muted relative to temperate ecosystems, so the greatest seasonal change experienced by subtropical and tropical wetlands is through the hydrologic response to pronounced seasonal differences in precipitation (McCormick *et al*., 1998; Thomas *et al*., 2006; Gottlieb *et al*., 2006). Seasonal changes in periphyton mats have been noted to occur within the Everglades, particularly a shift from dominance by filamentous cyanobacteria during the wet season, to diatoms during the dry season (McCormick *et al*., 1998). Although water depth is known to affect the spatial distribution of diatoms (Gaiser *et al*., 2009), differences in diatom assemblages between wet and dry periods have not been reported, and no such differences were found in the current study. Similarly, while spatial variation in water depth and periphyton TP are usually correlated (Gaiser *et al*., 2010), an examination of seasonal patterns in periphyton mat TP showed no differences between

periphyton mat TP during wet and dry periods, except for at the Belize sites where the lagoonal dry period samples exhibited elevated TP levels.

The relationship between diatom assemblages and TP availability demonstrated in experimental and observational studies in the Everglades (McCormick *et al*., Cooper *et al*., Gaiser *et al*., 2005) have led to the development of diatom-based prediction models (Gaiser *et al*., 2006) that are now employed in system-wide habitat assessment (Gaiser *et al*., 2009). While these models provide a more accurate and meaningful assessment of habitat state than previous work on the subject, their findings have highlighted yet another important consideration, i.e. the validity of cross-system applications of these models. In a study examining periphyton responses to eutrophication within the Everglades, Gaiser *et al*. (2006) found that "ambient" periphyton mat TP levels from un-impacted wetland areas varied from 97 to 430 μg P g-1 dry mass. This variation in periphyton mat TP levels among sites produced associated variations in diatom assemblage response to TP, such that a unique calibration model had to be produced for each individual wetland basin and no one model could be used to reliably infer quantitative TP levels across all sites. This indicated that instead of responding to absolute periphyton mat TP levels, diatom species were instead responding to relative changes in periphyton mat TP at each site.

In the current study, periphyton mat TP level at any given site was expressed as its deviation away from the local average periphyton mat TP level, instead of as an absolute value. Using this method, a clear pattern emerged, in which distinct "high" TP (above average) and "low" TP (below average) diatom assemblages could be identified at all locations. This implies that for a diatom assemblage within any given location, there

is a defined response to changes in TP, relative to the baseline TP level for that area, as opposed to a standard response to a general threshold TP value that applies across sites.

This pattern was also evident in the species optima and tolerances, which differed among locations, but when ranked, revealed a consistent pattern in which species "preferences" for low or high TP levels were similar among locations. Subsequent analyses also identified species that were indicative of either high or low TP levels, though only one of these species (*Eunotia flexuosa*, which indicated "high" mat TP concentrations) was shared by both Everglades and Caribbean locations. The Everglades indicator species identified in this study were the same as those identified by Gaiser *et al*., (2005), including *Eunotia flexuosa*, *Navicula cryptotenella*, *Eunotia incisa*, *Rhopalodia gibba* and *Nitzschia amphibia* as indicators of elevated periphyton mat TP levels and *Mastogloia smithii* as an indicator of low periphyton mat TP levels. Several other studies have identified *Mastogloia smithii* as an indicator of TP levels in the Everglades (McCormick *et al*., 1996; Cooper *et al*., 1999; Pan *et al*., 2000; Slate and Stevenson, 2007), and it has been proposed as potential keystone taxon in these mats (Gaiser *et al*., 2010).

At both Everglades and Caribbean locations there was a strong relationship between diatom-inferred and observed periphyton mat TP, confirming that diatom assemblages can be used to infer periphyton mat TP in these wetlands. While both models were strong, the model produced for the combined Caribbean locations was more robust with a higher R^2 and lower RMSE than the model for the Everglades location. This is likely due to fact that a greater number of sites were sampled in the Everglades, which would have introduced greater variability in habitat and environmental factors that

may influence diatom assemblages and reduce the strength of the phosphorus signal (Slate, 1998).

The results of this study are consistent with findings from other work examining relationships between diatom assemblages and water quality across spatial expanses, and support the growing concern regarding the cross-system application of diatom-based water-quality assessment tools (Potapova and Charles, 2007). Diatom species assemblages, as well as the specific responses of individual species to environmental factors, can vary considerably even within habitat and/or geographic boundaries (Pipp, 2002; Kelly *et al*., 1998; Charles *et al*., 2006; Gaiser *et al*., 2006) and this can reduce the predictive power of models developed outside the target system. In addition, discrepancies in diatom taxonomic identification often arise when work is conducted by multiple investigators and this can reduce comparability of data across systems. However, diatom based monitoring techniques remain a powerful tool for water quality assessment and the careful application of this technique for the purposes of wetland monitoring and management within karstic wetlands in the Caribbean region should be encouraged. The development of site-specific models relating diatom assemblages to water quality would provide the most reliable and accurate information for use in biomonitoring programs within these systems. However, in the absence of data to develop such models, the cross-system application of inference models developed for the well-studied Everglades system may suffice, but only as a means of determining relative, as opposed to absolute, water quality state.

CONCLUSIONS

The findings of this study have shown that the karstic wetlands of the South Florida Everglades share a number of similar features with those of Belize, Mexico and Jamaica, including a distinctive diatom flora that is likely characteristic of these types of habitats within the northern Caribbean region. Diatom assemblages within these habitats change in relation to periphyton mat TP concentrations, such that "low" and "high" TP assemblages can be identified. Species TP optima and indicator species differed between Everglades and Caribbean locations, however high-quality weighted averaging models effectively predicted mat TP concentrations from diatom assemblages for both Everglades and Caribbean locations.

The use of diatoms in aquatic biomonitoring programs has been well established for lakes (e.g. Dixit and Smol, 1994), rivers (e.g., Charles, 1996; Stevenson and Pan, 1999) and to a lesser extent, wetlands (e.g., Pan and Stevenson, 1996). The development of various standardized diatom indices (e.g., Lowe, 1974; van Dam *et al*., 1994) and diatom-based inference models (e.g., Gaiser *et al*., 2006) has allowed a more quantitative approach to water quality assessment and encourages cross system comparisons. Challenges arise, however, when intrinsic ecosystem variability reduces the predictive power of these indices and models, even when applied within and across similar systems (Gaiser *et al*., 2006; Weilhoefer and Pan, 2006; Charles *et al*., 2006).

This current study provides an example of the value of diatoms as bioindicators for inferring water quality in karstic wetlands, but emphasizes the need for caution when applying diatom inference models across systems. While this strategy may on occasion

be the only recourse available, in the absence of a robust monitoring program even moderate sampling within a given system can provide valuable supplementary information regarding water quality.

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Table 4-1. Location of Caribbean sampling sites, presented as latitudinal and longitudinal bounding GPS coordinates of sampling sites within each location.

	Sian Ka'an National Park, Quintana Roo, Mexico	New River Lagoon, Indian Church, Belize	Slipe River, Black River Morass, St. Elizabeth, Jamaica
EAST	087º30.585	88º37.958'	78 ˚ 46.972
WEST	087º57.579	88º39.212'	77 ˚ 48.874
NORTH	19º52.342	17º47.111'	18 ˚ 03.182
SOUTH	18º47.223	17 ˚ 37.166	18 ˚ 01.524

Table 4-2. Number of sites sampled (N), water characteristics and periphyton attributes for each location during wet and dry periods. Average values are given along with standard deviation values in brackets. Missing data are indicated with a dash (−).

SITE	N	pH	Conductivity ($\mu S\ cm^{-1}$)	Water depth (cm)	Total Biovolume ($ml\ m^{-2}$)	Biovolume ($ml\ m^{-2}$)	TP ($\mu g\ P\ g^{-1}$ DM)	Dry Mass ($g\ m^{-2}$)	Organic content (%)	Ash Free Dry Mass ($g\ m^{-2}$)	Chlorophyll ($\mu g\ m^{-2}$)	Chlorophyll concentration ($\mu g\ g^{-1}$ DM)
Belize Wet	12	7.3 (0.5)	441.8 (208.6)	73.2 (8.5)	876.0 (1474.8)	857.1 (1486.4)	239.7 (106.7)	77.1 (133.4)	67.8 (19.1)	30.1 (48.2)	140.2 (132.7)	48.3 (52.5)
Belize Dry	9	8.3 (0.2)	690.3 (104.0)	31.6 (11.8)	101.6 (264.6)	101.6 (264.6)	543.1 (187.9)	3.2 (6.7)	37.4 (17.9)	1.5 (3.0)	1288.5 (2602.0)	260.6 (175.0)
Jamaica Wet	5	7.9 (0.2)	522.6 (62.4)	9.6 (3.6)	-	-	405.2 (158.3)	-	-	-	-	-
Jamaica Dry	5	8.4 (0.5)	447.6 (137.3)	11.6 (12.7)	2251.3 (1712.6)	2251.3 (1712.6)	200.3 (16.5)	156.0 (104.8)	28.7 (7.2)	39.4 (25.5)	29693.0 (19940.6)	222.5 (83.1)
Mexico Wet	6	-	1259.0 (952.5)	37.9 (10.3)	7460.7 (3043.8)	6772.6 (2957.6)	212.5 (93.7)	365.0 (195.5)	37.9 (7.4)	121.4 (49.5)	37195.4 (12261.7)	129.7 (51.5)
Mexico Dry	4	9.2 (0.4)	15047.7 (16670.5)	30.3 (23.4)	4564.3 (2568.5)	4144.6 (2720)	193.7 (210.9)	317.4 (233.9)	42.5 (15.5)	109.4 (76.5)	133456.4 (153012.9)	465.3 (257.1)

Table 4-3. List of non-rare species (> 1% average abundance) showing the number of locations (N) at which each species was found, along with its average percentage abundance at each location: Everglades (E), Belize (B), Mexico (M), Jamaica (J) and Caribbean locations combined (C). Species absence from a location is indicated with a dash (−). TP optimum and tolerance values (TP Opt (Tol)) are given for the 22 species that were present at all locations and indicator species (I) are identified as indicating high or low TP for the Everglades (** = high TP; * = low TP) and Caribbean (ᵗᵗ = high TP; ᵗ = low TP) locations.

	N	Average % abundance				TP Opt (Tol)		I	
TAXON		E	B	M	J	E	C		
Achnanthidium neomicrocephalum H. Lange-Bertalot & F. Staab	4	1.4	27.0	0.7	1.2	191 (24)	442 (33)	ᵗᵗ	
Brachysira neoexilis Lange-Bertalot	4	7.8	25.3	5.9	7.6	147 (23)	273 (32)		
Cyclotella meneghiniana Kützing	4	0.4	0.4	1.2	0.4	163 (27)	289 (29)		
Diploneis oblongella (Naegelii ex. Kutzing) Ross	4	0.6	0.2	0.9	1.9	128 (19)	225 (27)		
Diploneis parma Cleve	4	0.7	0.2	0.3	1.5	137 (24)	235 (30)		
Encyonema evergladianum Krammer	4	23.2	16.3	20.3	29.6	146 (22)	229 (28)	ᵗ	
Encyonema sp. 5	4	3.4	1.7	5.8	3.3	177 (26)	230 (27)		**
Encyonema sp. 6	4	0.6	0.2	0.6	0.1	177 (26)	230 (27)		
Encyonopsis microcephala (Grunow) Krammer in Krammer	4	2.7	0.2	1.1	10.8	189 (29)	334 (25)		**
Eunotia flexuosa (Brébisson) Kützing	4	0.6	0.5	0.2	0.5	239 (30)	368 (25)	ᵗᵗ	**
Fragilaria nanana Lange-Bertalot	4	0.7	2.8	3.5	2.2	199 (26)	263 (29)		
Fragilaria synegrotesca Lange-Bertalot	4	11.2	14.0	6.0	6.6	168 (25)	266 (29)		**
Fragilaria ulna var. *ulna* (Nitzsch) Lange-Bertalot	4	1.0	2.3	0.2	0.6	266 (32)	281 (31)		
Gomphonema cf. *vibriodes* Reichardt & Lange-Bertalot	4	0.9	1.7	4.0	0.2	206 (26)	406 (32)	ᵗᵗ	
Gomphonema intricatum var. *vibrio* (Ehrenberg) Cleve	4	0.9	1.2	0.5	0.7	172 (26)	329 (32)		**
Mastogloia cf. *smithii* Thwaites ex. W. Smith	4	37.6	6.3	21.8	6.7	152 (24)	240 (29)		*
Mastogloia smithii var. *lacustris* Grunow	4	2.5	1.8	1.6	0.4	128 (20)	239 (26)		
Navicula cf. *radiosa* Kutzing	4	0.9	1.2	1.6	1.0	198 (27)	282 (35)		**

Table 4-3. C'tnd.

TAXON	N	Average % abundance				TP Opt (Tol)		I	
		E	B	M	J	E	C		
Navicula cryptotenella Lange-Bertalot	4	1.6	1.2	1.7	1.1	190 (29)	332 (30)		**
Navicula subtilissima Cleve	4	1.1	1.4	0.3	1.2	154 (24)	291 (35)		
Nitzschia palaea (Kutzing) W. Smith	4	4.3	2.3	6.6	7.1	120 (18)	222 (24)		*
Nitzschia serpentiraphe Lange-Bertalot	4	4.0	1.2	3.1	3.5	109 (17)	180 (18)		*
Sellaphora laevissima Krammer	4	0.6	0.2	0.5	0.4	138 (22)	321 (33)		
Caponea caribbea Podzorski	4	0.7	0.2	0.2	0.2				
Nitzschia lacunarum Hustedt in A. Schmidt *et al*.	4	0.4	0.2	0.2	0.3				
Encyonema silesiacum (Bleisch) Mann	3	4.5	0.4	0.3	-				**
Eunotia camelus Ehrenberg	3	6.7	5.1	0.9	-			‡‡	
Navicella pusilla (Grunow) Krammer	3	0.3	0.2	5.8	-				
Encyonopsis subminuta Krammer et Reichardt	3	-	0.2	3.2	3.5				
Navicula heimansioides Lange-Bertalot	3	-	0.9	0.3	0.3				
Nitzschia semirobusta Lange-Bertalot	3	-	4.5	9.6	12.0				
Achnanthidium sp. 2	3	0.8	0.5	-	0.3			‡‡	
Cocconeis placentula Ehrenberg	3	0.2	0.3	-	0.1				
Fragilaria capucina var. *vaucheriae*	3	0.1	0.2	-	0.1				
Gomphonema gracile Ehrenberg	3	0.8	0.3	-	0.2				
Nitzschia nana Grunow in Van Heurck	3	1.3	0.9	-	0.6				
Pinnularia microstauron (Ehrenberg) Cleve	3	0.6	0.2	-	0.2				
Sellaphora pupula (Kützing) Mereschkowsky	3	0.9	0.7	-	0.2				
Gomphonema affine Kützing	3	0.6	-	0.4	0.5				
Amphora sulcata (Brébisson) Cleve	3	8.9	-	3.0	2.4			‡	

Table 4-3. C'ntd.

TAXON	N	Average % abundance E	B	M	J	TP Opt (Tol) E	C	I
Brachysira brebissonii Ross	2	1.2	34.5	-	-			
Eunotia cf. *monodon* Ehrenberg	2	0.3	1.6	-	-			
Eunotia rhabenhorstiana (Patrick) Metzeltin & Lange-Bertalot	2	0.3	0.8	-	-			
Frustulia rhomboides var. *crassinervia* (Brebisson ex. W. Smith) Ross	2	0.6	0.3	-	-			
Neidium ampliatum (Ehrenberg) Krammer	2	0.3	0.3	-	-			
Nitzschia amphibia Grunow	2	0.7	14.9	-	-			
Stenopterobia curvula (W. Smith) Krammer	2	0.3	0.2	-	-			
Eunotia cf. *karenae* Metzeltin & Lange-Bertalot	2	-	1.8	0.4	-			tt
Gomphonema maclaughlinii Reichardt	2	-	0.2	0.2	-			
Nitzschia denticula Grunow	2	-	13.4	5.4	-			
Nitzschia microcephala Grunow	2	-	0.8	1.1	-			
Pinnularia sp. 1	2	-	0.3	0.3	-			
Plagiotropis sp. 1	2	-	1.8	0.2	-			
Diploneis oblongella (Naegeli ex Kuetzing) Ross	2	-	-	0.2	0.6			
Diploneis sp. 1	2	-	-	0.2	0.1			
Nitzschia tubicola Grunow	2	-	-	14.1	2.8			t
Rhopalodia sp. 1	2	-	-	0.6	1.1			
Achnanthidium exiguum (Grunow) Czarnecki	2	-	2.8	-	0.4			tt
Achnanthidium sp. 1	2	-	2.8	-	0.2			
Amphora ovalis (Kützing) Kützing	2	-	0.3	-	0.3			
Caloneis sp. 2	2	-	0.2	-	0.4			
Encyonopsis sp. 1	2	-	0.3	-	0.1			
Eunotia sp. 2	2	-	0.3	-	0.3			

Table 4-3. C'ntd.

TAXON	N	Average % abundance E	B	M	J	TP Opt (Tol) E	C	I	
Mastogloia elliptica (Agardh) Cleve	2	-	3.5	-	2.0				
Staurosira construens Ehrenberg	2	-	1.9	-	0.5				
Staurosirella pinnata var. *pinnata* (Ehrenberg) Williams & Round	2	-	5.5	-	0.1				
Synedra acus var. *angustissima* Ehrenberg	2	-	0.6	-	0.1			‼	
Navicula sp. 2	2	-	0.7	-	0.1				
Mastogloia lanceolata Thwaites ex. W. Smith	2	1.2	-	9.4	-				
Rhopalodia gibba (Ehrenberg) O. Muller	2	0.4	-	-	3.9				**
Amphora holsatica Hustedt	1	0.6	-	-	-				
Amphora sp.7	1	0.4	-	-	-				
Brachysira aponina Kützing	1	0.5	-	-	-				
Brachysira procera Lange-Bertalot & Moser	1	0.9	-	-	-				
Brachysira pseudoexilis Lange-Bertalot & Moser	1	1.5	-	-	-				*
Brachysira serians (Brebisson ex Kutzing) Round & Mann	1	0.2	-	-	-				
Brachysira vitrea (Grunow) Ross	1	0.7	-	-	-				
Cyclotella pseudostelligera	1	0.6	-	-	-				
Cymbella sp. 1	1	0.7	-	-	-				
Encynoconposis sp. 1	1	0.4	-	-	-				
Encyonema silesiacum var. *elegans* Krammer	1	1.7	-	-	-				
Encyonema sp. 1	1	0.6	-	-	-				
Encyonema sp. 2	1	0.3	-	-	-				
Encyonema sp. 4	1	0.9	-	-	-				
Eunotia incisa W. Smith ex. Gregory	1	0.4	-	-	-				**

Table 4-3. C'ntd.

TAXON	N	Average % abundance E	B	M	J	TP Opt (Tol) E	C	I
Eunotia naegelii Migula	1	0.4	-	-	-			**
Eunotia sp. 1	1	0.8	-	-	-			**
Fragilaria cf. *ulna* (Nitzsch) Lange-Bertalot	1	0.9	-	-	-			
Fragilaria sp. 1	1	0.4	-	-	-			
Fragilariforma virescens var. *capitata* (Ralfs) Williams & Round	1	0.5	-	-	-			
Gomphonema auritum Braun	1	0.4	-	-	-			
Gomphonema coronatum Ehrenberg	1	0.4	-	-	-			
Gyrosigma obscurum (W. Smith) Griffith & Henfrey	1	0.3	-	-	-			
Navicula radiosafallax Lange-Bertalot	1	0.6	-	-	-			
Nitzschia amphibia (Grunow) Lange-Bertalot	1	0.8	-	-	-			**
Nitzschia cf. *obtusa*	1	0.7	-	-	-			
Pauliella taeniata (Grunow) Round & Basson	1	0.7	-	-	-			
Pinnularia cf. *gibba*	1	0.5	-	-	-			
Pinnularia sp. 5	1	0.5	-	-	-			
Pinnularia stomatophora (Grunow) Cleve	1	0.4	-	-	-			
Pinnularia viridiformis Krammer	1	0.4	-	-	-			
Sellaphora sp. 1	1	0.4	-	-	-			
Stauroneis javanica (Grunow) Cleve	1	0.6	-	-	-			
Stauroneis phoenicentron (Nitzsch) Ehrenberg	1	0.3	-	-	-			
Anomoneis cf. sphaerophora morph 2	1	-	0.5	-	-			
Aulacoseira granulata (Ehrenberg) Simonsen	1	-	3.0	-	-			
Brachysira pumila Metzeltin & Lange-Bertalot	1	-	16.4	-	-			
Caloneis sp. 1	1	-	0.3	-	-			

Table 4-3. C'ntd.

TAXON	N	Average % abundance				TP Opt (Tol)		I
		E	B	M	J	E	C	
Craticula cuspidata (Kützing) Mann	1	-	0.2	-	-			
Craticula sp.1	1	-	0.2	-	-			
Cymbella aspera (Ehrenberg) Cleve	1	-	0.7	-	-			
Epithemia sp. 1	1	-	0.7	-	-			
Eunotia flexuosa (Brébisson) Kützing _2	1	-	0.4	-	-			
Eunotia implicata Nörpel, Lange-Bertalot & Alles	1	-	0.3	-	-			
Eunotia sp. 5	1	-	0.2	-	-			
Eunotia sp. 6	1	-	0.5	-	-			
Eunotia sp. 9	1	-	0.2	-	-			
Fallacia pygmaea (Kützing) Stickle & Mann	1	-	1.4	-	-			
Gomphonema parvulum (Kützing) Grunow	1	-	0.2	-	-			
Gomphonema sp. 1	1	-	3.5	-	-			
Hantzschia spectabilis (Ehrenberg) Hustedt	1	-	0.2	-	-			
Mastogloia elliptica var. *dansei* (Thwaites) Cleve	1	-	0.8	-	-			
Navicula brasiliana (Cleve) Cleve	1	-	0.4	-	-			
Navicula constans Hustedt	1	-	0.4	-	-			
Navicula densilineolata (Lange-Bertalot) Lange-Bertalot	1	-	0.2	-	-			
Neidium cf. densestriata Hustedt	1	-	0.2	-	-			
Nitzschia scalaris (Ehrenberg) W. Smith	1	-	0.2	-	-			tt
Pinnularia acrosphaeria (Brébisson) W. Smith	1	-	0.3	-	-			
Pinnularia neomajor	1	-	0.2	-	-			
Pinnularia sp. 3	1	-	0.4	-	-			

Table 4-3. C'ntd.

TAXON	N	Average % abundance				TP Opt (Tol)		I
		E	B	M	J	E	C	
Pinnularia stoermeri	1	-	0.2	-	-			
Pinnularia streptoraphe	1	-	0.3	-	-			
Sellaphora pupula var. *aquaeductae*	1	-	0.2	-	-			
Stauroneis phoenicentron	1	-	0.4	-	-			
Stauroneis smithii Grunow	1	-	0.7	-	-			
Surrirella elegans Ehrenberg	1	-	0.9	-	-			
Unknown species 05	1	-	0.2	-	-			
Amphora cymbifera var. *heritierarum* Wachnicka & Gaiser	1	-	-	0.5	-			
Amphora sp.3	1	-	-	0.2	-			
Amphora sp.6	1	-	-	0.5	-			
Amphora sp.8	1	-	-	0.2	-			
Anomoneis sphaerophora (Ehrenberg) Pfitzer	1	-	-	0.2	-			
Brachysira cf. *hofmanniae* Lange-Bertalot	1	-	-	1.1	-			
Cyclotella litoralis Lange & Syvertsen	1	-	-	0.2	-			
Diploneis sp. 2	1	-	-	0.4	-			
Hantzschia vivacior Lange-Bertalot	1	-	-	0.2	-			
Mastogloia braunii Grunow	1	-	-	1.0	-			
Mastogloia sp. 4	1	-	-	0.3	-			
Navicula palistinae Gerloff, Natour & Rivera	1	-	-	1.3	-			
Navicula palistinae morph 2	1	-	-	0.2	-			
Navicula pseudocrassirostris Hustedt	1	-	-	2.7	-			
Navicula sp. 5	1	-	-	0.2	-			
Navicula sp. 6	1	-	-	1.2	-			

Table 4-3. C'ntd.

TAXON	N	Average % abundance				TP Opt (Tol)		I
		E	B	M	J	E	C	
Nitzschia sp. 2	1	-	-	0.9	-			
Nitzschia sp. 4	1	-	-	2.2	-			
Pinnularia sp. 2	1	-	-	0.6	-			
Pleurosigma sp. 1	1	-	-	0.3	-			
Proschkinia sp. 1	1	-	-	1.5	-			
Seminavis eulensteinii (Grunow) Danielidis, Ford & Kennett	1	-	-	0.2	-			
Actinocyclus normanii (Gregory ex Greville) Hustedt	1	-	-	-	0.3			
Diploneis sp. 3	1	-	-	-	0.2			
Diploneis sp. 4	1	-	-	-	0.2			
Diploneis sp. 5	1	-	-	-	0.2			
Encyonema jemtlandicum var. *venezolanum* Krammer	1	-	-	-	4.0			
Encyonema sp. 3	1	-	-	-	0.8			
Encyonema vulgare var. *vulgare* Krammer	1	-	-	-	1.1			
Fragilaria (?) sp. 1 cf. *famelica* (Kützing) lange-Bertalot	1	-	-	-	1.7			
Mastogloia cf. *braunii*	1	-	-	-	0.5			
Navicula sp. 1	1	-	-	-	0.2			
Navicula sp. 7	1	-	-	-	0.4			
Neidium sp. 1 cf. *juba*	1	-	-	-	0.1			
Nitzschia sp. 5	1	-	-	-	0.4			
Nitzschia sp. 6	1	-	-	-	0.5			
Nitzschia thermaloides Hustedt	1	-	-	-	0.5			
Pinnularia sp. 4	1	-	-	-	0.1			
Tabularia tabulata (Agardh) Snoeijs	1	-	-	-	0.7			

Table 4-4. Average per-site species richness (S) and diversity (H) for all locations. Standard deviations are indicated in parentheses. Significantly low values ($p < 0.001$) are indicated with an asterisk (*).

Site	No. of samples	Total no. of species	S	H
Belize	21	113	18.48 (6.51)	1.67 (0.49) *
Mexico	10	84	18.70 (4.45)	2.00 (0.33)
Jamaica	10	87	21.90 (4.41)	2.01 (0.22)
Everglades	134	87	14.88 (3.40) *	1.59 (0.30) *

Figure 4-1. Benthic (a) and epiphytic (b) periphyton mat specimens collected from karstic marsh habitats.

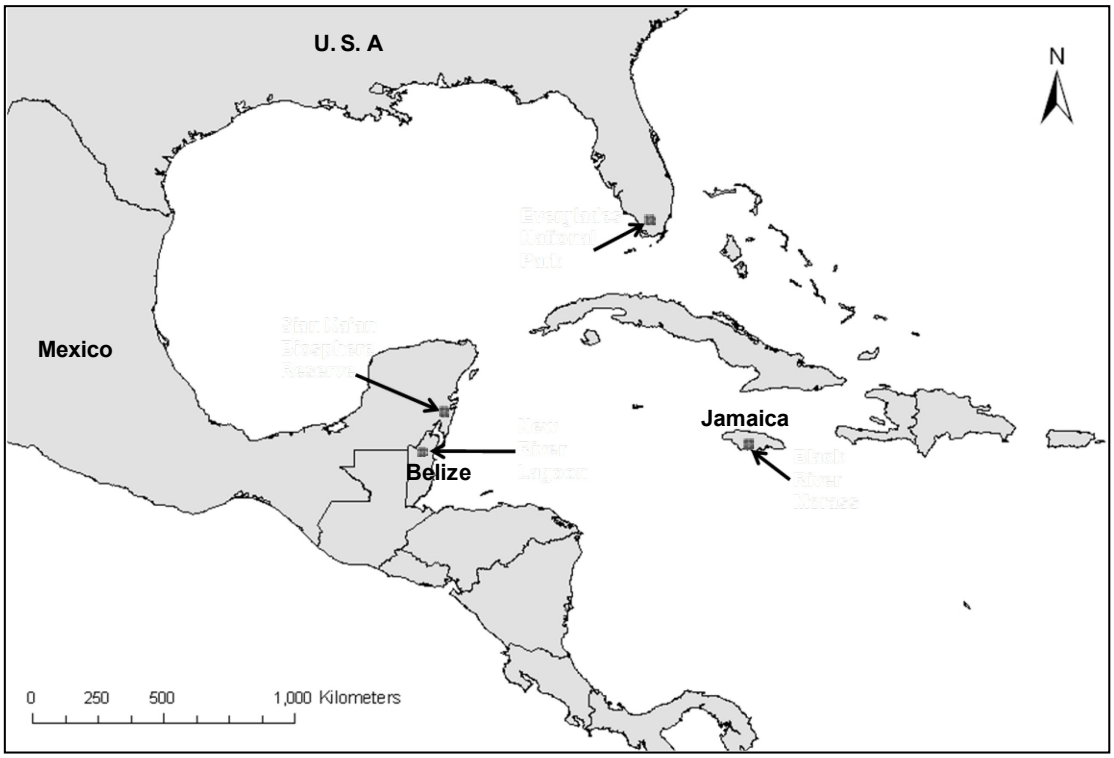

Figure 4-22. Map of northern Caribbean region showing the four sampling locations for this study.

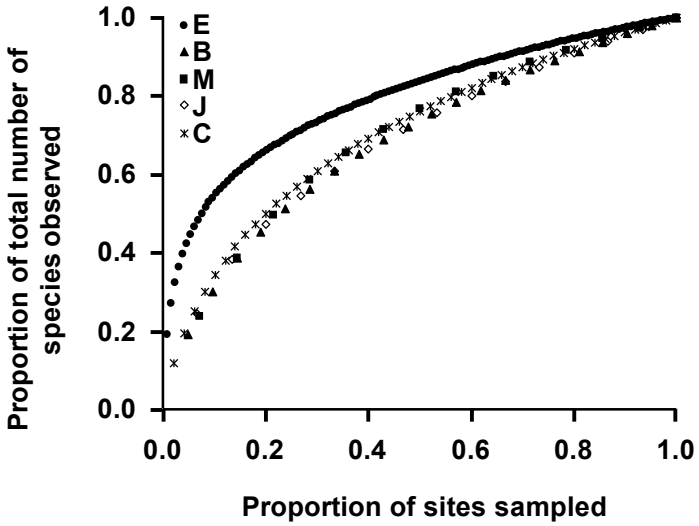

Figure 4-3. Rarefaction curves generated for Everglades samples (E), Belize samples (B), Mexico samples (M), Jamaica samples (J) and a composite of the Caribbean samples (C).

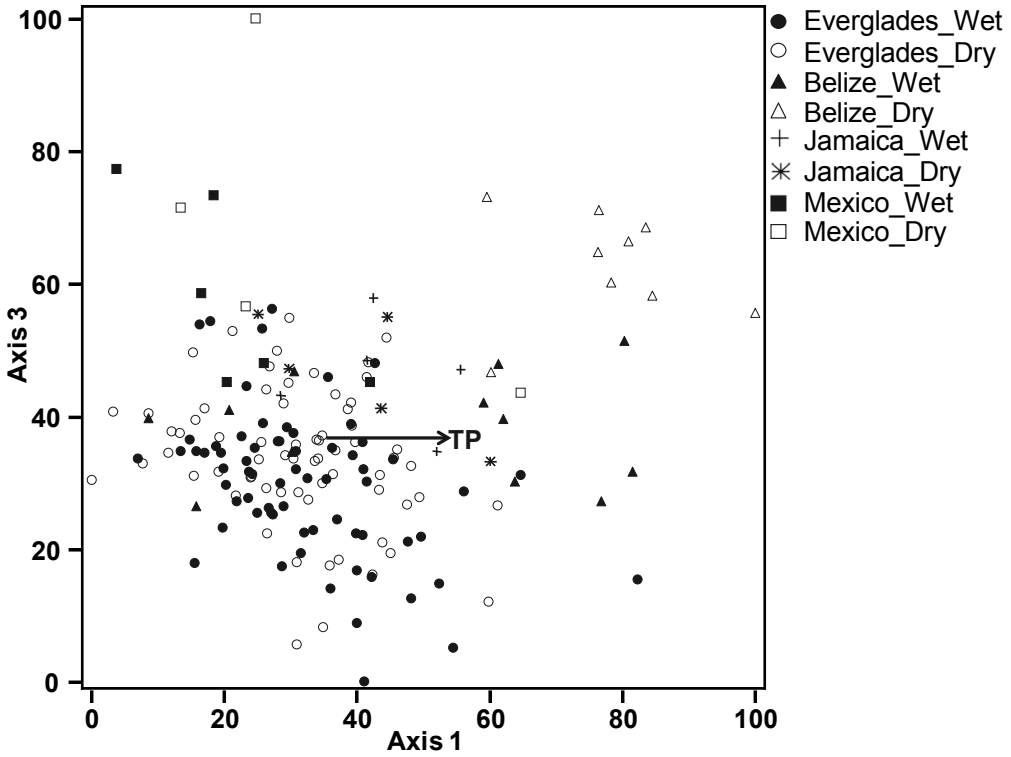

Figure 4-4. NMDS plot showing dissimilarity between diatom assemblages from Everglades (E), Belize (B), Mexico (M) and Jamaica (J) locations (Stress = 0.17). The vector representing the direction and strength of the relationship between mat TP and diatom assemblage dissimilarity is shown.

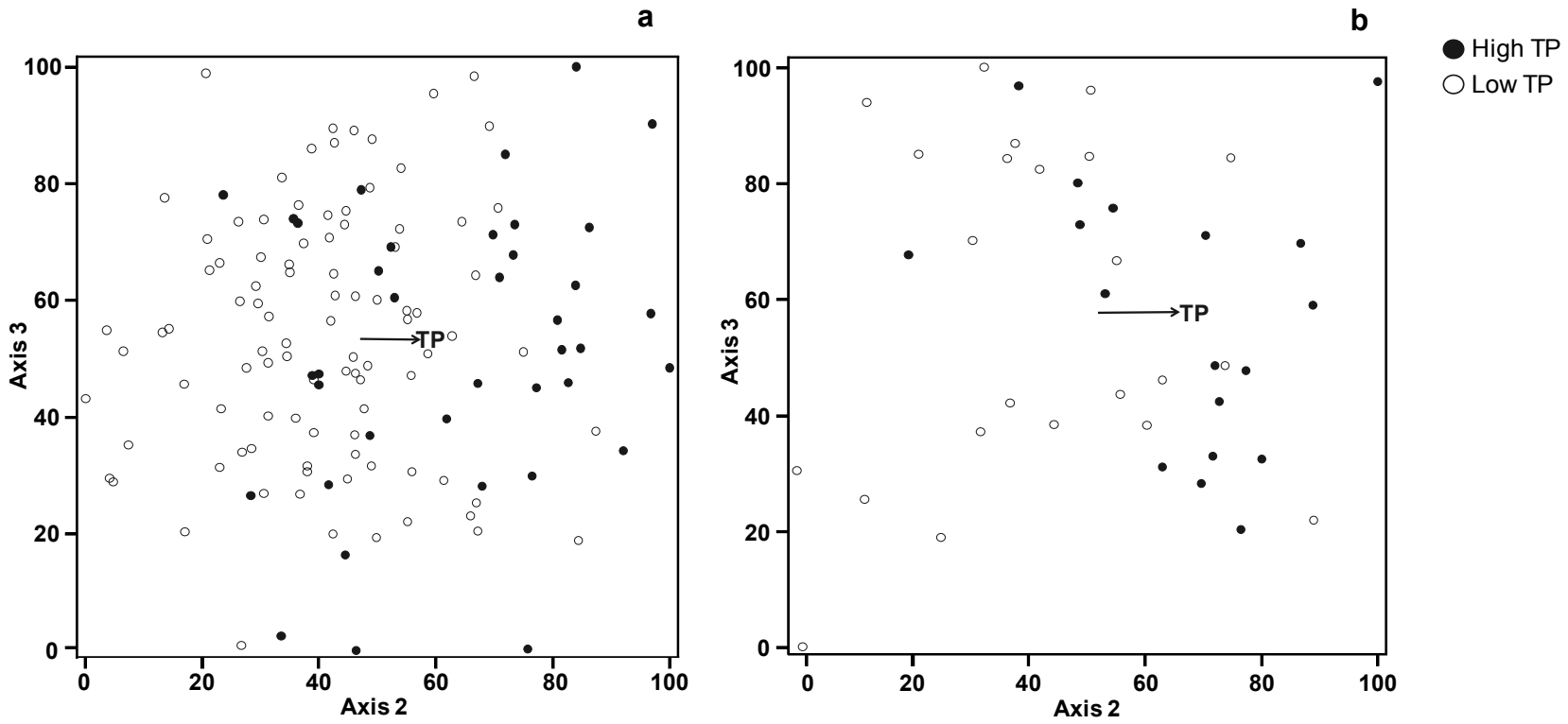

Figure 4-5. NMDS plot showing dissimilarity between "high" and "low" TP diatom assemblages from (a) Everglades (Stress = 0.19), (b) a composite of the Caribbean locations (Stress = 0.12). The vector representing the direction and strength of the relationship between mat TP and diatom assemblage dissimilarity is shown

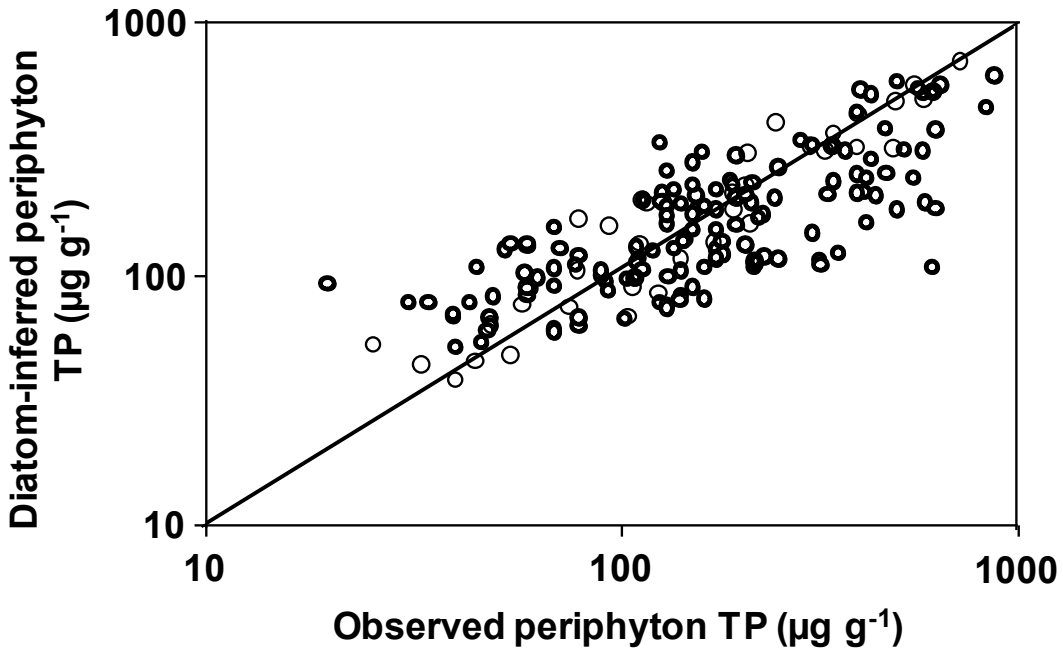

Figure 4-6. Scatter plot showing the relationship between diatom inferred periphyton mat TP concentrations and observed periphyton mat TP concentrations for Caribbean (●) (R^2 = 0.85, RMSE = 66.1 µg TP g^{-1}) and Everglades (O) sites (R^2 = 0.56, RMSE = 113.4 µg TP g^{-1}).

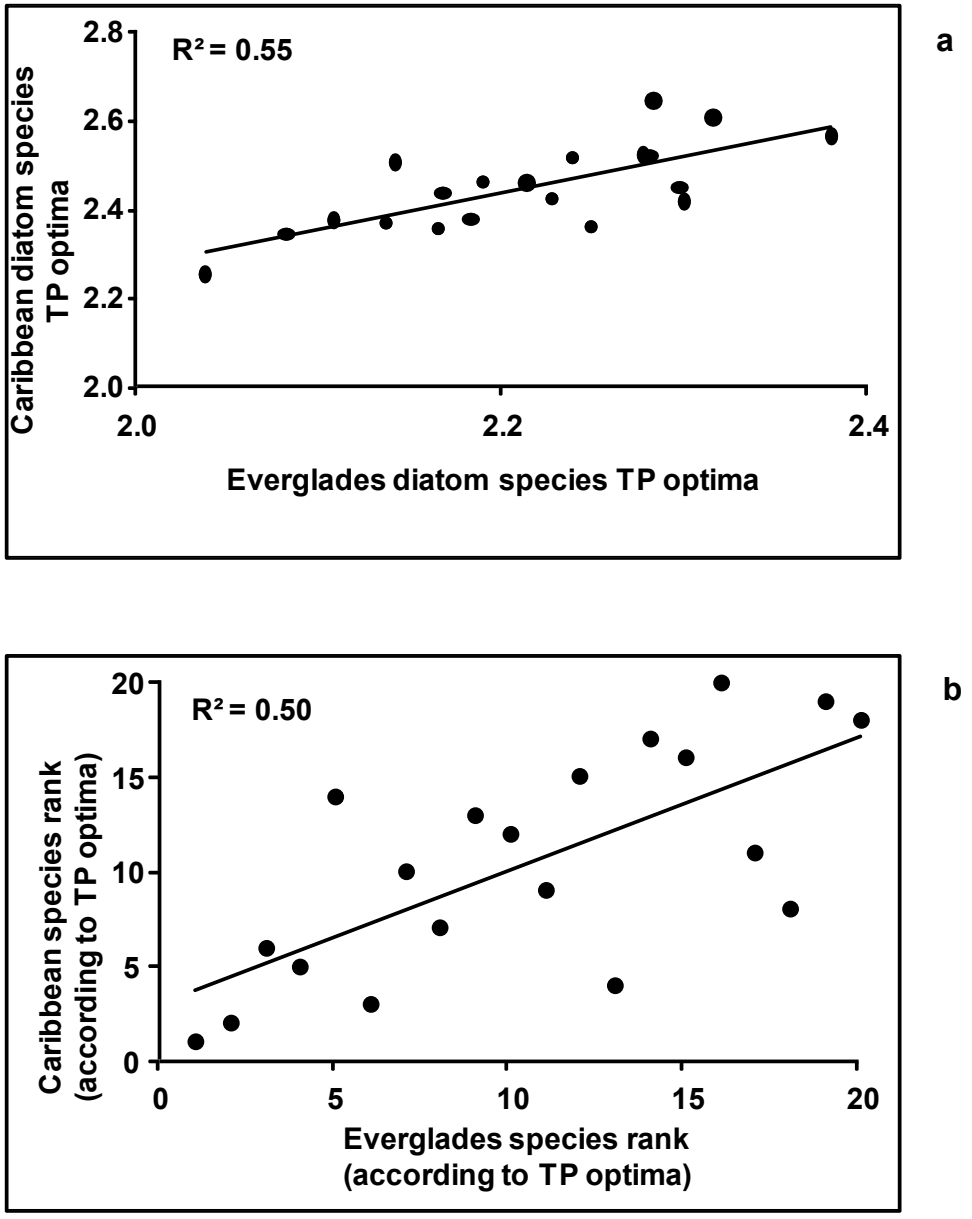

Figure 4-7. Scatter plot showing (a) the relationship between Everglades and Caribbean diatom species TP optima ($R^2 = 0.55$) and (b) the relationship between Everglades and Caribbean ranked diatom species TP optima ($R^2 = 0.55$).

CHAPTER V

General Conclusions

Regional wetland degradation as a result of agricultural and industrial activities is increasing and effective techniques to aid in wetland monitoring and management are greatly needed. Diatoms have proven to be a highly effective tool for use in monitoring water quality changes, and within the Everglades, where periphyton mats are noted for their high standing crop and productivity, as well as their response to changes in hydrology and water quality, models have already been developed which allow diatoms to be used for inferring changes in phosphorus availability within the system. The potential exists for using diatoms in this capacity in karstic wetlands throughout the Caribbean and Central American region, but this is contingent on the availability of baseline information and an understanding of the dynamics of periphyton mats in these habitats. This current study addressed these needs.

In Chapter II, (i) positive relationships between water depth and mat organic content and (ii) negative relationships between periphyton mat total phosphorus (TP) concentrations and biomass were identified in Everglades marshes. These relationships were also demonstrated at a number of similar karstic wetland habitats in Belize, Mexico and Jamaica, therefore strongly corroborating the patterns observed in the Everglades, and providing evidence to support the idea that the observed relationships are indeed characteristic of tropical karstic wetlands and not unique to the Everglades system. This

has effectively shown that water depth and, to a greater extent, periphyton TP content, are both drivers for periphyton dynamics in these systems.

Periphytic diatom assemblages are known to be extremely sensitive to changes in water chemistry. In the Everglades, established relationships between periphytic diatom assemblages and TP have been used to develop diatom based calibration models to infer water, soil and periphyton mat TP concentrations, as well as to indicate past environmental conditions and identify anthropogenically driven changes to the system using paleoecological techniques. These techniques can be employed in similar systems provided there is adequate information regarding (i) the species composition of local assemblages and (ii) the response of these assemblages to changes in water quality.

The first of these issues was addressed in Chapter III, which provides a taxonomic inventory of the diatom species associated with calcitic periphyton mats from karstic wetlands within the region. This comprehensive species list, along with photomicrographs, morphological descriptions and autecological information, provide the first account of diatom species from these habitats in Belize and Jamaica, and supplement the information from the single study conducted in the Yucatan region of Mexico. This taxonomic study has also identified a distinctive assemblage of diatom species (including *Brachysira neoexilis, Encyonema evergladianum, Encyonema* spp., *Fragilaria syngrotesca, Mastogloia smithii* var. *lacustris, Mastogloia smithii, Navicula cryptotenella, Nitzschia palaea* and *Nitzschia serpentiraphe*) which occurred across all locations. This assemblage, though commonly found in periphyton mats within Everglades marshes, has not been reported from other habitat types and is therefore possibly endemic to subtropical/tropical freshwater karstic wetlands.

The second issue, which involves an examination of the response of periphytic diatom assemblages to changes in water quality, was addressed in Chapter IV. The diatom assemblages from periphyton mats in Everglades, Belize, Mexico and Jamaica marshes all changed in relation to periphyton mat TP concentrations, such that "low" and "high" TP assemblages could be identified. Despite the fact that species composition overlapped across locations and weighted averaging models effectively predicted mat TP concentrations from diatom assemblages for both Everglades (R^2=0.56) and Caribbean (R^2=0.85) locations, there were significant differences among Everglades and Caribbean locations with respect to species TP optima and indicator species. These results highlight two important points. The first is that diatoms do serve as effective indicators of water quality in karstic wetlands within the Caribbean region. The second is that despite the similarity among systems and the overlapping diatom species assemblage, the specific response of individual species to changing water quality can differ among systems. As such, caution is necessary when attempting to apply a single diatom-based inference model across systems, as variations in the response of species to water quality reduces the accuracy of model based predictions.

VITA

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ACADEMIC PUBLICATIONS

Evelyn Gaiser, Josette M. La Hée, Franco A. C. Tobias, Anna H. Wachnicka (2010) "*Mastogloia smithii* var. *lacustris* Grun.: A structural engineer of calcareous mats in karstic subtropical wetlands" Proceedings of the Academy of Natural Sciences of Philadelphia (in press)

Josette M. La Hée, Evelyn E. Gaiser, Joel C. Trexler, William F. Loftus. "Phosphorus and hydrology as drivers of periphyton biomass in four tropical karstic wetland systems" Wetlands (in prep)

Josette M. La Hée, Evelyn E. Gaiser. "Phosphorus effects on diatom community composition and dynamics in four tropical karstic wetland systems" Journal of the North American Benthological Society (in prep)

ACADEMIC PRESENTATIONS

Phosphorus and hydrology as drivers of periphyton biomass in the Everglades and three tropical karstic wetlands.
Oral Presentation
95th Meeting of the Ecological Society of America, Pittsburgh, Pennsylvania, U.S.A.
J. M. La Hée and E. E. Gaiser, August 2010

The use of diatom communities as indicators of water quality in four tropical, karstic wetland systems
Oral Presentation
94th Meeting of the Ecological Society of America, Albuquerque, New Mexico, U.S.A.
J. M. La Hée and E. E. Gaiser, August 2009

"Sister systems: Comparisons of diatom communities from the Florida Everglades and the Black River Morass, Jamaica."
Oral Presentation
19th North American Diatom Symposium, Pellston, Michigan, U.S.A.
J. M. La Hée and E. E. Gaiser, September, 2007

"The effects of rum distillery effluent on the periphytic diatom community of the North Elim River, St. Elizabeth, Jamaica"
Oral Presentation
17th North American Diatom Symposium, Florida, U.S.A.
Josette La Hée, October, 2003

"The effects of rum distillery effluent on the macroinvertebrate and periphytic diatom community of the North Elim River, St. Elizabeth, Jamaica"
Oral presentation
Proceedings of the 12th Caribbean Academy of Sciences Conference, Havana, Cuba.
Josette La Hée, Kimberly John, Eric Hyslop, Dale Webber, April, 2000

AWARDS AND GRANTS

- Phycological Society of America Grant in Aid of Research 2007
- Latin American and Caribbean Center Research Travel Grant 2006
- Society of Wetland Scientists 2006
- Garden Club of America Scholarship 2006
- Iowa Lakeside Laboratory Merit Scholarship (2004)
- Christina Menendez Fellowship for Everglades Research 2004