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Mechanisms of Diatom Assembly in a Hydrologically-Managed Subtropical Wetland

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

MECHANISMS OF DIATOM ASSEMBLY IN A HYDROLOGICALLY-MANAGED SUBTROPICAL WETLAND

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Sylvia Seulbe Lee

2014

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

This dissertation, written by Sylvia Seulbe Lee, and entitled Mechanisms of Diatom Assembly in a Hydrologically-Managed Subtropical Wetland, having been approved in respect to style and intellectual content, is referred to you for judgment.

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

Mark Edlund

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Date of Defense: March 18, 2014

The dissertation of Sylvia Seulbe Lee is approved.

Dean Kenneth G. Furton
College of Arts and Sciences

Dean Lakshmi N. Reddi
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Florida International University, 2014

DEDICATION

This dissertation is dedicated to my parents, Peter D. Lee and Sye J. Lee, for all the sacrifices they made for our family and for their constant support and love.

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ABSTRACT OF THE DISSERTATION

MECHANISMS OF DIATOM ASSEMBLY IN A HYDROLOGICALLY-MANAGED SUBTROPICAL WETLAND

by

Sylvia Seulbe Lee

Florida International University, 2014

Miami, Florida

Professor Evelyn Gaiser, Major Professor

Diatoms are useful indicators of ecological conditions but the mechanisms driving assemblage distribution are not clearly defined. Understanding the mechanisms underlying assemblage distribution is necessary to make accurate predictions about the effects of environmental change, such as hydrologic management, restoration, and climate change. The examination of diatom distribution and key drivers across a large wetland over several years can provide a resolved spatio-temporal framework for determining the relative importance of environmental and spatial factors influencing assemblage patterns. I examined a 6-year record of diatom distribution across the Everglades, a large hydrologically-managed subtropical wetland. Successful restoration of this ecosystem depends on using reliable ecological targets and bioassessment strategies based on a comprehensive understanding of the biotic responses to the variables being manipulated, especially hydrology. The components of my research are: 1) characterizing the relationship between diatom distribution and environmental factors; 2) investigating the taxonomy of species presumably with little or no limitation to dispersal by spatial factors; and 3) examining the relative importance of environmental and spatial factors on diatom distribution patterns within a hydrologically-managed environment. Building upon the well-documented utility of Everglades diatom transfer functions for phosphorus based on species optima and tolerance ranges, I developed transfer functions for hydroperiod and biovolume of periphyton (consortium of algae, bacteria, and fungi) and evaluated the utility of resultant diatom-based inference models for bioassessment. Considering the importance of environmental factors, diatoms in the Everglades and Caribbean wetlands may have restricted distributions. My taxonomic investigation of two species with presumed continental distributions and the consequent description of two new species suggest spatial factors can restrict diatom dispersal. The importance of both environmental and spatial controls on Everglades diatom distribution may be related to the availability of calcareous (high mineral content) periphyton that diatoms inhabit because periphyton mineral content is correlated with environmental factors, which differ among compartments within the ecosystem because of hydrologic management. I found environmental factors were more important controls on the distribution of persistent inhabitants of calcareous periphyton, suggesting spatial factors are relatively less important when species are well-suited to the habitats made available by environmental conditions influenced by hydrologic management.

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CHAPTER I: GENERAL INTRODUCTION

Magnuson (1990) summarized the findings of key ecological studies that demonstrated the need to extend research efforts beyond the two or three year funding period to reveal the "invisible present," defined as the time period encompassing our lifetimes when important changes are occurring but at rates that are too slow to detect obvious cause-and-effect relationships. One reason for the invisible present is that human activities produce landscape legacies (Foster et al. 2003) that persist and complicate environmental responses even after conditions change, such as little or no recovery in stream aquatic diversity despite decades of reforestation of past agricultural areas (Harding et al. 1998). Sufficient temporal context is required to fully understand the changes observed in a single sampling period, such as patterns of phytoplankton richness and community stability associated with climate warming over 30 years (Pomati et al. 2011). In the same vein as the invisible present, Sparks and Swanson (1990) coined the term "invisible place" to illustrate the importance of spatial context to complement long-term studies so that findings are applicable to the whole ecosystem. Understanding both the spatial and temporal context of environmental systems is necessary to make robust predictions of the results of management activities. Long-term datasets are needed to determine what mechanisms structure biotic assemblages, how assemblages are changing through time, and how to improve management targets (Magurran et al. 2010). Further, long-term datasets provide the necessary temporal context to understand systems with high interannual variability in environmental conditions.

The ability to predict how assemblages will change in response to human activity and other causes of environmental change depends on knowing the mechanisms underlying the structuring of the assemblages themselves. Mechanisms regulating assemblage distribution include 1) niche-based processes that occur in response to environmental factors; and 2) dispersal-limiting processes that occur in response to spatial factors (Soininen 2007). Niche-based processes refer to controls on species abundances by the environment resulting from differences in species traits that limit species' environmental tolerance ranges (Hutchinson 1957). Dispersal-limiting processes refer to controls on species abundances resulting from the influence of space on immigration and emigration between assemblages (Hubbell 2001).

For microorganisms, the early Dutch scientist Baas Becking (1934) supported niche-based control on assemblage distribution with the phrase '*everything is everywhere*, but, *the environment selects.*' In other words, microorganisms should have unlimited dispersal ability made possible by their small size and large populations, but niche-based processes determine the species abundances we observe (de Wit and Bouvier 2006). If both niche-based and dispersal-limiting processes control assemblage distribution, microorganisms should show limited long-distance dispersal and evidence of adaptations to their environment, such as endemism and species richness related to regional habitat availability (Martiny et al. 2006, Telford et al. 2006, Soininen 2007). If only dispersal-limiting processes control assemblage distribution, the small size and large populations of microorganisms should allow random distribution throughout the world proportional to global population size, regardless of species dispersal abilities or how well species are suited to local environments (Hubbell 2001, Finlay 2002, Finlay et al.

2002). Sufficient spatial and temporal context is needed to determine which hypothesis concerning the roles of niche-based and dispersal-limiting processes is the most well-founded for microorganisms.

The importance of environmental controls on the distribution of diatoms, a diverse group of unicellular algae, is illustrated by the utility of diatoms as indicators of environmental change because of their sensitivity to water quality and habitat conditions. Diatoms also have rapid reproduction rates relative to higher plants or animals, which allow populations to respond quickly to environmental alterations (Smol and Stoermer 2010). Diatoms are sensitive to water quality parameters such as nutrients (Pan and Stevenson 1996, Cooper et al. 1999, Gaiser et al. 2006, Lane and Brown 2007, La Hée and Gaiser 2012), salinity (Taffs 2001, Hicks and Nichol 2007, Wachnicka et al. 2010, Wachnicka et al. 2011, Nodine and Gaiser 2013), dissolved oxygen (Zhang et al. 2011), and pH (Owen et al. 2004, Taffs et al. 2008). Diatoms are also sensitive to hydrologic parameters such as hydroperiod (Gaiser et al. 1998, Gottlieb et al. 2006, Mackay et al. 2011) and water depth (Finné et al. 2010). In hydrologically-managed systems, understanding the interactions between climate drivers, biotic assemblages, and management operations is important, as suggested for example, by algal blooms that may have resulted in part from flood control efforts responding to hurricane activity (Rudnick et al. 2006, Briceño and Boyer 2010). Repeated surveys of diatom distribution relative to drivers of environmental change elucidate mechanisms underlying assemblage distribution that can be used to improve management operations. Spatial resolution is especially important to consider in study designs because the relative importance of environmental and spatial control of diatom communities could depend on scale, with spatial factors becoming more important as study extent increases, because a larger study region captures a greater range in variability of biogeographical and environmental factors (Soininen 2007).

Recent studies acknowledge that both local and regional factors can structure diatom assemblages (Soininen 2007, Soininen et al. 2007, Vanormelingen et al. 2008, Soininen and Weckström 2009, Verleyen et al. 2009, Heino et al. 2010). The relative importance of each mechanism, however, is yet unclear and likely varies across habitat types. Heino et al. (2010) concluded that in boreal streams, purely spatial factors explained more variation than environmental factors in diatom species richness and assemblage distribution. Other studies found spatial factors are less important than environmental factors in controlling assemblage distribution (Vanormelingen et al. 2008, Soininen and Weckström 2009, Veryleyen et al. 2009). The majority of the abovementioned studies were done in temperate stream and lake habitats. There are few studies of what mechanisms structure diatom assemblages in wetlands, which pose unique environmental challenges to diatoms, such as frequent drying and variable light availability that may influence species dispersal abilities. Furthermore, accurate assessment of wetland environmental conditions is extremely important because although wetlands provide essential ecosystem services including water supply for humans and habitat for thousands of plants and animals, wetlands are one of the fastest disappearing ecosystems in the world (Mitsch and Gosselink 2007). Understanding the mechanisms that structure diatoms can improve our predictions about environmental change in wetlands and guide our efforts to restore these fragile ecosystems.

The Florida Everglades is a model system that highlights the need for spatial and temporal context to guide hydrologic management. The Everglades is spatially large (about 9000 km^2) even after drastic reductions in area were made to serve human needs (Davis et al. 1994, McVoy et al. 2011). A very long and complex history of interaction with humans has shaped the landscape into the compartmentalized and intensively-managed system it is today (Light and Dineen 1994, McVoy et al. 2011). Everglades restoration efforts officially began in 1994 with the Everglades Forever Act, but the progression toward restoration targets in response to implemented projects needs assessment. A long-term dataset that could help evaluate restoration effectiveness is the system-wide diatom assemblage composition data collected as part of the Monitoring and Assessment Program (MAP) of the Comprehensive Everglades Restoration Plan (RECOVER 2004). Initiated in 2005, the MAP has generated over 6 years of continuous data at unusually large spatial scales. There are few studies using data that have the spatial and temporal resolution to completely address the mechanisms driving diatom assembly. The spatially-balanced design and long-term data collection of the MAP (Philippi 2005) includes monitoring Everglades diatom assemblages; the sampling captures a broad range of variability in environmental factors and biogeography and has the temporal resolution to capture interannual variability needed to adequately quantify the relative importance of environmental and spatial factors.

Everglades diatoms are ideal for testing the importance of local and regional controls on assembly because their composition tracks a broad range of environmental conditions throughout the ecosystem. However, the hydrologically-managed wetland environment can also exert regional-scale historical, biogeographical, and evolutionary controls. In the Everglades and other wetlands with shallow and slow-moving water, diatoms associated with periphyton attached to surfaces are more abundant than planktonic forms. Periphyton is a matrix of algae, fungi, bacteria, and detritus (Browder et al. 1994) that contributes to Everglades ecosystem processes such as primary production (Ewe et al. 2006), mediation of trophic interactions in the food web (Chick et al. 2008), control of water chemistry by nutrient uptake (Thomas et al. 2006), and oxygenation of the water column (McCormick et al. 1997, Hagerthey et al. 2011). The local environment within the periphyton mat has a strong relationship with diatom assemblage composition. Measurements of periphyton phosphorus (P), rather than P in water or soil, have been used to indicate environmental conditions in the Everglades because of high correlation with and immediate response to P load by the periphyton itself (loss of biomass) and by assemblage composition (Gaiser et al. 2004). The strong relationship between diatom assemblage composition and periphyton P are well-known (Gaiser et al. 2004, 2006, Gaiser 2009, Gaiser et al. 2011). Compositional differences are also present in periphyton mats from long- (> 8 months) and short-hydroperiod (< 8 months) environments (Gottlieb et al. 2006). In addition to hydrology, habitat characteristics like periphyton mat mass also have strong relationships with diatom assemblage composition (refer to Chapter II) and may reflect additional mechanisms controlling assemblage distribution outside of strictly physicochemical environmental controls.

There is strong potential for spatial controls on assemblage distribution of diatoms in periphyton mats. While desiccation is the most significant hindrance to dispersal via air or waterbirds (Kristiansen 1996), Everglades diatoms may be adapted to survive seasonal drying (Thomas et al. 2006, Gaiser, et al. 2006) and are often encased in or produce extracellular polymeric substances (EPS) which could act as antidesiccants (reviewed in Hoagland et al. 1993; Hostetter and Hoshaw 1970, Davis 1972, Gaiser et al. 2010). However, potential dispersal limitation and control of species abundances by biogeographical and spatial factors are indicated by regional differences in species responses to environmental variables (Gaiser et al. 2006) and assemblages that are possibly endemic to tropical karstic wetlands (Slate 1998, La Hée and Gaiser 2012). The diatom flora of subtropical karstic wetlands, which is not well documented in comparison to the flora of temperate regions, may include taxa with dispersal limitations conferred by their preferred periphyton mat habitat. Notable floristic studies in the region include research on the diatoms of Jamaica (Podzorski 1985), Cuba (Foged 1984), the Everglades (Slate and Stevenson 2007), and Mexico (Novelo et al. 2007). La Hée and Gaiser (2012) determined the nutrient preferences of diatoms in the karstic wetlands of the Everglades, Jamaica, Belize, and the Yucatán and found regional differences in preferences, leading to more reliable estimates of P concentration from local rather than regional models. This finding supports the potential importance of biogeographical processes even within the relatively similar environments in the Everglades and Caribbean region.

The presence of diatoms that may have specific adaptations to forming or inhabiting periphyton mats in the Everglades and the Caribbean regions shows that spatial factors and differences in species dispersal abilities could underlie diatom distribution in wetlands. A numerically abundant and ecologically important Everglades diatom species has been identified as *Mastogloia smithii* Thwaites ex W. Smith 1856 (McCormick and O'Dell 1996, Gaiser et al. 2006, Slate and Stevenson 2007) and *M.*

smithii var. *lacustris* Grunow ex Schneider 1878 (Gaiser et al. 2010). However, *M. smithii* and *M. smithii* var. *lacustris* were originally described using specimens from Europe (Smith 1856, Grunow 1878, Van Heurck 1880, Van Heurck 1885) and were lacking in designated type material that could be used to resolve taxonomic discrepancies. Morphological comparison with newly designated type material demonstrated that the Everglades species is neither of the two designations, revealing evidence against the once presumed distributions of these species across continents (refer to Chapter III).

Periphyton mats may provide a particular kind of habitat for diatoms that mediate the environmental and spatial processes driving species distributions, especially if some taxa have greater biological dependence on or adaptations to living within a particular form of periphyton. Periphyton is distributed across the Everglades landscape in diverse forms, varying with the history and current hydrologic management of the environment (Gaiser et al. 2011, Hagerthey et al. 2011). In unenriched environments of the Everglades, low nutrient availability, high abundance of carbonate from dissolution of limestone, and frequent desiccation encourage the growth of periphyton mats that are abundant in cyanobacteria (Gaiser et al. 2011, Hagerthey et al. 2011). The EPS that coat filaments or encase coccoid forms of cyanobacteria contribute to mat cohesion and provide the main structure of thick, sometimes laminated, periphyton mats (Stal 1995), although some EPS-secreting diatoms can also contribute to the mat matrix (Gaiser et al. 2010). Thick, cyanobacteria-dominated periphyton mats in unenriched environments in the Everglades are often calcareous because calcium carbonate from the limestone bedrock can accumulate on the surfaces of cyanobacterial filaments by abiotic adsorption mediated by the EPS or biotic reprecipitation after inorganic carbon acquisition from the water column (Browder et al. 1994, Hagerthey et al. 2011). In enriched environments of the Everglades, higher phosphorus concentrations promote disintegration of the mat structure and an assemblage dominated by diatoms and green algae that are not mat-forming (Gaiser et al. 2006, Gottlieb et al. 2006). Enriched periphyton can be loosely attached to substrates or can form green, gelatinous clouds that are more typical of less alkaline and mesotrophic or eutrophic aquatic systems (Hagerthey et al. 2011). Regions of the Everglades with differing environmental histories and current hydrologic management have differing levels of environmental and spatial controls on diatom assemblage distribution that may be related to the suitability of habitats in enriched and unenriched periphyton (refer to Chapter IV).

In the following chapters, I present three components of my research. In Chapter II, I characterized the niche-based relationship between diatoms and habitat characteristics (physicochemical environmental variables and biological features of periphyton) by building upon the well-documented utility of Everglades diatom transfer functions of phosphorus based on species optima and tolerance ranges. I hypothesized that if niche-based processes are important to Everglades diatoms, their assemblage composition should also have strong associations with hydrology and habitat characteristics such as periphyton abundance. In Chapter III, I investigated the original specimens of *Mastogloia smithii* and *M. lacustris*, collected from the United Kingdom and Belgium, respectively, and whether the morphology of the species reported with these names from the Everglades and the Caribbean were consistent with the original specimens. I hypothesized that if spatial factors are also important controls on diatom distribution, morphological differences should indicate more restricted distributions and possibly regional endemism. In Chapter IV, I examined the relative importance of niche-based and dispersal-limiting processes on distribution patterns within the hydrologically-managed environment of the Everglades. I hypothesized that both niche-based and dispersal-limiting processes control diatom assemblage composition, but the relative importance of either process may differ for taxa that are persistent inhabitants of calcareous periphyton, as opposed to taxa with occasional spatial and temporal occurrence patterns, because persistent taxa may have biological, dispersal, and life history strategies that are advantageous for life in calcareous periphyton. I also hypothesized that the abundance of persistent taxa will have a strong relationship with the presence of calcareous periphyton, which is related to the environmental conditions manipulated by hydrologic management in the Everglades.

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CHAPTER II: DIATOM-BASED MODELS FOR INFERRING HYDROLOGY AND PERIPHYTON ABUNDANCE IN A SUBTROPICAL KARSTIC WETLAND: IMPLICATIONS FOR ECOSYSTEM-SCALE BIOASSESSMENT

Abstract

I developed diatom-based prediction models of hydrology and periphyton abundance to inform assessment tools for a hydrologically managed wetland. Because hydrology is an important driver of ecosystem change, hydrologic alterations by restoration efforts could modify biological responses, such as periphyton characteristics. In karstic wetlands, diatoms are particularly important components of mat-forming calcareous periphyton assemblages that both respond and contribute to the structural organization and function of the periphyton matrix. I examined the distribution of diatoms across the Florida Everglades landscape and found hydroperiod and periphyton biovolume were strongly correlated with assemblage composition. I present species optima and tolerances for hydroperiod and periphyton biovolume, for use in interpreting the directionality of change in these important variables. Predictions of these variables were mapped to visualize landscape-scale spatial patterns in a dominant driver of change in this ecosystem (hydroperiod) and an ecosystem-level response metric of hydrologic change (periphyton biovolume). Specific diatom assemblages inhabiting periphyton mats of differing abundance can be used to infer past conditions and inform management decisions based on how assemblages are changing. This study captures diatom responses to wide gradients of hydrology and periphyton characteristics to inform ecosystem-scale bioassessment efforts in a large wetland.

Introduction

In wetlands, hydrology is an important driver of ecosystem change because it maintains both the abiotic and biotic components that contribute to the defining features and function of wetland habitats (Mitsch & Gosselink 2007). Many wetlands undergo ecosystem-scale changes as anthropogenic agents, including accelerating rates of land-use and climate change (Batzer & Sharitz 2006), as well as restoration efforts, alter their hydrology. To predict the ecosystem effects of hydrologic changes and to direct adaptive assessment efforts, it is important to understand the complex relationships between hydrology and biotic assemblages. Because biotic assemblages can actively change wetland hydrology and physicochemistry through feedbacks (Mitsch & Gosselink 2007), hydrologic alterations by restoration efforts could modify these relationships if assemblage changes occur.

Bioassessment tools permit interpretation of the direction of environmental change and are useful for developing management targets to inform and assess restoration efforts (EPA 2011a). Diatom assemblages are sensitive to environmental changes, including hydrologic changes, so they can be used to develop robust inference models for early detection of shifts because of habitat degradation or restoration projects (Davis et al. 1996; Stevenson 1998). Sensitivity to hydrologic changes have been shown by the immediate recovery of diatom production in desiccated periphyton (benthic algae; Browder et al. 1994) upon rehydration (Thomas et al. 2006), and the influence of hydroperiod on the relative abundance of desiccation-resistant species inhabiting the periphyton matrix (Gottlieb et al. 2005). Periphyton is an important indicator of wetland degradation and restoration progress because it undergoes rapid and measurable structural, functional, and compositional responses to environmental changes (especially hydrology and water quality; Browder et al. 1994) at a large range of spatial scales (McCormick and Stevenson 1998; Gaiser 2009).

Diatom-based assessments conducted over long time periods should be used to inform wetland adaptive assessment tools about the rates, causes, and functional consequences of change to improve future management strategies (Gaiser & Rühland 2010). Because diatoms persist in the fossil record, they provide quantitative measures of past conditions that give ecologically-based context for current and future management plans (Smol & Stoermer 2010). Along with long-term monitoring, reconstructing the hydrologic history of wetlands is important, as past settings can provide hydrologic targets for restoration (Marshall et al. 2009), particularly in the face of changes in rainfall and inundation because of climate change (Mulholland et al. 1997). In addition to assessment over time, the inherent spatial attribute of diatom-based models provide an opportunity to examine responses at multiple spatial scales. The degree of consistency of species responses to ecosystem properties and the distribution of environmental gradients among hydrologically connected wetland subbasins determine whether models should be basin-specific (e.g., Gaiser et al. 2006) or regional.

Wetland assessment programs have lagged behind other aquatic systems, such as lakes and streams (EPA 2011b). Robust diatom-based inference models will provide a means for examining both the drivers and biological feedbacks of regulatory variables at a range of spatial scales. Most diatom-based assessments of wetlands have addressed water quality parameters such as nutrients (Pan & Stevenson 1996; Cooper et al. 1999; Gaiser et al. 2006; Lane & Brown 2007; Velinsky et al. 2011; La Hée & Gaiser 2012), salinity (Taffs 2001; Hicks & Nichol 2007; Wachnicka et al. 2010; Wachnicka et al. 2011), dissolved oxygen (Zhang et al. 2011), and pH (Owen et al. 2004; Taffs et al. 2008). Some studies have employed diatoms to assess wetland vegetation (Huvane & Cooper 2001; Gaiser et al. 2005a), and several have employed diatom-based assessment of wetland hydrologic characteristics such as hydroperiod (Gaiser et al. 1998; Mackay et al. 2011). To date, inference models that reflect biological feedbacks, such as periphyton characteristics, to hydrologic conditions have not been developed. Reconstructions of ecosystem properties using regional inference models were successful for several wetlands (Gaiser et al. 1998; Taffs 2001; Owen et al. 2004), while other studies used or advocated basin-specific models (Cooper et al. 1999; Gaiser et al. 2006; La Hée & Gaiser 2012).

In the Florida Everglades, restoration goals, targets, and assessment tools are at the forefront of scientifically-sound adaptive management of the multi-billion dollar, landscape-scale Comprehensive Ecosystem Restoration Plan (C & SF Project 1999). Restoration efforts propose to redirect unused fresh water to areas that historically had greater periods of inundation, as well as to areas that would benefit cities and farmers. Without robust inference models, however, changes to hydrology could result in unintended consequences for wetland structure and function (e.g., Surratt et al. 2012). While development of diatom response models to water quality parameters such as periphyton total phosphorus (TP) concentrations (McCormick et al. 1996; Pan et al. 2000; Gaiser et al. 2006; La Hée & Gaiser 2012) have allowed paleoecological reconstructions of historical environments (e.g., Cooper et al. 1999; Slate & Stevenson 2000), hydrologic reconstructions have been impeded by the lack of robust diatom-based inference models (but see Sanchez et al. 2012). Also, diatom responses to periphyton characteristics reflective of biological feedbacks and responses to hydrologic changes have not been defined. If specific diatom assemblages inhabit periphyton of differing characteristics (e.g., biovolume), diatoms could be used to infer past wetland conditions even though the characteristics of the periphyton itself are not conserved in monitoring or paleoecological records. The numerous biogeochemical processes attributed to periphyton make the maintenance of native periphyton structure an important aspect of Everglades restoration (Hagerthey et al. 2011). Examination of periphyton along hydroperiod gradients in a marl-based wetland area found little effect of hydroperiod on periphyton biomass (Wachnicka, unpublished data), but patterns across the long hydrologic gradients present in the larger Everglades landscape, including the hydrologically different (but connected) Water Conservation Areas (WCAs) and Everglades National Park (ENP) (Light & Dineen 1994), are expected. Extensive studies have been conducted on the periphyton and paleoecological indicators of the historically P-enriched and hydrologically-managed WCA-2A (e.g., McCormick et al. 1996; McCormick et al. 1998; Cooper et al. 2008). However, a quantitative evaluation of diatom sensitivity to periphyton characteristics occurring across the broader hydrologic gradients represented in the Greater Everglades could elucidate landscape-scale responses to hydrologic change.

In this study, I examined the diatom assemblages of periphyton samples that were gathered in 2006 as part of a landscape-scale monitoring program across the Everglades. My first objective was to quantify diatom assemblage patterns and associations with habitat characteristics. I used the term ‘habitat characteristics’ to include both the abiotic physicochemical factors of the environment and the biological features of the periphyton mat that influence, and are influenced by, the diatoms embedded in the mat matrix. I hypothesized that hydroperiod, periphyton biovolume, and periphyton TP concentration would be associated with the differences in diatom assemblages across the Everglades. My second objective was to test whether the responses of diatom assemblages across the Everglades were consistent throughout the landscape. I hypothesized that a spatially extensive dataset would enable detection of basin-specific responses, if they exist, but also provide an opportunity to develop landscape-scale models. My final objective was to evaluate the predictive capacity of diatom-based inference models. In addition, I mapped inferences relative to actual patterns to illustrate the utility of visualizing landscape-scale patterns for application in restoration planning and management.

Methods

Site Description

Located in Florida, USA, the Everglades is an expansive wetland (>6000 km^2) encompassing a mosaic of environmental conditions resulting from natural gradients and differences in biogeochemistry, as well as anthropogenic compartmentalization and eutrophication (Davis & Ogden 1994). Owing to the limestone bedrock underlying much of the southern Everglades, periphyton assemblages can contain an abundance of calcium carbonate precipitates that allows the formation of thick, calcareous mats. However, areas of higher nutrient levels contain organic, filamentous films that are easily disrupted (McCormick & O'Dell 1996; McCormick et al. 2001; Gaiser et al. 2005b; Gaiser et al. 2011). This study focuses on calcareous communities occurring throughout the spatially complex WCAs and ENP, exclusive of soft-water regions (the Arthur R. Marshall

Loxahatchee National Wildlife Refuge, also known as WCA-1) with a very different algal assemblage and suite of environmental stressors (Harvey & McCormick 2009; Gaiser et al. 2011; Hagerthey et al. 2011). The Everglades has a subtropical climate with a distinct wet and dry season, the duration of which are controlled by climate variability and water management and can have significant influences on variability in species abundances and ecosystem properties.

Sample Collection and Processing

Periphyton samples were collected during the 2006 wet season (September through December) as part of the Monitoring and Assessment Program of the Comprehensive Everglades Restoration Plan (RECOVER 2004). A total of 86 sites were included in this study (refer to Figure 2.5). Generalized random-tessellation stratification (Stevens & Olsen 2004) was used to choose a spatially balanced set of sampling locations. The landscape was divided into 800m x 800m grids and a representative sample of these was drawn as primary sampling units (PSU); three sampling sites were randomly selected from the samplable habitat in each PSU (Philippi 2005). Samplable habitat included all locations where vegetation was not too dense for the sampling device to enclose 1 m^3 of the water column and less than 1 m deep; primarily wet prairies and sloughs met these conditions (Gunderson 1994).

At each sampling location, water depth was measured, and water samples were taken for measurement of pH and conductivity ($\mu S\ cm^{-1}$). Other hydrologic variables, including hydroperiod (days flooded) and days since dry (number of days since flooding of the marsh surface after the latest drying event when water levels were <5 cm), were estimated by calibration to nearby continuous water level gauges using digital elevation models provided by the Everglades Depth Estimation Network (EDEN, http://sofia.usgs.gov/eden/stationlist.php). The sampling device used to delineate the sampling area was a 1 m^3 enclosure with mesh sides and open on the top and bottom (Jordan et al. 1997). Visual assessment for aerial cover (percent of the surface of the enclosed area covered by periphyton) was conducted before all periphyton within the enclosure was collected and measured for biovolume using a perforated graduated cylinder. Extraneous plant matter, animals, and other debris were on average less than 0.5% of the volume of the sample and did not affect biovolume measurements. If no benthic, epiphytic, or metaphytic periphyton was present, flocculent detritus from the benthos was collected (Troxler & Richards 2009; Pisani et al. 2011).

Periphyton samples were taken back to the laboratory and frozen before further processing. Animals, plant matter, and other debris were removed, and subsamples were taken for the measurement of dry weight (g m^{-2}) by drying at 80 °C to constant weight, ash-free dry mass (g m^{-2}) by combustion at 500 °C for 1.5 hours, chlorophyll *a* mass (µg m^{-2}) and chlorophyll *a* concentration (µg g^{-1} dry weight) by fluorometry (Welschmeyer 1994), total periphyton P (µg g^{-1} dry weight) by colorimetry after dry combustion (Solorzano & Sharp 1980; EPA 1983), and diatom species composition analysis. Organic content was calculated as the ratio of ash-free dry mass to total dry mass expressed as a percent. Periphyton P concentrations were used as a metric of P availability because periphyton P has a strong correlation with P load (Gaiser et al. 2004; Gaiser et al. 2005b; Gaiser et al. 2006). Diatom samples were cleaned of calcite and organic matter using strong acids and chemical oxidizers (Hasle & Fryxell 1970), and then permanently affixed to glass slides using Naphrax®. A minimum of 500 valves were counted and identified per slide (Weber 1973) using a compound light microscope at 1000x magnification. Identifications were made to the lowest taxonomic level possible (variety or forma) using a database of South Florida diatom taxa (http://fce.lternet.edu/data/database/diatom) and other references (e.g., Slate & Stevenson 2007).

Data analysis

Species abundances were relativized by the maximum abundance achieved by each species over all samples to reduce the differential impact of common and uncommon species on inferences. All species were included in the analyses after checking for outliers more than two standard deviations from the mean Sørenson distance measure (McCune & Grace 2002). Three categories of habitat characteristics were analyzed: hydrology, periphyton abundance, and periphyton quality (Table 2.1). Hydrology included days since dry (DSD), hydroperiod (HYPER), and water depth (DEPTH). Periphyton abundance included periphyton biovolume (PBIOV), aerial cover (AERCO), chlorophyll *a* mass (CHLMA), dry weight (DRYWT), and ash-free dry mass (AFDM). Periphyton quality included periphyton organic content (ORGCO), periphyton total phosphorus (TP), chlorophyll *a* concentration (CHLCO), water column pH (pH), and water column conductivity (CONDU). I used the term ‘periphyton quality’ to include measurements of periphyton and water column attributes because of the intimate relationship between water quality (nutrient and ion concentrations) and the composition and function of periphyton mats, including both the influence of the water column on

Table 2.1. Summary statistics of habitat characteristics (before transformations) and transformations used to bring skewness of values closest to zero. TP was transformed by taking the log of x+10 (the decimal constant) and then subtracting 1 (the order of magnitude constant) from the resulting value (refer to McCune and Grace 2002). Sample size = 86 sites.

Category	Habitat characteristics (units)	Code	Mean	Standard deviation	Minimum	Maximum	Trans-formation
Hydrology	Days since dry (days)	DSD	556	802	0	2523	Log(x+1)
	Hydroperiod (days)	HYPER	239	61	39	333	none
	Water depth (cm)	DEPTH	41.8	21.4	6.0	90.0	Square root
Periphyton abundance	Periphyton biovolume (mL m^{-2})	PBIOV	3000	3200	0	14000	Square root
	Aerial cover (% of 1 m^2 quadrat)	AERCO	50	40	0	100	Arcsine square root
	Chlorophyll *a* mass (µg m^{-2})	CHLMA	$1.35x10^{-4}$	$1.34x10^{-4}$	0	$5.80x10^{-4}$	Square root
	Periphyton dry weight (g m^{-2})	DRYWT	50.3	79.7	0	437	Log(x+1)
	Periphyton ash-free dry mass (g m^{-2})	AFDM	17.4	23.2	0	121	Log(x+1)
Periphyton quality	Organic content of periphyton (%)	ORGCO	51	18	23	84	Square root
	Total periphyton phosphorus (µg m^{-2})	TP	190	140	20	660	(Log(x+10))-1
	Chlorophyll *a* concentration (µg g^{-1})	CHLCO	927	1340	65.5	8260	Log(x+1)
	Water column pH	pH	7.9	0.34	7.2	9.1	Tenth root
	Conductivity of water (µS cm^{-1})	CONDU	284	216	2.13	1170	Square root

mats and the influence of mats on the surrounding water column (Gottlieb et al. 2005; Thomas et al. 2006; Hagerthey et al. 2011). Each habitat characteristic was transformed to bring skewness (a metric to assess normality) closest to zero, including square root, arcsine square root, tenth root, and log transformations (McCune and Grace 2002) (Table 2.1). Samples more than two standard deviations from the mean Euclidean distance measure were considered outliers and removed from the dataset; subsequent analysis of species confirmed the absence of outlier species. Samples were categorized *a priori* into three wetland subsets based on landscape pattern and management practices: Shark River Slough (SRS), Water Conservation Areas 2A and 2B (WCA-2), and Water Conservation Areas 3A and 3B (WCA-3).

To examine diatom assemblage patterns associated with gradients of habitat characteristics, I used non-metric multidimensional scaling (NMS) ordination (Kruskal & Wish 1978; Minchin 1987) with the Bray-Curtis dissimilarity measure (Bray & Curtis 1957). Because the data are observational, I did not attempt to identify causal relationships between assemblages and habitat characteristics. The statistical program DECODA (Database for Ecological Community Data; Minchin 1990) was used to run ordinations and to fit vectors of maximum correlation of habitat characteristics with assemblage difference. To detect whether assemblages had consistent responses to habitat characteristics throughout the landscape or if there were distinct regional differences, analysis of similarity (ANOSIM) was conducted using Primer-E statistical software (version 6.0) to determine differences in diatom assemblages among and within the three wetland subsets (Clarke & Gorley 2006). Following the results of the ANOSIM, separate ordinations of wetland subsets were conducted to determine any subset-specific assemblage patterns. To test the null hypothesis that species responses to habitat characteristics are not associated among subsets, I used Kendall's coefficient of concordance with correction for tied ranks, W_c (Zar 1996).

I used the Bio-Env (Biota-Environment) procedure in Primer to determine the habitat characteristics most correlated with differences in diatom assemblages (Clarke & Ainsworth 1993). Bio-Env determines the correlation (Spearman) between the ranked dissimilarities of all possible pairs of samples based on the assemblage matrix and the ranked dissimilarities based on subsets of the environmental (habitat characteristics) matrix (Clarke & Warwick 2001). Rank correlation ρ=1 indicates complete agreement, whereas ρ=-1 indicates complete opposition (Clarke & Warwick 2001; Clarke & Gorley 2006). Because Bio-Env attempts to match all possible combinations of habitat characteristics to explain differences in the assemblage data, correlations could be found by chance. I tested the null hypothesis that the biota and the environment are not linked by using the BEST (Biota Environment STepwise) permutations test (999 permutations) in Primer to determine statistical significance (Clarke et al. 2008).

For the selected habitat characteristics, weighted averaging calibration models were constructed using C2 software to obtain species optima and tolerance values (Juggins 2005). The weighted averaging models were tested by simulating prediction errors using the bootstrapping resampling method repeated 1000 times (Efron 1982; Birks et al. 1990). The resulting Root Mean Square Error of Prediction (RMSEP) and bootstrapped (boot) r^2 were used as more conservative estimates of model fit compared to the apparent Root Mean Square Error (RMSE) and r^2 (Efron 1983; Birks et al. 1990; ter Braak & Juggins 1993; Birks 1995). For variables that were previously transformed, I present the upper and lower limits of tolerance values because of transformation-generated scale changes. For the same reason, I present RMSE and RMSEP values in transformed units. Finally, observed, diatom-inferred, and the difference between the observed and diatom-inferred values were mapped using ArcGIS version 10 (ESRI 2011). Interpolation techniques were not applied because of the inaccuracies that could result from the use of a limited number of sampling points across a large area.

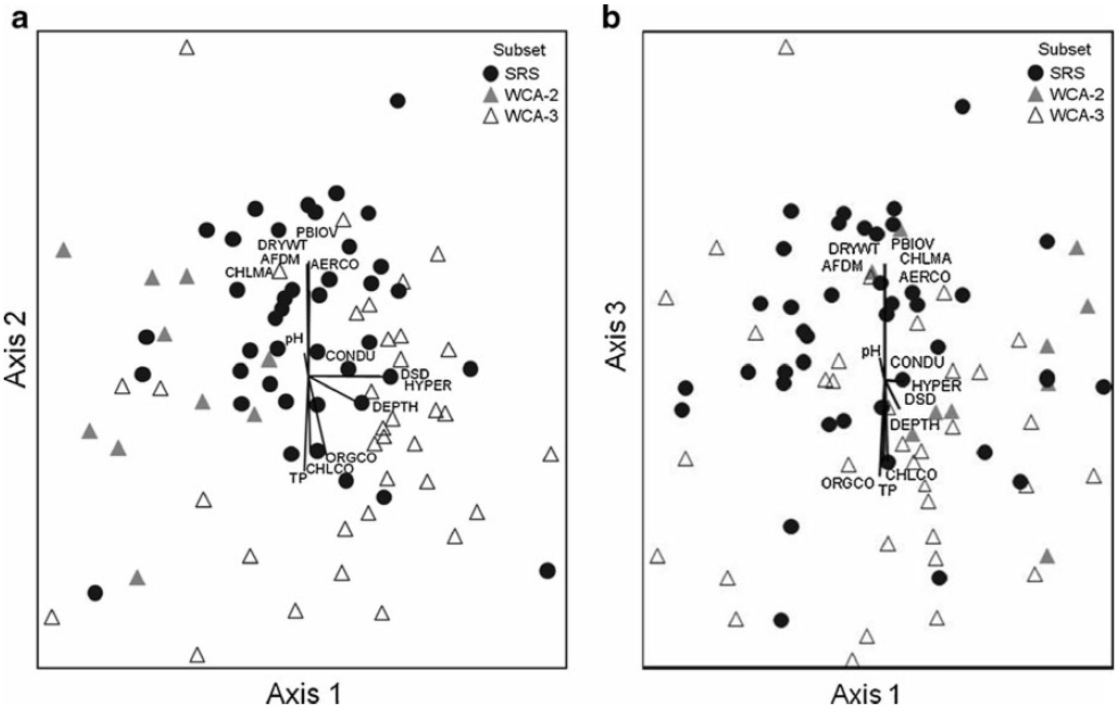
Results

Assemblage patterns and habitat characteristics

I observed 59 species of diatoms representing 21 genera. The most abundant species among all samples were *Mastogloia calcarea* (refer to Chapter III), *Encyonema evergladianum*, *Fragilaria synegrotesca*, and *Brachysira neoexilis*, making up 36%, 24%, 12%, and 9% of all diatom valves counted, respectively. *Mastogloia calcarea* was the most abundant species in WCA-3, SRS, and WCA-2 (38%, 35%, and 34% of all valves counted, respectively). There were 15 species common to all wetland subsets that contributed 95% of the total relative abundance, indicating high overlap of species among regions.

Differences among sites in the relative abundance of species generally grouped samples by wetland subset in the NMS ordination, though overlap was also common (Figure 2.1 a). A three-dimensional solution resulted in the greatest decrease in minimum stress level (stress=0.183) and was rotated by degree increments until the relative distribution of the vectors of habitat characteristics could be clearly depicted (Figure 2.1 a and b). The total rotation was 260°, which also maximized the association between

Figure 2.1. Non-metric multidimensional scaling ordination plot (multivariate representation of dissimilarities between samples based on rank order differences in assemblage composition). Three-dimensional ordination shown in two-dimensional plots for easier visualization: Axis 2 vs. 1 (a) and Axis 3 vs. 1(b). Plots rotated 260° (maximizing association between hydroperiod and Axis 1) to show relative distribution of environmental vectors. Wetland subsets: Shark River Slough (SRS), Water Conservation Areas 2A and 2B (WCA-2), and Water Conservation Areas 3A and 3B (WCA-3).



hydroperiod and Axis 1. The percentages of variance represented by Axis 1, 2, and 3 for the rotated ordination were 23%, 29%, and 20%, respectively. Periphyton biovolume, dry weight, AFDM, and TP had the largest magnitude of association with the ordination axes, as indicated by the length of the vectors (refer to Table 2.4 for exact correlation values). The relative placement and angles of the vectors showed patterns in diatom assemblages were correlated with hydrology (hydroperiod, days since dry, and water depth), periphyton quantity (periphyton biovolume, AFDM, dry weight, aerial cover, and chlorophyll *a* mass), and periphyton quality (TP, organic content, chlorophyll *a* concentration, and pH).

The habitats included in this study ranged from short (min=39 days) to very long (max=333 days) hydroperiod sites; periphyton biovolumes were as low as 0 mL m^{-2} (4 WCA-3 sites and 1 SRS site) to as high as 14,000 mL m^{-2} (Table 2.1). Most habitat characteristics were positively skewed; hydroperiod, however, was negatively skewed, indicating a greater number of long hydroperiod sites relative to short hydroperiod sites in the samples (Table 2.1). Habitat characteristics within the same category (hydrology, periphyton abundance, and periphyton quality) were correlated ($p<0.05$), except for conductivity; conductivity was only correlated with pH (Table 2.2). Organic content and other metrics of periphyton quality were correlated with metrics of periphyton abundance. SRS sites exhibited a negative relationship between hydroperiod and periphyton biovolume, while longer hydroperiod sites in WCA-2 and WCA-3 tended to have mats of higher periphyton biovolume but less organic content (Table 2.3).

Table 2.2. Pearson's correlation matrix of habitat characteristics (prior to transformations). Sample size = 86.

Category	Hydrology			Periphyton abundance					Periphyton quality				
	DSD	HYPER	DEPTH	PBIOV	AERCO	CHLMA	DRYWT	AFDM	ORGCO	TP	CHLCO	pH	CONDU
DSD													
HYPER	0.73[a]												
DEPTH	0.58[a]	0.47[a]											
PBIOV	-0.32[a]	-0.26	-0.50[a]										
AERCO	-0.23	-0.16	-0.41[a]	0.82[a]									
CHLMA	-0.30[a]	-0.23	-0.47[a]	0.92[a]	0.79[a]								
DRYWT	-0.32[a]	-0.30[a]	-0.54[a]	0.94[a]	0.82[a]	0.91[a]							
AFDM	-0.31[a]	-0.28[a]	-0.52[a]	0.95[a]	0.80[a]	0.92[a]	0.99[a]						
ORGCO	0.24	0.27[a]	0.46[a]	-0.60[a]	-0.65[a]	-0.57[a]	-0.76[a]	-0.65[a]					
TP	0.11	0.01	0.40[a]	-0.62[a]	-0.62[a]	-0.54[a]	-0.66[a]	-0.60[a]	0.72[a]				
CHLCO	0.38[a]	0.42[a]	0.56[a]	-0.65[a]	-0.57[a]	-0.47[a]	-0.73[a]	-0.68[a]	0.71[a]	0.59[a]			
pH	-0.21	-0.31[a]	-0.38[a]	0.42[a]	0.37[a]	0.41[a]	0.49[a]	0.48[a]	-0.40[a]	-0.25[a]	-0.43[a]		
CONDU	0.06	0.04	0.07	0.02	0.05	-0.02	0.00	-0.01	-0.01	-0.06	-0.07	-0.31[a]	

[a] Significant correlation at the 0.05 level

Table 2.3. Pairwise correlations between three habitat characteristics describing hydrology (HYPER), periphyton abundance (PBIOV), and periphyton quality (ORGCO) of wetland subsets: SRS (Shark River Slough) WCA-2 (Water Conservation Areas 2A and 2B), and WCA-3 (Water Conservation Areas 3A and 3B). Sample size = 86 sites.

	SRS			WCA-2			WCA-3	
	HYPER	PBIOV		HYPER	PBIOV		HYPER	PBIOV
PBIOV	-0.32[a]		PBIOV	0.20		PBIOV	0.24	
ORGCO	0.42[a]	-0.51[a]	ORGCO	-0.21	-0.42	ORGCO	-0.28	-0.53[a]

[a] Significant correlation at the 0.05 level

Landscape-scale patterns

Relative abundances of diatom species varied consistently among the three wetland subsets according to ANOSIM (Global R=0.26; p<0.01). Pairwise tests showed that SRS and WCA-2 were the most different (R=0.52), while SRS and WCA-3 were most similar (R=0.17), but differences between all pairs were statistically significant (p<0.01). Ordinations performed for the subsets (stress=0.17, 0.03, and 0.16; SRS, WCA-2, and WCA-3, respectively) showed that SRS assemblages had similar associations with habitat characteristics as the combined dataset (Figure 2.2a), except for responses to pH (Table 2.4). The WCA-3 assemblage also showed similar associations as those of the combined dataset (Figure 2.2b), except associations with days since dry, hydroperiod, chlorophyll *a* mass, conductivity and pH were not statistically significant. The WCA-2 assemblage was only associated with TP but, more importantly, had similar placement of vectors relative to each other as in the combined dataset (Figure 2.2c). Kendall's test of concordance between subset-specific species responses to habitat characteristics rejected the null hypothesis that species responses were not associated (W_c=0.76, χ^2=27.4, p<0.01; Table 2.4). Therefore, concordant associations of assemblage patterns among subsets allowed development of landscape-scale metrics using the entire dataset.

Weighted averaging models and maps

Hydroperiod, days since dry, water depth, periphyton biovolume, TP, and chlorophyll *a* concentration were selected by the Bio-Env procedure as the subset of habitat characteristics that formed the most correlated (ρ=0.27) ranked set of dissimilarities with that of the assemblage matrix. The procedure was repeated with

Figure 2.2. Non-metric multidimensional scaling. Three-dimensional ordination of wetland subsets: SRS (a), WCA-2 (b), and WCA-3 (c). Plots rotated to show relative distribution of environmental vectors.

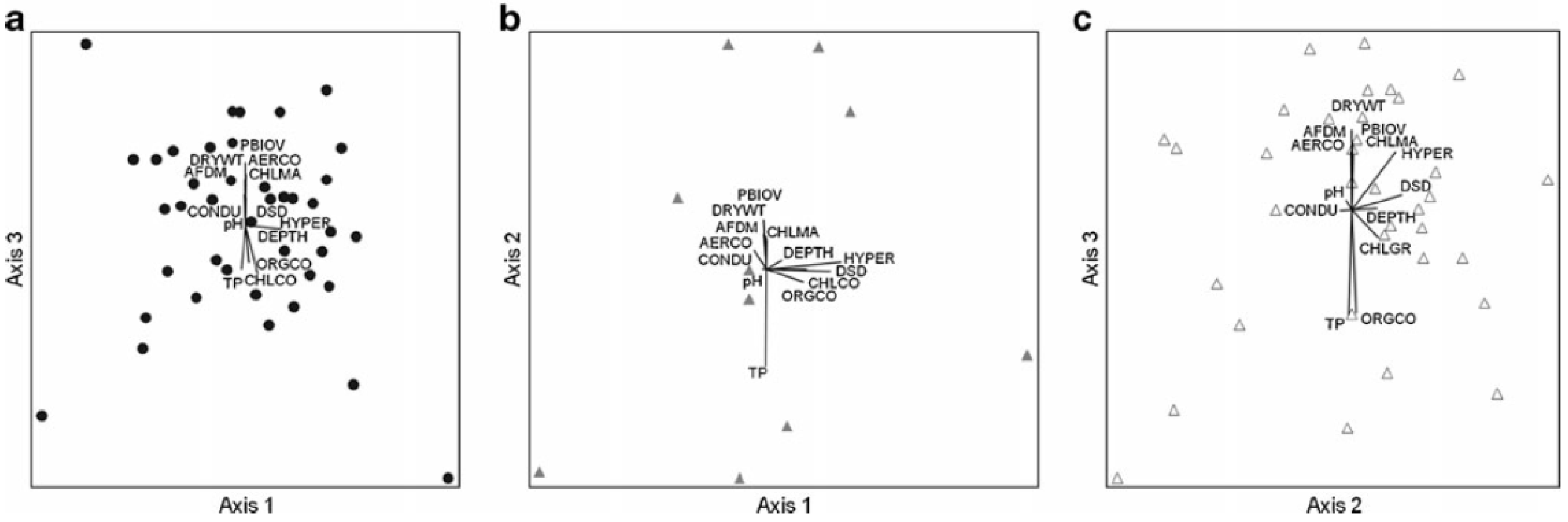


Table 2.4. Maximum correlation to vectors of habitat characteristics from non-metric multidimensional scaling of the entire dataset and each subset separately.

Habitat characteristics	All subsets (n=86)	SRS (n=41)	WCA-2 (n=10)	WCA-3 (n=35)
DSD	0.36[a]	0.37	0.52	0.37
HYPER	0.35[a]	0.57[a]	0.71	0.45
DEPTH	0.44[a]	0.59[a]	0.61	0.49[a]
PBIOV	0.61[a]	0.63[a]	0.42	0.52[a]
AERCO	0.56[a]	0.60[a]	0.50	0.52[a]
CHLMA	0.53[a]	0.48[a]	0.33	0.46
ORGCO	0.52[a]	0.67[a]	0.81	0.71[a]
DRYWT	0.61[a]	0.70[a]	0.42	0.55[a]
AFDM	0.59[a]	0.65[a]	0.34	0.47[a]
TP	0.59[a]	0.68[a]	0.80[a]	0.65[a]
CHLCO	0.53[a]	0.77[a]	0.76	0.57[a]
CONDU	0.27	0.36	0.48	0.27
pH	0.32[a]	0.33	0.27	0.31

[a] Significant correlation at the 0.05 level.

forced exclusions because of high correlations between hydroperiod and days since dry, hydroperiod and water depth, and between TP and chlorophyll *a* concentration (refer to Table 2.2). In the second run, hydroperiod, periphyton biovolume, and TP were selected as the subset to reach the highest rank correlation (ρ=0.25), with no improvement with the addition of any number of the remaining variables. Because the observed rank correlation could not be obtained after 999 permutations using randomized environmental matrices, I rejected the null hypothesis that there is no link between the assemblages and the environment (p<0.001). The variance in assemblage composition explained by hydroperiod, periphyton biovolume, and TP was 12.4%, 13.6%, and 17.9%, respectively (p<0.005 for all).

Because hydroperiod, periphyton biovolume, and TP best matched assemblage patterns, these three metrics best informed inference models for assessment applications. The TP weighted averaging models were comparable to previous models generated from Everglades diatom assemblages (Gaiser et al. 2006; La Hée & Gaiser 2012). Thus, I do not reiterate the results in this study. I evaluated the performance of weighted averaging models constructed for hydroperiod and periphyton biovolume by comparing diatom-inferred values with observed values (Figure 2.3). Diatom-inferred hydroperiod was correlated with observed values with r^2=0.63 (RMSE=35 days) and boot r^2=0.19 (RMSEP=55 days); diatom-inferred periphyton biovolume was correlated with observed values with r^2=0.56 (RMSE=19 square root mL m^{-2}) and boot r^2=0.41 (RMSEP=23 square root mL m^{-2}) (Table 2.5).

Hydroperiod optima of diatom species ranged from 99 to 303 days and tolerances ranged from 8 to 81 days above and below optima; periphyton biovolume optima ranged

Figure 2.3. Diatom-inferred vs. observed hydroperiod (a) and periphyton biovolume (b). Diatom-inferred values calculated using weighted averaging models with bootstrapping cross validation method. Weighted averaging method with the lowest RMSEP (Root Mean Square Error of Prediction) chosen. Strength of model prediction indicated by r^2 of trendline (apparent and bootstrapped r^2 values (boot r^2) shown). Dashed line indicates 1:1 line of 100% correlation. Axes scaled to back-transformed values for periphyton biovolume.

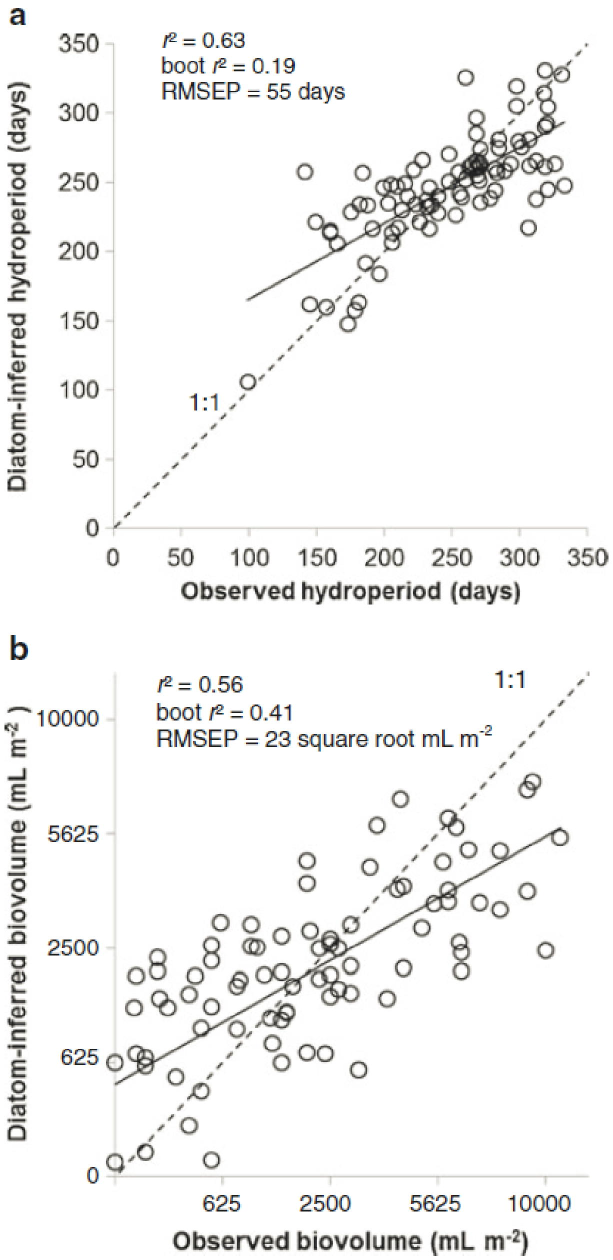


Table 2.5. Performance of weighted-averaging models by linear regression of diatom-inferred values against observed values of entire dataset and each subset separately. Slope of regression line (r^2) and Root Mean Square Error (RMSE) compared to slope of regression line of bootstrap cross-validated values (boot r^2) and Root Mean Square Error of Prediction (RMSEP).

		All subsets (n=86)	SRS (n=41)	WCA-2 (n=10)	WCA-3 (n=35)
Hydroperiod	r^2	0.63	0.67	0.71	0.76
	RMSE (days)	35	29	28	29
	boot r^2	0.19	0.26	0.1	0.23
	RMSEP (days)	55	48	54	54
Periphyton biovolume	r^2	0.56	0.57	0.59	0.67
	RMSE (square root mL m^{-2})	19	18	12	14
	boot r^2	0.41	0.37	0.02	0.31
	RMSEP (square root mL m^{-2})	23	23	23	22

from 0 to 6000 mL m^{-2} and tolerances ranged from as low as 0 mL m^{-2} (where flocculent matter from the benthos, rather than periphyton, was sampled) and as much as 11,000 mL m^{-2} (Table 2.6). *Pinnularia microstauron* was associated with shorter hydroperiod sites, while *Encyonema* sp. 02 was associated with longer hydroperiod sites; *Eunotia naegelii* was associated with low periphyton biovolume, while *Nitzschia serpentiraphe* was associated with high periphyton biovolume, though it had a wide tolerance range of 850 to 8700 mL m^{-2} (Figure 2.4).

Maps of observed values, diatom-inferred values, and differences (observed minus inferred values) for hydroperiod (Figure 2.5 a, b and c) and periphyton biovolume (Figure 2.5 d, e and f) allowed visualization of the spatial distribution of these important habitat characteristics and the accuracy of diatom-based inferences. The highest predicted values of hydroperiod were in WCA-3, while the northern part of SRS had the lowest predicted values. In SRS, very long hydroperiod conditions (>280 days) were underestimated and shorter hydroperiod conditions (<190 days) were overestimated. Inferred periphyton biovolume estimates were very similar to observed values, with the highest predicted values in SRS, and lower values (<5000 mL m^{-2}) in WCA-2 and WCA-3. Differences between observed and diatom-inferred values were generally no more than one standard deviation of the observed variability in hydroperiod and periphyton biovolume (Figure 2.5 c and f, respectively).

Discussion

Hydroperiod, periphyton biovolume, and periphyton TP content were the habitat characteristics most strongly associated with diatom assemblage structure in the

Table 2.6. Frequency, maximum abundance, and weighted-average optima and tolerance ranges of diatom species for hydroperiod (HYPER) and periphyton biovolume (PBIOV). Species sorted from low to high hydroperiod optima. PBIOV tolerance lower and upper limits reported because of transformation-generated changes in scale. Sample size = 86 sites.

			HYPER		PBIOV		
Taxon Name	Freq. (%)	Max. abund. (%)	opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Caponea caribbea Podzorski	0.005	0.397	99	50	3500	1300	6900
Nitzschia cf. *obtusa* W. Smith	0.005	0.395	145	50	1600	300	4000
Nitzschia amphibia var. *frauenfeldii* Grunow	0.009	0.781	157	50	6000	2900	10200
Pinnularia cf. *gibba* Ehrenberg	0.002	0.188	173	50	3700	1400	7100
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	0.005	0.302	178	50	400	0	1900
Eunotia camelus Ehrenberg	0.151	13.200	181	50	0	0	600
Gomphonema gracile Ehrenberg	0.014	1.200	181	50	0	0	600
Frustulia rhomboides var. *crassinervia* (Brébisson) Ross	0.023	1.208	192	44	700	100	1900
Pinnularia microstauron (Ehrenberg) Cleve	0.071	2.000	192	57	1500	0	5400
Frustulia sp. 01	0.005	0.378	196	50	0	0	600
Stenopterobia curvula (W. Smith) Krammer	0.005	0.378	196	50	0	0	600
Rhopalodia gibba (Ehrenberg) Muller	0.048	1.439	203	43	1400	200	3600

Table 2.6. Continued.

Taxon Name	Freq. (%)	Max. abund. (%)	opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Diploneis parma Cleve	0.503	7.273	205	53	1500	100	4400
Gomphonema affine Kützing	0.050	1.186	208	62	1600	200	4700
Diploneis oblongella (Naegeli ex Kuetzing) Ross	0.190	2.183	209	60	2200	600	4900
Navicula subtilissima Cleve	0.343	7.031	216	64	2800	700	6300
Nitzschia palea var. *debilis* (Kützing) Grunow	3.300	16.80	219	51	3100	800	6700
Brachysira brebissonii Ross	0.114	3.021	227	77	1000	0	3300
Encyonopsis microcephala (Grunow) Krammer	1.560	34.170	230	46	1600	100	5000
Nitzschia serpentiraphe Lange-Bertalot	2.461	33.100	230	52	4400	1400	9300
Cyclotella meneghiniana Kützing	0.263	1.188	233	50	1800	200	5000
Nitzschia amphibia (Grunow) Lange-Bertalot	0.192	1.727	234	57	700	0	2100
Brachysira neoexilis morph. 1 Lange-Bertalot & Moser	0.149	4.626	234	43	4400	900	10700
Navicula cryptotenella Lange-Bertalot	0.835	7.364	237	46	1000	100	3200
Eunotia naegelii Migula	0.069	3.008	237	45	100	0	1100
Eunotia monodon Ehrenberg	0.007	0.377	239	81	1100	500	2000

Table 2.6. Continued.

Taxon Name	Freq. (%)	Max. abund. (%)	opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Nitzschia palea (Kutzing) Smith	0.828	23.730	239	38	2000	500	4500
Amphora sulcata (Brébisson) Cleve	1.630	43.380	241	46	2000	500	4500
Eunotia flexuosa (Brébisson) Kützing	0.194	8.271	242	37	100	0	900
Brachysira neoexilis morph. 2 Lange-Bertalot	9.106	50.850	242	61	2200	400	5700
Brachysira pseudoexilis Lange-Bertalot & Moser	0.341	2.923	243	56	4100	1400	8300
Mastogloia calcarea Lee, Gaiser, Van de Vijver, Edlund & Spaulding	36.37	75.900	243	55	2100	300	5600
Brachysirea vitrea (Grunow) Ross	0.023	1.547	244	47	5200	2300	9400
Gomphonema intricatum var. *vibrio* (Ehrenberg) Cleve	0.595	7.200	245	48	900	0	3400
Sellaphora laevissima (Kützing) Krammer	0.133	0.985	245	54	1500	100	4600
Mastogloia lanceolata Thwaites	0.091	2.603	248	42	2600	900	5100
Navicula radiosa Kützing	0.464	4.494	251	47	1400	200	4000
Encyonema evergladianum Krammer	23.30	60.790	252	53	2200	400	5600
Achnanthes minutissima f. *gracillima* (Meister) Cleve-Euler	0.078	1.912	253	53	1100	100	3100
Fragilaria synegrotesca Lange-Bertalot	12.58	72.540	258	48	900	0	2900

Table 2.6. Continued.

Taxon Name	Freq. (%)	Max. abund. (%)	opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Enyconema silesiacum var. *elegans* Krammer	0.229	6.667	260	40	900	0	3100
Gomphonema coronatum Ehrenberg	0.005	0.355	260	50	100	600	5000
Amphora holsatica Hustedt	0.005	0.562	260	50	2300	0	900
Encyonema sp. 01	2.387	31.670	261	51	1400	100	3900
Eunotia incisa Gregory	0.018	0.388	262	10	300	0	1600
Nitzschia nana Grunow	0.174	5.618	263	61	1400	200	3700
Sellaphora pupula (Kützing) Mereschkowsky	0.027	1.509	265	8	100	0	1200
Aulacoseira italica (Ehrenberg) Simonsen	0.002	0.192	265	50	4400	1800	8100
Gomphonema vibriodes Reichardt & Lange-Bertalot	0.297	4.610	266	55	1000	0	3200
Encyonema silesiacum (Bleisch) Mann	0.220	14.750	268	50	100	0	100
Brachysira serians (Brébisson) Round & Mann	0.002	0.217	268	50	100	0	1100
Fragilaria nanana Lange-Bertalot	0.153	2.000	272	52	100	100	3100
Achnanthes caledonica Lange-Bertalot	0.300	11.260	280	62	1300	300	3100
Fragilaria ulna var. *ulna* (Nitzsch) Lange-Bertalot	0.027	0.901	287	56	1200	200	3300

Table 2.6. Continued.

Taxon Name	Freq. (%)	Max. abund. (%)	opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Navicula radiosafallax Lange-Bertalot	0.014	0.538	291	41	200	0	500
Stauroneis javanica (Grunow) Cleve	0.002	0.186	298	50	2500	1000	6100
Achnanthes cf. *minutissima* v. *gracillima* (Meister) Lange-Bertalot	0.005	0.407	298	50	3000	700	5400
Encyonema sp. 02	0.018	0.377	303	28	1200	200	3000
Fragilaria delicatissima (W. Smith) Lange-Bertalot	0.009	0.538	303	50	300	0	700

Figure 2.4. Relative abundances of diatom species indicating preferences (optima and tolerance ranges) for a range of hydroperiod (a-f) and periphyton biovolume (g-l). Second order polynomial trendlines. Note different y-axis scales for each taxon.

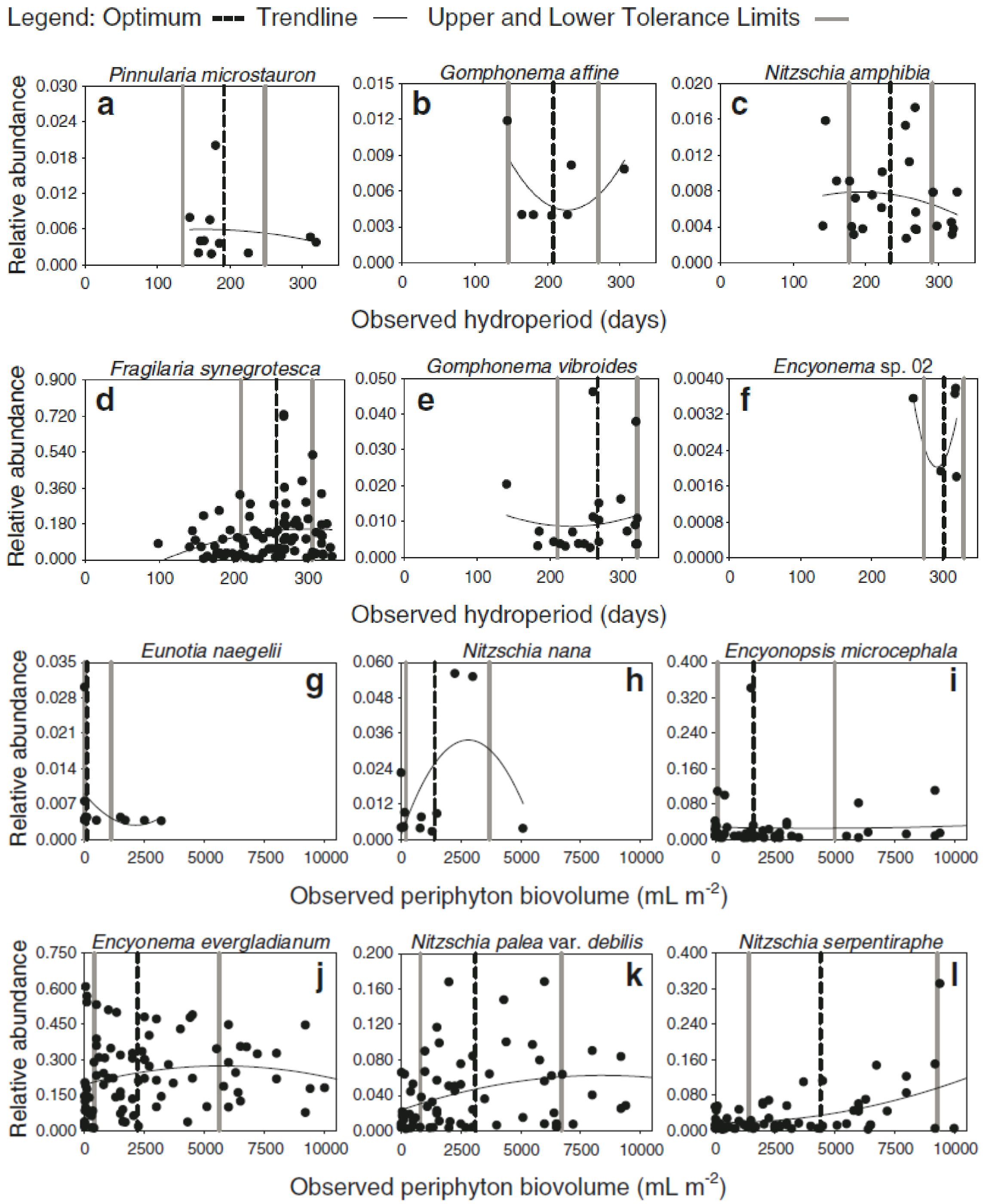
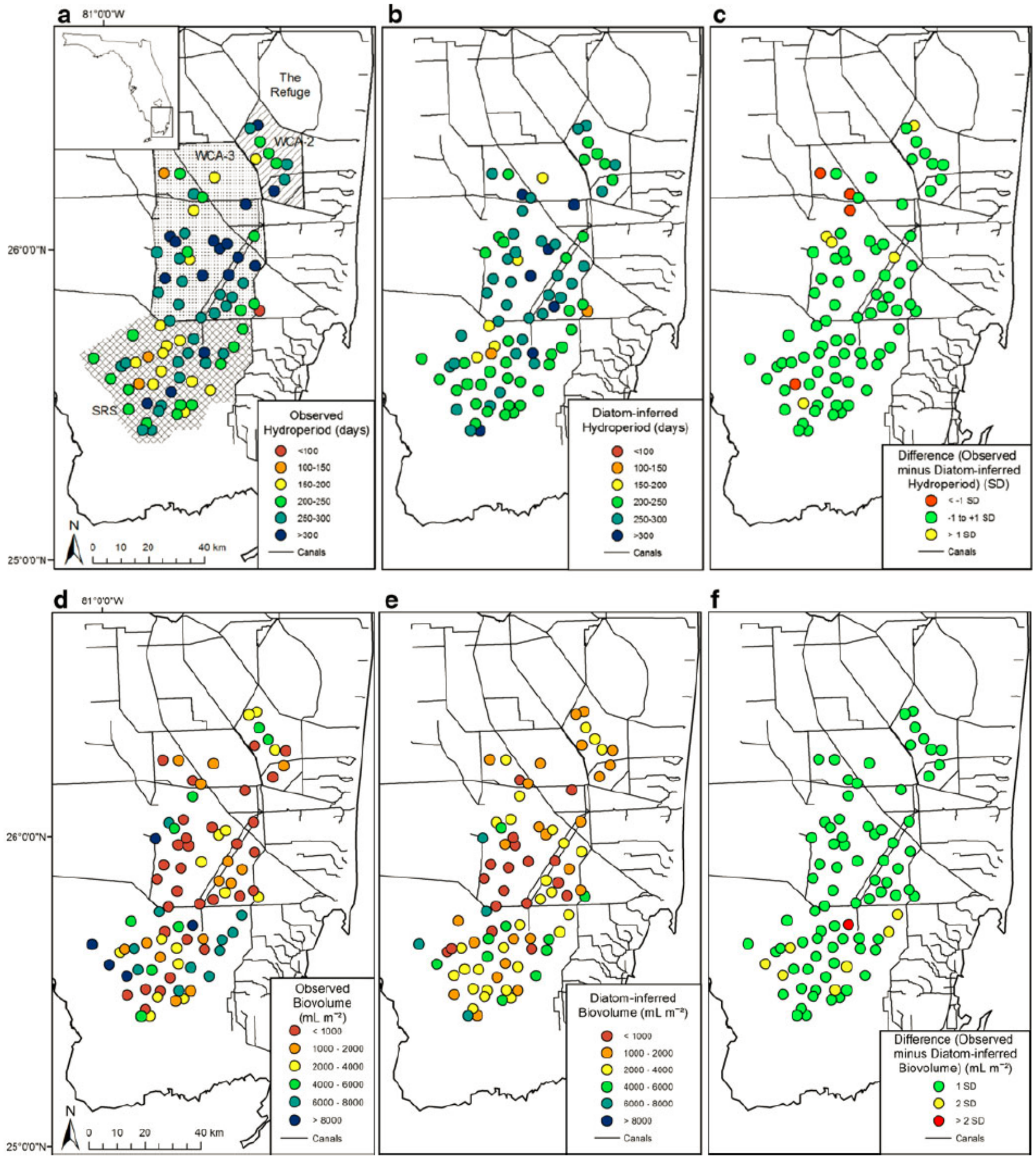


Figure 2.5. Observed, diatom-inferred, and difference (observed minus diatom-inferred values) maps of hydroperiod (a, b, c) and periphyton biovolume (d, e, f), respectively. Black values in difference maps (c and f) indicate values within one standard deviation of observed values. Standard deviations of hydroperiod and periphyton biovolume are 61 days and 3200 mL m^{-2}, respectively. Patterning in (a) delineates wetland subset boundaries.



Everglades. The underlying geology and geomorphology influence the natural hydropatterns of the Everglades (McVoy et al. 2011), while an extensive system of canals, levees and water control structures control the present flow of water (Sklar et al. 2002). Alterations to the hydrology of the Everglades influence periphyton biovolume and nutrient content, especially when canal inputs increase delivery of minerals or P and encourage the development or disintegration of periphyton communities (Iwaniec et al. 2006; Hagerthey et al. 2011; McCormick et al. 2011). Periphyton biovolume has been used as a metric of productivity (e.g., Ewe et al. 2006; Iwaniec et al. 2006), but has not been analyzed as a habitat characteristic for diatom assemblages. Because mats of high and low abundance appear to support distinct diatom assemblages, assemblage composition is useful for inferring the abundance of periphyton in given wetland locations in the past (before drainage and management) to inform restoration target-setting. A known relationship between assemblage composition and periphyton biovolume would also aid restoration assessment because obtaining measurements of periphyton biovolume in the field is simple compared to the additional processing required to obtain measurements of chlorophyll *a* or nutrients in the laboratory. Because certain diatom species (e.g., *Eunotia camelus*, *Gomphonema gracile*, and *Stenopterobia curvula*) are associated with flocculent detrital material but absent or infrequent at sites with periphyton (zero minimum biovolume optimum and tolerance), their relative abundances can indicate the absence of periphyton. Thus, diatoms are comprehensive indicators of periphyton abundance that can provide inferences about a range of wetland environments that may or may not support periphyton.

While the relationship between phosphorus concentrations and diatom assemblage structure is well-documented (McCormick et al. 1996; McCormick et al. 1998; Pan et al. 2000; Gaiser et al. 2006; Cooper et al. 2008; La Hée & Gaiser 2012), this study shows the important effects of hydroperiod and periphyton biovolume on diatom composition. The exact mechanisms driving diatom assemblage composition are undefined, but feedbacks among hydroperiod, periphyton biovolume, and composition likely shape wetland structure and function. The tendency to have high periphyton abundance in short hydroperiod areas (Gottlieb et al. 2006) indicates the periphyton mats in these areas could favor desiccation-resistant species capable of surviving annual drying. In turn, desiccation-resistant diatoms and other algal species produce biomass, including anti-desiccative mucilage (Hoagland et al. 1993), that contribute to high biovolume periphyton mats, while also playing a role in controlling nutrient and mineral concentrations in the surrounding water column (Gottlieb et al. 2005; Thomas et al. 2006; Hagerthey et al. 2011). Further investigations are needed to understand how changes in hydrology affect these feedbacks.

The responses of individual diatom species, especially species with narrow tolerance ranges, had a key role in determining predictive relationships of diatom assemblages with hydroperiod and periphyton biovolume. For example, *Fragilaria synegrotesca* preferred long hydroperiod habitats; this agreed with previous findings by Gottlieb et al. (2005) and Gaiser et al. (2011). The diatom species with the longest hydroperiod optimum was *Fragilaria delicatissima*, a planktonic species (Patrick & Reimer 1966). *Pinnularia microstauron* was associated with shorter hydroperiod habitats; the type specimen of this species was found in soil on the roots of plants from Rio de

Janeiro, Brazil, indicating its ability to survive in drier conditions (Patrick & Reimer 1966). The holotype of *Caponea caribbea*, which had the shortest hydroperiod optimum in this study, was collected by Podzorski (1985) from algal mats on the surface of a Jamaican peat swamp that had experienced a fire some months prior. Podzorski's (1985) findings suggest that *C. caribbea* is adapted to surviving periodic desiccation and fire, which are frequent in short-hydroperiod wetlands; this species may even indicate time since fire. Species associated with habitats with very little periphyton, such as *Eunotia camelus* and *Stenopterobia curvula,* are acidophilic diatoms not usually found in calcium-rich habitats like calcareous periphyton mats (Patrick & Reimer 1966; Krammer & Lange-Bertalot 1988; Furey 2010). *Gomphonema gracile* and *G. coronatum* have been reported to prefer high P habitats with pH<7 (Tobias & Gaiser 2006; Slate & Stevenson 2007).

Some of the more common diatom species in the flora of Everglades calcareous periphyton had broad tolerance ranges that were not useful for inferring habitat characteristics. *Nitzschia serpentiraphe*, a very common species in slough periphyton mats with a moderate (Slate & Stevenson 2007) to low TP optimum (Gaiser et al. 2006), reached its highest abundance in the thick, calcareous mats from SRS. Calcareous periphyton mats disintegrate because of a shift in community structure from a calcite-precipitating filamentous flora (species of *Utricularia* and cyanobacteria that provide substrates for diatom growth) to dominance by green algae and eutrophic diatoms following P enrichment (McCormick & O'Dell 1996; McCormick et al. 2001; Gaiser et al. 2005b; Gaiser et al. 2006; Gaiser et al. 2011). This phenomenon supports the association of *N. serpentiraphe* with high periphyton biovolume and correspondingly low to moderate TP habitats. However, *N. serpentiraphe* also had a wide tolerance range, which is expected because species in this genus are known to tolerate eutrophic conditions (Van Dam et al. 1994). The species with the highest periphyton biovolume optima (including *N. amphibia* var. *frauenfeldii*, *N. serpentiraphe*, *Brachysira vitrea*, and *B. neoexilis*) had an average tolerance range of greater than 8000 mL m^{-2}. The wide tolerance ranges of these species restrict optima from reaching higher values, even though periphyton abundance can exceed 10,000 mL m^{-2}. Inferences about periphyton abundance and enrichment based on diatoms with wide tolerance ranges should be made with caution because other factors may allow some species to thrive in both enriched and unenriched habitats.

I found that although the wetland subsets in this study differed in species' relative abundances, similar assemblage responses to habitat characteristics allowed development of a landscape-scale model encompassing gradients broader than those present in individual subsets. None of the NMS ordinations captured a response to conductivity, likely because of the shorter conductivity gradient encompassed by this study's focus on alkaline freshwater habitats (where calcareous periphyton thrives) relative to gradients of other habitat characteristics. The lack of response by WCA-3 assemblages to metrics of inundation (days since dry and hydroperiod) may reflect how the impoundment of water for flood control in the WCAs limits the natural variability of inundation (Light & Dineen 1994; Romanowicz & Richardson 2008). In contrast, historic P enrichment in WCA-2 affected nutrient removal (Craft & Richardson 1993), peat accretion (Reddy et al. 1993), and vegetation (Urban et al. 1993). In this study, species assemblages in WCA-2 were not associated with any of the variables measured except TP. The lack of response to the other habitat characteristics could be attributed to the low sample size of the subset (n=10). Despite these differences, hydroperiod and periphyton biovolume weighted averaging models made separately for each subset had lower boot r^2 values (especially models for WCA-2) or only slightly improved boot r^2 values (the hydroperiod models for SRS and WCA-3) (Refer to Table 2.5), probably because of the decrease in sample size (Birks et al. 1990; Reavie & Juggins 2011). The lack of improvement in correlation values of subset-specific models validated combining wetland subsets for landscape-scale assessment.

The weighted averaging models for hydroperiod and periphyton biovolume showed the utility of diatom assemblages for wetland assessment. The Everglades model in this study was not as strong as the hydroperiod model by Gaiser et al. (1998) for diatoms from surface sediments of intermittent ponds on the Atlantic Coastal Plain (r^2=0.81), because the Everglades model underestimates long hydroperiod conditions and overestimates short hydroperiod conditions. The limitations of the Everglades model could be a result of higher spatial and temporal variability within a wetland compared to ponds that are similar in geology, vegetation, and water source but range broadly in hydroperiod, permitting a more extreme gradient for developing inferences. Because unimodal-based calibration methods are prone to the 'edge effect' (ter Braak & Juggins 1993; Birks 1998), which biases inferred values towards the mean of the observed values, I evaluated but did not employ weighted averaging models using partial least squares regression (ter Braak & Juggins 1993) to conserve parsimony and because improvements were not statistically significant.

Visualizing the weighted averaging models showed that for both hydroperiod and periphyton biovolume, most of the differences between observed and diatom-inferred values were within the variability (one standard deviation) of the observed values. Because wetlands are spatially complex, maps are useful for summarizing biotic responses to the environment by visualization of biological patterns across a landscape in a way that integrates spatial and environmental heterogeneity. Maps can complement tools already developed for restoration assessment (Gaiser 2009), to visualize compliance or deviation of current conditions from reference or restoration targets.

Analyzing diatom assemblage composition is a useful way to develop predictive models about the environment that coarser metrics may not always capture, especially in dynamic systems such as wetlands. Unlike one-time direct measurement of physical or chemical conditions such as periphyton biomass or water quality, assemblage composition is less prone to sampling variability because it integrates environmental conditions over larger spatial and temporal scales (Stevenson 1998). The relationship between diatom assemblages and hydrology is especially important in the Everglades because hydrologic manipulation is the basis of current restoration plans. As advances in diatom taxonomy continue to develop, it is imperative to make identifications to the species level in order to reconcile any current taxonomic discrepancies with future datasets (Julius & Theriot 2010). This effort would facilitate the combination of datasets for analyses at larger spatial and temporal scales. While assessment based on the presence or absence of a few indicator species can be less time consuming and costly, this method is prone to non-detection resulting from variable species detectability or inadequate sampling (MacKenzie 2005). Gottlieb (2003) found that long and short hydroperiod assemblages differed in species relative abundances, rather than in the presence or absence of species. Likewise, I found that wetland subsets had differing species relative abundances, not species identities, which permitted development of inference models at the landscape scale. The laborious process involved in species identification and enumeration is worthwhile, considering the wealth of information it provides about how the species within assemblages respond, as a whole, to the environment and should be incorporated in assessments of other wetland systems.

Sound ecologically-based assessment of change in wetlands requires an understanding of how assemblages respond to ecosystem parameters to make interpretations about past conditions, develop targets for the future, and aid assessment. This study found diatom assemblage composition has predictable relationships with two very important habitat characteristics of wetland ecosystem function: hydroperiod and periphyton biovolume. Wetland management programs should use this information to infer landscape-scale biological responses to hydrologic change and to inform restoration targets, especially in the Everglades where hydroperiod regimes no longer follow natural spatial and temporal patterns (Romanowicz & Richardson 2008). The hydroperiod and periphyton biovolume optima and tolerance ranges of Everglades diatom taxa defined by this study are important autecological information that should be used to further investigate the poorly described flora of tropical karstic wetlands (La Hée & Gaiser 2012). Finally, this study found landscape-scale models are possible in the Everglades because diatom assemblage patterns were consistent across wetland subsets. Spatially-explicit visualizations of these models are useful for assessing the performance of diatom-based inferences over a large area. Landscape-scale diatom-based models from the Everglades should be used as an example for other large wetlands around the world with high hydrologic connectivity, such as boreal wetlands (Spence et al. 2011), the Pantanal (Alho et al. 1988), and the Okavango Delta (McCarthy et al. 2000). Although most tropical wetlands have received inadequate attention to date, advancements made by monitoring, restoration, and assessment efforts for the subtropical Everglades can guide newly developing wetland protection programs.

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CHAPTER III: MORPHOLOGY AND TYPIFICATION OF *MASTOGLOIA SMITHII* AND *M. LACUSTRIS*, WITH DESCRIPTIONS OF TWO NEW SPECIES FROM THE FLORIDA EVERGLADES AND THE CARIBBEAN REGION

Abstract

The names *Mastogloia smithii* Thwaites ex Smith and *M. smithii* var. *lacustris* Grunow have been attributed to a variety of related diatom morphologies, partly because of poor availability of type material and complicated nomenclatural history. The history is detailed, clarifying the type morphologies of *M. smithii* and re-confirming a neglected elevation of *M. smithii* var. *lacustris* to *M. lacustris* (Grunow) Grunow. Populations reported as *M. smithii* and *M. lacustris* from the temperate zone (Ontario, Canada and Iowa and Michigan, USA), karstic wetlands of the subtropical Everglades (Florida, USA) and the tropics (Jamaica, Mexico, and Belize) are compared to each other. Based on morphological differences including density of partecta, striae, and areolae, *M. calcarea* sp. nov. and *M. pseudosmithii* sp. nov. are described from the Everglades and the Caribbean region, and a lectotype of *M. smithii* and a neotype of *M. lacustris* are designated.

Introduction

Diatoms within the genus *Mastogloia* Thwaites ex W. Smith have naviculoid valves with rounded to capitate apices, areolate striae, and modified valvocopulae with chambers called partecta (Smith 1856, Stoermer et al. 1964, Ross et al. 1979, Round et al. 1990, Paddock & Kemp 1990). *Mastogloia* is highly diverse, with an estimated 410 taxa (Novarino 1989) distinguished by various morphological features including the stria arrangement across the valve surface, the orientation, size, shape, and number of partecta, the shape of the raphe and raphe ends, and other internal and external ultrastructural characters (Hustedt 1933, Voigt 1942, Stephens & Gibson 1980, Novarino 1990, Paddock & Kemp 1990, Pennesi et al. 2011). Hustedt (1933) divided *Mastogloia* into 11 eco-morphological groups, two of which are pertinent to the taxa studied in this investigation: Apiculatae and Lanceolatae. *Mastogloia* is a predominantly marine genus (e.g., Pennesi et al. 2011, 2012), but also has brackish and freshwater representatives (Round et al. 1990).

Mastogloia smithii Thwaites ex W. Smith is a common, presumably cosmopolitan, benthic diatom (Zafar 1964, Krammer & Lange-Bertalot 1986, Caljon & Cocquyt 1992, García-Rodríguez et al. 2002, Townsend & Gell 2005) that can attain high abundances in freshwaters with high conductivity and pH (Laird et al. 1996, Snoeijs 2001, Townsend & Gell 2005). Along with *M. lacustris* (Grunow) Grunow, more commonly reported as *M. smithii* var. *lacustris* Grunow, *M. smithii* has been described as dominant in the karstic wetlands of the Florida Everglades (Slate & Stevenson 2007, Gaiser et al. 2010) and the Caribbean, including Jamaica, Belize, and Mexico (Novelo et al. 2007, Ibarra et al. 2009, Gaiser et al. 2010, La Hée 2010, La Hée & Gaiser 2012).

However, the identity of these karstic wetland specimens is questionable in some of these reports; the name *M. smithii* is sometimes erroneously used for specimens that show more resemblance to *M. lacustris* (Gaiser et al. 2010). Moreover, some morphological features of subtropical and tropical populations reported under these names vary from those reported in the literature, and further investigations into their differences have been suggested (Gaiser et al. 2010). Investigation of subtropical and tropical populations must include the assessment and validation of the original taxonomic concepts of *M. smithii* and *M. lacustris* by examination of the type material. This validation, as well as the resolution of any major taxonomic discrepancies within the literature, is necessary to accurately represent the true diversity of diatoms, especially in regions with poorly known floras such as the Caribbean (La Hée 2010, La Hée & Gaiser 2012).

Mastogloia smithii has a complicated nomenclatural history because of variability in the descriptions and specimen sources used by diatomists, leading to confusion in the literature. *Mastogloia smithii* was originally described by Smith (1856, p. 65) from fresh and brackish water samples collected on 10 sampling dates from eight locations in England, including the "Little Sea" in Dorset: "Valve elliptical, extremities produced; loculi 6 to 24; striae 42 in .001″. Breadth of valve .0003″ to .0008″ " (16.5 striae in 10 µm and 7.6–20.3 µm wide) (Tables 3.1–3.2). Smith (1856) also recognized an unnamed *"β"* form of *M. smithii* with capitate ends: *"β*. Extremities produced and inflated." He (Smith 1856) distinguished *M. smithii* from *M. danseii* (Thwaites) W. Smith and *M. lanceolata* Thwaites by "its freshwater habitat, distinctly produced, and occasionally capitate extremities and variable breadth." In this statement, Smith (1856) did not appear to consider the capitate *"β"* form a separate entity from the nominate variety. Smith's

Table 3.1. Source material (samples) and slides examined for the study of *Mastogloia* species.

Taxa examined	Source information	Collection location	Latitude (N)	Longitude (W)	Date
M. smithii lectotype	Material and slide VI-43-B5 (BR)	Dorset, UK	nd	nd	Oct. 1848
M. lacustris neotype	Material and slide III-24-A9 (BR)	Bergh, Brabant, Belgium	nd	nd	nd
M. lacustris isoneotype	Slide Types du synopsis des diatomées de Belgique. no. 47. *M. smithii* var. *lacustris* Grun. Belgique (FH)	Bergh, Brabant, Belgium	nd	nd	nd
M. lacustris confirmed distribution records	Slide EEG 08-24-10 Alvar rock pool periphyton (FIU)	Misery Bay Provincial Nature Reserve, Ontario, Canada	45°48.349	82°46.315	Aug. 2010
	Slide 2011-13 Periphyton on buoy (ILH)	Little Miller's Bay, Milford, Iowa, USA	43°22.693	95°10.844	May 2011
	Slide JPK 5591-5 (FIU)	O'Neal Lake, Michigan, USA	45°42.758	84°53.264	Mar. 2011
M. calcarea holotype	Material GCM 4841 and slide GC 58993 (ANSP)	Everglades National Park, Florida, USA	25°41.883	80°39.249	Oct. 2008
M. calcarea isotype	Slide 4298 (BR)	Everglades National Park, Florida, USA	25°41.883	80°39.249	Oct. 2008
M. calcarea paratypes	Slides 4311 (BR) and GC 16009 (ANSP)	Broad River, Black River Morass, St. Elizabeth, Jamaica	18°01.524	77°48.874	May 2008
	Slides 4312 (BR) and GC 30902 (ANSP)	New River Lagoon, Orange Walk, Belize	17°45.527	88°38.456	Nov. 2007
	Slides 4313 (BR) and GC 30903 (ANSP)	Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico	19°49.619	87°30.585	Dec. 2006

Table 3.1. Continued.

Taxa examined	Source information	Collection location	Latitude (N)	Longitude (W)	Date
M. pseudo-smithii holotype	Material GCM 4842 and slide GC 58994 (ANSP)	Everglades National Park, Florida, USA	25°28.935	81°2.907	Nov. 2011
M. pseudo-smithii isotype	Slide 4314 (BR)	Everglades National Park, Florida, USA	25°28.935	81°2.907	Nov. 2011
M. pseudo-smithii	Material and slide CERP 034 851 1 19 (FIU)	Water Conservation Area 2A, Florida, USA	26°12.874	80°22.101	Oct. 2011
	Material and slide CERP 009 884 1 19 (FIU)	Water Conservation Area 3A, Florida, USA	26°14.275	80°38.956	Oct. 2011
M. aff. *smithii* 1	Material JPK 5591 (CU); slides JPK 5591-1 to JPK 5591-4 (FIU)	O'Neal Lake, Michigan, USA	45°42.758	84°53.264	Mar. 2011
M. aff. *smithii* 2	Material and slide III-24-A8 (BR)	South Africa	nd	nd	nd
	Slide Types du synopsis des diatomées de Belgique. no. 46. *M. smithii* Thwaites Afrique méridionale (FH)	South Africa	nd	nd	nd

Note. BR: National Botanic Garden of Belgium; FH: Farlow Herbarium; ANSP: Academy of Natural Sciences, Philadelphia; FIU: Florida International University; ILH: Iowa Lakeside Laboratory Reimer Herbarium; CU: University of Colorado; nd: no data.

Table 3.2. Morphometric data and morphological features of *Mastogloia smithii* from relevant reference sources, with LM measurements of *M. smithii* lectotype and mean values in parentheses. Information from references obtained directly from the text.

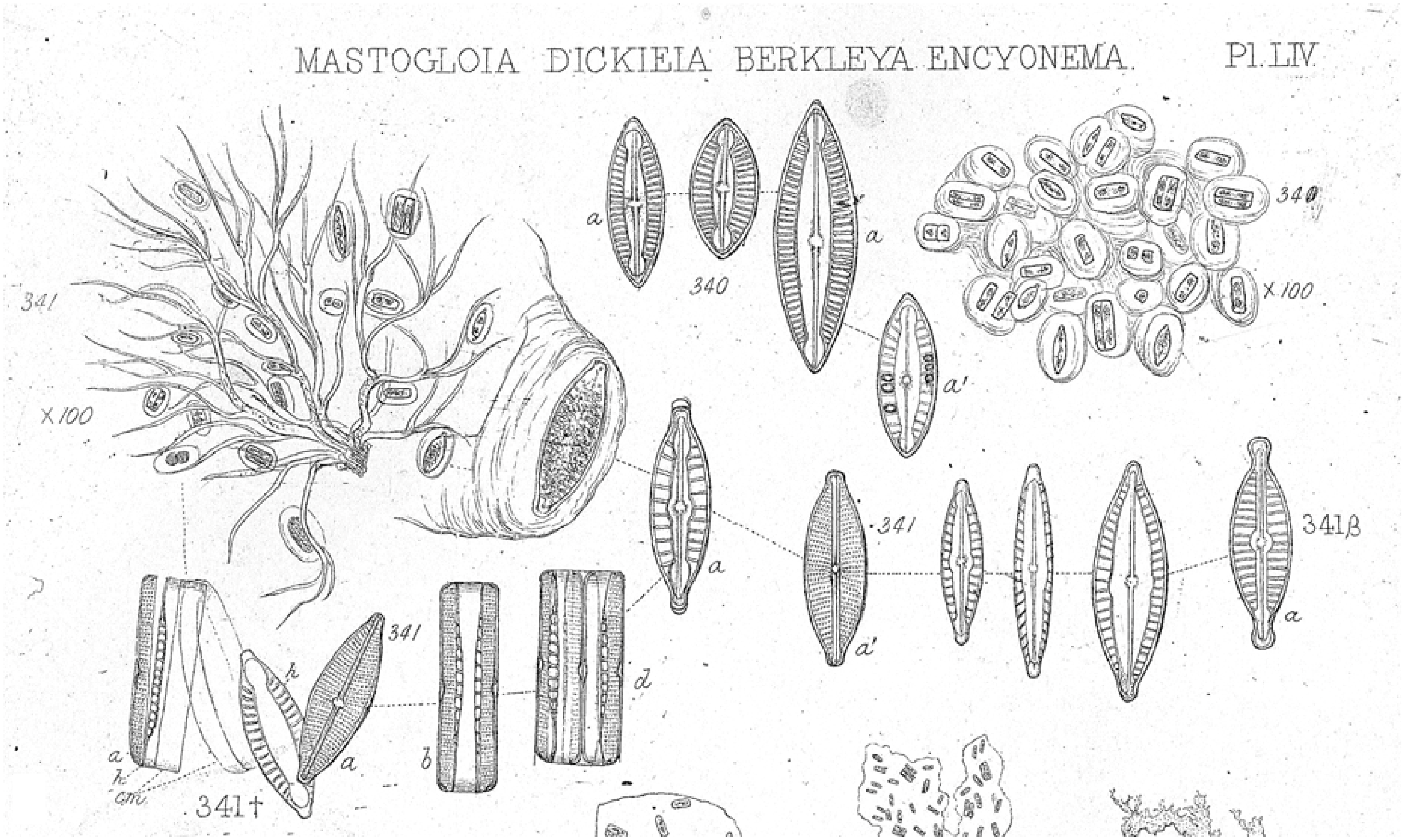
Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (μm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
Smith (1856)	nd	nd	7.6–20.3	nd	16.5	nd	nd	nd	nd	nd	Elliptical	Produced; *“β”* form: produced and inflated
Van Heurck (1885)	nd	30–45	nd	nd	15–17	nd	nd	nd	Slightly extended laterally	Radiating to apices	Elliptical	Slightly reduced-rostrate, attenuated
Patrick & Reimer (1966)	nd	20–45	8–14	nd	18–19	14–17	6–8	nd	Small, elliptical to quadrangular	Parallel or slightly radiate	Elliptical to elliptical-lanceolate	Short, protracted, subrostrate to subcapitate
Krammer & Lange-Bertalot (1986)	nd	20–60	8–14	nd	18–20	15–21	nd	nd	Small, round to elliptical or rectangular	nd	Linear-elliptical	Capitate
Lectotype VI-43-B5, Dorset, UK	20	25–50 (35)	11–15 (13)	2.7	20–21	23–26	6–8	3.9	Elliptical 6–12 (9)	166–174 (170)	Elliptical-lanceolate	Rostrate to capitate

Note. n: number of specimens measured; nd: no data.

(1856) drawing of *M. smithii* (Figure 3.1) showed variability in valve width, but consistently featured a very narrow central area and longitudinal lines on either side of the raphe that could indicate axial costae (Ross et al. 1979, Stephens & Gibson 1980); however, the size of the central area and presence of axial costae were not mentioned in the written description.

The taxonomic concept of *M. smithii* began shifting shortly after the taxon was described. According to VanLandingham (1971), the first published use of *M. smithii* after Smith (1856) was Grunow (1860), but Grunow (1860) was skeptical of the status of *M. smithii sensu* Smith as a distinct taxon from *M. lanceolata sensu* Smith. Nevertheless, *M. smithii* was subsequently reported from Ireland (O'Meara 1871), the Caspian Sea (Grunow 1878), France (Brun 1880), South Africa (Van Heurck & Grunow 1882–1885), Belgium (Van Heurck 1880, 1885), and North America (Wolle 1894), among other locations (VanLandingham 1971). Evidence of a major shift in the concept of *M. smithii sensu* Smith was found in Patrick & Reimer (1966), who reported *M. smithii* as widely distributed within the United States, especially in freshwater lakes. However, their figure of *M. smithii*, was based not on type nor even United States material, but on South African material used by Van Heurck (exact location not provided in Van Heurck & Grunow 1882–1885, Type no. 46; note that this publication and other exsiccatae in the Van Heurck and Grunow collection are not types as defined by the International Code of Nomenclature for algae, fungi, and plants). The taxonomic concept of *M. smithii* presented by Van Heurck (1885) and Patrick & Reimer (1966) did not include axial costae on either side of the raphe. Patrick & Reimer's (1966) figure of *M. smithii* has a distinctly asymmetrical and panduriform central area not present in *M. smithii sensu*

Figure 3.1. Original line drawing of *Mastogloia smithii*, labeled 341 and 341β from Smith (1856).



Smith. Furthermore, Krammer & Lange-Bertalot (1986, pl. 201, figs 2–5, 7–9) showed micrographs of *M. smithii* specimens with varying valve widths and apices, all lacking evidence of axial costae, from three locations: Belgium, Northern Europe, and South Africa. Because subsequent researchers did not reconcile these discrepancies, problems arose when taxa identified as *M. smithii* in other collections were studied. For example, Novarino (1990) studied the morphology of specimens from the Rabenhorst collection (Cesati Herbarium in Rome, Italy) identified as *M. smithii*, but noted several differences from earlier descriptions: the undulate rather than straight raphe, the rectangular rather than circular central area, the presence of pseudopartecta (protuberances between the terminal partecta and the partectal ring apices), and the absence of axial costae.

Misinterpretations also arose when *M. smithii* was reported from regions of the world with relatively poorly studied floras, such as subtropical and tropical wetlands in the western hemisphere. When Podzorski (1985) reported *M. smithii* from Jamaica, he referred to the description by Patrick & Reimer (1966), even though his micrographs show narrower valves (pl. 5, figs 21–22) than *M. smithii sensu* Patrick & Reimer, and only the partectal ring of a slightly wider valve (pl. 5, fig. 18). Difficulty with nomenclature and morphological diversity of *M. smithii* became further apparent when Slate & Stevenson (2007) reported two morphotypes of *M. smithii* from the Florida Everglades, USA; the morphotypes were distinguished by valve outline (linear-lanceolate in Morphotype I and almost elliptical in Morphotype II) and slightly larger lengths in Morphotype I. Slate & Stevenson (2007) noted that Morphotype I resembled *M. lacustris*, but with higher areola and stria density than that given in the literature. Gaiser et al. (2010) reviewed the ecology and morphology of subtropical and tropical populations, distinguishing the dominant morphotype from *M. smithii* (to which it is often referred in Everglades literature) after reviewing type material, and aligning it more closely to *M. lacustris* (referred to as *M. smithii* var. *lacustris* Grunow).

The nominate variety of *M. smithii* has been closely allied to, and often confused with, *M. lacustris. Mastogloia lacustris* was originally described as a variety of *M. smithii* by Grunow (1878, p. 111): "*Eine ziemlich abweichende Form der* M. Smithii*, welche ich einstweilen als var. lacustris bezeichne, findet sich in Süsswasserseen. Sie hat einen viel grösseren und starker seitlich erweiterten freien Raum um den Mittelknoten,15–16 Querstreifen und nähert sich der* M. Dansei" [A rather different form of *M. smithii*, that I call for the time being var. *lacustris,* is found in freshwater lakes. It has a much bigger and more strongly laterally extended free space around the central nodule, 15–16 striae and approaching *M. dansei*] (Table 3.3). Because Grunow (1878) did not clearly identify the locality of *M. smithii* var. *lacustris,* provide any figures of the taxon, or designate a holotype, it became difficult to establish its taxonomic identity, either as a variety of *M. smithii* as Grunow originally intended, or as a separate entity. However, Grunow (1878) gave three characteristics that distinguished this taxon from the nominate variety: found in freshwater lakes rather than brackish localities, a much larger and laterally expanded central area, and 15–16 rather than 15–17 striae in 10 µm.

The evolution of the taxonomic concept of *M. lacustris* continued with a short description of *M. smithii* var. *lacustris* in Van Heurck (1885): "*Diffère du type par sa forme plus étroite et par le nodule beaucoup plus élargi latéralement*" [Differs from the type by its narrower shape and much more laterally expanded nodule]. Previously, however, Van Heurck (1880, pl. 4, fig. 14) had included a line drawing (Figure 3.2) that

Table 3.3. Morphometric data and morphological features of *Mastogloia lacustris* from relevant reference sources, with LM measurements *of M. lacustris* neotype specimens and confirmed distribution records with mean values in parentheses. Information from references obtained directly from text.

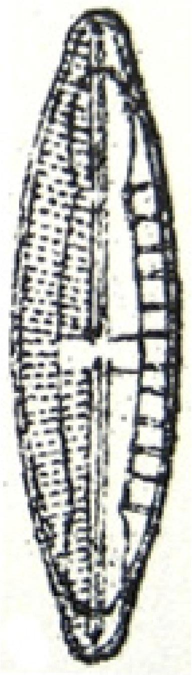
Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (µm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
Grunow (1878)	nd	nd	nd	nd	15–16	nd	nd	nd	More laterally extended	nd	nd	nd
Van Heurck (1885)	nd	30–45	Narrower than *M. smithii*	nd	15–17	nd	nd	nd	More laterally extended	Radiating to apices	Elliptical	Slightly reduced-rostrate, attenuated
Patrick & Reimer (1966)	nd	20–45	8–11	nd	15–16	13–15	6–8	nd	Larger, more rectangular, extending to outer border of loculi	More radiate than *M. smithii*	Linear-lanceolate	As in *M. smithii*
Krammer & Lange-Bertalot (1986)	nd	20–60	8–14	nd	15–18	15–21	nd	nd	nd	nd	Linear-lanceolate	More or less stubby, projecting
Novarino (1990)	nd	28–41 (33.5)	7.5–10.0 (8.5)	nd	15–20	nd	nd	nd	Circular, more frequently rectangular	Radiate	Narrowly lanceolate	Slightly produced, obtuse

Table 3.3. Continued.

Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (µm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
Neotype III-24-A9, Belgium	20	28–55 (38)	8–10 (9)	4.3	16–17	16–20	5–7	3.4	Asymmetrical, elliptical to polygonal 5–14 (8)	147–164 (156)	Elliptical-lanceolate	Rostrate (rounded in post-initial valves)
EEG 08-24-10, Canada	25	27–51 (35)	7–9 (8)	4.3	16–17	16–20	5–6	4.4	Asymmetrical, elliptical to polygonal 5–13 (8)	142–162 (152)	Elliptical-lanceolate	Rostrate (rounded in post-initial valves)
2011-13, Iowa	20	20–49 (35)	7–10 (9)	4.0	17–18	16–20	5–6	4.2	Asymmetrical, elliptical to polygonal 3–11 (6)	149–164 (155)	Elliptical-lanceolate	Rostrate (rounded in post-initial valves)
JPK 5591-5, Michigan	20	29–49 (36)	8–10 (9)	4.0	16–18	18–20	5–7	4.3	Asymmetrical, elliptical to polygonal 4–10 (6)	150–159 (153)	Elliptical-lanceolate	Rostrate (rounded in post-initial valves)

Note. n: number of specimens measured; nd: no data.

Figure 3.2. Original line drawing of *M.* (*Smithii* var?) *lacustris* Grun. from Van Heurck (1880).



assigned the name, "*M.* (*Smithii* var?) *lacustris* Grun." to the taxon. This status change to specific rank, *M. lacustris* (Grunow) Grunow, was apparently never followed by later researchers, even by Van Heurck (1896). In the literature, the name *M. lacustris* (e.g., Cox 2006) has rarely been used, unlike *M. smithii* var. *lacustris* (e.g., Patrick & Reimer 1966, Krammer & Lange-Bertalot 1986, Novarino 1989, California Academy of Sciences 2011). A slide containing the taxon was included in the *Types du Synopsis des Diatomées de Belgique* as exsiccatum Type no. 47, *Mastogloia* (*Smithii* var.) *lacustris* Grun. from Bergh, Brabant, Belgique (Van Heurck & Grunow 1882–1885). In addition to the laterally expanded central area originally mentioned by Grunow (1878), Van Heurck (1885) distinguished *M. lacustris* from the nominate variety by its narrower width, but not by geographical distribution or stria density. Later researchers were mostly faithful to the taxonomic concept of *M. lacustris sensu* Van Heurck & Grunow Type no. 47, especially because of the accessible exsiccatae (Edgar 2008), though Type no. 47 was never formally designated as type material of *M. lacustris*. Patrick & Reimer (1966) used exsiccatum Type no. 47 to further distinguish this taxon from *M. smithii* by its more radiate and coarser striae (15–16 in 10 µm for *M. lacustris,* 18–19 in 10 µm for *M. smithii sensu* Van Heurck & Grunow's Type no. 46, 16.5 in 10 µm for *M. smithii sensu* W. Smith) and linear-lanceolate rather than elliptical-lanceolate (*sensu* Van Heurck & Grunow Type no. 46) or elliptical (*sensu* W. Smith) valve outline. Krammer & Lange-Bertalot (1986) also used exsiccatum Type no. 47 when they extended the maximum valve length of *M. lacustris* from 45 µm *sensu* Van Heurck (1885) to 60 µm to include post-initial valves (pl. 201, fig. 1).

Inconsistent descriptions of stria density and other features that distinguish *M. lacustris* from *M. smithii* have led to inconsistent identifications. Features of subtropical (Slate & Stevenson 2007) and tropical populations (Novelo et al. 2007) reported under these names vary from those reported in the literature (Gaiser et al. 2010). Novelo et al. (2007) identified a taxon from Mexico with a stria density of 18–20 in 10 µm and a width of 7.6–9.5 µm as *M. smithii*; these measurements were consistent with Krammer & Lange-Bertalot (1986) although a maximum width of 14 µm was reported in the reference (Krammer & Lange-Bertalot 1986). Ecophenotypes (Stoermer 1967) and variation in valve morphology during size diminution among many species of *Mastogloia*, resulting in the normally rostrate apices becoming less so (Gaiser et al. 2010, fig. 4), add to the problem. Furthermore, initial valves of *M. smithii* (Stickle 1986) and *M. grevillei* W. Smith ex Gregory (Main 1995) have a strikingly different appearance with broadly rounded apices. However, this variability in valve morphology in relation to shape changes during size diminution was ignored (e.g., Krammer & Lange-Bertalot 1986, pl. 201, fig. 1) or has only been briefly mentioned (e.g., Slate & Stevenson 2007, Gaiser et al. 2010). For example, Slate & Stevenson (2007) suspected that rounded apices could be characteristics of initial valves, and Gaiser et al. (2010) showed the size variation for subtropical and tropical populations, identifying specimens with rounded apices as initial valves. The present study characterizes and establishes a lectotype for *M. smithii* and a neotype for *M. lacustris*, then establishes the identity and morphology of subtropical (Florida, USA) and tropical (Jamaica, Belize, and Mexico) inland *Mastogloia* taxa by comparing these populations to the types and temperate populations (Ontario, Canada and Iowa and Michigan, USA) of *M. smithii* and *M. lacustris*.

Methods

Material and slides containing specimens identified as *M. smithii* and *M. lacustris* (or *M. smithii* var. *lacustris*) were obtained from herbaria and modern collections (see Figure 3.3 and Table 3.1 for location details and accession numbers):

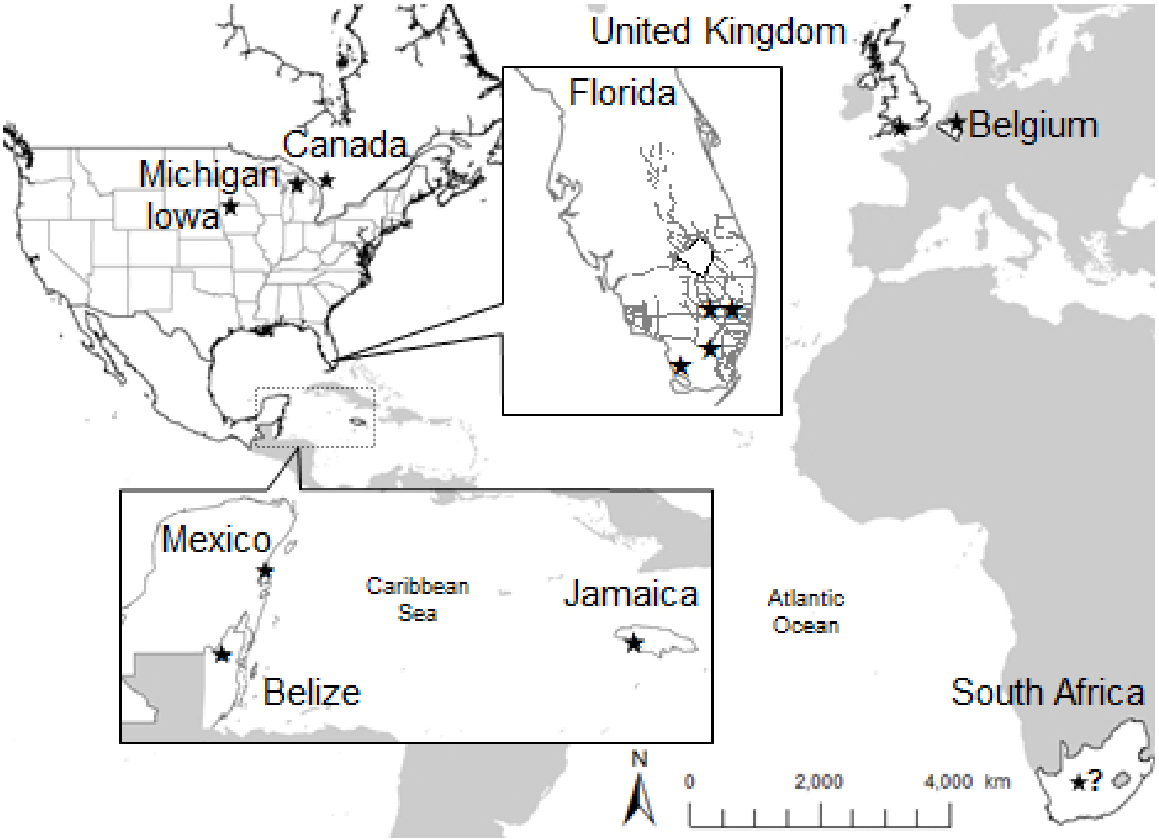
- Smith reported 10 collections in the original description of *M. smithii*, one of which (the oldest material) was "Little Sea," Dorset, United Kingdom, collected by Smith in October 1848, and likely shared with Thwaites [see Smith's (1856, p. 64) discussion of providing Thwaites with additional material of *M. danseii* in October 1848]. These collections can be considered syntypes. The Dorset material was obtained from the Van Heurck collection housed at the National Botanic Garden of Belgium (BR). The original slide (BR VI-43-B5) made from this material was also investigated.
- *Mastogloia smithii* from material collected by Van Heurck from an unknown location in South Africa (*Afrique méridionale*) used to make exsiccatum slide Type no. 46 (Van Heurck & Grunow 1882–1885) and referenced by Patrick & Reimer (1966) for their figure of *M. smithii* was obtained from BR.
- *Mastogloia smithii* from exsiccatum slide Type no. 46 (Van Heurck & Grunow 1882–1885), presumably containing material identical to the BR material, was obtained from the Farlow Herbarium at Harvard University (FH).
- Material related to *M. lacustris* from the Caspian Sea (Grunow 1878) in the Grunow collection could not be retrieved from the Naturhistorisches Museum in Vienna (A. Igersheim, pers. comm.). *Mastogloia smithii* var. *lacustris* from

material originating from Bergh, Brabant, Belgium used to make exsiccatum slide Type no. 47 (Van Heurck & Grunow 1882-1885) was obtained from BR.

- *Mastogloia smithii* var. *lacustris* from exsiccatum slide Type no.47 (Van Heurck & Grunow 1882-1885), presumably containing material identical to the BR material, was obtained from FH.
- Specimens identified as *M. lacustris* from modern periphyton samples were collected from northeast Everglades National Park, Florida, USA.
- Specimens identified as *M. smithii* from modern periphyton samples were collected from southwest Everglades National Park, Water Conservation Area 2A, and Water Conservation Area 3A, Florida, USA.
- Specimens identified as *M. lacustris* from modern periphyton samples were collected from Jamaica (Broad River in the Black River Morass, St. Elizabeth), Belize (New River Lagoon in Orange Walk), and Mexico (Sian Ka'an Biosphere Reserve in Quintana Roo).
- Specimens identified as *M. smithii* and *M. lacustris* from modern periphyton samples were collected from O'Neal Lake, Bliss, Michigan, USA.
- Specimens identified as *M. lacustris* from modern periphyton samples were collected from Canada (Misery Bay Provincial Nature Reserve, Burpee and Mills, Ontario) and Iowa, USA (Little Miller's Bay in Milford).

Material from Florida, the Caribbean, and Canada was archived at Florida International University (FIU), material from Iowa was archived at the Iowa Lakeside Laboratory Reimer Diatom Herbarium (ILH), material from Michigan was archived at the University of Colorado Diatom Herbarium (CU), and holotypes and some paratypes

Figure 3.3. Map of sample locations from herbarium (United Kingdom, Belgium, South Africa) and current (Canada, Michigan, Iowa, Florida, Jamaica, Mexico, Belize) *Mastogloia* collections.



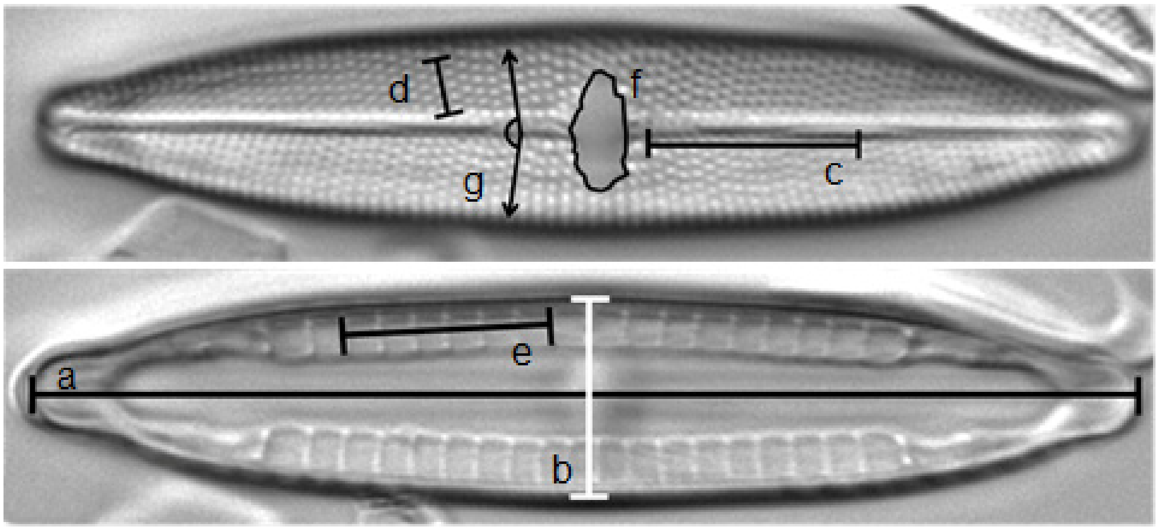
of the newly described species were archived at the Academy of Natural Sciences, Philadelphia (ANSP). Original material from BR was cleaned following the method of Van der Werff (1955). Different cleaning methods were necessary to oxidize higher levels of organic matter in lake samples from Iowa and Michigan (Patrick & Reimer 1966) and to remove very high levels of calcium carbonate in karstic wetland samples from Canada, Florida, and the Caribbean (Hasle & Fryxell 1970). For scanning electron microscopy (SEM), a portion of all samples except Michigan material were filtered through polycarbonate membrane filters with a pore diameter of 3 µm. After air drying, pieces of the filters were fixed on aluminium stubs, sputter-coated with 50 nm gold (Cressington 208HR, Watford, UK) and studied on a Zeiss ULTRA SEM microscope at 3 kV at the Natural History Museum, London, UK. Samples from Michigan were sputter-coated with 50 nm gold and examined on a FEI Quanta FEG 450 field emission SEM. For all modern samples and exsiccatae slides no. 46 and 47, light microscopy (LM) was conducted using a Zeiss Axioskop 2 equipped with differential interference contrast (Nomarski) and a Leica DFC425 digital camera. For the syntype material of *M. smithii*, LM observations were made using an Olympus BX51 microscope, equipped with differential interference contrast (Nomarski) and the Colorview I Soft Imaging System.

In each of the modern samples at least 500 valves were counted to determine the relative abundances of specimens resembling *M. smithii* and *M. lacustris* (Weber 1973). Digital images of at least 20 specimens from each population were captured by LM with effort to include the widest possible range in valve length, including post-initial valves (valves recently divided from initial valves). Morphometric data (length, width, stria density, areola density, partectum density, area of the central area, and angle of striae from the apical axis) were obtained from LM images using ImageJ (Rasband 1997–2012) (Figure 3.4). Area of the central area was measured by drawing a polygon around the empty space in the center of the valve. Angle of striae was measured as the angle created by the striae on both sides of the raphe, so that an angle of 180° would be the measurement of parallel striae.

Multivariate analyses were performed to compare all modern specimens to each other and to specimens from type material, based on differences in morphometric data (controlling for size-dependent metrics): angle of striae, area of the central area, stria, areola and partectum densities, length:width ratio, and length:partecta ratio (Novarino & Muftah 1992). All variables were standardized to zero mean and unit variance. DECODA version 3.01 beta 58 (Minchin 2005–2012) was used to perform non-metric multidimensional scaling (NMS) ordination based on a Euclidean distance dissimilarity matrix and to perform vector fitting (Kantvilas & Minchin 1989) (i.e., calculating the maximum Spearman rank correlation coefficient between each morphometric variable and the final ordination scores). NMS rather than principal components analysis was used because the assumption of linear relationships between all morphometric variables could not be made (Kruskal & Wish 1978). Analysis of similarity (ANOSIM) was performed using Primer-E version 6 (Clarke & Gorley 2006) to test the null hypothesis that there is no difference between specimens from different locations (by comparing the dissimilarities within and among groups).

Terminology for *Mastogloia* ultrastructure followed that of Hustedt (1933), Voigt (1942), Ross et al. (1979), Stephens & Gibson (1980), Novarino (1990), Paddock & Kemp (1990), and Round et al. (1990).

Figure 3.4. Valve of *Mastogloia lacustris* in two different LM focal views with markings showing measurement methods of morphometric data: a) length, b) width, c) stria density, d) areola density, e) partectum density, f) area of central area, g) angle of striae.



Results

Mastogloia smithii

The valve morphology of *M. smithii* from Dorset, UK was consistent with Smith's (1856) original description (Table 3.2) and line drawing (Figure 3.1) of the taxon. No other *Mastogloia* taxa that could be confused with Smith's description were found on the slide. Thus, this single syntype reported by Smith (1856) provided the basis of the following description and was designated the lectotype of *M. smithii.*

Mastogloia smithii Thwaites ex W. Smith (Figures 3.5–3.6)

Description. Cells solitary. Valves elliptical-lanceolate with rostrate to subcapitate apices, 25–50 µm length, 11–15 µm width, 20–21 striae per 10 µm, 23–26 areolae per 10 µm (Figure 3.5). Striae areolate, gently radiate, becoming parallel at the apices, stria arrangement on the valve face continues unchanged onto the mantle; central area elliptical (Figure 3.6a). Areolae rounded, some reduced around the central area (Figure 3.6b), internally occluded by a cribrum (velum perforated by regularly arranged pores; Figures 3.6b–c). Raphe straight with a median kink (Figure 3.6a), proximal raphe ends slightly expanded and opening into a spathulate groove (Figure 3.6b), distal raphe ends slightly expanded, extending centrally over the mantle, hooked to the same side, with a small hyaline area where the curve occurs (Figure 3.6c). Internally, raphe more or less straight, within a thin raphe sternum, lying in an axial area with raised 'axial costae' that create a 'gutter' which widens slightly at the central nodule and does not extend to the distal raphe ends (Figures 3.6d–e). Internal proximal raphe ends slightly expanded and

Figure 3.5. Valves of *Mastogloia smithii* from lectotype slide VI-43-B5, Dorset, UK showing size reduction, LM. Note: axial costae (arrow). Figures b, d, g. Valves showing partectal ring. Figures c–d. Lectotype specimen. Scale bars =10 µm.

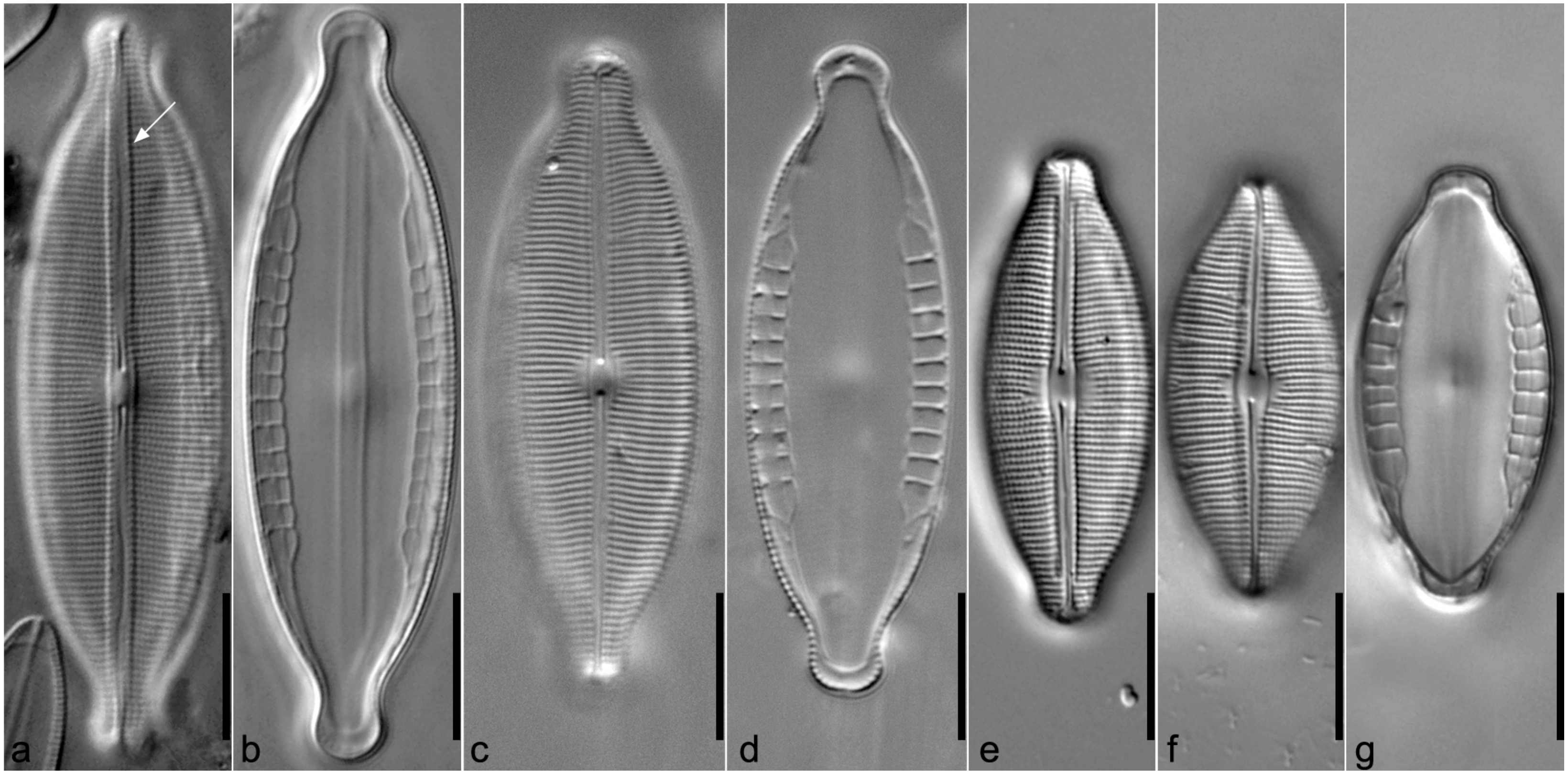
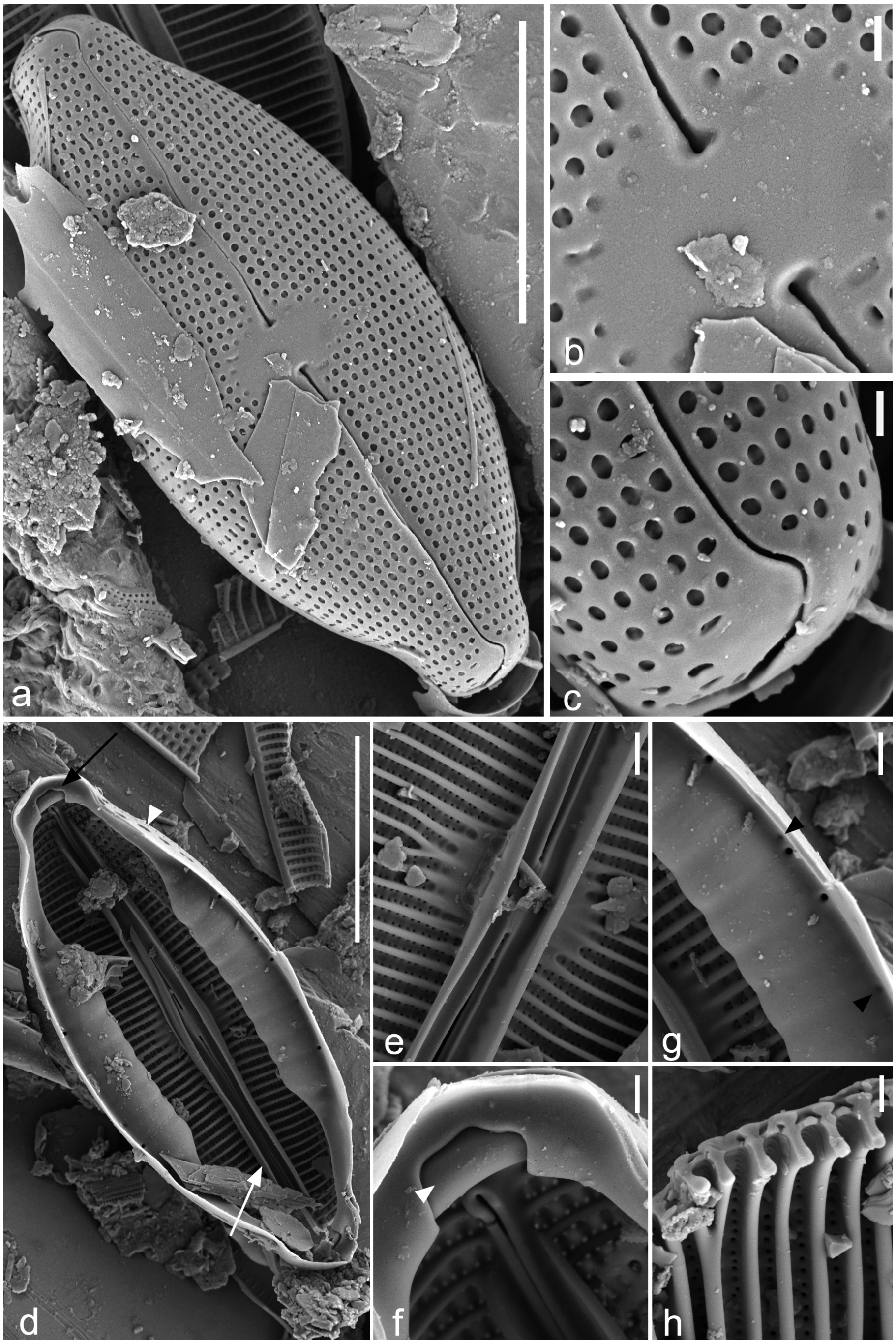


Figure 3.6. *Mastogloia smithii* from lectotype material, Dorset, UK, SEM external (a–c) and internal views (d–h): a) whole valve, b) detail of central area showing reduced areolae, c) detail of valve apex, d) whole valve with partectal ring showing axial costae (white arrow), broad cleft at apex (black arrow), and partectal pore (arrowhead), e) detail of central area and axial costae, f) detail of pseudoseptum (arrowhead) and helictoglossa, g) detail of pores between partecta, some appearing occluded (arrowheads), h) broken valve showing costa-like virgae. Scale bars =10 µm (a, d), 1 µm (e, f), 0.5 µm (b–c, g–h).



raphe sternum elevated toward the raised central nodule (Figures 3.6d–e). Internal distal raphe ends straight, slightly expanded, ending in simple helictoglossae (Figures 3.6f). Partectal ring ‘closed’ (forming a complete band around the cell), without a flange separating the ring from the valve margins, with a broad cleft at both apices exposing the pseudoseptum (Figures 3.6d, f), with pores between some pairs of partecta near the advalvar edge of the partectal ring arranged in no obvious pattern, some pores appearing occluded (Figures 3.6d, g). Partecta distributed along both sides of the partectal ring, except near the apices, partecta visibly distinguishable, slightly larger towards the apices (Figures 3.6d, g). Virgae (solid silica between striae) thickened to form costae, present throughout the valve interior (Figures 3.6d, h). Five partectal pores located near both sides of the apices (Figure 3.6d).

Lectotype (here designated). Slide VI-43-B5 in the Van Heurck collection at the National Botanic Garden of Belgium (BR), Meise, Belgium based on the “Little Sea,” Dorset, United Kingdom material collected by W. Smith in October 1848. Lectotype specimen illustrated in Figures 3.6c–d.

Mastogloia lacustris

The status change for *M. smithii* var. *lacustris* to *M. lacustris* proposed by Grunow (Van Heurck 1880) is a valid publication of *M. lacustris* (P. Compère and M. Wynne, pers. comm.). The LM and SEM observations of the lectotype material of *M. smithii* (Figures 3.5–3.6) and specimens in the Van Heurck type material of *M. lacustris* from Belgium (Figures 3.7–3.8) showed several important morphological differences (refer to

Figure 3.7. Valves of *Mastogloia lacustris* from neotype slide III-24-A9, Brabant, Belgium showing size reduction, LM. Figures b, d, g. Valves showing partectal ring. Figures c–d. Neotype specimen. Scale bars =10 µm.

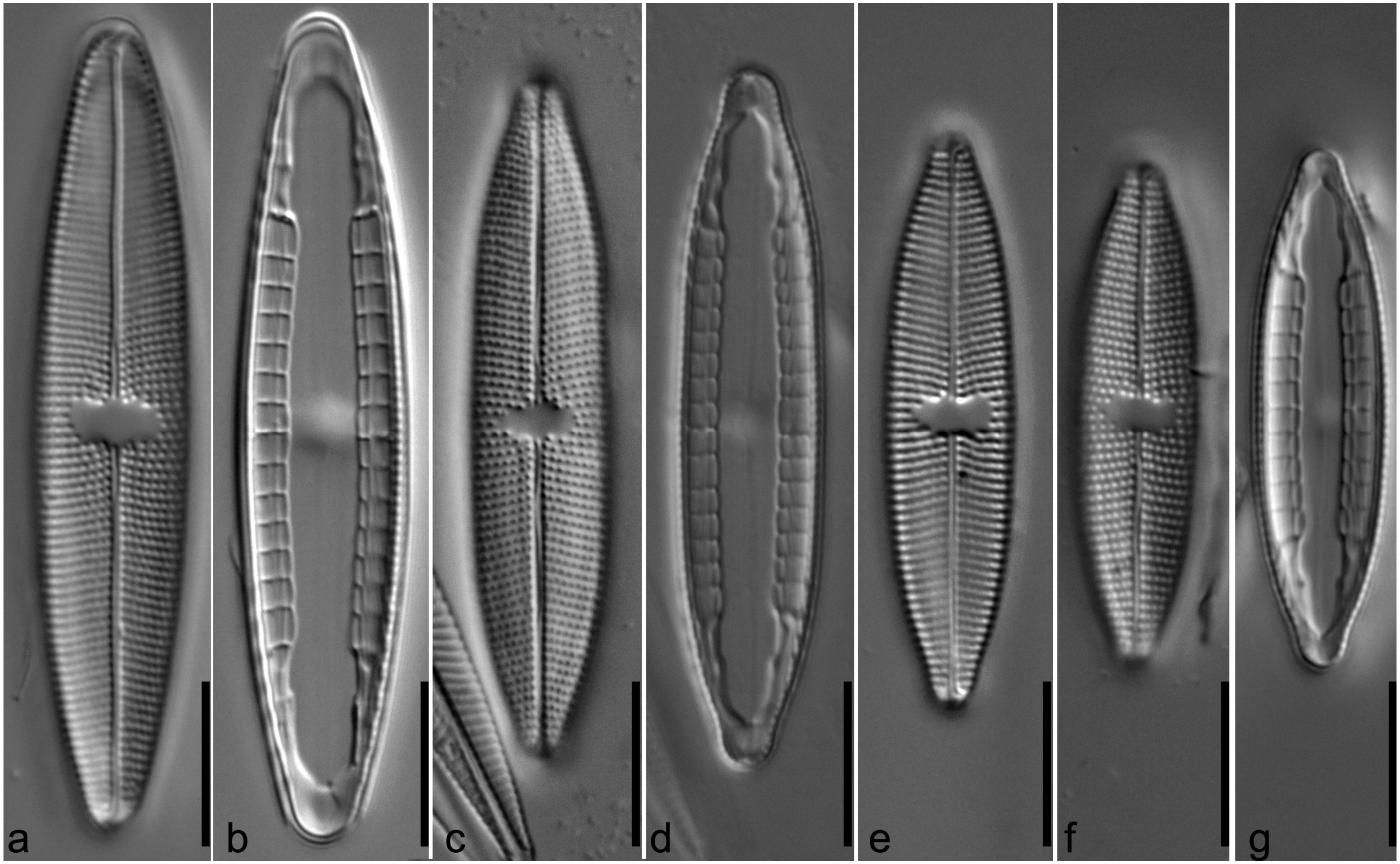
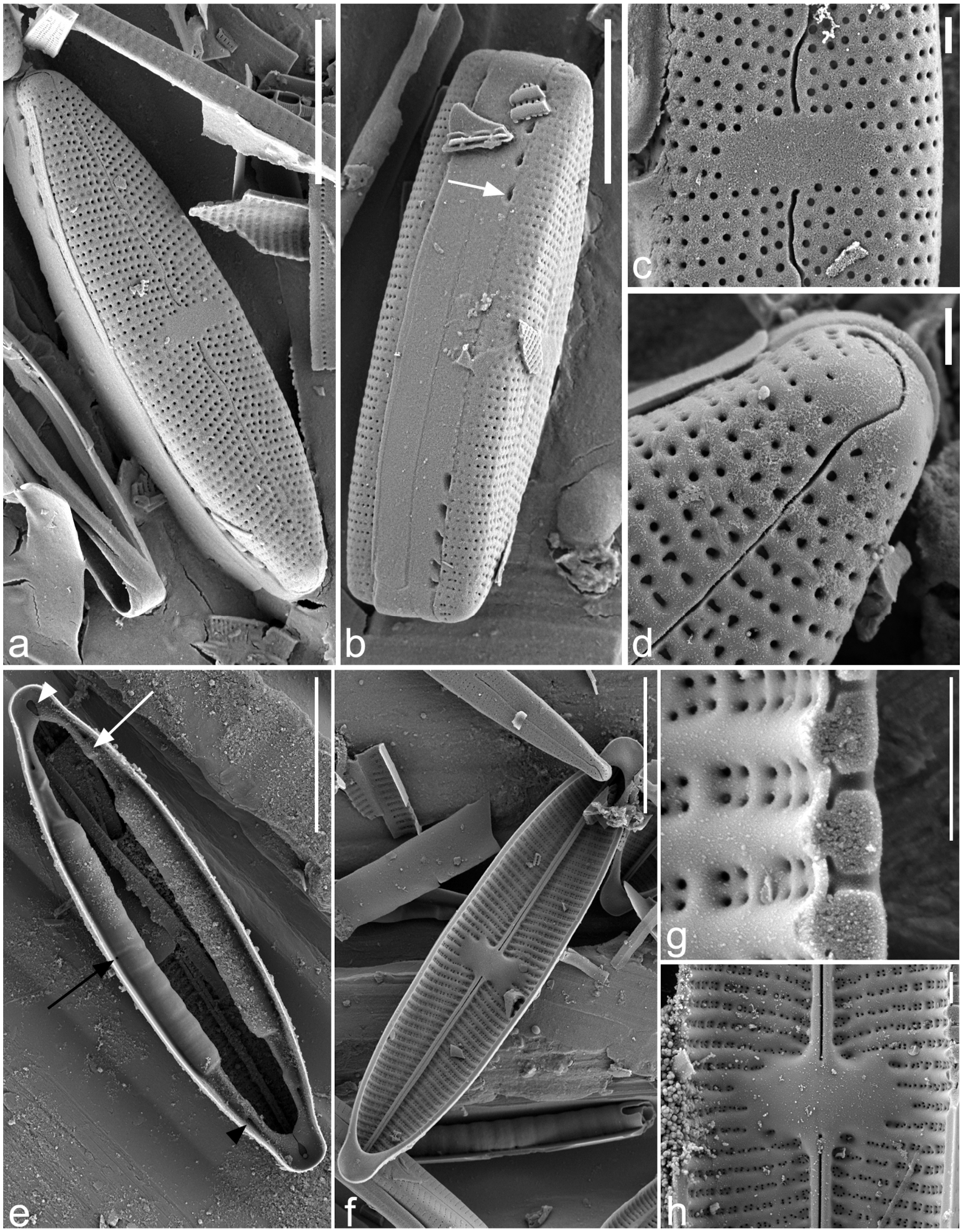


Figure 3.8. *Mastogloia lacustris* from neotype material, Brabant, Belgium, SEM external (a–d) and internal views (e–h): a) whole valve, b) frustule in girdle view showing partectal pores (arrow), c) detail of central area, d) detail of valve apex, e) whole valve with partectal ring showing lacuna (white arrowhead), pseudopartectum (white arrow), areola between centermost pair of partecta (black arrow), and furrow near apices (black arrowhead), f) whole valve, g) broken valve showing thickened virgae and cribrum, h) detail of central area. Scale bars = 10 µm (a–b, e–f), 1 µm (c–d, g–h).



Discussion) that further support the recognition of *M. lacustris* at the species level. While Grunow (1878) originally described *M. lacustris* in a publication describing diatoms from the Caspian Sea, he noted that the taxon was found in freshwater lakes and did not provide any detailed provenance for his source material. Furthermore, Grunow material from the Caspian Sea or environs associated with *M. lacustris* could not be found. Therefore, my characterization of *M. lacustris* is based on Van Heurck's material from Belgium, on which he and Grunow based their observations for the *Synopsis des diatomées de Belgique* and from which they prepared the slides that were distributed as part of the *Types du synopsis des diatomées de Belgique* (Van Heurck & Grunow 1882–1885). A neotype for *M. lacustris* was designated from this material obtained from BR, recognizing its significance as the source material for Van Heurck's *Synopsis* and numerous and widely distributed *Types* exsiccatae. Morphological and NMS analyses (Figure 3.9) confirmed the distribution of *M. lacustris* in Canada (Figure 3.10), Iowa (Figure 3.11), and Michigan (Figure 3.12).

Mastogloia lacustris (Grunow) Grunow (Figures 3.7–3.8)

Description. Cells solitary. Valves elliptical-lanceolate with rostrate apices (post-initial valves with rounded apices, small valves with subrostrate apices), 25–55 µm length, 7–10 µm width, 16–18 striae in 10 µm, 16–20 areolae in 10 µm (Figure 3.7). Striae areolate, radiate, weakly curved at the central area, becoming parallel at the apices, stria arrangement on the valve face continues unchanged onto the mantle (Figures 3.8a–b). Central area rectangular to elliptical (Figure 3.8c). Areolae rounded, internally occluded

Figure 3.9. Two-dimensional non-metric multidimensional scaling ordination plot, with axes 1 and 2 representing 88% of the total variance, and vectors representing the magnitude and direction of the maximum Spearman rank correlation coefficient between morphometric data and the final ordination scores. Group 1 (green): *Mastogloia smithii* lectotype, UK; Group 2 (black): *M. lacustris* neotype, Belgium and specimens from Canada, Iowa, and Michigan; Group 3 (red): *M. calcarea* from Florida, Jamaica, Belize, and Mexico; Group 4 (blue): *M. pseudosmithii* from Florida, *M.* aff. *smithii* 1 from South Africa (*M. smithii sensu* Van Heurck), and *M.* aff. *smithii* 2 from Michigan.

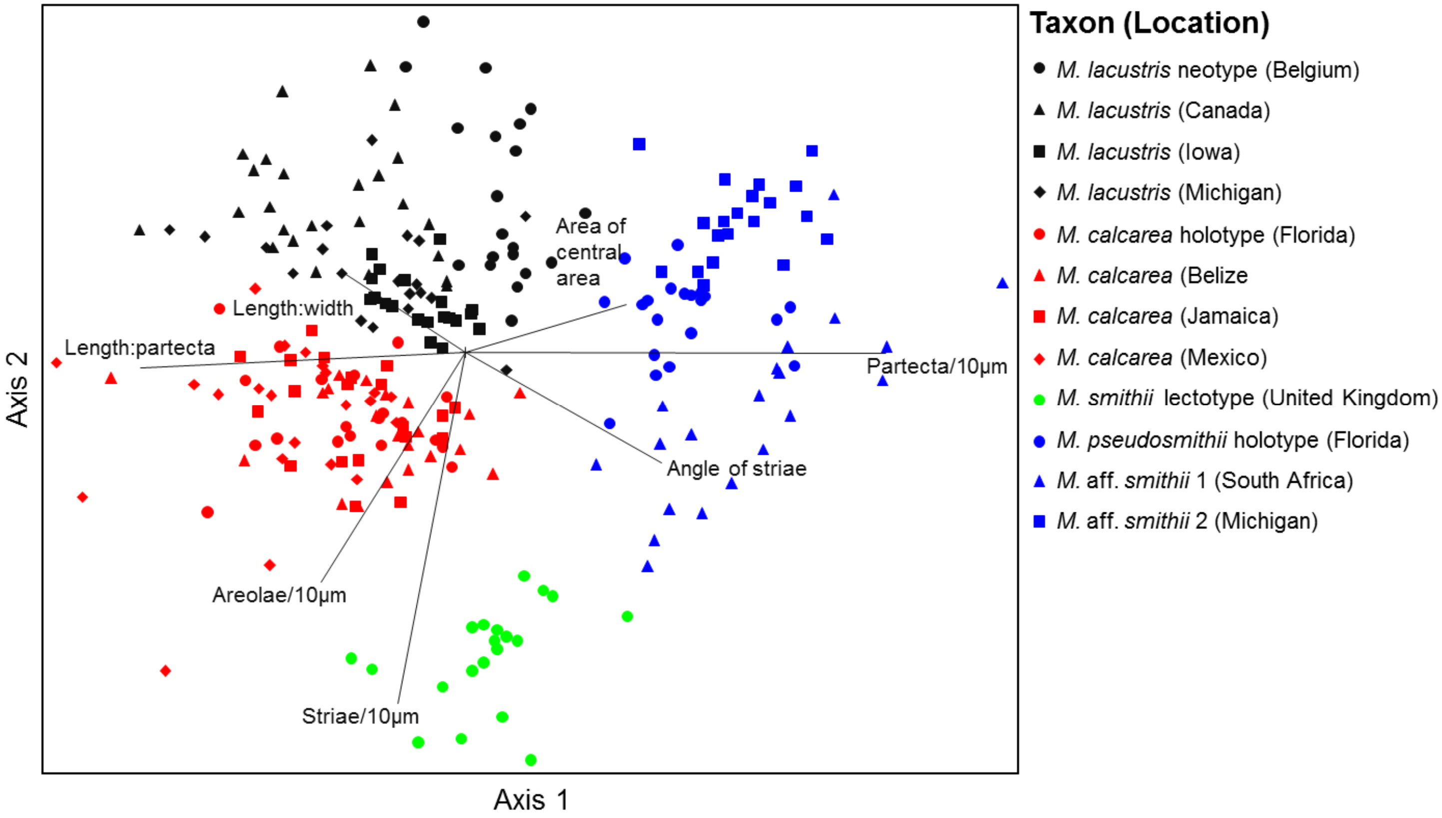


Figure 3.10. Valves of *Mastogloia lacustris* from confirmed distribution in Canada showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.

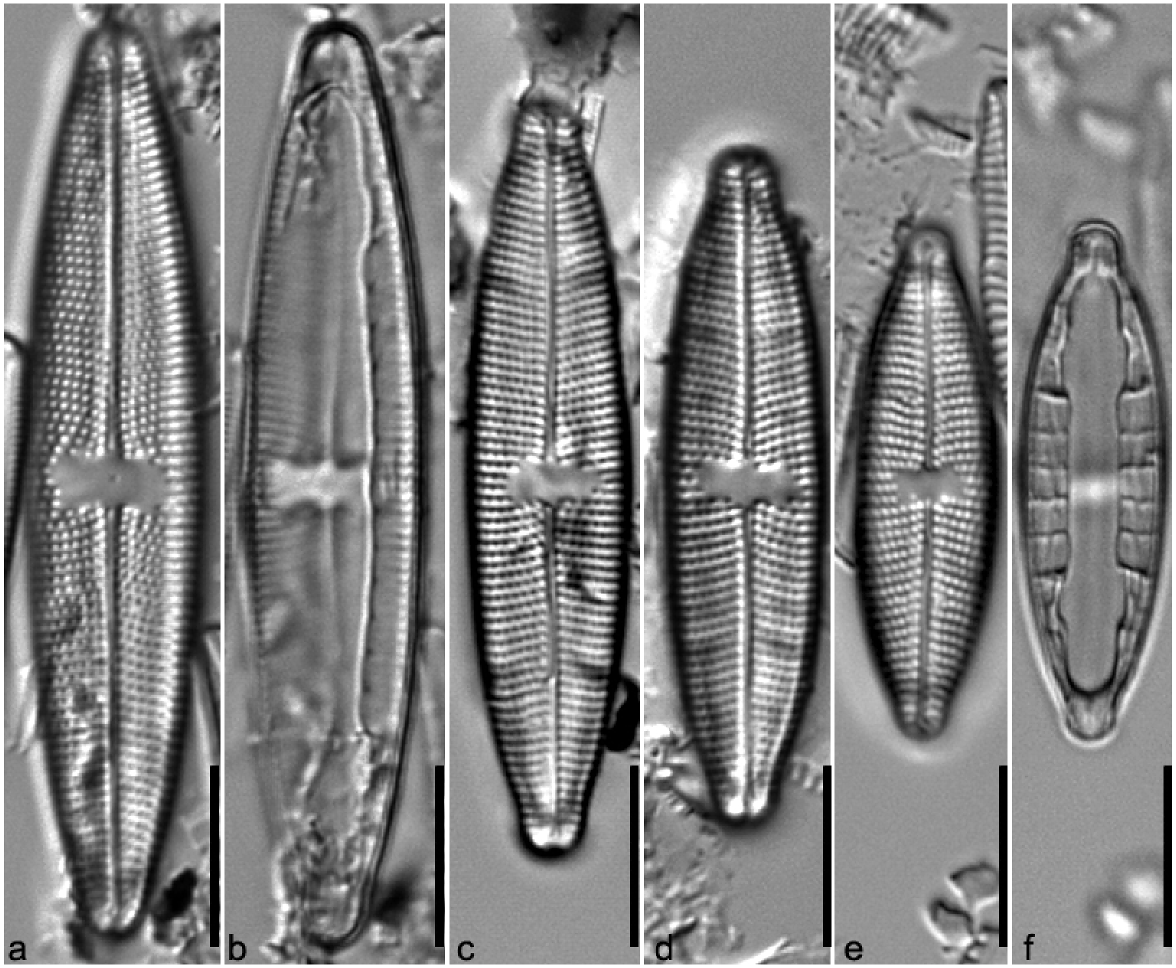


Figure 3.11. Valves of *Mastogloia lacustris* from confirmed distribution in Iowa showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.

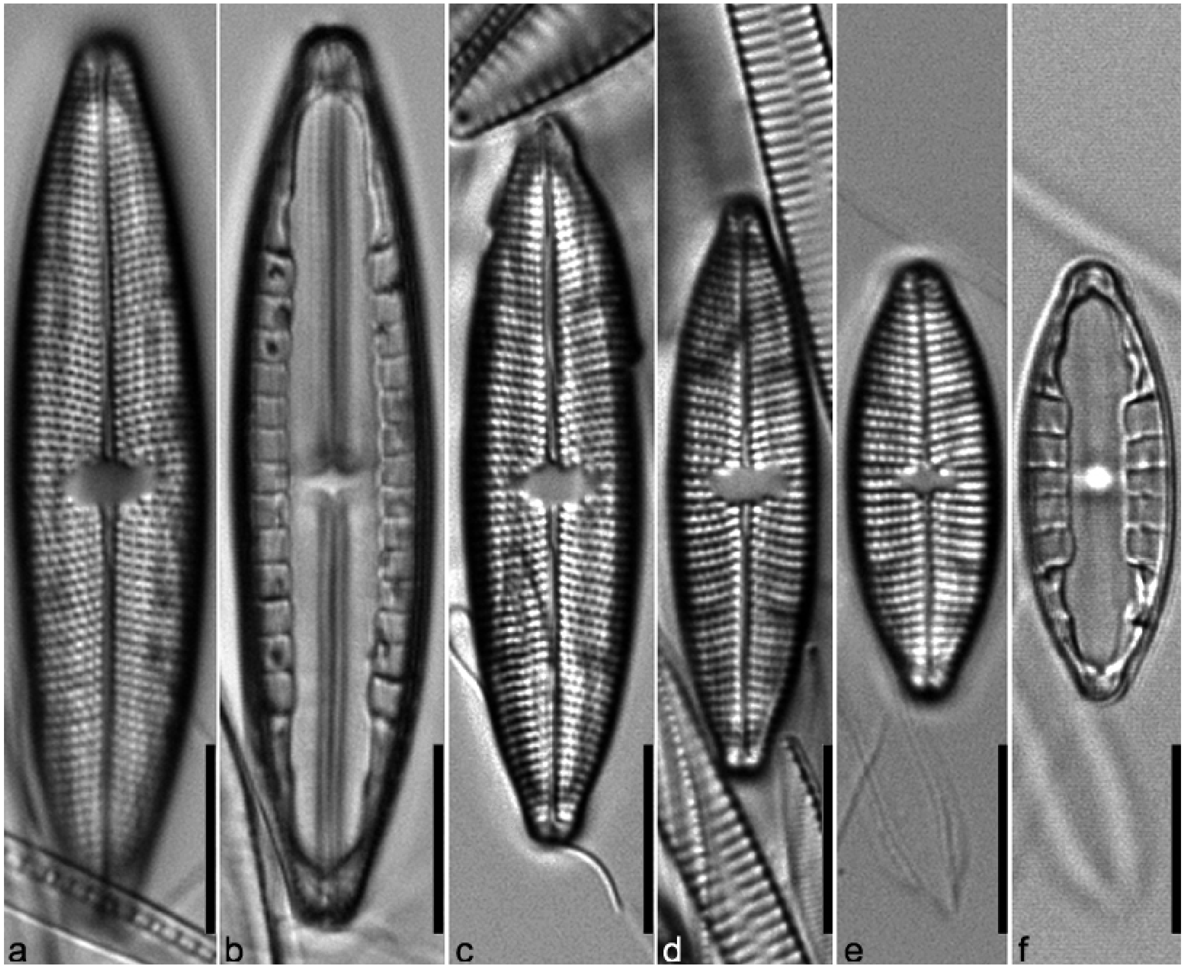
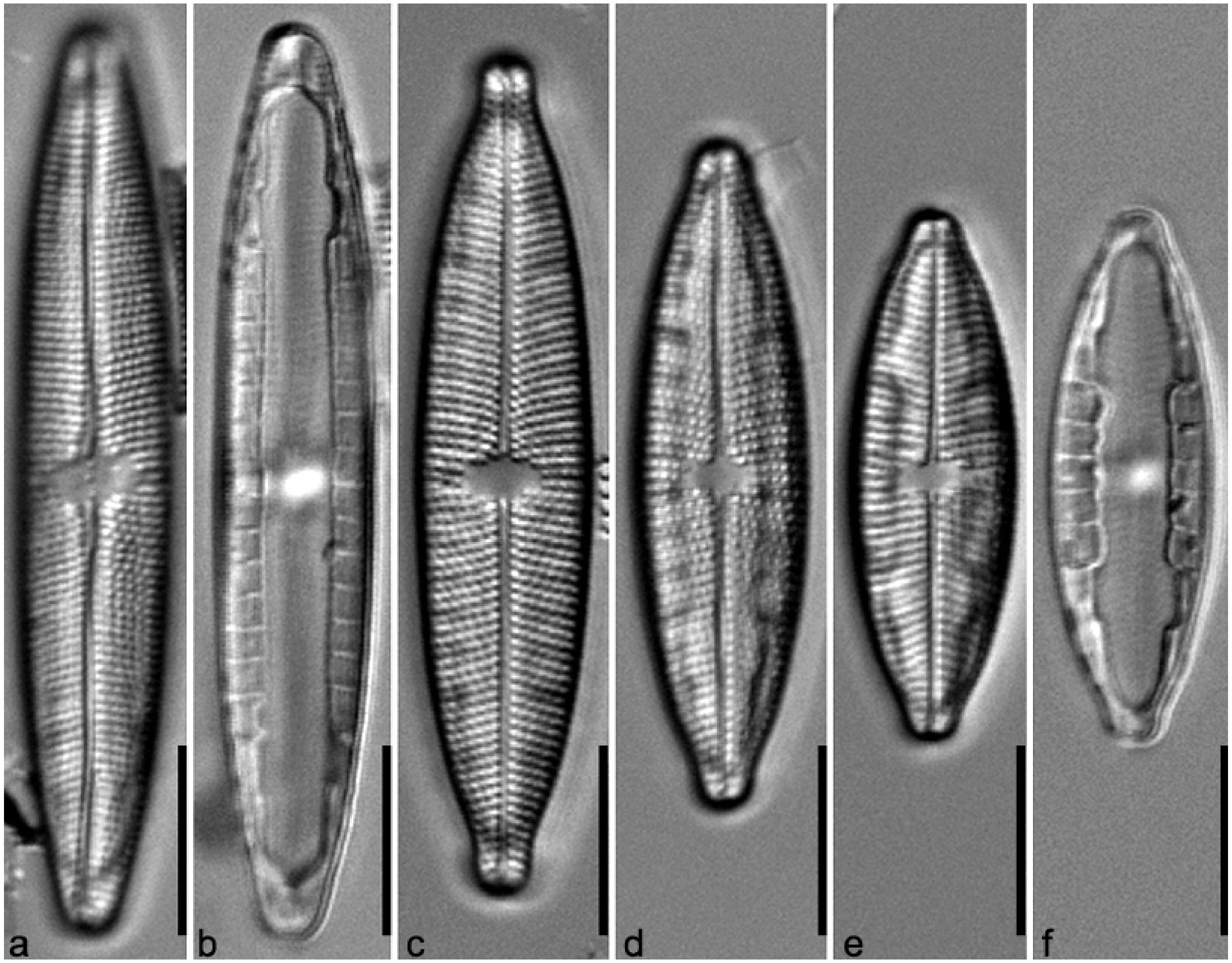


Figure 3.12. Valves of *Mastogloia lacustris* from confirmed distribution in Michigan showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.



by a cribrum (Figure 3.8g). Raphe straight with a kink near the central area (Figures 3.8a, c), proximal raphe ends slightly expanded, deflected in the same direction (Figures 3.8a, c), distal raphe ends slightly expanded, extending centrally over the mantle, hooked to the same side, with a small hyaline area where the curve occurs (Figure 3.8d). Internally, raphe straight, encased in a thickened sternum (Figures 3.8e–f). Internal proximal raphe ends slightly expanded, raphe sternum fused into the thickened central nodule (Figures 3.8f, h). Internal distal raphe ends occluded by pseudosepta (Figure 3.8f). Partectal ring closed, lacking a flange separating the ring from the valve margin, apices with a narrow cleft which expands into a pyriform lacuna (pear-shaped gap), with a pseudopartectum and a furrow opening into a pore-like cavity on each side of both apices, and with one pore between the centermost pair of partecta on each side of the partectal ring (Figure 3.8e). Partecta distributed along both sides of the partectal ring, except near the apices, partecta visibly distinguishable, evenly sized although slightly larger at the apices (Figure 3.8e). Thickened virgae present throughout the valve interior (Figures 3.8f–h). Cribral pores become highly irregular near the raphe sternum and central nodule (Figure 3.8h). Four or five partectal pores located near both sides of the apices (Figures 3.8a–b).

Neotype (here designated). Slide III-24-A9 in the Van Heurck collection at the National Botanic Garden of Belgium (BR), Meise, Belgium based on Bergh material from Brabant, Belgium used for the *Types du synopsis des diatomées de Belgique*, exsiccatum VH Type no. 47. Neotype specimen illustrated in Figures 3.7c–d.

Isoneotype (here designated). Slide labeled “Dr. Henri Van Heurck Types du Synopsis des Diatomées de Belgique. No. 47. *Mastogloia smithii* var. *lacustris* Grun. *Belgique”* in the Farlow Herbarium (FH) at Harvard University, Cambridge, USA based on Bergh material from Brabant, Belgium used for the *Types du synopsis des diatomées de Belgique*, exsiccatum VH Type no. 47.

Confirmed distribution records.

- Slide FIU EEG 08-24-10, Canada (45°48.349 N, 82°46.315 W), alvar rock pool periphyton, collected by E. Gaiser, August 2010 (Figure 3.10).
- Slide ILH 2011-13, Iowa, USA (43°22.693 N, 95°10.844 W), periphyton on buoy, collected by the 2011 Ecology and Systematics of Diatoms class at Iowa Lakeside Laboratory, May 2011 (Figure 3.11).
- Slide FIU JPK 5591-5, Michigan, USA (45°42.758 N, 84°53.264 W), periphyton, collected by J. P. Kociolek, March 2011 (Figure 3.12).

Mastogloia calcarea sp. nov. and *M. pseudosmithii* sp. nov.

Specimens identified as *M. smithii* were rare (<1% of total diatom abundance in Michigan, Florida and Jamaica) in modern samples. Specimens identified as *M. lacustris* were found in higher abundances in the samples from Canada (3%), Iowa (2%), Michigan (8%), Florida (67%), Belize (5%), Jamaica (4%), and Mexico (57%). The multivariate analyses were based on a two-dimensional NMS of morphometric data of the ten discrete populations because it had stress=0.16, which did not significantly decrease with additional dimensions. Four groups can be distinguished (Figure 3.9): Group 1 consisted of the *M. smithii* lectotype; Group 2 consisted of the *M. lacustris* neotype and specimens identified as *M. lacustris* from Canada (Figure 3.10), Iowa (Figure 3.11), and Michigan (Figure 3.12); Group 3 consisted of specimens identified as *M. lacustris* from Florida (Figures 3.13–3.15), Jamaica (Figure 3.16), Belize (Figure 3.17), and Mexico (Figure 3.18); and Group 4 was a heterogeneous group that consisted of specimens identified as *M. smithii* from Florida (Figures 3.19–3.20), *M.* aff. *smithii* 1 from South Africa (Figures 3.21–3.22), and *M.* aff. *smithii* 2 from Michigan (Figures 3.23–3.24). In Group 4, there was more overlap in ordination space among specimens from Florida and Michigan than with specimens from South Africa. Axis 1 and 2 represented 88% of the total variance in morphology. Partectum density was most correlated with the distribution of specimens in ordination space. Stria and areola densities also showed strong correlations with the distribution of specimens in ordination space (Table 3.4). ANOSIM pairwise comparisons showed that most populations were statistically different between and within groups, with the exception of *M. lacustris* from Michigan, Canada, and Iowa (Group 2, note that an exclusive comparison between Canada and Iowa was statistically significant), and all populations within Group 3 (Table 3.5). Therefore, based on ultrastructure, morphology, and ecological differences, two new species are proposed:

- *Mastogloia calcarea*, the taxon from Florida and the Caribbean (Group 3) formerly reported as *M. smithii* (Podzorski 1985, pl. 5, figs 21–22)*, M. smithii* Morphotype I (Slate & Stevenson 2007), and *M. smithii* var. *lacustris* (Gaiser et al. 2010).

- *Mastogloia pseudosmithii*, the Floridian taxon from Group 4 (also found in Jamaica but not included in this study) formerly reported as *M. smithii* (Podzorski 1985, pl. 5, fig. 18) and *M. smithii* Morphotype II (Slate & Stevenson 2007).

Mastogloia calcarea sp. nov. Lee, Gaiser, Van de Vijver, Edlund & Spaulding (Figures 3.13–3.15; Table 3.6)

Description. Cells solitary, live specimens producing mucilage strands near the apices, with 2 H-shaped plastids, one at each pole (Figures 3.13a–c). Valves linear-lanceolate (post-initial and small valves elliptical-lanceolate) with rostrate apices (post-initial valves with rounded apices, small valves with subrostrate apices), 27–54 µm length (up to 71 µm from Mexico), 7–9 µm width, 19–20 striae in 10 µm, 16–20 areolae in 10 µm (Figure 3.14). Striae areolate, radiate, weakly curved at the central area, becoming parallel at the apices, stria arrangement on the valve face continues unchanged onto the mantle (Figures 3.15a, c). Central area elliptical to polygonal, usually asymmetrical (Figure 3.15b). Areolae rounded, internally occluded by a cribrum (Figures 3.15d–f). Raphe straight (weakly undulate) with a kink near the central area; proximal raphe ends slightly expanded, deflected in the same direction; distal raphe ends slightly expanded, extending centrally over the mantle, hooked to the same side, with a small hyaline area where the curve occurs (Figure 3.15a). Internally, raphe straight, encased in a thickened sternum (Figures 3.15d–h). Internal proximal raphe ends straight, raphe sternum fused into the thickened central nodule (Figures 3.15e–g). Internal distal raphe ends occluded by pseudosepta (Figure 3.15e).

Figure 3.13. Valves of *Mastogloia calcarea* from Florida, USA: a–b) LM of live specimen from Water Conservation Area 3A (26°7.1703 N, 80°46.089 W) collected by F. Tobias on 8 October 2012 showing mucilage strands exuding from partectal pores situated toward apices, two H-shaped plastids, and numerous oil droplets, and c) SEM of unprocessed Everglades periphyton material showing specimen with numerous strands of mucilage exuding from partectal pores. Scale bars =10 µm.

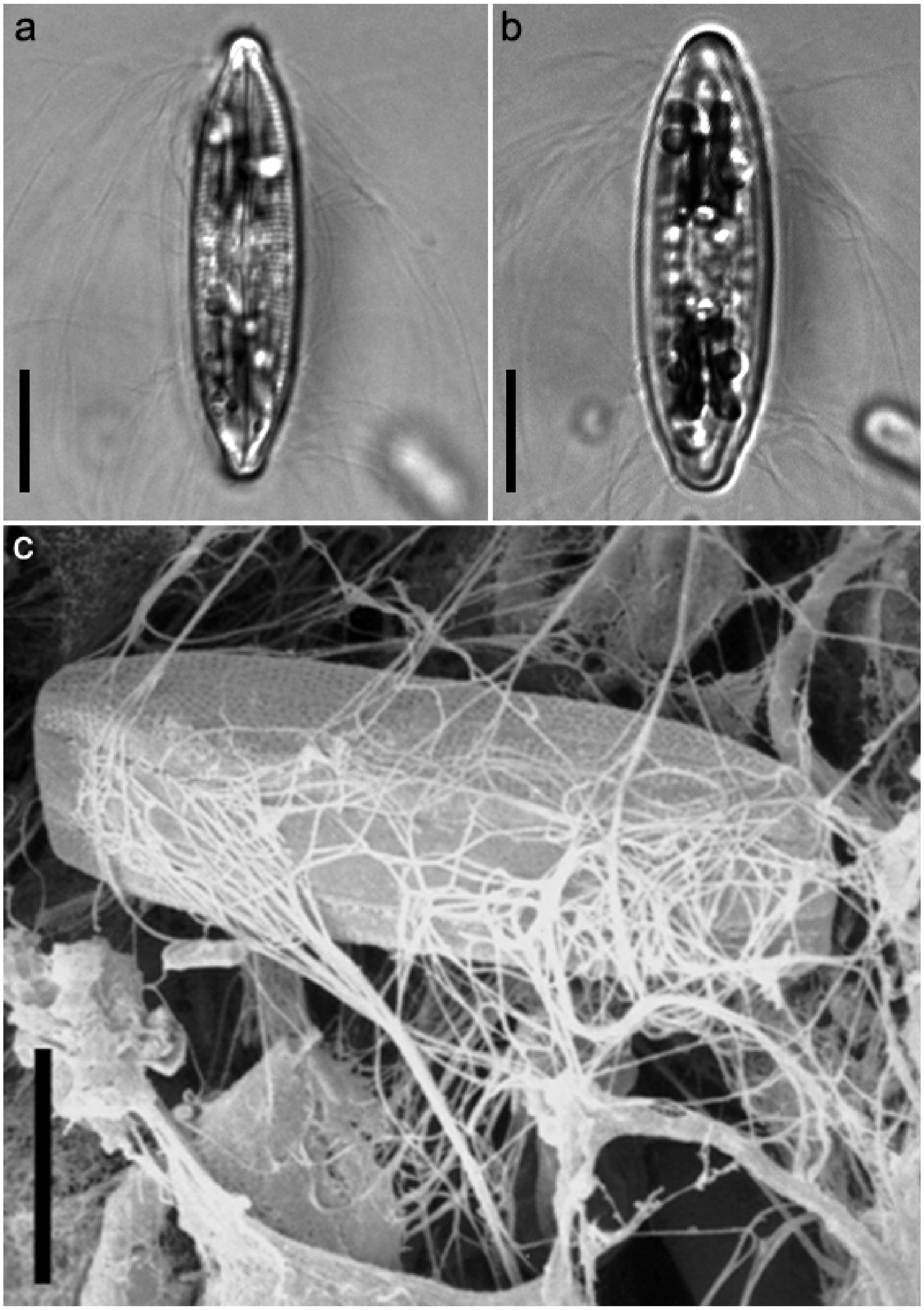


Figure 3.14. Valves of *Mastogloia calcarea* from holotype material ANSP GCM 4841 showing size reduction, LM. Figures b, e, g. Valves showing partectal ring. Figures d–e. Holotype specimen from ANSP GC 58993. Scale bars =10 µm.

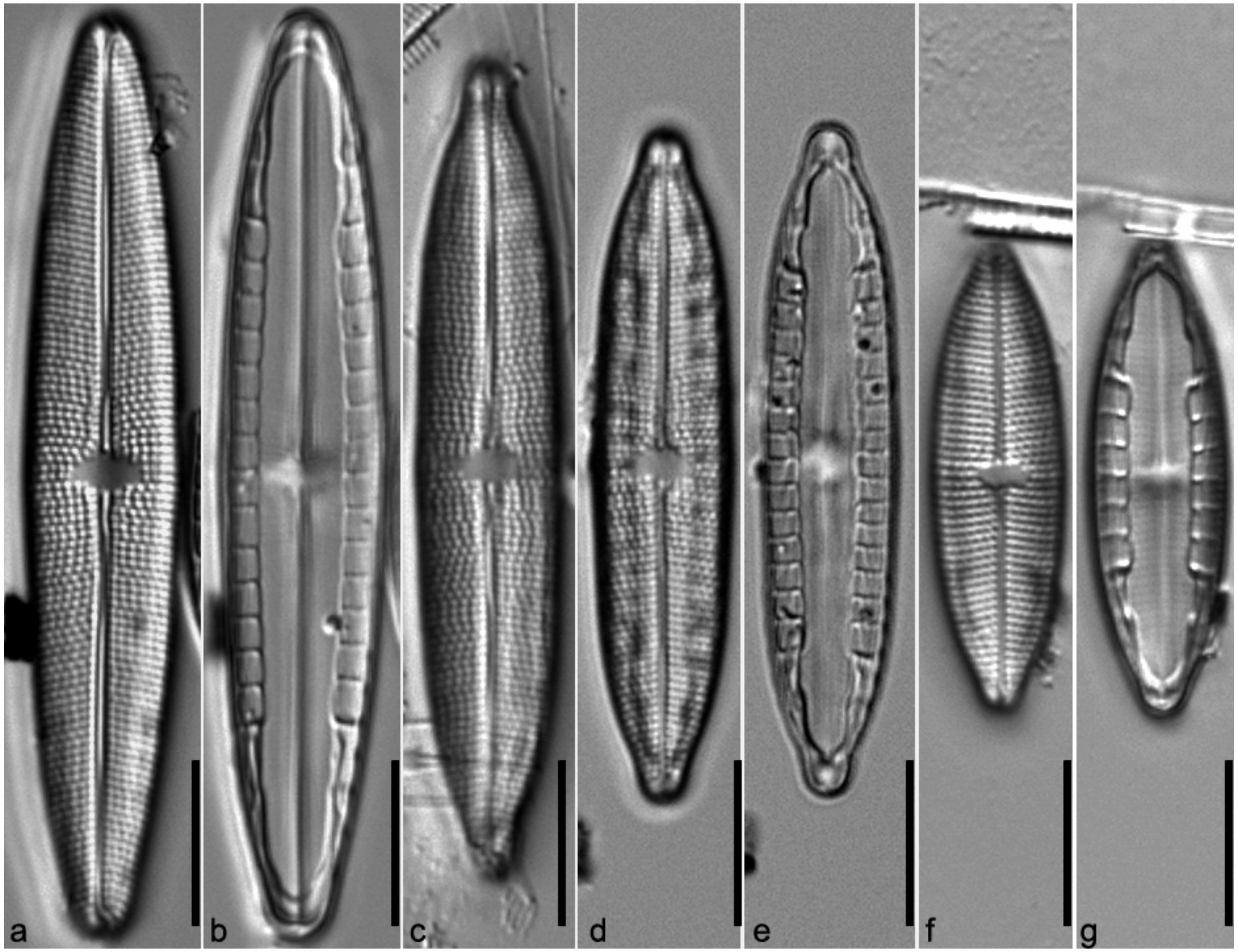


Figure 3.15. *Mastogloia calcarea* from holotype material ANSP GCM 4841, Florida, USA, SEM external (a–c) and internal views (d–h): a) whole valve, b) detail of central area showing asymmetry, c) frustule in girdle view showing partectal pore (arrow) partially covered by valve edge, d) whole valve with partectal ring showing pseudopartectum (arrow), e) whole valve, f) detail of central area, g) detail of pores (arrowheads) between centermost pairs of partecta, h) detail of valve apex showing narrow cleft (arrowhead) and furrow with pore-like cavity (arrow) in partectal ring. Scale bars =10 µm (a, c–e), 1 µm (b, f–h).

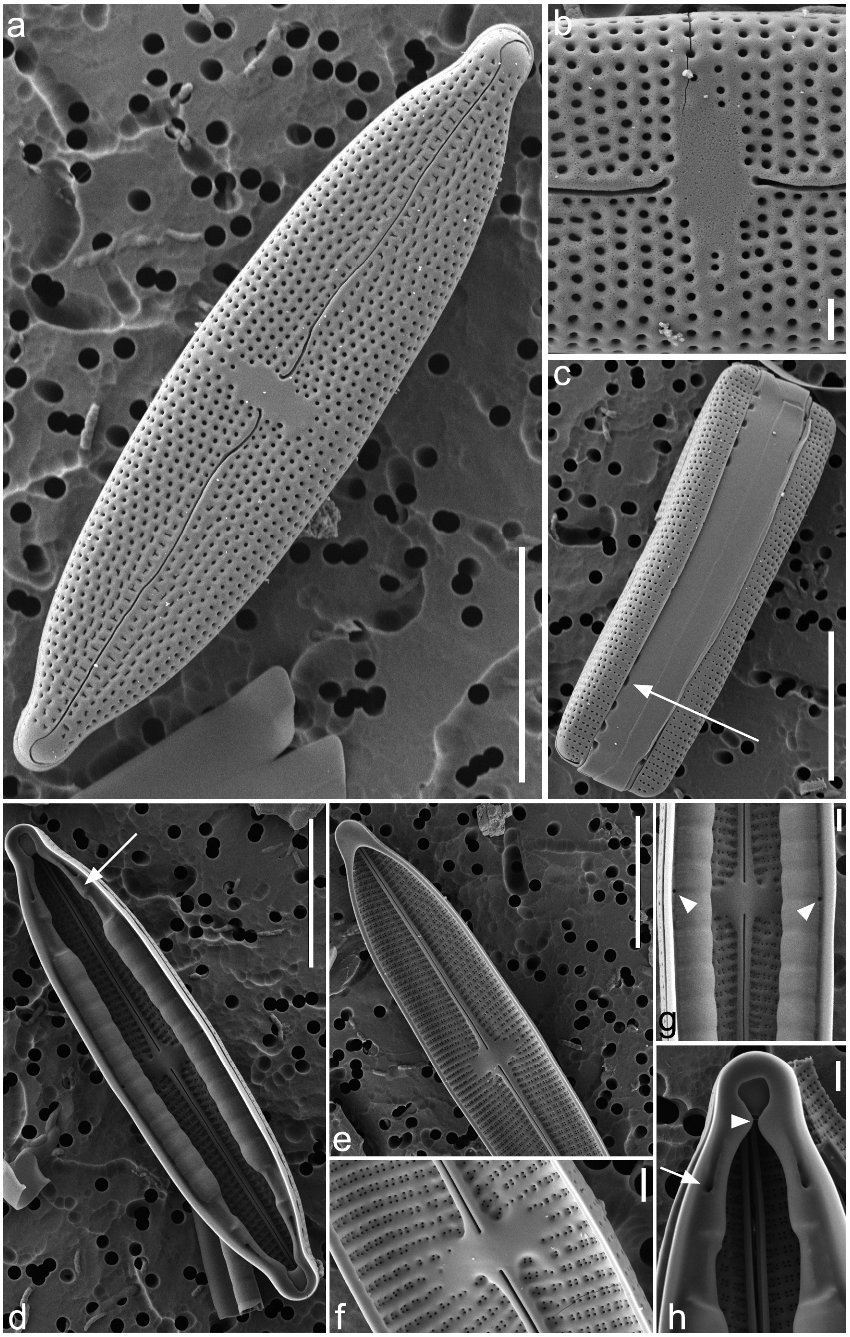


Figure 3.16. Valves of *Mastogloia calcarea* from confirmed distribution in Jamaica showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.

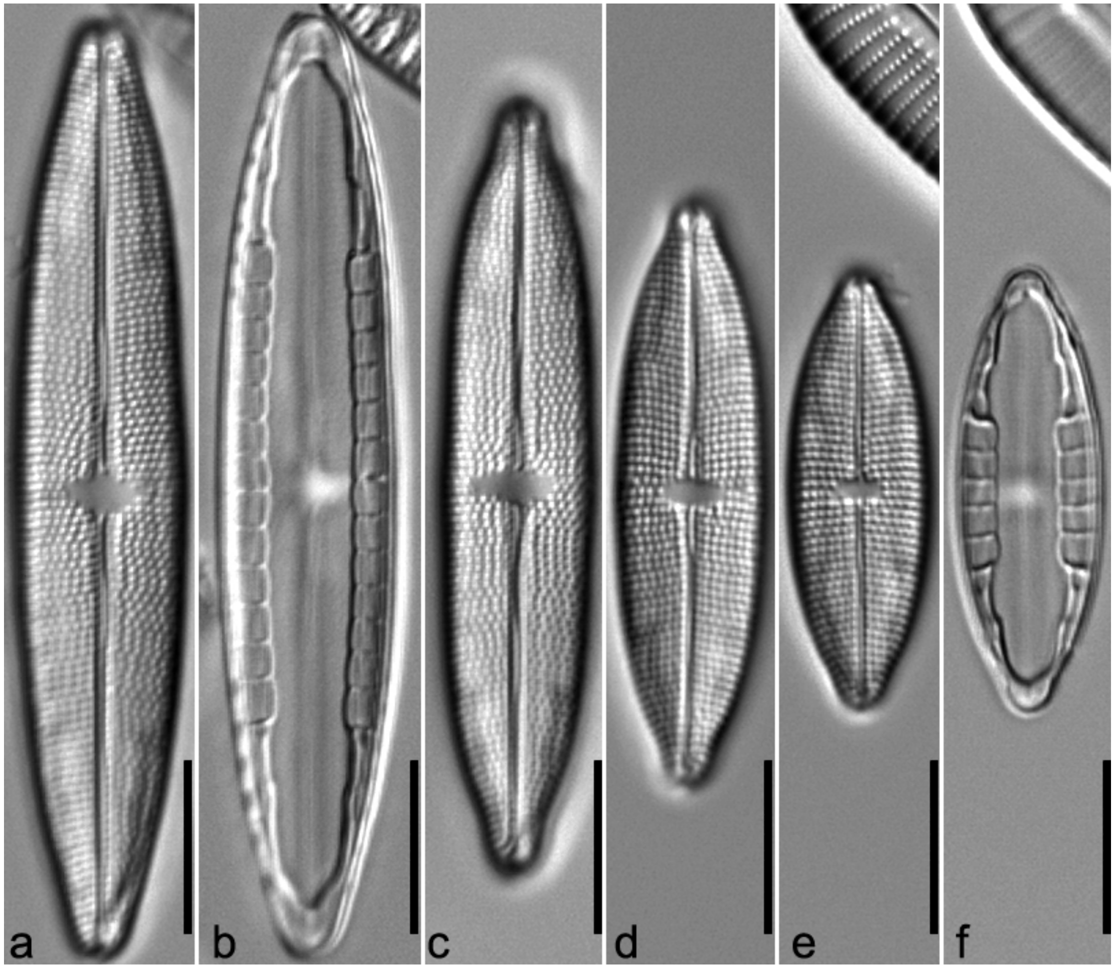


Figure 3.17. Valves of *Mastogloia calcarea* from confirmed distribution in Belize showing size reduction, LM. Figures b, f. Valves

showing partectal ring. Scale bars =10 µm.

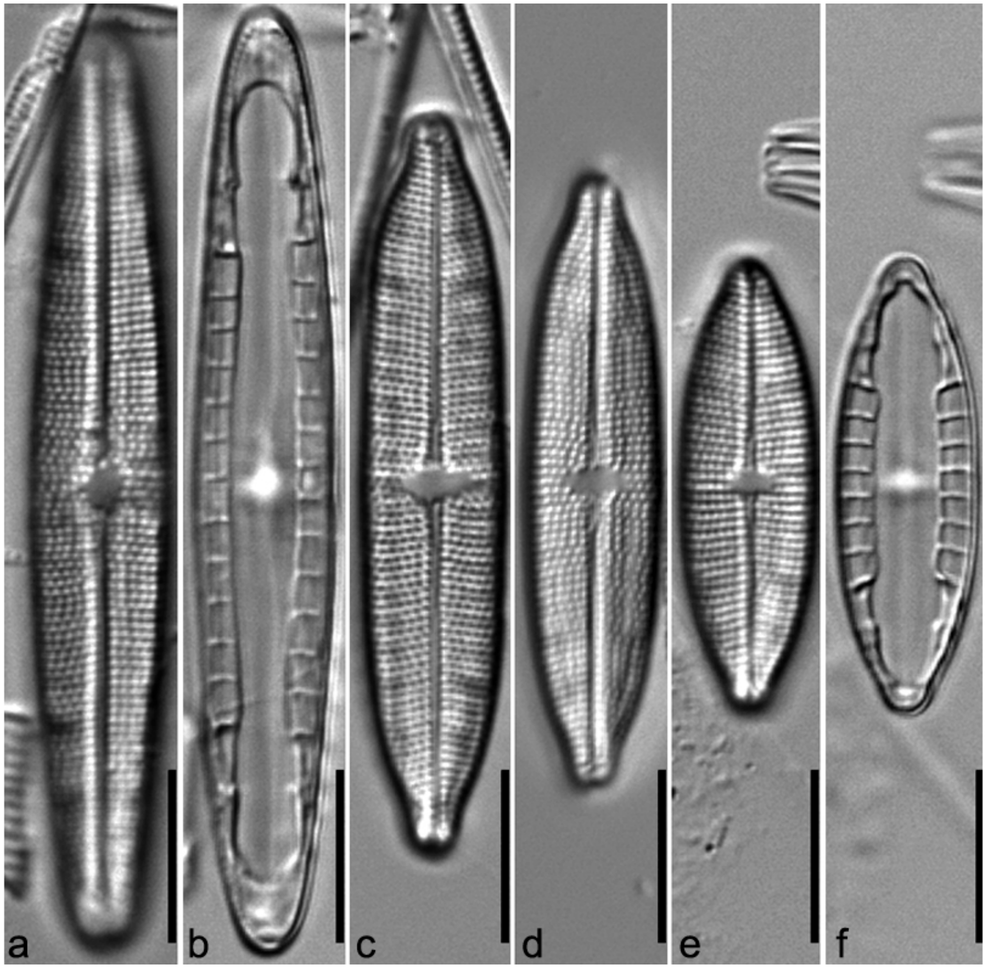


Figure 3.18. Valves of *Mastogloia calcarea* from confirmed distribution in Mexico showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.

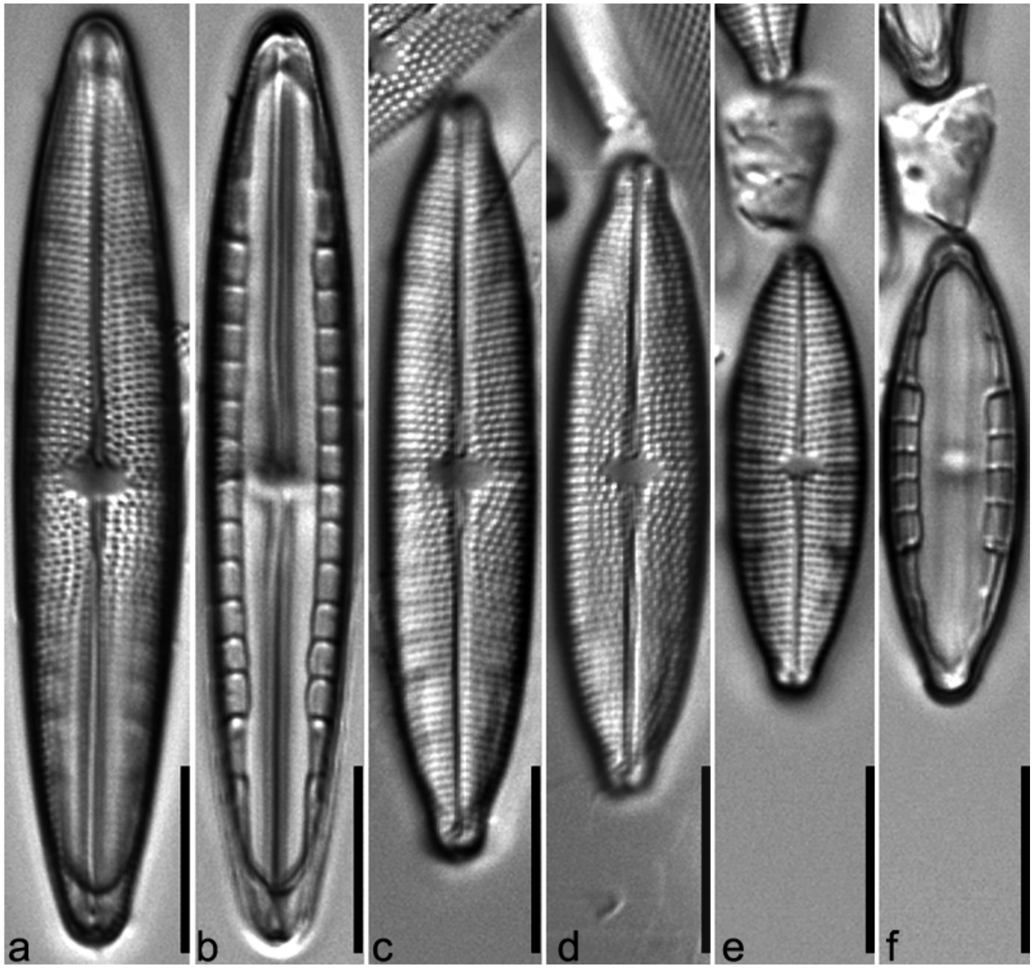


Figure 3.19. *Mastogloia pseudosmithii* from holotype material ANSP GCM 4842, Florida, USA, showing size reduction, LM. Figures b, e, g. Valves showing partectal ring. Figures d–e. Holotype specimen from ANSP GC 58994. Scale bars =10 µm.

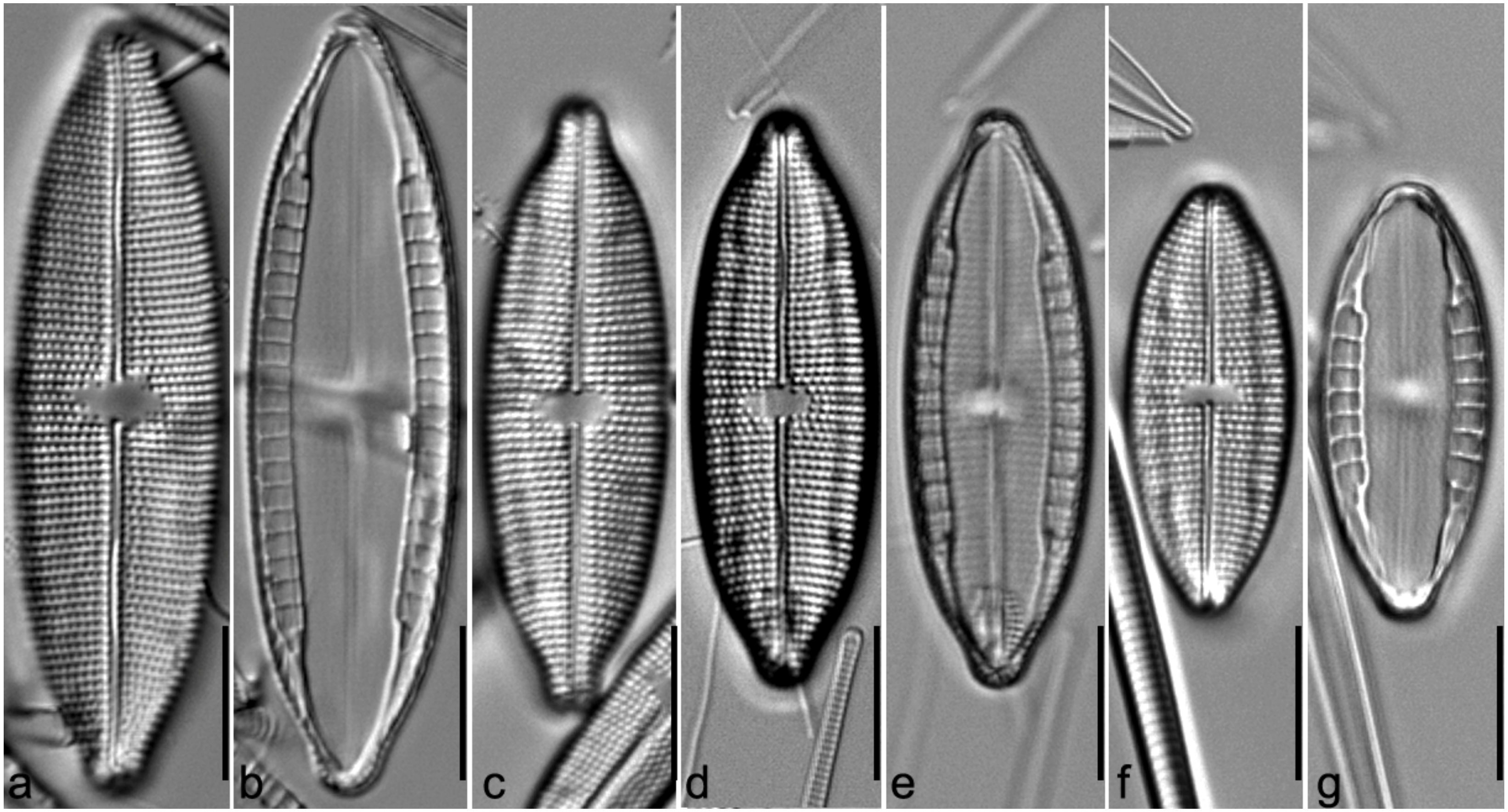

a
b
c
d
e
f
g

Figure 3.20. *Mastogloia pseudosmithii* from holotype material ANSP GCM 4842, Florida, USA, SEM, external (a) and internal views (b–c): a) whole valve, b) whole valve with partectal ring, c) detail of valve showing virgae and vimines of same thickness and irregular arrangement of pores between some partecta. Scale bars = 10 µm (a–b), 1 µm (c).

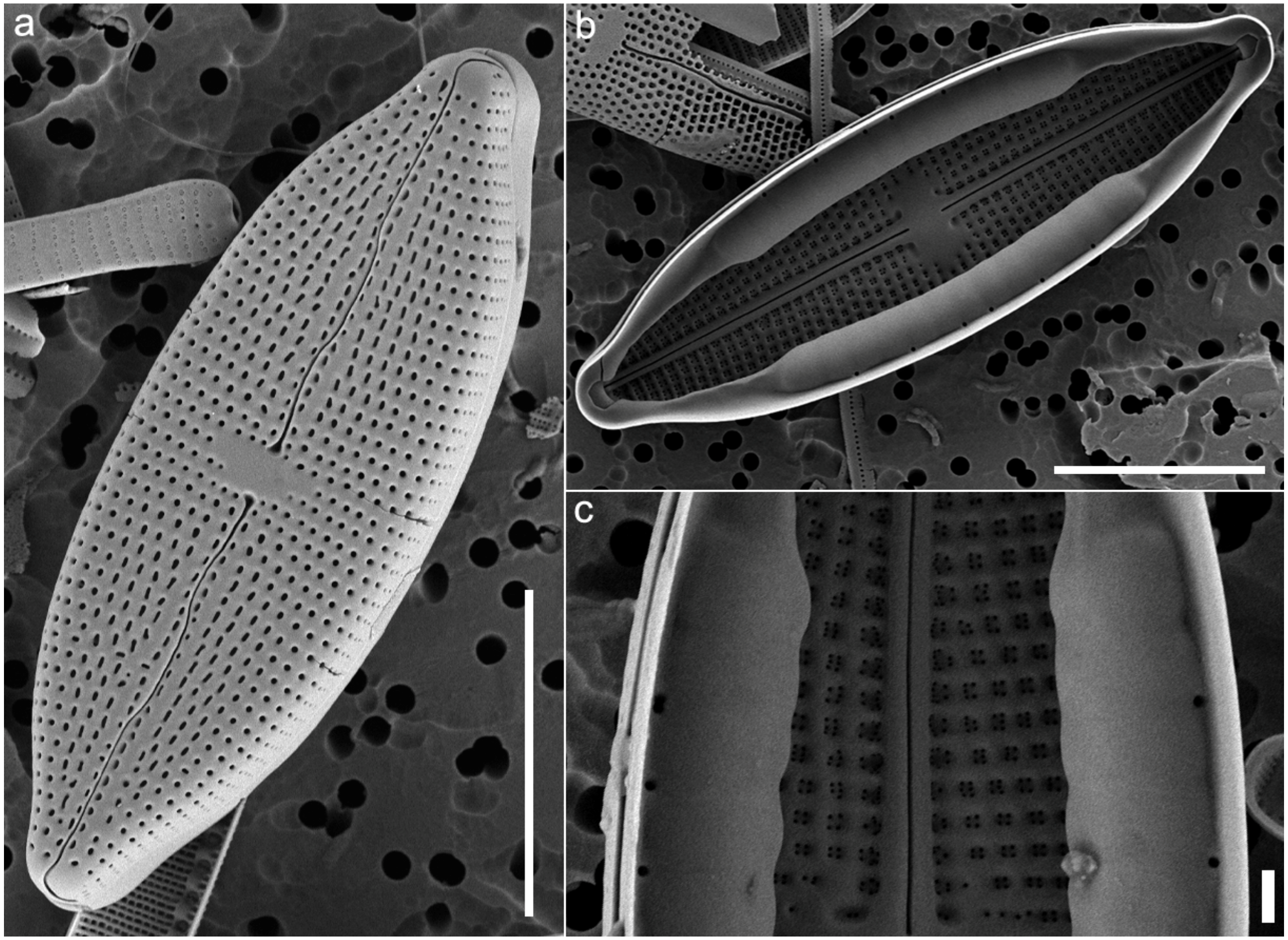


Figure 3.21. *Mastogloia* aff. *smithii* 1 from Van Heurck exsiccatum no. 46 material, South Africa showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.

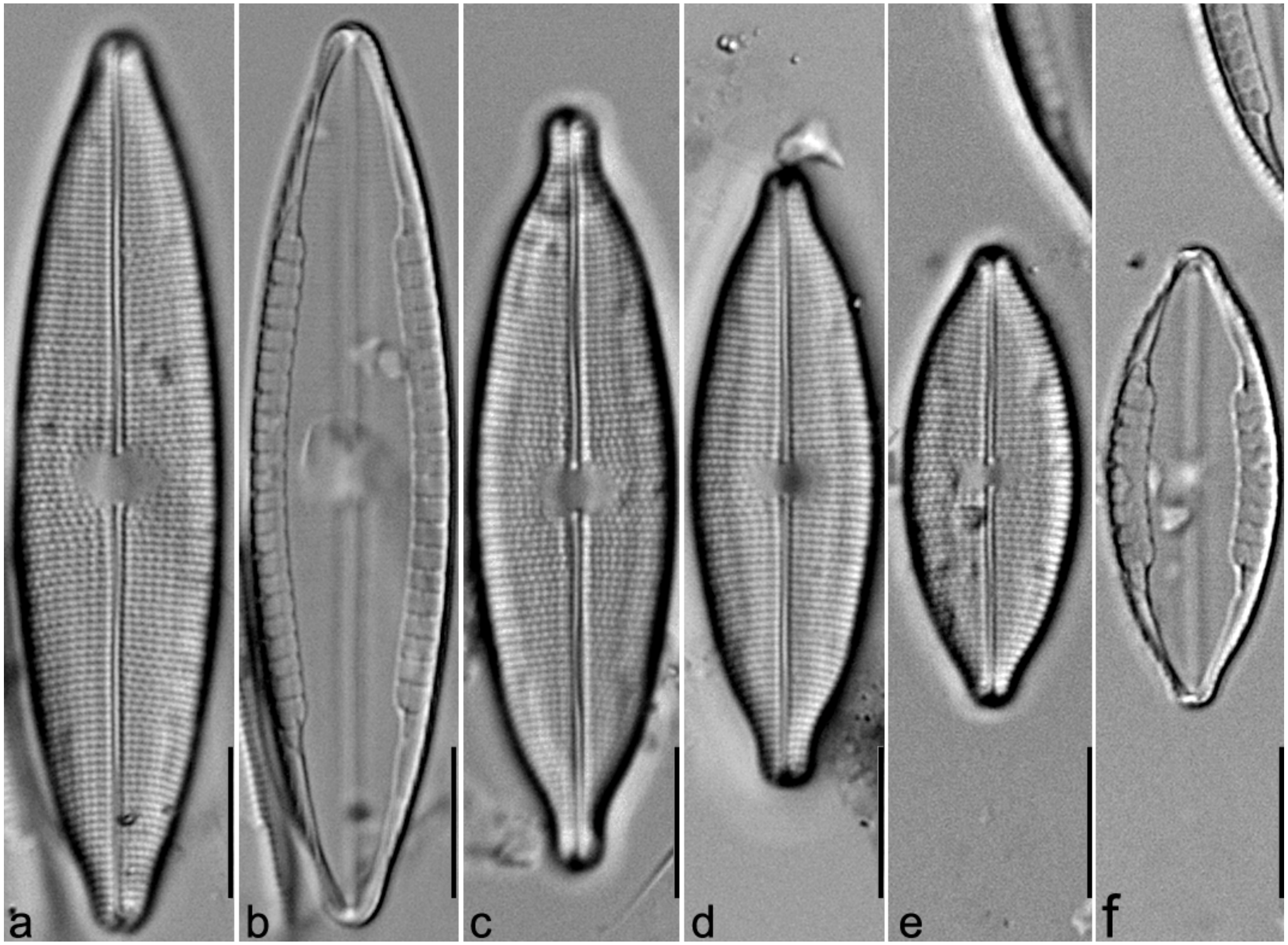


Figure 3.22. *Mastogloia* aff. *smithii* 1 from Van Heurck exsiccatum no. 46 material, South Africa, SEM, external (a) and internal views (b–d): a) whole valve, b) whole valve with partectal ring, c) detail of central area (note panduriform shape) and cribrum, d) detail of valve apex without partectal ring. Scale bars =10 µm (a–b), 1 µm (c–d).

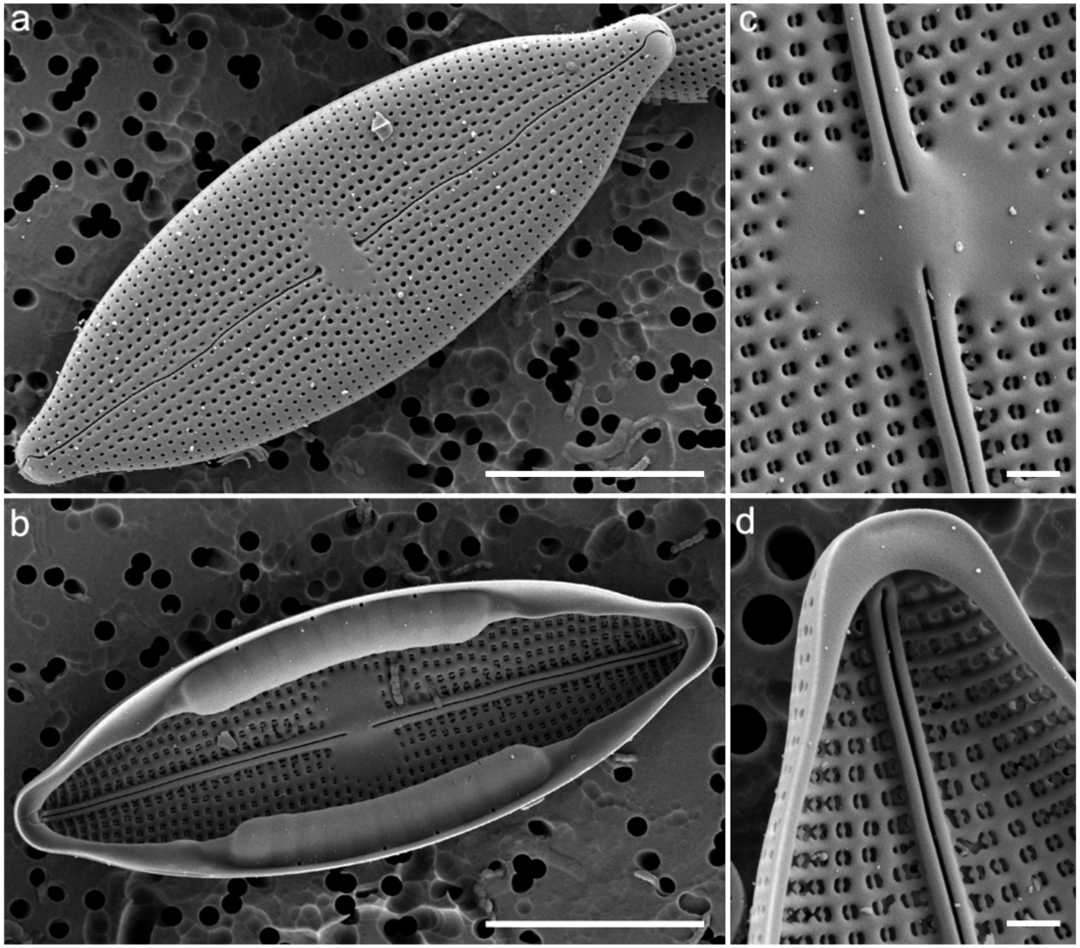


Figure 3.23. *Mastogloia* aff. *smithii* 2 from Michigan showing size reduction, LM. Figures b, f. Valves showing partectal ring. Scale bars =10 µm.

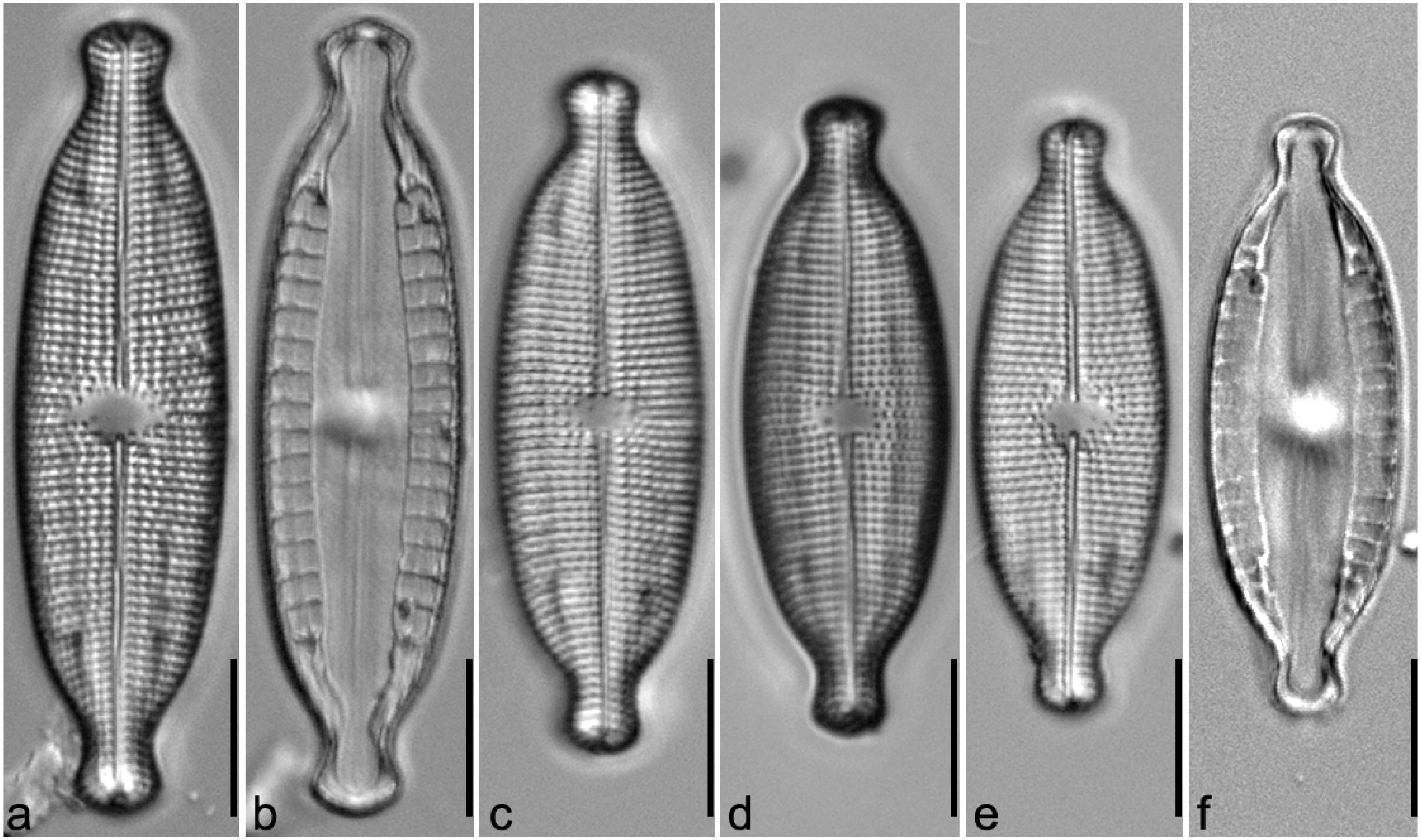


Figure 3.24. *Mastogloia* aff. *smithii* 2 from Michigan, SEM external (a) and internal views (b): a) whole valve, b) whole valve with partectal ring. Scale bars =10 µm.

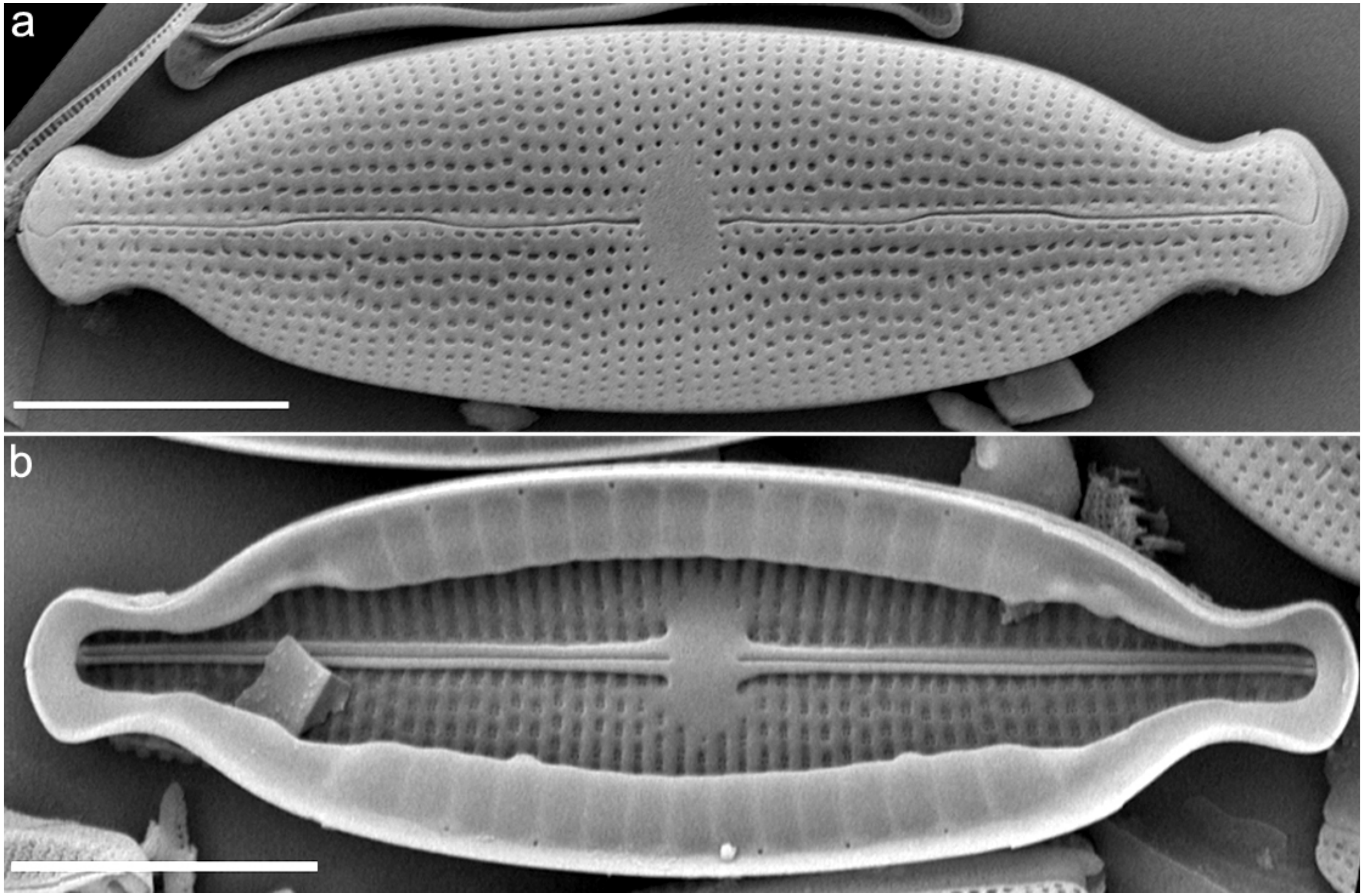


Table 3.4. Maximum Spearman rank correlations between morphometric variables and final ordination scores.

Morphometric data	Spearman rank correlation coefficient
Partectum density	0.91*
Stria density	0.87*
Areola density	0.82*
Angle of striae	0.81*
Length:partectum ratio	0.80*
Length:width ratio	0.65*
Area of central area	0.61*

Note. *: significant correlation at $p<0.001$.

Table 3.5. ANOSIM *R* statistics from pairwise comparisons of *Mastogloia* populations based on morphometric data: angle of striae radiation, area of the central area, densities of striae, areolae and partecta, length:width and length:partectum ratios.

Taxon	Location	Belgium	Canada	Iowa	Michigan	Florida	Belize	Jamaica	Mexico	United Kingdom	Florida	South Africa
M. lacustris	Belgium											
	Canada	0.46*										
	Iowa	0.51*	0.27*									
	Michigan	0.42*	0.06	0.13								
M. calcarea	Florida	0.80*	0.77*	0.69*	0.62*							
	Belize	0.80*	0.82*	0.70*	0.64*	0.07						
	Jamaica	0.83*	0.75*	0.67*	0.59*	-0.03	0.05					
	Mexico	0.73*	0.67*	0.55*	0.50*	0.01	0.13	0.01				
M. smithii	United Kingdom	1.00*	1.00*	1.00*	0.98*	0.97*	0.96*	0.99*	0.89*			
M. pseudosmithii	Florida	0.75*	0.97*	0.97*	0.95*	0.98*	0.95*	0.99*	0.91*	1.00*		
M. aff. *smithii* 1	South Africa	0.89*	0.98*	0.92*	0.95*	0.93*	0.90*	0.94*	0.91*	0.88*	0.60*	
M. aff. *smithii* 2	Michigan	0.83*	0.99*	1.00*	0.98*	1.00*	0.99*	1.00*	0.97*	1.00*	0.40*	0.71*

Note. *: significant difference between populations at $p<0.001$.

Table 3.6. Morphometric data and morphological features of *Mastogloia calcarea* from relevant reference sources, with LM

measurements of *M. calcarea* holotype and paratype specimens and mean values in parentheses. Information from references obtained directly from the text.

Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (µm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
Podzorski (1985)[1], Jamaica	nd	20–45	8–14	nd	18–19	14–17	6–8	nd	Small, elliptical to nearly quadrangular	Parallel or slightly radiate	Elliptical to elliptical-lanceolate	Short, protracted, subrostrate to subcapitate
Novelo et al. (2007)[2], Mexico	nd	28.5–56	7.6–9.5	nd	18–20	16–20	5–9	nd	Small, elliptical to rectangular	Slightly radiate	Elliptical-lanceolate	Subrostrate
Slate & Stevenson (2007)[3], Florida	nd	25–57	7–9	nd	18–20	20	5–6	nd	nd	nd	Linear-lanceolate	nd (rounded in initial valves)
Gaiser et al. (2010)[4], Florida	20	28–55 (42)	9–10 (9.6)	4.3	16–20	nd	nd	nd	nd	nd	nd	nd
Holotype ANSP GC 58993, Florida	20	27–54 (38)	7–9 (8)	4.6	19–20	16–20	5–6	3.9	Asymmetrical, elliptical to polygonal 3–7 (5)	157–168 (163)	Linear-lanceolate	Rostrate (rounded in post-initial valves)

Table 3.6. Continued.

Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (µm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
Paratype ANSP GC 30902, Belize	21	22–54 (34)	7–9 (8)	4.3	18–20	16–20	5–7	3.8	Asymmetrical, elliptical to polygonal 2–5 (3)	157–172 (163)	Linear-lanceolate	Rostrate (rounded in post-initial valves)
Paratype ANSP GC 16009, Jamaica	20	26–50 (38)	8–10 (9)	4.4	19–20	16–20	4.5–6	3.9	Asymmetrical, elliptical to polygonal 2–7 (4)	152–167 (162)	Linear-lanceolate	Rostrate (rounded in post-initial valves)
Paratype ANSP GC 30903, Mexico	22	19–53 (38)	7–10 (8)	4.7	19–20	16–20	4.25–6	4.4	Asymmetrical, elliptical to polygonal 1–7 (4)	154–167 (162)	Linear-lanceolate	Rostrate (rounded in post-initial valves)

Note. n: number of specimens measured; nd: no data.

[1] pl 5; figs 21–22 as *M. smithii* in Patrick & Reimer 1966.

[2] as *M. smithii*.

[3] as *M. smithii* morphotype I.

[4] as *M. smithii* var. *lacustris*.

Partectal ring closed, without a flange separating the ring from the valve margins, with a pseudopartectum (Figure 3.15d), apices with a narrow cleft which expands into a pyriform lacuna, with a furrow opening into a pore-like cavity on each side of both apices (Figure 3.15h), and with one pore between the centermost pair of partecta on each side of the partectal ring (Figure 3.15g). Partecta distributed along both sides of the partectal ring, except near the apices, partecta visibly distinguishable, evenly sized although slightly larger close to the apices (Figure 3.15d). Thickened virgae present throughout the valve interior (Figures 3.15e–f). Cribral pores becoming highly irregular near the raphe sternum and central nodule (Figure 3.15f). Five partectal pores located near both sides of the apices, increasingly occluded by the valve edge away from the apices (Figure 3.15c).

Holotype (here designated). Marked specimen on slide ANSP GC 58993, Academy of Natural Sciences, Philadelphia, USA. Holotype specimen illustrated in Figures 3.14d–e.

Isotype (here designated). Slide BR-4298, National Botanic Garden of Belgium, Meise, Belgium.

Confirmed distribution records (paratypes here designated):

- Slides BR-4311 and ANSP GC 16009, Jamaica (18°01.524 N, 77°48.874 W), periphyton, collected by E. Gaiser and J. La Hée, 3 May 2008 (Figure 3.16).
- Slides BR-4312 and ANSP GC 30902, Belize (17°45.527 N, 88°38.456 W), periphyton, collected by E. Gaiser and J. La Hée, 13 November 2007 (Figure 3.17).

- Slides BR-4313 and ANSP GC 30903, Mexico (19°49.619 N, 87°30.585 W), periphyton, collected by E. Gaiser and J. La Hée, 10 December 2006 (Figure 3.18).

Type locality. Periphyton on sawgrass (*Cladium jamaicense*), sample material ANSP GCM 4841, Everglades National Park (25°41.883 N, 80°39.249 W), Florida, USA. Collected by F. Tobias, 6 October 2008.

Etymology. The specific epithet refers to the taxon's dominance in calcareous periphyton mats, especially in subtropical and tropical wetlands with seasonal drying and flooding (Gaiser et al. 2010).

Distribution. Subtropical and tropical karstic wetlands of Florida, USA, Mexico, Jamaica and Belize (Novelo et al. 2007, Slate & Stevenson 2007, Gaiser et al. 2010, La Hée 2010, La Hée & Gaiser 2012).

Ecology. Lives embedded within microbial communities dominated by filamentous and coccoid cyanobacteria that form extensive mats upon the sediment or bedrock surface and around the submersed stems of aquatic plants in shallow water, limestone-based environments with seasonal desiccation (Gaiser et al. 2010). Weighted-averaging optima: water depth 52 cm, salinity 0.1, total phosphorus 225 $\mu g\ g^{-1}$, and pH 7.6 (referred to as *M. smithii* in Gaiser et al. 2006, and *M. smithii* var. *lacustris* in Gaiser et al. 2010).

Mastogloia pseudosmithii sp. nov. Lee, Gaiser, Van de Vijver, Edlund & Spaulding (Figures 3.19–3.20; Table 3.7)

Description. Cells solitary. Valves elliptical-lanceolate with rostrate apices (small valves with subrostrate to rounded apices), 28–51 µm length, 11–14 µm width, 16–17 striae in 10 µm, 16 areolae in 10 µm (Figure 3.19). Striae areolate, gently radiate, becoming parallel at the apices, stria arrangement on the valve face continues unchanged onto the mantle (Figure 3.20a). Central area elliptical to polygonal, commonly asymmetrical (Figures 3.19–3.20a). Areolae rounded to elliptical, some reduced around the central area, internally occluded by a cribrum (Figures 3.20a–c). Raphe straight with a median kink (Figure 3.20a). Proximal raphe ends expanded and pore-like, opening into a spathulate groove (Figure 3.20a). Distal raphe ends extending centrally over the mantle, hooked to the same side, with a small hyaline area where the curve occurs (Figure 3.20a). Internally, raphe straight, encased in a thickened sternum (Figure 3.20b). Internal proximal raphe ends straight, raphe sternum fusing into the thickened central nodule (Figure 3.20b). Internal distal raphe ends occluded by pseudosepta (Figure 3.20b). Partectal ring closed, without a flange separating the ring from the valve margins, with a broad cleft at both apices, with pores between partecta near the advalvar edge of the partectal ring sometimes arranged in a pattern (Figures 3.20b–c). Partecta distributed along both sides of the partectal ring except near the apices, visibly distinguishable, evenly sized except slightly larger close to the apices (Figure 3.20c). Virgae and vimines (cross connections between virgae) of the same thickness present throughout the valve interior (Figure 3.20c). Cribral pores becoming irregular near the raphe sternum and central nodule (Figures 3.20b–c).

Holotype (here designated). Marked specimen on slide ANSP GC 58994, Academy of Natural Sciences, Philadelphia, USA. Holotype specimen illustrated in Figures 3.19d–e.

Isotype (here designated). Slide BR-4314, National Botanic Garden of Belgium, Meise, Belgium.

Type locality. Floating periphyton mat in brackish marsh, sample material ANSP GCM 4842, Everglades National Park (25°28.935 N, 81°2.907 W), Florida, USA. Collected by A. Scharnagl, 3 November 2011.

Etymology. The specific epithet refers to the close resemblance of this new taxon to *M. smithii*, with which it was often confused.

Distribution. At present, only reported from the coastal marshes of Florida (Trexler & Gaiser 2012) and Jamaica (Podzorski 1985), and some inland locations such as Water Conservation Areas 2A (Slate & Stevenson 2007) and 3A of Florida (referred to as *M. smithii* var. *lacustris* in Trexler & Gaiser 2012).

Ecology. Comprises <1% of total diatom abundance in non-calcareous periphyton assemblages in waters of high conductivity, such as brackish areas near the coastal marsh, slightly acidic pH, and slightly higher total phosphorus (referred to as *M. smithii* in Gaiser et al. 2006, Trexler & Gaiser 2012). Weighted-averaging optima: water depth 41 cm, pH 6.7, conductivity 2500 $\mu S\ cm^{-1}$, and total phosphorus 480 $\mu g\ g^{-1}$ (Trexler & Gaiser 2012).

Discussion

There is growing evidence of unrecognized diversity among diatoms because of a lack of knowledge of types and/or original collections, a lack of resources for resolving taxonomic discrepancies, and assignment of names to taxa with morphologies that are not faithful to the original taxonomic concepts. The complicated nomenclatural histories highlighted in this paper show that *M. smithii* and *M. lacustris* exemplify all three problems: the original material of both taxa was either impossible or very difficult to locate, both taxa had inconsistent published morphological descriptions, and the names were assigned to taxa from many parts of the world with morphological variability beyond the range of the original descriptions. However, by clarifying species boundaries, discriminatory methods, including molecular sequence analyses (Behnke et al. 2004, Mann et al. 2004), mating experiments (Mann et al. 1999), and multivariate morphological analyses (Edlund & Soninkhishig 2009) are improving our understanding of diatom diversity.

Table 3.7. Morphometric data and morphological features of *Mastogloia pseudosmithii* and *M.* aff. *smithii* 1 from relevant reference sources and LM measurements of *M. pseudosmithii* holotype, *M* aff. *smithii* 1, and *M.* aff. *smithii* 2 with mean values in parentheses. Information from reference source obtained directly from the text.

Taxon	Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (µm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
M. pseudosmithii	Slate & Stevenson (2007)[1], Florida	nd	22–45	10–13	nd	14–15	17–18	6–8	nd	nd	nd	Almost elliptical	nd
	Holotype ANSP GC 58994, Florida	20	28–51 (38)	11–14 (12)	3.2	16–17	16	6–8	3.1	Asymmetrical, rectangular to elliptical 4–10 (7)	170–175 (173)	Elliptical-lanceolate	Rostrate (blunt in small valves)
M. aff. *smithii* 1	Patrick & Reimer (1966)[2]	nd	20–45	8–14	nd	18–19	14–17	6–8	nd	Small, elliptical to nearly quadrangular	Parallel or slightly radiate	Elliptical to elliptical-lanceolate	Short, protracted, subrostrate to subcapitate
	Van Heurck & Grunow (1882–1885)[3], South Africa	20	28–60 (42)	10–14 (12)	3.4	18–20	16–20	7–8	3.1	Panduriform 5–18 (11)	170–176 (173)	Elliptical-lanceolate	Rostrate

Table 3.7. Continued.

Taxon	Reference source	n	Valve length (µm)	Valve width (µm)	Mean length: width ratio	Striae in 10 µm	Areolae in 10 µm	Partecta in 10 µm	Mean length: partectum ratio	Shape and area of central area (µm^2)	Angle of striae (°)	Outline of medium-sized valve	Apices
M. aff. *smithii* 2	Michigan	20	35–51 (43)	11–14 (13)	3.3	15–16	12–16	6–8	3.0	Elliptical 7–13 (10)	167–173 (171)	Elliptical-lanceolate	Capitate

Note. n: number of specimens measured; nd: no data.

[1] as *M. smithii* morphotype II.

[2] as *M. smithii.*

[3] Type no. 46 *M. smithii*.

Diatoms assigned to *M. smithii* and *M. smithii* var. *lacustris* can now be attributed to at least four entities: *M. smithii, M. lacustris, M. calcarea,* and *M. pseudosmithii.* Smith (1856) did not formally recognize varieties of *M. smithii*, though he recognized an unnamed *"β"* form of *M. smithii* with capitate apices. As such, Smith's (1856) concept of *M. smithii* was very broad, including a wide width range and both rostrate and capitate forms. The material collected by Smith from Little Sea, Dorset, UK, was designated as the *M. smithii* lectotype because it is the oldest material (1848) among the syntypes. While Smith (1856) reported a maximum valve width of 20.3 µm, no specimen with valve width >15 µm was found in the *M. smithii* lectotype slide. My observations showed that axial costae are an important distinguishing feature of the taxon. This is consistent with Hustedt (1933), who separated taxa into Apiculatae if axial costae were present and into Lanceolatae if not present; the otherwise shared features of the two groups are partecta situated close to the valve margins (i.e., no flange between the partectal ring and the valve margin) and a generally straight raphe. Smith's (1856) drawing of *M. smithii* (Figure 3.1) suggests the presence of axial costae in all forms, including the *"β"* form. Because Grunow (1860), Van Heurck (1880, 1885), and Patrick & Reimer (1966) did not demonstrate the presence of axial costae in their text or figures of *M. smithii*, their descriptions could not be unequivocally determined as *M. smithii sensu* W. Smith. Moreover, there is no evidence that these researchers inspected the original specimens identified by Smith (1856) as *M. smithii.* Despite the broad taxonomic concept of *M. smithii sensu* W. Smith, morphological evidence clearly shows that it does not include taxa without axial costae such as *M. lacustris, M. calcarea,* and *M. pseudosmithii.*

Novarino (1990) was correct to note this difference between *M. smithii* and the taxon he obtained from the Rabenhorst collection, which is most probably *M. lacustris*, based on the description provided. Another variety of *M. smithii* that needs further investigation is *M. smithii* var. *amphicephala* Grunow (Van Heurck 1880, pl. 4, fig. 27), shown by a line drawing in the *Atlas* as a taxon with distinctly capitate apices. Following Van Heurck (1880), Patrick & Reimer (1966) described *M. smithii* var. *amphicephala* as resembling the nominate variety, except for the distinctly capitate apices, but included a caveat that only a small size range had been examined and that further observations could confirm that the taxon was part of the nominate variety. The morphology of *M. smithii* var. *amphicephala* needs further investigation to determine whether it is Smith's (1856) *"β"* form, a variety of *M. smithii* distinct from the *"β"* form, or a completely separate entity, as shown for *M. lacustris, M. calcarea,* and *M. pseudosmithii.*

SEM, LM, and multivariate analyses of morphometric data clearly differentiated *M. lacustris* and *M. smithii* as distinct species. Neotype specimens of *M. lacustris* possessed a very different valve structure from the lectotype specimens of *M. smithii*: (1) *M. lacustris* had much smaller external areolae, which are big enough in *M. smithii* to reveal the cribrum at certain angles (Figures 3.6b–c, Figures 3.8c–d); (2) *M. lacustris* lacked the internal axial costae and costa-like virgae exhibited by *M. smithii* (Figures 3.6d–e, h) and instead, possessed simpler, thickened virgae and a raphe encased within a thickened raphe sternum (Figures 3.8f–h); (3) *M. lacustris* had a narrow cleft at each apex of the partectal ring that expands into a pyriform lacuna (Figure 3.8e), while *M. smithii* had a broad cleft without a lacuna (Figures 3.6d, f); (4) *M. lacustris* had pseudopartecta and furrows on either side of the partectal ring apices (Figure 3.8e), while *M. smithii* lacked both (Figure 3.6d); and (5) *M. lacustris* had fewer pores between partecta than *M. smithii* (Figures 3.6d, g; Figure 3.8e). Moreover, the two taxa differed significantly in LM measurements of stria density, partectum density, length:width and length:partectum ratios (Tables 3.2–3.3; Figure 3.9). Krammer & Lange-Bertalot (1986) provided only two figures of *M. lacustris*: a post-initial valve (pl. 201, fig. 1) with rounded apices, and a very short specimen (pl. 201, fig. 6) with subrostrate to round apices (exact outline difficult to discern from photomicrograph cutout) as a result of variable valve morphology during size diminution. There has been no discussion of this variability in any of the previously mentioned descriptions of *M. lacustris* (except Slate & Stevenson 2007 and Gaiser et al. 2010 for *M. calcarea*), partly because the taxonomic concept of *M. lacustris* was unclear until now. It is possible that since Krammer & Lange-Bertalot (1986), interpretations of *M. lacustris* were limited to valves with rounded apices while interpretations of *M. smithii* were limited to specimens with rostrate apices, especially in subtropical and tropical karstic wetlands where specimens (now allocated to *M. calcarea*) more closely matched the stria density of *M. smithii* (Gaiser et al. 2006, Novelo et al. 2007, Ibarra et al. 2009, Gaiser & Rühland 2010, Gaiser et al. 2010, La Hée 2010, La Hée & Gaiser 2012). The rounded apices of *M. calcarea* post-initial valves were correctly pointed out by Slate & Stevenson (2007) and, more extensively, by Gaiser et al. (2010, fig. 4a, m, x). In the multivariate analyses, *M. lacustris* specimens from North America were statistically different from the Belgian neotype. The difference was mostly attributed to a lower length:partectum ratio in the Belgian population. All other attributes overlapped in range or mean values with those of the North American populations, precluding taxonomic separation of the two groups.

Mastogloia calcarea differed from the neotype and the North American populations of *M. lacustris* by its linear-lanceolate, rather than elliptical-lanceolate, valve outline (excluding post-initial and small valves) and all morphometric data examined by multivariate analyses. Gaiser et al. (2010) was the first to recommend a more thorough exploration of *M. lacustris* type material because of the consistent differences between *M. calcarea* and the morphological descriptions of *M. lacustris* given in references, particularly the higher stria density and narrower width range of *M. calcarea*. Morphometric data taken for *M. calcarea* did not concur with the large central area and coarse striae of the *M. lacustris* neotype. Gaiser et al. (2010) recognized *M. calcarea* as a structural engineer and keystone species (like cyanobacteria) in microbial mat assemblages because of its sensitivity to phosphorus enrichment and the strong positive relationship between its relative abundance and mat biomass. At present, the distribution of *M. calcarea* appears to be limited to karstic wetlands of subtropical and tropical regions in the western hemisphere. However, because of the limited number of studies on the diatom flora of tropical and other karstic wetlands where periphyton mats occur, *M. calcarea* may prove to be more widely distributed.

It is clear that *M. smithii sensu* W. Smith, *M. pseudosmithii, M.* aff. *smithii* 1, and *M.* aff. *smithii* 2 are separate entities. *Mastogloia pseudosmithii* lacks internal axial costae and costa-like virgae, has lower stria and areola densities, a larger length:width ratio, and a smaller length:partectum ratio than *M. smithii sensu* W. Smith. *Mastogloia* *pseudosmithii* is morphologically similar to *M.* aff. *smithii* 1, but *M. pseudosmithii* has lower stria density. *Mastogloia pseudosmithii* also has a rectangular to elliptical central area and cribral pores mostly arranged in groups of four or greater (Figure 3.20c), while *M.* aff. *smithii* 1 has a nearly panduriform central area (depicted in Patrick & Reimer 1966) and cribral pores that are elongated and mostly arranged in groups of two forming a circular depression (Figure 3.22c). *Mastogloia pseudosmithii* is also similar to *M.* aff. *smithii* 2, but *M.* aff. *smithii* 2 has coarser striae and areolae, in addition to highly capitate apices without a cleft in the partectal ring (Figure 3.24b). Slate & Stevenson (2007) reported slightly different stria and areola densities for *M. smithii* Morphotype II, but their figures 37a–c concur with the morphological features of *M. pseudosmithii,* as does Podzorski's (1985, pl. 5, fig. 18). The ecology of *M. pseudosmithii* differs from that of *M. calcarea* because it is a rare taxon that prefers brackish conditions where a combination of factors, including phosphorus input from seawater and pH lowered by peat accumulation, encourages algal assemblages that do not form the cohesive calcareous periphyton mats that dominate the Everglades landscape (Gaiser et al. 2006, 2010).

This investigation of *M. smithii, M. lacustris,* and populations previously identified as these two taxa in the temperate, subtropical, and tropical regions clearly shows the importance of careful taxonomic analyses in uncovering the true diversity of diatoms. The results of careful examination of original material, and the designation of lecto- and neotypes of *M. smithii* and *M. lacustris,* respectively, allow justification of subsequent divergences from the original taxonomic concepts. In regions without focused taxonomic work, such as the type locality of *M. calcarea* and *M. pseudosmithii,* multiple populations must be compared to develop a representative idea of a taxon's morphological variability. Finally, in lieu of molecular or reproductive taxon discrimination, multivariate analyses of morphometric data provide quantitative evidence that supports taxonomic differences determined from analyzing ultrastructure and ecological preferences. Using a combination of these methods permitted the description of two new *Mastogloia* species from the Florida Everglades and the Caribbean region.

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CHAPTER IV: BENTHIC DIATOM METACOMMUNITY SPATIAL AND TEMPORAL BETA DIVERSITY ARE RELATED TO HABITAT AVAILABILITY IN A HYDROLOGICALLY-MANAGED WETLAND

Abstract

While spatial and temporal turnover (beta diversity) are important ecological metacommunity attributes for understanding the relative contribution of local (niche-based) and regional (dispersal-related) controls on assemblage composition, rarely are data sufficiently resolved to fully distinguish mechanisms of compositional change in both space and time. Further, mechanisms underlying compositional change may be misunderstood if all taxa are treated equally, as opposed to addressing differences between taxa with persistent or occasional spatial and temporal occurrence patterns. Here, I determined controls on spatial beta diversity of a benthic diatom metacommunity and made spatially-explicit comparisons of temporal beta diversity across 64 sites through 6 years. I also made comparisons of beta diversity between two regions with differing hydrologic management that encourage the development of either suitable or unsuitable habitats (high or low periphyton mineral content, respectively) for benthic diatoms that are persistent in calcareous wetlands. Both environmental and spatial factors were important components of beta diversity, suggesting dispersal limitation is an important assembly mechanism for benthic diatoms. However, the relative importance of environmental factors was greatest for persistent taxa in suitable habitats. Persistent taxa had higher temporal beta diversity in unsuitable habitats than suitable ones, while

occasional taxa had the opposite result. Differences between persistent and occasional taxa in the relative importance of local and regional controls, as well as their temporal turnover in suitable and unsuitable habitats, inform hypotheses related to life history differences that could be used to further investigate assembly mechanisms of benthic diatoms.

Introduction

While human activities continue to alter ecosystem structure and function from global to local scales (Vitousek et al. 1997, Hillebrand and Matthiessen 2009), the mechanisms underlying biodiversity remain unresolved for many groups of organisms and landscapes. Reasons for this shortcoming include insufficient spatial and temporal context to capture the complexity of natural ecosystems (Hillebrand and Matthiessen 2009) and treating all taxa in a system equivalently even though their spatial and temporal occurrence patterns may differ as a result of differing biological, dispersal, and life history strategies (Magurran and Henderson 2003, Coyle et al. 2013).

Both spatial and temporal contexts are necessary to understand the mechanisms underlying biodiversity because assembly mechanisms operate at multiple spatial (e.g., local and regional) and temporal (e.g., seasonal, interannual, successional) scales. The concept of a metacommunity, a group of assemblages potentially linked by dispersal-related processes such as immigration and emigration (Leibold et al. 2004), is useful for understanding the influence of local and regional controls on biodiversity at multiple spatial scales and over time. Local controls of community assembly include niche-based, local-scale environmental processes (Hutchinson 1957), while regional controls include dispersal-limiting, broad-scale biogeographical processes (Hubbell 2001).

Spatial beta diversity, the variability of assemblage composition in space, can be used to distinguish the importance of local and regional controls on a metacommunity, which is essential for understanding how and why communities change (Borcard et al. 1992). The relative importance of local and regional controls on beta diversity may depend on spatial scale (Soininen 2007, Bramburger et al. 2008, Sokol et al. 2013a). In addition, local diversity dynamics may not represent ecosystem-scale functioning and services (Loreau et al. 2003), so it is important to characterize beta diversity using adequate spatial resolution.

In temporally heterogeneous systems (i.e., high interannual variability), the relative importance of local and regional controls on assemblage distribution may not be stationary, so a temporal component of diversity is critical for obtaining a general characterization of the metacommunity and for detecting long-term trends from this baseline. If the timescale of the dataset is too short, trends in beta diversity are probably sensitive to sampling effects, such as the interannual variability within the window of time captured by the dataset (Korhonen et al. 2010). At intermediate timescales (weeks to years), however, local colonization and extinction are effectively driven by temporal variation in environmental or dispersal patterns, especially for organisms at low trophic positions with large species pools and rapid generation times (Korhonen et al. 2010). For microorganisms, intermediate timescales can be used to compare temporal beta diversity in a spatial framework.

Important aspects of assemblage distribution may be overlooked if there is no distinction made between taxa that differ in occurrence patterns over space and time (Magurran 2007). Persistent taxa are often called core species, although most studies use definitions of this term based on patterns of incidence or abundance distributions (Magurran and Henderson 2003, Ulrich and Zalewski 2006, Dolan et al. 2009, Coyle et al. 2013), rather than Hanski's (1982) mechanistic definition (*K*-selected species with low probability of local extinction). In contrast to core species, occasional taxa have been called satellite species if they are *r*-selected species with high probability of local extinction (Hanski 1982), or fugitive species if abundances are related to availability of patches lacking superior competitors (Hutchinson 1951, Horn and MacArthur 1972). Until life histories and biotic interactions between these groups are understood, I use the terms persistent and occasional taxa to categorize species based on incidence across space and time. Persistent taxa may dominate because of biological, dispersal, or life history strategies that are advantageous for survival in a particular habitat, such as estuarine fish associated with muddy substratum or anadromous/catadromous life histories (Magurran and Henderson 2003). Occasional taxa co-occur in lower abundances and inconsistently across space and time. The spatial and temporal patterns of persistent and occasional taxa may reflect biological, dispersal, and life history differences influencing abundances within a particular habitat if the patterns are correlated with habitat availability.

The mechanisms underlying the biodiversity of microorganisms, such as benthic diatoms, remain unresolved. Microbial distributions may simply be a function of global population sizes because of large populations and small body sizes (Finlay et al. 2002). However, global dispersal of diatoms must be slow enough for regional metacommunity characteristics to develop (Telford et al. 2006). Recent studies acknowledge that both local and regional controls structure diatom assemblages (Soininen 2007; Vanormelingen et al. 2008; Soininen & Weckström 2009; Verleyen et al. 2009; Heino et al. 2010). Many of these studies were conducted in streams and lakes, while few studies have examined mechanisms structuring diatoms in wetlands. The shallow water depths in wetlands promote development of benthic, rather than planktonic, assemblages. Unlike streams or lakes with high dispersal potential by water flow or seasonal mixing, there may be strong constraints against dispersal if diatoms are dependent on the protective structure and resource-rich environment of biofilms in wetlands. With sufficient spatial and temporal context, benthic diatoms in wetlands have high potential for challenging the idea that microorganisms are not dispersal limited.

I examined the spatio-temporal turnover patterns in the benthic diatom metacommunity of the Everglades, consisting of persistent and occasional taxa, represented by 64 sites and 6 years of data. In addition to analyses of the whole study system, I examined two large basins within the Everglades with the same sample size but with differing hydrologic management that promotes the development of suitable or unsuitable habitats (high or low periphyton mineral content, respectively) for benthic diatoms. In the Everglades and other calcareous wetlands, diatoms are most abundant within the protective and resource-rich environment of periphyton with high mineral content; phosphorus-enrichment or prolonged periods of deep water, often consequences of hydrologic management, lead to dissolution of this type of periphyton (Browder et al. 1994, Gaiser et al. 2011, 2013, Lee et al. 2013, Sokol et al. 2013b). I pose the following hypotheses concerning regulation of spatio-temporal turnover of this metacommunity:

1. Spatial beta diversity will be regulated by both local (environmental) and regional (spatial) factors but environmental factors will be more important in sites with suitable habitats because species turnover will be less influenced by the ability to disperse to suitable habitats.

2. Environmental factors will be more important regulators of spatial turnover of persistent taxa because of adaptations to and dispersal limitation conferred by their preferred habitat (periphyton with high mineral content).
3. If persistent taxa have biological, dispersal, or life history strategies specific to their preferred habitat, they will be superior competitors relative to occasional taxa and have the lowest temporal beta diversity in sites where suitable habitats occur consistently over time, whereas occasional taxa will have the highest temporal beta diversity in the same sites.

Methods

Site Description

My study was carried out in the Everglades, a large wetland (about 9,000 km^2) located in south Florida, USA that encompasses several compartmentalized regions, including Water Conservation Areas (WCAs) and Everglades National Park (ENP) (Davis and Ogden 1994). Water Conservation Area 2A (2A) and WCA 3A (3A) are leveed compartments north of ENP, Shark River Slough (SRS) is the main drainage of ENP, and Taylor Slough is a smaller drainage in the southeastern corner of ENP (Appendix A). The two main basins compared in this study, SRS and 3A, have differing environmental histories and current hydrologic management that influence landscape structure and composition of the biota (Liston 2006, Wetzel et al. 2008). The Everglades has a distinct wet and dry season controlled by the subtropical climate and hydrologic management. The seasonal drying and flooding of the marsh has been preserved in most areas within SRS, but management practices in 3A have overly drained the northern portion and prolonged flooding in the southern portion (Light and Dineen 1994, David 1996).

Sampling and Processing for Diatom Assemblages

Periphyton was collected from 64 sites each year during 6 wet seasons (September to December) from 2006 to 2011 as part of the Monitoring and Assessment Program of the Comprehensive Everglades Restoration Plan (RECOVER 2004). Sites outside of SRS and 3A were included in whole-system analyses, but small sample sizes precluded region-specific analyses other than SRS and 3A (22 sites each). Generalized random-tessellation stratification was used to choose a spatially balanced set of sampling locations (Stevens and Olsen 2004). Field sampling, sample processing, and diatom identification and enumeration follow the methods described in Lee et al. 2013.

Statistical Analyses

Proportional environmental variables (aerial cover and organic content) were arcsine squareroot transformed to improve asymmetry and peakiness of the distributions (McCune and Grace 2002). All other environmental variables were log (x + c) transformed, where c is a constant representing the first percentile value (following Sokol et al. 2013a). Subsequently, all environmental variables were standardized to zero mean and unit variance. The pairwise.t.test function in R (R Development Core Team 2013) was used to compare environmental variables in SRS and 3A.

Assemblage data were reduced to 30 taxa that were present in at least one site every year. To categorize taxa as persistent or occasional, I used each taxon's mean incidence at a site over the 6 year study period; taxa with incidence >2 were categorized as persistent and the remaining taxa were categorized as occasional (i.e., occasional taxa, on average, were not observed at the same site more than once) (Appendix C). After relativization by sample totals in the three assemblage matrices, I made no further modifications because of inherent rescaling properties of the dissimilarity measure used in subsequent analyses (Jost 2007).

To define suitable habitat, I related periphyton mineral content with abundance of persistent taxa. Periphyton mineral content (the ratio of periphyton ash-free dry mass to total dry mass expressed as a percent) is naturally high in regions of the Everglades with low water depths and low peat accretion because the limestone bedrock has a strong influence on water chemistry, but hydrologic management has negatively affected mineral content by P-enrichment near canal inflows and prolonged periods of deep water in the WCAs (Gaiser et al. 2011, Harvey and McCormick 2009, Hagerthey et al. 2011). Previous investigations in the Everglades and Caribbean wetlands have provided abundant evidence of diatoms that prefer to inhabit periphyton with high mineral content (Browder et al. 1994, Slate and Stevenson 2007, Gaiser et al. 2011, La Heé and Gaiser 2012, Lee et al. 2014). I defined a mineral content threshold that corresponds to a strong positive relationship between the incidence of suitable habitat (periphyton with above-threshold mineral content) and the abundance of persistent taxa.

I performed diversity partitioning of all, persistent, and occasional taxa into alpha, beta, and gamma diversity components at the regional (SRS and 3A) and whole-study (including sites outside of SRS and 3A) levels for each year. Diversities are based on Hill numbers or species equivalents (Jost 2007). I used the order of $q = 1$, which weighs species exactly by their frequencies, does not favor common or rare species, and equals the exponential of Shannon entropy (Hill 1973, Jost 2007). The means of diversity components were averaged over time and compared using the pairwise.t.test function in R.

To examine spatial beta diversity, I used variation partitioning to determine the relative contributions of environmental and spatial factors to beta diversity following the methods of Sokol et al. (2013a). To examine temporal beta diversity, I used the d function in the vegetarian package in R to calculate beta diversity of assemblages from a single site at each time step (Charney and Record 2013). Temporal beta diversity ranged from 1 (equivalent assemblages within a time step) to 2 (distinct assemblages within a time step). Serial autocorrelation was detected using the Durbin-Watson test (following Angeler 2013) in the car package in R (Fox and Weisberg 2011). Three sites with positive autocorrelation and 1 site with negative autocorrelation were removed from further analyses. Sites with complete absence of occasional taxa were removed from further analyses. Mean temporal beta diversities of each site were mapped using ArcMap$^{\mathrm{TM}}$ 10.0 (ESRI 2010). I used R 3.0.1 for all statistical analyses unless otherwise specified.

Results

Suitable Habitat Availability in SRS and 3A

I defined suitable habitat for persistent taxa as periphyton with >40% mineral content (Figure 4.1a) because at this threshold, the mean abundance of persistent taxa had the strongest correlation ($R^2 = 0.73$) with suitable habitat availability (Figure 4.1b). Suitable habitats occurred more consistently in SRS than 3A (Figure 4.1b). Greater suitable habitat availability in SRS was related to >2 times lower water depth, hydroperiod, and P levels than in 3A (Figure B1 in Appendix B). Mean periphyton mineral content was >3 times greater, and periphyton biovolume, dry weight, ash-free dry mass, and chlorophyll *a* mass were >2 times greater in SRS than 3A.

Diversity Partitioning

Diversity of the reduced 30-species metacommunity was about 7 taxa at the whole-study scale (mean gamma), 5 taxa at the local assemblage scale (mean alpha), and 2 distinct assemblages (mean beta) within the metacommunity (Table 4.1). Regional diversity (mean gamma) of occasional taxa was greater than persistent taxa by up to 4 taxa at the whole-study scale and within SRS ($p<0.01$), but no more than 2 taxa in 3A. Local assemblage diversity (mean alpha) of persistent taxa was greater than occasional taxa by about 2 taxa at the whole-study scale and within regions ($p<0.001$). The number of distinct assemblages (mean beta) of occasional taxa was about 3 times greater than persistent taxa at the whole-study scale and within regions ($p<0.001$). There were about 4 distinct assemblages of occasional taxa and only 1 assemblage of persistent taxa.

Figure 4.1. (a) Relationship between mean mineral content and mean abundance of persistent taxa in SRS, 3A, and all sites. Dashed line indicates suitable habitat threshold. (b) Availability of suitable habitat (>40% inorganic content) in SRS and 3A and abundance of persistent taxa.

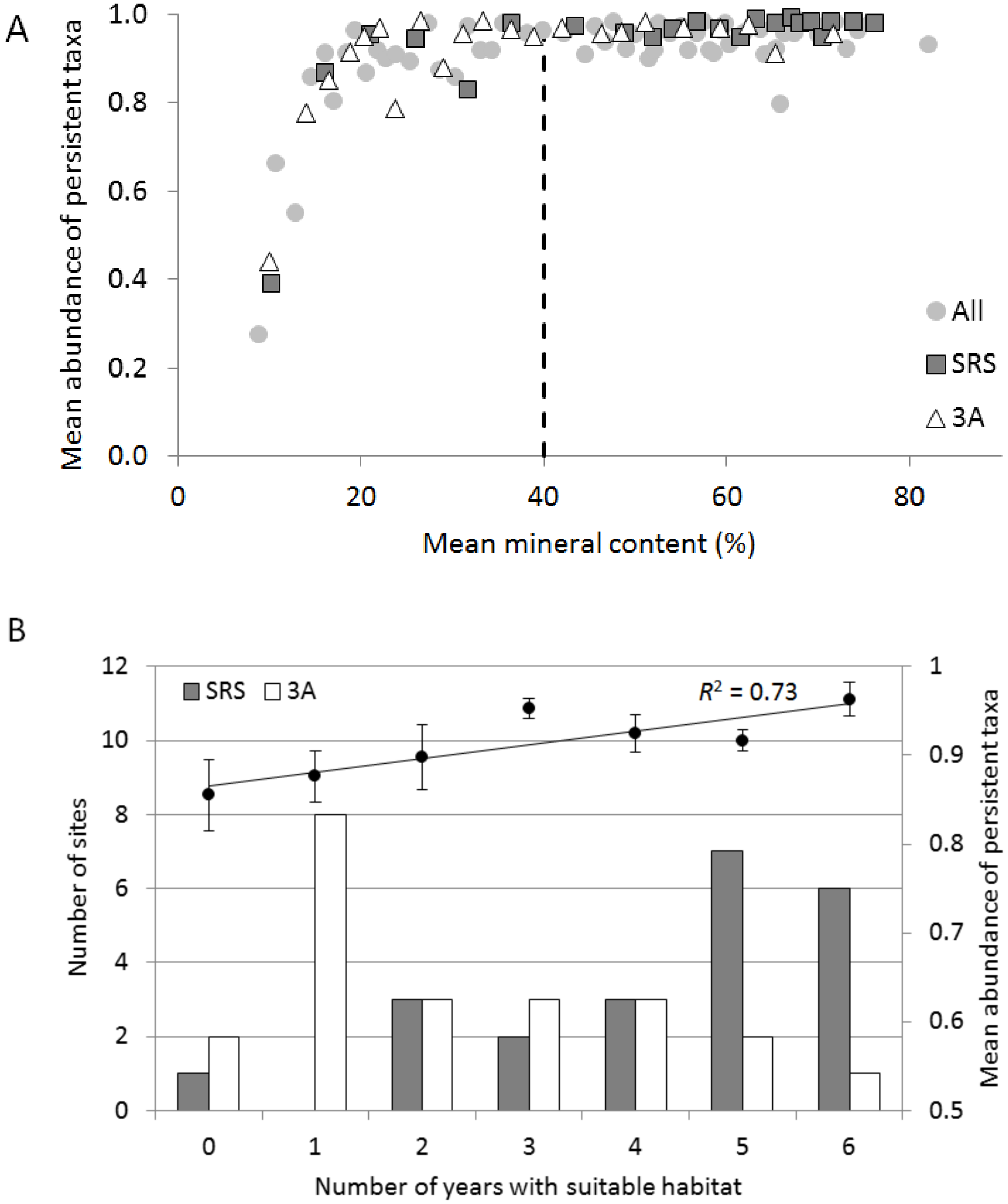


Table 4.1. Results of diversity partitioning performed for each year from 2006-2011 using N number of samples and order of $q = 1$ (species weighed by their frequencies without bias towards common or rare taxa). Mean values of each diversity partition are averages over 6 years ± 1 standard error: alpha (local diversity), beta (number of distinct assemblages over space), and gamma (regional diversity).

Region and taxon category	N	Mean alpha	Mean beta	Mean gamma
All	64	4.66 ± 0.12	1.57 ± 0.07	7.36 ± 0.49
Persistent	64	4.21 ± 0.11	1.45 ± 0.05	6.13 ± 0.36
Occasional	64	1.82 ± 0.05	5.29 ± 0.39	9.55 ± 0.55
SRS	22	4.61 ± 0.18	1.28 ± 0.02	5.91 ± 0.28
SRS Persistent	22	4.31 ± 0.17	1.24 ± 0.02	5.36 ± 0.25
SRS Occasional	22	1.82 ± 0.05	4.26 ± 0.28	7.79 ± 0.65
3A	22	4.48 ± 0.1	1.63 ± 0.08	7.32 ± 0.48
3A Persistent	22	4.08 ± 0.07	1.53 ± 0.07	6.27 ± 0.36
3A Occasional	22	1.82 ± 0.11	4.14 ± 0.68	7.23 ± 0.79

Spatial Beta Diversity

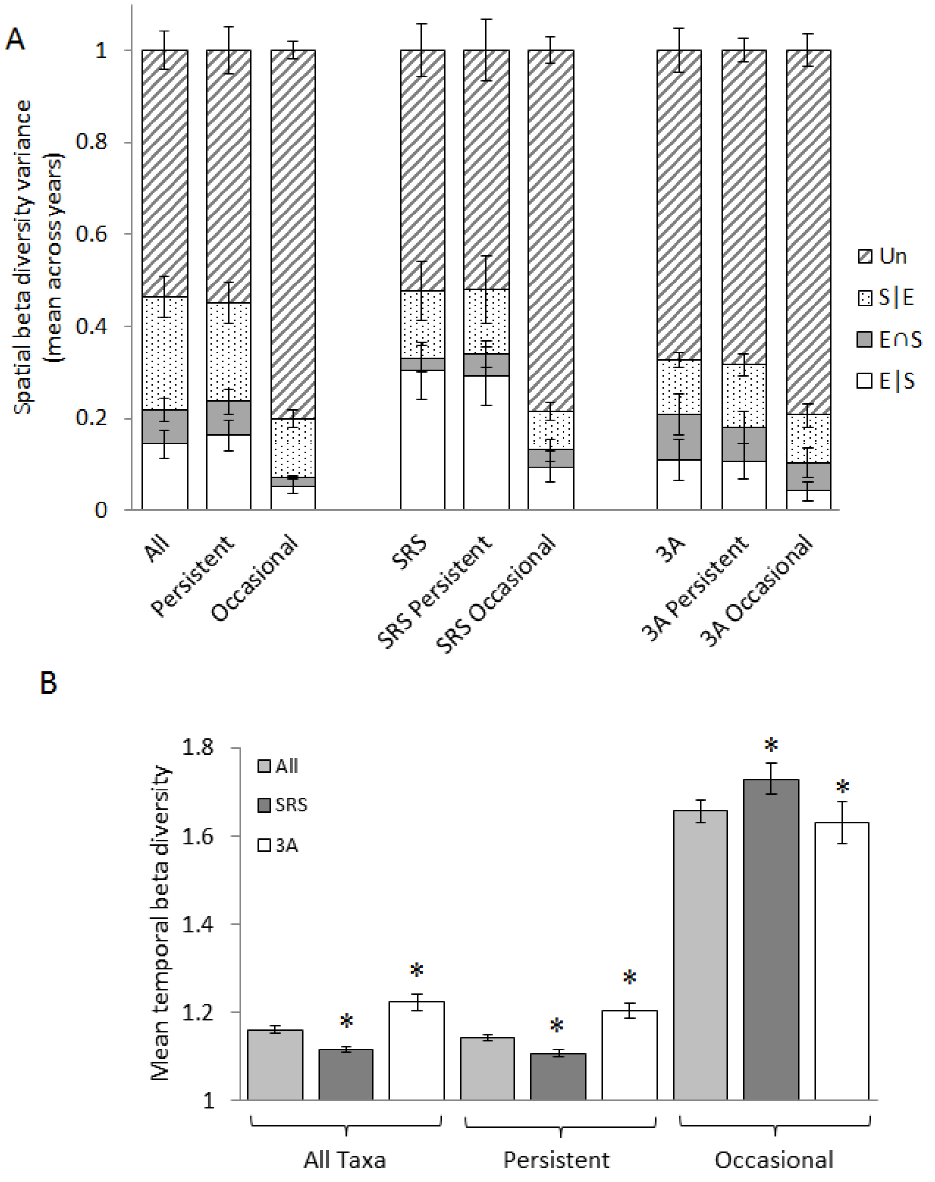
At the whole-study scale, both environmental and spatial factors were important contributors to the beta diversity of all taxa, but environmental factors explained more variation of persistent taxa than occasional taxa (Figure 4.2a, see Appendix D for year-specific results). Both hydrology and mineral content or hydrology and periphyton mass best explained variation of persistent taxa, but single environmental variables often best explained variation of occasional taxa. Generally, occasional taxa had broader-scale spatial filtering than persistent taxa. The unknown component of beta diversity was largest (about 80%) for occasional taxa.

At the regional scale, SRS and 3A did not have distinct assemblages (mean beta diversity = 1.05). Within regions, however, environmental factors better explained variation in SRS than 3A. In SRS, mineral content or periphyton mass differences best explained variation of persistent taxa, but either mineral content or hydrology best explained variation of occasional taxa. Generally, there was finer-scale spatial filtering in SRS than 3A. Spatial and spatially structured environmental factors explained the most variation in 3A. Mineral content usually best explained variation in 3A. Unexplained variation was lowest (52%) for SRS persistent taxa.

Temporal Beta Diversity

Mean temporal beta diversity (averages across 5 time steps from 2006-2011) ranged from 1.04 (nearly identical assemblages) to 2.0 (distinct assemblages). At the whole-study scale, persistent taxa had lower turnover than occasional taxa (Figure 4.2b).

Figure 4.2. (a) Spatial beta diversity of Everglades diatoms (all, persistent, and occasional taxa). Beta diversities were partitioned into four components: pure environment (E|S), spatially structured environment (E∩S), pure space (S|E), and unexplained (Un). Error bars represent 1 standard error. Number of sites = 64. (b) Mean temporal beta diversity of Everglades diatoms (all, persistent, and occasional taxa). Temporal beta diversities were calculated using assemblage dissimilarities between time steps (5 time steps from 2006-2011) at each site. Values range from 1 (identical assemblages) to 2 (distinct assemblages). Error bars represent standard errors. Asterisks represent significant pairwise t-statistics ($p<0.05$) between SRS and 3A. Number of sites = 60 and 22 at the whole-study scale and in both SRS and 3A, respectively.



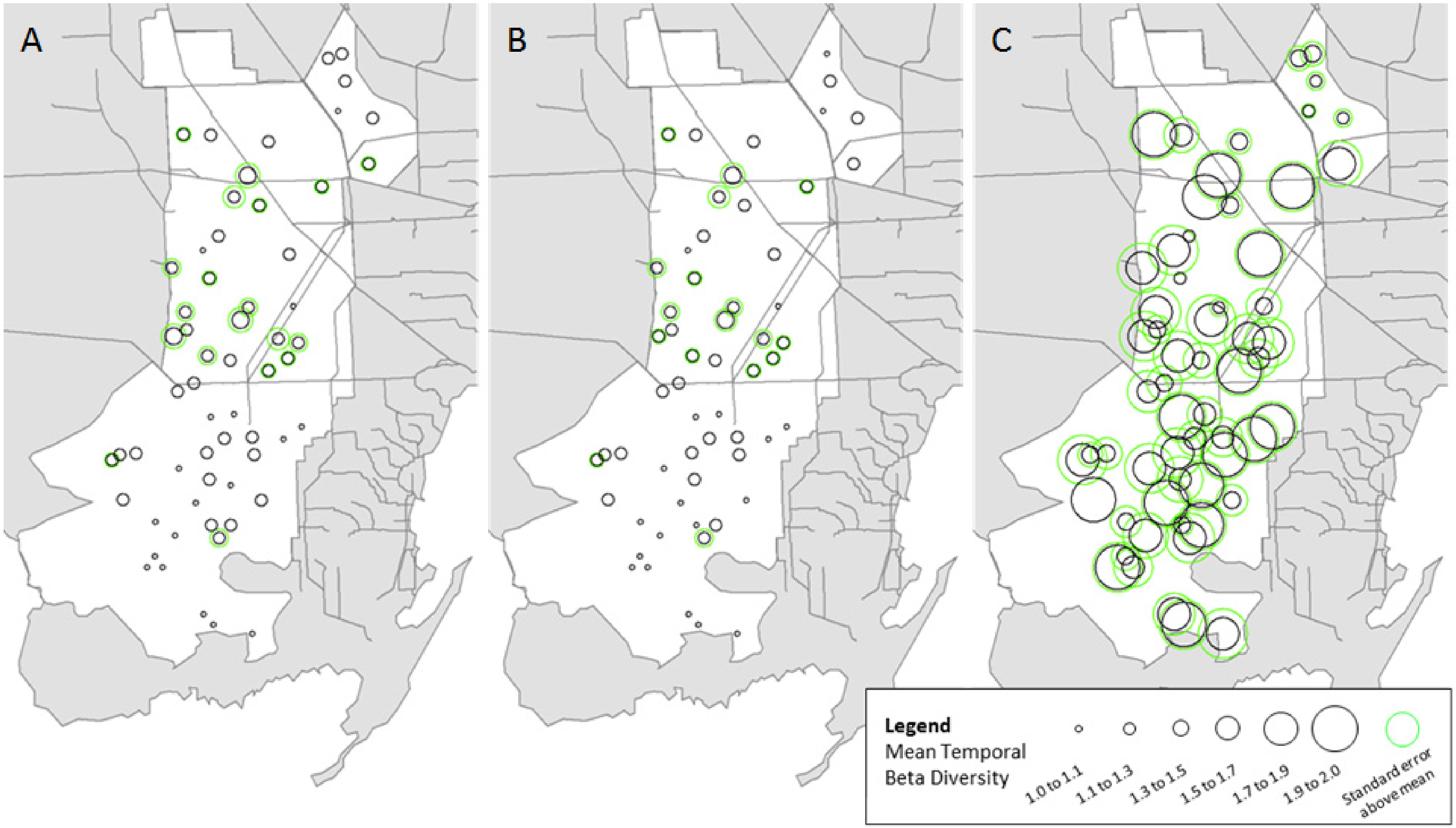
At the regional scale, persistent taxa had higher turnover in 3A, while occasional taxa had higher turnover in SRS (Figure 4.2b). For all and persistent taxa, sites with the highest turnover were in southern 3A, while the lowest turnover was in southern SRS and in Taylor Slough (Figure 4.3a-b). For occasional taxa, the lowest turnover was in southern 3A and in 2A, while the highest turnover was in SRS and northern 3A (Figure 4.3c). Refer to Appendix A for locations of Taylor Slough and 2A.

Discussion

Spatial Beta Diversity

Spatial beta diversity showed strong control of the metacommunity by both local environmental factors and broad-scale spatial factors. The importance of spatial factors indicates dispersal limitation is an important assembly mechanism of benthic diatom despite their small size and large populations. Spatial diversity patterns in Everglades periphyton have been observed through region-specific P optima (Gaiser et al. 2006), characteristic periphyton mat types and algal assemblages in different parts of the Everglades (Browder et al. 1994, Slate and Stevenson 2007, Gaiser et al. 2011), and boundary effects in response to hydrologic restoration (Gaiser et al. 2013). Spatially structured environmental factors explained more variation across species components in 3A than SRS because the natural north to south decrease in ground elevation of the Everglades, combined with hydrologic impediments at the southern end of 3A, produce an increasing surface water depth gradient from north to south (Light and Dineen 1994).

Figure 4.3. Mean temporal beta diversity of Everglades diatom assemblage types: (a) all taxa, (b) persistent taxa, and (c) occasional taxa. Beta diversities were averaged across all time steps (5 time steps from 2006-2011) at each site. Green circles represent 1 standard error above the mean. Absence of standard errors indicates near zero values.



Unexplained variation, which was highest for occasional taxa, could result from stochastic processes such as founder effects, or complex intra- or interspecific interactions within the periphyton mat. Söderström (1989) concluded that core bryophyte species have higher local growth rate and dispersal ability because they reproduce both sexually and asexually, unlike satellite species that reproduce sexually. While diatoms undergo both sexual and asexual reproduction, asexual reproduction is more common and sexual reproduction has been related to density-dependent nutrient limitation in later stages of periphyton development (Stevenson 1990). Persistent taxa may undergo more frequent sexual reproduction in their preferred habitat (periphyton with high mineral content and low P), while occasional taxa reproduce asexually and disperse to less nutrient-limited habitats. In contrast to occasional taxa, evidence of sexual reproduction was frequently observed for persistent taxa such as *Mastogloia calcarea* (Gaiser et al. 2010, Lee et al. 2014) and *Encyonema evergladianum* (Lee pers. obs.). Thus, density dependence of reproduction is an example of intraspecific interactions within periphyton that may contribute to unexplained variation.

Temporal Beta Diversity

With a moderately long and spatially-resolved dataset, I showed regional differences in the turnover of persistent and occasional taxa were related to differences in suitable habitat availability. Persistent taxa, which I hypothesized would have lower turnover in sites with suitable habitats, had the lowest turnover in southern SRS and Taylor Slough, and the highest turnover in southern 3A. Assessment of Taylor Slough in 2006 found acceptable ranges of P and no hydrologic modifications that would affect periphyton composition (Gaiser 2009). In 3A, however, prolonged flooding in the southern portion discourages development of periphyton with high mineral content (Gaiser et al. 2011).

Occasional taxa, which I hypothesized would have the highest turnover in sites where persistent taxa have the lowest turnover, had the highest turnover in SRS, while the lowest turnover was in southern 3A and in 2A. My finding that persistent taxa have lower turnover (i.e., more stable assemblages) in SRS is consistent with less stable populations of occasional taxa in the same sites if persistent taxa have adaptations that make them superior competitors in their preferred habitat, which occur with greater regularity in sites within SRS than 3A. Low turnover of occasional taxa in 2A is consistent with the region's current and historical P-enrichment by inflows from agricultural areas that have altered periphyton to have consistently lower mineral content than what is suitable for persistent taxa (McCormick et al. 1996, Slate and Stevenson 2000).

Persistent and Occasional Taxa

Although I objectively divided the assemblage into persistent and occasional taxa using spatial and temporal incidence, the differences in spatial and temporal beta diversity between these two species components were ecologically meaningful. My hypothesis that persistent taxa are biologically dependent on the availability of suitable habitat was supported by greater variation explained by environmental factors and lower turnover in SRS, where shorter hydroperiods and lower P are related to greater suitable habitat availability (refer to Fig. B1 in Appendix B). Lee et al. (2013) showed that the integrity of the periphyton mat is a critical biological factor associated with Everglades diatom abundance. The distinction between persistent and occasional taxa may reveal finer-scale mechanisms controlling spatial and temporal distributions within regions with differing environmental histories and management.

The persistent inhabitants of inorganic (calcareous) periphyton mats may be highly dispersal limited. Calcareous periphyton is abundant in karst wetlands, especially in the Everglades and the Caribbean (Rejmánková and Komárková 2000, Novelo et al. 2007, Gaiser et al. 2011, La Heé and Gaiser 2012), but also in temperate fens and alvars (Gaiser, unpublished data). Calcareous periphyton includes diatoms that can directly contribute to mat structure by exuding extracellular polymeric substances (EPS), like *Mastogloia calcarea* (Gaiser et al. 2010, Lee et al. 2014), or are dependent on cyanobacterial EPS as substrates for colonization and protection from desiccation and excess UV (Rejmánková and Komárková 2000, Elasri and Miller 1999, Sirová et al. 2006, Thomas et al. 2006), as well as the nitrogen fixed by cyanobacteria (Paerl et al. 2000). In sites with abundant calcareous periphyton, environmental factors explain relatively more variation than spatial factors because dispersal from suitable habitat is not necessary. Given their strong dependence on the periphyton mat, persistent taxa are unlikely to have strong dispersal ability. In sites where calcareous periphyton is not abundant, dispersal limitation of persistent taxa may explain more turnover and relatively greater control by spatial factors.

Taxa encountered only occasionally in the Everglades may be widely distributed elsewhere, but may not have adaptations to live in calcareous periphyton. Taxa that I defined as occasional, such as *Nitzschia amphibia* and *N. palea*, are not abundant in calcareous periphyton because they have high P optima (Gaiser et al. 2006). Occasional taxa had the greatest amount of unexplained variation, indicating regulation by mechanisms other than local environmental control or dispersal limitation. Higher abundance and lower turnover of occasional taxa were observed in regions with P-enrichment, such as 2A, or deep water, such as southern 3A, where calcareous periphyton is not abundant. Occasional taxa may prefer sites with less calcareous periphyton because of a decrease in the dominance of persistent taxa. If so, occasional taxa in this metacommunity may play the role of fugitives that opportunistically colonize patches lacking superior competitors (Hutchinson 1951, Horn and MacArthur 1972). Benthic assemblages are likely to support complex interspecific interactions because they have complex structures and temporally-dynamic successional patterns (Stevenson 1990, Passy 2002, 2007).

Differences between persistent and occasional taxa in the relative importance of local and regional controls, as well as their temporal turnover in suitable and unsuitable habitats, can inform hypotheses related to life history strategies. Phytoplankton studies have considered diatoms as *r*-selected organisms because blooms occur with high light and nutrients during mixing events (Kilham and Hecky 1988), but this generalization does not account for the diverse morphology and life histories of diatoms. Reynolds (1988) proposed the CSR (colonial, stress tolerant, or ruderal) classification for phytoplankton based on morphology and function. Recently, Law et al. (2014) found the best method to explain variation in stream phytobenthic assemblages was a combination of Reynold's (1988) CSR classification and life-forms (e.g., motile or stalked). Law et al. (2014) observed that R-type species were the most competitive in the benthos because their high surface area to volume ratio (s:v) allows greater nutrient and light assimilation and their motility allows movement out of shaded areas. Persistent taxa in my study included highly motile species (e.g., *Mastogloia, Nitzschia,* and *Navicula* spp.) that can move within periphyton to find optimal microhabitats and mates, unlike the occasional taxa in my study with limited or no motility (e.g., *Achnanthidium, Eunotia,* and *Fragilaria* spp.). Law et al. (2014) also found C-type species, colonizers that track high light and nutrient levels (Reynolds 1988), were present in sites with disturbance by high flow velocity or grazers and appeared to colonize newly opened niches, similar to occasional taxa in my study. Both R and C-type species exhibit high growth rates because of their high s:v (Reynolds 1988), but R-type species may outcompete C-type species in benthic assemblages, leading to R-type species that are persistent and C-type species that are occasional. If so, R-type species should be under mostly local controls (i.e., environmental gradients) and have low turnover in their preferred habitat, while C-type species are controlled by competition and disturbances that open niches previously occupied by R-type species and have high turnover.

Conclusions

Spatial and temporal beta diversity are important attributes of ecological metacommunities for understanding the mechanisms of biodiversity, which requires adequate spatial and temporal resolution. Additionally, distinguishing persistent and occasional taxa in a metacommunity can aid detection of finer-scale patterns. I found both environmental and spatial factors were important components of beta diversity of benthic diatoms, which is not consistent with the idea of global distribution of microorganisms. I found local environmental control was greatest in sites with environmental conditions that encourage development of suitable habitat for persistent taxa. My site-specific comparisons of temporal beta diversity showed greater overall turnover in hydrologically-managed localities. From the strong relationship between suitable habitat availability and the spatial and temporal turnover of persistent taxa, I can infer that persistent taxa have biological, dispersal, and life history strategies that are advantageous in their preferred habitats and are different from those of occasional taxa.

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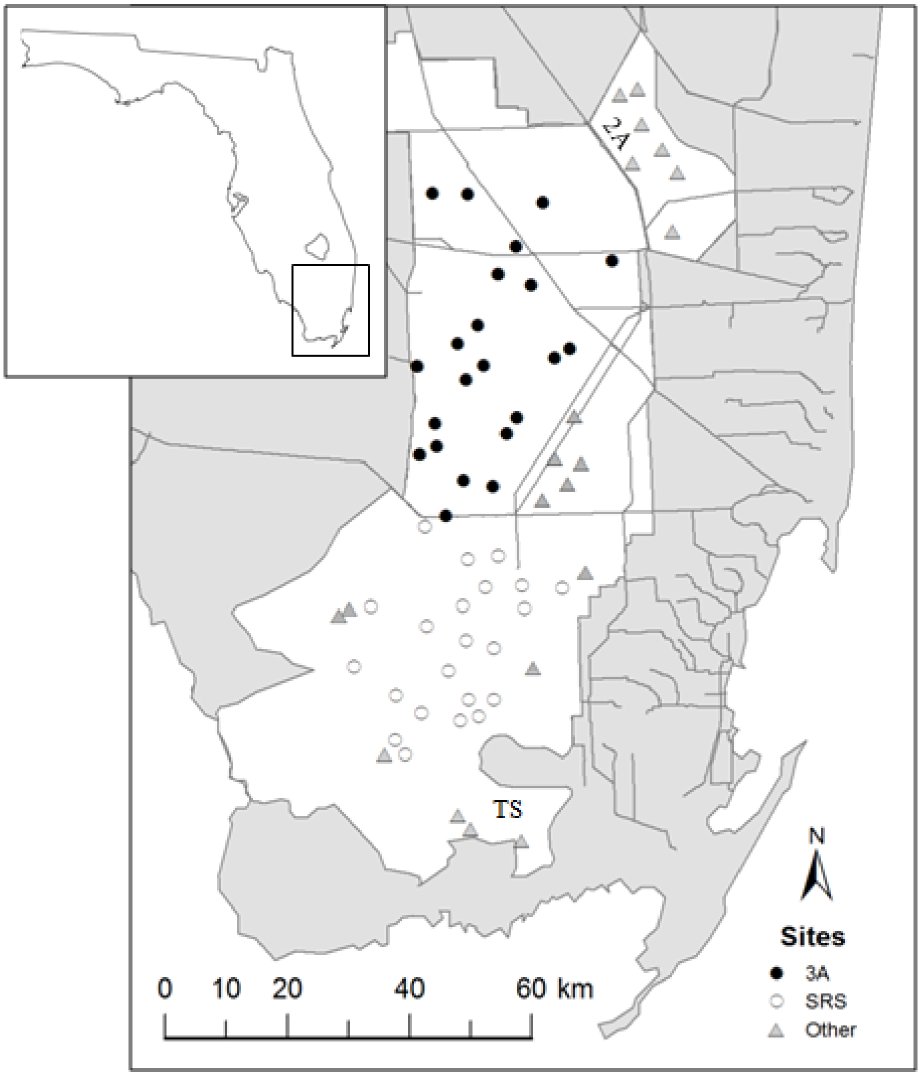
Appendices to Chapter IV

Appendix A

Figure A1. Map of sampling sites showing inset of Florida, USA. Lines represent canals. All sites were included in whole-study scale analyses but not in comparisons between SRS and 3A. Also shown are locations of Water Conservation Area 2A (2A) and Taylor Slough (TS).

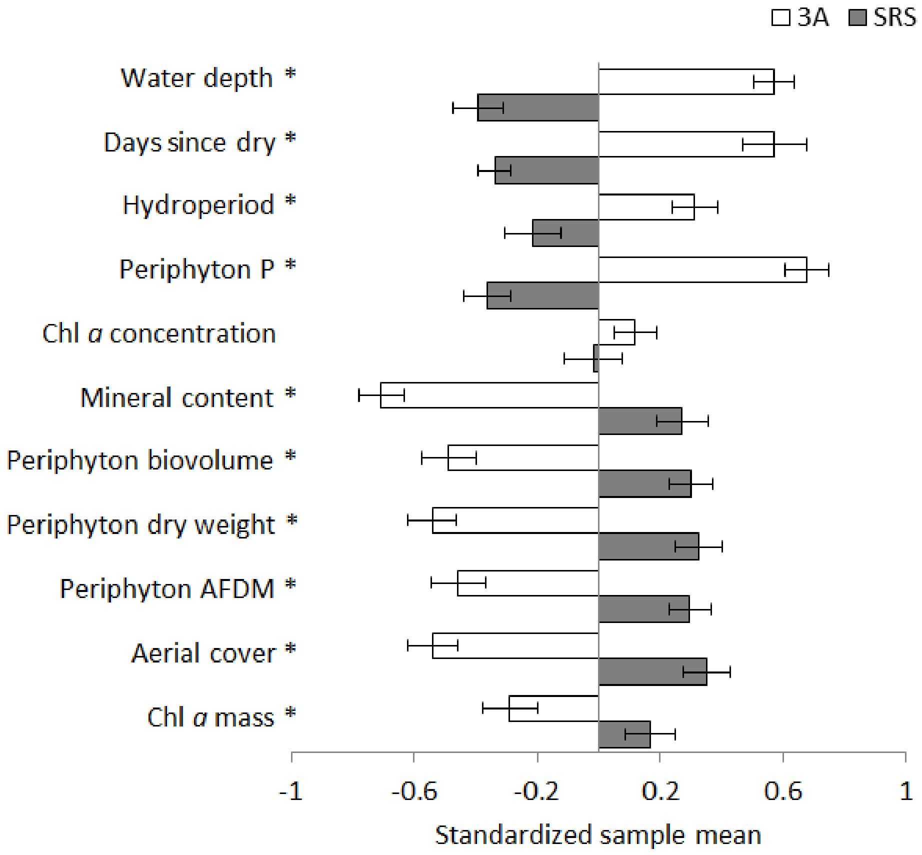


Appendix B

Table B1. Summary of environmental characteristics in the whole study area (All), Shark River Slough (SRS), and Water Conservation area 3A (3A). Means are averages across all sites and all years. Interannual standard deviation is the spread across sites of the within-site means across years. Inter-site standard deviation is the spread across years of the within-year means across sites. Number of sites in the whole study area, SRS, and 3A = 64, 22, and 22, respectively. Number of years = 6.

	Mean			Interannual standard deviation			Inter-site standard deviation		
Region	All	SRS	3A	All	SRS	3A	All	SRS	3A
Water depth (cm)	48	38	62	18	10	17	9	11	12
Days since dry (days)	691	265	1404	1010	258	1397	193	115	350
Hydroperiod (days)	238	221	262	55	53	49	33	41	29
Periphyton P (µg g^{-1})	170	128	249	89	56	85	37	47	50
Chl a concentration (µg g^{-1})	3420	4564	1163	4021	4141	1082	7849	10839	2016
Inorganic content (%)	48	53	34	16	15	13	3	4	5
Periphyton biovolume (ml m^{-2})	3198	4158	1458	2231	1974	1164	580	894	361
Aerial cover (%)	59	72	38	24	16	17	8	12	11
Chl a mass (µg g^{-1})	10203	12734	5147	6469	5698	4185	5497	7437	2933
Periphyton dry weight (g m^{-2})	151	211	33	179	165	34	72	114	13
Periphyton AFDM (g m^{-2})	52	70	17	48	40	14	24	38	6

Figure B1. Comparison of environmental conditions and periphyton mass in 3A and SRS. Interannual sample means are within-site means across years that were averaged across sites within each region. Environmental data were standardized across the whole study system, including sites outside of 3A and SRS. Error bars represent 1 standard error from the mean. Asterisks indicate variables with significant pairwise t-statistics ($p<0.001$) in comparisons between 3A and SRS.



Appendix C

Table C1. Names of taxa and abundance information: P is persistence (mean incidence at a site over 6 years), I is incidence (proportion of samples present out of 384 total samples), and A is abundance (mean relative abundance in a sample). Taxa 1-15 were categorized as persistent and taxa 16-30 were categorized as occasional.

	Taxon	P	I	A
1	*Encyonema evergladianum* Krammer 1997	5.94	0.99	0.276
2	*Mastogloia calcarea* Lee, Gaiser, Van de Vijver, Edlund & Spaulding 2014	5.88	0.98	0.339
3	*Brachysira microcephala* (Grunow) P. Compère 1986	5.81	0.97	0.098
4	*Fragilaria synegrotesca* Lange-Bert. 1993	5.80	0.97	0.091
5	*Encyonema mesianum* (Cholnoky) D.G. Mann in Round, R.M. Crawford & D.G. Mann 1990	5.25	0.88	0.044
6	*Nitzschia palea* var. *debilis* (Kütz.) Grunow in Cleve & Grunow	5.19	0.86	0.039
7	*Nitzschia serpentiraphe* Lange-Bert. 1993	4.56	0.76	0.035
8	*Gomphonema intricatum* var. *vibrio* Ehrenb. *sensu* Fricke 1902	4.22	0.70	0.015
9	*Navicula cryptotenella* Lange-Bert. in Krammer & Lange-Bert. 1985	3.98	0.66	0.023
10	*Diploneis parma* Cleve 1891	3.75	0.63	0.009
11	*Encyonopsis microcephala* (Grunow) Krammer 1997	3.31	0.55	0.031
12	*Stephanocyclus meneghenia*na (Kütz.) Skabitschevsky 1975	3.11	0.52	0.006
13	*Navicula radiosa* Kütz. 1844	2.63	0.44	0.008
14	*Kobayasiella* cf. *parasubtilissima* (H. Kobayasi & T. Nagumo) Lange-Bert.	2.52	0.42	0.008
15	*Diploneis oblongella* (Naegeli in Kütz.) Cleve-Euler in Cleve-Euler & Osvald	2.39	0.40	0.006
16	*Encyonema silesiacum* var. *elegans* Krammer 1997	1.73	0.29	0.065
17	*Achnanthidium minutissimum* var. *gracillima* (Meister) Lange-Bert. 1989	1.55	0.26	0.019
18	*Nitzschia amphibia* Grunow 1862	1.47	0.24	0.020
19	*Nitzschia palea* (Kütz.) W. Sm. 1856	1.39	0.23	0.018
20	*Sellaphora laevissima* (Kütz.) D.G. Mann 1989	1.39	0.23	0.005

Table C1. Continued.

	Taxon	P	I	A
21	*Encyonema* sp. 1	1.22	0.20	0.014
22	*Fragilaria nanana* Lange-Bert. in Krammer & Lange-Bert. 1991	1.03	0.17	0.009
23	*Amphora sulcata* (Bréb.) Cleve 1895	0.92	0.15	0.052
24	*Eunotia flexuosa* (Bréb. in Kütz.) Kütz. 1849	0.91	0.15	0.012
25	*Gomphonema* cf. *vibrioides* Reichardt & Lange-Bert. 1991	0.84	0.14	0.010
26	*Eunotia naegelii* Migula 1907	0.69	0.11	0.009
27	*Pinnularia microstauron* (Ehrenb.) Cleve 1891	0.61	0.10	0.012
28	*Frustulia crassinervia* (Bréb.) Lange-Bert. *et* Krammer in Lange-Bert. & Metzeltin 1996	0.25	0.04	0.004
29	*Eunotia monodon* Ehrenb. 1843	0.20	0.03	0.004
30	*Rhopalodia gibba* (Ehrenb.) O. Müller 1895	0.16	0.03	0.005

Appendix D

Table D1. Results of spatial beta diversity variance partitioning performed for each year from 2006-2011 including number of sites (N), maximum and minimum distances between sites, and variance partitions of spatial beta diversity: pure environment (E|S), spatially structured environment (E∩S), pure space (S|E), and unexplained. Spatial (PCNM) and environmental variables list the spatial filters or variables explaining the most variance in assemblage dissimilarities across space. PCNM1 represents the broadest spatial filters and each successive PCNM represents finer-scale filtering. The E|S and S|E *p* values show significance of pure environment and pure space components of beta diversity. Note: components of spatial beta diversity with negative values indicate non-linear relationships or interactions that are difficult to interpret, but are negligible when values are near zero.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
All	N	64	64	64	64	64	64
	$\text{Distance}_{\text{max}}$ (km)	124.38	124.73	123.94	124.16	124.33	124.50
	$\text{Distance}_{\text{min}}$ (km)	1.97	1.74	1.93	1.30	2.19	1.48
	E|S	0.13	0.21	0.07	0.26	0.07	0.11
	E∩S	0.03	0.02	0.03	0.08	0.12	0.17
	S|E	0.28	0.22	0.23	0.05	0.35	0.34
	Unexplained	0.56	0.54	0.67	0.60	0.45	0.39
	Environmental variables	Chl a concentration + Hydroperiod	Periphyton biovolume + Hydroperiod	Inorganic content	Periphyton P + Hydroperiod	Inorganic content + Chl a mass	Periphyton dry weight + Days since dry + Periphyton biovolume

Table D1. Continued.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
All	Spatial variables	PCNM5 + PCNM3 + PCNM6 + PCNM13 + PCNM26	PCNM5 + PCNM3 + PCNM12 + PCNM22	PCNM12 + PCNM1 + PCNM5 + PCNM7	PCNM1 + PCNM14	PCNM5 + PCNM9 + PCNM3 + PCNM1 + PCNM13 + PCNM11	PCNM1 + PCNM4 + PCNM3 + PCNM5 + PCNM14
	E|S *p* value	0.005	0.005	0.005	0.005	0.017	0.005
	S|E *p* value	0.005	0.005	0.005	0.048	0.005	0.005
Persistent	N	64	64	64	64	64	64
	Distance$_{\text{max}}$ (km)	124.38	124.73	123.94	124.16	124.33	124.50
	Distance$_{\text{min}}$ (km)	1.97	1.74	1.93	1.30	2.19	1.48
	E|S	0.18	0.23	0.08	0.28	0.12	0.09
	E∩S	0.01	0.01	0.03	0.09	0.14	0.17
	S|E	0.22	0.19	0.15	0.05	0.32	0.35
	Unexplained	0.58	0.57	0.75	0.58	0.43	0.39
	Environmental variables	Chl a concentration + Hydroperiod	Periphyton dry weight + Hydroperiod	Inorganic content	Periphyton P + Hydroperiod	Inorganic content + Hydroperiod + Chl a mass	Periphyton dry weight + Days since dry

Table D1. Continued.

Region and taxon	Year	2006	2007	2008	2009	2010	2011

category							
Persistent	Spatial variables	PCNM6 + PCNM13 + PCNM5 + PCNM26	PCNM5 + PCNM12 + PCNM22	PCNM12 + PCNM1	PCNM1 + PCNM14	PCNM5 + PCNM9 + PCNM13 + PCNM3 + PCNM1 + PCNM7	PCNM1 + PCNM4 + PCNM3 + PCNM5 + PCNM14
	E|S *p* value	0.005	0.005	0.015	0.005	0.013	0.005
	S|E *p* value	0.005	0.005	0.010	0.059	0.005	0.005
Occasional	N	60	50	61	55	60	57
	$\text{Distance}_{\text{max}}$ (km)	124.38	124.73	123.94	121.18	124.33	124.50
	$\text{Distance}_{\text{min}}$ (km)	1.97	2.69	1.93	1.30	2.19	1.48
	E|S	0.01	0.01	0.04	0.12	0.05	0.08
	E∩S	0.02	0.02	0.02	0.02	0.01	0.03
	S|E	0.16	0.08	0.17	0.05	0.16	0.14
	Unexplained	0.81	0.89	0.77	0.80	0.79	0.75
	Environmental variables	Water depth	Days since dry	Water depth	Periphyton P + Chl a concentration + Hydroperiod	Periphyton biovolume	Chl a concentration

Table D1. Continued.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
Occasional	Spatial	PCNM2 +	PCNM3 +	PCNM5 +	PCNM4 +	PCNM3 +	PCNM3 +

	variables	PCNM4 + PCNM1 + PCNM9	PCNM1	PCNM4 + PCNM9 + PCNM11 + PCNM1	PCNM24	PCNM16 + PCNM32	PCNM1 + PCNM7
	E|S *p* value	0.160	0.150	0.005	0.005	0.005	0.005
	S|E *p* value	0.005	0.005	0.005	0.005	0.005	0.005
SRS	N	22	22	22	22	22	22
	$\text{Distance}_{\text{max}}$ (km)	37.44	37.13	37.74	37.00	37.22	36.80
	$\text{Distance}_{\text{min}}$ (km)	2.86	2.88	2.88	2.44	2.58	2.87
	E|S	0.17	0.56	0.27	0.18	0.24	0.40
	E∩S	-0.05	0.07	0.06	0.13	-0.03	-0.02
	S|E	0.42	0.01	0.11	0.00	0.11	0.22
	Unexplained	0.46	0.36	0.56	0.69	0.68	0.40
	Environmental variables	Chl a concentration	Periphyton biovolume	Inorganic content	Chl a concentration	Inorganic content	Chl a mass + Aerial cover
	Spatial variables	PCNM14	PCNM1	PCNM12	PCNM5	PCNM9	PCNM2
	E|S *p* value	0.010	0.005	0.005	0.010	0.015	0.005
	S|E *p* value	0.015	0.440	0.054	0.670	0.051	0.005

Table D1. Continued.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
SRS Persistent	N	22	22	22	22	22	22
	$\text{Distance}_{\text{max}}$	37.44	37.13	37.74	37.00	37.22	36.80

	(km)						
	$\text{Distance}_{\text{min}}$ (km)	2.86	2.88	2.88	2.44	2.58	2.87
	E|S	0.19	0.57	0.27	0.18	0.16	0.37
	E∩S	-0.05	0.07	0.07	0.14	0.09	-0.02
	S|E	0.44	0.01	0.12	0.01	0.00	0.26
	Unexplained	0.42	0.34	0.54	0.68	0.75	0.39
	Environmental variables	Chl a concentration	Periphyton biovolume	Inorganic content	Chl a concentration	Inorganic content	Chl a mass + Aerial cover
	Spatial variables	PCNM14	PCNM1	PCNM12	PCNM5	PCNM10	PCNM2
	E|S *p* value	0.015	0.005	0.005	0.010	0.036	0.010
	S|E *p* value	0.010	0.640	0.067	0.660	0.540	0.010
SRS Occasional	N	18	17	19	18	20	18
	$\text{Distance}_{\text{max}}$ (km)	37.44	37.13	37.74	37.00	37.22	36.80
	$\text{Distance}_{\text{min}}$ (km)	2.86	2.88	2.97	2.44	2.58	2.87
	E|S	0.04	0.08	0.06	0.13	0.01	0.24

Table D1. Continued.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
SRS Occasional	E∩S	0.12	-0.02	-0.02	-0.01	0.10	0.04
	S|E	0.12	0.12	0.13	0.07	0.02	0.05
	Unexplained	0.73	0.81	0.83	0.81	0.87	0.67
	Environmental	Chl a	Water depth	Chl a	Chl a	Periphyton	Periphyton P

	variables	concentration		concentration	concentration	AFDM	+ Hydroperiod
	Spatial variables	PCNM5 + PCNM10	PCNM2	PCNM3	PCNM9	PCNM12	PCNM6
	E|S *p* value	0.170	0.090	0.170	0.005	0.360	0.005
	S|E *p* value	0.066	0.023	0.027	0.037	0.320	0.100
3A	N	22	22	22	22	22	22
	Distance_{max} (km)	53.60	53.30	53.57	53.45	53.26	53.73
	Distance_{min} (km)	2.94	3.17	3.10	2.97	2.97	3.12
	E|S	0.06	0.14	-0.02	0.29	0.04	0.16
	E∩S	0.05	0.02	0.12	0.01	0.30	0.11
	S|E	0.07	0.12	0.14	0.11	0.17	0.08
	Unexplained	0.83	0.72	0.76	0.59	0.49	0.65
	Environmental variables	Chl a concentration	Chl a concentration	Inorganic content	Inorganic content + Periphyton biovolume	Inorganic content	Inorganic content + Water depth

Table D1. Continued.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
3A	Spatial variables	PCNM1	PCNM4	PCNM1	PCNM4	PCNM1	PCNM1
	E|S *p* value	0.130	0.023	0.940	0.005	0.190	0.030
	S|E *p* value	0.200	0.025	0.026	0.033	0.013	0.066
3A Persistent	N	22	22	22	22	22	22
	Distance_{max}	53.60	53.30	53.57	53.45	53.26	53.73

	(km)						
	$\text{Distance}_{\text{min}}$ (km)	2.94	3.17	3.10	2.97	2.97	3.12
	E|S	0.10	0.14	-0.02	0.22	0.01	0.18
	E∩S	0.00	0.02	0.11	0.00	0.22	0.10
	S|E	0.17	0.13	0.16	0.13	0.20	0.03
	Unexplained	0.72	0.72	0.74	0.65	0.57	0.70
	Environmental variables	Chl a concentration	Chl a concentration	Inorganic content	Inorganic content	Inorganic content	Inorganic content + Water depth
	Spatial variables	PCNM12	PCNM4	PCNM1	PCNM4	PCNM1	PCNM1
	E|S *p* value	0.070	0.018	0.810	0.005	0.540	0.042
	S|E *p* value	0.023	0.032	0.036	0.020	0.015	0.340
3A Occasional	N	22	16	22	20	20	19

Table D1. Continued.

Region and taxon category	Year	2006	2007	2008	2009	2010	2011
3A Occasional	$\text{Distance}_{\text{max}}$ (km)	53.60	53.30	53.57	53.45	53.26	53.73
	$\text{Distance}_{\text{min}}$ (km)	2.94	3.17	3.10	2.97	2.97	3.12
	E|S	0.06	0.07	0.02	0.12	-0.02	0.00
	E∩S	0.04	-0.01	0.17	0.00	0.14	0.04
	S|E	0.03	0.05	0.13	0.08	0.19	0.15
	Unexplained	0.87	0.88	0.68	0.81	0.69	0.82
	Environmental	Inorganic	Periphyton P	Inorganic	Chl a mass	Inorganic	Aerial cover

variables	content		content		content	
Spatial variables	PCNM1	PCNM1	PCNM1 + PCNM3	PCNM8	PCNM1	PCNM1
E|S p value	0.082	0.029	0.340	0.010	0.830	0.640
S|E p value	0.240	0.100	0.037	0.029	0.005	0.015

CHAPTER V: GENERAL CONCLUSIONS

The availability of a 6-year record of diatom distribution with high spatial resolution across the Florida Everglades allowed me to investigate assembly mechanisms of diatoms in periphyton. I took a different approach from previous studies by relating diatom assemblage composition to non-physicochemical habitat characteristics, such as periphyton abundance and mineral content. Periphyton abundance and mineral content may be metrics that integrate the influence of environmental and spatial controls on the assemblage composition of its diatom inhabitants. If we consider the periphyton matrix as a micro-ecosystem that provides habitats for its constituents, the availability and quality of habitats should determine species abundances. The availability and quality of habitats in periphyton are strongly related to local environmental factors, evidenced by thick, calcareous mats in unenriched environments with seasonal desiccation and loose, organic aggregates in more enriched environments that may have extended hydroperiods. However, historical, biogeographical, and evolutionary processes also have potential regional-scale control on the availability and quality of habitats in periphyton.

Environmental history and current hydrologic management have divided the Everglades into distinct, but connected, wetlands with differing hydrologic and nutrient histories that persistently encourage the growth of particular forms of periphyton each year. In regions of the Everglades with histories of drastic drainage, extended dry seasons have likely encouraged the dominance of thick periphyton mats inhabited by taxa adapted to periods of desiccation. Conversely, the growth of thick periphyton mats have not been encouraged in impounded regions with generally longer hydroperiod and deeper water. In

Chapter II, I found a strong relationship between assemblage composition and hydroperiod, but many taxa had tolerance ranges >50 days, indicating potential desiccation resistance. In addition, I found a strong relationship between assemblage composition and periphyton biovolume, indicating the dependence of diatoms on the availability and quality of habitats. Availability of habitat (periphyton mats) is important for diatoms, because the periphyton mat can provide protection from moisture extremes and other environmental fluctuations that can stress diatom inhabitants.

Consistent morphological differences may support dispersal limitation of diatoms by spatial factors and potential regional endemism, rather than distribution across continents. In Chapter III, I found the dominant taxon in Everglades and Caribbean periphyton assemblages has a more limited distribution than previously thought when the taxon was reported as *Mastogloia smithii* or *M.* (*smithii* var.) *lacustris*. The taxonomic confusion stemmed from lack of accessible type material for both taxa and relatively poorly studied diatom flora in tropical wetlands. In addition, within-taxon morphological variability from post-initial valves to increasingly smaller valves produced by asexual reproduction required quantitative analyses of valves across full size ranges from multiple populations to define the taxonomy of the newly described species, *M. calcarea* and *M. pseudosmithii*. The availability of an accessible lectotype of *M. smithii* newly designated by this study may allow researchers to find that, upon comparison with populations found in their own study systems, *M. smithii* is not cosmopolitan, after all. Diatoms like *M. calcarea* that are key contributors to their benthic habitats have potentially strong biogeographical constraints by spatial factors that can limit their dispersal.

Strong niche-based control at the local assemblage scale did not exclude the contribution of spatial, dispersal-limiting processes to assemblage composition of Everglades diatoms. In Chapter IV, I found both environmental and spatial factors are important controls on the assemblage distribution of the overall Everglades diatom metacommunity, despite the small size and large populations of diatoms. I found the relative importance of environmental and spatial factors on assemblage distribution differ among compartments of the Everglades under differing hydrologic management. In Shark River Slough (SRS), where lower nutrients and shorter hydroperiods encourage development of calcareous periphyton mats, environmental controls are relatively more important than spatial controls. In Water Conservation Area 3A (3A), where higher nutrients and longer hydroperiods do not encourage development of calcareous periphyton mats, spatial controls are relatively more important than environmental controls. The differences I observed may be related to the influence of hydrologic management on the availability of habitat for taxa that have either persistent or occasional incidence in calcareous periphyton mats.

Differences between persistent and occasional taxa in the relative importance of environmental and spatial controls on assemblage distribution suggest large-scale biogeographical processes limit the dispersal of some diatom taxa; dispersal limitation then allows time for species to develop adaptations to local habitat characteristics. Even after determining the contributions of environmental and spatial factors to assemblage variability, however, unexplained variation remains, most notably for occasional taxa. Stochastic processes (e.g., founder effects, random genetic drift, or disturbances) and complex biotic interactions within the periphyton matrix (e.g., competition or density dependence), may also contribute to unexplained variance in diatom biodiversity. Future studies should examine how traditional theories about life history strategies (e.g., *r/K* selection) and population dynamics (e.g., competition or density dependence) apply to diatoms, especially benthic diatom assemblages with complex spatial structuring and temporal dynamics. Investigation of successional changes in composition as periphyton development (and dissolution) occurs and biological traits and life history characteristics of each species could elucidate which taxa have truly evolved into superior competitors in periphyton mat habitats, which taxa occur in the same habitats but are inferior competitors, and which taxa are truly cosmopolitan. In the Everglades, continued monitoring and data collection are essential for future detection of long-term trends (outside of background interannual variability captured by 6 years), especially to fully understand the effects of restoration upon ecosystem-scale implementation. Finally, the taxonomy of many Everglades and Caribbean diatoms that remain unresolved needs further attention in anticipation of comparative studies aimed at understanding global-scale processes.

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