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Diatom Indicators of Ecosystem Change in Subtropical Coastal Wetlands

Evelyn Gaiser, Anna Wachnicka, Pablo Ruiz, Franco Tobias, and Michael Ross

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Introduction

Coastal ecosystems often support a diverse benthic microalgal community that, together with associated bacteria, fungi, and macroalgae, forms prolific periphyton growths on sediments and the grasses and/or wet forest vegetation that inhabit the coastline. Particularly in the subtropics and tropics, coastal periphyton communities form the base of a productive and diverse food web both in the marsh and the adjacent offshore marine environment as tides transport both periphyton products and consumers across the marine–freshwater interface (Admiraal, 1984; Day et al., 1989). Coastal wetlands at this interface present a diversity of environmental conditions because of the strong gradients in salinity, water availability, and nutrient supply inherent in this transitional environment. A variety of habitat types result (depending on latitude), including interior freshwater forested marshes, supertidal graminoid marshes, intertidal estuarine lagoons, hypersaline pools, mangrove swamps, and grassy salt marshes. Consequently, coastal periphyton communities contain some of the most compositionally diverse algal floras in the world (de Wolf, 1982). Because algae are strongly influenced by their surrounding chemical and structural environment, they provide a useful tool for environmental monitoring in complex coastal systems (Vos and de Wolf, 1993; Sullivan, 1999; Cooper et al., 1999).

Several anthropogenic influences threaten the existence and viability of coastal systems worldwide, including nutrient enrichment, overharvesting of consumable resources, landscape modification, and saltwater encroachment (National Research Council, 1993). Documentation of detrimental ecological effects of the last has, in recent decades, been increasing in frequency and extent around the globe (Park

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et al., 1989), as the rate of saltwater encroachment into coastal ecosystems increases due to sea-level rise exacerbated by diversion and depletion of coastward overland freshwater flow. The history of coastal ecosystems in South Florida provides an unfortunate example of the magnitude and complexity of effects that decades of canalization and sea-level rise can have on intertidal communities. Rates of saltwater encroachment in coastal South Florida exceed 400 m per decade in some areas (Ross et al., 2000), resulting in the disappearance of vast areas of freshwater marsh and interior migration of mangrove swamps.

Because salinity has an overriding influence on microbial community composition, algae (particularly diatoms) have been used to track rates of saltwater encroachment in both modern monitoring and paleoecological studies (Gasse et al., 1983; Juggins, 1992; Ross et al., 2001). Algal populations respond on timescales of weeks to months to changes in environmental conditions, integrating much of the small-scale temporal variation that is often the source of unwanted "noise" in continuous salinity recording data (Snoeijs, 1999). Transfer functions have been created from the modern distribution of diatoms along salinity gradients (in coastal areas and closed-basin "saline" lakes, e.g., Campeau et al., 1995; Fritz et al., 1999, respectively) that allow salinity to be predicted from diatom community composition with a very high degree of accuracy. However, while many coastal diatom taxa are thought to be widely distributed, application of salinity preferences for diatoms collected in regions (e.g., Baltic Sea, Snoeijs, 1999; Thames River, England, Juggins, 1992; Chesapeake Bay, Cooper, 1995; Mississippi salt marsh, Sullivan, 1982) other than South Florida would be problematic because there would likely be a low degree of taxonomic overlap with these data sets. Subtropical wetlands in general and specifically the Everglades have been poorly explored taxonomically, resulting in incompletely defined ecological and range size distributions. Further, coastal environments of the subtropics are dominated by mangrove swamps, and other than studies by Siqueiros-Beltrones and Castrejón (1999, Balandra Lagoon, Baja CA), Navarro and Torres (1987, Indian River, FL), Sullivan (1981, Mississippi salt marsh), Reimer (1996, Bahamas), and Podzorski (1985, Jamaica), there have been few explorations of coastal mangrove diatoms. The composition and range size distribution of mangrove diatoms and associated microflora, and their response to environmental variation, are practically unknown.

The objectives of the present study were to survey the algal flora of periphyton communities in coastal wetlands in the Everglades of southeast Florida. Periphyton mats are a dominant feature in both freshwater and saline Everglades wetlands (Browder et al., 1982; Ross et al., 2001). The specific purposes of this work were to (1) document the taxonomic composition of algal assemblages, particularly diatoms, in periphyton of the coastal Everglades and (2) determine environmental drivers of assemblage composition, in order to (3) create algae-based inference models that could be used to track trajectories of environmental change. Our goal was to produce a taxonomic guide to aid in identifying subtropical coastal diatoms and to create algae-based environmental inference models that can be employed in long-term monitoring and/or paleoecological studies to document ecological response to habitat alteration along the South Florida coastline.

Methods

Study Site

The southeastern edge of Florida was historically characterized by expansive coastal mangrove wetlands that were dissected by tidal creeks flowing from the freshwater Everglades to the coast. Egler (1952) was able to distinguish distinct vegetation zones lying in bands parallel to the coast, driven by gradients of salinity, water availability, nutrients, and susceptibility to drought and fire, including a coastward sequence of graminoid freshwater wetlands (to the interior), followed by dwarf mangrove scrub swamps in intertidal areas, bounded by fringing mangrove forest on the coast. Throughout the last several decades, an extensive network of drainage canals has been constructed in South Florida, effectively draining much of the interior and coastal Everglades for urban and agricultural development. By the turn of the 21st century, the wetland bands had been diminished to the periphery of the coastline: freshwater graminoid

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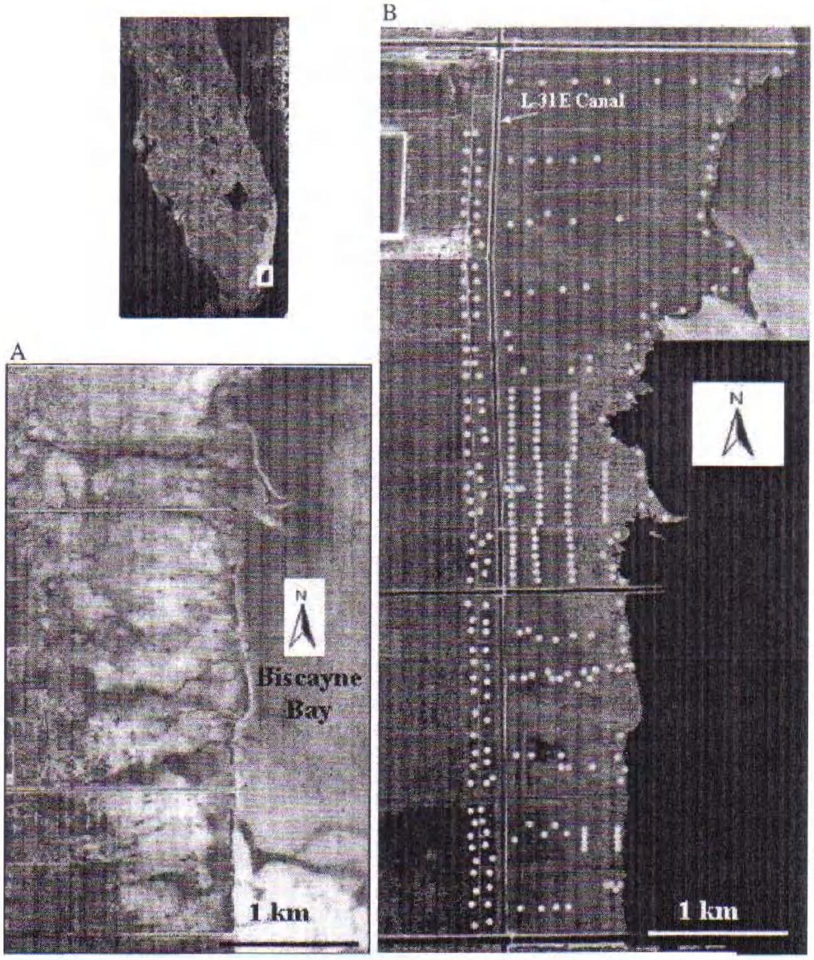

FIGURE 10.1 Location of study area in southeast Florida. (A) Aerial photograph from 1940 showing east–west canals, north–south drainage ditches, and remnant tidal creeks. (B) Aerial photograph from 1990 showing additional canals built since 1940, including the L-31E canal, the disappearance of tidal creeks, and the distribution of collecting sites among the 13 wetland sub-basins.

marshes had been largely displaced by an enroaching mangrove scrub community and most tidal creeks had disappeared (Ross et al., 2000; Figure 10.1B).

The present study focuses on an area of remnant coastal wetlands, parts of which are protected in Biscayne National Park (Figure 10.1). The ~7 km long study area is bounded to the north and south by major east–west drainage canals (Princeton and Mowry, respectively) and bisected north–south by a secondary canal (L-31E). The region is dissected by many smaller east–west ditches, which compartmentalize the area longitudinally into 13 hydrologically distinct wetland basins that range in width from about 0.5 to 2 km. To the west of the L-31E canal, freshwater marshes are now hydrologically isolated from the coast and bounded to the west by agricultural lands, the periphery of which is heavily invaded by exotic trees including *Schinus terebinthifolius* (Brazilian peppertree) and *Casuarina equisetifolia*

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(Australian pine). To the east of the L-31E canal, mangrove communities predominate, with strands of upland forest now occupying the remnant tidal creek beds.

We used a stratified–random design to select study sites within each of the 13 sub-basins. Using aerial photos of the area, each sub-basin was divided into four to six units, including, to the west of the L-31E canal, a freshwater swamp forest dominated by exotics that have invaded abandoned agricultural land and remnant freshwater graminoid marsh and, to the east of the L-31E canal, mangrove forests that can be characterized by canopy height and cover as dwarf, transitional, and fringing (along the coastline). Within each unit a north–south transect was randomly located, and one to five sampling stations were evenly distributed along its length. A total of 226 stations were sampled within the 12-km^2 area (Figure 10.1B).

Data Collection and Processing

At each station, we assessed the vegetation community structure, roughly described the sediments, and sampled periphyton and several chemical parameters in surface and/or pore water. Vegetation was assessed using methods of Ross et al. (2001), where species cover and canopy height were estimated separately for upper (~2 m height) and lower (<2 m) strata in repeated quadrats. Depth of sediments to the limestone bedrock was measured at five stations with a probe-rod, and using a soil auger, sediments were extracted to measure depths of readily apparent compositional and textural transitions. Using a polyvinylchloride (PVC) pipe, five small (3.8 cm^2, 1 to 2 cm thick) sections of surface soil, commonly occupied by periphyton, were extracted from each location and composited. A portable meter was used to measure pH and conductivity in surface water, if present, or in pore water that filled the auger hole. Conductivity (μS cm^{-1}) was converted to salinity (ppt) using a model provided from a previous study in a nearby basin where both variables were directly measured (Ross et al., 2001).

In the laboratory, periphyton was picked free of large plant fragments, homogenized, diluted, and subsampled for analysis of dry weight (DM, 2 days at 100°C), ash-free dry weight (AFDM, 1 h at 500°C), total phosphorus (TP, by automated colorimetry), and soft-algae and diatom composition. Diatoms were cleaned of calcite and organic matter by chemical oxidation and permanently fixed to a glass microslide using Naphrax® mounting medium. At least 500 diatom valves were counted on random, measured transects on a compound light microscope at 1000×. Nondiatom algae ("soft algae") were analyzed from one station within each unit in sub-basins 1 to 8 by preparing semipermanent water-mounted slides. At least 500 units (cells, colonies, or filaments) were counted and identified on random transects on the slide at 400 to 1000× magnification. Abundance estimates were converted to biovolume using critical dimensions (length, width, breadth) of 20 representatives of each morphologically distinct unit and applying volumetric formulas for the closest geometric shape. Diatom and soft algal samples, permanent slides, photographs of all taxa, database links, and all references used in taxonomic determination can be accessed through our Web site at http://serc.fiu.edu/periphyton/index.htm and are archived in a curated collection in the microscopy laboratory at Florida International University.

Data Analysis

Stations were sorted into five vegetation type categories based on survey data and aerial photographs, including a freshwater swamp forest, freshwater graminoid marsh, and dwarf, transitional, and fringing mangrove forest. The distinctiveness of the categories based on relative cover of species present in more than 5% of the sites was confirmed using analysis of similarity (among community types) employing the Bray-Curtis similarity metric in PRIMER-E/ANOSIM® software. Plant species significantly influencing the five community types were identified using Dufrene and Legendre's (1997) "Indicator Species Analysis," where taxa having an indicator value (based on relative abundance and frequency among sites) above 40% of perfect indication ($P < 0.05$) were considered reliable indicators.

Using the spatial modeling and analysis (V2.0) module in Arcview GIS 3.2®, we mapped the distribution of the vegetation community types and other environmental variables (soil depth, canopy height, salinity, and periphyton AFDM and TP content). To interpolate between points, we used the IDW method, which weights the value of each point by the distance that point is from the cell being analyzed and

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then averages the values. The output grid cell size was 10 m and the number of neighbors was 3 points. Means of each parameter were calculated within each vegetation type and compared using a Student's *t*-test, and correlations among parameters were determined using the Pearson correlation coefficient on log-transformed data, with $P < 0.001$.

Patterns in relative abundances and biovolumes of diatom and nondiatom taxa, respectively, were determined using nonmetric multidimensional scaling ordination (NMDS), analysis of similarity, and weighted-averaging regression. Species by station data matrices were established and species present in fewer than 1% of samples and having a mean relative abundance (when present) of <0.05% were removed prior to analysis. Assortment of sites in the NMDS ordinations based on the Bray-Curtis similarity metric were related to environmental variables using vector fitting. The significance of algal community patterns relative to vegetation type (a categorical variable) was determined using analysis of similarity on the same similarity matrix as used for the NMDS.

We used weighted-averaging regression and calibration to determine the strength of the relationship of species composition to salinity and vegetation type. This approach assumes that species abundance responses can be characterized by an optimum or mode where abundances are greatest and a tolerance that defines the breadth of appearance along a gradient. The value of an environmental variable can then be calculated for a sample from an unknown environment, using the average of the optima of the species present, weighted by their abundances and possibly tolerances. Using the weighted-averaging program C2 (Juggins, 2003), we estimated the salinity and vegetation optimum and tolerance for each species as the average among sites in which the taxon occurred and then tested the prediction power by estimating the salinity and vegetation type from a random set of sites (bootstrapping with replacement) and plotted predictions against observed values. Predicted values for salinity and vegetation type from diatom and soft-algae calibration models were mapped using the same approach as for the environmental variables (described above).

Results

Vegetation

The five major vegetation community types distinguished through interpretation of aerial photographs and used to determine selection of sampling sites were confirmed to be compositionally distinct based on relative cover of 45 of the most abundant of the 84 plant species found in the study area (ANOSIM, all combinations, global $R = 0.48$, $P < 0.01$). Compositional differences within freshwater units (upland forest and freshwater marsh) and interior mangrove units (dwarf and transitional) were less ($R = 0.2$ and 0.3, $P < 0.05$, respectively) than differences between freshwater and mangrove units (mean $R = 0.4$, $P < 0.01$), and the fringing mangrove forest was highly distinguishable from all other units (mean $R = 0.8$, $P < 0.001$). Although the coastward sequence of vegetation zones was consistent among sub-basins, there was variation in the breadth of each zone along the 7-km study area (Figure 10.2A), and we acknowledge that additional distinct community types occur within these units, most notably including a densely vegetated, heavily canopied mangrove forest growing in historic drainages that meander through adjoining units and forests occupying tree islands that punctuate all units of the landscape. Vegetation canopy height was significantly higher in the upland forest and transitional and fringing mangroves than in the freshwater marsh and dwarf mangrove community (see Figure 10.4A below).

Environmental Variation

Compositional differences among units were associated with variation in several environmental parameters. In pore water, while no significant pattern was observed in pH (mean = 7.2), a strong west–east increase in salinity was observed in many of the sub-basins, with the L-31E clearly separating freshwater (salinity < 5 ppt) from marine (5 to 20 ppt) conditions (Figure 10.3A). Soils were significantly deeper in the fringing mangrove forest than other units (126 cm vs. mean 104 cm, respectively), and although

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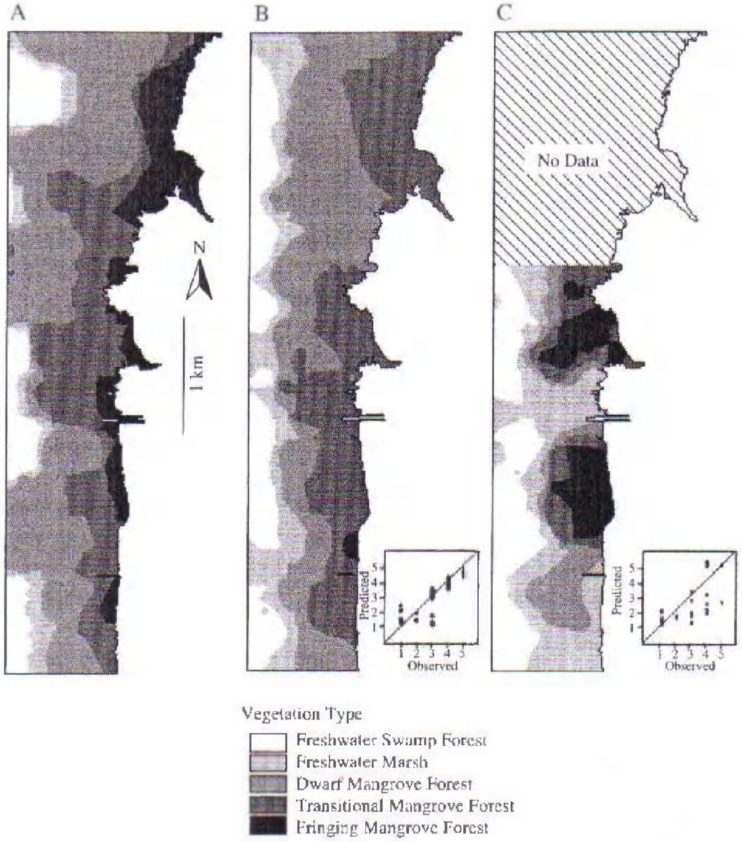

FIGURE 10.2 Observed distribution of the five major vegetation types within the study area (A) and distribution of vegetation types predicted from diatom community composition (B) and nondiatom algal community composition (C) using weighted-averaging regression. Insets are plots of observed vs. inferred vegetation type based on diatom and soft-algae optima and tolerances (R^2 = 0.69, 0.42 and RMSE = 0.77 and 1.2, for diatoms and algae, respectively). Plant species significantly associated with each community type were (1) Freshwater swamp forest: *Casuarina equisetifolia* (Australian pine), *Conocarpus erectus* (buttonwood), *Schinus terebinthifolius* (Brazilian pepper); (2) Freshwater marsh: *Cladium jamaicense* (sawgrass), *Juncus rhomerianus* (black rush), *Typha domingensis* (cattail); (3) Dwarf mangrove forest: *Laguncularia racemosa* (white mangrove), *Rhizophora mangle* (red mangrove); (4) Transitional mangrove forest: *Avicennia germinans* (black mangrove); and (5) Fringing mangrove forest: *R. mangle*, *L. racemosa*, *A. germinans*.

nearly all cores were characterized by an upper heavily rooted peat, this layer was deepest in the fringing mangroves and gradually became shallower to the interior freshwater marsh (66 cm vs. 12 cm, respectively; Figure 10.4B). With implications for linking biotic patterns to environmental variation, several variables were significantly correlated with each other, including soil, peat depth, salinity, and pH.

Periphyton Biomass and TP Content

Algae were organized into periphyton communities of considerable mass throughout the wetland units (Figure 10.4C). Periphyton DM was highest in the dwarf mangrove and freshwater marsh units (903 and 575 g m^{-2}, respectively) and lower in the forested units (mean = 266 g m^{-2}). A considerable portion of this mass in all units was composed of calcite, particularly in the dwarf mangrove and freshwater units, such that when this portion that is not combustible is subtracted from the dry mass (in the AFDM calculation), some of the pattern in periphyton distribution disappears, although AFDM biomass remains significantly higher in the dwarf mangrove forest than other units (Figure 10.4C). Likewise, the portion

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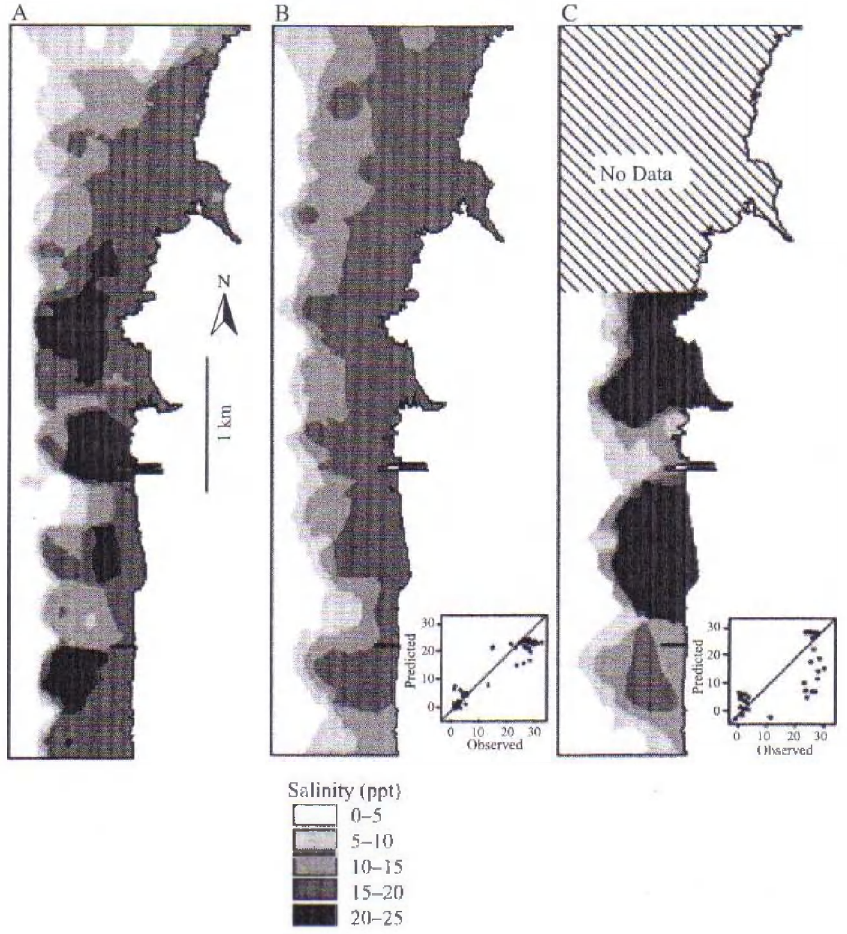

FIGURE 10.3 Observed distribution of pore water salinity (ppt) within the study area (A) and distribution of salinity predicted from diatom community composition (B) and nondiatom algal community composition (C) using weighted-averaging regression. Insets are plots of observed vs. inferred salinity based on diatom and soft-algae optima and tolerances (R^2 = 0.91, 0.58 and RMSE = 0.14, 0.34 for diatoms and soft-algae, respectively).

of the periphyton composed of organic (rather than calcitic) mass was significantly higher in the forested units than in the dwarf mangroves and freshwater marsh. The DM, AFDM, and organic carbon content of the periphyton mats were, by nature of their analysis, correlated and also strongly negatively related to canopy height, and less so to peat depth in the sediments.

Very strong trends in the TP content of periphyton mats were evident in the system, with periphyton in the freshwater marsh having significantly lower P than all other units and mats in the transitional and fringing mangrove forest having more than an order of magnitude higher P content than other units (Figure 10.4D). Patterns of variation in periphyton TP content were positively correlated with peat depth, canopy height, and salinity.

Algal Community Composition

A total of 405 diatom taxa representing 64 genera were collected from periphyton in the study area. Genera represented by the most taxa (number given in parentheses) were *Amphora* (59), *Navicula* (55), *Mastogloia* (51), *Nitzschia* (39), *Fragilaria* (21), *Achnanthes* (16), and *Diploneis* (15). The NMDS ordination (two dimensions, stress = 0.12) of relative abundance of 133 of the most abundant taxa found clear separation of diatom communities occupying the freshwater units (forest and marsh) from the

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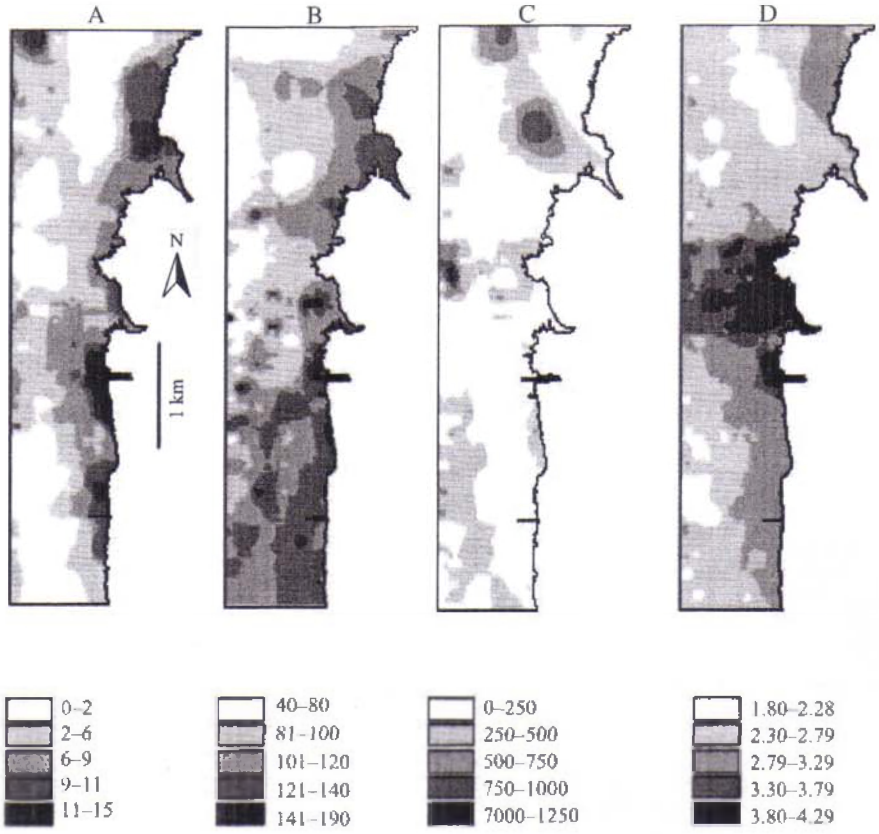

FIGURE 10.4 Distribution of (A) mean vegetation canopy height (m), (B) soil depth (cm), (C) periphyton AFDM (g m^{-2}), and (D) periphyton tissue total phosphorus concentration (log μg g^{-1}) within the study area.

marine mangrove units. This pattern was verified by the analysis of similarity, which showed that significant separation between freshwater units 1 and 2 vs. marine units 3, 4, and 5 (global $R > 0.6$ for all comparisons, $P < 0.001$), but little distinction in comparisons within freshwater and marine units (global $R < 0.2$ for all comparisons, $P > 0.1$). While the ANOSIM analysis suggested two groups (freshwater vs. marine), the weighted-averaging regression model revealed a more linear gradient from interior to coastal communities (Figure 10.2B). A total of 35 indicator taxa were identified, 6 for the upland forest, 5 for the freshwater marsh, 2 for the dwarf mangroves, 7 for the transitional mangrove forest, and 15 for the fringing mangrove forest (pictured in Figure 10.5 and Figure 10.6). When mapped spatially, diatom-based vegetation type predictions appear similar to measured values (Figure 10.2B).

The NMDS ordination also revealed significant patterns in diatom composition among sites relative to salinity, canopy height, organic content, peat depth, and TP (maximum vector $R^2 = 0.34$, 0.30, 0.29, 0.24, and 0.23, respectively). Effects of canopy height and TP on diatom composition were positively correlated and together negatively correlated with the influence of organic content of the periphyton mats. The effect of salinity, the strongest variable influencing composition, was correlated with that of peat depth. Because salinity had an overriding effect on composition and was only correlated with one other variable, we examined this relationship further using weighted-averaging regression.

Because the frequency distribution of salinity values among sites was bimodal, with sites in the freshwater units confined to the west of the L-31 E canal having much lower values than mangrove sites to the east, the linear model used in the weighted-averaging regression may not provide the best fit to these data. Even so, the model has strong predictive power because most of the taxa incorporated in the model have well-defined salinity optima and narrow tolerances (provided in the appendix to this chapter). When mapped spatially, diatom-based salinity predictions appear similar to measured values (Figure 10.3B).

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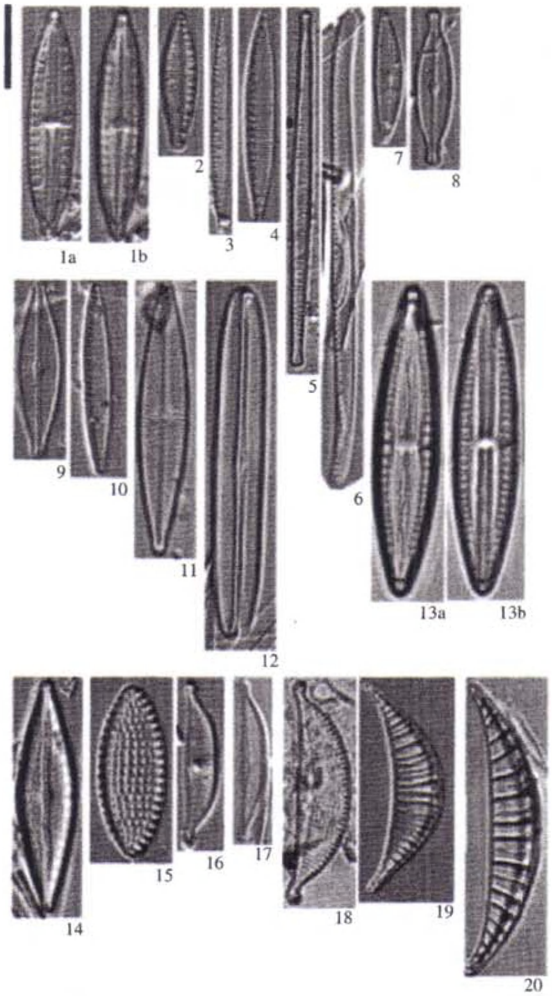

FIGURE 10.5 Digital photographs of diatom taxa that were significantly associated with each vegetation community type. From the freshwater forest: (1) *Mastogloia smithii* (a = midvalve focus showing internal partectae and b = surface of valve), (2) *Nitzschia semirobusta*, (3) *N. amphibia* f. *frauenfeldii*, (4) *N. amphibia*, (5) *Fragilaria synegrotesca*, and (6) *N. nana*; from the freshwater marsh: (7) *Encyonema evergladianum*, (8) *Brachysira neoexilis* (Typ 3), (9) *B. neoexilis* (Typ 2), (10) *N. palea* var. *debilis*, and (11) *Navicula podzorski*; from the dwarf mangrove forest: (12) *N. palestinae* and (13) *M. reimeri* (a = surface of valve and b = midvalve focus showing internal partectae); and from the transitional mangrove forest: (14) *M. angusta*, (15) *Tryblionella granulata*, (16) *Amphora* cf. *fontinalis*, (17) *A. coffeaeformis* var. *aponina*, (18) *A. costata*, (19) *Rhopalodia acuminata*, and (20) *R. gibberula*. Scale bar = 10 µm; original magnification: figures 1 to 15, 17, 19, and 20, ×1008; figure 16, ×1600; figure 18, ×1250.

In the study, 57 additional nondiatom algal taxa were found and identified co-occurring with diatoms in the periphyton communities at the reduced set of sites. The soft-algae flora was taxonomically dominated by coccoid and filamentous cyanophytes (39 and nine taxa, respectively), but also included two coccoid, two desmid, and three filamentous chlorophyte taxa, one dinoflagellate taxon and one purple-sulfur bacterium (non-algal, but included in counts). Taxa comprising more than 1% of the total biovolume of soft algae included, in decreasing order of abundance, the three filamentous chlorophytes (undetermined branching filaments resembling *Rhizoclonium*; 42%), followed by the blue-green filament *Scytonema* cf. *hofmannii* C. Agardh *ex* Bornet (35%) and three other unidentifiable blue-green filaments (resembling *Schizothrix* spp., 6.5%), seven *Chroococcus* spp. (5.8%), five *Gloeothece* spp. (3.4%), six *Aphanothece* spp. (2.5%), and the purple-sulfur bacterium (1.3%).

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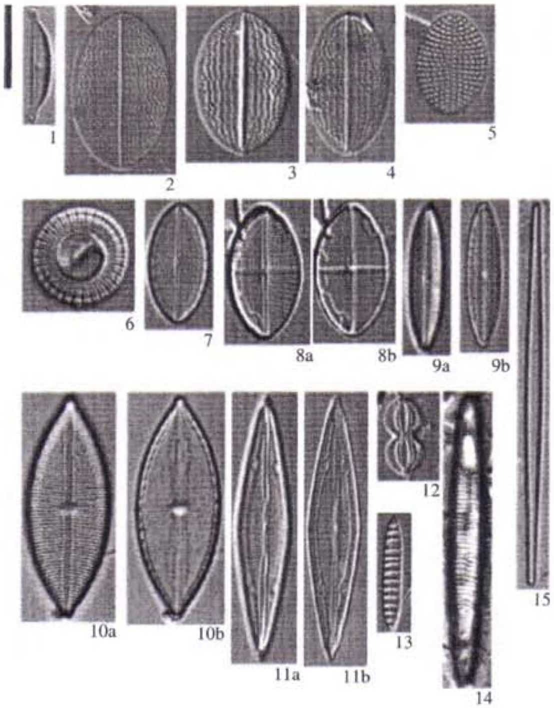

FIGURE 10.6 Digital photographs of diatoms taxa that were significantly associated with the fringing mangrove forest: (1) *Amphora subacutiuscula*, (2) *Cocconeis placentula*, (3) *C. placentula* var. *lineata*, (4) *C. placentula* var. *euglipta*, (5) *C. scutellum*, (6) *Cyclotella distinguenda*, (7) *Mastogloia ovalis*, (8) *M. crucicula* (a = surface of valve and b = midvalve focus showing internal partectae), (9) *M. pusilla* (a = surface of valve and b = midvalve focus showing internal partectae), (10) *M. nabulosa* (a = surface of valve and b = midvalve focus showing internal partectae), (11) *M. erythraea* (a = surface of valve and b = midvalve focus showing internal partectae), (12) *Diploneis caffra*, (13) *Denticula subtilis*, (14) *Rabdonema adriaticum*, and (15) *Hyalosynedra leavigata*. Scale bar = 10 μm; original magnification ×1008.

Both nondiatom and diatom algae responded similarly to measured environmental variables. The NMDS ordination (two-dimensional stress = 0.11) of relative biovolume of 35 of the most abundant taxa separated freshwater forest and marsh sites from marine mangrove units, and this distinction was shown to be significant in the analysis of similarity ($P < 0.001$). Several sites were distinctly grouped apart from other sites because they were uniquely dominated by a filamentous chlorophyte-resembling *Rhizoclonium*. These included most of the coastal sites in sub-basins 4 and 7. The ANOSIM analysis showed clear separation of algal communities occupying the freshwater units (forest and marsh) from the marine mangrove units. The weighted-averaging regression model for habitat types was strong but less predictive than the diatom-based model (Figure 10.2C). Five species were significantly indicative of three of the vegetation units, including, for the freshwater forest, two blue-green filaments resembling *Schizothrix calcicola* (Agardh) Gomont and the coccoid blue-green *Gomphosphaeria semenvitis*; for the dwarf mangrove scrub, an unidentified *Gloeothece* sp.; and for the fringing mangroves, an unidentified chlorophyte resembling *Rhizoclonium*. When mapped spatially, algae-based vegetation type predictions appear similar to measured values (Figure 10.2C).

The NMDS ordination showed the same variables to be important in explaining soft-algal distribution as the diatoms, including salinity, peat depth, canopy height, TP, and organic content (maximum vector $R^2 = 0.34, 0.33, 0.25, 0.21$, and 0.20, respectively). Effects of canopy height, TP, and peat depth on soft-algal species composition were positively correlated and together negatively correlated with the influence of organic content of the periphyton mats. The effect of salinity, the strongest variable influencing composition, was independent of other variables, and we examined this relationship further using weighted-averaging regression. The model to predict salinity from algal species composition is strong. When mapped spatially, the algal-based predictions are less consistent with actual measured values (in

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comparison to diatoms; Figure 10.3C), although sites to the east and west of the L-31E canal can be clearly distinguished.

Discussion

The freshwater–saltwater ecotone lining the coast of southeast Florida coast is migrating rapidly westward. In our 7-km study area, four canals constructed over the last several decades now discharge the majority of overland freshwater flow directly into Biscayne Bay. Comparing the current locations of the five vegetation zones to those observed in the 1940 aerial photograph, several changes are obvious: (1) tidal creeks linking the interior freshwater marsh to the coast have disappeared, so that most fresh water is now delivered in large volumes to point locations where canals terminate, (2) the freshwater marsh has been drained and native vegetation displaced to the west by invasive exotic trees and to the east by the expanding dwarf mangrove forest, and (3) all coastal vegetation bands are now restricted to the east of canals that, by running parallel to the coastline, prohibit natural mixing of fresh water and salt water during the tidal cycle. Together with sea-level rise (the regional rate is estimated to be 3 to 4 mm yr^{-1}; Wanless et al., 1994), massive freshwater drainage has caused a rapid rate of saltwater encroachment that forces mangrove communities to shift landward to the canal boundary, which disrupts natural exchange across the coastal ecotone.

Evidence of shifts in the width and location of the vegetation zones can be interpreted from the soil profiles. All of our soil cores contained a substantial marl layer below a surficial peat. In the Everglades, marl soils are generally associated with freshwater marsh communities, particularly wet-prairie meadows (defined as graminoid marshes that are inundated 6 to 9 months per year). Peat soils are indicative of deeper water, more prolonged flooding, and mangrove communities along coastlines. We interpret the peat layer upper soils across the wetland basins to be indicative of (1) invasion by forest elements into the freshwater marsh due to water diversion from areas west of the L-31E canal, and (2) invasion of mangroves into areas previously occupied by freshwater marsh in areas east of the L-31E. Sedimentation rates from studies in similar communities nearby (1 to 3 mm/yr^{-1}; Scholl et al., 1969) suggest the contact is coincident with the establishment of the drainage canal network.

The microbial community in the Biscayne Bay coastal wetlands was, in most areas, organized into a cohesive periphyton mat. Organic biomass, measured by AFDM, was high (mean = 190 g m^{-2}) throughout the study area exceeding values found in a nearby mangrove marsh (5 to 20 g m^{-2}; Ross et al., 2001), where saltwater encroachment has caused a rapid expansion of a broad band of low productivity (referred to as the "white zone"). The highest values in the shallow freshwater marsh units (mean = 317 g m^{-2}) were comparable to marshes in the interior Everglades, where periphyton biomass can exceed that of emergent plants (Browder et al., 1982). Notably, the percent organic carbon in periphyton mats was highest toward the coast where marl deposition is minimized.

Of the measured environmental variables, only canopy height was correlated with periphyton biomass, with lowest values in heavily canopied fringing forests and highest in open areas of freshwater marsh. It is not unexpected that light availability would control periphyton biomass, although Beanland and Woelkerling (1983) found no effect of canopy on periphyton algal biomass in an *Avicennia* forest in South Australia, and, in our study, biomass was still relatively high in the heavily canopied fringe. Ambient daytime irradiance to the surface of Everglades periphyton mats can exceed 1000 µmol m^{-2} s^{-1}, an intensity that has been shown to photo-inhibit photosynthesis (Underwood, 2002). Typically, periphyton mats have distinct vertical structure, with green productive layers underlying a calcitic, inactive (possibly light-inhibited) surface. In this study, mats in open areas in this study were thick and structured, whereas periphyton in shaded areas usually comprised a thin, green film growing attached to roots and leaf litter. This community may be encouraged by the higher TP availability in coastal areas, and contribute to the inverse relationship between periphyton organic content and P availability. It was somewhat remarkable that although P availability (as measured by the TP content of the periphyton mats) varied an order of magnitude in the study area, there was no measurable correlation with periphyton DM or AFDM biomass, although it has been shown to control periphyton biomass in other areas of the Everglades (Gaiser et al., 2004). However, although biomass may be similar to or lower than interior

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areas, turnover of periphyton in the fringing mangroves may be higher as a result of increased nutrient availability. Other studies have found particularly high algal productivity in fringing mangrove ecosystems and in neighboring seagrass beds (Koch and Madden, 2001). Total algal biomass in one *Rhizophora mangle* forest in Puerto Rico was actually found to exceed the total annual leaf litterfall (Rodriguez and Stoner, 1989), pointing to the impact of benthic periphyton to the food web of mangroves and neighboring lagoons and estuaries.

Periphyton mat biomass was high across the broad range of salinity experienced by this system. This shows that the complicated, intricately connected communities forming highly structured periphyton mats can be created in both freshwater and marine conditions, even though the composition (at all levels, macro- and microalgal, bacterial, fungal, etc.) differs due to the strong osmotic gradient represented from freshwater to marine environments.

Indeed, we did find that salinity had an overriding control on algal composition throughout the coastal wetlands. While mats were dominated throughout the system by green algal filaments, *Scytonema* spp., and small coccoid blue-green algae, their morphologies (and, thus, our taxonomic designations) differed along the salinity gradient. The difficulty of assigning names to most of the taxa stems from the fact that coastal mangrove microalgal communities are poorly explored taxonomically. That we could not find many of the taxa collected here listed, described, or pictured in studies from similar system suggests either that these studies misdiagnosed taxa because of the paucity of appropriate taxonomic literature or that there is more regionality to the coastal microalgal flora than previously thought.

However, at higher levels of taxonomic organization, this flora did resemble that of other microbial mangrove mats collected elsewhere and, at those levels, responded similarly to salinity variation in the system. Phillips et al. (1994) found that horizontal zonation of algae on pneumatophores of *Avicennia* marina in South Africa was controlled primarily by salinity and wetting frequency, with the green alga *Rhizoclonium* dominating wet areas and providing support for numerous filamentous cyanophyte taxa (notably, *Lygbya confervoides* and *Microcoleus chthonoplastes*, belonging to genera also found in this study). *Rhizoclonium* and other green-algal filaments are often abundant in mangrove periphyton communities, often forming a tertiary layer over the macroalgae that are directly attached to the mangrove roots (Phillips et al., 1994). The macroalgae have been shown to be an important component of mangrove marshes, both in terms of their own productivity and diversity and also through their support of a diverse epiphytic community: it is not uncommon to find upward of 20 species of macroalgae inhabiting mangrove benthos, providing support for hundreds of microalgal taxa (Collado-Vides, 2000). Although we excluded macroalgae from our detailed analyses, we did note in field collections that *Bostrichia* was abundant on prop-roots and often coated with a thin green-algal mat (likely *Rhizoclonium* spp.). These *Rhizoclonium*-based communities were particularly important in coastal sites in sub-basins 4 and 7, which was what influenced the separation of these sites in the NMDS ordination.

The filamentous chlorophytes and macroalgae were joined by cyanobacterial filaments, particularly *Scytonema* and *Schizothrix* species, which often form the backbone of microbial mats across the full salinity range, from shallow, freshwater calcareous wetlands in the Everglades and Belize (Rejmánková and Komárková, 2000) to intertidal mangroves (Collado-Vides, 2000) to subtidal marine stromatolites (Rasmussen et al., 1993)) and hypersaline lagoons (Hussain and Khoja, 1993). These genera both contain species representing the full salinity spectrum, and indeed some of the species (*Scytonema hofmannii*) appear capable themselves of thriving in vastly different salinity regimes. In this study, the *Scytonema* and *Schizothrix* were most abundant in the freshwater marsh where they appeared, upon microscopic examination, to be coated with calcium carbonate crystals, which has been noted elsewhere (Browder et al., 1982). These were displaced by noncalcite precipitating blue-green algae in communities closer to the coast. Similar *Lyngbya*- and *Microcoleous*-dominated blue-green algae have been collected from mangrove pneumatophores elsewhere (Hussain and Khoja, 1993). While the periphyton matrix appears throughout the system to be macroscopically strung together by filamentous green or blue-green algae, the interstices of this web are often "glued" together by mucilaginous polysaccharide produced by abundant and diverse coccoid blue-green algae, which may increase desiccation resistance, provide a barrier to fluctuations in salinity, and concentrate nutrients and enzymes that control nutrient cycling.

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The most diverse algal component in the periphyton mats studied here was the diatoms. It is common to find a large number of diatom genera in estuaries and near-coast environments because typically genera are confined to either fresh or salt water, and rarely mix except in brackish situations (Snoeijs, 1999). The dominance of *Amphora* and *Mastogloia* in the coastal flora is similar to findings in other parts of Florida and the Caribbean (Montgomery, 1978; Sullivan, 1981; Navarro, 1982; Foged, 1984; Podzorski, 1985; Reimer, 1996). These genera, together with *Navicula, Nitzschia, Cocconeis, Fragilaria,* and *Achnanthes*, are probably important in coastal floras circumglobally, at least in the Northern Hemisphere. At lower taxonomic levels we found several taxa with consistent morphologies that have not appeared elsewhere (or only in the regional literature — Montgomery, 1978; Navarro, 1982; Foged, 1984; Podzorski, 1985) that may be unique to the subtropical/tropical Atlantic Coast.

Diatoms organized into distinct freshwater and marine assemblages on either side of the L-31 E canal that effectively deterred mixing of tidal and overland freshwater flow. To the east of the canal, the freshwater marsh flora was dominated by *Encyonema evergladianum*, *Brachysira neoexilis*, and *Nitzschia palea* var. *debilis*, which are all common in un-enriched periphyton mats throughout the freshwater Everglades (Slate, 1998; Cooper et al., 1999). The freshwater swamp forest contained many of the same taxa as the freshwater marsh, but was the preferred habitat for *Mastogloia smithii, Fragilaria synegrotesca*, and four species of *Nitzschia* (*N. semirobusta, N. amphibia* f. *frauenfeldii, N. amphibia,* and *N. nana*). While these are all common elsewhere in the Everglades (Slate, 1998; Cooper et al., 1999), the predominance of *Nitzschia* taxa in the forest relative to the marsh is notable, and may reflect a higher stress tolerance for members of this genus (i.e., disturbance and low light intensities).

To the east of the L-31 E canal, the mangrove system was dominated by pennate benthic taxa. Mangrove-inhabiting taxa appear to be capable of withstanding a broad range of salinity and frequent desiccation. Taxa in the genus *Amphora, Achnanthes,* and *Tryblionella* became gradually more dominant toward the coast, indicating an affinity for higher salinities. These taxa appeared to assort better along the salinity gradient than by the vegetation type categories, likely because of the effect of tidal transport from the coastline to the canal levee. Transport was also probably responsible for the presence of notably marine planktonic taxa, such as *Cyclotella striata, Catacombas gaillonii, Biddulphia* spp., and *Terpsinoë musica*, in benthic samples.

Applications

The algal flora of coastal South Florida is not only prolific in terms of biomass and richness, but is highly correlated with salinity and vegetation type — two factors that will be influenced most by continued saltwater encroachment. Models provided here allow salinity to be predicted from diatom composition with an error of <10% of the actual value. Considering the high degree of variation in continuous salinity recordings, diatoms not only offer a means of monitoring salinity more accurately in the modern environment, but also provide a tool for reconstructing past salinity from fossil assemblages. Further, diatom composition offers a tool for "hindcasting" an ecological variable (vegetation type) from past communities. The predictive power of these models can be strengthened by those of Ross et al. (2001) who created a diatom-based transfer function that predicts distance from the coast in a neighboring South Florida wetland with 100 m resolution. The use of diatoms in coastal environments should receive increased attention in coming years as the realization of their tight linkages to the strong zonation typical of coastal environments is recognized in different regions. While long-term preservation of diatoms in sediments of coastal mangrove systems is sometimes poor (Ross et al., 2001), locations slightly displaced offshore appear to offer better preserved records that have been useful in salinity reconstructions (Huvane and Cooper, 2001). This work strongly advocates the use of diatoms in tracking habitat shifts in response to restoration at the freshwater–marine coastal interface.

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Appendix

Number of occurrences, maximum relative abundances, and weighted-averaging (WA) salinity optima and tolerances (ppt) of the 132 most common diatom taxa in the southeast Florida coastal wetland study area. Taxa are listed in order of estimated WA salinity optima.

Taxon	No. Occ.	Max. Abund.	Salinity Optimum	Salinity Tolerance
Achnanthidium minutissimum (Kütz.) Czar.	8	0.29	1.80	0.20
Nitzschia nana Grun. in V. H.	11	0.14	1.83	0.72
Navicula subrostellata Hust.	5	0.07	1.84	0.21
Encyonopsis microcephala (Grun.) Kr.	18	0.43	1.84	0.85
Nitzschia amphibia f. *frauenfeldii* (Grun.) L-Bert.	6	0.13	1.84	0.28
Pinnularia maior (Kütz.) Rab.	9	0.02	1.95	0.35
Encyonema carina L-Bert. & Kr.	5	0.04	1.96	0.23
Brachysira neoexilis L-Bert. (Typ2)	16	0.09	2.04	0.66
Nitzschia palea var. *debilis* (Kütz.) Grun. in Cl. & Grun.	23	0.18	2.06	1.24
Nitzschia amphibia Grun.	13	0.06	2.08	1.08
Nitzschia semirobusta L-Bert.	18	0.25	2.19	0.86
Navicula cryptotenella L-Bert.	17	0.32	2.25	1.84
Encyonema evergladianum Kr.	33	0.57	2.25	1.51
Encyonema neomesianum Kr.	14	0.20	2.26	1.09
Encyonema silesiacum (Bl.) Mann	13	0.07	2.32	1.47
Diploneis ovalis (Hilse in Rab.) Cl.	28	0.10	2.39	1.44
Gomphonema intricatum var. *vibrio* (Ehr.) Cl.	5	0.01	2.44	1.44
Mastogloia smithii Thw. *ex* Sm.	38	0.65	2.44	1.53
Diploneis vacilans (Schm.) Cl.	5	0.05	2.62	1.78
Brachysira neoexilis L-Bert. (Typ1)	9	0.04	2.69	1.77
Navicula veneta Kütz.	18	0.09	2.89	2.36
Brachysira neoexilis L-Bert. (Typ3)	7	0.06	2.92	1.52
Navicella pusilla Kr.	29	0.39	3.00	1.88
Nitzschia palea (Kütz.) Sm.	14	0.04	3.11	2.31
Caponea caribbea Podz.	14	0.02	3.40	2.47
Fragilaria synegrotesca L-Bert.	29	0.16	3.41	2.68
Rhopalodia operculata (Ag.) Håkansson	6	0.21	3.66	2.24
Rhopalodia gibba (Ehr.) Müller	9	0.04	3.68	2.89
Nitzschia bergii Cl.-Eul.	4	0.11	3.72	2.23
Amphora sulcata A. Schm.	20	0.57	3.87	2.61
Nitzschia intermedia Hantzsch *ex* Cl. & Grun.	4	0.02	3.89	2.30
Nitzshia dissipata (Kütz.) Grun.	8	0.05	3.94	3.00
Selaphora stroemii (Hust.) Mann	5	0.01	4.15	3.17
Mastogloia smithii var. *lacustris* Grun.	13	0.02	4.20	2.75
Diploneis litoralis (Donkin) Cl.	9	0.03	4.36	3.06
Diploneis oblongella (Nae.g.) Cl.-Eul.	39	0.35	4.58	2.90
Diploneis parma Cl.	14	0.02	5.22	3.53
Nitzschia sigmoidea (Nitzsch) Sm.	5	0.01	5.34	3.23
Nitzschia serpentiraphe L-Bert.	4	0.07	5.89	2.83
Navicula erifuga L-Bert.	16	0.02	5.98	3.85
Kolbesia amoena (Hust.) Kingston	10	0.04	6.14	3.61
Gomphonema vibrioides Reich. & L-Bert.	8	0.01	6.31	3.68
Navicula podzorski L-Bert.	11	0.06	6.46	3.49
Rhopalodia musculus (Kütz.) Müller	5	0.03	7.07	2.89
Nitzschia gracilis Hantzsch	14	0.03	7.20	3.66
Caloneis sp. 02L31E	4	0.02	7.31	3.04
Navicula sp. 03L31E	23	0.34	8.17	3.03
Fragilaria fasciculata (Ag.) L-Bert.	18	0.27	8.85	3.98

(continued)

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Taxon	No. Occ.	Max. Abund.	Salinity Optimum	Salinity Tolerance
Nitzschia graciliformis L-Bert. & Simonsen	5	0.01	9.15	4.41
Seminavis strigosa (Hust.) Danielidis & Economou-Amilli	14	0.17	9.45	4.15
Fragilaria capensis Grun.	4	0.02	10.37	2.25
Mastogloia braunii Grun.	15	0.05	10.55	3.60
Fragilaria femelica (Kütz.) L-Bert.	31	0.36	11.60	2.51
Amphora sp. 22L31E	8	0.10	11.79	1.57
Nitzschia microcephala Grun. in Cl. & Möller	27	0.05	11.97	3.20
Navicula tenelloides Hust.	12	0.07	12.41	3.27
Nitzschia sigma (Kütz.) Sm.	4	0.09	12.74	2.85
Navicula cryptocephala Kütz.	5	0.05	13.07	3.92
Rhopalodia gibberula (Ehr.) Müller	25	0.69	13.09	3.88
Nitzschia scallpeliformis (Grun.) Grun. in Cl. & Grun.	4	0.09	13.13	3.79
Amphora subacutiuscula Sch.	23	0.30	13.26	2.44
Brachysira aponina Kütz.	12	0.11	13.54	3.78
Amphora cymbifera Greg	7	0.03	13.73	2.00
Mastogloia halophila John	20	0.27	13.89	2.80
Cyclotella meneghiniana Kütz.	12	0.10	14.38	3.88
Proszkinia bulnheimii Grun. Karayeva	4	0.08	14.43	1.47
Nitzschia frustulum (Kütz.) Grun.	12	0.16	14.44	3.82
Amphora eulensteinii Grun.	9	0.05	14.60	2.16
Amphora coffeaeformis Kütz.	15	0.18	14.61	2.02
Entomoneis sp.02L31E	11	0.01	14.69	1.92
Denticula subtilis Grun.	20	0.21	15.18	3.03
Grammatophora oceanica (Ehr.) Grun.	6	0.01	15.30	1.61
Amphora acutiuscula Kütz.	10	0.04	15.31	1.31
Amphora coffeaeformis var. *borealis* (Kütz.) Cl.	4	0.01	15.51	1.40
Amphora coffeaeformis var. *aponina* (Kütz.) Arch. & Sch.	27	0.36	15.55	1.98
Mastogloia reimeri John	11	0.06	15.69	2.96
Cocconeis placentula var. *lineata* (Ehr.) V. H.	9	0.16	15.75	1.77
Bacillaria paradoxa Gmelin	8	0.06	16.02	0.70
Mastogloia erythraea var. *grunowii* Foged	7	0.02	16.06	0.88
Planothidium rostratum (Østrup) Round & Bukhtiyarova	4	0.05	16.34	3.07
Cocconeis scutellum var. *ornata* Grun.	6	0.04	16.48	0.39
Amphora normani Hust.	9	0.09	16.54	0.94
Rhopalodia constricta (Sm.) Kr.	8	0.03	16.59	1.24
Rhopalodia acuminata Kr.	22	0.49	16.60	2.11
Cocconeis placentula Ehr.	10	0.24	16.84	0.96
Mastogloia recta var. *pumila* Hust.	4	0.04	16.85	0.54
Melosira sp. 01L31E	10	0.02	17.02	2.69
Navicula recens L-Bert.	8	0.05	17.02	2.50
Mastogloia angusta Hust.	17	0.17	17.06	2.38
Cocconeis scutellum Ehr.	4	0.13	17.12	0.55
Mastogloia ovalis Schm.	6	0.06	17.24	0.26
Achnanthes nitidiformis L-Bert.	5	0.02	17.28	0.51
Amphora sp. 02L31E	8	0.04	17.30	0.57
Hyalosynedra leavigata (Grun.) Will. & Round	16	0.41	17.31	1.48
Cyclotella distinguenda Hust.	22	0.21	17.38	1.12
Mastogloia braunii f. *minuta* Voigt	10	0.02	17.45	2.41
Licmophora normaniana (Grev.) Wahrer	11	0.03	17.50	0.80
Mastogloia crucicula (Grun.) Cl.	5	0.05	17.57	0.54
Rhabdonema adriaticum Kütz.	5	0.21	17.57	0.68
Navicula palestinae (Gerloff)	17	0.37	17.61	1.70
Seminavis sp. 02L31E	4	0.00	17.62	1.22
Mastogloia pumila (Grun.) Cl.	4	0.01	17.67	0.99

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Taxon	No. Occ.	Max. Abund.	Salinity Optimum	Salinity Tolerance
Amphora sp. 39L31E	9	0.03	17.74	0.80
Cocconeis placentula var. *euglipta* (Ehr.) Grun.	5	0.08	17.90	0.91
Mastogloia pusilla Grun.	6	0.03	18.23	0.81
Mastogloia sp. 04L31E	5	0.08	18.29	0.88
Diploneis gruendleri (Schm.) Cl.	6	0.02	18.33	0.73
Tryblionella granulata (Grun. in Cl. & Möller) Mann	6	0.05	18.38	0.92
Mastogloia biocellata Navarino & Muftah	7	0.01	18.40	1.27
Mastogloia erythraea Grun.	12	0.06	18.43	2.22
Amphora costata W. Sm.	6	0.13	18.45	0.84
Navicula sp. 01L31E	4	0.11	18.59	0.76
Tryblionella coarctata (Grun. in Cl. & Grun.) Mann	4	0.00	18.66	0.90
Seminavis gracilenta (Grun. *ex* Schm.) Mann	12	0.02	18.72	1.12
Grammatophora macilenta Sm.	4	0.00	18.74	1.16
Navicula cincta (Ehr.) Ralfs in Pritchard	5	0.07	18.86	0.75
Mastogloia cyclops Voigt	9	0.03	18.93	0.86
Diploneis caffra Giffen	14	0.21	19.07	0.98
Amphora ostrearia var. *lineata* (Bréb. *ex* Kütz.) Cl.	8	0.14	19.11	0.76
Navicula tripunctata (Müller) Bory	5	0.01	19.12	1.21
Amphora veneta Kütz.	4	0.13	19.16	1.04
Planothidium lanceolatum (Bréb.) Round & Bukhtiyarova	4	0.07	19.28	1.08
Melosira nummuloides (Dillwyn) Ag.	4	0.09	19.32	1.29
Nitzschia vitrea Norman	9	0.03	19.38	1.85
Seminavis robusta Danielidis & Mann	12	0.01	19.67	1.01
Navicula pseudocrassirostris (Hust.)	8	0.03	19.73	1.33
Mastogloia nabulosa Voigt	10	0.09	20.00	0.92
Fragilaria tenera (Sm.) L-Bert.	8	0.04	20.25	1.39
Caloneis sp. 01L31E	4	0.00	20.52	1.06
Tryblionella debilis Arnott	7	0.07	20.86	1.33
Mastogloia elegans Levis	13	0.09	20.99	1.03
Amphora sp. 24L31E	6	0.02	21.38	0.66

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