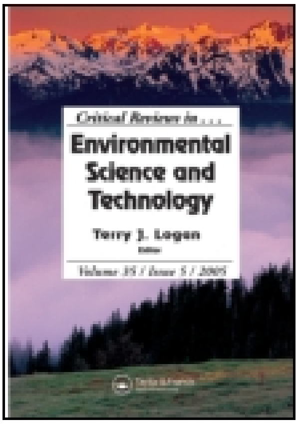

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Landscape Patterns of Periphyton in the Florida Everglades

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Periphyton is an abundant and ubiquitous feature of the Florida Everglades, often forming thick mats that blanket shallow sediments and submersed plants. They are considered to be primary ecosystem engineers in the Everglades by forming and stabilizing soils, controlling concentrations of nutrients and gases, and supplying food and structure for other organisms. Distribution patterns are related to underlying physicochemical gradients as well as those hydrologic changes imposed by water management. Because communities respond rapidly to environmental change, their use has been advocated to provide indication of system degradation or restoration. The authors review studies on the distribution of periphyton in the Everglades, highlighting major findings relevant to water management, and also areas where additional exploration is necessary.

KEYWORDS: algae, benthic mats, Everglades, hydrology, restoration, periphyton, phosphorus

INTRODUCTION

Submerged surfaces in wetlands, littoral zones, and shallow ponds often support abundant quantities of benthic algae. The Everglades is no exception, where benthic algae and associated bacteria, fungi, and microfauna

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(colloquially, periphyton) form thick mats that blanket shallow limestone sediments, coat submersed stems of macrophytes, and form floating rafts that drift along the surface of the water. Except in areas that are unnaturally enriched in phosphorus or have a significantly shortened hydroperiod, periphyton can be found in abundance throughout the Everglades ecosystem, from the loose, flocculent aggregations in the soft-water Loxahatchee National Wildlife Refuge, to the thick, calcareous mats of the central Everglades sloughs, to benthic mats found in marl prairies, to the aggregations around mangrove pneumatophores in estuary ecotones. Although widespread, not all Everglades periphyton communities are the same. There is significant spatial variability in abundance, appearance, and species composition that is not only functionally meaningful but also can indicate areas of concern for water management in the highly regulated Everglades ecosystem (Gaiser, 2009).

Because of their abundance and widespread distribution, periphyton communities are considered to be primary ecosystem engineers in the Everglades (McCormick and Stevenson, 1998). Thick accumulations full of mucopolysaccharides secreted by algae and bacteria can stabilize underlying sediments and retain moisture during droughts, preventing desiccation (Donar et al., 2004; Thomas et al., 2006a). They also sequester nutrients from the water column and can serve as sites for long-term nutrient storage and recycling by resident algae, bacteria, and animals that mutualistically interact in these tightly aggregated assemblages (Iwaniec, 2008). Estimates of annual net primary production ranging from 100–10,000 g m^{-2} yr^{-1} (Ewe et al., 2006; Iwaniec et al., 2006) compared with reported averages of 10–50 g m^{-2} yr^{-1} from other wetland types (Vymazal and Richardson, 1995) appear paradoxical given the oligotrophic nature of the Everglades (water total phosphorus concentrations in the un-enriched interior averages < 10 μg l^{-1}; McCormick et al., 2002; Noe et al., 2001). At these rates, periphyton may constitute a significant sink for atmospheric CO_2, although the ultimate fate of this production is unknown. Although it is clear that periphyton can regulate water column oxygen concentrations (McCormick et al., 1997; McCormick and Laing, 2003) and aquatic metabolism (Hagerthey et al., 2010), periphytic algae are also converting dissolved inorganic carbon to both organic and particulate inorganic form (as calcium carbonate soil, or marl, in the calcareous Everglades). Periphyton thereby regulates the cycling of inorganic carbon between dissolved and particulate forms but also contributes to the formation of the thick flocculent detritus that forms the fluff over most deeper water Everglades sediments and eventually to dissolved organic carbon, both of which can be transported to adjacent systems (Gleason 1972; Gleason and Spackman, 1974; Wood, 2005). Together, periphyton mats and their detrital products supply energy to planktonic and benthic food webs, as well as habitat for a diversity of small animals (Dorn et al., 2006). In this way, periphyton communities are not only a resource capital supporting the rest of the Everglades ecosystem, but also contribute to its biodiversity, from their own speciose microbial assemblages to those of the organisms dependent on their structural or nutritional provisioning.

Due to their multidimensional influence on the Everglades ecosystem, the interaction of periphyton communities with their biogeochemical environment and dependent biological communities has been examined, particularly relative to the primary biophysical drivers in the Everglades, including nutrient enrichment, hydrology, and ion availability. As has been found for other benthic algal communities (Stevenson et al., 1996), periphyton assemblages of the Everglades respond in meaningful structural, functional, and compositional ways to these gradients that can be modeled and used for predictive purposes (McCormick and Stevenson, 1998). A variety of large-scale surveys and experimental studies have defined the patterns and mechanisms of periphyton response to nutrient enrichment (Gaiser et al., 2004a, 2005; McCormick and O'Dell, 1996; McCormick et al., 1996, 1998) and hydrology (Gottlieb et al., 2005, 2006; Thomas et al., 2006a), whereas interactions with naturally existing and disturbance-derived ion gradients are only recently being revealed (McCormick and Harvey, 2011). Their utility as indicators of ecosystem change has been proven; their time scale of response (days to months) is relevant to adaptive management and circumvents frustrating dependence on otherwise noisy data of the drivers themselves (Gaiser et al., 2004a; McCormick and Stevenson, 1998). Because changes in periphyton productivity or composition can elicit a response cascade affecting the experience of dependent organisms or regulatory biophysical features of the Everglades, it can serve as an early warning signal of impending change that provides an opportunity for corrective action before other less malleable wetland features are irrevocably altered (Gaiser et al., 2005). Their rapid, well-defined response to the variables targeted by restoration and their widespread distribution in the system has prompted integration of periphyton attributes into an ongoing system-wide assessment of ecosystem status (Doren et al., 2009; Gaiser, 2009). The consequences of changes in periphyton structure and function to other biophysical and ecological attributes are in some places measurable, in others delayed or confounded by temporal lags and complex linkages, and in many being revealed in pioneering synoptic multidimensional surveys and novel exploratory and experimental research.

The purpose of this chapter is to review existing Everglades studies to reveal underlying patterns of periphyton distribution throughout the Everglades ecosystem. The results of landscape surveys and experimental studies are examined to determine how natural patterns have been altered by changes in the primary environmental drivers in the Everglades. Although the implementation of periphyton-based tools in system-wide environmental assessment is a relatively new science in the Everglades, this chapter provides a review of the latest approaches and outcomes from recent and innovative assessment programs. Research on Everglades periphyton evolved sporadically, with only a few studies conducted prior to the 1990s (i.e., Browder et al., 1981, 1982, 1994; Grimshaw et al., 1993; Swift and Nicholas, 1987; Van

Meter-Kasanof, 1973; Wood and Maynard, 1974), followed by more concerted efforts as it became recognized as a salient ecological feature and evaluative tool in the system. As a result of this late blooming and then rapidly maturing scientific history, some particularly applied areas of periphyton biology are well understood in the Everglades whereas other topics, particularly taxonomic and ecophysiological aspects, are poorly understood relative to other ecosystems (Gaiser and Rühland, 2009). Here, we review the status of current research and end with a discussion of research needs in order to stimulate activity toward the most pressing issues.

PRESENT DISTRIBUTION PATTERNS OF PERIPHYTON IN THE EVERGLADES

The pre-disturbance distribution of periphyton in the Everglades ecosystem is difficult to hindcast because few early studies incorporated periphyton collections and paleoenvironmental records are poorly resolved owing to shallow, frequently oxidized sediments, and poor microfossil preservation. However, large-scale pattern relative to less mutable gradients in elevation and geology are reflected in the abundance, structure, and composition of periphyton communities according to the biogeochemical mosaic and resultant habitat types that characterize the managed ecosystem. The proximal driver of this mosaic of habitats is the underlying geology and geomorphology that influences water chemistry and hydrology, the ultimate drivers of periphyton structure and function (Browder et al., 1994). Here we distinguish periphyton communities of four distinct Everglades habitat types where it is abundant and has been at least cursorily studied: (a) the marl prairies and rocky glades, (b) the ridge and slough drainages of the central Everglades, (c) the soft-water marshes of Loxahatchee National Wildlife Refuge (Water Conservation Area 1 [WCA-1]), and (d) the coastal mangroves lining the coastlines of Florida and Biscayne Bays. We focus on the central Everglades ecosystem south of Lake Okeechobee; studies of periphyton in the lake have shown considerable compositional and functional similarity to southern Everglades communities (Havens et al., 1999), but we do not include the lake specifically in this review. Also, although periphyton is known to occur in sporadic abundance in the sink holes of tree islands and in the Big Cypress National Park, research on these communities is sparse if not entirely lacking. Calcareous epiphytic periphyton communities also occur in abundance in the expansive seagrass beds of Florida Bay, which are examined in detail in Frankovich et al. (2006, 2009) and Wachnicka (2009).

Marl Prairies and Rocky Glades

Along the shallow, intermittently flooded edges of the modern Everglades drainage, periphyton forms thick carbonate-rich accretions on the bedrock

FIGURE 1. Photos of Everglades periphyton: (A) epilithic mat in marl prairie, (B) epiphytic sweaters on *Eleocharis cellulosa* in wet prairie, (C) dried mat draped over scenscent vegetation in marl prairie, (D) thick epiphytic growth on *Bacopa macrocarpa* in Taylor Slough, (E) floating metaphytic mat in Shark River Slough, and (F) mats floating in the dwarf mangrove ecotone along Taylor River.

and on the stems of emergent macrophytes (Figures 1A and 1A). These extensive benthic mats occur in wetlands where hydroperiods of ~2–9 months limit the accretion of peat soils (Craft and Richardson, 1993) and are part of what distinguishes the southern marl prairies from other physiographic regions of the Everglades (Davis et al., 2005). Instead of peat, marl soils predominate, as calcium carbonate is dissolved from the limestone into the overlying dilute, shallow water where it is reprecipitated as productive benthic algae acquire dissolved inorganic carbon from the water column (see Hagerthey et al., 2011). Marl soils accrete at rates dependent on the spatial extent and production of mats (Gleason, 1972). A distinct and diverse wet prairie plant community described by Olmstead and Loope (1984) and Gunderson (1994) is rooted in the mat-covered marl, including sawgrass (*Cladium jamaicense*) and the prairie grasses *Schoenus nigricans*, *Muhlenbergia capillaris* var. *filipes*, *Schizachuyrium rhizomatum*, *Rhynchospora colorata*, and *Rhynchospora traycii*.

Periphyton production in marl prairies is regulated by water delivery and nutrient availability (Iwaniec et al., 2006) and is therefore highly seasonal. In the dry season, floating mats and thick epiphytic accumulations on plant stems (locally referred to as sweaters for their thick, fluffy, protective appearance) form a dry drapery over the vegetation that has been conjectured to smother supporting plants and thereby possibly exert some level of control on plant composition (Pimm, 1995; Figure 1C). Although the outer coating of this material can be desiccated, the underlying material often remains moist (Thomas et al., 2006a). This moisture is largely retained by copious polysaccharides produced in the wet season by coccoid cyanobacteria (Donar et al., 2004) and can sustain the algae, other microbes, plant roots, and inhabiting microfauna through the dry season. Upon rewetting in the wet season (through direct rainfall or managed water delivery), nutrients and enzymes can be rapidly desorbed from the periphyton mat into the water column (Gottlieb et al., 2005; Thomas et al., 2006a), stimulating new production. Recovering periphyton then sequesters most of the desorbed nutrients out of the water column quickly after reflooding and is thought to be responsible for maintaining the ambient marsh phosphorus levels of 5–10 μg L^{-1} indicative of oligotrophy (Noe et al., 2001; Thomas et al., 2006a). Biomass production in submersed periphyton mats then continues to exceed decomposition for approximately 3–4 months after rewetting at rates that can exceed 10,000 g m^{-2} yr^{-1} (Iwaniec et al., 2006). The thick mats can float up and down in the water column as gas builds up during the day and is then lost at night (Iwaniec et al., 2006), and this sloughed material, including sweaters cast from decaying stems, can be observed drifting downstream on the surface (Thomas et al., 2002). Periphyton biomass estimates during the peak of the wet season range from 2,000–4,000 g m^{-2} in the wet prairie (Ewe et al., 2006; Iwaniec et al., 2006), in most cases exceeding plant biomass and being an order of magnitude higher than comparable long-hydroperiod mats (Figure 1D; Gottlieb et al., 2005). The interaction between this large mass of periphyton and plant growth is not well understood, although shade manipulation experiments have failed to produce a considerable affect on production by either community (Thomas et al., 2006a).

Periphyton communities living in carbonate-rich water associated with such karstic features have a unique composition that is quite different from the soft-water communities characterizing most shallow depressions. As a result, most Everglades algal communities bear little compositional similarity to the well-documented algal floras of temperate North America or Europe and instead have a high degree of endemism or resemble those of other karstic freshwater wetlands (Rejmánková and Komárková, 2000), intertidal mangrove communities (Collado-Vides, 2000) and subtidal marine stromatolites (Rasmussen et al., 1993), although the biogeography of this flora has only been sparsely and recently examined (Gaiser and Rühland, 2009). *Chara* spp. (L.) is a common macroalgae in the short-hydoperiod mats and is often found interspersed with several poorly studied species of *Utricularia*, including *U. gibba* and *U. subulata*. These plants can facilitate the production of marl sediments when their production exceeds respiration, increasing the pH and causing calcium carbonate precipitation (McConnaughey, 1991). They form the backbone of support for filamentous cyanobacteria, particularly *Schizothrix calcicola* and *Scytonema hofmanni* (Gleason and Spackman, 1974), which also precipitate calcium carbonate in the microenvironment around their sheaths. These filamentous plants create a matrix that supports the growth of numerically dominant coccoid cyanobacteria, including species in the genera *Chroococcus*, *Chroococcidiopsis*, and *Aphanothece*, which are encased in a thick polysaccharide sheath that further serves to bind the periphyton mat together (Gottlieb et al., 2005) and resist drying (Thomas et al., 2002; Figure 2). The polysaccharide can comprise up to 90% of the volume of benthic periphyton mats (Donar et al., 2004) and serves as a substrate for colonization by other algae and bacteria. Compared to long-hydroperiod marshes, diatoms and green algae are rare in short-hydroperiod wetlands (<2% of biovolume), presumably due to their limited ability to withstand frequent drying (Gottlieb et al., 2005). These unique communities are among the most threatened in the Everglades because of the extent of short-hydroperiod habitat that has been lost along the margins of the system or due to the strong hydrologic manipulation in these habitats (shortened hydroperiods and artificially low water levels).

Ridges and Sloughs

In the Shark and Taylor River Slough drainages and in areas of the Water Conservation Areas where annual hydroperiods exceed 9 months on a regular basis, water lily (*Nymphaea odorata*) marshes are interspersed with wet prairies dominated by *Utricularia purpurea*, *Eleocharis cellulosa*, *Panicum hemitomon*, and *Sagittaria lancifolia* and higher elevation ridges dominated by *Cladium jamaicense* (Gunderson, 1994). These areas accrete peat soils yet generally remain replete in dissolved calcium carbonate, supporting periphyton communities that contain about 30% mineral matter (Gaiser et al., 2006a). Although the thick epilithic mats common in the marl prairie can be found in drier or higher elevation pockets in the ridges and sloughs,

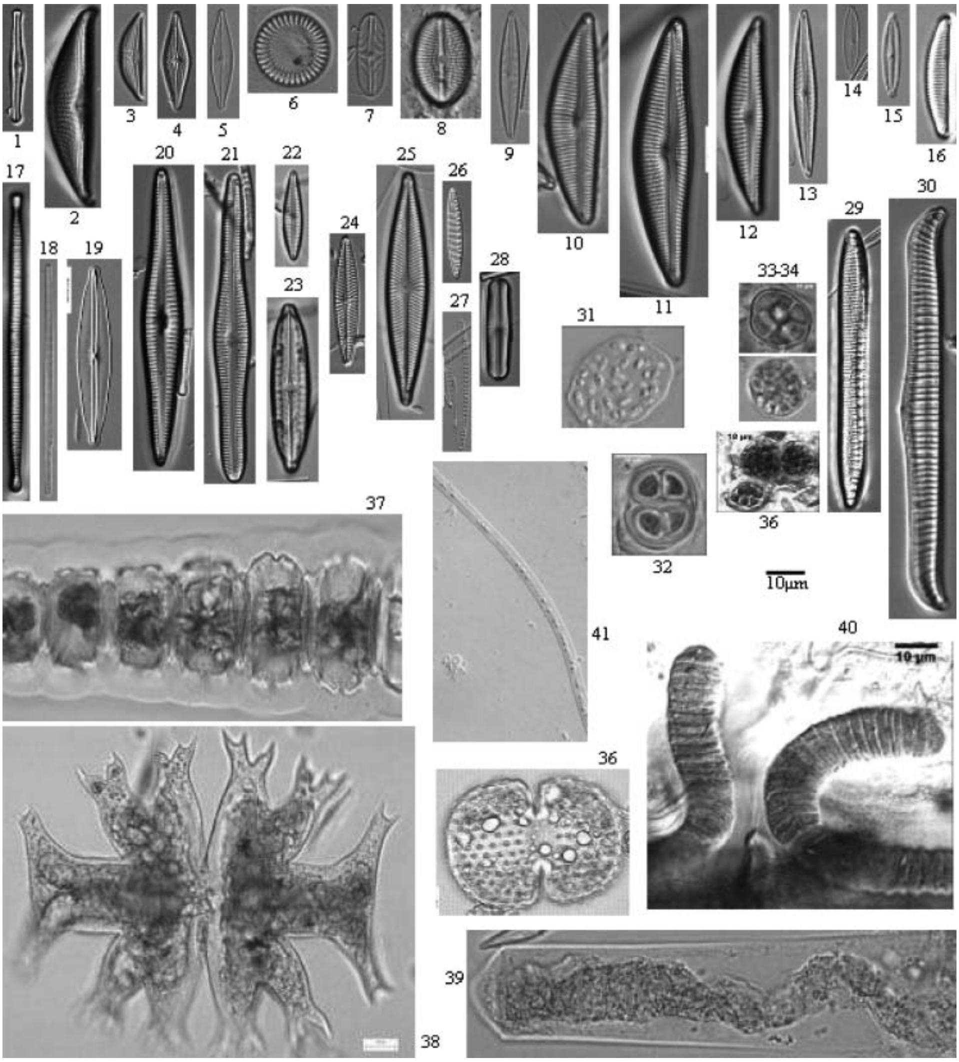

FIGURE 2. Photos of common Everglades algae: (1) *Achnanthes caledonica*, (2) *Amphora sulcata*, (3) *Amphora veneta*, (4) *Brachysira brebissonii*, (5) *Brachysira neoexilis*, (6) *Cyclotella meneghiniana*, (7) *Diploneis oblongella*, (8) *Diploneis parma*, (9) *Encyonema evergladianum*, (10) *Encyonema ftsp01*, (11) *Encyonema ftsp02*, (12) *Encyonema silesiacum* var. *elegans*, (13) *Encyonopsis egsp01*, (14) *Encyonopsis microcephala*, (15) *Encyonopsis subminuta*, (16) *Eunotia incisa*, (17) *Fragilaria synegrotesca*, (18) *Fragilaria nana*, (19) *Frustulia rhomboides* var. *crassinervia*, (20) *Gomphonema* cf. *intricatum* var. *vibrio*, (21) *Gomphonema* cf. *vibrioides*, (22) *Gomphonema parvulum*, (23) *Mastogloia smithii*, (24) *Navicula cryptotenella*, (25) *Navicula radiosa*, (26) *Nitzschia amphibia*, (27) *Nitzschia palea* var. *debilis*, (28) *Sellaphora laevissima*, (29) *Nitzschia serpentiraphe*, (30) *Rhopalodia gibba*, (31) *Aphanothece sp.*, (32) *Chroococcus sp.*, (33–34) *Chroococcidiopsis sp.*, (35) Unknown colonial alga, (36) *Cosmarium reniforme*, (37) *Desmidium grevilii*, (38) *Micrasterias crux-melitensis*, (39) *Mougeotia sp.*, (40) *Scytonema hofmannii*, (41) *Schizothrix calcicola*.

periphyton is more commonly found in loosely aggregated associations with the most common submersed macrophyte, *Utricularia purpurea*, and on the stems of the other emergent plants (Figure 1E). In very dense stands of tall *Cladium jamaicense*, periphyton biomass can be quite low relative to that of the neighboring slough (Gottlieb et al., 2005). However, strong winds and tropical storm activity have been observed to cause slough-generated periphyton to pile up on the edges of sawgrass ridges, perhaps contributing to organic matter accretion while also supplying nutrients.

Gottlieb et al. (2006) compared the composition of periphyton communities in marl prairie and slough, and found that although there was significant compositional overlap (77% of species were found in both habitats), larger differences were observed in the relative abundances of common taxa. Cyanobacteria dominate both communities, and slough mats are similarly dominated by *Schizothrix calcicola* and *Scytonema hofmannii*; however, diatoms comprised a greater proportion than observed in the marl prairie. Common diatoms in slough periphyton mats include *Achnanthes caledonica*, *Brachysira neoexilis*, *Cyclotella meneghiniana*, *Encyonema evergladianum*, *Mastogloia smithii*, *Nitzschia palea* var. *debilis*, and *Nitzschia serpentiraphe* (Figure 2; Slate and Stevenson, 2007), as well as a diversity of poorly defined morphotypes related to the *Gomphonema vibrio* complex (Tobias and Gaiser, 2006). In permanently inundated sites, *F. synegrotesca* is particularly abundant, and possibly a reliable indicator of the absence of periodic drying. These highly endemic communities are very susceptible to nutrient enrichment and are quickly replaced by widespread eutrophic taxa when exposed to above-ambient sources of P (Slate and Stevenson, 2007). Although enriched communities occur naturally, for instance in the deeper sloughs surrounding P-rich tree islands, they are expanding as discussed in great detail subsequently.

Soft-Water Communities

Although calcareous periphyton mats are emblematic of the central Everglades, equally important are soft-water algal communities, best represented in WCA-1. Surface waters in WCA-1 are derived largely from rainfall in contrast to other parts of the ridge and slough region that are more strongly influenced by mineralized canal discharges. Consequently, they provide an ion-depleted environment to the algae that more closely resembling that of the isolated wetlands and ponds of the Atlantic Coastal Plain (Gaiser and Johansen, 2000; Siver et al., 2005). Although some species are held in common with the calcareous Everglades, instead of being dominated by cyanobacteria, communities in the Refuge contain diverse and abundant chlorophytes, particularly desmids, and a diverse diatom community (McCormick and Harvey, 2011; Swift and Nicholas, 1987). Water draining into conveyance canals surrounding the Refuge have caused mineral levels around the Refuge perimeter and, in some places, several kilometers into the interior, to increase (McCormick and Harvey, 2011). Evidence from paleoecological and ongoing monitoring efforts in the northeast Everglades (northern WCA-2A) suggest that the system was once less calcareous than it was and that canal excavation and flows have increased calcium carbonate supply to the interior (Slate and Stevenson, 2000; Winkler et al., 2001). These issues are discussed in the following section on salinity.

Mangrove Ecotone

As water meanders through the Everglades drainage toward the coast, salinity increases and plant communities change but calcareous mats remain a conspicuous component of the ecosystem. The shallowly inundated mangrove marshes along existing and historic drainages, particularly those now occupied by sparse, dwarf mangrove forests, often support thick benthic and floating mats similar in appearance to those occurring in the upstream freshwater marsh (Figure 1F). These are particularly abundant in the Taylor River drainages and along the coastline of Biscayne Bay (the Biscayne Coastal Wetlands; Gaiser et al., 2004b). Encrustations of algae are commonly seen around the prop roots of *Rhizophora mangle*, and wide expanses of epilithic periphyton mats are observed in the white zone ring of low vegetation density, described by Egler (1952) and Ross et al. (2001). Some of the same stromatolitic species predominate in these mats, particularly *Scytonema* and *Schizothrix* species (Wachnicka and Gaiser, 2007). These genera both contain species representing the full salinity spectrum, and indeed some of the species appear capable of thriving across a broad range of salinity regimes (Gaiser et al., 2004b; Ross et al., 2001). In the Everglades, these communities are sometimes displaced by noncalcite precipitating cyanobacteria in communities closer to the coast, including *Lyngbya* and *Microcoleous*, which have been collected from mangrove pneumatophores elsewhere (Hussain and Khoja, 1993). These taxa are indicative of higher phosphorus availability (McCormick and O'Dell, 1996), and the high biomass of some mangrove communities may be enhanced by associations with N-fixing pneumatophore bacteria as well as coastal supplies of phosphorus, observed to enhance mat TP concentrations along the coastal fringe. Although 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 polysachharide produced by abundant and diverse coccoid cyanobacteria, which may increase dessication resistance, provide a barrier to fluctuations in salinity, and concentrates nutrients and enzymes that control nutrient cycling.

The most diverse algal components in the periphyton mats of the mangrove ecotone are 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 (Cooper et al., 2009). The dominance of *Amphora* and *Mastogloia* in the coastal flora is similar to findings in other parts of Florida and the Caribbean (for a review, see Wachnicka, 2009). These genera, together with *Navicula*, *Nitzschia*, *Cocconeis*, *Fragilaria*, and *Achnanthes*, are probably important in coastal floras circumglobally, at least in the Northern Hemisphere. However, at lower taxonomic levels many taxa not reported elsewhere (or insufficiently described) may be unique to the subtropical and tropical Atlantic coast (Wachnicka 2009). Wachnicka and Gaiser (2007) described 21 new species in two common genera from the mangrove zone and shallow seagrass beds of Florida and Biscayne Bays, and many more remain to be described, indicating both the respectable degree of endemism and paucity of taxonomic attention received by the coastal Caribbean diatom flora.

CHANGES IN DISTRIBUTION CAUSED BY ANTHROPOGENIC DISTURBANCE

Although some of the distinctive landscape patterns observed in the Everglades result from natural underlying biogeochemical gradients (Davis et al., 1994), the biophysical template of the Everglades has been fundamentally altered by land conversion and water management that greatly modify the current expression of the ecosystem. In the absence of quality predrainage data on Everglades periphyton, it is difficult to discern natural from disturbed settings, and in any respect, the entire ecosystem can be considered disturbed and is likely quite different from the predrainage setting. However, with attempts toward restoring more natural water flow and quality on the horizon, we can observe how the present configuration of anthropogenic influences have modified and continue to transform communities by tracking them over time and in space relative to known stressors. Here we review ongoing periphyton assessments and experimental studies that have revealed the relationships between periphyton attributes and water quantity and quality parameters, particularly phosphorus, hydrology, and ion concentration, which have received the most attention. We emphasize periphyton parameters that appear to reliably indicate ecosystem change in response to alterations in these abiotic drivers and highlight regions of the Everglades where evidence exists for change in response to management actions.

Effects of Phosphorus Enrichment

Enrichment by phosphorus draining to canals, then marshes, from surrounding fertilized agriculture and urban landscapes poses one of the greatest water quality threats to the ecology of the historically oligotrophic Everglades (Noe et al., 2001). The productivity and composition of benthic algal communities change quickly in response to elevated concentrations of limiting nutrients due to the short-generation times and differing competitive abilities of algal taxa (Stevenson et al., 1996). For this reason, algae are regularly employed in water quality assessments (McCormick and Cairns, 1994; Stevenson, 2000) although applications in wetlands have lagged behind other ecosystems (Gaiser and Rühland, 2009; Pan et al., 2000). Indeed, the past several decades of research on periphyton responses to phosphorus in the Everglades have set the stage for indicator development, not just for the Everglades but for other wetland ecosystems experiencing similar water quality impairments (Gaiser, 2009; McCormick and Stevenson, 1998). The effects of phosphorus enrichment on periphyton in the Everglades have been examined through descriptive work along known P-enrichment gradients and through controlled experiments to determine the mechanisms, loads, and concentrations that cause the observed patterns (Browder et al., 1982; Cooper et al., 1999; Gaiser et al., 2006a; Grimshaw et al., 1993; Hagerthey et al., 2008; McCormick et al., 1997; McCormick et al., 2009; McCormick and O'Dell, 1996; McCormick et al., 1996; McCormick et al., 1998; Pan et al., 2000; Raschke, 1993; Swift and Nicholas, 1987; Vymazal and Richardson, 1995). Together, these studies have shown that any sustained P enrichment beyond what would naturally be experienced in the marsh causes measurable changes in periphyton production and composition. One of the easiest and most reliable measures of increased P exposure is the increased P concentration in the periphyton biomass (Gaiser et al., 2004a). Because the system is shallow and oligotrophic, any excess P delivered to the system is quickly sequestered by the microbial community at rates and concentrations reflective of P load. Unless this community is saturated in P, excess P delivered to the system is not recognized in a water column TP measurement (unlike pelagic ecosystems, where this P would be measurable in a water sample containing plankton). Therefore, in the Everglades and other naturally oligotrophic benthic environments, water quality surrogates are necessary to accurately detect and quantify enrichment (Gaiser et al., 2004a).

As periphyton sequesters excess P from the water column, productivity of the more competitive taxa of both algae and bacteria increases. Least competitive in this interaction are the calcareous filamentous and coccoid cyanobacteria and endemic Everglades diatoms, whereas green algal taxa, especially *Mougeotia* spp., and widespread eutrophic diatoms, such as *Gomphonema parvulum* and *Nitzschia amphibia*, found in low abundance in native mats, are favored (Gaiser et al., 2006a; McCormick and O'Dell, 1996; Figure 2). Bacterial productivity is also stimulated, shifting the balance between autotrophy and heterotrophy in the mat, although compositional and functional changes in bacterial communities have not been examined. A common consequence of enrichment, observed experimentally and along enrichment gradients in the Everglades, is disintegration of the calcareous, cyanobacterially dominated mat and replacement by a mucilaginous,

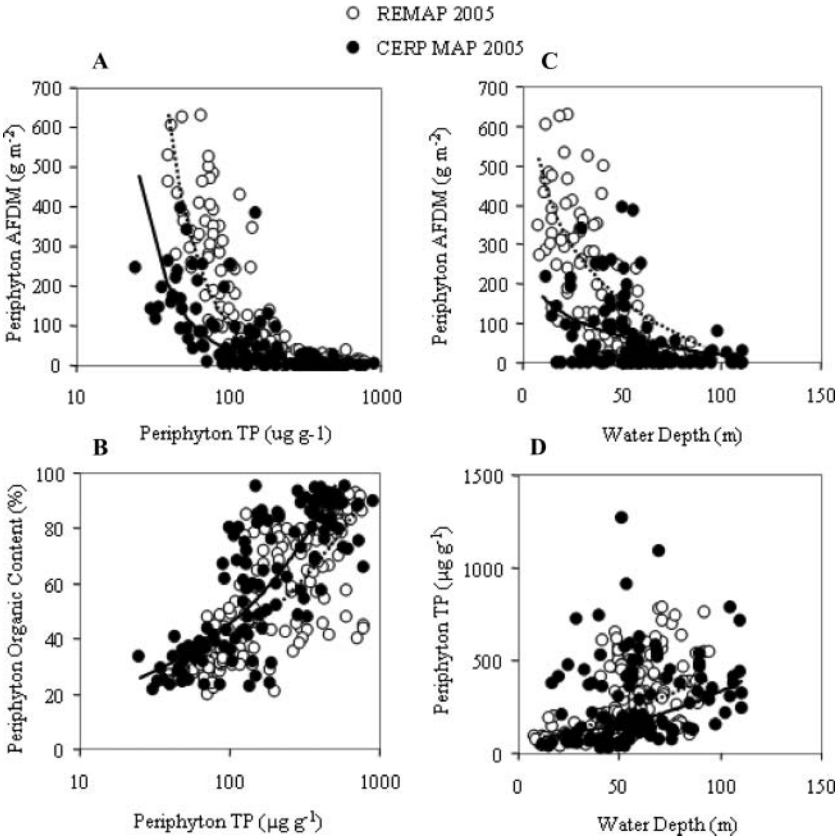

FIGURE 3. Relationships between periphyton attributes in system-wide USEPA REMAP (white circles) and RECOVER (filled circles) surveys: (A) pervasive inverse relationship between periphyton ash-free dry mass (AFDM) and total phosphorus (TP), (B) positive relationship between periphyton organic content and TP, (C) negative relationship between periphyton AFDM and water depth, and (D) positive relationship between periphyton TP content and water depth.

green-algal-dominated community (Gaiser et al., 2005; McCormick and O'Dell, 1996; McCormick et al., 2001; Figure 3A).

Metabolically, increased O_2 production has been measured during this transition (McCormick et al., 1997), whereas the absolute organic biomass of periphyton mat declines (Gaiser et al., 2005; Figure 3B). A three-step process has been postulated for the disintegration of periphyton mats upon phosphorus exposure: (a) increased production of bacteria that consume accumulated polysaccharide and detritus that leads to (b) increased CO_2 consumption and dissolution of calcium carbonate matrix that is (c) gradually replaced by a more competitive green-algal community. Although the mechanism of this shift is poorly understood (see Hagerthey et al., 2011), the loss of calcareous mat and replacement by loosely aggregated green algal assemblage is well described for most regions of the calcareous Everglades. However, eutrophic assemblages appear to be a transient community, as sustained eutrophication commonly leads to monospecific cattail stands that do not support periphyton, either because of shading (Grimshaw et al., 1993) or allelopathy conferred by the dense stands (McCormick et al., 1998; Thomas et al., 2006b).

Data from periphyton collections along known enrichment gradients and from large-scale system-wide surveys are key to assessing patterns of water quality degradation, particularly when it is acknowledged that these microbial assemblages can offer an early warning of changes that could be reversed before cascading to a persistent, highly modified ecosystem state. Gaiser et al. (2006a) reported changes in periphyton attributes from collections taken in 1999 and 2000 along transects downstream of water control structures in WCA-1, WCA-2A, WCA-3A, Shark River Slough (SRS), and Taylor Slough (TS). Total P concentrations in periphyton provided a better indication of P loading history than water column TP concentrations, and reached asymptotic levels in WCA-1, WCA-3A and SRS at 3, 1, and 1 km downstream of the sources, respectively. Though periphyton TP also declined exponentially in WCA-2A, values 14 km from the source were higher (500 μg P g^{-1}) than levels measured in the interior of SRS ($\sim$150 μg P g^{-1}). By contrast, concentrations in calcareous mats of TS were low throughout ($M = 124$ μg P g^{-1}) and unrelated to distance from the canal phosphorus source. Periphyton biomass was negatively correlated with TP within and among these marshes. Taxonomic responses to P enrichment were strong, and included changes in both diversity and composition. Diatom diversity in native Everglades calcareous periphyton communities is low compared to other wetland ecosystems (average 22 taxa per sample) and has been shown to increase in response to enrichment (Raschke, 1993). Significant reductions in diversity (Shannon-Weiner H') with distance from canal P sources were shown in WCA-1A, SRS, TS, and WCA-2A, although the site closest to the canal and most severely enriched in WCA-2A had very low diversity (only 7 taxa; Figures 4A and 4B).

Transects in SRS and WCA–3A sampled by Gaiser et al. (2006a) were aligned closely with those of the 1990–1991 survey reported by Raschke (1993), enabling a temporal comparison of diversity trends. Although taxonomic inconsistencies between these studies preclude interpretation of absolute H' values, the trends are similar, although it is possible that the earlier study shows water quality impairment further to the interior of both marshes than the Gaiser et al. (2006a) study (Figure 4A). Both studies showed a strong relationship between diversity and metrics of phosphorus availability—sediment TP in Raschke (1993), periphyton TP in Gaiser et al. (2006a for SRS, $R^2 = .65$ and .93, respectively (Figure 4C). The taxonomic responses responsible for these changes were difficult to compare between studies because of changes in nomenclature, but in Gaiser et al.'s (2006a)

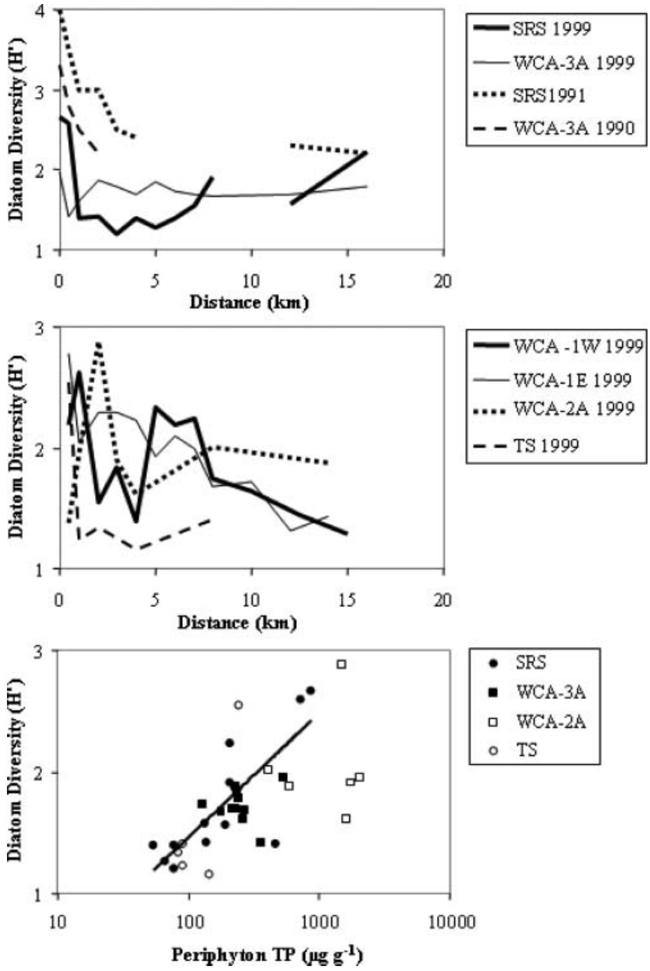

FIGURE 4. Relationships between Shannon-Weiner Diversity (H') and (A) distance into Shark River Slough (SRS) and Water Conservation Area 3A (WCA-3A) from the C-12 discharge gates on the Tamiami canal, measured in 1990 and 1991 by Raschke (1991; redrawn from graphics) and in 1999 by Gaiser et al. (2006a); (B) distance away from canal inputs in Water Conservation Area 1 (WCA-1), Water Conservation Area 2A (WCA-2A), and Taylor Slough (TS); and (C) periphyton TP concentration in SRS, WCA-3A, WCA-2A, and TS.

study, taxa were identified as significant indicators of P availability according to their optimal location along the measured gradient (calculated by weighted averaging, in μg P g^{-1}). Low P taxa (100–300) included *B. neoexilis*, *M. smithii*, *E. evergladianum*, *E. microcephala*, and *F. synegrotesca*; medium P taxa (300–500) included *Eunotia flexuosa* and *Navicula cryptotenella*; and high P taxa (>800) included *Eunotia incise*, *Rhopalodia gibba*, *Amphora veneta*, *Nitzschia amphibia*, and *Gomphonema parvulum* (Figure 2).

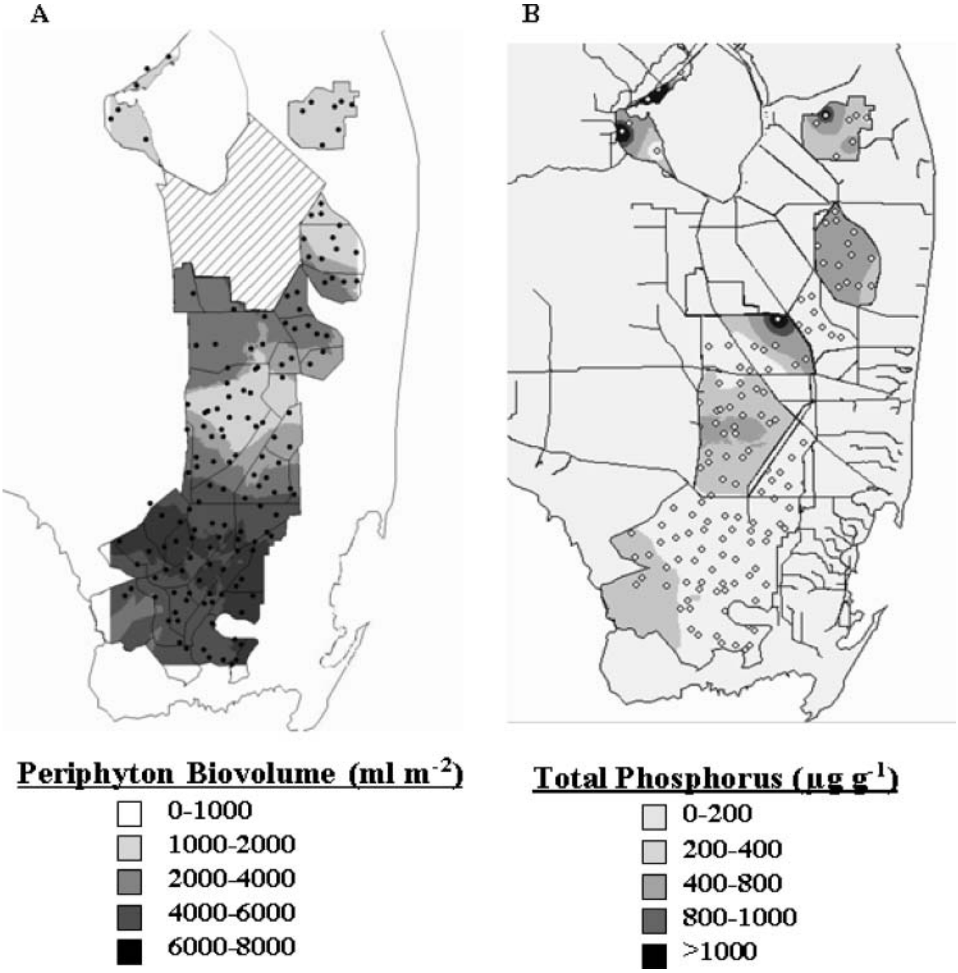

FIGURE 5. Distribution of the (A) volume and (B) total phosphorus content of periphyton collected in 2005 REMAP and RECOVER surveys.

Large-scale assessment efforts by the RECOVER Monitoring and Assessment (Comprehensive Everglades Restoration Plan, 2005) and the U.S. Environmental Protection Agency REMAP (Scheidt and Kalla, 2007) programs include collections of a full suite of chemical, physical, and biological parameters relevant to restoration assessment, including periphyton (Trexler et al., 2008). Results of the fall 2005 survey revealed an inverse relationship between periphyton biovolume and TP concentration (Figure 5). For assessment purposes, absolute values were compared to expectations derived from Gaiser et al.'s (2006a) cross-system transect and experimental study. Standing stocks and TP values in the interior of WCA-3A were found to be lower and higher, respectively, than expected, indicating a combination of increased

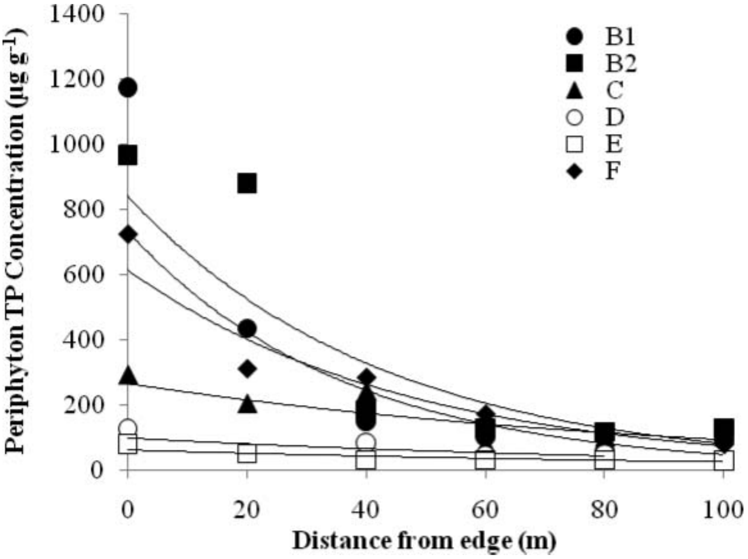

FIGURE 6. Periphyton phosphorus concentration gradients along 100-m transects perpendicular to the S-332 detention basins on the eastern boundary of Everglades National Park, measured in November 2005 (B1, B2 downstream of basin B (north and south), C and D, respectively; E and F are north of basin B).

hydroperiod and phosphorus loading to this marsh. This contrasts to the interpretation of relatively high TP concentrations in WCA-1 and the estuary of SRS, where prior data would suggest values are naturally elevated in these areas. Because these surveys are designed to detect impairment in the less susceptible marsh interior, they are coupled with continued transect surveys closer to canal P sources. Cause for concern has emerged from collections along the eastern boundary of Everglades National Park, where overflow from the S-332 detention basins or seepage from enriched groundwater are causing enrichment gradients 100–200 m to the west of the levee edge of the basins (Gaiser et al., 2008; Figure 6). This is particularly obvious in elevated periphyton TP concentrations, lower than expected periphyton biomass and the presence of high-TP diatoms near detention ponds B and C near the head of Taylor Slough, and these trends appear to be worsening with time (Gaiser et al., 2008).

Effects of Hydrologic Modification

The creation of WCAs, in combination with agricultural and urban development, has caused a loss in spatial extent and connectivity in the Everglades. In places where natural patterns of water flow from the north were cut off,

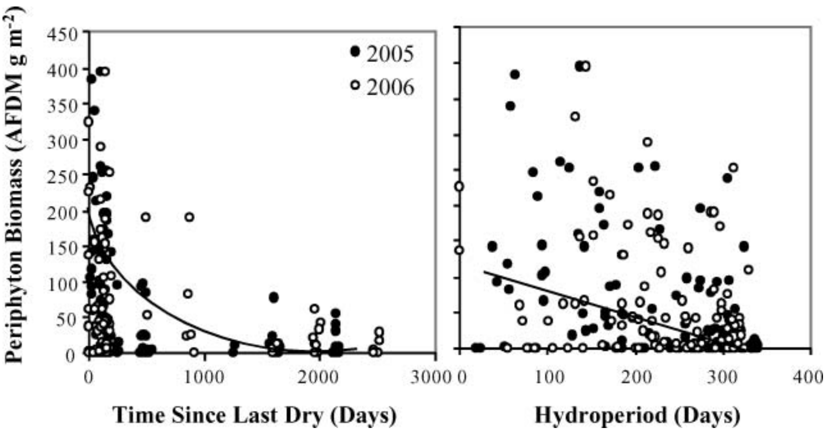

FIGURE 7. Inverse relationship between periphyton biomass and time since last dry and hydroperiod from the RECOVER (2005, 2006) and REMAP (2005) whole-system assessments.

such as in northeast SRS, much of WCA-2A, and northern WCA-3A, hydroperiods have shortened and droughts have more severe consequences (Davis et al., 2005). Much native ridge and slough habitat has been converted to marl prairie (particularly the northeastern portions of SRS) and former marl prairie and rocky glades habitats have been converted to farmland and housing (Davis et al., 1994). On the other hand, some places are experiencing extended hydroperiods and drying pattern reversals, such as southern WCA-3A where the Tamiami Trail (and associated L-29 stage constraints) and the S-12A and S-12B gate closures create extended hydroperiods even during extended dry seasons. Similarly, the L-31 and C-111 canal systems have resulted in very flashy and unseasonable flows into TS.

The shortening of hydroperiods due to drainage activities has influenced periphyton structure and composition, increasing the extent of benthic mats where hydroperiods have shortened and eliminating them in the vast areas that have been converted to urban use or agriculture. It is likely that benthic mats once extended well to the east of the present Everglades, lining the transverse glades that are now virtually absent (Ruiz and Ross, 2004). Further reduction in hydroperiod in existing marl prairies can result in loss of diatom and green algal species in the periphyton mat, leaving the mat to comprise mostly mat-forming filamentous cyanobacteria and associated calcitic matrix (Gottlieb et al., 2005). Short-hydroperiod mats have an order of magnitude higher areal dry weight and ash-free dry weight (organic) biomass than long-hydroperiod mats and the inorganic (primarily calcitic) portion of the biomass is much larger in short- than long-hydroperiod periphyton mats (70–90% vs. 30–70%, respectively; Gottlieb et al., 2005, Figure 7). This shift can influence consumer communities, as short-hydroperiod periphyton assemblages are coated with calcium carbonate crystals that impede digestion by most grazers (Browder et al., 1994; Trexler et al., 2008) and the matrix of cyanobacterial filaments creates pocketed refuges for more edible algae, making them less accessible or potentially inaccessible to consumers (Geddes and Trexler, 2003). The effect of decreased hydroperiod on net annual production of periphyton mats has not been elucidated, but because periphyton production is limited to periods during which the mats are flooded, the severe reductions in wet season duration experienced in the eastern Everglades likely has substantially decreased annual production. Reduced periphyton production would decrease marl soil accretion rates in areas with hydroperiods reduced below 1–2 months per year. Interpreting changes in water depth or hydroperiod from periphyton attributes is complicated by complex interactions of these attributes with water quality parameters. Increased periphyton TP concentrations and organic matter content are associated with increasing water depth. Indeed, tracking hydrologic change from periphyton attributes is promising, as periphyton mats have been shown to converge structurally and compositionally when exposed for long duration to the same hydroperiod regime (Gottlieb et al., 2006). Additional solution holes, found in the marl prairie landscape, which have intermediate hydroperiods, fall somewhere in the middle structurally and functionally between long- and short-hydroperiod mats. This indicates that shifts in periphyton composition due to changes in water delivery to the Everglades should be readily visible, making periphyton a useful early indicator of impending change at the ecosystem level.

The Recovery Monitoring and Assessment (RECOVER 2005, 2006) and U.S. Environmental Protection Agency REMAP (REMAP 2005) surveys showed a decrease in water depth and hydroperiod from the Water Conservation Areas to the base of Shark River and Taylor Sloughs that roughly corresponded to patterns in periphyton biovolume. Biovolume increased significantly with decreasing hydroperiod and number of days since last dry, although sites in the driest parts of northeast SRS fell below the best fit line, indicating lower biomass than would be predicted by the model (Figure 7). It is likely that the low biovolume values to the interior of WCA-3A are due to the combination of extended hydroperiods and increased P availability in this wetland. The absence of long-term monitoring or paleoecological data from these regions precludes an interpretation of the direction of change in periphyton attributes experienced by these wetlands. However, the optimal hydroperiod for each algal species collected in the RECOVER and REMAP programs was estimated using the hydroperiods estimated from the EDEN network (Conrads and Petkewich, 2009). The site hydroperiod for each site was then estimated by weighting the abundance of each species by its hydroperiod optimum. About one third of the variability of hydroperiod (estimated by EDEN) was explained by diatom and soft algae species composition ($R^2 = .34$), with an estimate error of only 73 days of the measured hydroperiod value (Trexler et al., 2008). Species showing strong individual responses to hydrologic variables included the diatoms *Nitzschia serpentiraphe* and *Nitzschia palea* var. *debilis* and the cyanobacterium *Scytonema hoffmannii* that were most abundant in shallow, short-hydroperiod sites throughout SRS and TS; and the green alga *Mougeotia* spp., the blue-green algae *Schizothrix calcicola* and *Rhabdonema linearis*, and the diatoms *Encyonema* ftsp01 and *Fragilaria synegrotesca* that were most abundant in deeper, long-hydroperiod sites of WCA-3A (Figure 2). Together, these results support those suggested from experimental work of Gottlieb et al. (2006) but this is the first study to show concordance of these relationships at very large spatial scales.

Effects of Changing Ion Concentrations

Changes in ion chemistry, an expected result of canal excavation and drainage, can modify $CaCO_3$ delivery and, also, possibly, ion seepage from groundwater (McCormick and Harvey, 2011; Price et al., 2006). Swift and Nicholas (1987) showed that periphyton growth rates in the Everglades were significantly influenced by site differences in water quality (i.e., major ion content, pH, and phosphorus composition) independent of hydrologic factors. Increased water delivery from canals increases the supply of calcium and bicarbonate as well as other ions including magnesium, sodium, potassium, chloride, and sulfate (McCormick and Harvey, 2011). Increased mineral loads encourage development of benthic periphyton dominated by calcite-precipitating blue-green algae. In fact, shifts from high-diversity green algae, diatom, and cyanobacteria assemblages to mats dominated by filamentous cyanobacteria have been noted in paleoecological studies of areas adjacent to canals, where water management alterations increased pH and ion concentrations in downstream marshes (Slate and Stevenson, 2000). Northern areas of WCA-2A were found to have been peat-accreting environments prior to the dredging of peripheral drainage canals, providing a buffer between the water column and limerock underneath. Acidity and conductivity were likely lower than at present, and under such conditions, extensive calcareous mats in this region would have been improbable. Instead, WCA-2A may have supported communities similar to those of the interior of WCA-1 (Slate and Stevenson, 2000).

The transition of periphyton communities in northern WCA-2A from low- to high-conductivity characteristics may have occurred abruptly in the 1960s after modifications to the water-management system (Slate and Stevenson, 2000). The effects extend through the interior of WCA-2A as indicated by the dominance of calcareous cyanobacteria mats (McCormick et al., 1996, McCormick et al., 2009). Similar changes have occurred in WCA-1, where conductivity measured along the margins of the peripheral canal system is elevated due to canal water intrusion into this rainfall-driven wetland (Figure 8A; Hagerthey et al.,). At a near-canal site in the WCA-1 marsh,

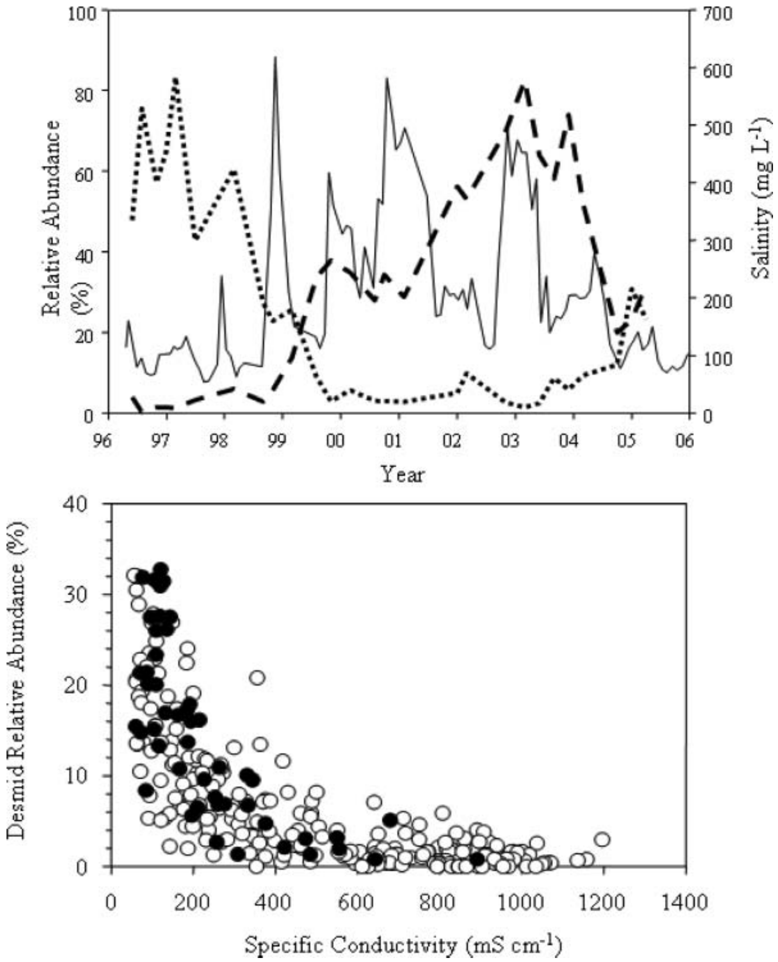

FIGURE 8. (A) Change in periphyton species composition at a site (X4) in WCA-1 as a function of variable salinity (conductivity). Dotted line represent the total relative abundance of algae indicative of low salinity (e.g., desmids and the diatom *Brachysira brebissonii*). Dashed line represents the total relative abundance of taxa indicative of high salinity (e.g., the diatoms *Mastogloia smithii* and *Encyonema evergladianum*). (B) Change in the relative abundance of desmids along a salinity gradient in WCA-1.

high conductivity values were associated with increases in diatom taxa normally associated with calcareous periphyton mats of the southern Everglades, including *Mastogloia smithii* and *Encyonema evergladianum* (Figure 8A). These have displaced desmid algae, which show a strong negative response to increasing conductivity (Figure 8B). Where desmids are abundant, low-conductivity diatoms typical of historical conditions in WCA-1 are also present (*Brachysira serians*, *Cymbella amphioxys*, *Frustulia rhomboides* var. *crassinervia*) but these are displaced toward the periphery of the marsh by high-conductivity diatoms, *M. smithii*, *E. evergladianum*, *Cymbella ruttneri*, *Fragilaria vaucheriae* v. *longissima*, and *M. smithii* v. *lacustris*.

Biological effects of increases in conductivity have also been noted in coastal mangrove communities subject to saltwater encroachment, particularly along the Biscayne coastline where the L-31E canal has reduced freshwater dispersion to the coast and thwarted any interior-ward migration of communities as sea level rises. As a result, freshwater gramminoid communities normally supporting prolific periphyton mats have been nearly eliminated and the white zone, an area of very low productivity visible from satellite imagery, have been expanding (Ross et al., 2001). Periphyton-associated mollusks were used to reconstruct the rates of these changes from dated sediment cores to reveal over 90% of freshwater wetlands have been lost from the Biscayne coastline due to lateral saltwater encroachment rates, calculated to average 3.1 m yr^{-1} for the last 70 years (compared to 0.14 m yr^{-1} for the predrainage period; Gaiser et al., 2006b). Diatom assemblages associated with very high conductivities have been expanding in the white zone and in former transverse glade depressions that are no longer regularly connected to freshwater (Gaiser, 2004b).

INDICATOR DEVELOPMENT AND FUTURE WORK

Major advances have been made in last two decades in our knowledge of the distribution of periphyton abundance and composition in the Everglades. Experimental research has led to a better understanding of the drivers of compositional pattern, although strong interactions among many drivers complicate inferences about the source of changes observed in contemporary survey and deserve attention through multifactorial controlled experiments. Interpreting the direction of restorative change, or further degradation, from ongoing monitoring and assessment programs is promising. However, these interpretations could be strengthened by further attention to the following topics: (a) development of a web-accessible algal taxonomy archive to improve concordance among researchers, meta-analyses of past and ongoing collections, and our interpretation of species' autecologies and biogeography; (b) coordinating multiagency periphyton monitoring efforts to improve ability to detect change at multiple spatial and temporal scales; (c) molecular exploration of microbial components, including bacteria and fungi, that would contribute to better resolved interpretations of periphyton distribution in space and time at all levels of organization species; (d) better understanding of multidimensional drivers of change, including those not yet well investigated (i.e., micronutrients and contaminants); (e) continued long-term collections at permanent monitoring sites to improve evaluations of natural temporal variability to guide management expectations; (f) continued quest for well-preserved paleoecological records of diatoms or other proxies to improve periphyton targets for natural systems models; (g) increased attention to threats to endemic species and their engineering function in the coastal ecotone, confronted by both short-term management changes and long-term sea level rise; (h) increased attention to functional metrics of change, including physiological and metabolic attributes that have not been well investigated (Hagerthey et al., 2011); and (i) effects of hydroperiod on community biogeochemical function (Will structural shifts toward blue-green algae lead to changes in N concentration and loads entering estuarine systems?). With added attention to these topics, it may be possible to integrate periphyton into a model of whole-ecosystem response to further human disturbance, management, and restoration in this threatened landscape.

The managed Everglades differs from the predrainage ecosystem in fundamental ways, including spatial extent and connectivity, hydrologic (hydroperiod, depth, and flow) regimes, and water quality. Likewise, the composition and distribution of periphyton across the managed system also differs from predrainage times and current characterizations of reference or minimally impacted conditions may be poor predictors of future restored conditions in some areas. In fact, the absence of historical accounts of conspicuous periphyton communities within the Everglades prior to significant drainage suggests that periphyton may not have been as abundant, at least across portions of the ecosystem, as it is at present. Restoration of historic flow regimes would convert presently impounded, static wetlands into flowing environments and would certainly influence periphyton attributes in affected areas. And, achieving hydrologic restoration using waters that are elevated in phosphorus or major ions such as calcium also alter periphyton landscape patterns. Understanding periphyton responses to projected flow regimes and attainable water quality conditions under different restoration scenarios allows scientists and managers to evaluate the ecological consequences of restoration and the potential for unanticipated periphyton responses that may not be deemed desirable by the metrics contained in present assessment programs (e.g., Gaiser et al., 2008).

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