

1 **Landscape Patterns of Periphyton in the Florida Everglades**

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9 **Running Head: Everglades Periphyton Distribution**

10
11 **Abstract**

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

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23 **Keywords:** periphyton, algae, Everglades, benthic mats, phosphorus, hydrology, restoration

1 **Introduction**

2

3 Submerged surfaces in wetlands, littoral zones and shallow ponds often support abundant
4 quantities of benthic algae. The Everglades is no exception, where benthic algae and associated
5 bacteria, fungi and microfauna (colloquially, “periphyton”) form thick mats that blanket shallow
6 limestone sediments, coat submersed stems of macrophytes and form floating rafts that drift
7 along the surface of the water. Except in areas that are unnaturally enriched in phosphorus or
8 have a significantly shortened hydroperiod, periphyton can be found in abundance throughout
9 the Everglades ecosystem, from the loose, flocculent aggregations in the soft-water Loxahatchee
10 National Wildlife Refuge, to the thick, calcareous mats of the central Everglades sloughs, to
11 benthic mats found in marl prairies, to the aggregations around mangrove pneumatophores in
12 estuary ecotones. Although widespread, not all Everglades periphyton communities are the same.
13 There is significant spatial variability in abundance, appearance and species composition that is
14 not only functionally meaningful but also can indicate areas of concern for water management in
15 the highly regulated Everglades ecosystem (Gaiser 2009).

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17 Because of their abundance and widespread distribution, periphyton communities are considered
18 to be primary ecosystem engineers in the Everglades (McCormick & Stevenson 1998). Thick
19 accumulations full of mucopolysaccharides secreted by algae and bacteria can stabilize
20 underlying sediments and retain moisture during droughts, preventing desiccation (Donar et al.
21 2004; Thomas et al. 2006). They also sequester nutrients from the water column and can serve as
22 sites for long-term nutrient storage and recycling by resident algae, bacteria and animals that
23 mutualistically interact in these tightly aggregated assemblages (Iwaniec 2008). Estimates of

1 annual net primary production ranging from 100-10,000 g m⁻² yr⁻¹ (Iwaniec et al. 2006, Ewe et
2 al. 2006) compared to reported averages of 10-50 g m⁻² yr⁻¹ from other wetland types (Vymazal
3 et al. 1995), appear paradoxical given the oligotrophic nature of the Everglades (water total
4 phosphorus concentrations in the un-enriched interior averages <10 µg l⁻¹; Noe et al. 2001,
5 McCormick et al. 2002). At these rates, periphyton may constitute a significant sink for
6 atmospheric CO₂, although the ultimate fate of this production is unknown. While it is clear that
7 periphyton can regulate water column oxygen concentrations (McCormick et al. 1997,
8 McCormick and Laing 2003) and aquatic NEP, GPP, and R (Hagerthey et al. submitted),
9 periphytic algae are also converting dissolved inorganic carbon to both organic and particulate
10 inorganic form (as calcium carbonate soil, or marl, in the calcareous Everglades). Periphyton
11 thereby regulates the cycling of inorganic carbon between dissolved and particulate forms but
12 also contributes to the formation of the thick flocculent detritus that forms the ‘fluff’ over most
13 deeper water Everglades sediments and eventually to dissolved organic carbon, both of which
14 can be transported to adjacent systems (Gleason 1972; Gleason and Spackman 1974; Wood
15 2005). Together, periphyton mats and their detrital products supply energy to planktonic and
16 benthic food webs, as well as habitat for a diversity of small animals (Dorn et al. 2006). In this
17 way, periphyton communities are not only a resource capital supporting the rest of the
18 Everglades ecosystem, but also contribute to its biodiversity, from their own speciose microbial
19 assemblages to those of the organisms dependent on their structural or nutritional provisioning.
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21 Due to their multidimensional influence on the Everglades ecosystem, the interaction of
22 periphyton communities with their biogeochemical environment and dependent biological
23 communities has been examined, particularly relative to the primary biophysical drivers in the

1 Everglades, including nutrient enrichment, hydrology and ion availability. As has been found for
2 other benthic algal communities (Stevenson et al. 1996), periphyton assemblages of the
3 Everglades respond in meaningful structural, functional and compositional ways to these
4 gradients that can be modeled and used for predictive purposes (McCormick & Stevenson 1998).
5 A variety of large-scale surveys and experimental studies have defined the patterns and
6 mechanisms of periphyton response to nutrient enrichment (McCormick & O'Dell 1996;
7 McCormick et al. 1996, 1998; Gaiser et al. 2004, 2005) and hydrology (Gottlieb et al. 2005,
8 2006; Thomas et al. 2006), while interactions with naturally-existing and disturbance-derived ion
9 gradients are only recently being revealed (reviewed by McCormick & Harvey this issue;
10 Hagerthey et al. submitted). Their utility as indicators of ecosystem change has been proven;
11 their timescale of response (days to months) is relevant to adaptive management and circumvents
12 frustrating dependence on otherwise noisy data of the drivers themselves (McCormick &
13 Stevenson 1998; Gaiser et al. 2004). Because changes in periphyton productivity or composition
14 can elicit a response cascade affecting the experience of dependent organisms or regulatory
15 biophysical features of the Everglades, it can serve as an early-warning signal of impending
16 change that provides an opportunity for corrective action before other less malleable wetland
17 features are irrevocably altered (Gaiser et al. 2005). Their rapid, well-defined response to the
18 variables targeted by restoration and their widespread distribution in the system has prompted
19 integration of periphyton attributes into an ongoing system-wide assessment of ecosystem status
20 (Doren et al. 2009; Gaiser 2009). The consequences of changes in periphyton structure and
21 function to other biophysical and ecological attributes are in some places measurable, in others
22 delayed or confounded by temporal lags and complex linkages, and in many being revealed in
23 pioneering synoptic multidimensional surveys and novel exploratory and experimental research.

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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 will be 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 will provide 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 1990's (i.e., Van Meter-Kasanof 1973; Wood & Maynard 1974; Browder et al. 1981, 1982, 1994; Swift & Nicholas 1987; Grimshaw et al. 1993), 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 then rapidly maturing scientific history, some particularly applied areas of periphyton biology are well understood in the Everglades while other topics, particularly taxonomic and ecophysiological aspects, are poorly understood relative to other ecosystems (Gaiser & 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.

Current Distribution Patterns of Periphyton in the Everglades

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The pre-disturbance distribution of periphyton in the Everglades ecosystem is difficult to hindcast, since few early studies incorporated periphyton collections and paleoenvironmental

1 records are poorly resolved owing to shallow, frequently oxidized sediments and poor
2 microfossil preservation. However, large-scale pattern relative to less mutable gradients in
3 elevation and geology are reflected in the abundance, structure and composition of periphyton
4 communities according to the biogeochemical mosaic and resultant habitat types that
5 characterize the managed ecosystem. The proximal driver of this mosaic of habitats is the
6 underlying geology and geomorphology which influences water chemistry and hydrology, the
7 ultimate drivers of periphyton structure and function (Browder et al. 1994). Here we distinguish
8 periphyton communities of four distinct Everglades habitat types where it is abundant and has
9 been at least cursorily studied: (1) the marl prairies and rocky glades, (2) the ridge and slough
10 drainages of the central Everglades, (3) the soft-water marshes of Loxahatchee National Wildlife
11 Refuge (Water Conservation Area 1; WCA 1) and (4) the coastal mangroves lining the coastlines
12 of Florida and Biscayne Bays. We focus on the central Everglades ecosystem south of Lake
13 Okeechobee; studies of periphyton in the Lake have shown considerable compositional and
14 functional similarity to southern Everglades communities (Havens et al. 1999), but we do not
15 include the Lake specifically in this review. Also, although periphyton is known to occur in
16 sporadic abundance in the sink holes of tree islands and in the Big Cypress National Park,
17 research on these communities is sparse if not entirely lacking. Calcareous epiphytic periphyton
18 communities also occur in abundance in the expansive seagrass beds of Florida Bay, which are
19 examined in detail in Frankovich et al. (2006, 2009) and Wachnicka (2009).

20

21 *Marl Prairies and Rocky Glades:* Along the shallow, intermittently flooded edges of the modern
22 Everglades drainage, periphyton forms thick carbonate-rich accretions on the bedrock and on the
23 stems of emergent macrophytes (Fig 1a,b). These extensive benthic mats occur in wetlands

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

12
13 Periphyton production in marl prairies is regulated by water delivery and nutrient availability
14 (Iwaniec et al., 2006) and is therefore highly seasonal. In the dry season, floating mats and thick
15 epiphytic accumulations on plant stems (locally referred to as “sweaters” for their thick, fluffy,
16 protective appearance) form a dry drapery over the vegetation that has been conjectured to
17 smother supporting plants and thereby possibly exert some level of control on plant composition
18 (Pimm 1995, Fig 1c). While the outer coating of this material can be desiccated, the underlying
19 material often remains moist (Thomas et al. 2006). This moisture is largely retained by copious
20 polysaccharides produced in the wet season by coccoid cyanobacteria (Donar et al. 2004) and
21 can sustain the algae, other microbes, plant roots and inhabiting microfauna through the dry
22 season. Upon rewetting in the wet season (through direct rainfall or managed water delivery),
23 nutrients and enzymes can be rapidly desorbed from the periphyton mat into the water column

1 (Gottlieb et al. 2005; Thomas et al. 2006), stimulating new production. Recovering periphyton
2 then sequesters most of the desorbed nutrients out of the water column quickly after reflooding
3 and is thought to be responsible for maintaining the ambient marsh phosphorus levels of 5-10 μg
4 L^{-1} indicative of oligotrophy (Noe et al., Thomas et al. 2006). Biomass production in submersed
5 periphyton mats then continues to exceed decomposition for approximately 3-4 months after
6 rewetting at rates that can exceed $10,000 \text{ g m}^{-2} \text{ yr}^{-1}$ (Iwaniec et al. 2006). The thick mats can
7 float up and down in the water column as gas builds up during the day and is then lost at night
8 (Iwaniec et al. 2006), and this sloughed material, including “sweaters” cast from decaying stems,
9 can be observed drifting downstream on the surface (Thomas et al. 2002). Periphyton biomass
10 estimates during the peak of the wet season range from 2,000-4,000 g m^{-2} in the wet prairie
11 (Iwaniec et al. 2006; Ewe et al. 2006), in most cases exceeding plant biomass and being an order
12 of magnitude higher than comparable long-hydroperiod mats (Fig. 1d; Gottlieb et al. 2005). The
13 interaction between this large mass of periphyton and plant growth is not well understood,
14 although shade manipulation experiments have failed to produce a considerable affect on
15 production by either community (Thomas et al. 2006).

16

17 Periphyton communities living in carbonate rich water associated with such karstic features have
18 a unique composition that is quite different from the soft-water communities characterizing most
19 shallow depressions. As a result, most Everglades algal communities bear little compositional
20 similarity to the well-documented algal floras of temperate North America or Europe and instead
21 have a high degree of endemism or resemble those of other karstic freshwater wetlands
22 (Rejmánková & Komárková 2000), intertidal mangrove communities (Collado-Vides 2000) and
23 subtidal marine stromatolites (Rasmussen et al. 1993), although the biogeography of this flora

1 has only been sparsely and recently examined (Gaiser & Rühland 2009). *Chara* spp. (L.) is a
2 common macroalgae in the short-hydroperiod mats and is often found interspersed with several
3 poorly studied species of *Utricularia*, including *U. gibba* and *U. subulata*. These plants can
4 facilitate the production of marl sediments when their production exceeds respiration, increasing
5 the pH and causing calcium carbonate precipitation (McConnaughey 1991). They form the
6 backbone of support for filamentous cyanobacteria, particularly *Schizothrix calcicola* and
7 *Scytonema hofmanni* (Gleason and Spackman 1974), which also precipitate calcium carbonate in
8 the microenvironment around their sheaths. These filamentous plants create a matrix that
9 supports the growth of numerically-dominant coccoid cyanobacteria, including species in the
10 genera *Chroococcus*, *Chroococcidiopsis*, and *Aphanothece*, which are encased in a thick
11 polysaccharide sheath that further serves to bind the periphyton mat together (Gottlieb et al.
12 2005) and resist drying (Thomas et al. 2002; Fig. 2). The polysaccharide can comprise up to
13 90% of the volume of benthic periphyton mats (Donar et al. 2004) and serves as a substrate for
14 colonization by other algae and bacteria. Compared to long-hydroperiod marshes, diatoms and
15 green algae are rare in short-hydroperiod wetlands (< 2 % of biovolume), presumably due to
16 their limited ability to withstand frequent drying (Gottlieb et al. 2005). These unique
17 communities are among the most threatened in the Everglades because of the extent of short-
18 hydroperiod habitat that has been lost along the margins of the system or due to the strong
19 hydrologic manipulation in these habitats (shortened hydroperiods and artificially low water
20 levels).

21

22 *Ridges and Sloughs:* In the Shark and Taylor River Slough drainages and in areas of the Water
23 Conservation Areas where annual hydroperiods exceed 9 months on a regular basis, water lily

1 (*Nymphaea odorata*) marshes are interspersed with wet prairies dominated by *Utricularia*
2 *purpurea*, *Eleocharis cellulosa*, *Panicum hemitomon* and *Sagittaria lancifolia* and higher
3 elevation ridges dominated by *Cladium jamaicense* (Gunderson 1994). These areas accrete peat
4 soils yet generally remain replete in dissolved calcium carbonate, supporting periphyton
5 communities that contain about 30 % mineral matter (Gaiser et al. 2006). While the thick
6 epilithic mats common in the marl prairie can be found in drier or higher elevation pockets in the
7 ridges and sloughs, periphyton is more commonly found in loosely aggregated associations with
8 the most common submersed macrophyte, *Utricularia purpurea* and on the stems of the other
9 emergent plants (Fig 1e). In very dense stands of tall *Cladium jamaicense*, periphyton biomass
10 can be quite low relative to that of the neighboring slough (Gottlieb et al. 2005). However, strong
11 winds and tropical storm activity have been observed to cause slough-generated periphyton to
12 pile up on the edges of sawgrass ridges, perhaps contributing to organic matter accretion while
13 also supplying nutrients (C. Saunders, unpublished data).

14

15 Gottlieb et al. (2006) compared the composition of periphyton communities in marl prairie and
16 slough, and found that while there was significant compositional overlap (77% of species were
17 found in both habitats), larger differences were observed in the relative abundances of common
18 taxa. Cyanobacteria dominate both communities, and slough mats are similarly dominated by
19 *Schizothrix calcicola* and *Scytonema hofmannii*; however, diatoms comprised a greater
20 proportion than observed in the marl prairie. Common diatoms in slough periphyton mats
21 include *Achnanthes caledonica*, *Brachysira neoexilis*, *Cyclotella meneghiniana*, *Encyonema*
22 *evergladianum*, *Mastogloia smithii*, *Nitzschia palea* var. *debilis*, *Nitzschia serpentiraphe* (Fig 2.,
23 Slate & Stevenson 2007) as well as a diversity of poorly defined morphotypes related to the

1 *Gomphonema vibrio* complex (Tobias & Gaiser 2006). In permanently inundated sites, *F.*
2 *synegrotesca* is particularly abundant, and possibly a reliable indicator of the absence of periodic
3 drying. These highly endemic communities are very susceptible to nutrient enrichment and are
4 quickly replaced by widespread eutrophic taxa when exposed to above-ambient sources of P
5 (Slate & Stevenson 2007). Although enriched communities occur naturally, for instance in the
6 deeper sloughs surrounding P-rich tree islands, they are expanding as discussed in great detail
7 below.

8
9 *Soft-water Communities:* While calcareous periphyton mats are emblematic of the central
10 Everglades, equally important are soft-water algal communities, best represented in WCA 1.
11 Surface waters in WCA 1 are derived largely from rainfall in contrast to other parts of the ridge
12 and slough region that are more strongly influenced by mineralized canal discharges.
13 Consequently, they provide an ion-depleted environment to the algae that more closely
14 resembling that of the isolated wetlands and ponds of the Atlantic Coastal Plain (Gaiser &
15 Johansen 2001; Siver et al. 2005). Although some species are held in common with the
16 calcareous Everglades, instead of being dominated by cyanobacteria, communities in the Refuge
17 contain diverse and abundant chlorophytes, particularly desmids, and a diverse diatom
18 community (Swift and Nicholas 1987, Hagerthey et al. submitted). Water draining into
19 conveyance canals surrounding the Refuge have caused mineral levels around the Refuge
20 perimeter and, in some places, several kilometers into the interior, to increase (McCormick &
21 Harvey this issue). Evidence from paleoecological and ongoing monitoring efforts in the
22 northeast Everglades (northern WCA-2A) suggest that the system was once less calcareous than
23 it was and that canal excavation and flows have increased calcium carbonate supply to the

1 interior (Slate & Stevenson, 2000; Winkler and others, 2001). These issues are discussed in the
2 salinity section below.

3
4 *Mangrove Ecotone:* As water meanders through the Everglades drainage toward the coast,
5 salinity increases and plant communities change, but calcareous mats remain a conspicuous
6 component of the ecosystem. The shallowly inundated mangrove marshes along existing and
7 historic drainages, particularly those now occupied by sparse, dwarf mangrove forests, often
8 support thick benthic and floating mats similar in appearance to those occurring in the upstream
9 freshwater marsh (Fig. 1f). These are particularly abundant in the Taylor River drainages and
10 along the coastline of Biscayne Bay (the Biscayne Coastal Wetlands; Gaiser et al. 2004).

11 Encrustations of algae are commonly seen around the prop roots of *Rhizophora mangle*, and
12 wide expanses of epilithic periphyton mats are observed in the “white zone” ring of low
13 vegetation density, described by Egler (1952) and Ross et al. (2001). Some of the same
14 stromatolitic species predominate in these mats, particularly *Scytonema* and *Schizothrix* species
15 (Wachnicka & Gaiser 2007). These genera both contain species representing the full salinity
16 spectrum, and indeed some of the species appear capable of thriving across a broad range of
17 salinity regimes (Ross et al. 2001; Gaiser et al. 2004). In the Everglades, these communities are
18 sometimes displaced by non-calcite precipitating cyanobacteria in communities closer to the
19 coast, including *Lyngbya* and *Microcoleus*, which have been collected from mangrove
20 pneumatophores elsewhere (Hussain & Khoja 1993). These taxa are indicative of higher
21 phosphorus availability (McCormick & O’Dell 1996), and the high biomass of some mangrove
22 communities may be enhanced by associations with N-fixing pneumatophore bacteria as well as
23 coastal supplies of phosphorus, observed to enhance mat TP concentrations along the coastal

1 fringe. While the periphyton matrix appears throughout the system to be macroscopically strung
2 together by filamentous green or blue-green algae, the interstices of this web are often “glued”
3 together by mucilaginous polysachharide produced by abundant and diverse coccoid
4 cyanobacteria, which may increase dessication resistance, provide a barrier to fluctuations in
5 salinity, and concentrates nutrients and enzymes that control nutrient cycling.

6
7 The most diverse algal component in the periphyton mats of the mangrove ecotone are the
8 diatoms. It is common to find a large number of diatom genera in estuaries and near-coast
9 environments because typically genera are confined to either fresh or salt water, and rarely mix
10 except in brackish situations (Cooper et al. 2009). The dominance of *Amphora* and *Mastogloia* in
11 the coastal flora is similar to findings in other parts of Florida and the Caribbean (see Wachnicka
12 2009 for a review). These genera, together with *Navicula*, *Nitzschia*, *Cocconeis*, *Fragilaria* and
13 *Achnanthes*, are probably important in coastal floras circumglobally, at least in the Northern
14 Hemisphere. However, at lower taxonomic levels many taxa not reported elsewhere (or
15 insufficiently described) may be unique to the subtropical/tropical Atlantic coast (Wachnicka
16 2009). Wachnicka & Gaiser (2007) described 21 new species in two common genera from the
17 mangrove zone and shallow seagrass beds of Florida and Biscayne Bays, and many more remain
18 to be described, indicating both the respectable degree of endemism and paucity of taxonomic
19 attention received by the coastal Caribbean diatom flora.

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21 **Changes in Distribution Caused by Anthropogenic Disturbance**

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

17

18 ***Effects of Phosphorus Enrichment:*** Enrichment by phosphorus draining to canals, then
19 marshes, from surrounding fertilized agriculture and urban landscapes poses one of the greatest
20 water quality threats to the ecology of the historically oligotrophic Everglades (Noe et al. 2001).
21 The productivity and composition of benthic algal communities change quickly in response to
22 elevated concentrations of limiting nutrients due to the short-generation times and differing
23 competitive abilities of algal taxa (Stevenson et al. 1996). For this reason, algae are regularly

1 employed in water quality assessments (McCormick & Cairns 1994; Stevenson et al. 2001)
2 although applications in wetlands have lagged behind other ecosystems (Pan et al. 2000; Gaiser
3 & Rühland 2009). Indeed, the past several decades of research on periphyton responses to
4 phosphorus in the Everglades have set the stage for indicator development, not just for the
5 Everglades but for other wetland ecosystems experiencing similar water quality impairments
6 (McCormick & Stevenson 1998; Gaiser 2009). The effects of phosphorus enrichment on
7 periphyton in the Everglades have been examined through descriptive work along known P-
8 enrichment gradients and through controlled experiments to determine the mechanisms, loads,
9 and concentrations that cause the observed patterns (Browder et al. 1982; Swift & Nicholas
10 1987; Grimshaw et al. 1993; Raschke 1993; Vymazal & Richardson 1995; McCormick et al.
11 1996; McCormick & O'Dell 1996; McCormick et al. 1997; Cooper et al. 1999; Pan et al. 2000;
12 McCormick et al. 1998; Gaiser et al. 2006; Hagerthey et al. 2008, McCormick et al. 2009).
13 Together, these studies have shown that any sustained P enrichment beyond what would
14 naturally be experienced in the marsh causes measurable changes in periphyton production and
15 composition. One of the easiest and most reliable measures of increased P exposure is the
16 increased P concentration in the periphyton biomass (Gaiser et al. 2004). Because the system is
17 shallow and oligotrophic, any excess P delivered to the system is quickly sequestered by the
18 microbial community at rates and concentrations reflective of P load. Unless this community is
19 saturated in P, excess P delivered to the system will not be recognized in a water column TP
20 measurement (unlike pelagic ecosystems, where this P would be measurable in a water sample
21 containing plankton). Therefore, in the Everglades and other naturally oligotrophic benthic
22 environments, water quality surrogates are a necessity to accurately detect and quantify
23 enrichment (Gaiser et al. 2004).

1
2 As periphyton sequesters excess P from the water column, productivity of the more competitive
3 taxa of both algae and bacteria will increase. Least competitive in this interaction are the
4 calcareous filamentous and coccoid cyanobacteria and endemic Everglades diatoms, while green
5 algal taxa, especially *Mougeotia* spp., and widespread eutrophic diatoms, such as *Gomphonema*
6 *parvulum* and *Nitzschia amphibia*, found in low abundance in native mats, are favored
7 (McCormick & O'Dell 1996; Gaiser et al. 2006; Fig. 2). Bacterial productivity is also stimulated,
8 shifting the balance between autotrophy and heterotrophy in the mat, although compositional and
9 functional changes in bacterial communities have not been examined. A common consequence
10 of enrichment, observed experimentally and along enrichment gradients in the Everglades, is
11 disintegration of the calcareous, cyanobacterially-dominated mat and replacement by a
12 mucilaginous, green-algal-dominated community (McCormick & O'Dell 1996; McCormick et
13 al. 2001; Gaiser et al. 2005; Fig. 3a).

14
15 Metabolically, increased O₂ production has been measured during this transition (McCormick et
16 al. 1997), while the absolute organic biomass of periphyton mat declines (Gaiser et al. 2005; Fig.
17 3b). A three-step process has been postulated for the disintegration of periphyton mats upon
18 phosphorus exposure: (1) increased production of bacteria that consume accumulated
19 polysaccharide and detritus that leads to (2) increased CO₂ consumption and dissolution of
20 calcium carbonate matrix that is (3) gradually replaced by a more competitive green-algal
21 community. While the mechanism of this shift is poorly understood (see Hagerthey et al. this
22 issue), the loss of calcareous mat and replacement by loosely aggregated green algal assemblage
23 is well-described for most regions of the calcareous Everglades. However, eutrophic

1 assemblages appear to be a transient community, as sustained eutrophication commonly leads to
2 monospecific cattail stands that do not support periphyton, either because of shading (Grimshaw
3 et al. 1993) or allelopathy conferred by the dense stands (McCormick et al. 1998; Thomas et al.
4 2006).

5
6 *Regions of concern:* Data from periphyton collections along known enrichment gradients and
7 from large-scale system-wide surveys are key to assessing patterns of water quality degradation,
8 particularly when it is acknowledged that these microbial assemblages can offer an early warning
9 of changes that could be reversed before cascading to a persistent, highly modified ecosystem
10 state. Gaiser et al. (2006) reported changes in periphyton attributes from collections taken in
11 1999 and 2000 along transects downstream of water control structures in Water Conservation
12 Areas (WCA) 1, 2A, 3A, Shark River Slough (SRS) and Taylor Slough (TS). Total P
13 concentrations in periphyton provided a better indication of P loading history than water column
14 TP concentrations, and reached asymptotic levels in WCA-1, 3A and SRS at 3, 1, and 1 km
15 downstream of the sources, respectively. Though periphyton TP also declined exponentially in
16 WCA-2A, values 14 km from the source were higher ($500 \mu\text{g P g}^{-1}$) than levels measured in the
17 interior of SRS ($\sim 150 \mu\text{g P g}^{-1}$). By contrast, concentrations in calcareous mats of TS were low
18 throughout (mean $124 \mu\text{g P g}^{-1}$) and unrelated to distance from the canal phosphorus source.
19 Periphyton biomass was negatively correlated with TP within and among these marshes.
20 Taxonomic responses to P enrichment were strong, and included changes in both diversity and
21 composition. Diatom diversity in native Everglades calcareous periphyton communities is low
22 compared to other wetland ecosystems (average 22 taxa per sample) and has been shown to
23 increase in response to enrichment (Raschke 1993). Significant reductions in diversity (Shannon-

1 Weiner H') with distance from canal P sources were shown in WCA-1A, SRS, TS, and WCA-
2 2A, although the site closest to the canal and most severely enriched in WCA-2A had very low
3 diversity (only 7 taxa; Fig. 4a,b).

4

5 Transects in SRS and WCA-3A sampled by Gaiser et al. (2006) were aligned closely with those
6 of the 1990-1991 survey reported by Raschke (1993), enabling a temporal comparison of
7 diversity trends. Although taxonomic inconsistencies between these studies preclude
8 interpretation of absolute H' values, the trends are similar, although it is possible that the earlier
9 study shows water quality impairment further to the interior of both marshes than the Gaiser et
10 al. (2006) study (Fig. 4a). Both studies showed a strong relationship between diversity and
11 metrics of phosphorus availability (sediment TP in Raschke (1993), periphyton TP in Gaiser et
12 al. (2006) for SRS, $R^2=0.65$ and 0.93 , respectively, Fig 4c). The taxonomic responses
13 responsible for these changes were difficult to compare between studies because of changes in
14 nomenclature, but in the Gaiser et al. (2006) study, taxa were identified as significant indicators
15 of P availability according to their optimal location along the measured gradient (calculated by
16 weighted averaging, in $\mu\text{g P g}^{-1}$). Low P taxa (100-300) included *B. neoexilis*, *M. smithii*, *E.*
17 *evergladianum*, *E. microcephala* and *F. synegrotesca*, medium P taxa (300-500) included
18 *Eunotia flexuosa* and *Navicula cryptotenella* and high P taxa (>800) included *Eunotia incise*,
19 *Rhopalodia gibba*, *Amphora veneta*, *Nitzschia amphibia* and *Gomphonema parvulum* and (Fig.
20 2).

21

22 Large-scale assessment efforts by the RECOVER Monitoring and Assessment (RECOVER
23 2005) and the U.S. Environmental Protection Agency Re-MAP (Scheidt & Kalla 2007) programs

1 include collections of a full suite of chemical, physical and biological parameters relevant to
2 restoration assessment, including periphyton (Trexler et al. 2008). Results of the fall 2005 survey
3 revealed an inverse relationship between periphyton biovolume and TP concentration (Fig. 5).
4 For assessment purposes, absolute values were compared to expectations derived from the Gaiser
5 et al. (2006) cross-system transect and experimental study. Standing stocks and TP values in the
6 interior of WCA-3A were found to be lower and higher, respectively, than expected, indicating a
7 combination of increased hydroperiod and phosphorus loading to this marsh. This contrasts to
8 the interpretation of relatively high TP concentrations in WCA-1 and the estuary of SRS, where
9 prior data would suggest values are naturally elevated in these areas. Because these surveys are
10 designed to detect impairment in the less susceptible marsh interior, they are coupled with
11 continued transect surveys closer to canal P sources. Cause for concern has emerged from
12 collections along the eastern boundary of Everglades National Park, where overflow from the S-
13 332 detention basins or seepage from enriched groundwater are causing enrichment gradients
14 100-200 m to the west of the levee edge of the basins (Gaiser et al. 2008; Fig. 6). This is
15 particularly obvious in elevated periphyton TP concentrations, lower than expected periphyton
16 biomass and the presence of high-TP diatoms near detention ponds B and C near the head of
17 Taylor Slough, and these trends appear to be worsening with time (Gaiser et al. 2008).

18

19 ***Effects of Hydrologic Modification:*** The creation of Water Conservation Areas, in combination
20 with agricultural and urban development, have caused a loss in spatial extent and connectivity in
21 the Everglades. In places where natural patterns of water flow from the north were cut off, such
22 as in northeast SRS, much of WCA-2A, and northern WCA3A, hydroperiods have shortened and
23 droughts have more severe consequences (Davis et al. 2005). Much native ridge and slough

1 habitat has been converted to marl prairie (particularly the northeastern portions of Shark River
2 Slough) (and former marl prairie and rocky glades habitats to farmland and housing (Davis et al.
3 1994). On the other hand, some places are experiencing extended hydroperiods and drying
4 pattern reversals, such as southern WCA 3A where the Tamiami Trail (and associated L-29 stage
5 constraints), and the S-12A and S-12B gate closures create extended hydroperiods even during
6 extended dry seasons. Similarly, the L-31 and C-111 canal systems have resulted in very
7 “flashy” and unseasonable flows into TS.

8
9 The shortening of hydroperiods due to drainage activities has influenced periphyton structure and
10 composition, increasing the extent of benthic mats where hydroperiods have shortened and
11 eliminating them in the vast areas that have been converted to urban use or agriculture. It is
12 likely that benthic mats once extended well to the east of the current Everglades, lining the
13 transverse glades that are now virtually absent (Ruiz & Ross 2004). Further reduction in
14 hydroperiod in existing marl prairies can result in loss of diatom and green algal species in the
15 periphyton mat, leaving the mat to be comprised of mostly mat-forming filamentous
16 cyanobacteria and associated calcitic matrix (Gottlieb et al. 2005). Short-hydroperiod mats have
17 an order of magnitude higher areal dry weight and ash-free dry weight (organic) biomass than
18 long-hydroperiod mats and the inorganic (primarily calcitic) portion of the biomass is much
19 larger in short- than long-hydroperiod periphyton mats (70-90% vs. 30-70%, respectively;
20 Gottlieb et al. 2005, Fig. 7). This shift can influence consumer communities, as short-
21 hydroperiod periphyton assemblages are coated with calcium carbonate crystals that impede
22 digestion by most grazers (Browder et al. 1994; Trexler et al. 2008) and the matrix of
23 cyanobacterial filaments creates pocketed refuges for more edible algae, making them less

1 accessible or potentially inaccessible to consumers (Geddes and Trexler 2003). The effect of
2 decreased hydroperiod on net annual production of periphyton mats has not been elucidated, but
3 because periphyton production is limited to periods during which the mats are flooded, the
4 severe reductions in wet season duration experienced in the eastern Everglades likely has
5 substantially decreased annual production. Reduced periphyton production would decrease marl
6 soil accretion rates in areas with hydroperiods reduced below 1-2 months per year. Interpreting
7 changes in water depth or hydroperiod from periphyton attributes is complicated by complex
8 interactions of these attributes with water quality parameters. Increased periphyton TP
9 concentrations and organic matter content are associated with increasing water depth. Indeed,
10 tracking hydrologic change from periphyton attributes is promising, as periphyton mats have
11 been shown to converge structurally and compositionally when exposed for long duration to the
12 same hydroperiod regime (Gottlieb et al. 2006). Additionally solution holes, found in the marl
13 prairie landscape, which have intermediate hydroperiods, fall somewhere in the middle
14 structurally and functionally between long and short hydroperiod mats. This indicates that shifts
15 in periphyton composition due to changes in water delivery to the Everglades should be readily
16 visible, making periphyton a useful early indicator of impending change at the ecosystem level.

17

18 *Regions of concern:* The Recovery Monitoring and Assessment (RECOVER 2005, 2006) and
19 U.S. Environmental Protection Agency Re-MAP (RE-MAP 2005) surveys showed a decrease in
20 water depth and hydroperiod from the water conservation areas to the base of Shark River and
21 Taylor Slough that roughly corresponded to patterns in periphyton biovolume. Biovolume
22 increased significantly with decreasing hydroperiod and number of days since last dry, although
23 sites in the driest parts of northeast SRS fell below the best fit line, indicating lower biomass than

1 would be predicted by the model (Fig. 7). It is likely that the low biovolume values to the interior
2 of WCA-3A are due to the combination of extended hydroperiods and increased P availability in
3 this wetland. The absence of long-term monitoring or paleoecological data from these regions
4 precludes an interpretation of the direction of change in periphyton attributes experienced by
5 these wetlands. However, the optimal hydroperiod for each algal species collected in the
6 RECOVER MAP and RE-MAP program was estimated using the hydroperiods estimated from
7 the EDEN network (Conrads and Petkewich 2009). The site hydroperiod for each site was then
8 estimated by weighting the abundance of each species by its hydroperiod optimum. About one
9 third of the variability of hydroperiod (estimated by EDEN) was explained by diatom and soft
10 algae species composition ($R^2 = 0.34$), with an estimate error of only 73 days of the measured
11 hydroperiod value (Trexler et al. 2008). Species showing strong individual responses to
12 hydrologic variables included the diatoms *Nitzschia serpentiraphe*, *Nitzschia palea* var. *debilis*
13 and the cyanobacterium *Scytonema hoffmannii* that were most abundant in shallow, short-
14 hydroperiod sites throughout SRS and TS and the green alga *Mougeotia* spp., the blue-green
15 algae *Schizothrix calcicola*, *Rhabdonema linearis* and the diatoms *Encyonema ftsp01*, *Fragilaria*
16 *syngrotesca* that were most abundant in deeper, long-hydroperiod sites of WCA 3-A (Fig. 2).
17 Together, these results support those suggested from experimental work of Gottlieb et al. (2006)
18 but this is the first study to show concordance of these relationships at very large spatial scales.
19
20 ***Effects of Changing Ion Concentrations:*** Changes in ion chemistry, an expected result of canal
21 excavation and drainage, can modify CaCO_3 delivery and, also, possibly, ion seepage from
22 groundwater (Price et al. 2006; Hagerthey et al. submitted). Swift & Nicholas (1987) showed
23 that periphyton growth rates in the Everglades were significantly influenced by site differences

1 in water quality (i.e., major ion content, pH and phosphorus composition) independent of
2 hydrologic factors. Increased water delivery from canals increases the supply of calcium and
3 bicarbonate as well as other ions including magnesium, sodium, potassium, chloride, and sulfate
4 (McCormick & Harvey this issue; Hagerthey et al. submitted). Increased mineral loads
5 encourage development of benthic periphyton dominated by calcite-precipitating blue-green
6 algae. In fact, shifts from high-diversity green algae, diatom and cyanobacteria assemblages to
7 mats dominated by filamentous cyanobacteria have been noted in paleoecological studies of
8 areas adjacent to canals, where water management alterations increased pH and ion
9 concentrations in downstream marshes (Slate and Stevenson 2000). Northern areas of WCA 2-A
10 were found to have been peat accreting environments prior to the dredging of peripheral drainage
11 canals, providing a buffer between the water column and limerock underneath. Acidity and
12 conductivity were likely lower than today, and under such conditions, extensive calcareous mats
13 in this region would have been improbable. Instead, WCA-2A may have supported communities
14 similar to those of the interior of WCA-1 (Slate and Stevenson 2000).

15
16 *Regions of Concern:* The transition of periphyton communities in northern WCA-2A from low-
17 to-high conductivity characteristics may have occurred abruptly in the 1960's after modifications
18 to the water-management system (Slate and Stevenson 2000). The effects extend through the
19 interior of WCA-2A as indicated by the dominance of calcareous cyanobacteria mats
20 (McCormick et al. 1996, McCormick et al. 2009). Similar changes have occurred in WCA-1,
21 where conductivity measured along the margins of the peripheral canal system is elevated due to
22 canal water intrusion into this rainfall-driven wetland (Fig. 8a; Hagerthey et al. submitted). At a
23 near-canal site in the WCA-1 marsh, high conductivity values were associated with increases in

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

9
10 Biological effects of increases in conductivity have also been noted in coastal mangrove
11 communities subject to salt-water encroachment, particularly along the Biscayne coastline where
12 the L-31E canal has reduced freshwater dispersion to the coast and thwarted any interior-ward
13 migration of communities as sea-level rises. As a result, freshwater gramminoid communities
14 normally supporting prolific periphyton mats have been nearly eliminated and the “white zone,”
15 an area of very low productivity visible from satellite imagery, have been expanding (Ross et al.
16 2001). Periphyton-associated mollusks were used to reconstruct the rates of these changes from
17 dated sediment cores to reveal over 90% of freshwater wetlands have been lost from the
18 Biscayne coastline due to lateral salt-water encroachment rates, calculated to average 3.1 m yr^{-1}
19 for the last 70 years (compared to 0.14 m yr^{-1} for the pre-drainage period; Gaiser et al. 2006).
20 Diatom assemblages associated with very high conductivities have been expanding in the white
21 zone and in former ‘transverse glade’ depressions that are no longer regularly connected to
22 freshwater (Gaiser 2004).

23

1 **Indicator development and future work**

2

3 Major advances have been made in last two decades in our knowledge of the distribution of
4 periphyton abundance and composition in the Everglades. Experimental research has led to a
5 better understanding of the drivers of compositional pattern, although strong interactions among
6 many drivers complicate inferences about the source of changes observed in contemporary
7 survey and deserve attention through multi-factorial controlled experiments. Interpreting the
8 direction of restorative change, or further degradation, from ongoing monitoring and assessment
9 programs is promising. However, these interpretations could be strengthened by further attention
10 to the following topics: (1) development of a web-accessible algal taxonomy archive to improve
11 concordance among researchers, meta-analyses of past and ongoing collections, and our
12 interpretation of species' autecologies and biogeography, (2) coordinating multi-agency
13 periphyton monitoring efforts to improve ability to detect change at multiple spatial and temporal
14 scales, (3) molecular exploration of microbial components, including bacteria and fungi, that
15 would contribute to better resolved interpretations of periphyton distribution in space and time at
16 all levels of organization species, (4) better understanding of multi-dimensional drivers of
17 change, including those not yet well investigated (i.e., micronutrients, contaminants), (5)
18 continued long-term collections at permanent monitoring sites to improve evaluations of natural
19 temporal variability to guide management expectations, (6) continued quest for well-preserved
20 paleoecological records of diatoms or other proxies to improve periphyton targets for natural
21 systems models, (7) increased attention to threats to endemic species and their engineering
22 function in the coastal ecotone, confronted by both short-term management changes and long-
23 term sea-level rise, and (8) increased attention to functional metrics of change, including

1 physiological and metabolic attributes that have not been well investigated (Hagerthey et al. this
2 issue). 9) effects of hydroperiod on community biogeochemical function (will structural shifts
3 toward b-g algae lead to changes in N concentration and loads entering estuarine systems). With
4 added attention to these topics, it may be possible to integrate periphyton into a model of whole-
5 ecosystem response to further human disturbance, management, and restoration in this threatened
6 landscape.

7
8 The managed Everglades differs from the predrainage ecosystem in fundamental ways, including
9 spatial extent and connectivity, hydrologic (hydroperiod, depth, and flow) regimes, and water
10 quality. Likewise, the composition and distribution of periphyton across the managed system
11 also differs from predrainage times and current characterizations of reference or “minimally
12 impacted” conditions may be poor predictors of future restored conditions in some areas. In fact,
13 the absence of historical accounts of conspicuous periphyton communities within the Everglades
14 prior to significant drainage suggests that periphyton may not have been as abundant, at least
15 across portions of the ecosystem, as it is today. Restoration of historic flow regimes would
16 convert currently impounded, static wetlands into flowing environments and would certainly
17 influence periphyton attributes in affected areas. And, achieving hydrologic restoration using
18 waters that are elevated in phosphorus or major ions such as calcium will also alter periphyton
19 landscape patterns. Understanding periphyton responses to projected flow regimes and
20 attainable water quality conditions under different restoration scenarios will allow scientists and
21 managers to evaluate the ecological consequences of restoration and the potential for
22 unanticipated periphyton responses that may not be deemed desirable by the metrics contained in
23 current assessment programs (e.g., Gaiser 2008).

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2

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9 This is SERC contribution #

10

11

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- 19

1 **Figure Legends:**

2

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

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

21 Fig. 3. Relationships between periphyton attributes in system-wide USEPA R-EMAP (white
22 circles) and RECOVER MAP (filled circles) surveys: (A) pervasive inverse relationship between
23 periphyton ash-free dry mass (AFDM) and total phosphorus (TP), (B) positive relationship

1 between periphyton organic content and TP, (C) negative relationship between periphyton
2 AFDM and water depth and (D) positive relationship between periphyton TP content and water
3 depth.

4 Fig. 4. Relationships between Shannon-Weiner Diversity (H') and (A) distance into Shark River
5 Slough (SRS) and Water Conservation Area 3A (WCA-3A) from the C-12 discharge gates on the
6 Tamiami canal, measured in 1990 and 1991 by Raschke (1991)* and in 1999 by Gaiser et al.
7 (2006); (B) distance away from canal inputs in Water Conservation Area 1 (WCA-1, West and
8 East of x and x gates, respectively), Water Conservation Area 2A (WCA-2A) and Taylor Slough
9 (TS); and (C) periphyton TP concentration in SRS, WCA-3A, WCA-2A and TS.

10 *Redrawn from graphics in Raschke (1991)

11 Fig. 5. Distribution of the (A) volume and (B) total phosphorus content of periphyton collected
12 in 2005 R-EMAP and RECOVER MAP surveys.

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

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

19 Fig. 8. (A) Change in periphyton species composition at a site (X4) in WCA-1 change as a
20 function of variable salinity (conductivity). Dotted line represent the total relative abundance of
21 algae indicative of low salinity (e.g., desmids and the diatom *Brachysira brebissonii*). Dashed
22 line represents the total relative abundance of taxa indicative of high salinity (e.g., the diatoms

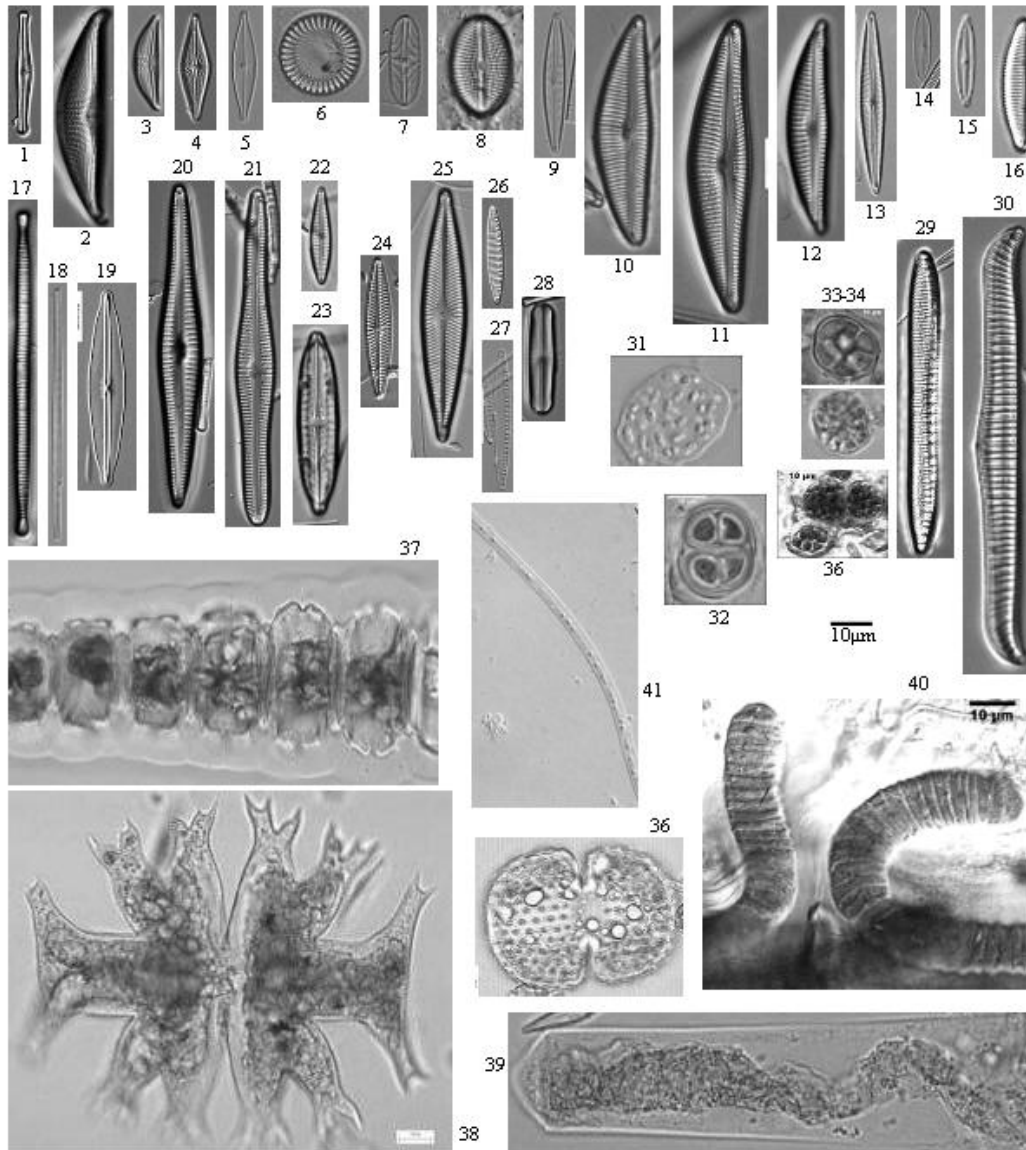
- 1 *Mastogloia smithii* and *Encyonema evergladianum*). (B) Change in the relative abundance of
- 2 desmids along a salinity gradient in WCA-1.
- 3

1 Fig. 1.



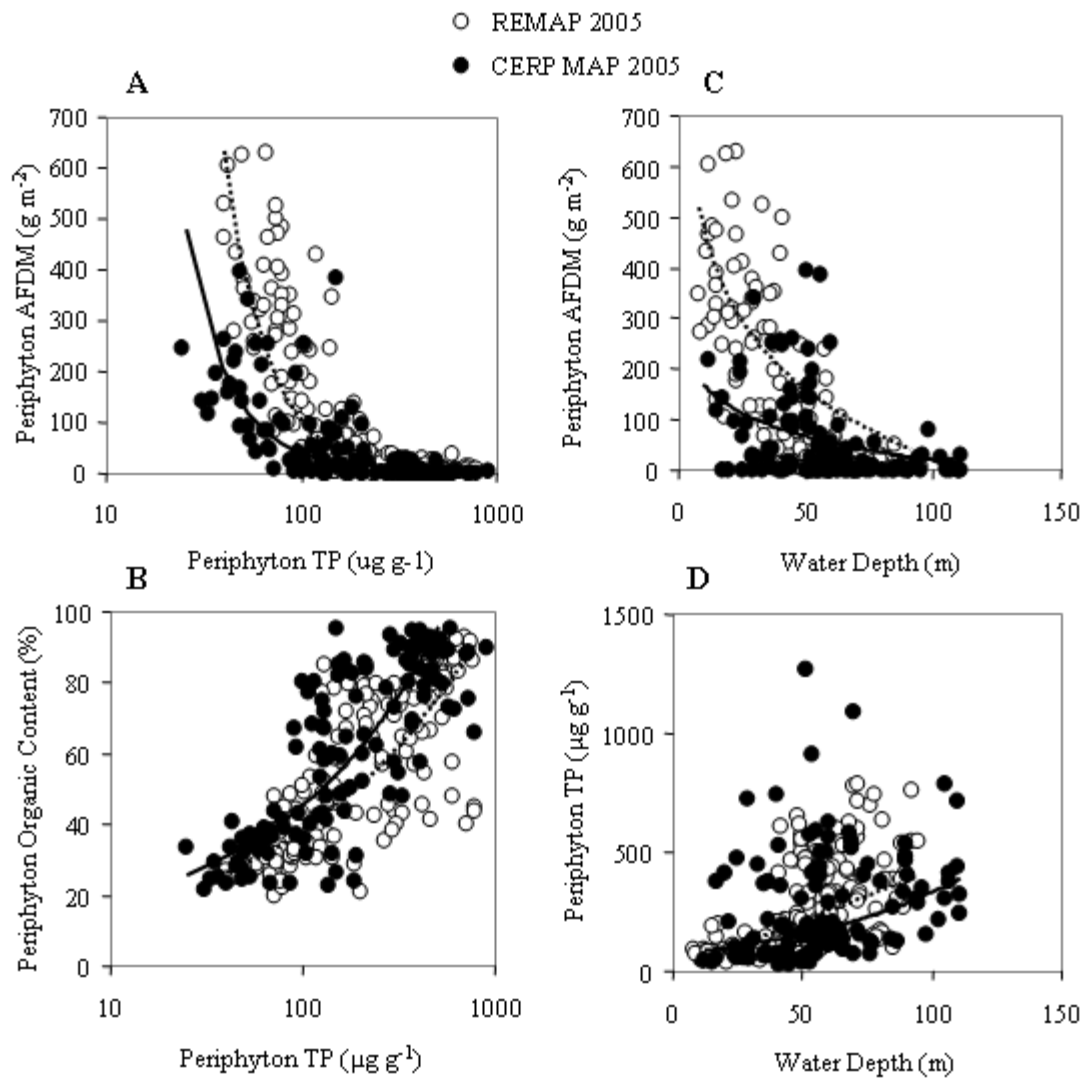
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1 Fig. 2.



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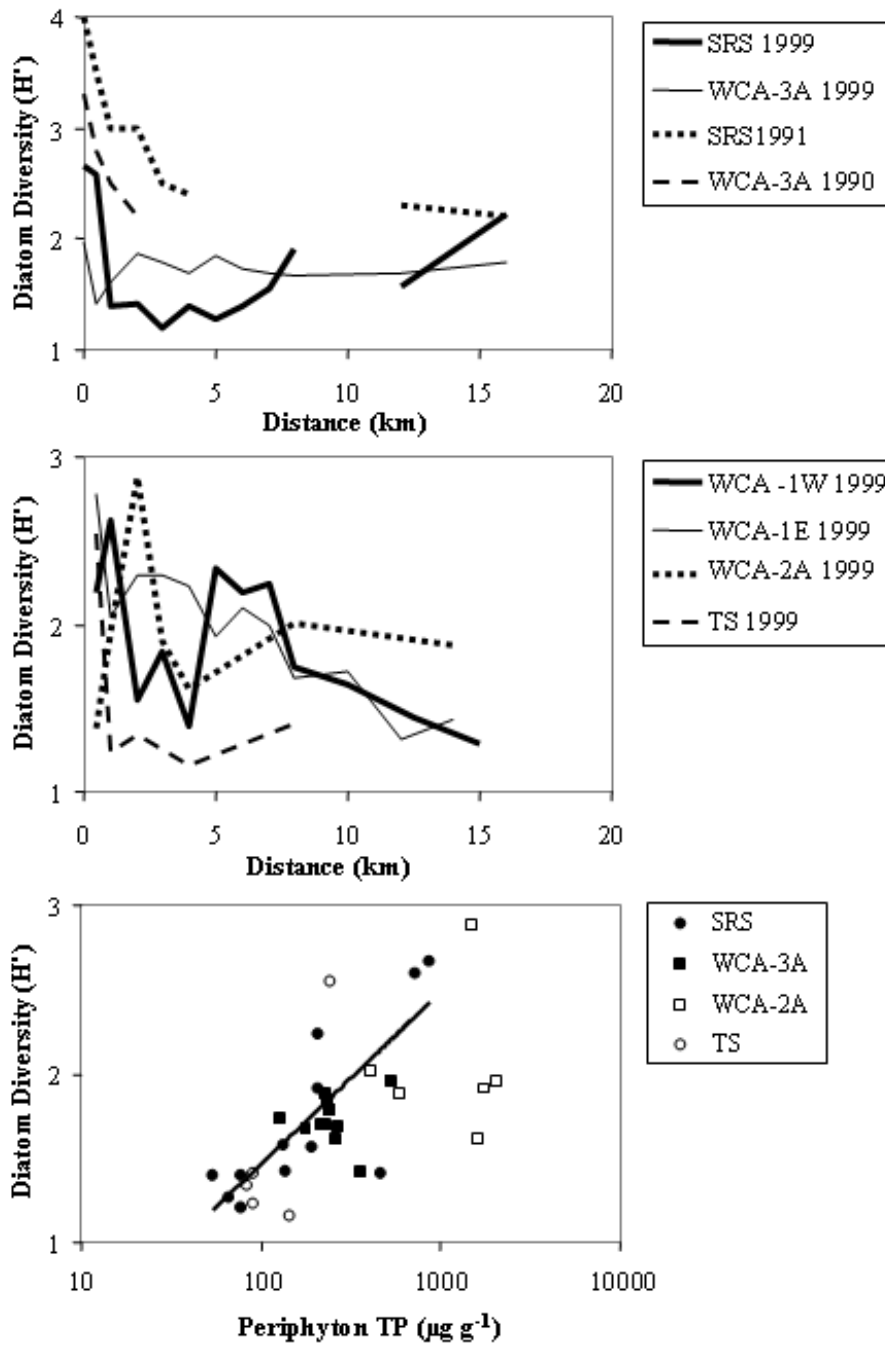
1 Fig. 3.



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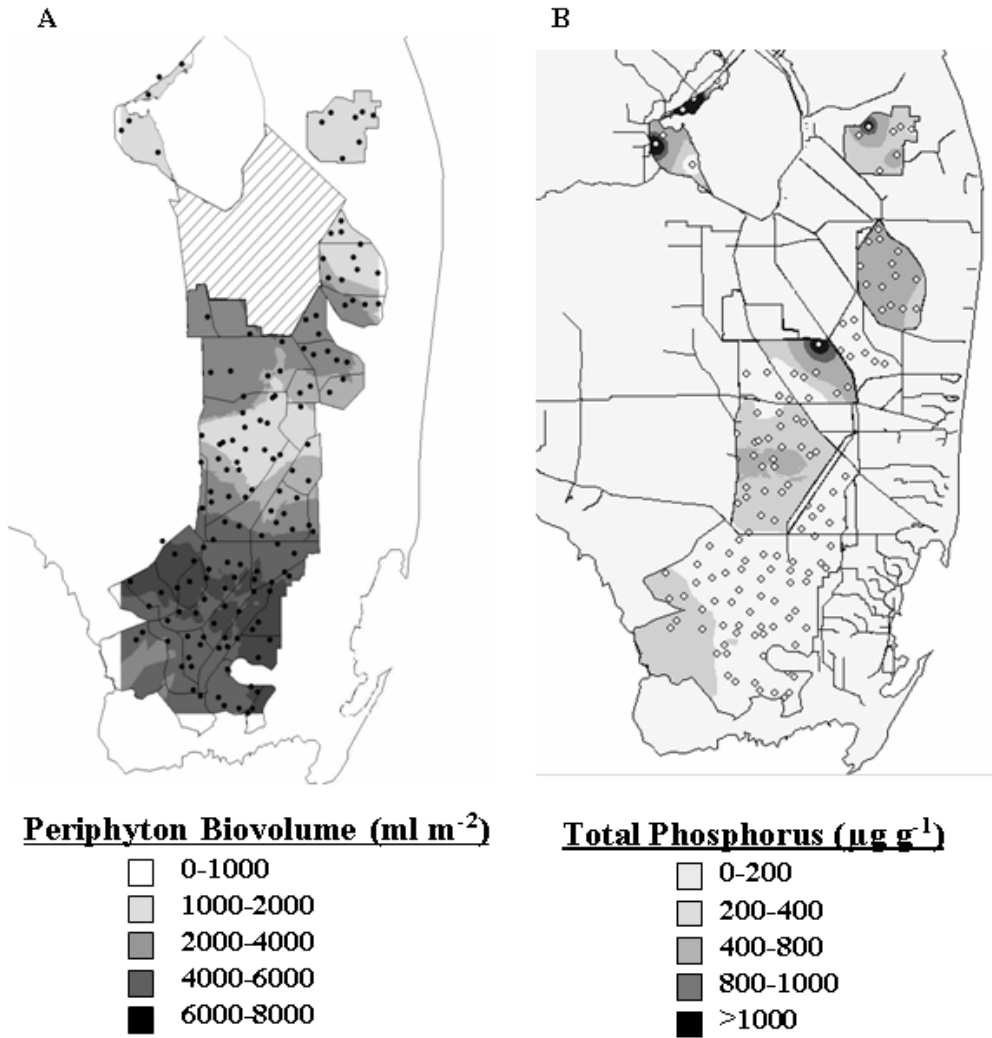
1 Fig. 4.



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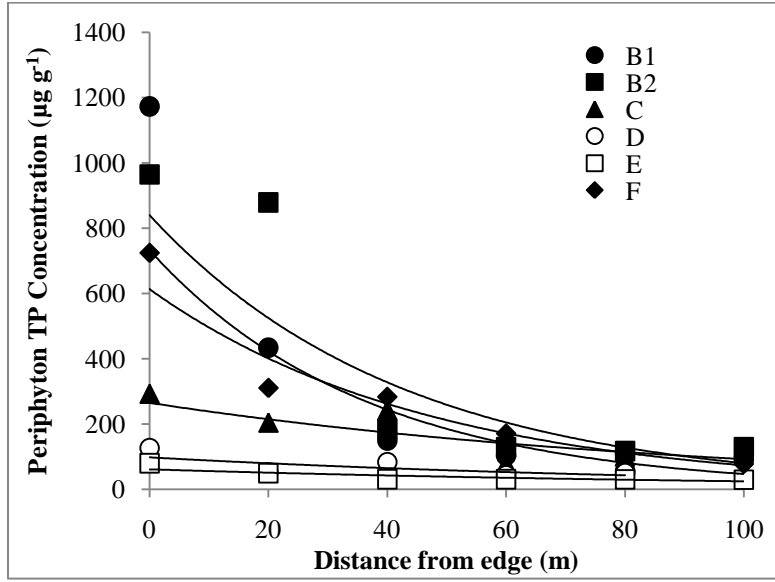
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1 Fig. 5.



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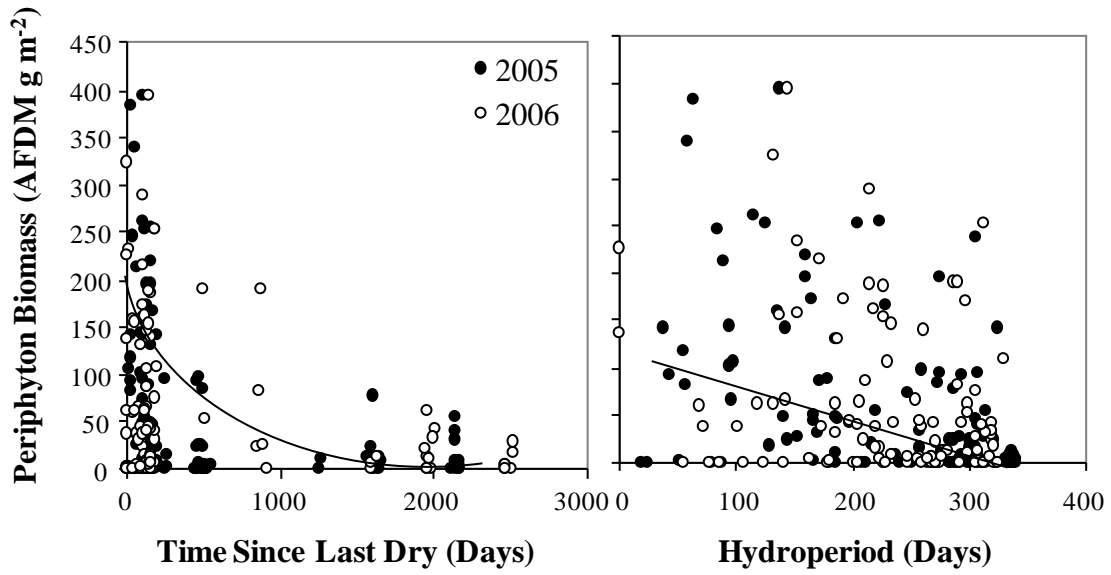
1 Fig. 6.



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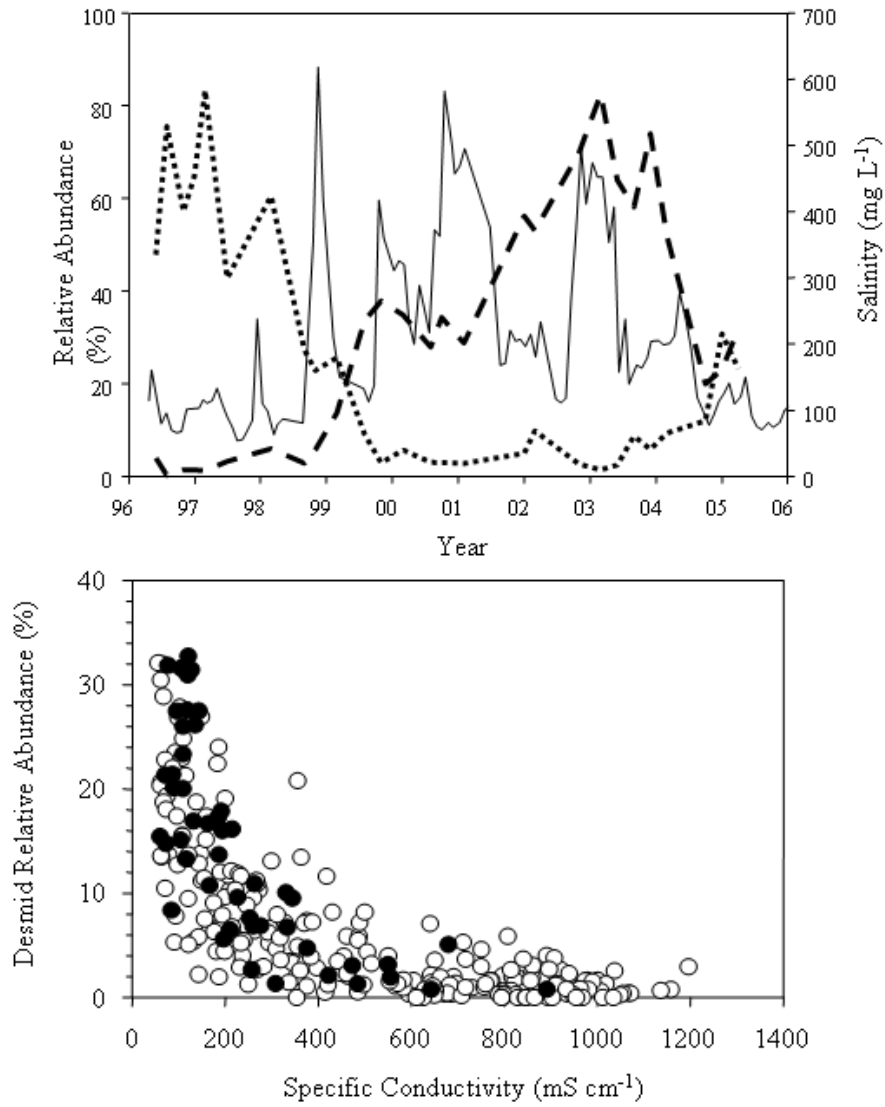
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1 Fig. 7.



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1 Fig. 8.



2