Hydrobiologia (2006) 569:195–207

J.C. Trexler, E.E. Gaiser & D.L. Childers (eds), Interaction of Hydrology and Nutrients in Controlling Ecosystem Function in Oligotrophic Coastal Environments of South Florida
DOI 10.1007/s10750-006-0132-1

Comparative study of periphyton community structure in long and short-hydroperiod Everglades marshes

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Key words: Everglades, hydrology, algae, diatoms, cyanobacteria and community structure

Abstract

The Florida Everglades is a mosaic of short and long-hydroperiod marshes that differ in the depth, duration, and timing of inundation. Algae are important primary producers in widespread Everglades' periphyton mats, but relationships of algal production and community structure to hydrologic variability are poorly understood. We quantified differences in algal biomass and community structure between periphyton mats in 5 short and 6 long-hydroperiod marshes in Everglades National Park (ENP) in October 2000. We related differences to water depth and total phosphorus (TP) concentration in the water, periphyton and soils. Long and short-hydroperiod marshes differed in water depth (73 cm vs. 13 cm), periphyton TP concentrations (172 μg g^{-1} vs. 107 μg g^{-1}, respectively) and soil TP (284 μg g^{-1} vs. 145 μg g^{-1}). Periphyton was abundant in both marshes, with short-hydroperiod sites having greater biomass than long-hydroperiod sites (2936 vs. 575 grams ash-free dry mass m^{-2}). A total of 156 algal taxa were identified and separated into diatom (68 species from 21 genera) and "soft algae" (88 non-diatom species from 47 genera) categories for further analyses. Although diatom total abundance was greater in long-hydroperiod mats, diatom species richness was significantly greater in short- hydroperiod periphyton mats (62 vs. 47 diatom taxa). Soft algal species richness was greater in long-hydroperiod sites (81 vs. 67 soft algae taxa). Relative abundances of individual taxa were significantly different among the two site types, with soft algal distributions being driven by water depth, and diatom distributions by water depth and TP concentration in the water and periphyton. Periphyton communities differ between short and long-hydroperiod marshes, but because they share many taxa, alterations in hydroperiod could rapidly promote the alternate community.

Introduction

The structure and function of benthic communities in temporary wetlands is strongly linked to the timing, distribution and duration of flooding (or hydroperiod, as in Townsend, 2001). The Everglades of southern Florida, U.S.A., contains wetlands that span the hydroperiod continuum from rarely to permanently flooded. This mosaic has been classified into slough and wet-prairie communities that are flooded for relatively long (≥8 month) or short (< 8 month) duration each year (Gunderson, 1994). Short-hydroperiod marshes are found on the edges of the Everglades, and hydroperiod generally increases toward the interior sloughs. Hydroperiod distribution is frequently changing in this system due to human manipulations of water inputs through canal structures that control water movement into the Everglades (Fennema et al., 1994). Therefore, it is important to identify short and long-term ecological effects (and indicators) of hydrologic change in this wetland.

Several studies have identified hydroperiod as a primary driver of plant (Gunderson, 1994), invertebrate (Bruno et al., 2001) and fish (Kushlan, 1989; DeAngelis et al., 1997) communities in the Everglades, although effects on the prolific periphyton mats distributed across the hydroperiod gradient has been noted only anecdotally (Browder et al., 1981; Thomas et al., 2002). Gunderson (1994) classified plant community distribution among Everglades sloughs and wet prairies and generally described long-hydroperiod Everglades sloughs as having sparse macrophyte communities with abundant floating periphyton mats (usually associated with submersed macrophytes) and organic-rich sediments. These marshes generally lack epipelic and epilithic mats. In contrast, short-hydroperiod wet prairies were characterized as having a rich emergent macrophyte community interspersed with thick, epipelic and epilithic mats that overlay mineral soils and calcium carbonate bedrock. Short-hydroperiod marshes usually lack *Utricularia purpurea* and associated epiphyton (Gottlieb et al., 2005).

Everglades periphyton mats contain a matrix of algae, fungi, bacteria and dead organic matter and are an important food resource for invertebrates and fish (Cattaneo & Mousseau, 1995; Lamberti, 1996; Shaver et al. 1997; Sheldon & Walker, 1997) and play a key role in the biogenic formation of short-hydroperiod marl soils (Gleason & Spackman, 1974). Despite the importance of periphyton to the Everglades ecosystem, the variability in periphyton community composition between short and long-hydroperiod marshes has not been well defined. A few early studies provide general descriptions of the floristic composition of short-hydroperiod epipelic periphyton mat communities (Van Meter-Kasanof, 1973; Browder et al., 1981). Most work has focused on long-hydroperiod periphyton mats, particularly defining response to changes in nutrient availability in both experimental studies and descriptive gradient analyses (Vymazal & Richardson, 1995, McCormick et al., 1998). Taxonomic composition and nutrient concentrations in periphyton tissues appear to be important early indicators of changing nutrient availability in the Everglades and have been advocated as water quality metrics (Gaiser et al., 2004). Although studies elsewhere have shown periphyton also responds strongly to water availability (Gaiser et al., 1998; Wolin & Duthie, 1999), their relationships to hydroperiod in the Everglades are poorly defined. Hydroperiod may be an important driver of periphyton composition in the Everglades (Gottlieb et al., 2005), and periphyton could provide an important index of altered hydropatterns, similar to their utility in detecting nutrient change (Gaiser et al., 2004).

This study compares periphyton community structure between short and long- hydroperiod marshes in Everglades National Park (ENP). Periphyton, soil, and water samples were collected from short-hydroperiod wet prairie marshes and long-hydroperiod Everglades sloughs in order to (1) provide the first comprehensive description of algal composition of short- hydroperiod marshes, (2) distinguish this community from that of long-hydroperiod settings, and (3) relate biomass and compositional differences to physiochemical variation between short and long-hydroperiod habitats.

Methods

Site and habitat description

In October 2000, samples were collected from five short and six long-hydroperiod sites in ENP (Fig. 1). The short-hydroperiod sites (S1A, B and C, S2, and S3) were located in the eastern edge of ENP in habitat characterized as wet prairie/rocky glades (Gunderson, 1994) and dominated by *Cladium jamaicense*, *Rhynchospora colorata*, and *Rhynchospora traycii* (Wunderlin, 1998). The long-hydroperiod sites (L1A, B and C, L2, L3, and L4) were located in Shark River Slough in a plant community dominated by *Eleocharis cellulosa* and *Utricularia purpurea* (Wunderlin, 1998). Site L4 is located in the slough-mangrove ecotone where estuarine waters moving inland may seasonally affect salinity and nutrients (Fig. 1). Three replicate samples were collected at each site.

A modification of the 1995 Base South Florida Water Management Model (SFWMM) v3.5 was used to select short-hydroperiod sites submerged from 30 to 180 days per year and long-hydroperiod sites flooded for 300–365 days (http://www.sfwmd.gov/org/pld/restudy/hpm/frame1/maps/indmaps.htm). Although short-hydroperiod sites are dominated by marl soils, many also contain solution holes. Solution holes can remain inundated several months longer than the surrounding short-hydroperiod environment (Kobza

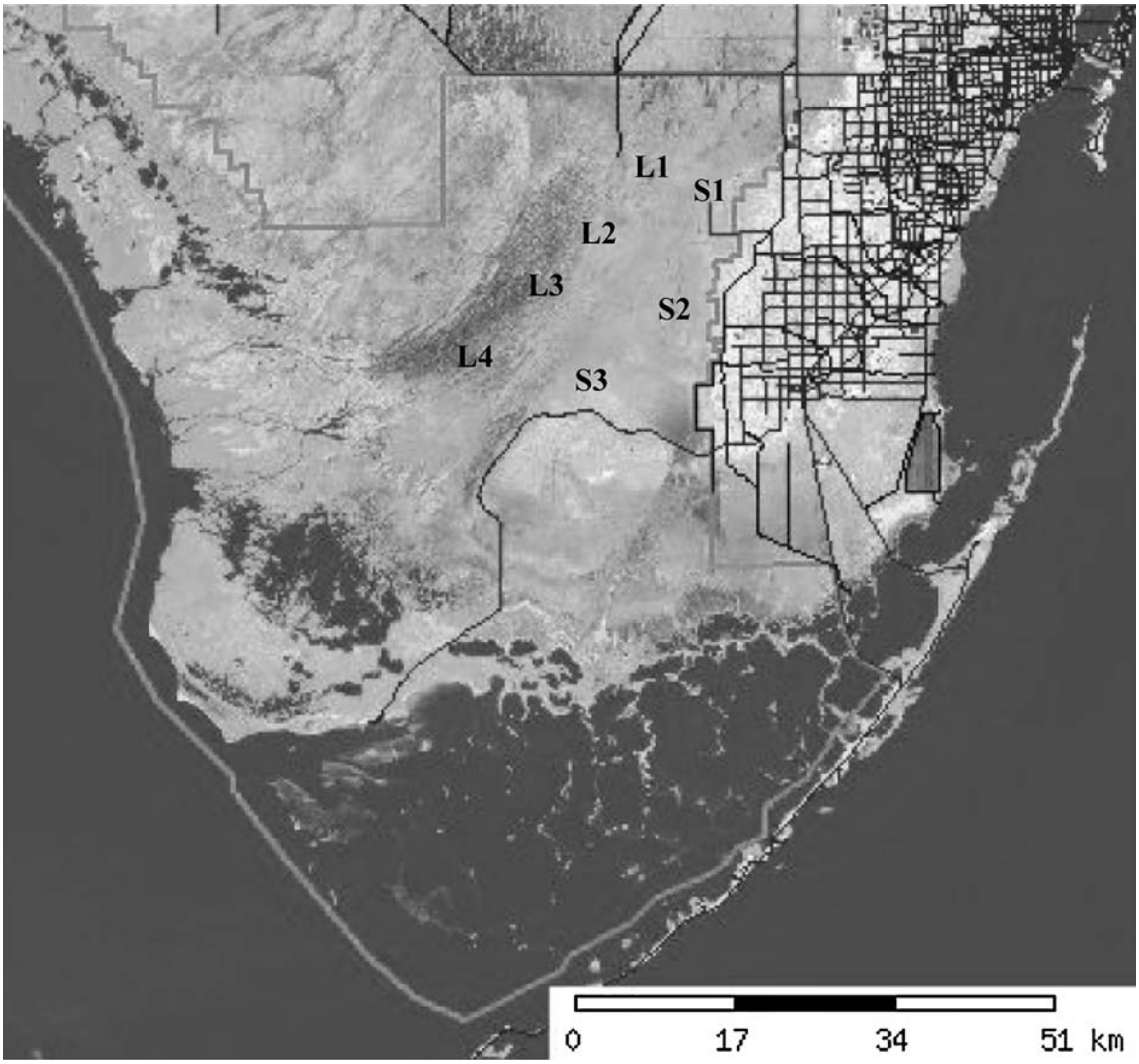

Figure 1. Sample stations within Everglades National Park. L1, L2, L3, and L4 are long-hydroperiod sites and S1, S2, and S3 are short-hydroperiod sites.

et al., 2004) and contain relatively organic-rich soils, therefore having a hydroperiod intermediate between typical short and long-hydroperiod sites. Samples were collected from three solution holes at both sites S1 and S2; selected holes were at least 10 cm deep and greater than 50 cm wide.

Periphyton samples

In order to avoid substrate bias, such as that of glass slides toward diatoms (Marszalek et al., 1979, Cattaneo & Amireault, 1992, Danilov & Ekelund, 2001, Jaskowiak et al., 2001), we sampled extant periphyton instead of using artificial substrates. Fifteen cores (3.25 cm^2) of floating *Utricularia*-associated periphyton and benthic epilithic and epipelic periphyton were collected and pooled for each mat sample. The Daubenmire (1959) 2×5 dm plot method was used to estimate mat coverage in the field. Fragments of plant and animal debris and *U. purpurea* were removed from the periphyton samples. Cores were homogenized in a known volume of deionized water (Fairchild et al., 1985) and then divided into three fractions. Two fractions were used to analyze the algal communities, while the third was used to determine periphyton nutrient content and biomass, as described below. Algal community analysis was purposefully separated into two fractions – a "soft algal" component which included all diatom and non-diatom algae and a diatom only fraction. This separation was necessary to discern specific diatom responses apart from the rest of the community. Soft-algae were identified to the lowest possible taxonomic entity given considerable nomenclatural inconsistency and uncertainty with this poorly explored flora (often genus-level identification was necessary; Gaiser et al., 2004), while diatoms were identified to the lowest taxonomic entity (species or variety).

Soft algal samples were frozen prior to enumeration. A known volume of thawed, homogenized sample was placed on a cover slip, partially dried, inverted onto a slide with 0.02 ml deionized water and sealed with clear fingernail polish to obtain a semipermanent (1–2 week viability) mount (Stevenson & Bahls, 1997). Viable cells (pigmented) were identified at 1000× magnification until 500 "units" were identified. Units were either single cells (of unicellular or colonial taxa) or 60 μm sections of filaments. Algal taxa were identified using standard literature and a taxonomic database developed for South Florida taxa (Desikachary, 1959; Starmach, 1966; Patrick & Reimer, 1975; Whitford & Schumaker, 1984; Komárek & Anagnostidis, 1986, 1989; Komárek & Hindak, 1988, http://www.serc.fiu.edu/periphyton/). Diatoms encountered in soft counts were identified to genus to measure the relative abundance of diatoms verse other soft algae.

The diatom fraction was cleaned (Hasle & Fryxell, 1970) and a known volume of pooled sample was dried on cover slips which were mounted to glass slides using Naphrax®. A minimum of five hundred valves per slide were identified and counted (Weber, 1973). Identifications followed Patrick & Reimer (1975), Krammer & Lange-Bertalot (1991), Krammer (1992), Lange-Bertalot (1993) and an online database of South Florida diatom taxa (http://www.serc.fiu.edu/periphyton/).

The third fraction was used to determine periphyton dry weight (DW), ash-free dry weight (AFDW), and nutrient content (Weber, 1973). A subsample of dried material was used to estimate periphyton total nitrogen (TN) and total carbon (TC) on a Carlo Erba NA1500 series analyzer. A second subsample of dried material was used to measure total phosphorus (TP) content colorimetrically (Solarzano & Sharp, 1980). A final subsample was used to determine periphyton AFDW (1 h at 500 °C: Weber, 1973). Measures of periphyton biomass determined from cores were multiplied by coverage estimates to scale biomass estimates to a m^{-2} basis.

Soil samples

Soil samples (10 cm depth) were collected from each site using a modified 140 ml syringe. Dry weight (80 °C) and AFDW (450 °C) were determined. Bulk density was calculated as dry weight (DW) cm^{-3}. Samples were homogenized and divided into subsamples for TN, TC, and TP analyses using methods described above for periphyton.

Water Samples

Six water samples were collected from each site and stored on ice. Three of these samples were filtered through 25 mm Whatman GF/F glass fiber filters and three remained unfiltered. The unfiltered samples were analyzed for TN, TC, and TP using methods described above and filtered samples were analyzed for soluble reactive phosphorus (SRP), nitrite (NO_2), nitrate (NO_3), and ammonium (NH_4) using a four channel Alpkem RFA 300 series auto analyzer (EPA Standard Methods 365.1, 353.2, 353.2, and 350.1, respectively).

Statistical analysis

Patterns of diatom and soft algal species distribution among and within the two hydroperiod classes were visualized using nonmetric multidimensional scaling (NMDS) ordination, employing the Sorenson (Bray-Curtis) dissimilarity metric (PC-ORD Version 4-1, Gleneden Beach, Oregon, U.S.A.). To determine the significance of patterns noted in the ordination, we used analysis of similarity (ANOSIM; PRIMER V 5, Plymouth, UK

2002, Clarke, 1993; Clarke & Warwick, 1994). ANOSIM uses the same similarity matrix as in the ordination to test whether among group exceeds within group dissimilarity, and the degree of difference is expressed as a "Global *R*" value which increases from 0 to 1 with increasing among sample dissimilarity. When analyzing the soft algal data with NMDS and ANOSIM, all *Chroococcus*, *Aphanothece*, *Cosmarium*, *Desmidium*, and *Staurastrum* species were pooled at the generic level. Species patterns were linked to environmental data using vector biplot overlays and Pearson correlations. Physiochemical data were compared across and within hydroperiods using general linear model (GLM) analysis of variance (ANOVA) followed by Tukey's studentized range test with SAS Version 8.0 (SAS, Kerry, NC) statistical software.

Results

Periphyton biomass

Periphyton biomass ranged from 286 to 3665 g AFDM m^{-2}, with the epilithic and epipelic mats of the short-hydroperiod sites having significantly higher average biomass than the floating mats in the long-hydroperiod sites (2936 vs 575 g AFDM m^{-2}, respectively; Fig. 2; $F_{1,31} = 421.25$; $p < 0.001$). Biomass in solution holes was greater than that of long-hydroperiod sites (2618 g AFDM m^{-2}). Mats from long-hydroperiod sites contained proportionally more organic matter than short-hydroperiod sites (53% vs. 37%, respectively; $p < 0.001$.).

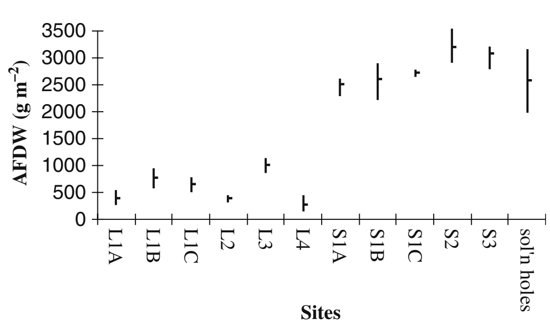

Figure 2. Periphyton ash-free dry weight (AFDW) by site, $n = 3$/site. L indicates long-hydroperiod sites and S indicates short-hydroperiod sites. Solution hole samples are from sites S1 and S2.

Periphyton community composition

Soft algae

Ninety-six taxa of chlorophytes, cyanophytes and diatoms were counted in the soft algal analyses, representing 47 genera (see Electronic Supplemental Materials[1] – Appendix A). Species richness was higher at long- hydroperiod sites than short-hydroperiod sites (78 vs. 69 taxa, respectively). Coccoid cyanobacteria, particularly *Chroococcus* spp., dominated the taxonomic diversity at all sites (see Electronic Supplemental Materials – Appendix A). *Scytonema hofmanii*, *Schizothrix calcicola* and two unidentified cyanobacteria (paired coccoid cyanobacteria (2–4 μm) sp. 2 and nonheterocystic cyanobacterial filament 8) were common in short-hydroperiod sites. Long-hydroperiod sites contained greater *Oedogonium* spp. and *Bulbochaeta* sp. than short-hydroperiod sites and had greater desmid diversity and abundance (see Electronic Supplemental Materials – Appendix A).

Although not numerically abundant in the short-hydroperiod sites, diatoms were well represented in many of the long-hydroperiod sites. Relative diatom abundance was significantly greater in long-hydroperiod periphyton mats than short-hydroperiod mats (29.00% vs. 0.96%, respectively). In particular, *Fragilaria* spp. and *Encyonema* spp. were the most common diatoms represented (see Electronic Supplemental Materials – Appendix A). The top ten algal taxa represented in both short and long-hydroperiod sites made up over 70% of all soft algal counts (see electronic supplemental materials – Appendix A).

Analysis of similarity indicates short and long-hydroperiod sites differed significantly in soft algal community composition (Global $R = 0.814$, $p < 0$ .001). All long-hydroperiod sites are seen on the right side of axis 1, while all short-hydroperiod sites are grouped on the left side of axis 1 (Fig. 3). The NMDS loss function describing the degree to which each dimension contributes to representing full compositional dissimilarity declined appreciably between one and two dimensions but not thereafter, so we retained a 2-dimensional result for visualization (stress = 23.9).

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[1] Electronic Supplementary material is available for this article at http://dx.doi.org/10.1007/s10750-006-0132-1

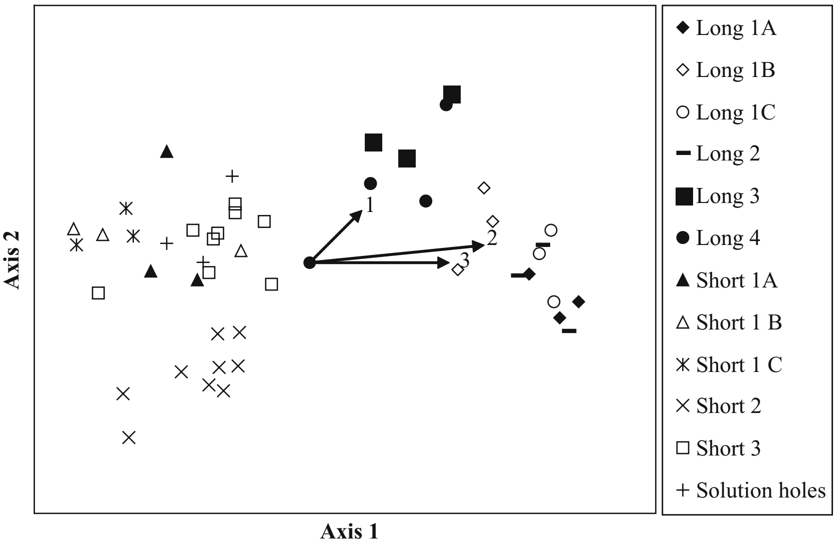

Figure 3. Two-dimensional non-metric multidimensional scaling (NMDS) ordination of soft algae communities. Long-hydroperiod, short-hydroperiod and solution hole communities are plotted along with biplot vector overlays of physiochemical data where vector 1 = Soil TP, 2 = water depth, 3 = periphyton TP, water TP and SRP. The direction of the vector indicates increases in the measured parameter(s).

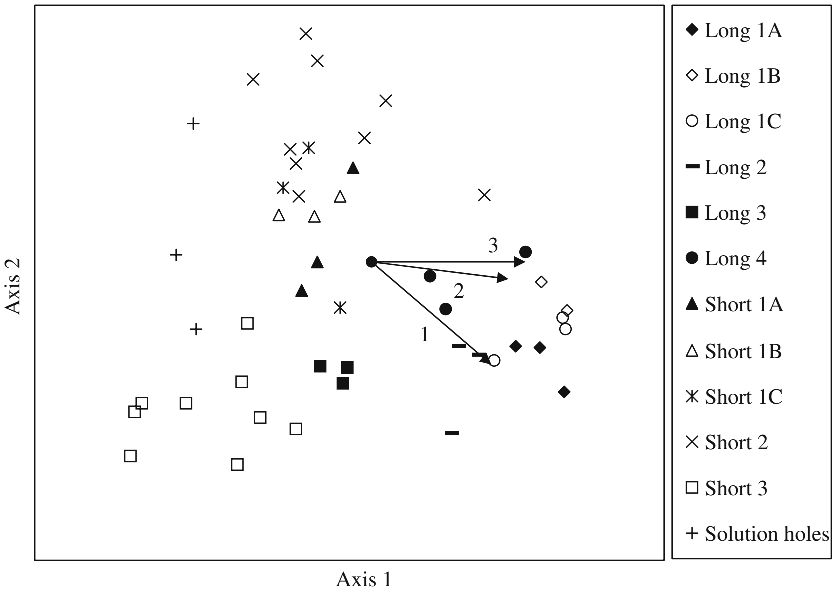

Figure 4. Two-dimensional non-metric multidimensional scaling (NMDS) ordination of diatom communities. Long-hydroperiod, short-hydroperiod and solution hole communities are plotted along with biplot vector overlays of physiochemical data where vector 1 = water depth, 2 = water column SRP and TP, 3 = periphyton TP. The direction of the vector indicates increases in the measured parameter(s).

Diatom counts

Sixty-eight diatom taxa representing 21 genera were identified. Sixty-two species were found in short-hydroperiod sites, while 47 species were found in long-hydroperiod sites. *F. synegrotesca* and *Mastogloia smithii* were dominant taxa in long-hydroperiod sites, while *E. evergladianum*, *M. smithii*, *Encyonema microcephala*, *Nitzschia* *palea var. debilis* and *Brachysira neoexilis* were dominant in the short-hydroperiod (see Electronic Supplemental Materials – Appendix B).

Diatom communities differed compositionally between long and short-hydroperiod sites (Global $R = 0.623$, $p = 0.001$). A two dimensional model reduced stress from 23.2 to 18.9; adding more axes did not appreciably reduce this level, so the 2-dimensional ordination was retained for visualization of this pattern (Fig. 4).

Periphyton nutrients

The TP concentration in periphyton tissue was greater in long-hydroperiod sites than in short-hydroperiod sites (172 and 107 μg g^{-1}, respectively; Fig. 5; $F_{2,45} = 24.37$, and $p < 0.001$). Periphyton TP from solution holes did not differ significantly from long or short-hydroperiod mat TP. Periphyton at site L4 contained higher levels of TP than all other long-hydroperiod sites (251 μg P g^{-1}; Fig. 5; $F_{5,12} = 9.0$, $p < 0.001$). Site S2 had greater mat TP than all other short-hydroperiod sites (131 μg P g^{-1}; $F_{4,22} = 12.44$, $p < 0.001$).

Physiochemical parameters

Water depth

Water depth at the time of sampling was linearly related to hydroperiod class, as was found by Gunderson (1994) throughout ENP. Short and long-hydroperiod average water depths were 13 ± 11 cm (± S.D.) and 73 ± 4 cm, respectively.

Water column nutrients

Total P, TC, SRP, NH_4, NO_2, and NO_3 did not differ significantly between long and short-hydroperiod sites (Table 1). A significant difference was found in TN ($F = 8.83$, $p = 0.007$), but this was driven mainly by one extreme sample from site L4. If this sample was removed from the analysis, there were no significant differences in water chemistry between groups.

Soils nutrients and organic content

Excluding site L4 and the solution holes, soil TP was significantly greater in long-hydroperiod than short-hydroperiod sites (284 μg g^{-1} vs. 145 μg g^{-1}; Fig. 6a; $F_{2,33} = 11.58$, $p < 0.001$). Soil TP was lower in long-hydroperiod sites if TP was standardized for soil bulk density rather than dry mass (82 vs. 40 μg cm^{-3}, respectively; Fig. 6b; $F_{1,16} = 9.10$, $p = 0.008$). Soil TP and periphyton TP were correlated in long-hydroperiod sites but not in short-hydroperiod sites (Fig. 6a, b). The correlation between long-hydroperiod periphyton TP and soil TP increased when soil TP was standardized for bulk density (Fig. 6b; $R^2 = 0.48$ for soil TP in μg g^{-1} vs. $R^2 = 0.85$ for soil TP in μg cm^{-3}). The solution holes and site L4 had greater TP than the other five short and five long-hydroperiod sites (Fig. 7a).

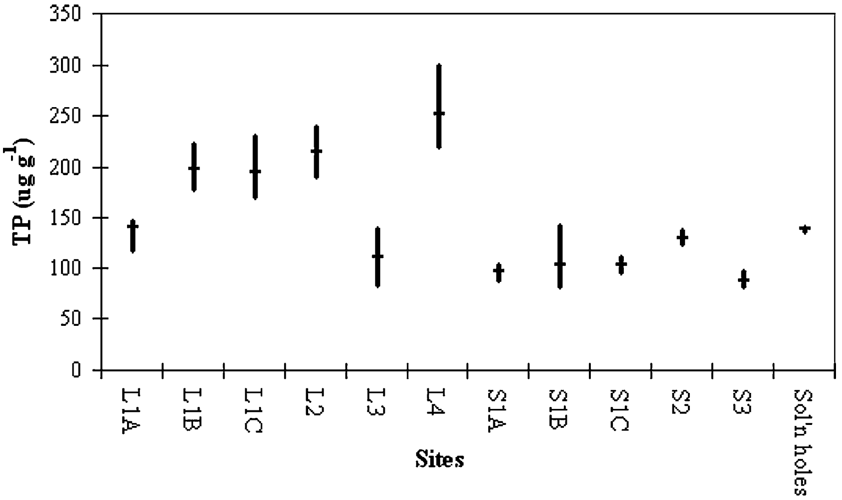

Figure 5. A. Periphyton total phosphorus (μg TP g^{-1} DW) by site showing high, low and average TP, $n = 3$/site. Bars show range; horizontal tics indicate average.

Table 1. Mean water column nutrients of the 6 long and 5 short-hydroperiod sites with standard deviations in parenthesis, $n = 3$/site. NS indicates no significant difference between long and short-hydroperiod sites

Nutrient	Short-Hydroperiod (μM)	Long-Hydroperiod (μM)	*p*
TP	0.16 (0.03)	0.10 (0.03)	NS
TN	26.50 (3.49)	41.21 (18.57)	0.007
TOC	648.71 (123.23)	727.98 (109.91)	NS
NO_2	0.00 (0.00)	0.00 (0.00)	NS
NO_3	0.21 (0.14)	0.50 (0.14)	NS
NH_4	0.64 (0.79)	0.79 (0.79)	NS
SRP	0.10 (0.03)	0.10 (0.03)	NS

Soil C:N was significantly greater in short than long-hydroperiod sites (25 vs. 12, respectively; Fig. 7b; $F_{2,33} = 63.88$, $p < 0.001$). Site L3 had higher soil C:N than the four other long-hydroperiod sites (16.24 vs. 11.98, respectively; Fig. 7b; $F_{5,12} = 20.83$, $p < 0.001$).

Solution hole soil C:N did not differ from either short or long-hydroperiod soils (Fig. 7b).

The average organic content of soils from short-hydroperiod sites, solution holes, and long-hydroperiod sites was 10%, 35%, and 80% respectively.

Relationship of periphyton communities to physiochemical parameters

When the physiochemical parameters were analyzed in relation to the NMDS axes generated from the soft algae counts, a strong correlation was found between NMDS axis 1 and water depth, soil TP, periphyton TP, water column TP and TN, and water column SRP (Table 2). Axes were rotated to maximize the fit of each variable. The variation among sites along axis 2 was not correlated to the above factors (Table 2, Fig. 3).

Analysis of the relation of the physiochemical parameters to the NMDS axes generated from the diatom counts showed that differences in diatom communities were correlated with differences in water depth, water column TP and SRP, and periphyton TP (Table 2). Water depth, water TP, SRP, soil TP, and periphyton TP were all strongly correlated to axis 1 (Table 2, Fig. 4). Axis 2 was also positively correlated with water depth (Table 2). *F. synegrotesca* was abundant in deep water, long-hydroperiod sites, while this species was rare in short-hydroperiod sites (see Electronic Supplemental Materials – Appendix B).

Discussion

Periphyton community structure

Algal community structure varied significantly between short and long-hydroperiod mats (Figs. 3 and 4), but differences between communities were primarily due to differences in relative abundance rather than presence/absence. Of the 96 taxa in soft algae counts, 77% were found in both short and long-hydroperiod periphyton mat types, while 65% of the 68 taxa in the diatom counts were found in both mat types. Cyanobacteria were the dominant taxa observed in both short and long-hydroperiod sites. This study and that of Wood & Maynard (1974) indicate that *Chroococcus* spp. are

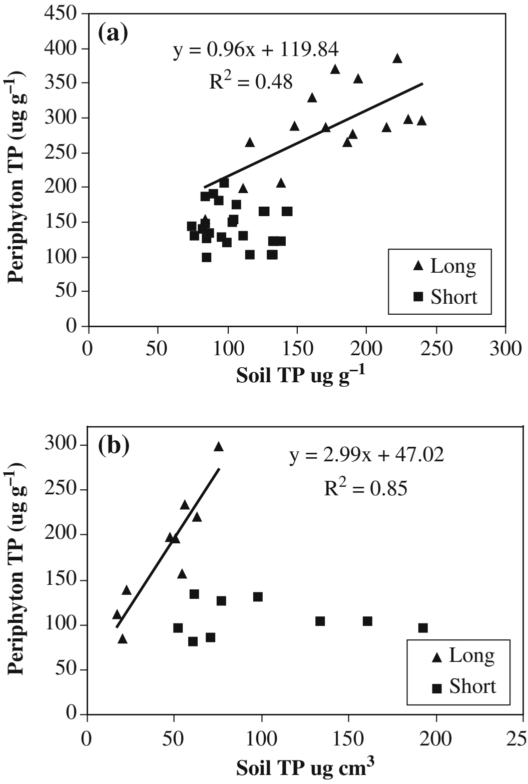

Figure 6. Soil total phosphorus (TP) vs. periphyton TP in long (triangles) and short (squares) hydroperiod marshes. Regression lines are for long-hydroperiod data only. (a) Soil TP is standardized for dry weight (DW). (b) Soil TP is standardized for bulk density.

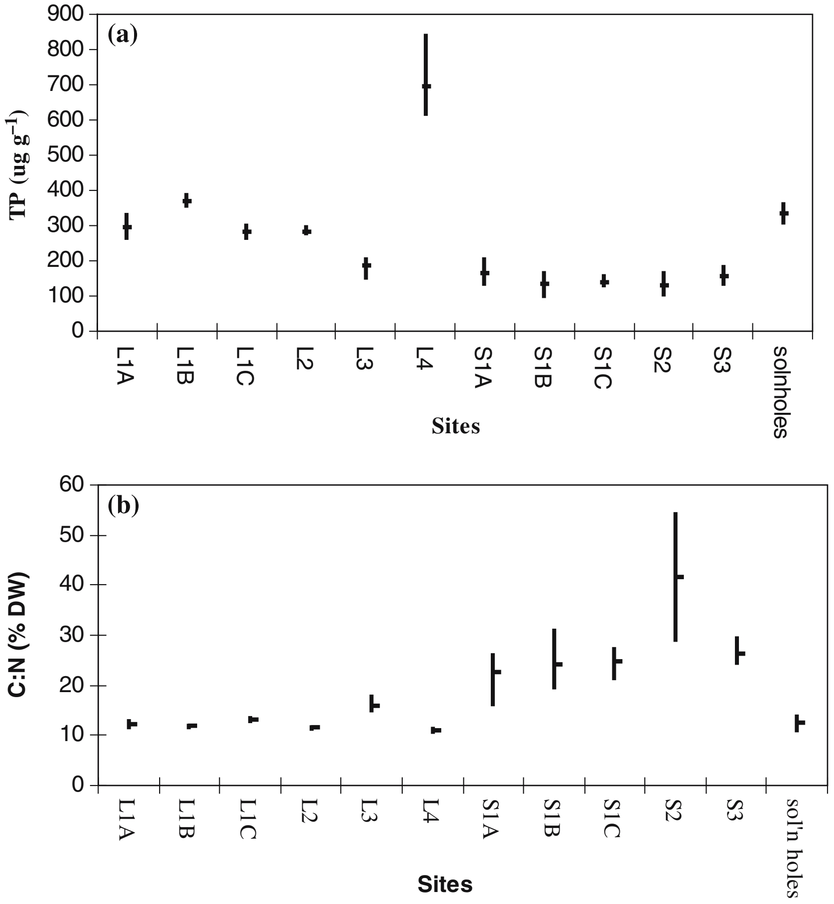

Figure 7. (a) Soil total phosphorus (TP) at all sites showing high, low and average TP, $n = 3$/site. (b) Ratios of % DW carbon to % DW nitrogen in soil. Bars show data range; horizontal tics are average C:N, $n = 3$/site. Abbreviations are the same as in Figure 4.

common in both short and long-hydroperiod mats, but *Chroococcus* spp. were conspicuously absent from the Browder et al. (1981) study.

Diatom communities in ENP were considerably more diverse than previously reported. Our study identified 68 diatom taxa from 24 genera, whereas previous studies of the short and long-hydroperiod periphyton communities identified only 7 (Browder et al., 1981) and 14 genera (Vymazal & Richardson, 1995) of diatoms, respectively. Similar to our study, *F. synegrotesca* was abundant in long-hydroperiod Everglades sites studied by Vymazal & Richardson (1995), McCormick et al. (2001), and Childers et al. (2002).

Diatom numeric abundance in short-hydroperiod sites was less in our study as compared to Browder et al. (1981). Browder et al. (1981) reported the annual average abundance of diatoms at site S1 made up approximately 14% of the algal material, with seasonal variability ranging from 5% in July to a maximum of 25% in November. In our study, diatoms in all short-hydroperiod sites made up less than 1% of enumerated algae. Water management activities have shortened the length of flooding by several months in short-hydroperiod habitats (Fennema et al., 1994). Shortened hydroperiod increases desiccation stress, possibly leading to the observed decline in diatom numbers (Gottlieb et al., 2005) when comparing our results to those of Browder et al. (1981).

Periphyton in short-hydroperiod sites have significantly greater mean DW and AFDW biomass than periphyton in long-hydroperiod sites (Fig. 2). There are 3 possible explanations for these results. First, short-hydroperiod mats are benthic and adhere to the sediment or rock sub-

Table 2. Pearson and Kendall Correlations with soft algae and diatom NMDS ordination axes 1 and 2

	Soft Algae NMDS		Diatom NMDS	
	Axis 1 R^2	Axis 2 R^2	Axis 1 R^2	Axis 2 R^2
Water Depth	0.79	0.11	0.39	0.33
Water TP	0.42	0.00	0.48	0.03
Water TN	0.15	0.07	0.14	0.02
SRP	0.48	0.00	0.50	0.05
Soil TP	0.31	0.17	0.23	0.03
Periphyton TP	0.46	0.00	0.52	0.00

strate. Although some benthic mats become detached from the substrate, mats in our study were tightly associated with the marl sediments. This stability leads to seasonal and annual accrual, resulting in laminated mats. Defining which layer is the start of a growing season is problematic and can lead to error in distinguishing annual biomass and standing stock.

Secondly, part of the variation in periphyton biomass results from problems separating benthic mats from the substrate. It is difficult to remove all of the sediment without the loss of algal filaments and frustules (Smith, 1944). Filamentous forms found in dry environments often penetrate the substrate to cope with desiccation (Garcia-Pichel & Pringault, 2001). This is a common strategy also found in desert algae. In contrast, floating long-hydroperiod mats associated with the macrophyte *Utricularia purpurea* are much easier to sample. As *U. purpurea* and the associated periphyton age, much of the mat is lost due to sloughing. This loss does not accumulate in the mat, but instead falls to the sediment; thus biomass of floating long- hydroperiod mats is much lower than short-hydroperiod mats. This helps explain the strong relationship between floating mat TP and sediment TP. Samples of floating mats are a relatively recent accumulation of periphyton.

Third, short-hydroperiod periphyton biomass is also greater due to the dominance of calcite-precipitating cyanobacterial filaments, such as *S. hofmanii*, in short-hydroperiod periphyton. Calcite accumulation in dense mats increases mat DW more than a comparable volume of organic matter.

Physiochemical variation between short and long-hydroperiod habitats

The long-hydroperiod marsh sites had peat soils with high organic content, low C:N, and high TP on a dry weight basis, as compared to short-hydroperiod sites, although TP per volume was greater in short-hydroperiod marshes. When comparing peat and marl soils, or organic and mineral soils, controlling for bulk density provides a more complete description of nutrient variability between the two soil types and a different way to consider nutrient availability (Newman et al., 1998). The lower bulk density of long-hydroperiod peat soils explains this difference in TP. When periphyton TP was graphed against soil TP, calculated on a volume basis, the relation of long-hydroperiod periphyton TP to soil TP was much stronger than when soil TP was calculated on a DW basis (Fig. 6a and b).

Water column dissolved nutrients and total nutrients varied little between long and short-hydroperiod sites (Table 2). The efficient uptake of nutrients from the water by periphyton and macrophytes leads to low levels of SRP and TP in the water column at both types of sites. Everglades algae drive down the water column nutrient concentrations to extremely low levels, thereby precluding the growth of species with higher nutrient requirements. The low variability in water column nutrients and totals, as compared to the relatively large changes in periphyton mat nutrients, suggests that periphyton nutrient content may be a better indicator of the actual trophic status of Everglades marshes (Childers et al., 2002; Gaiser et al., 2004).

As predicted, mat community structure across the Everglades landscape was strongly related to water depth and, thus, hydroperiod. In the NMDS analyses, water depth was correlated with axis 1 for both soft algae and diatoms and was the major correlate between diatoms and axis 2 (Table 2). Soft algae distributions were most strongly related to water depth, while diatom distributions were correlated with water depth, water column phosphorus and periphyton phosphorus. Even with large variation in periphyton TP (Fig. 5), however, diatom and soft algae communities differed greatly between hydroperiods. This indicates, again, that hydroperiod plays a strong role in structuring Everglades algal communities.

Although the physiochemical parameters affected short and long-hydroperiod communities, responses differed in the two communities. For example, the short-hydroperiod periphyton TP was unrelated to soil TP, but soil TP was strongly correlated to periphyton TP concentrations in long-hydroperiod communities (Fig. 6). Conversely, short-hydroperiod periphyton had a stronger relationship to water depth than long-hydroperiod communities. Because the long-hydroperiod communities sampled remained wet for most, if not all, of the year, inundation was not the driving variable within their environments, whereas for communities that suffered desiccation annually, water depth was much more important. The one exception to this was long-hydroperiod site L3. Although still a long-hydroperiod site, L3 dries nearly annually resulting in a diatom community that was more similar to short-hydroperiod communities (Fig. 4).

A major state and federal attempt to restore what remains of the Everglades began in 1994 with the Everglades Forever Act (Florida Statute §373.4592 [1994]). Restoration will provide additional inputs of fresh water into Everglades National Park (ENP). Proposed changes in duration and amount of flow may result in expanding long-hydroperiod areas within the current park boundaries and adding short-hydroperiod sites on the Park's border. This study provides data on the distribution and abundance of algae in different Everglades marshes prior to restoration. The lack of literature on short-hydroperiod community structure makes this landscape-scale survey of particular importance. Results of our study suggest that as short-hydroperiod marshes are inundated for longer periods, their periphyton mats should begin to resemble long-hydroperiod mats, having fewer cyanobacterial filaments and greater diatom abundance. This periphyton community change may alter Everglades trophic structure. Prolonged increases in hydroperiod will also affect soil formation through decreased calcium carbonate deposition associated with a decrease in cyanobacterial filament abundance and an increase in organic rich sediments.

Acknowledgements

Special thanks to Drs. Dan Childers, Joel Trexler, Len Scinto, Rudolf Jaffe, Tom Philippi, and Serge Thomas for helpful comments throughout the research and writing stages of this project. Members of the FIU Periphyton and Macrophyte labs also deserve special thanks for field and laboratory assistance during all stages of this research. We would like to acknowledge the FIU Tropical Biology Program and the Southeast Environmental Research Center for partially funding the above research. Additional support was provided by the National Science Foundation through the Florida Coastal Everglades LTER program (DEB−9910214). This is contribution #295 of the Southeast Environmental Research Center at Florida International University.

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