Periphyton as an indicator of restoration in the Florida Everglades

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1. Introduction

Periphyton communities, comprised of algae, floating plants, and associated animals, are a ubiquitous feature of Everglades marshes. Periphyton is responsible for over half of the primary production in the Everglades (Ewe et al., 2006) and is the primary food source for small fish, crayfish, grass shrimp and other small consumers at the base of the food web. Therefore, understanding changes in periphyton is critical to determine causes for alterations in communities of charismatic mega-fauna (i.e., large fish, wading birds, alligators). In addition, through interactions with the physiochemical environment and other biota, periphyton influences many other features of the Everglades ecosystem including soil quality, concentration of nutrients, and dissolved gasses. Periphyton responds predictably and quickly (days to weeks) to changes in environmental conditions at a large range of spatial scales (meters to tens of kilometers). It therefore serves as an excellent early responder and can be used as a warning of impending change (Gaiser et al., 2005). Detecting change quickly in this system is important, as the difficulty and cost of restoration increases with the duration of damage. For example, it is much easier to stop an impending cattail invasion through diversion of eutrophic water than to replace a large cattail stand with sawgrass.
Studies of variation in Everglades periphyton along naturally existing and experimentally created gradients have found strong relationships between species composition, nutrient content, structure (growth form), calcite content, and physiology (e.g., nutrient uptake and productivity) to water quality and quantity (Browder et al., 1982; Swift and Nicholas, 1987; Grimshaw et al., 1993; Raschke, 1993; Vymazal and Richardson, 1995; McCormick et al., 1996, 1997, 1998; McCormick and O’Dell, 1996; Cooper et al., 1999; Pan et al., 2000; Gaiser et al., 2006). The total phosphorus (TP) content of periphyton tissue is one of the best measures of P load history (McCormick and Stevenson, 1998; Gaiser et al., 2005, 2006). While increases in water as well as soil P are only detectable after years of enhanced P loading (because of rapid microbial and physical uptake), effects upon periphyton TP concentration are immediate (Gaiser et al., 2004a,b). Large-scale losses of periphyton throughout the system have occurred in response to excessive P enrichment from canals (Gaiser et al., 2006) and these losses have had cascading effects throughout the Everglades ecosystem (Gaiser et al., 2005). For this reason, periphyton TP concentration and correlated variables (i.e., calcite content, species composition) are now regularly monitored in most Everglades programs. Additionally, changes in periphyton biomass and composition are apparent along spatial and temporal hydrologic gradients, indicating that periphyton collections will improve detections of hydrologic changes as well (Thomas et al., 2006; Gottlieb et al., 2006).

The utility of periphyton to expose ecological ramifications of restorative or deconstructive change is due to its bearing several of the most desirable features of a reliable ecological indicator which include (1) being distributed throughout the system of study, and (2) having rapid response to environmental change that is (3) quantifiable at several levels of biological organization (individual, species, population and community) with (4) consequences to levels above and below its placement in the food web (Karr, 1999). Reliance on periphyton to indicate environmental change is well justified by scientific research conducted in the Everglades (McCormick and Stevenson, 1998; Gaiser et al., 2006), which adds regional applicability to the existing body of literature in aquatic sciences that supports the widespread employment of periphyton monitoring in aquatic ecosystem management (Hill et al., 2000; Stevenson, 2001). We anticipate that patterns of periphyton production, nutrient content and composition among and within mapping assessments will reliably indicate changes driven by hydrology and nutrient enrichment. Alterations in periphyton attributes then cascade through the system to affect higher organisms through changes in food composition and quality, concentration of gasses and nutrients in the water column, and ecosystem structure (i.e., soil formation and quality, physical habitat structure).

1.1. Factors that drive the use of periphyton indicators

The following hypotheses relative to periphyton were formulated using data from descriptive and experimental studies and are now being used to guide monitoring programs in the Greater Everglades (RECOVER, 2005).

The proportion of floating, calcareous periphyton mats increase with longer hydroperiods, but are replaced by epiphytic non-calcareous algal communities once water depths exceed ~1–2 m.

1.1.1. Supporting data

Studies along transects in Everglades wetlands showed hydrologically driven gradients in periphyton mat structure (Gaiser et al., 2006). Sloughs and marl prairies were dominated by thick, highly productive calcareous mats, but algal communities became non-calcareous when water depths exceeded about 1.5 m. Other long-term studies showed that calcareous mat productivity is highest in the short-hydroperiod wet prairie (Iwaniec et al., 2006; Ewe et al., 2006) where benthic, sediment-associated mats predominate. Floating mats associated with purple bladderwort, Utricularia purpurea, in slough sites are less productive but production increases during the peak of the wet season (Gaiser et al., 2006).

Nutrient enrichment elevates periphyton nutrient content, reduces the proportion of calcareous floating and epiphytic periphyton mats, and replaces native species by non-mat forming filamentous species.

1.1.2. Supporting data

Throughout the Everglades, periphyton has been shown to rapidly and accurately indicate water quality changes; periphyton responses were critical to establishing the P criterion for freshwater sloughs (McCormick et al., 1996; Gaiser et al., 2004a,b), indicated rates of coastal salt water encroachment in mangroves (Ross et al., 2001; Gaiser et al., 2004a,b) and detected of nutrient enrichment in adjacent offshore seagrass beds (Frankovich et al., 2006). Several studies have shown that periphyton not only responds to but also regulates water quality (Thomas et al., 2006; Gaiser et al., 2006) by quickly and efficiently removing excess P from the water column. Gaiser et al. (2005) recommends using periphyton P content, rather than water or soil P, to measure P-enrichment history, because periphyton P content has repeatedly been shown to more reliably indicate P load history. This has been adopted in most large-scale monitoring programs in the Everglades (i.e., the EPA R-EMAP assessment).

1.2. Areas of the Everglades covered by this periphyton indicator

Periphyton covers virtually all of the Everglades freshwater wetlands and the southern estuarine areas. The area this indicator covers includes the Greater Everglades, Florida Bay and southern estuaries, Lake Okeechobee, and the Kissimmee River basin (see Fig. 1 in Doren et al., 2009).

1.3. Indicator history

Periphyton has been studied extensively in the Everglades because of its utility as an early warning indicator of impending ecosystem change and the significant consequences of altered periphyton communities on the rest of the food web. Increased nutrient delivery to natural Everglades...
marshes causes periphyton mats to disintegrate and collapse (Gaiser et al., 2006), altering food availability to grazers at the base of the food web. Research shows periphyton losses are initiated upon exposure to very low nutrient enhancements (>10 ppb TP; Gaiser et al., 2005). Models have been developed to determine the extent of periphyton losses driven by nutrient enrichment of the Everglades ecosystem (Gaiser et al., 2006). Further, hydrologic changes strongly affect the function and structure of periphyton. Sites that are dry for a majority of the year have minimal production values, while sites that are flooded for >6 months are most productive (Thomas et al., 2006; Gottlieb et al., 2005; Iwaniec et al., 2006). The timing of re-flooding of previously dried periphyton mats is also important, as dried periphyton releases large quantities of nutrients into the water column upon re-flooding that subsequently may negatively affect downstream systems (Thomas et al., 2006).

Periphyton biomass in the Everglades is significantly higher than occurs in other wetlands, with dry mass values often exceeding plant biomass in many areas of freshwater marsh as well as offshore marine seagrass beds (Ewe et al., 2006). This primary biomass supports the remainder of the food web, including invertebrates, fish and wading birds (Williams and Trexler, 2006). Periphyton grows on any substrate available in the marsh; as a result, substrate associations vary throughout the Everglades. In the marl prairie, periphyton grows attached to the sediment or bedrock and stems of emergent macrophytes, whereas deeper sloughs contain periphyton communities that are primarily attached to floating macrophytes such as U. purpurea (Gaiser et al., 2006). Therefore, hydrology affects periphyton not only directly but also indirectly, by affecting the substrate available for colonization.

Changes in the hydrologic regime (i.e., duration and timing of flooding, water depth) can greatly influence periphyton community structure and function. During the dry season in short-hydroperiod marshes, periphyton communities are dormant and unproductive (Thomas et al., 2006). Following re-flooding, periphyton recovers within days, but not before large quantities of nutrients have been released back into the water column (Thomas et al., 2006). In stagnant situations, these nutrients may be re-sequestered by the community upon recovery but if water is flowing, the released nutrients can affect downstream communities. Gottlieb et al. (2005) showed that periphyton communities can quickly transition in composition and structure if exposed to alternating hydrologic regimes. These fast responses to environmental changes strongly advocates for the use of periphyton as an indicator for environmental monitoring in the Everglades.

Across the hydrologic spectrum, periphyton has been shown to respond directly and quickly to above-background concentrations of nutrients. The response is rapid and easily detected, as low-level nutrient enhancements lead to a demise of the periphyton community altogether (Gaiser et al., 2006). This has substantial consequences to the invertebrate and fish communities dependent on this biomass for food (Turner et al., 1999; Gaiser et al., 2005). Periphyton mats have also been shown to be extremely diverse, with more than 700 algal taxa having been documented from the Florida Everglades thus far (see www.serc.edu/~periphyton and Slate and Stevenson, 2007). Taxonomic changes driven by changes in nutrient availability can be measured prior to the collapse of the community itself. The history of nutrient loading to a particular site can be interpreted with a high degree of accuracy from periphyton community composition (Gaiser et al., 2005). A variety of models exist that accurately predict the nutrient status of water from periphyton (Cooper et al., 2005), and these can be applied to monitoring and paleoecological studies to determine trends in water quality over time (Slate and Stevenson, 2000).

1.4. Significance of the indicator to Everglades restoration

The periphyton indicator is relevant to the Everglades ecosystem because it responds to variability at a scale that makes it applicable to the entire ecosystem or to large portions of the ecosystem. Periphyton productivity and community structure are directly linked to hydrology. Periphyton productivity (e.g., abundance and standing stock) is a performance measure in most conceptual ecological models for the Comprehensive Everglades Restoration Program (CERP, http://www.evergladesplan.org), including interim goals to assess the progress of CERP. Periphyton performance measures identified by CERP include biomass and cover, community composition in both short- and long-hydroperiod wetlands, and response to frequency and duration of dry-downs.
The periphyton indicator is feasible to implement and is scientifically defensible. Periphyton metrics such as abundance and community structure are statistically correlated to ecosystem drivers in South Florida, resulting in reliable models that have been developed to determine the impacts of water management on these communities (McCormick and Stevenson, 1998; Gaiser et al., 2006).

The periphyton indicator is sensitive to system drivers (stressors). Key ecosystem drivers (rainfall, water quantity, water quality) are statistically correlated with periphyton species abundance and community composition (Cooper et al., 1999; Gaiser et al., 2006). Periphyton biomass and community composition have been causally linked to hydrological factors (water depth, days since last dry-down, and length of dry-down; Thomas et al., 2006). Finally, short- and long-hydroperiod wetlands have distinct periphyton biomass and community composition (Gottlieb et al., 2006).

The periphyton indicator is integrative (Fig. 1), as periphyton production is linked to fish and macroinvertebrate production, which, in turn, is linked to wading bird nesting success (this issue). In addition to CERP recognition of periphyton’s food-web contributions, periphyton has been identified as a relevant metric for landscape connectivity, or intactness of the system. Ultimately, periphyton is integrative in that community responses are representative of hydrological improvement (i.e., water management).

2. Communicating the periphyton indicator

2.1. Indicator performance measures and metrics

Several metrics provide reliable measure of periphyton response to hydrologic and water quality changes in this system. They can be broadly grouped into three categories: abundance, quality and community composition. Within these categories, at least three measures are recorded within the context of the CERP assessment. These include, for abundance, wet biovolume (ml m$^{-2}$), dry biomass (g m$^{-2}$) and ash-free dry biomass (g m$^{-2}$); for quality, organic content ($\mu$g dry g$^{-1}$), chlorophyll a content ($\mu$g dry g$^{-1}$) and total phosphorus content ($\mu$g dry g$^{-1}$); and, for community composition, algal and diatom composition measured using similarity metrics in multi-dimensional ordination space and substrate affiliation (percent cover by substrate type).

Within each of the categories, all of the parameters respond in the same direction (positive or negative) to changes in water quality as well as hydrologic conditions, including water depth, duration, timing, and spatial extent (Gaiser et al., 2006). The periphyton biomass metrics of wet biovolume, dry biomass and ash-free dry biomass are correlated and all decline with increasing water depth and hydroperiod as well as with increasing availability of phosphorus (Gaiser et al., 2006; Ewe et al., 2006). The periphyton quality metrics of organic, chlorophyll a, and total phosphorus content are correlated and increase with increasing water depth and hydroperiod and with increasing phosphorus availability (Gaiser et al., 2005, 2006). The community metrics are based on compositional similarity to expected community structure, established from collections at reference locations (according to Gaiser et al., 2006). The metric for periphyton cover by substrate type is also multivariate, where optima and tolerances are calculated for each substrate type along each gradient, and then site water quality predictions are based on those optima weighted by relative cover.

2.2. Stoplight report card system applied to periphyton

The stoplight system for periphyton involves first calibrating the tri-color code by the deviation of values for each metric from an expected baseline condition for each sampling point. Triplicate samples from Principal Sampling Units (PSUs, randomly selected locations within Landscape Sampling Units, LSUs) visited annually in the mid-wet season are analyzed for each periphyton metric. PSU means are then compared to expected values for background conditions defined for the respective LSU. Background conditions are defined from data collected or inferences made from locations within the LSU that are considered un-impacted by human activities and are not static; that is, ranges of acceptable conditions may change depending on modifications by external drivers not under our control (i.e., climate variability) and advancements in the understanding of the ecosystem. Development of a consistent baseline necessitates long-term data, so we do expect targets to evolve as the duration of monitoring programs grows. However, any changes in baseline expectations will be documented and then hindcast through the stoplight system to re-calibrate former values.

2.3. Determining thresholds for periphyton success (green), caution (yellow) or failure (red)

Once baseline expectations for each of the 9 variables are established, color codes are assigned to each PSU based on deviation from that expectation. If the value is within one standard error of the mean, it is designated green (natural), within two standard errors is designated yellow (caution) and beyond three standard errors is designated red (altered). The PSU is then assigned a color for biomass, quality and community composition. The distribution of color designations can then be mapped by PSU for each of these three performance measures. The final color designation for each LSU is then based on the percentage of yellow and red sites. An LSU is given a final yellow designation if more than 25% of sites are coded yellow or red and a red designation if more than 50% of the sites are red, with these cut-offs being based on variability determined within un-impacted background sites (Gaiser et al., 2006).

Baseline expectations for periphyton TP content, ash-free dry biomass and composition for some LSUs are fairly well-defined and so we provide an example using those data. The expected ranges for these variables for un-impacted conditions for Water Conservation Area 1 (WCA-1) and 3 (WCA-3), Shark River Slough (SRS) and Taylor Slough (TS) were defined by transect surveys conducted in these areas in 1999 by Gaiser et al. (2006). This study did not find un-impacted conditions in Water Conservation Area 2 (WCA 2), but because this is an important wetland of considerable management interest, we
estimated the un-impacted condition for this wetland to be close to that defined for periphyton-dominated areas of SRS. This contention is supported by the work of McCormick and O’Dell (1998) who found the abundance and composition of periphyton in the interior of this wetland to resemble that described for SRS. Establishment of appropriate baseline expectations is a challenging process, since it involves choosing targets based on values observed a selected temporal

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![Fig. 2 - Distribution of values for periphyton TP, ash-free dry mass and compositional similarity for surveys in 2005 and 2006 in Water Conservation Areas 1 (WCA-1), 2A (WCA-2A) and 3A (WCA-3A), Shark River Slough (SRS) and Taylor Slough (TS). Green coding was used to define acceptable ranges defined by the mean values of un-impacted sites ±1 standard error of that mean, yellow for values between 1 and 2 standard errors and red for sites departing more than 2 standard errors from mean values of sites surveyed in the same basins in 1999 (Gaiser et al., 2006). Compositional assessments for 2006 have not yet been completed.](image-url)
or spatial distance from perceived unnatural perturbations. Effective targets also encompass the range of natural variability experienced by a system, requiring long-term datasets that are rarely available. We expect this to be an area of rapid development as new, large-scale surveys generate applicable data. The Gaiser et al. (2006) provides a starting point, however, and Fig. 2 shows how each basin has unique ranges of acceptable values and how each attribute scales differently. Data from 2005 and 2006 CERP Mapping surveys were plotted on these graphs to show the proportion of sites falling in each of the colored regions.

For annual assessments, a map of the distribution of the periphyton TP indicator is displayed (Fig. 3) to show within and among-region pattern. Because of inter-basin differences in targets, areas showing high values (dark shading) do not necessarily indicate altered conditions (red coding) unless they exceed the range acceptable for that region. Pattern and suspected causes are displayed in the “Summary Findings” section (Fig. 3). Each basin is then assigned a value using the green-yellow-red coding, based on the proportion of sites falling into these ranges (explained above). Explanation is then provided for causes of current conditions and prospects for the next two years if water management remains the same (Fig. 4).

3. Discussion

Conversions of large areas of short-hydroperiod wetlands (marl prairies) east of Everglades National Park and the Water Conservation Areas into agricultural and urban uses has resulted in a large loss of the spatial area once inhabited by periphyton and associated populations of fish and macroinvertebrates. These irreversible land-use changes have had a major impact on both the abundance and structure of these communities.

Periphyton cover, biomass, productivity and composition are affected by the duration and frequency of droughts. The reduction of hydroperiod resulting from long-term water management changes has limited the production period for periphyton in Everglades’ wetlands for many decades (Davis et al., 2006). Increases in duration of flooding and depth of water in the southern Everglades (eastern portions of Everglades National Park) that were over-drained for
many decades have allowed periphyton to recover, with subsequent improvements in fish and macroinvertebrate populations (Trexler et al., 2005). Further improvement in water management is needed. Additional hydrological restoration is expected to improve habitat for periphyton production in both long and short-hydroperiod wetlands. In long-hydroperiod wetlands, improvements in water management should reduce the incidence and severity of drying, further lengthening the production period and primary biomass available to the food chain. In short-hydroperiod

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Fig. 4 – Example of system assessment report based on periphyton. Each wetland basin with significant background data is scored with a red, yellow or green symbol for each indicator, based on the proportion of sites falling within these categories in assessment. In this case, biomass = ash-free dry mass (g m⁻²), quality = total phosphorus content (µg g⁻¹) and community composition = diatom similarity (%). Trends in current status are explained and prospects for conditions in 2-years are projected based on the assumption of no change in water management.
wetlands, improved water management should encourage more prolific periphyton growth, including more edible taxa (Gottlieb et al., 2006; Geddes and Trexler, 2003), and facilitate recovery of dependent macroinvertebrates and fish.

This periphyton-based tool effectively indicates departures in the system from the natural un-impacted state. Because periphyton responds over short time scales to manipulations in the system, it is likely that year-to-year patterns in ecosystem response to management will be observed. This is particularly true in the case of water quality variables (TP content) which respond very directly to P supply and more quickly than P in other system components like the water column, soils or plants (Gaiser et al., 2005). Responses to hydrologic manipulation may take longer to be detected in periphyton, particularly because the variability in response to hydrologic change is greater than for water quality. As the availability of experimental and observational data on periphyton response to hydrology expands, predictions will be enabled at smaller spatial scales that may be more sensitive to change.

4. Longer term science needs

The productivity and composition of periphyton mats throughout the Everglades is fairly well understood. Models of periphyton response to hydrology and water quality are also being developed, but few studies have examined the combination of these effects on periphyton and the rest of the food web. Models that operate on smaller scales than the landscape units presented here need to be employed as it is widely recognized that periphyton exhibits unique natural qualities at different points along the Everglades gradient. In addition, longer term effects of alterations in periphyton composition and function are necessary to determine consequences to the food web and to soil formation. Paleocological studies, where possible, would also provide baseline information about past water quality and hydrology, to provide a better guide to restoration.

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