Hydrobiologia (2009) 621:105–114
DOI 10.1007/s10750-008-9635-2

PRIMARY RESEARCH PAPER

Landscape responses to wetland eutrophication: loss of slough habitat in the Florida Everglades, USA

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Received: 15 April 2008 / Revised: 6 October 2008 / Accepted: 16 October 2008 / Published online: 14 November 2008

Abstract Much of the historical Everglades has been either lost or degraded as a result of human activities. Among the aquatic habitats that comprise the Everglades landscape mosaic, open-water sloughs support critical ecological functions and appear especially sensitive to both hydrologic and water-quality perturbations. We used a combination of remote sensing and on-the-ground sampling to document spatial changes in the extent and vegetative composition of sloughs along a phosphorus (P) gradient in the northern Everglades. Increasing levels of water and soil P were associated with a decline in slough coverage, loss of the abundant native periphyton community, and a shift in dominant macrophyte species. The characteristic slough macrophyte species *Eleocharis cellulosa* and *Nymphaea odorata* exhibited different sensitivities to P enrichment, but both species declined with enrichment as slough habitats were invaded by *Typha domingensis*, a species that is known to expand aggressively in response to enrichment. A limited amount of open-water habitat occurred in highly enriched areas, but these habitats were maintained largely as a result of airboat disturbance and did not contain characteristic slough vegetation. Many changes in slough coverage and composition occurred in areas where water and soil P concentrations were only marginally higher than background levels. Our findings support the need for Everglades hydrologic restoration efforts to adhere to strict water-quality standards for P to avoid further degradation of this key landscape feature.

Keywords *Eleocharis* · Everglades · Hydrology · *Nymphaea* · Periphyton · Phosphorus · Sloughs · *Typha* · Vegetation · Wetlands

Handling editor: L. M. Bini

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Introduction

The Florida Everglades is at the forefront of ecosystem restoration efforts, as Federal and State agencies attempt to reverse more than a century of human impacts that include hydrological alterations, water-quality degradation, and the introduction of invasive exotic species to this extensive subtropical peatland. Roughly half of the Everglades has been drained for agricultural and urban uses, and presently these surrounding lands exert substantial influence on environmental conditions across much of the remaining wetland. The overarching ecological goal of the

Comprehensive Ecosystem Restoration Plan (CERP—www.evergladesplan.org) is the recovery of key habitats, communities, and threatened and endangered species by "getting the water right"—that is restoring the quantity, quality, timing, and distribution of flows to the remnant Everglades ecosystem (South Florida Ecosystem Restoration Task Force, 2000). The success of this multi-decadal, multi-billion dollar effort hinges upon a clear understanding of the relationships between key environmental drivers such as water depth, flow, and nutrients and the ecological targets for restoration.

The predrainage landscape of the remnant Everglades consisted largely of a habitat mosaic dominated by alternating sawgrass (*Cladium jamaicense* Crantz) "ridges" and deeper water sloughs aligned in the direction of flow (Science Coordination Team, 2003). The recovery of this "ridge and slough" feature is a primary target of Everglades restoration (Ogden, 2005). Within this mosaic, sloughs provide critical habitat supporting native populations and ecological processes and must be maintained as a dominant landscape feature if restoration efforts are to succeed. Sloughs are characterized by low cover of floating and emergent macrophyte species, including *Nymphaea odorata* and *Eleocharis* spp., and extremely high primary productivity due to an abundance of periphyton often in association with the submersed macrophyte purple bladderwort (*Utricularia purpurea*) (McCormick et al., 1998). High productivity in these habitats maintains an oxygenated water column (McCormick & Laing, 2003) and is associated with an abundant and diverse community of aquatic consumers relative to other natural Everglades habitats (Rader, 1994; Trexler et al., 2002). Sloughs provide refugia for fish and invertebrates during the dry season, concentrating prey and in turn providing optimal foraging conditions for top predators such as wading birds during the nesting season (Kushlan, 1989; Hoffman et al., 1994; Gawlik, 2002). Thus, sloughs play a pivotal role in the maintenance of the native Everglades food web.

Both the spatial extent and condition of slough habitat have declined substantially within the remnant Everglades (Davis et al., 1994). Several anthropogenic factors are believed to have contributed to this decline. Roughly 26% of the historical ridge and slough landscape has been drained for agricultural and urban development (Davis et al., 1994), and much of the remainder has been diked to form a series of impoundments or water conservation areas (WCAs) where flow is regulated by a network of pumps and spillways (Light & Dineen, 1994). This disruption of natural flow patterns is believed responsible for the gradual conversion of slough to *Cladium* (Science Coordination Team, 2003). In addition to these hydrologic modifications, Davis et al. (1994) proposed that fire suppression may promote the replacement of slough habitats by *Cladium*. Influences of water quality on Everglades vegetation are also well recognized (Vaithiyanathan & Richardson, 1999; McCormick et al., 2002; Childers et al., 2003). These studies have implicated P enrichment as the cause of the loss of native periphyton communities and vascular plants such as *U. purpurea* from slough habitats and the replacement of these habitats by emergent macrophytes, particularly cattail (*Typha domingensis* Pers.). Thus, multiple anthropogenic factors may constrain the recovery of slough habitats in the current managed ecosystem.

Hydrologic restoration is increasingly viewed as the key to revitalizing and maintaining the remaining ridge and slough landscape and is a major focus of CERP projects in the Everglades. These projects are being implemented with the assumption that state water-quality goals for P will be met and, therefore, sufficient low-P water will be available for restoration activities. We documented spatial changes in the extent and vegetative characteristics of sloughs across a P gradient in the northern Everglades to determine the degree of P enrichment that resulted in a decline in these habitats. Our findings illustrate the importance of attaining water-quality standards to assure that minimally impacted slough habitats are maintained across the restored landscape.

Methods

Study location

Measurements were conducted in WCA 2A, an impounded wetland in the northern Everglades (Fig. 1). Phosphorus-rich canal waters began entering this wetland in the early 1960s upon completion of its compartmentalization as part of the Central and Southern Florida Flood Control Project (Light & Dineen, 1994; Rutchey et al., 2008). These waters

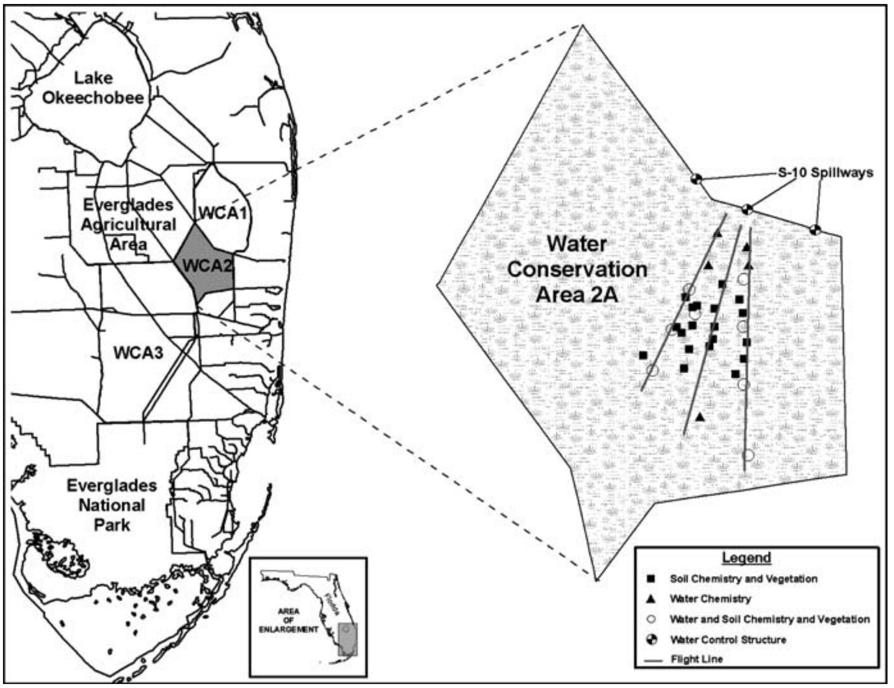

Fig. 1 Study location within the Florida Everglades

enter the wetland through gated spillways located along the northern levee and flow southward to create a P enrichment gradient with surface-water and soil P concentrations declining exponentially with distance downstream of the inflows (McCormick et al., 2002). Hydrologic parameters such as water depth also vary along this gradient but are not correlated with phosphorus concentrations or distance from the inflow (McCormick et al., 1996). Historically, this part of WCA 2A was part of the ridge and slough landscape (Davis, 1943). Interior areas of this wetland still approximate this historic condition and contain a balance of slough and *Cladium*, while highly enriched areas near canal inflows have gradually been transformed to dense cattail stands (Rutchey & Vilchek, 1999).

Remote sensing

Color infrared positive transparencies were obtained on February 20, 1999 by flying three separate flight lines along the enrichment gradient (Fig. 1). Each flight line began at a canal discharge structure and ended at a long-term monitoring station used to characterize reference P conditions in the interior of this wetland. The data were captured at an altitude of 1,000 feet resulting in a photograph scale of 1:2,000 (1 cm = 20 m). A total of 94 photographs were taken to provide a continuous record of vegetation changes along each flight line. Photo centerpoint locations were collected using airborne GPS.

Each photograph encompassed an area of roughly 200,000 m^2. Coverages were estimated for an area of 25,000 m^2 in the center of each photograph by overlaying a grid of 400 equally spaced points. Limiting coverage measurements to the center of each photograph avoided problems with overlap and glare near the edges of the photographs. The vegetation type at each point was recorded to determine percent cover for the grid. Fifteen representative photographs from across the gradient were groundtruthed by helicopter and airboat to assess our ability to consistently distinguish different coverage types.

Vegetation types were classified into categories, with an emphasis on open-water habitats. Stands of emergent vegetation (mostly *Cladium*, *Typha*, or willow) were classified into a single category to distinguish these habitats from open water. As the photographs were taken during the winter dry season when the wetland was drying out, open-water habitats first had to be classified as either flooded or dry; this distinction was necessary as periphyton and macrophyte coverages could only be obtained for areas that were still flooded. Coverages in flooded areas were then classified into four major categories as follows: (1) open water (no plant or periphyton cover); (2) airboat trails (also no plant or periphyton cover); (3) *N. odorata*; and (4) floating periphyton mats, which in some cases were mixed with *U. purpurea*. It was also necessary to record mixtures of these coverages (e.g., lily-periphyton) when a grid point included more than one category in roughly equal proportion. *Eleocharis* spp. also was present in open-water habitats near the downstream end of the gradient, but ground-truthing showed that the coverage of this taxon could not be reliably distinguished from open water. Therefore, some points classified as open water contained sparse stands of *Eleocharis* in minimally enriched areas.

On-the-ground sampling

The abundance of two common slough indicator species, *N. odorata* and *E. cellulosa*, and the invasive species *T. domingensis* were measured in 27 sloughs at varying distances downstream of the canal inflows in the vicinity of the flight lines used to collect aerial photography. Sampling was limited to locations >4 km downstream of the canal because no discernible slough habitat was present in closer proximity to this discharge point. A 50-m line transect was established in each slough and plant frequency of occurrence was measured in 25 1-m^2 quadrats spaced at 2-m intervals along this transect.

Environmental conditions

Measurements of water quality and hydrology were not collected at every point we sampled. Instead, data collected between 1996 and 1999 from routine monitoring at 13 permanent sampling sites downstream of canal discharges into WCA 2A (see Fig. 1) were used to characterize changes in surface-water P and hydrology along this gradient. Water samples were collected monthly when at least 10 cm of surface water was present and analyzed colorimetrically for TP following acid digestion (USEPA, 1983). Water depth was measured monthly at a fixed staff gauge at each of these sites when surface water was present. Continuous water-depth measurements were collected at three of the monitoring sites located at approximately 2, 7, and 11 km downstream.

Soil samples were collected in March 1997, concomitant with vegetation frequency measurements. Using a thin-walled 10-cm i.d. aluminum open barrel coring tube, three surface (0–10 cm depth) soil samples were collected from each of the line transects in the 27 slough locations. Samples were dried at 85–90°C for 48–72 h and analyzed colorimetrically for TP following acid digestion (USEPA, 1983, 1986).

Statistical analysis

The location of significant shifts in water and soil P concentrations and associated population, community, and landscape features along the gradient were detected using one of two different regression models. Phosphorus concentration data were best described using piecewise regression (Neter et al., 1996), which allowed multiple linear functions to be fit to the data for different distance ranges. A breakpoint—the location along the gradient where an increase in P concentration occurred—was identified as the point where these functions intersected. The low model standard error of the piecewise models compared to alternative models (single linear function, exponential function, and the change-point model described below) indicated that this approach provided the best statistical fit to both the water and soil P data.

Response variables tended to show a rapid shift between alternative states and were best described (i.e., lowest model standard error) using a second regression method, change-point analysis (Niu et al., 2000). This iterative procedure for detecting shifts along environmental gradients is based on methods developed by Chang et al. (1988) for detecting shifts in time series analysis. Response data were ordered by distance downstream of canal discharges, and a series of dummy variable regression models were then generated to separate the data into all possible sequential pairs across this gradient. Regression coefficients corresponding to the difference in mean values between each pair were calculated, and the statistical significance of the largest coefficient was tested using a Student's *t*-test. If significant, this separation represented the first change point. Data were then subdivided into these two groups and reanalyzed using the same procedure to detect a second significant change point. This procedure was repeated until no more significant change points were found. Diagnostic statistics presented by Niu et al. (2000) showed that this statistical method is appropriate for detecting changes in these ecological data sets across this wetland P gradient. This model provided a superior statistical fit to the response data compared with other models described above.

The same series of models were applied to mean water depth data across the gradient to detect a spatial trend. Continuous stage data were averaged by month for each of the three sites with stage recorders, and temporal trends in these data were compared among the sites by calculating Pearson product–moment correlation coefficients (Sokal & Rohlf, 1995) to further determine the degree of correspondence in hydrologic conditions across the gradient.

Results

Changes in open-water area and composition based on remote sensing

The extent of open-water habitats was substantially lower in areas of the wetland near canal discharges compared with those in the wetland interior as indicated by change-point analysis ($P < 0.001$, Fig. 2). At locations ≥9 km from the canal, open-water habitats accounted for between 15% and 70% of wetland area, with change-point analysis showing an average contribution of 42%. By contrast, open-water accounted for just 0–22% of wetland area at locations <7 km from the canal, with an average contribution of 4%. Change-point analysis showed two change points associated with this decline at 9.5 and 7.4 km, respectively.

The composition of open-water habitats also changed significantly downstream of canal discharges (Fig. 3). Open-water areas located approximately 8–9 km or farther from the canal consisted largely of slough-wet prairie habitats indicative of minimally enriched areas of the Everglades. *Nymphaea* and floating mats of calcareous periphyton and *Utricularia* were the dominant vegetation types in these habitats and, collectively, comprised >80% of the cover at most locations. Change-point analysis indicated that the coverage of both declined significantly with enrichment ($P < 0.001$). The change point for mat cover occurred at 9.2 km, and this vegetation type was generally absent from sites <8 km from the canal. *Nymphaea* cover was greatest at sites 6–8 km from the canal but was low or absent at sites closer to the canal. The change point for this vegetation type

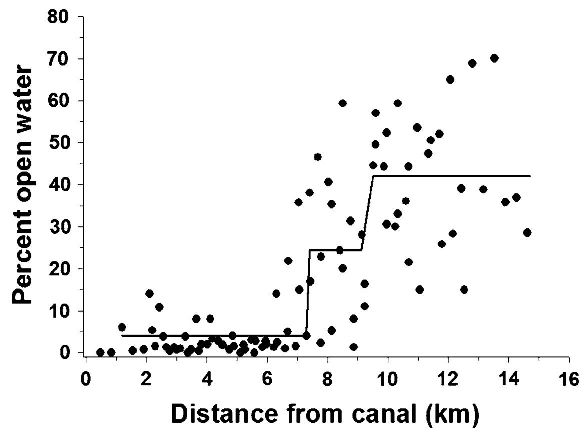

Fig. 2 Percent cover of open-water areas with distance downstream of P-rich canal discharges. The *line* shows the change-point model, which provides locations of significant change points (*vertical portion* of the *line*) and mean values for the dependent variable between these change points (*horizontal portion* of the *line*)

occurred at 6.3 km. Closer to the canal, much or all open-water habitat was clearly created by airboat activity and these areas were devoid of both floating periphyton mats and *Nymphaea*. A change point at 4.4 km ($P < 0.001$) showed the increasing importance of this classification type at locations nearest to the canal. The remainder of the habitat in this area was classified as unvegetated (change point between 6 and 7 km), although some of this may have also resulted from past airboat activity.

Changes in slough vegetation based on quadrat sampling

The abundance of all three indicator macrophyte species changed significantly with distance downstream of canal discharges. Sloughs in the wetland interior were dominated by *Eleocharis* and *Nymphaea* in varying abundances and were devoid of *Typha* (Fig. 4). The frequency of occurrence of *Eleocharis* typically was 80% or more along transects in sloughs >8 km downstream of the canals, dropped abruptly to <10% at sites closer to the canal, and was absent from all sites <6.5 km from the canal. A significant change point for this species occurred at 7.82 km ($P < 0.001$). The occurrence of *Nymphaea* was highly variable among interior slough sites, ranging from 12% to 100%. However, *Nymphaea* had a consistently high (>80%) frequency of occurrence at sites at intermediate distances downstream and was

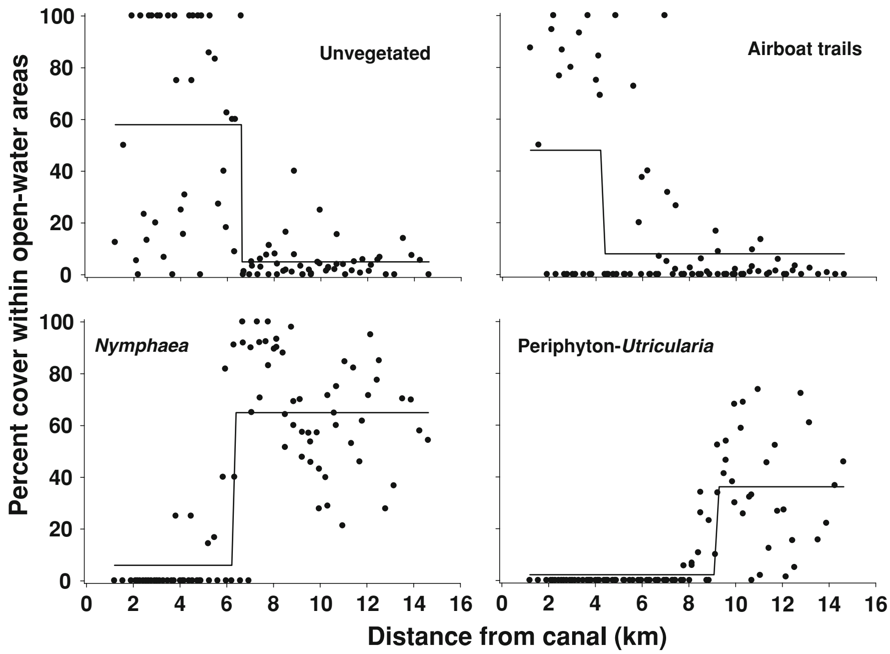

Fig. 3 Percentage of open-water areas containing different cover types with increasing distance downstream of canal discharges. See text for details on classification types and Fig. 2 for interpretation of change-point results

only absent from sites sampled closest to the canal (<5.5 km). Change-point analysis detected a significant decline in this species at 5.5 km ($P < 0.001$). *Typha* was not detected at sites >8 km downstream, was present at low abundance (12%) in some sloughs between 7 and 8 km, and increased sharply to 100% occurrence at a distance of 6–7 km. A significant change point for this species was detected at 6.75 km ($P < 0.001$).

Changes in phosphorus and hydrology along the gradient

Annual geometric mean water-column TP concentrations averaged <10 μg l^{-1} (range 7–12 μg l^{-1}) at five sampling sites >8 km downstream of the canal (Fig. 5). Concentrations averaged 15 μg l^{-1} (range 14–17 μg l^{-1}) at the next two farthest sites located approximately 7 km downstream. Phosphorus concentrations increased steadily with decreasing distance from the canal and averaged 89 μg l^{-1}, with a mean annual high of 115 μg l^{-1}, at the closest site less than 2 km away. Piecewise regression analysis detected an increase in concentration between sites located at 6.91 and 8.17 km downstream ($P < 0.001$). Soil TP was strongly correlated with water-column TP and increased from <400 mg kg^{-1} at sites >7.5 km downstream to 1,400 mg kg^{-1} at the site closest to the canal (Fig. 5). Piecewise regression analysis showed a breakpoint indicating an increase in concentration between sites located at 7.50 and 7.80 km downstream ($P < 0.001$).

While there was considerable temporal variation in water levels, hydrologic conditions exhibited little variation along the gradient. Variation in monthly water depths during the 4-year period of record was nearly identical at the three continuous stage-monitoring sites located across the gradient ($r \geq 0.886$, $P < 0.001$). Based on monthly readings of staff gauges at all 13 permanent monitoring sites, mean water depth was lowest at sites approximately 7 km from the canal (0.46–0.48 m) and identical at sites nearest and farthest from the canal (0.61 m) (Fig. 6). None of the statistical models we used showed a significant trend across the gradient for this hydrologic parameter. The range of variation in water depth was also similar among these 13 sites as indicated by the standard deviation.

Discussion

Our findings show that slough habitats are extremely sensitive to anthropogenic P loading and can be degraded and even lost from the Everglades landscape at relatively low levels of enrichment. Our

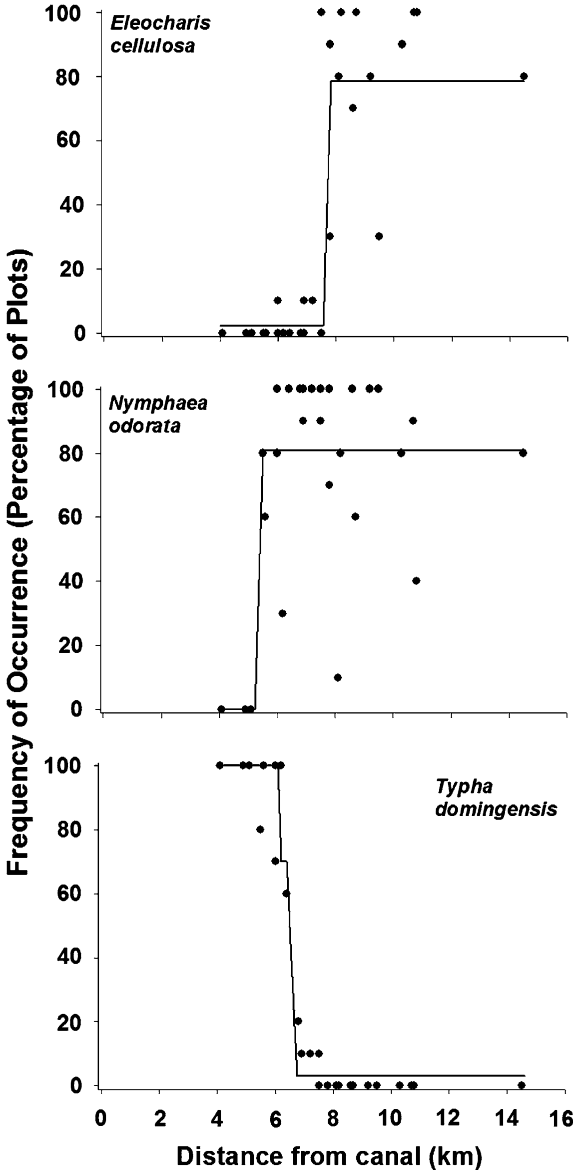

Fig. 4 Frequency of occurrence of dominant macrophyte species in open-water habitats with distance downstream of canal discharges. See text for sampling methods and Fig. 2 for interpretation of change-point results

remote sensing and ground-based sampling detected significant shifts in the spatial extent and vegetative composition of sloughs in response to small increases in water and soil P above background levels. Our sampling was conducted across an area of similar hydrology and, thus, these habitat changes could not be attributed to hydrologic modification. These findings have important implications for Everglades

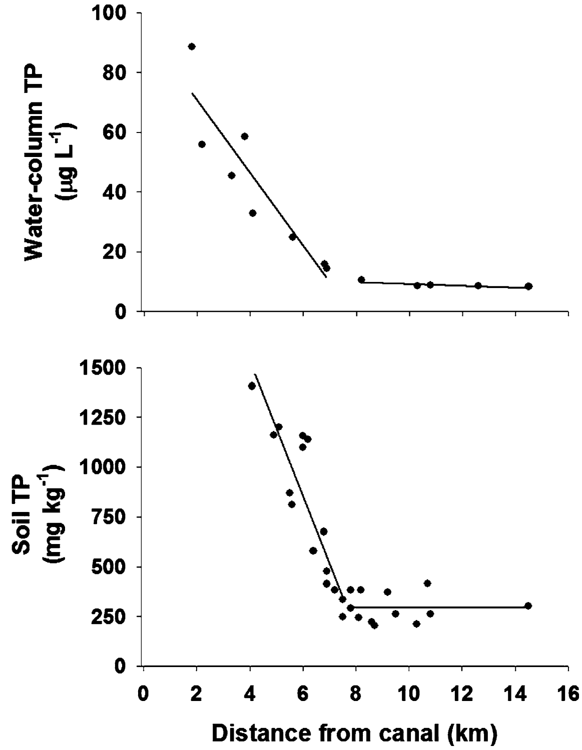

Fig. 5 Changes in surface-water and soil TP for the period 1996–1999. Surface-water TP concentrations are average annual geometric mean values; soil concentrations are based on a single collection in 1997

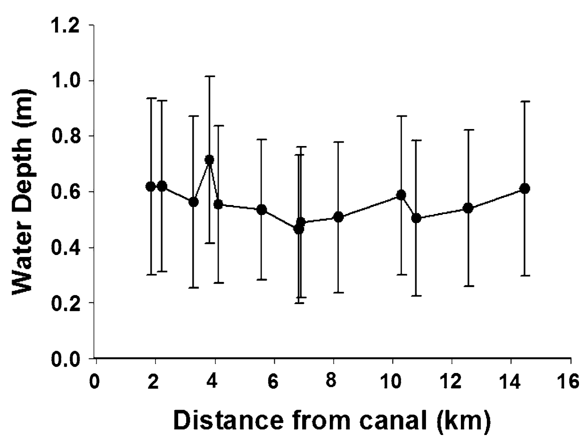

Fig. 6 Mean (±1 standard deviation) water depths (averages of monthly data) for 13 sites across the gradient during the period 1996–1999

restoration, a primary goal of which is the recovery and maintenance of the historic ridge-and-slough landscape, and illustrate the need to explicitly include water-quality targets as a part of this restoration element.

Several changes in slough vegetation occur simultaneously in response to P enrichment, and these changes in turn alter the functional characteristics of these habitats. Loss of the calcareous periphyton assemblage was the most sensitive indicator we measured, declining at about the same point (9.2 km) as the initial decline in slough extent (9.5 km). Experimental studies (McCormick et al., 2001) have established the link between P enrichment and the loss of this community, with consequent effects on dissolved oxygen regimes (McCormick & Laing, 2003) and higher trophic levels (Gaiser et al., 2005; Liston et al., 2008). The emergent macrophyte *E. cellulosa* also appeared sensitive to P enrichment. This species provides important habitat for fish and invertebrates (Loftus & Eklund, 1994; Rader, 1994) as well as substrate for periphyton growth (McCormick et al., 1998). A recent controlled study demonstrated that *E. cellulosa* responds to elevated P concentrations with increased growth rates, greater biomass, and a higher rate of photosynthesis (Chen et al., 2005). Therefore, the decline in *Eleocharis* with P enrichment under field conditions may have been caused by the concomitant increase in the dominance of *Nymphaea*. *Nymphaea* was the dominant cover type in enriched sloughs, covering an average of nearly 90% of the water surface at remotely sensed locations near the 7-km distance compared to an average cover near 60% in unenriched sloughs. This pattern is consistent with experimental findings that *Nymphaea* cover increases in response to controlled P enrichment (Newman et al., 2004). The dense cover of *Nymphaea* in enriched sloughs is associated with low water-column dissolved oxygen and periphyton productivity, a condition quite different from that found in unenriched sloughs (McCormick & Laing, 2003). The significant decline in *Nymphaea* cover and abundance in sloughs closer to the canal P source most likely was due to shading from and perhaps below-ground competition with *Typha*, which increased significantly between 7 and 6 km.

Several of the changes associated with slough decline (reduction in slough coverage, loss of sensitive periphyton and macrophytes) occurred at a similar point along the enrichment gradient and, therefore, at a similar levels of P enrichment. Within this zone of initial change (roughly 7–9 km downstream of canal discharges), average water-column TP concentrations increased from as low as 7 μg l^{-1} to as high as 15 μg l^{-1}, and soil TP concentrations increased from background concentrations of 200–400 mg kg^{-1} to >500 mg kg^{-1}. As reported by McCormick et al. (1996), water-quality parameters other than TP showed either modest or no change along this gradient, and our hydrologic monitoring showed no relationship between water-depth regimes and distance that would explain these ecological changes. These patterns combined with the results of controlled P dosing studies support the conclusion that P enrichment was the environmental factor driving vegetation and landscape changes across this gradient.

The loss of slough habitats from the enriched Everglades landscape ultimately occurs as a result of the filling-in of these open-water areas with *Typha*. Vegetation maps of northern WCA 2A (Rutchey & Vilchek, 1999) clearly show how the spread of *Typha* through this wetland has occurred by the selective colonization of sloughs. On these maps, the shape and arrangement of *Typha* stands in highly enriched areas without sloughs are identical to the patterning of sloughs farther down the enrichment gradient. The susceptibility of sloughs to *Typha* encroachment may be due to the relatively sparse, low-stature vegetation in these habitats, which offers comparatively little above- and below-ground competition to more robust species such as *Typha*. By contrast, *Cladium* stands appear more resistant to *Typha* expansion, and some form of stress (e.g., high water) or severe disturbance (e.g., peat fires) may be required to weaken or eradicate *Cladium* and facilitate *Typha* establishment in these habitats (Newman et al., 1998; Gunderson, 2001). In a project that expanded on our study, Hagerthey et al. (2008) further determined that while *Cladium* ridges and sloughs are co-located in the landscape, their response to P is independent and indicative of unique regime shifts.

Our remote-sensing results indicate that the spatial extent of slough habitat begins to decline farther down the gradient (change points of 9.5 and 7.4 km) than the location where our ground-based sampling documented a significant increase in *Typha* frequency in individual sloughs (change point of 6.75 km). Our field observations are that *Typha* often establishes first around the edges of a slough and then encroaches inward by rhizomatous growth. Our ground-based method, which involved sampling a transect across the center of the slough, did not account for *Typha* growth at the edges of sloughs. Therefore, while not quantified in this study, our observations indicate that *Typha* encroachment accounts for at least some of the reduction in the size of individual sloughs between 9.5 and 7.4 km.

In addition, our remote sensing analysis of open-water areas in highly enriched parts of our study area determined that they are not natural sloughs and have been created and maintained largely by airboats. These habitats are not enduring features of the landscape as they quickly revert to *Typha* within a few years following the cessation of airboat activity (personal observation). The frequent disturbance required to prevent *Typha* establishment also inhibits the growth of other rooted macrophytes such as *Nymphaea* but allows for some growth of submersed taxa such as *Ceratophyllum* that are adapted to high nutrient conditions and are found exclusively in these highly enriched open-water habitats near the canals (Vaithiyanathan & Richardson, 1999). There is some functional equivalence between these artificially created areas and natural sloughs. For example, Crozier & Gawlik (2002) found that wading bird usage of enriched areas of WCA 2A was greater than that in unenriched areas, despite the presence of significantly less open-water habitat, which these species require for foraging. This likely is due to higher productivity and prey densities in enriched areas (Rader & Richardson 1994; Turner et al., 1999), which compensates for the smaller foraging area. These observations have led to the recognition that artificial sloughs in densely vegetative areas may play a role in restoring ecological function to nutrient-enriched areas, while external P loads to the system are being reduced (Newman et al., 2006). However, these human-maintained habitat features bear little resemblance to natural Everglades sloughs.

The causes of slough loss appear to be complex and may vary in importance among locations within the remnant Everglades. For example, hydrology is an important driver of Everglades vegetative and landscape patterns (Davis et al., 1994), and the loss of natural flow regimes is considered a key factor contributing to the deterioration of the ridge-and-slough landscape (Science Coordination Team, 2003). However, hydrologic modifications alone cannot explain patterns of slough loss within WCA 2A, the entire area of which has been impounded and experiences similar patterns of fluctuation in water flow and depth. In this and other Everglades wetlands exposed to canal discharges, slough loss is strongly correlated with water-quality changes and with vegetation changes directly linked to P enrichment. These patterns indicate that restoration of predrainage landscape features hinges not only upon the re-establishment of favorable flow regimes, but on a return to the oligotrophic conditions that most of this regional wetland experienced prior to human alterations. Our conclusions are consistent with a recent synthesis of the entire Everglades restoration process (Sklar et al., 2005), which emphasizes the need for strict P-load reductions as well as hydrologic modifications to achieve restoration goals.

Acknowledgments We thank Kirk Gallagher for assistance with photointerpretation and Michelle Rau and Chad Kennedy for assistance with field sampling.

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