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Relating precipitation and water management to nutrient concentrations in the oligotrophic ''upside-down'' estuaries of the Florida Everglades

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Abstract

We present 8 yr of long-term water quality, climatological, and water management data for 17 locations in Everglades National Park, Florida. Total phosphorus (P) concentration data from freshwater sites (typically <0.25 μmol L^{-1}, or 8 μg L^{-1}) indicate the oligotrophic, P-limited nature of this large freshwater–estuarine landscape. Total P concentrations at estuarine sites near the Gulf of Mexico (average ≈ 0.5 μ mol L^{-1}) demonstrate the marine source for this limiting nutrient. This ''upside down'' phenomenon, with the limiting nutrient supplied by the ocean and not the land, is a defining characteristic of the Everglade landscape. We present a conceptual model of how the seasonality of precipitation and the management of canal water inputs control the marine P supply, and we hypothesize that seasonal variability in water residence time controls water quality through internal biogeochemical processing. Low freshwater inflows during the dry season increase estuarine residence times, enabling local processes to control nutrient availability and water quality. El Niño–Southern Oscillation (ENSO) events tend to mute the seasonality of rainfall without altering total annual precipitation inputs. The Niño3 ENSO index (which indicates an ENSO event when positive and a La Niña event when negative) was positively correlated with both annual rainfall and the ratio of dry season to wet season precipitation. This ENSO-driven disruption in seasonal rainfall patterns affected salinity patterns and tended to reduce marine inputs of P to Everglades estuaries. ENSO events also decreased dry season residence times, reducing the importance of estuarine nutrient processing. The combination of variable water management activities and interannual differences in precipitation patterns has a strong influence on nutrient and salinity patterns in Everglades estuaries.

Nutrient enrichment and cultural eutrophication affect virtually all aquatic systems to some degree (Carpenter et al. 1999; Boesch 2002). Effects tend to accumulate along hydrologic flow gradients, from primary streams, through large rivers and reservoirs, and ultimately to estuaries. Perhaps for this reason, freshwater ecosystems should be more likely to be oligotrophic than estuaries; most estuaries and coastal ecosystems are currently experiencing some degree of cultural eutrophication (Howarth et al. 2000; Castro et al. 2003). Oligotrophic freshwater systems are particularly vulnerable to even low levels of nutrient addition, and Vounatsou and Karydis (1991) suggested the use of oligotrophic aquatic systems as reference sites in eutrophication studies. We propose that oligotrophic estuarine systems provide the same reference function. In this paper, we present long-term water quality data from two freshwater–estuarine systems in the Florida Everglades that are characterized by low concentrations and availability of the limiting nutrient. These characteristics have been demonstrated in the freshwater Everglades (Noe et al. 2001; Gaiser et al. 2004) and in

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Everglades estuaries (Boyer et al. 1999; Sutula et al. 2003). Rudnick et al. (1999) calculated annual nutrient loads (1979–1996) along three transects in Everglades National Park that ran from canal inputs to the Gulf of Mexico, effectively coupling freshwater and estuarine systems. However, these two Everglades systems have not been explicitly coupled on a finer temporal scale (days to months) in a long-term, regional biogeochemical assessment.

The oligotrophic estuaries of the Florida Everglades are hydrologically coupled with upstream freshwater wetland systems by the flow of water, since most estuaries are coupled to their upstream watersheds. Most estuaries are also nitrogen limited (Vitousek and Howarth 1991), while the upstream freshwater systems tend to be phosphorus limited (Smith 1990). In the Everglades, macrophyte production in both the oligotrophic upstream wetlands and the estuaries is phosphorus limited (Fourqurean et al. 1992; Boyer et al. 1999; Noe et al. 2001). This low-nutrient status of the terrestrial boundary systems is an important defining feature of Everglades estuaries: the ocean, rather than the land, is the source of phosphorus (Fourqurean et al. 1992; Chen and Twilley 1999). Thus, the Everglades aquatic landscape is unusual both because of its oligotrophic nature and because of this marine supply of the limiting resource. Additionally, Everglades estuaries are unusual because macrophyte production is phosphorus limited. We used long-term water quality data sets to demonstrate each of these defining characteristics and to explore biogeochemical relationships among nutrients and with salinity.

Hydrologic modifications over the last 100 yr (including construction of over 2,500 km of canals and levees and hundreds of water control structures) have dramatically changed the Everglades (Light and Dineen 1994; Sklar et al. 2002). In this time, canals and levees have segmented the remaining Everglades into several large impoundments, known as water conservation areas (WCAs). The WCAs store water and curtail the natural tendency of water to flow south—downstream—through the Everglades landscape to the Gulf of Mexico. Everglades National Park (ENP), which is south of the WCA network, is the only region of the remaining Everglades that exhibits some natural flow patterns. Hydrologic compartmentalization has also caused the remaining wetlands to receive surface water, mainly as point-source inputs at canal structures. Swart et al. (1999) showed a long-term shift in Florida Bay salinity patterns, toward higher and less variable salinities, beginning around 1910, and related this shift to the cumulative effect of a number of human activities. Today, the first steps in the hydrologic restoration of the Everglades have already begun. Key goals of this restoration include longer hydroperiods, deeper water, and enhanced water flow. Hydrologic restoration efforts in the freshwater Everglades will necessarily affect the water entering the downstream estuaries. In fact, freshwater inputs to the Florida Bay estuary have already increased with the removal of a key levee along a major canal in 1997 (Rudnick et al. 1999; Parker 2000).

Because the Everglades is a wetland-dominated landscape, ecosystem structure and function as well as cross-system connectivity are driven by the hydrologic regime. Anthropogenic control of this regime via water management, as summarized above, defines the Everglades as a human-dominated system. However, regional climate also plays an important role in Everglades hydrology. The climatic template is neotropical, with about 80% of total annual precipitation occurring between June and November—the wet season. Total annual rainfall also follows a (roughly) decadal cycle between wet and dry years, such that the amplitude of this decadal pattern roughly equals the long-term average rainfall (Duever et al. 1994). Periodic interannual variations from this decadal pattern also occur, often in response to large-scale climatic forcing.

Larger scale quasi-global phenomena, such as El Niño–Southern Oscillation (ENSO) events, have been shown to affect coastal ecosystems in the northern Gulf of Mexico (Childers et al. 1990), lake ecosystems of the northern United States (Anderson et al. 1996), as well as all of North America (Trenberth et al. 1988). In northern and central Florida, Schmidt et al. (2001) showed that ENSO events were associated with higher than average rainfall in fall and winter, and Schmidt and Luther (2002) demonstrated ENSO control of salinity patterns in Tampa Bay, Florida. In south Florida, Beckage et al. (2003) showed that ENSO events were generally associated with wetter than average dry seasons, but their analysis related ENSO to fire patterns in the Everglades and they did not discuss wet season precipitation anomalies. To our knowledge, ENSO events have not been linked to complete annual precipitation records, to water quality patterns in the Everglades, or to salinity patterns in Everglades estuaries.

In this paper, we present long-term water quality data (1996–2003) from 17 sites in Everglades National Park (ENP). This research is part of the Florida Coastal Everglades long-term ecological research program (FCE LTER), which is the only LTER site located exclusively in a national park (Parsons 2004). Our objectives are (1) to describe the oligohaline character of the coupled freshwater–estuarine systems in ENP and the upside down nature of these systems in which the ocean, rather than the land, is the source of the limiting nutrient; (2) to investigate how relationships between organic and inorganic nutrient concentrations and relationships between salinity and nutrients vary across space in ENP estuaries; and (3) to demonstrate how climatological forcing (primarily via ENSO and drought events) and water management may control seasonal and interannual patterns in salinity and nutrient concentrations across ENP.

Materials and methods

Study area—This study was conducted in Everglades National Park, Florida, at the 17 permanent sites of the Florida Coastal Everglades long-term ecological research program (FCE LTER; Fig. 1). The freshwater landscape is dominated by sawgrass marshes and tree islands, interspersed with wet prairie and slough communities (Gunderson 1994). The estuarine tidal wetlands are mangrove forest, and the subtidal Florida Bay estuary includes seagrass beds, shallow carbonate banks, and numerous mangrove keys. Hydrologic modifications during the last 100 yr have reduced freshwater inputs to this system, resulting in shorter hydroperiods,

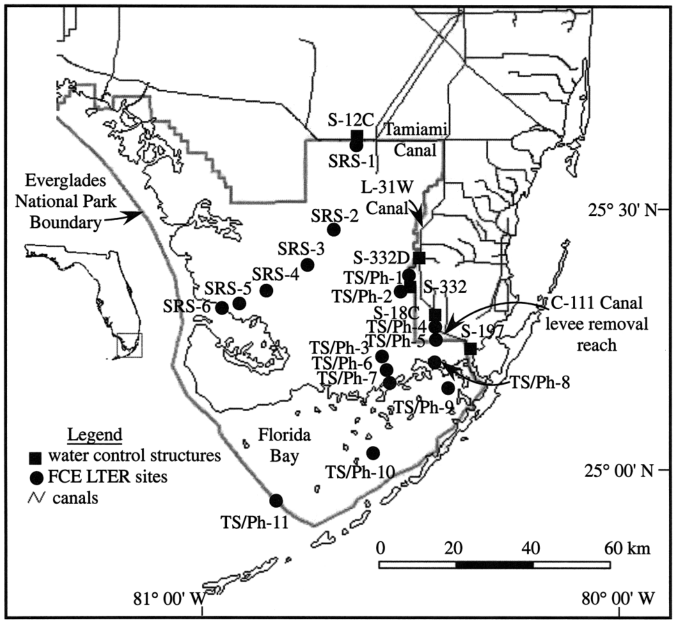

Fig. 1. Map of Everglades National Park showing the 17 FCE LTER sites. SRS-1 through -6 are along the Shark River Slough transect, TS/Ph-1, -2, -3, -6, and -7 are in Taylor Slough, TS/Ph-4, -5, and -8 in the C-111 basin/ENP panhandle, and TS/Ph-9, -10, and -11 are in Florida Bay. The 11 TS/Ph sites collectively form the southern Everglades Y-shaped transect. Key water control structures are shown as boxes, and key canals are indicated with arrows.

reduced water flow, saltier conditions in Florida Bay, and an inland shift of the estuarine ecotone (Light and Dineen 1994; Nuttle et al. 2000; Ross et al. 2000). Seasonal variability in water levels, inundation patterns, and the estuarine salinity regime in ENP are now largely controlled by local rainfall, evapotranspiration, and canal surface water inputs that are regulated by water management.

Our 17 water quality sites are located along transects that follow water flow from where surface water enters from canals through the estuaries to the Gulf of Mexico. Shark River Slough (SRS) canal inputs are controlled by the S-12 structures along the Tamiami Canal, and the first of our SRS sites (SRS-1) is located at the S-12C structure (Fig. 1). We define the oligohaline estuarine ecotone as the region where freshwater marsh (primarily sawgrass marsh and spikerush slough) and mangrove (primarily red mangrove) mix. In Shark River Slough, this ecotone region is relatively wide; our SRS-3 and SRS-4 sites bound the freshwater and estuarine margins of this ecotone, respectively (Fig. 1). The tidal range at the SRS-6 site, 2 km from the Gulf of Mexico, averages about 1 m. Tidal influence attenuates slightly up-estuary to SRS-4, and SRS-3 is nontidal.

Our southern Everglades transect is Y-shaped because this region is characterized by two dominant flow paths—one anchored at the L-31W canal and one at the C-111 canal. Surface water currently enters Taylor Slough (TS/Ph-1, -2, -3, -6, and -7) indirectly as bank overflow from the L-31W canal, and canal water levels are controlled by the S-332D pump structure (Fig. 1). Prior to January 2000, the S-332 structure pumped L-31W canal water directly into Taylor Slough (this structure was retired in early 2000; Fig. 1). Canal water enters the C-111 basin/ENP panhandle region (TS/Ph-4, -5, and -8) by C-111 canal overflow. In 1997, the levee along a 7-km length of the C-111 Canal was removed to enhance water flow into this region (Parker 2000). These surface water inputs are regulated by the S-18C structure immediately upstream and the S-197 structure immediately downstream. The S-197 is closed except in extreme flood threats, so most of the time water flow at the S-18C approximates total water flow entering the landscape once the C-111 canal has reached bankfull stage (Parker 2000).

Our Taylor Slough and C-111 basin/ENP panhandle transects join in northeastern Florida Bay (Fig. 1). Florida Bay is a triangular lagoonal estuary bounded by the Everglades to the north, the Florida Keys to the south, and the Gulf of Mexico to the west. The estuary is naturally compartmentalized into a network of shallow basins by carbonate mud banks that restrict water circulation, creating strong gradients in salinity, turbidity, and nutrient concentrations (Fourqurean et al. 1993). As a result, our three sites in Florida Bay (TS/Ph-9, -10, and -11) are not actually located along a predominant water flow path (as are our other 14 sites). Tidal advection from the Gulf of Mexico is quickly attenuated by the western mud banks, reducing astronomical tides at TS/Ph-10. Wind forcing dominates tidal fluctuations at TS/Ph-9 and at our oligohaline estuarine ecotone sites (TS/Ph-6, -7, and -8; Davis et al. 2004). Although precipitation is the largest source of freshwater to Florida Bay (Nuttle et al. 2000), freshwater inputs from Taylor Slough and the C-111 basin/ENP panhandle do affect salinity in the eastern bay (Boyer and Jones 1999; Nuttle et al. 2000).

Water quality sampling—Freshwater sites: Water quality sampling at the eight freshwater LTER sites began at various times, but we followed the same basic protocol at all sites. We began monitoring water quality at the two C-111 basin/ENP panhandle sites (TS/Ph-4 and -5; Fig. 1) in August 1998 and at the three Taylor Slough sites (TS/Ph-1, -2, and -3; Fig. 1) in July 1999. Shark River Slough sampling (SRS-1, -2, and -3; Fig. 1) began in November 2000. At all sites, samples were collected from the middle of the water column using ISCO automated water samplers powered by solar panels. In most cases, we interfaced rain level gauges to the autosamplers at these freshwater sites, and daily total rainfall data were downloaded monthly. We also outfitted all sites with an acoustic water level gauge that measured relative water height hourly. Samplers were programmed to collect a 250-ml sample every 18 h and to composite four such samples into the same 1-liter bottle. Thus, each tridaily sample contained a subsample collected roughly at noon, midnight, dawn, and dusk during that 3-d interval. Autosamplers were serviced monthly, and water samples were returned to the lab for nutrient analysis.

Some protocols call for preservation (by acidification or refrigeration, mostly) of such samples, but we chose to not field preserve our samples. We ran a field preservation experiment to verify this strategy in which paired samplers were deployed for a month at two sites and programmed to simultaneously sample from the same location in the water column. Bottles in one sampler contained 50 ml of 10 N

H_2SO_4 as a preservative; the other sampler had no preservative. Our analysis of these samples showed no significant difference in total phosphorus (TP) concentration (preserved [TP] = 1.09 × unpreserved [TP] + 0.01, $r^2 = 0.44$, $n = 26$). However, we found a consistent gain in total nitrogen (TN) in the acidified samples (of over 10 μmol L^{-1} in our case) relative to unpreserved samples (preserved [TN] = 0.98 × unpreserved [TN] + 10.6, $r^2 = 0.38$, $n = 26$). Notably, we found no evidence of hypoxic or anoxic conditions in either the preserved and unpreserved samples—conditions favorable to denitrification. Our strategy of not preserving field samples may only be appropriate in oligotrophic systems such as ours, where microbial activity in sample bottles stored in a field autosampler is minimal.

In May 2001, we began collecting a ''grab'' water sample during the monthly site visits. These samples were collected from 10 cm below the surface in sample-rinsed bottles and placed on ice in the dark for transport. In the lab, a subsample was filtered (Whatman GF/F filters) into a 60-ml acid-washed bottle for dissolved nutrient analysis. In this paper, we present nutrient concentration data from these eight sites through 2003.

Unfiltered water samples were analyzed for TN and TP. TN was measured using an ANTEK 7000N nitrogen analyzer using O_2 as carrier gas instead of argon to promote complete recovery of the nitrogen in the water samples (Frankovich and Jones 1998). TP was determined using the dry ashing, acid hydrolysis technique (Solorzano and Sharp 1980). Filtered samples were analyzed for soluble reactive phosphorus (SRP), nitrate + nitrite (NN), nitrite (NO_2^-), and ammonium (NH_4^+) using standard colorimetric techniques (Alpkem model RFA 300). Dissolved organic carbon was also measured on filtered water samples by direct injection onto hot platinum catalyst in a Shimadzu TOC-5000 after first acidifying to pH < 2 and purging with CO_2-free air.

Estuarine mangrove sites—Water quality sampling at the six estuarine mangrove LTER sites also began at various times but followed the sampling protocol described above for the freshwater sites. These sites were not instrumented with rain level gauges. We began sampling water quality at TS/Ph-7 in April 1996, at TS/Ph-6 in May 1998, and at TS/Ph-8 in November 1999 (Fig. 1). Sampling at SRS-4, -5, and -6 began in November 2000 (Fig. 1). Initially, autosamplers at TS/Ph-6 and -7 collected a 250-ml subsample every 6 h, composited into a single 1-liter sample every day. In October 1998 we switched to the tridaily composite sample protocol described above. The other four mangrove sites have always followed this tridaily composite protocol. We followed the same sample preparation and analytical methods described above, except that we also measured salinity in all samples using either a refractometer or a YSI salinometer. We present nutrient concentration data from these six sites through 2003.

Florida Bay—The three sites located in Florida Bay (TS/Ph-9, -10, and -11; Fig. 1) were sampled monthly. At each site we collected a grab water sample for total nutrient analysis from 10 cm below the surface. These samples were kept at ambient temperature in the dark during transport. We also collected a sample for dissolved nutrient analysis, which was immediately filtered (Whatman GF/F) into sample-rinsed 60-ml bottles and placed on ice in the dark for transport. Near surface and near bottom salinity was measured at each site using Hydrolab probes, and we present surface salinity data here. Laboratory analyses were performed following the protocols listed above. The three sites we present here are part of a larger water quality monitoring program that began in 1989. In this paper, we present data from these three sites from 1996 to 2003.

Climatological and water management data—Water flow and water levels in Shark River Slough are regulated by the S-12 structures along the northern ENP boundary. We used mean monthly water flow (m^3 s^{-1}) at the S-12C structure (where SRS-1 is located) to represent whether canal water was entering ENP. Water flows into the C-111 basin/ENP Panhandle at TS/Ph-4 are controlled by the S-18C (input) and S-197 (outflow) structures (Fig. 1). Bankfull canal stage (overflow) at our TS/Ph-4 site occurred when S-18C water levels were 0.61 m (2 feet) or greater. We calculated water flow into this landscape as S-18C flow minus S-197 flow for all days in which this water level exceeded 0.61 m, then generated monthly total water inputs by summing these daily values for each month (all structure data provided by the South Florida Water Management District). We were unable to estimate either the timing or rates of surface water inflow for Taylor Slough because S-332D pump flow data did not relate well to diffuse L-31W canal overflow at TS/Ph-1.

We obtained daily rainfall data from the Royal Palm weather station in ENP, which is centrally located relative to our 17 LTER sites (Fig. 1), and we present these data as monthly total rainfall (cm) for the period of our water quality record. We used monthly precipitation data from this site to calculate annual rainfall totals and ratios of dry season to wet season rainfall from 1963 to 2003. We also obtained monthly data for the Niño3 ENSO index from 1963 to 2003 from the NOAA Climate Prediction Center (Childers et al. 1990). We could not calculate calendar year annual means of the Niño3 index to compare with the annual rainfall values because dry season rainfall for a given year was based on December precipitation from the previous calendar year. For this reason, and to allow for lagged-response times (for teleconnections between the equatorial Pacific and south Florida), we calculated each year's Niño3 index as a monthly mean from June of the previous year through May of that year (which also encompassed a full wet and dry season for each year).

Statistical analyses—We summarized nutrient concentration (abbreviated as [X]) and salinity data at the 14 sites with continuous water quality records by calculating arithmetic means of monthly data as well as a mean for each site for the period of record. Conservative mixing relationships were generated by relating nutrient concentrations to their corresponding salinity values using linear and curvilinear regression. We ran these regressions for both grab sample data and for monthly means of total nutrient content and salinity. Curvilinear relationships were also investigated using polynomial regression, and we report results where ability of salinity to explain nutrient concentrations increased substantially with nonlinear regressions. We interpreted concave relationships as showing a nutrient sink within the estuary, while convex relationships suggested a nutrient source. Finally, we also used regression analysis to investigate the ability of TN and TP concentrations to predict dissolved inorganic nitrogen (DIN) and SRP content, respectively. These relationships allowed us to extrapolate a continuous time series of dissolved nutrient concentrations, using TN and TP content as surrogates, at the 14 of our 17 sites for which we have continuous TN and TP data. We linked ENSO activity with the south Florida climate by correlated the dry/wet rainfall ratios and total rainfall amounts with the corresponding Niño3 index for the 1963–2003 time period.

Results

Shark River Slough—Description: The six sites in SRS are located along a transect over 60 km long, from Tamiami Canal inputs to the Gulf of Mexico. The SRS-1 site, at the canal, was located in a deep pool immediately downstream of the S-12C structure. Total P concentrations were highly variable and averaged 0.75–1.0 μmol L^{-1} when this structure was closed—and water was not flowing into Shark River Slough, or SRS—while [TP] averaged about 0.25 μmol L^{-1} when the structure gates were open (Fig. 2A, 2C). Mean monthly [TP] at the interior freshwater site (SRS-2) were typically less variable and averaged less than 0.25 μmol L^{-1} (Fig. 2C). Mean monthly [TP] at the upper ecotone site (SRS-3) was somewhat higher (0.3–0.4 μmol L^{-1}) during the late dry season (April–June) and were similar to SRS-2 values during most other months (Fig. 2C). Total P concentrations at the estuarine sites (SRS-4, -5, and -6) showed less seasonal variation than the freshwater sites (Fig. 2C). In most months, mean [TP] increased down-estuary, with the highest [TP] at the SRS-6 site. This pattern was most consistent during wet season months when the S-12C structure was open and freshwater was flowing along this transect. Estuarine [TP] tended to be higher when this structure was closed, and was not always highest at SRS-6.

Some distinctive temporal and spatial patterns were observed in our [TN] data set. The most prominent of these patterns was higher mean [TN] at the freshwater sites (SRS-1 to -3) when the S-12C structure was closed (Fig. 2D). In these months, interior freshwater marsh [TN] were often more than double those at SRS-1. The other consistent pattern that we found along the SRS transect was declining [TN] down-estuary (SRS-4 to -6). Total N concentrations at SRS-6 were consistently low, and in almost all months estuarine [TN] was lower than at the freshwater sites (Fig. 2D).

Salinity along the SRS transect showed a longitudinal pattern typical of tidal estuaries, and a seasonal pattern typical of Everglades aquatic landscapes. The ecotone-marine gradient was strongest during the dry season, but the pattern also held when freshwater inputs were strong (Fig. 2A,B). We observed measurable salinity at the upper ecotone site (SRS-3) only in May and June 2001, immediately following a 2-month whole-system dry-down in SRS. We observed few if any temporal lags in mean monthly maximum or minimum salinities along the SRS-3 through SRS-6 estuarine gradient. From 2001 through 2003, we observed a steady decline in maximum (monthly mean) dry season salinity but no decline in minimum wet season salinity (Fig. 2B).

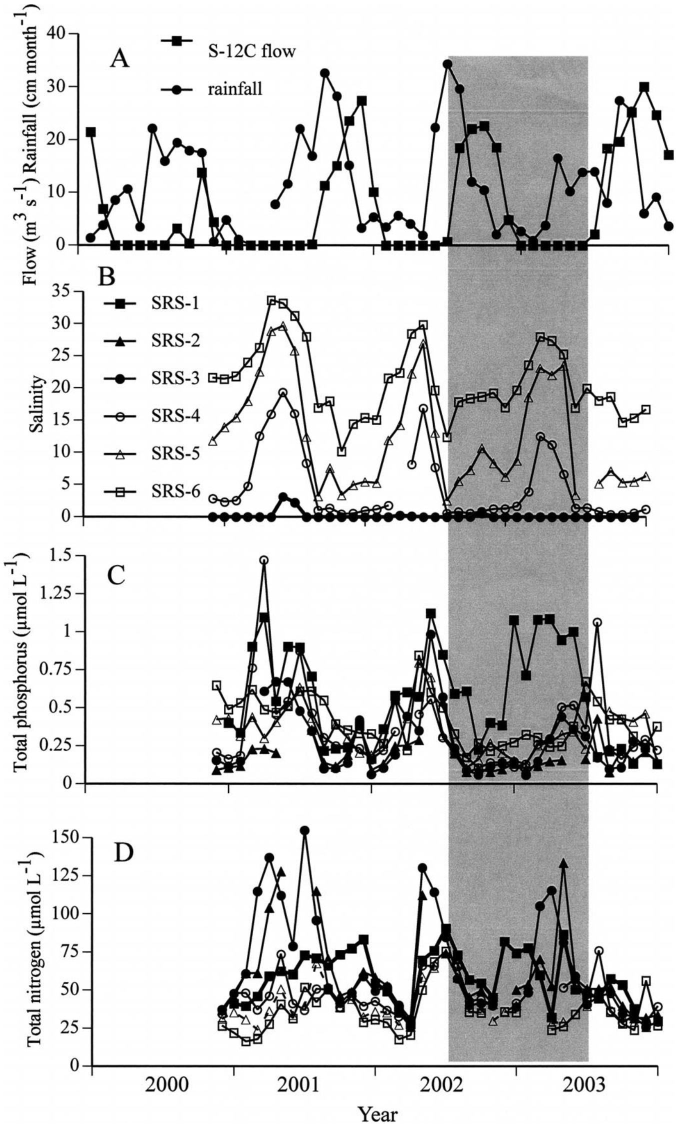

Fig. 2. Water quality, hydrologic, and climatological data from the SRS transect sites. (A) Total monthly rainfall at the Royal Palm met station, ENP and monthly mean water flow through the S-12C structure on Tamiami Trail, at SRS-1 (note that when S-12C flows were >0, the structure was open); (B) salinity at the oligohaline estuarine ecotone sites (SRS-3 and -4) and mangrove estuarine sites (SRS-5 and -6); (C) monthly mean [TP] at all SRS sites; (D) monthly mean [TN] at all SRS sites. The gray box approximates the temporal influence of the 2002–2003 ENSO event.

Climate and water management—Local rainfall and surface water inflow from the Tamiami Canal at the S-12 structures dominated freshwater inputs to the SRS drainage. Of the years for which we show a record (2000–2003), 2000 was the driest (Fig. 2A) with a total annual rainfall at the Royal Palm ENP meteorological station of 126.7 cm. The 2001 water restrictions and water management decisions in south Florida were largely blamed on low rainfall during 2000. Notably, all of central SRS dried during the 2001 dry season, and our SRS-2 site was dry for most of April and May 2001. Annual total rainfall at this same location in 2001 totaled 144.6 cm, and 2002 and 2003 totals were 134.1 and 139.6 cm, respectively. The long-term (1951–1980) average annual precipitation for ENP is 155 cm (Duever et al. 1994).

Contrasting with these relatively minor interannual rainfall differences, we found that average monthly inflow at the S-12C structure showed dramatic interannual differences. From January 2000 to July 2001, this structure was closed for 13 of 18 months, and flows when it was open were low (Fig. 2A). This time period contrasts with the 2001, 2002, and 2003 wet seasons, in which the S-12C was open consistently for 5–6 months and average monthly flows tracked monthly precipitation patterns—albeit with a 2-month lag (Fig. 2A).

A moderate ENSO event occurred during the 2000–2003 SRS period of record, from mid-2002 through mid-2003. During this time, we observed reduced wet season rainfall and enhanced dry season rainfall, and a negative Niño3 index for 2002 (Table 1). Rainfall during the 2002 wet season (June–November) totaled 93.8 cm compared with 118.6 cm during the previous season, and dry season 2003 (December 2002–May 2003) totaled 48.2 cm compared with 25.4 cm during the 2001 dry season. The dry : wet season rainfall ratios were high for both years ($= 0.46$ and 0.53), as typically happens during ENSO events (Table 1). The 2002 dry season total rainfall was 43 cm, but 22.4 cm of this fell in May 2002, which may have been an ENSO onset phenomenon. The Niño3 index from 1963 to 2003 was positively correlated with the dry : wet season rainfall ratio ($r = 0.38$, $p = 0.019$, $n = 38$) and with total annual rainfall ($r = 0.34$, $p = 0.037$, $n = 38$).

Nutrient–salinity relationships—Conservative mixing diagrams are often used to relate nutrient concentrations and salinity along a spatial gradient in estuaries. In our analysis, we regressed salinity and nutrient content along both spatial and temporal gradients. Using our estuarine SRS water quality sites (SRS-4, -5, and -6), we found significant salinity–[TP] relationships using both monthly mean and grab sample data, although salinity explained much more variability in grab sample [TP] (Table 2). Both showed increasing [TP] with increasing salinity, and the slope of the relationship using grab sample data was significantly greater than with monthly mean data. This increase in [TP] down-estuary holds true for the entire period of record. We found a similar positive relationship between grab sample [SRP] and salinity while the relationship between salinity and [TOC] was negative (Table 2).

All inorganic : organic nutrient concentration relationships from the SRS-4, -5, and -6 sites combined were significant. Total N content in monthly grab samples explained 73% of the variance in both [NH_4^+] and [NN] in the same samples, and the slopes of these relationships were not significantly different (Table 3). These slopes implied that, at our SRS estuarine sites, approximately 3.5–4% of TN was either NH_4^+ or NN at any given time. Similarly, [TP] explained 58% of variability in grab sample [SRP], such that SRP comprised about 15% of TP at our SRS estuarine sites (Table 3).

Table 1. ENSO index and south Florida precipitation data for 1963–2003. Dry season : wet season ratios are calculated from total rainfall from December (of the previous year) to May (dry season) and June to November (wet). Niño3 index values are means of monthly values from June of the previous year to May (*see text* for justification for 6-month lag). Total annual rainfall is dry season plus wet season rain for each year. Years shown in bold were ENSO event years, with the severity of the event shown in column 2.

Year	El Niño?	Dry season/ wet season rain	Niño3 index (June–May)	Total annual rain (mm)
1963		0.266		1,303
1964		0.341	0.20	1,595
1965		0.206	−0.64	1,318
1966	**Moderate**	**0.282**	**0.81**	**1,848**
1967		0.147	−0.47	1,397
1968		0.535	−0.87	2,200
1969		0.374	0.42	2,094
1970		0.556	0.43	1,203
1971		0.136	−1.23	867
1972	**Strong**	**0.573**	**1.06**	**1,575**
1973	**Strong**		**1.17**	
1974		0.329	−1.15	1,151
1975		0.292	−0.53	1,345
1976		0.382	−1.03	1,447
1977	**Moderate**	**0.537**	**0.56**	**1,414**
1978		0.513	−0.08	1,926
1979		0.636	−0.21	1,343
1980		0.327	0.24	1,915
1981		0.319	−0.14	1,560
1982		0.462	−0.03	1,612
1983	**Strong**	**0.558**	**2.04**	**1,846**
1984		0.529	0.07	1,218
1985		0.321	−0.90	1,221
1986		0.456	−0.61	978
1987		0.522	0.71	1,204
1988		0.210	0.67	1,453
1989		0.216	−1.41	920
1990		0.417	−0.19	1,082
1991		0.564	0.02	1,524
1992	**Moderate**	**0.265**	**1.04**	**1,236**
1993		0.548	0.16	1,137
1994		0.579	0.08	1,134
1995			0.19	
1996		0.361	−0.63	1,261
1997		0.214	−0.33	1,494
1998	**Strong**	**0.436**	**2.62**	**1,543**
1999		0.224	−0.70	1,624
2000		0.369	−0.93	1,256
2001		0.216	−0.40	1,441
2002	**Moderate**	**0.458**	**−0.23**	**1,367**
2003	**Moderate**	**0.534**	**0.52**	**1,386**

Southern Everglades Description—The southern Everglades transect was somewhat more complex because it had two freshwater marsh legs (Y-shaped; Fig. 1). Our Taylor Slough sites had different temporal records, but nonetheless showed some interesting landscape-level patterns. Mean [TP] at the three freshwater sites were consistently lower than at the estuarine mangrove sites, with the exception of

Table 2. Coefficients for relationships of salinity regressed with various nutrient constituents. MoMn, monthly mean of tridaily TN and TP concentration samples; Grab, concentration of total or dissolved nutrients from discrete grab samples collected monthly. In all cases, slope values are in μmol L^{-1} ppt^{-1} and intercepts are in μmol L^{-1}. * = relationships that improved considerably with curvilinear regressions (demonstrating an estuarine source or sink; *see text*). Those relationships in bold are significant but ecologically questionable (*see text*).

Basin	Sites	Sample type	Nutrient	Slope (±SE)	Intercept (±SE)	*p* value	r^2	*n*
SRS	4, 5, 6	MoMn	TP	0.009 (0.002)	0.26 (0.032)	<0.0001	0.16	109
SRS	4, 5, 6	Grab	TP	0.014 (0.001)	0.21 (0.02)	<0.0001	0.56	74
SRS	4, 5, 6	Grab	TOC	−122.4 (2.84)	1236 (43.2)	<0.0001	0.24	62
SRS	4, 5, 6	Grab	SRP	0.002 (0.001)	0.037 (0.007)	0.0002	0.20	67
TS/Ph		MoMn	TN	0.33 (0.15)	55.7 (2.05)	0.029	0.20	122
TS/Ph	6, 7	MoMn	TP	0.014 (0.002)	0.229 (0.024)	<0.0001	0.28	155
TS/Ph	6, 7	Grab	TP	0.006 (0.002)	0.278 (0.032)	0.012	0.13	49
TS/Ph	6, 7	Grab	NH_4^+	0.08 (0.027)	3.06 (0.39)	0.005	0.13	57
TS/Ph	6, 7	Grab	NN	−0.11 (0.01)	4.37 (0.32)	<0.0001	0.31	282
TS/Ph	**9, 10, 11**	**Grab**	**NH_4^+**	**−0.16 (0.04)**	**7.88 (1.35)**	**<0.0001**	**0.05**	**288**
TS/Ph	**9, 10, 11**	**Grab**	**TN**	**−0.54 (0.19)**	**52.7 (6.17)**	**0.005**	**0.02**	**288**
TS/Ph	**9, 10, 11**	**Grab**	**SRP**	**0.001 (0.0003)**	**0.08 (0.01)**	**0.001**	**0.04**	**286**
TS/Ph	**9, 10, 11**	**Grab**	**TOC**	**−5.72 (2.44)**	**766 (79.0)**	**0.019**	**0.02**	**285**
TS/Ph	6, 7, 9, 10, 11	Grab	NN*	−0.03 (0.005)	1.65 (0.15)	<0.001	0.08	347
TS/Ph	**6, 7, 9, 10, 11**	**Grab**	**NH_4^+**	**−0.05 (0.02)**	**4.27 (0.58)**	**0.02**	**0.01**	**345**
TS/Ph	**6, 7, 9, 10, 11**	**Grab**	**TN**	**−0.37 (0.10)**	**47.3 (3.11)**	**0.0003**	**0.04**	**324**
TS/Ph	6, 7, 9, 10, 11	Grab	TOC	−10.1 (1.41)	921 (43.7)	<0.0001	0.14	321
TS/Ph	8, 9, 10, 11	Grab	NN*	−0.03 (0.006)	1.74 (0.20)	<0.0001	0.07	318
TS/Ph	**8, 9, 10, 11**	**Grab**	**NH_4^+**	**−0.07 (0.02)**	**5.02 (0.76)**	**0.005**	**0.03**	**317**
TS/Ph	**8, 9, 10, 11**	**Grab**	**TN**	**−0.41 (0.13)**	**48.4 (3.97)**	**0.001**	**0.03**	**306**
TS/Ph	**8, 9, 10, 11**	**Grab**	**TP**	**0.004 (0.001)**	**0.15 (0.05)**	**0.006**	**0.03**	**311**
TS/Ph	8, 9, 10, 11	Grab	TOC	−9.42 (1.70)	894 (53.5)	<0.0001	0.09	304

a late 2003 TP incursion at TS/Ph-1, where L-31W canal water entered upper Taylor Slough (Fig. 3C; note that TS/Ph-1, -2, and -3 dry out for several months every dry season). At the estuarine mangrove sites (TS/Ph-6 and -7), [TP] were generally greater in the dry season, when salinities were higher (Figs. 3B, 5B). Additionally, monthly mean [TP] at these two sites peaked in 2000 and 2001 (the driest years of our record); they were lower before this, and have been steadily declining since. Total P concentrations were less variable at our three Florida Bay sites (TS/Ph-9, -10, and -11; Fig. 3C) and often were lower than mangrove site [TP]. This pattern held true even when [TP] data were summarized for the entire period of record (Fig. 7). In most months, [TP] measured at TS/Ph-11 (closest to the Gulf of Mexico) was highest among the Florida Bay sites.

Total N concentrations in Taylor Slough showed a pattern opposite that seen in SRS—mean monthly [TN] rates at freshwater sites were typically lower than those observed at the estuarine mangrove sites. As with [TP], [TN] was typically higher in the mangrove zone during the wet season (Fig. 4A, hollow vs. solid symbols; note that the freshwater sites dry down every dry season). Also, the mangrove sites

Table 3. Coefficients for total : inorganic nutrient relationships for N and P. Note that all regressions were forced through the intercept (*see text*). Grab = concentration of total or dissolved nutrients from discrete grab samples collected monthly. In all cases, slope values are dimensionless and intercepts are in μmol L^{-1}.

Basin	Sites	Sample type	Nutrient	Slope (±SE)	*p* value	r^2	*n*
SRS	4, 5, 6	Grab	NH_4^+ (*y*), TN (*x*)	0.04 (0.004)	<0.0001	0.73	45
SRS	4, 5, 6	Grab	NN (*y*), TN (*x*)	0.034 (0.003)	<0.0001	0.73	44
SRS	4, 5, 6	Grab	SRP (*y*), TP (*x*)	0.15 (0.02)	<0.0001	0.58	66
TS/Ph	6, 7	Grab	NH_4^+ (*y*), TN (*x*)	0.09 (0.01)	<0.0001	0.79	34
TS/Ph	6, 7	Grab	NN (*y*), TN (*x*)	0.024 (0.003)	<0.0001	0.62	35
TS/Ph	6, 7	Grab	SRP (*y*, TP (*x*)	0.10 (0.02)	<0.0001	0.38	39
TS/Ph	9, 10, 11	Grab	NN (*y*), TN (*x*)	0.02 (0.002)	<0.0001	0.35	282
TS/Ph	9, 10, 11	Grab	NH_4^+ (*y*), TN (*x*)	0.08 (0.01)	<0.0001	0.45	288
TS/Ph	9, 10, 11	Grab	SRP (*y*), TP (*x*)	0.04 (0.005)	<0.0001	0.18	286
TS/Ph	6, 7, 9, 10, 11	Grab	NH_4^+ (*y*), TN (*x*)	0.09 (0.005)	<0.0001	0.48	322
TS/Ph	6, 7, 9, 10, 11	Grab	NN (*y*), TN (*x*)	0.02 (0.002)	<0.0001	0.38	323
TS/Ph	6, 7, 9, 10, 11	Grab	SRP (*y*), TP (*x*)	0.08 (0.007)	<0.0001	0.27	319
TS/Ph	8, 9, 10, 11	Grab	NN (*y*), TN (*x*)	0.02 (0.002)	<0.0001	0.35	306
TS/Ph	8, 9, 10, 11	Grab	NH_4^+ (*y*), TN (*x*)	0.09 (0.005)	<0.0001	0.47	306
TS/Ph	8, 9, 10, 11	Grab	SRP (*y*), TP (*x*)	0.08 (0.007)	<0.0001	0.27	305

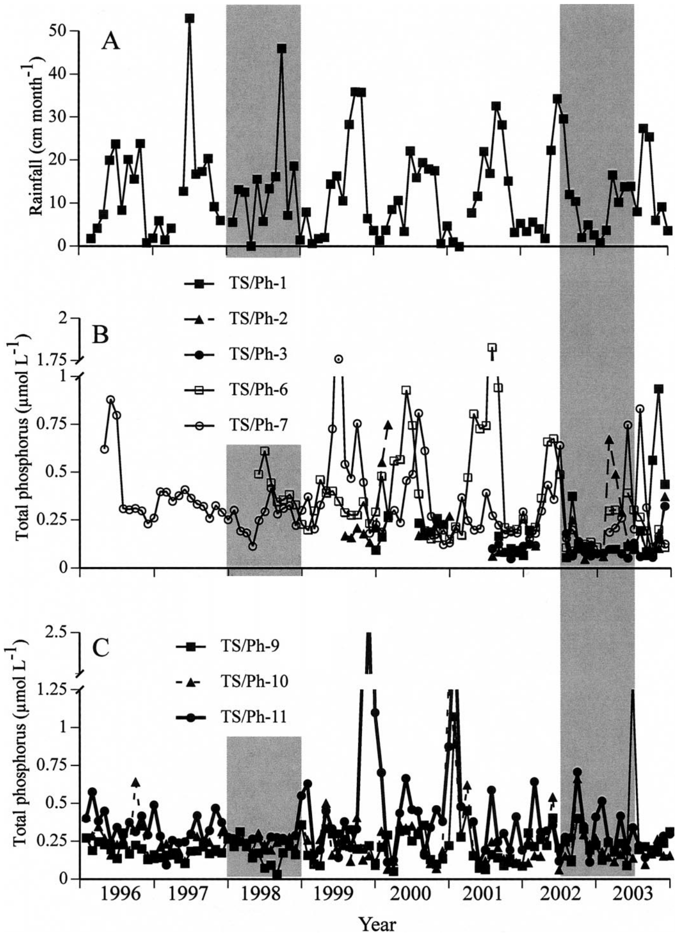

Fig. 3. Water quality and climatological data from the Taylor Slough sites on the southern Everglades transect. (A) Total monthly rainfall at the Royal Palm met station, ENP; (B) monthly mean [TP] at the freshwater and oligohaline estuarine ecotone sites (TS/Ph-1, -2, -3, -6, and -7); (C) [TP] at the Florida Bay estuarine sites (TS/Ph-9, -10, and -11). The gray boxes approximate the temporal influence of the 1998 and the 2002–2003 ENSO events.

often showed higher [TN] than the Florida Bay sites (Figs. 4, 7). There is some suggestion that [TN] measured at the TS/Ph-7 site has been declining since 1996 (Fig. 4A), and this decline was more noticeable at the TS/Ph-9 and -10 Florida Bay sites (Fig. 4B). This decline did not hold at the TS/Ph-11 Gulf of Mexico site.

Salinity patterns at the southern Everglades estuarine mangrove sites showed clear annual patterns, with lowest values during the wet season at TS/Ph-6 (Fig. 5). We observed the most protracted high-salinity dry season event in 2001, and the highest salinities also occurred in this year. In most years, dramatic salinity declines at the onset of the wet season occurred in parallel at TS/Ph-6 and -7, whereas the more gradual increases in salinity during the dry season typically occurred first at TS/Ph-7, followed 1–2 months later at TS/Ph-6 as freshwater drained from the Taylor Slough system (Fig. 5A). In Florida Bay, we saw little interannual or seasonal variation in salinity at the marine site (TS/Ph-11; Fig. 5B). However, the 1996–2003 record does show an interannual pattern of decreasing intersite salinity difference from

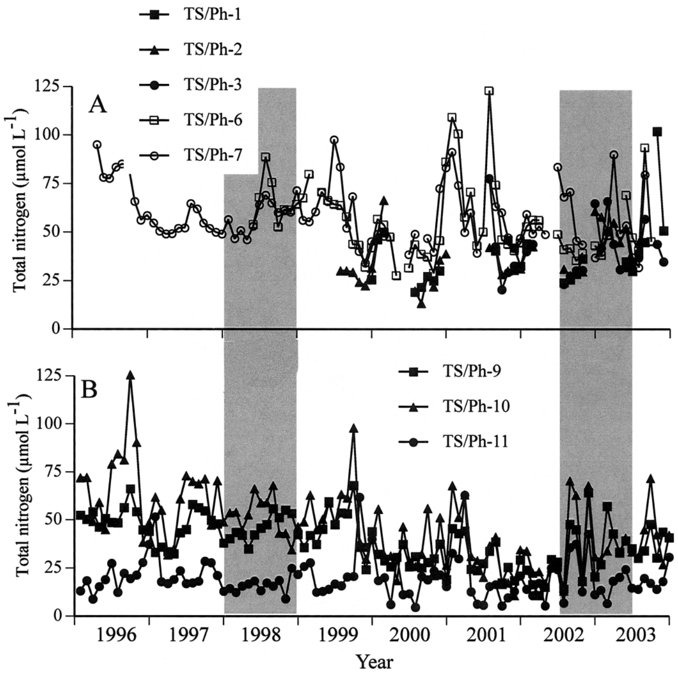

Fig. 4. Water quality data from the Taylor Slough sites on the southern Everglades transect (Fig. 3A shows rainfall). (A) monthly mean [TN] at the freshwater and oligohaline estuarine ecotone sites (TS/Ph-1, -2, -3, -6, and -7); (B) [TN] at the Florida Bay estuarine sites (TS/Ph-9, -10, and -11). The gray boxes approximate the temporal influence of the 1998 and the 2002–2003 ENSO events.

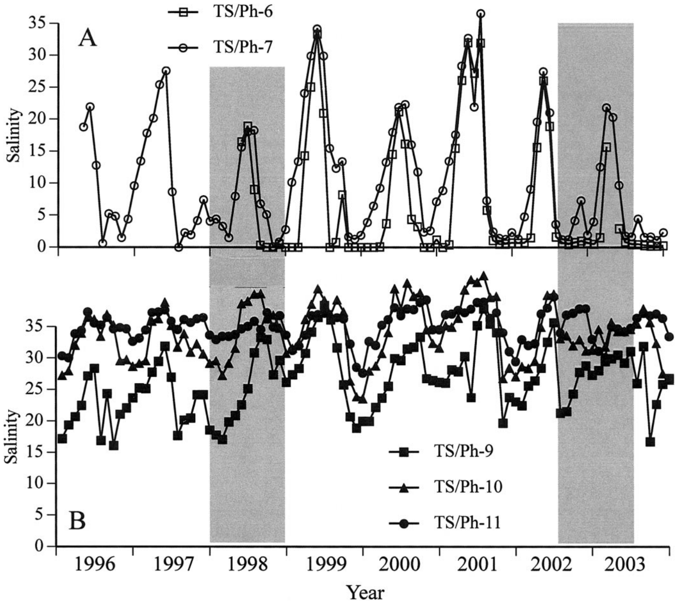

Fig. 5. Salinity data from the Taylor Slough sites on the southern Everglades transect (Fig. 3A shows rainfall). (A) average monthly salinity at the oligohaline estuarine ecotone sites (TS/Ph-6, and -7); (B) salinity at the Florida Bay estuarine sites (TS/Ph-9, -10, and -11). The gray boxes approximate the temporal influence of the 1998 and the 2002–2003 ENSO events.

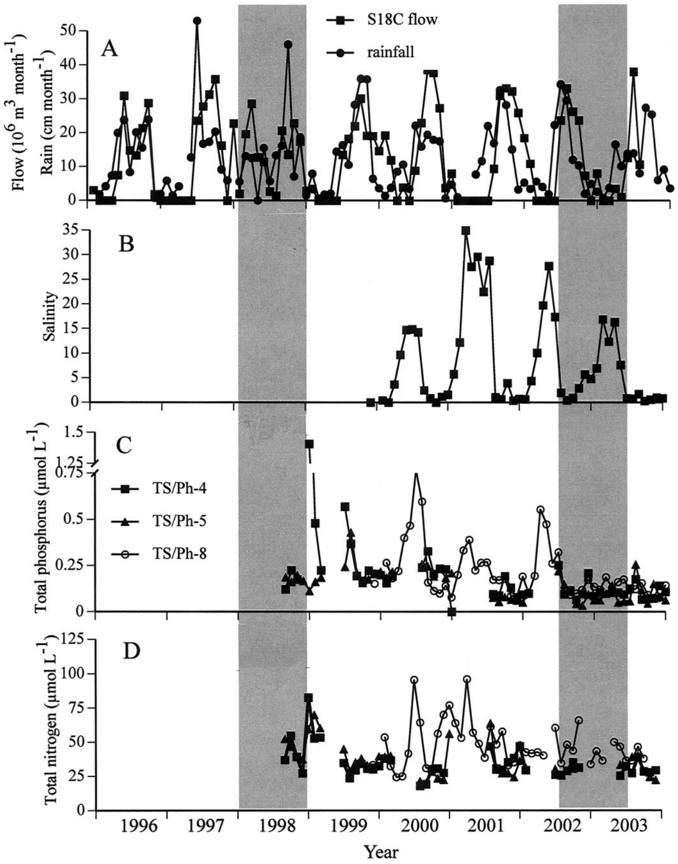

Fig. 6. Water quality, hydrologic, and climatological data from the C-111 basin/ENP Panhandle sites on the southern Everglades transect. (A) Total monthly rainfall at the Royal Palm met station, ENP and total monthly water flow into the landscape (= daily S-18C flow when WL ≥ 0.61 m minus S-197 flow); (B) salinity at the oligohaline estuarine ecotone site (TS/Ph-8); (C) monthly mean [TP] at the freshwater sites (TS/Ph-4 and -5) and the mangrove ecotone site; (D) monthly mean [TN] at the freshwater sites (TS/Ph-4 and -5) and the mangrove ecotone site. The gray boxes approximate the temporal influence of the 1998 and the 2002–2003 ENSO events.

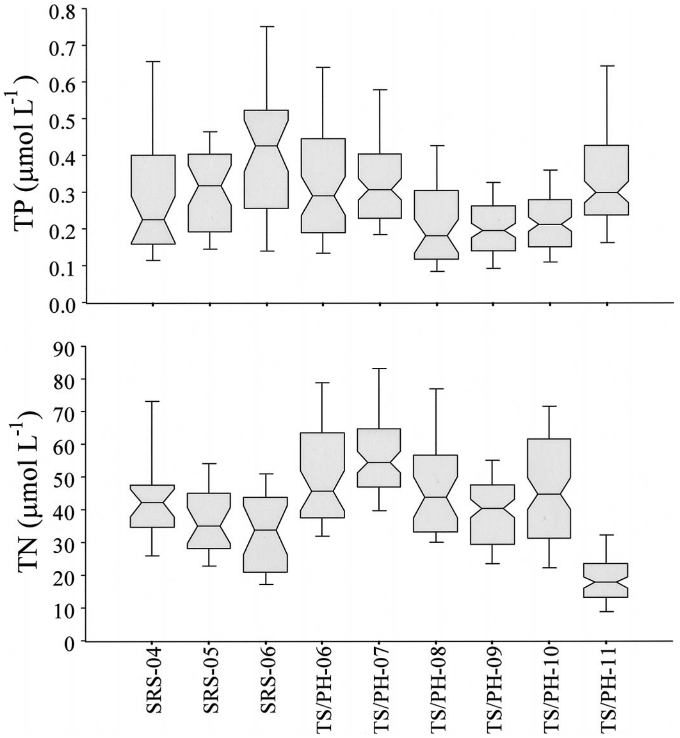

Fig. 7. Box-and-whisker plots of (A) [TP] and (B) [TN] for the period of record at all estuarine sites. The center horizontal line is the median of the data, top and bottom of the boxes are 25th and 75th percentiles (quartiles), and the ends of the whiskers are 5th and 95th percentiles. Box notches identify the 95% confidence interval about the median.

1996 to 1999/2000, then increasing cross-bay salinity gradient from 1999/2000 to 2003, suggesting a long-term periodicity in freshwater inputs across Florida Bay during this time (Fig. 5B).

Our C-111 basin/ENP Panhandle leg of the southern Everglades transect was shorter, and had only three sites (TS/Ph-4, -5, and -8). We found little difference in mean monthly [TP] at our freshwater sites (TS/Ph-4 and -5) compared with our mangrove site (TS/Ph-8), but there did appear to be a gradual but steady decline in [TP] at all sites from 1998 to 2003 (Fig. 6B). We observed the same declining trend in [TN] at these same sites. It also appeared that, in many months (both wet and dry season), mangrove site [TN] concentrations were higher than upstream freshwater TN values (Figs. 6B, 7). Over the 1999–2003 record, this mangrove site showed its lowest dry season salinity peak in 2000 followed by the highest dry season salinities in 2001 (Fig. 6A). 2001 also had a protracted high-salinity season, with salinity above 9 for 10 consecutive months compared with 6–7 months in most other dry seasons. The 2002–2003 dry and wet seasons were also atypical, since salinities began to increase in September 2002 but only peaked at 17 during the dry season.

Climate and water management—We had no direct measure of surface water input to Taylor Slough, but salinity at both mangrove sites (TS/Ph-6 and -7) tracked rainfall closely (Figs. 3A, 5A). In addition to the moderate 2002–2003 ENSO event, described above, there was a strong ENSO event in 1998 (Table 1). As with the later event, dry season rainfall was high while wet season rainfall was low, with a dry : wet season ratio of 0.436 (December 1997–May 1998 rainfall = 47.0 cm and June–November 1998 rainfall = 107.4 cm; Table 1). Notably, nearly half of this ENSO wet season rainfall occurred in September (46.1 cm), and much of that occurred on September 15 and 16 during Hurricane Irene (28.5 cm in 2 d). Without this event, the 1998 ENSO year had average rainfall (125.9 cm; Table 1).

In the C-111 basin/ENP Panhandle, we found that surface water inputs from the C-111 canal tracked seasonal rainfall patterns reasonably closely from 1996 to 2003 (Fig. 6A). This included the strong 1998 ENSO event in which water flowed from the canal in virtually every month, and the 2002–2003 moderate ENSO event when canal water entered this system in all but 3 months. The 2000 dry season showed anomalously high freshwater inputs in terms of both rainfall at the Royal Palm met station and inflows from the C-111 canal (Fig. 6A).

Nutrient–salinity relationships—There are several estuarine site configurations in our Y-shaped southern Everglades transects for which nutrient–salinity relationships could be calculated. We chose to analyze four groupings of sites: (1) the Taylor Slough mangrove sites (TS/Ph-6 and -7); (2) the Florida Bay sites (TS/Ph-9, -10, and -11); (3) TS/Ph-6, -7, -9, -10, and -11; and (4) TS/Ph-8, -9, -10, and -11 (*see Fig. 1*). The first site grouping (TS/Ph-6 and -7) included monthly means of continuous data as well as grab sample data. We found that both monthly mean [TN] and [TP] were positively related to salinity at TS/Ph-6 and -7, although the explanatory power was not strong ($r^2 = 0.20$ and 0.28, respectively; Table 1). Using grab sample data, however, we found considerably more relationships (Table 2). Of these, the strongest relationships were for [NN] and salinity at (1) the Florida Bay sites; (2) the TS/Ph-6, -7, -9, -10, and -11 combination, and; (3) the TS/Ph-8, -9, -10, and -11 combination (all were negative relationships; Table 2). For the latter two combinations of sites, a convex curvilinear relationship better represented this [NN] : salinity pattern—the pattern that conservative mixing diagrams argue suggests a midsalinity nutrient source ($[\text{NN}] = 0.109(\text{sal}) - 0.003(\text{sal})^2 + 0.896$, $r^2 = 0.23$, $p < 0.0001$ and $[\text{NN}] = 0.137(\text{sal}) - 0.004(\text{sal})^2 + 0.472$, $r^2 = 0.24$, $p < 0.0001$).

We found significant relationships between [TN] and both [NH_4^+] and [NN], and between [TP] and [SRP] for all estuarine site combinations discussed above (Table 3). There was no significant difference among site combinations in the NH_4^+ : TN ratio (0.08–0.09), and [TN] explained 45–75% of the variability in [NH_4^+]. The same was true for NN : TN, where we found a ratio of 0.02–0.024 and explanatory power ranging from 35% to 62% (Table 3). With the TP : SRP ratio, however, we found the Florida Bay sites to be significantly lower (0.04) than any combination that included mangrove sites (0.08–0.10). Notably, the former relationship was highly significant, but [TP] only explained 18% of the variability in [SRP] concentrations at the three Florida Bay sites (Table 3).

Discussion

Oligotrophy defines the aquatic landscape of ENP—Most estuaries and many freshwater bodies show some degree of cultural eutrophication today, and trajectories of change in these systems are often toward increased human influence on biogeochemical cycles (Castro et al. 2003). Oligotrophic systems may provide valuable end-member references for cross-system eutrophication studies, such as the synthesis objective of this special issue. In the freshwater Everglades, we have demonstrated that oligotrophic reference sites provide a valuable context for assessing nutrient effects in other parts of the landscape (Noe et al. 2001). Such low-nutrient end-member data were critical to the recent determination of the 0.3 μmol L^{-1} (10 ppb) class III phosphorus water quality standard for water entering the Everglades (Gaiser et al. 2004). We propose that the oligotrophic nature of our freshwater–estuarine Everglades landscape provides a similar reference function for this special synthesis on aquatic eutrophication.

With the exception of localized water quality effects immediately adjacent to some canal inputs (Childers et al. 2003), the aquatic ecosystems of ENP are uniquely oligotrophic and P limited (Boyer et al. 1999; Noe et al. 2001). Total P concentrations in the freshwater marshes of Shark River Slough are typically less than 0.25 μmol L^{-1}. Monthly mean [TP] at our SRS-1 site is very closely tied to S-12C structure activities, such that concentrations at this site are higher (0.5–1.0 μmol L^{-1}) when the structure is closed compared with when it is open ($\approx$0.25 μmol L^{-1}). This water quality site is actually located in a deep pool immediately downstream of the gated structure. We suspect that local remineralization in this deep water pool and long water residence times when the S-12C is closed are the primary reasons for these higher [TP] when the SRS-1 site is hydrologically decoupled from the downstream SRS-2 and -3 sites. Our TN data show an opposite pattern, though, with lower [TN] at the freshwater SRS sites when the S-12C gates are open and water is actively flowing down-slough. There is considerable evidence that freshwater Everglades wetlands are sources of dissolved organic N (DON; Davis et al. 2003; Lu et al. 2003; Parker 2000). This internal N source appears to be associated with slower processes that are most evident during the dry season, when the S-12 structures are closed and water residence times are longer.

Hydrologic control on biogeochemical cycling in southern Everglades freshwater marshes is dominated by regular dry-down events experienced by these shorter hydroperiod wetlands. Early wet season (June) spikes in [TP] occurred periodically at our Taylor Slough and C-111 basin/ENP Panhandle sites. In most cases, this June TP event occurred only at the canalside sites, suggesting a brief early wet season canal source of P. Similarly, in some years we observed a late wet season, pre–dry-down increase in [TP]—often at the interior marsh sites. We suspect that this phenomenon was a combination of evaporative concentration of the remaining standing water and both biotic and abiotic processes associated with annual marsh dry-down. In particular, Trexler et al. (2002) have shown that aquatic fauna actively concentrate in deeper water refugia as water levels drop in shorter hydroperiod wetlands. The late wet season P increases we observed may be partly a result of this concentration of animals and their activities during this time.

Lu et al. (2003), Parker (2000), and others have reported that southern Everglades freshwater marshes are sources of DON during much of the wet season. Our monthly data from this landscape confirm this pattern, although the concentration increases along our transects are not dramatic. Total N concentrations (>90% of which were DON) were higher at our downstream C-111 basin/ENP Panhandle site in 19 of the 34 months from 1998 to 2003 for which we had data at both sites. In Taylor Slough, concentrations at TS/Ph-2 or -3 were higher than at TS/Ph-1 in 11 of 20 months. Calcareous periphyton mats are a dominant component of these shorter hydroperiod southern Everglades marshes (Childers et al. 2003; Gottlieb 2003), and cyanobacteria are an important component of these mats (McCormick and Scinto

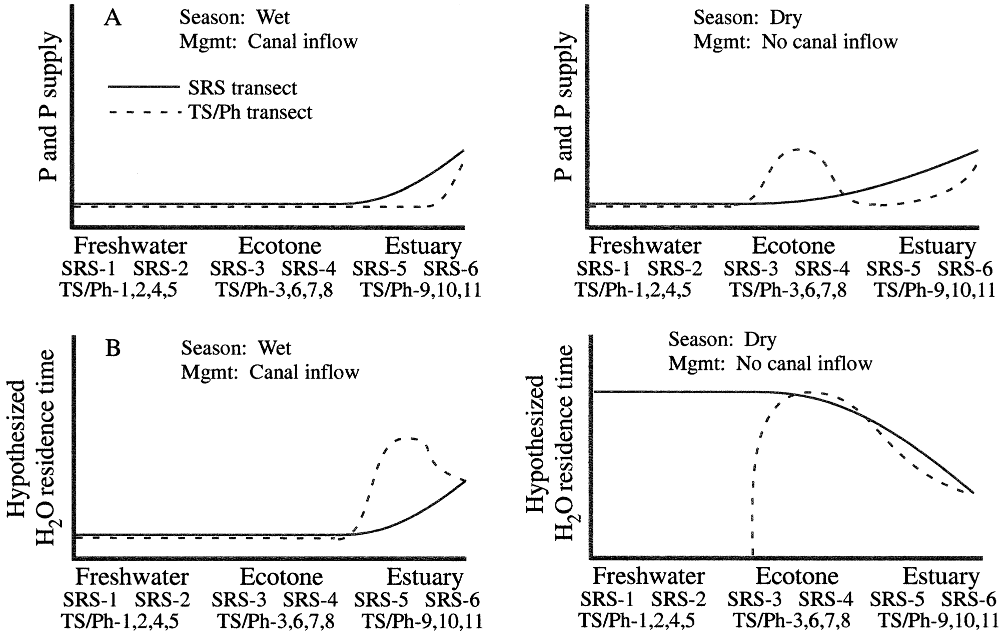

Fig. 8. (A) Conceptual model of the marine P source to the upside down estuaries of the Everglades, and how neotropical climatic seasonality and water management (manifest as canal inputs) alter patterns; (B) hypothesized conceptualization of how water residence time varies between the Shark River Slough (SRS) and southern Everglades (TS/Ph) transects, and how neotropical climatic seasonality and water management (manifest as canal inputs) alter patterns.

1999). It is likely that these nitrogen-fixing mats are responsible for much of the organic N source in these marshes—an intriguing phenomenon given that these are P-limited oligotrophic systems.

The upside down estuaries of ENP—Biogeochemical cycling and nutrient dynamics are strongly influenced by freshwater and terrestrial nutrient inputs in most estuaries. Anthropogenic control of those nutrient inputs is also a characteristic feature of many estuaries, often leading to trajectories of increasing cultural eutrophication. The data we present here for our 17 sites in ENP show a different picture, though. The freshwater ecosystems in the coastal Everglades landscape are oligotrophic and are characterized by very low [TP] (*see previous*). Furthermore, P—the limiting nutrient—is supplied by the Gulf of Mexico, not by upstream sources. We suggest that the marine source of the limiting nutrient is a defining characteristic of our Everglades estuaries, and we present a conceptual model depicting the upside down nature of these marine-driven systems (Fig. 8). Our conceptual model reflects the importance of season (wet vs. dry) as a key climatological driver in the neotropical Florida Everglades. Eyre and Balls (1999) demonstrated a similar climatological forcing of biogeochemical cycling in tropical estuaries that was manifest primarily through variability in freshwater inputs. Figure 8 also demonstrates how managed inflows of freshwater drive dynamics in our estuaries.

Our Shark River Slough transect follows water as it flows down this historical flow path to a direct connection with the Gulf of Mexico. Once this water entered the mangrove estuary, [TP] increased along with salinity. This relationship was highly significant and suggested an increase of 0.09 to 0.14 μmol L^{-1} TP for every 10 parts per thousand (ppt) increase in salinity. The 0-salinity intercepts of these regressions were 0.21–0.26 μmol L^{-1} P (6.5–8 parts per billion), which confirmed the oligotrophic nature of the freshwater entering this estuary from Shark River Slough (Noe et al. 2001). Based on these freshwater end-member concentrations, [TP] increased roughly 150% with a down-estuary salinity increase of 30. We also found a relationship between [SRP] and salinity, with [SRP] increasing 0.02 μmol L^{-1} for every 10-salinity increment from a freshwater end-member low of 0.037 ($\pm$0.007) μmol L^{-1} (also an approximate 150% increase down-estuary). These data and relationships all indicate that the source of P to the SRS estuary is the Gulf of Mexico, not the freshwater Everglades (Fig. 8A). Mangrove soil P and forest structure reflect this pattern, showing a wedge of productivity along the SRS estuarine gradient that is oriented toward the Gulf of Mexico (Chen and Twilley 1999). Seasonally, wet season freshwater inflows tend to compress the estuarine P gradient toward the marine end member, whereas during the dry season, reduced freshwater inflow allows incursions of marine P further up-estuary (Fig. 8A).

In the southern Everglades, the mangrove zone is isolated from this Gulf of Mexico source of P by Florida Bay. The marine P source is apparent in our Florida Bay water quality data, since TP concentrations are consistently highest at the TS/Ph-11 site. As in the Shark River Slough system, this validates our upside down estuarine model. Unlike in SRS, though, we did not find a salinity : TP relationship for the three Florida Bay sites. This is likely because salinity was relatively high (>15) at all of these sites. Also, Florida Bay is made up of a series of basins that are relatively isolated from each other by shallow mudbanks and mangrove keys. This compartmentalized geography means that our three Florida Bay sites were not hydrologically connected along a traditional freshwater to marine gradient. When considered with the TS/Ph-8 mangrove site (as a lower salinity end member), however, [TP] was positively related to salinity—although the explanatory power of this conservative mixing relationship was not strong.

Total P concentrations at the two mangrove sites in Taylor Slough (TS/Ph-6 and -7) were also positively related to salinity, such that salinity explained 13–28% of the variability in [TP] for grab samples and monthly means, respectively. The freshwater end-member concentration was 0.23–0.28 μmol L^{-1}, and [TP] in this mangrove zone increased 0.06 to 0.14 μmol L^{-1} for every 10 increase in salinity. Although this pattern held true when we summarized TP data for the entire period of record, it was a strongly seasonal pattern. We observed both higher [TP] and higher salinity during the dry seasons—as shown in our conceptual model (Fig. 8A). Water residence times in these mangrove wetlands are considerably longer during this time (Jaffe et al. 2001; Sutula et al. 2003). We attribute high [TP] in the mangrove zone and the positive salinity : TP relationship seen for sites TS/Ph-6 and -7 to a combination of the influx of P-rich carbonate particles from Florida Bay (Sutula et al. 2003) and to internal biogeochemical processing during these periods of longer residence time. We do not attribute this pattern to an upside down Gulf of Mexico supply of P. Davis et al. (2001*a*,*b*) found that the mangroves in this region took up TP, particularly during the higher salinity dry season. It is likely that higher TP concentrations during this time are a result of water column or subtidal processes, and these higher concentrations may actually stimulate intertidal wetland uptake of some of this P. Holmes et al. (2000) reported high rates of internal biogeochemical processing in the oligohaline zone of the Parker River estuary Massachusetts, when freshwater inputs were minimal (*see also* Vallino and Hopkinson 1998). Boynton and Kemp (2000) made a similar linkage between the seasonality of riverine inputs and nutrient cycling dynamics in the Chesapeake Bay.

We present this interaction between water residence time and biogeochemical cycling in our upside down Everglades estuaries as a conceptual hypothesis (Fig. 8B). During the wet season, water residence times along our SRS transect are low until near the Gulf of Mexico because of the flushing effect of large freshwater inputs. The compartmentalized geography of Florida Bay prevents similar freshwater effects, though, and water residence times tend to remain long at our Florida Bay sites (Fig. 8B). During the dry season, water residence times are long in the freshwater SRS while our freshwater TS/Ph sites dry down during this time. We hypothesize that the most dramatic seasonal effect on water residence times occurs during the dry season in the southern Everglades mangrove zone (TS/Ph-6, -7, and -8) and further hypothesize that these long dry season residence times play a major role in biogeochemical cycling in this oligohaline region (Fig. 8B). Jaffe et al. (2001) posed a similar question relative to organic matter diagenesis in this region. Research is needed to elucidate how water column or benthic processes in this mangrove zone are controlling [TP] during the higher salinity, longer residence time dry season.

Nitrogen is not a major factor in our upside down estuary model because it is not the nutrient limiting most primary production (i.e., mangroves and seagrass) in these estuaries (Fourqurean et al. 1992; Boyer et al. 1997). However, there does appear to be a long-term trend of declining [TN] in Florida Bay, at both the TS/Ph-9 and -10 sites (Fig. 4B). We also observed some interesting salinity : N relationships. Most notably, both southern Everglades estuarine transects showed significant convex curvilinear relationships between [NN] and salinity, such that salinity explained 23% and 24% of the variation in [NN] compared with 8% and 7% for the linear relationships (Taylor Slough and the C-111 basin/ENP Panhandle, respectively). The overall trend was of marine dilution of NN. These patterns suggest a midsalinity source of NN to the water column, and much of this pattern was driven by data from the three mangrove sites. This is consistent with mangrove flux data that showed uptake of NH_4^+ and release of NN, particularly during the higher salinity dry season (Davis et al. 2001*a*,*b*) when we hypothesize relatively long water residence times in this area (Fig. 8B). It is possible that dry season P and N dynamics are somewhat decoupled in our southern Everglades estuaries—with P cycling perhaps controlled by water column or subtidal processes and N cycling controlled by the mangrove wetlands, but with strong overall control by the seasonality of water residence time.

Organic : inorganic nutrient relationships—In most estuaries and many freshwater systems, relationships between patterns of dissolved and total nutrient concentrations are complicated by inorganic sediments, which potentially contribute only to the total nutrient pool. Freshwater Everglades wetlands are characterized by very low suspended sediment concentrations, though (Noe et al. 2001). Suspended sediment content is typically low at our estuarine sites as well (Boyer et al. 1997; Sutula et al. 2003). As such, TN and TP in most of our water samples were predominantly comprised of dissolved inorganic nutrients and dissolved organic N or P (Davis et al. 2003). We investigated how dissolved and total nutrients were related along subsets of our estuarine transects in an attempt to differentiate biogeochemical processing in different environments. Approximately 8% of TN at our SRS mangrove sites was DIN, split evenly between NH_4^+ and NN, while about 15% of TP was SRP. This contrasted with the Taylor Slough mangrove zone, where 11% of TN was DIN but most of that (9%) was NH_4^+. Total P was also more organic at the southern Everglades sites—10% of TP was SRP. We found no change in the relative contribution to TN by NH_4^+ (9–10%) or by NN (about 2%), or the relative contribution of SRP to TP (8–10%) when we included Florida Bay in our analyses. However, TP at only the three Florida Bay sites was considerably more organic (SRP = 4% of TP). Overall, we found that [TN] or [TP] concentration explained variability in NH_4^+, NN, or SRP concentration at our mangrove sites surprisingly well (58–73% in SRS, 62–79% in Taylor Slough). This relationship was not as strong for the three Florida Bay sites (18–45%). We suggest that the strong relationships at our mangrove sites lend confidence to the use of our long-term continuous total nutrient concentration data sets as surrogates for long-term changes in dissolved inorganic nutrients at these sites.

Climate and water management as biogeochemical drivers—The hydrologic regime is a key driver in all wetland ecosystems (Mitsch and Gosselink 2000). Our ENP study region is wetlands dominated—Florida Bay being the exception. The neotropical regional climate and human water management activities are the two primary controls on Everglades hydrology, and by extension on water quality patterns in ENP. The S-12 water control structures on Tamiami Canal control most surface water inputs to Shark River Slough, and their management has a dramatic effect on salinity and nutrient concentrations along our entire SRS transect. Over our 1996–2003 period of record, the wettest year was 1999 (164.7 cm) and the driest was 2000 (126.7 cm). Flow through the S-12C structure was low and sporadic during 2000, and substantive wet season discharge occurred only in October. After this low-rainfall, low-flow year, regulatory schedules required that the S-12C structure be kept closed from December 2000 until August 2001, in spite of the fact that 2001 was a relatively normal rainfall year (144.6 cm). As a result, the entire Shark River Slough system dried down in April and May of 2001, and salinity was detectable from late April through early July at our upper estuarine ecotone site (SRS-3). Salinities were higher for more months in 2001 at all estuarine sites, compared with 2002 and 2003. The reduced freshwater flow was coincident with higher [TP] in the SRS estuary in 2001, suggesting that the marine influence along this transect is strongly controlled by freshwater flow from upstream (as shown in Fig. 8A).

In the southern Everglades, our C-111 basin/ENP Panhandle subtransect was anchored at the C-111 canal, where the southern levee was removed in 1997 to increase freshwater inputs to this system (Parker 2000). These inputs are controlled by the S-18C structure just upstream from our TS/Ph-4 site. In most years, this structure is open for most or all of the wet season and closed for most of the dry season. However, S-18C flows did not follow this pattern in 1999 and 2000. The structure was open, and surface water entered our transect landscape, from the 1999 dry season through the end of the 2000 wet season, with March and May 2000 being the only exceptions. Thus, the C-111 basin/ENP Panhandle was receiving normal to above normal flow in 2000 even as SRS was receiving dramatically less surface water input. Downstream salinities, at TS/Ph-8, were lower in 2000 relative to 2001–2003 observations, in spite of low rainfall in this year. Thus, differential water management in these two drainages led to markedly different hydrologic regimes and salinity characteristics, although both regions received (essentially) the same precipitation.

The neotropical climate of south Florida is characterized by six wet months (June–November) and six dry months. Interannual variation in total rainfall can be fairly high (Duever et al. 1994). Between 1963 and 2003, the range of annual rainfall (maximum–minimum = 133.3 cm) was nearly as great as the 40-yr mean (142.2 cm), but during our period of record (1996–2003) annual precipitation varied by less than 40 cm (126.7 to 164.7 cm). We did observe considerable variability in the interannual wet–dry seasonal rainfall patterns during this time, though. 1998 was characterized by an abnormally wet dry season and a dry wet season, creating a pattern of relatively constant rainfall throughout the year. Similarly, the 2002 wet season appeared to end abruptly in August, rather than November, and was followed by an unusually wet dry season in 2003. In both cases, these abnormal precipitation patterns coincided with ENSO events—a strong event in 1998 and a moderate event in 2002–2003. In fact, the ratio of dry : wet season rainfall during ENSO events from 1963 to 2003 was considerably higher (mean = 0.455) compared with non-ENSO years (mean = 0.373, SE = 0.025). ENSO events coincide with drought conditions and abnormally low tidal inundation patterns along the northern Gulf of Mexico (Childers et al. 1990), and the recent ''brown marsh'' wetland die-off in southern Louisiana has been related to the strong 1998 ENSO event (R. Twilley, Louisiana State University, pers. comm.). Across North America, drought years have been linked to ENSO events (Trenberth et al. 1988) while ENSO events are associated with higher than average rainfall in central Florida (Schmidt and Luther 2002). Beckage et al. (2003) showed that south Florida typically has wetter than average dry seasons during ENSO events, and our analysis further demonstrated drier than average wet seasons during these events (both of which elevate the dry : wet season rainfall ratio). ENSO events do not necessarily affect total rainfall in the Everglades, but they do strongly modify the interannual timing of that rainfall. Effectively, during ENSO years the wet and dry season patterns generalized in Fig. 8 become more similar.

Earlier, we demonstrated how water management may strongly influence water quality patterns in ENP estuaries through controls on surface water inflows to the freshwater Everglades. ENSO events also affect salinity patterns and nutrient concentrations in these estuaries through shifts in the timing of rainfall. In the SRS estuary, the relative evenness of rainfall from mid-2002 through mid-2003 coincided with a muted seasonal pattern in salinity at all estuarine sites and markedly lower [TP]. Salinity responses to the 1998 and 2002–2003 ENSO events were not as strong. Neither ENSO had a dramatic effect on the seasonal patterns at our southern Everglades mangrove sites (TS/Ph-6, -7, and -8), but both events were marked by our lowest peak salinities of record and by shortened high-salinity seasons. In a pattern that paralleled the SRS estuary, the southern Everglades mangrove sites also showed lower [TP] during both ENSO events. Interestingly, salinities in Florida Bay appeared to be largely unaffected by the ENSO events. It appears that, by modifying the timing of rainfall without dramatically affecting total rainfall amounts, ENSO events increase freshwater influence (and decrease the marine influence) in the SRS estuary, but less so in the estuaries of the southern Everglades. This difference is probably a function of basin size. Shark River Slough is a large freshwater wetland basin that focuses freshwater flow into a relatively small estuarine ecotone. In contrast, the Taylor Slough and C-111 basin/ENP Panhandle drainages are much smaller and flow into a large subtidal system—Florida Bay. Variability in rainfall, as with ENSO events, would be expected to have a larger effect on the larger basin—SRS—and this is what our data show.

In this paper, we present up to 8 yr of long-term water quality, climatological, and hydrologic data for 17 locations in Everglades National Park that comprise the sampling network of the Florida Coastal Everglades LTER Program. These data demonstrate the oligotrophic, P-limited nature of this large freshwater–estuarine landscape. The limiting nutrient is supplied to these Everglades estuaries by the Gulf of Mexico, not by upstream sources, and we argue that this upside down estuary phenomenon is a defining characteristic of the Everglades landscape. We present a conceptual model to demonstrate how seasonality of rainfall inputs and the management of canal water inputs control the marine supply of P and, further, hypothesize that seasonal variability in water residence time is a strong driver of water quality through its control on internal biogeochemical processing. ENSO events are an important feature of the neotropical climatological template in south Florida, such that the seasonality of rainfall is largely muted during these events. This ENSO-driven disruption in seasonal rainfall patterns affects salinity patterns and tends to reduce marine inputs of P to Everglades estuaries. Oligotrophic end-member reference sites are important in analyses of how eutrophication phenomena are affecting aquatic ecosystems. We suggest that the Everglades landscape is an excellent low-nutrient reference for syntheses of human effects on biogeochemical cycles in both freshwater and estuarine ecosystems.

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