Estuaries and Coasts: J CERF (2008) 31:204–214
DOI 10.1007/s12237-007-9007-6

Indirect Hurricane Effects on Resource Availability and Microbial Communities in a Subtropical Wetland-Estuary Transition Zone

Clayton J. Williams · Joseph N. Boyer · Frank J. Jochem

Received: 16 May 2007 / Revised: 4 October 2007 / Accepted: 18 October 2007 / Published online: 19 December 2007

Abstract Three sequential hurricanes made landfall over the South Florida peninsula in August and September 2004. The storm systems passed north of the Everglades wetlands and northeastern Florida Bay, but indirect storm effects associated with changes in freshwater discharge during an otherwise drought year occurred across the wetland–estuary transition area. To assess the impacts of the 2004 hurricane series on hydrology, nutrients, and microbial communities in the Everglades wetlands to Florida Bay transition area, results are presented in the context of a seasonal cycle without hurricane activity (2003). Tropical activity in 2004 increased rainfall over South Florida and the study area, thereby temporarily relieving drought conditions. Not so much actual rainfall levels at the study site but more so water management practices in preparation of the hurricane threats, which include draining of an extensive freshwater canal system into the coastal ocean to mitigate inland flooding, rapidly reversed hypersalinity in the wetlands-estuary study area. Although annual discharge was comparable in both years, freshwater discharge in 2004 occurred predominantly during the late wet season, whereas discharge was distributed evenly over the 2003 wet season. Total organic carbon (TOC), ammonium (NH_4^+), and soluble reactive phosphorus (SRP) concentrations increased during the hurricane series to concentrations two to five times higher than long-term median concentrations in eastern Florida Bay. Spatiotemporal patterns in these resource enrichments suggest that TOC and SRP originated from the Everglades mangrove ecotone, while NH_4^+ originated from the bay. Phytoplankton biomass in the bay increased significantly during storm-related freshwater discharge, but declined at the same time in the wetland mangrove ecotone from bloom conditions during the preceding drought. In the bay, these changes were associated with increased nanophytoplankton and decreased picophytoplankton biomass. Heterotrophic bacterial production increased in response to freshwater discharge, whereas bacterial abundance decreased. Hydrochemical and microbial changes were short-lived, and the wetland–bay transition area reverted to more typical oligotrophic conditions within 3 months after the hurricanes. These results suggest that changes in freshwater discharge after drought conditions and during the hurricane series forced the productivity and P-enriched characteristics of the wetland's mangrove ecotone, although only briefly, to the south into Florida Bay.

Keywords Bacteria · Florida Bay · Florida Everglades · Phytoplankton

C. J. Williams · F. J. Jochem (✉)
Marine Biology Program, Florida International University,
3000 N.E. 151st Street,
North Miami, FL 33181, USA
e-mail: frank@jochemnet.de

J. N. Boyer
Southeast Environmental Research Center,
Florida International University,
Miami, FL 33199, USA

Introduction

Hurricanes and episodic storm events are common occurrences to wetland, estuarine, and coastal environments (Mallin et al. 1999; Paerl et al. 2001; Houston and Powell 2003; McKinnon et al. 2003; Davis et al. 2004). However, their impact on resource availability and microbial communities in these ecosystems is quite variable. Ecosystem responses are influenced by the environmental conditions preceding the storm event, magnitude of the event (i.e., duration, wind strength, amount of precipitation, and proximity to ecosystem), and post-storm climatic and environmental conditions (Tilmant et al. 1994; Mallin et al. 1999; Paerl et al. 2001; Davis et al. 2004). Hurricanes can cause catastrophic physical damage at landfall, but their impact is not limited to the areas hit directly. Aquatic systems adjacent to the central storm track can experience indirect hurricane effects, which could stem from increased freshwater discharge, direct precipitation, sediment resuspension, and nutrient loading and from moderate to high wind speeds and physical forcing. Passing near the North Carolina coast, Hurricane Gordon increased wind forcing and resuspended bottom sediments and nutrients, which caused chlorophyll *a* concentrations to increase up to sixfold and bacterial production to increase more than twofold (Fogel et al. 1999). In northeastern Florida Bay, Tropical Storm Harvey and Hurricane Irene induced 60% of annual freshwater inputs from the Everglades within a 4-week period, which carried 65% of annual nitrogen (N) and phosphorus (P) inputs into the bay and induced a short-lived phytoplankton bloom (Davis et al. 2004).

In August and September 2004, three hurricanes (Charley, 08/13/2004, Category (Cat) 4; Frances, 09/04/2004, Cat 2; and Jeanne, 09/26/2004, Cat 3 Saffir–Simpson Hurricane Scale) struck the western and eastern coastlines and Lake Okeechobee regions of Florida, USA. These systems passed to the north of the southeastern Everglades wetlands and Florida Bay, but indirect hurricane impacts were observed. Indirect storm effects originated from widespread inland flooding and rainfall, which altered freshwater discharge patterns to the coastal ocean. This late wet season freshwater discharge ended drought conditions and altered hydrochemistry and microbial communities across the wetland–bay transition area. To address ecosystem impact of 2004 freshwater discharge, field data combined with long-term monitoring data for wetland stations in the southeastern Everglades during 2004 are compared to monitoring data collected during 2003, which lacked hurricane activity. Thereby, this study aims at gauging the impact of freshwater released after drought conditions and during the 2004 hurricane series as compared to a more typical dry–wet season cycle in the wetland–bay transition zone.

Materials and Methods

Study Site and Sampling

Florida Bay is a shallow (<3 m), seasonally hypersaline, oligotrophic estuary bounded to the south and east by the Florida Keys, to the west by the Gulf of Mexico, and to the north by the Everglades wetlands (Fig. 1). Water circulation and lunar tides are restricted throughout much of Florida Bay by biogenic carbonate mudbanks and mangrove islands that compartmentalize the estuary into semi-isolated

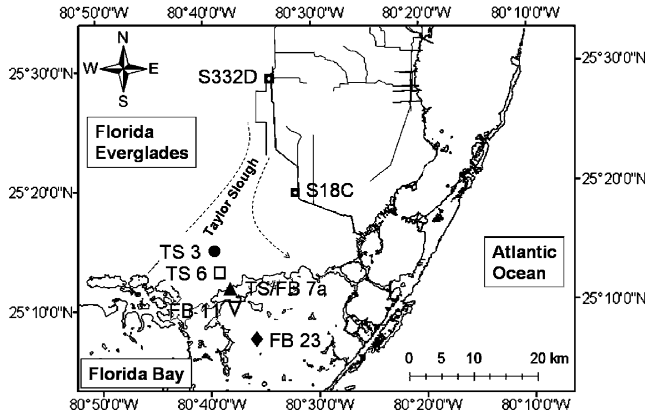

Fig. 1 Map of Florida Everglades and Bay. Sampling stations and canal control structures (S332D and S18C) are indicated

basins (Boyer et al. 1999). P is considered the limiting nutrient throughout the Everglades (wetland and estuary) landscape, and the Gulf of Mexico is an important P source to these ecosystems (Boyer et al. 1999; Noe et al. 2003). The climate is subtropical with a distinct wet (June–November) and dry season (December–May).

Overland freshwater enters Florida Bay in the northeast from the Everglades Taylor Slough/C-111 canal basin, but freshwater flow is not natural. Water is released into this basin by two South Florida Water Management District (SFWMD) canal control pump structures (S332D and S18C; Fig. 1). These structures control water levels in subsequent catchment canals that overflow into the Everglades wetlands. This nutrient-deplete freshwater overflow then flows southwards into Florida Bay through the Taylor Slough basin. The convergence of the P-limited freshwater and marine end-members creates an ecotone dominated by mangrove wetlands and characterized by increased organic matter (OM) production and P availability (Childers et al. 2006).

Conservative mixing models cannot explain the increased P concentrations within the ecotone. P enrichments are suspected to occur through ion exchange and carbonate mineral dissolution within the below aquifer and transport into the ecotone through terrestrial brackish ground water discharge (Price et al. 2006). The resource enrichments associated with the ecotone are more distinct during the dry season when freshwater flow is absent, surface water levels are low, and low-productive marine Florida Bay water enters the mangrove wetlands (Rudnick et al. 1999; Price et al. 2006). When freshwater flow is restored during the wet season, enhanced production and biogeochemical cycles found in the ecotone disappear without observed downstream enrichment in the northeastern bay (Childers et al. 2006). The fate of the P and OM enrichments is not well understood; P and OM could be retained in the ecotone sediments, taken up by local biota, and/or diluted by increased water levels and freshwater delivery (Rudnick et al. 1999; Sutula et al. 2001; Price et al. 2006).

Study sites were located along a 16-km Taylor Slough to Florida Bay transect encompassing the mangrove ecotone; station TS3 was upstream of, TS6 and TS/FB7a within, and FB11 and FB23 downstream of the ecotone (Fig. 1). Study sites corresponded to NSF-Florida Costal Everglades Long-Term Ecological Research (FCE-LTER) monitoring stations (http://fcelter.fiu.edu) TS/Ph 3, TS/Ph 6a, and TS/Ph 7a and Southeast Environmental Research Center (SERC) water quality monitoring stations 11 and 23, respectively (Boyer and Briceño 2006). Samples were collected monthly from January 2003 through April 2004, weekly or monthly from May through July 2004, and monthly from August 2004 through January 2005. Temporal schemes varied because different variables were collected as either part of FCE-LTER and SERC monitoring programs or this project to determine the effects of freshwater discharge on Florida Bay microbial communities.

Water samples were collected from 10 cm below the surface into acid-washed, sample-rinsed polycarbonate or polyethylene bottles kept cool and dark until laboratory processing. Salinity, inorganic and organic nutrient, and chlorophyll *a* concentrations were determined for the complete sampling period and allow comparison of seasonal cycles without (2003) and with (2004) hurricane activity. Bacterial production and flow cytometric analysis of bacterial and phytoplankton abundances (see below) were only determined or methodologically comparable for TS/FB7a, FB11, and FB23 from May 2004 through January 2005. Although temporally limited, these variables serve to evaluate microbial responses to changes in freshwater discharge associated with the 2004 hurricane series.

Analytical Methods

Hourly wind speed and direction measured at C-MAN station MLRF1 located approximately 35 km southeast of the study site were obtained from NOAA's National Data Buoy Center (www.ndbc.noaa.gov). Wind speeds recorded at the Miami International Airport (about 90 km north of the study site) were comparable to those measured at the C-MAN station, suggesting that wind observations at MLRF1 are representative for Taylor Slough and north-eastern Florida Bay. Wind data were converted to a wind stress vector plot using SigmaPlot 8.0 graphics software. Near-surface temperature and salinity were recorded with a YSI 556 MPS probe.

Rainfall and canal discharge flow rates were obtained through the SFWMD online database, DBHYDRO (www.sfwmd.gov), for pump structures S332D and S18C. To calculate local rainfall, daily rainfall at both structures was averaged. Daily mean canal discharge rates were summed for both structures to obtain an estimate of maximum daily flow rate into the Taylor Slough/C-111 canal basin (Rudnick et al. 1999). Combined canal discharge rates can overestimate freshwater flow into Taylor Slough due to recent SFWMD modifications to S332D. S332D pumps water indirectly into Taylor Slough through a catchment canal (L-31W), which overflows into Taylor Slough. Bank overflow from L-31W did not relate well to S332D discharge (Childers et al. 2006), but downstream changes in salinity corresponded to S332D discharge (Fig. 2).

Filtered (Whatman GF/F) water samples were analyzed for ammonium (NH_4^+), nitrate + nitrite (NO_x), and soluble reactive phosphorus (SRP) with an Alpkem RFA 300 flow-injected autoanalyzer using standard colorimetric techniques (Boyer and Briceño 2006). Unfiltered water samples were analyzed for total organic carbon (TOC) and total P. TOC was measured with a Shimadzu TOC-5000 by direct injection onto hot platinum catalyst after acidification to pH<2 and purging with CO_2-free air. Total P was measured by dry ashing and acid hydrolysis (Solorzano and Sharp 1980). Total organic phosphorus (TOP) was calculated as the difference between total and inorganic P.

Chlorophyll *a* (Chl *a*) as a proxy for phytoplankton biomass was extracted in ice-cold 90% acetone from particles collected on GF/F filters from 0.25–1.0 l water samples. Chl *a* extracts were measured with a spectrophotometrically calibrated Turner 111 fluorometer or a Gilford Fluoro IV spectrofluorometer. Pico- and nano-sized phytoplankton (i.e., cell sizes 0.2–2.0 and 2.0–20 μm, respectively) were counted on a Becton-Dickinson FACSort flow cytometer from 1% (final concentration) formalin-preserved water samples within 12 h of collection. Based on cell size (light scatter) and pigment autofluorescence (red chlorophyll

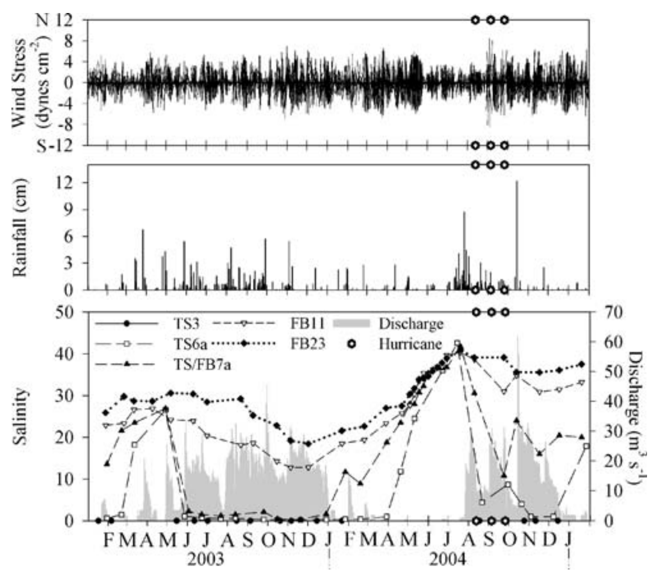

Fig. 2 Time-series of wind stress, average daily rainfall at S332D and S18C, and combined canal discharge from South Florida Water Management District canal pump structures S332D and S18C into the Taylor Slough/C-111 canal basin and salinity (*left*) at Taylor Slough and Florida Bay stations

fluorescence, >650 nm; yellow phycoerythrin fluorescence, 575±25 nm), phytoplankton counts were divided into three subgroups: eukaryotic phytoplankton (EUK), phycocyanin-type cyanobacteria (CYANO), and phycoerythrin-type, *Synechococcus*-like cyanobacteria (SYN). As compared to SYN, CYANO cells were defined by relatively lower yellow fluorescence and higher red fluorescence, although red (chlorophyll) autofluorescence was less than that produced by small eukaryotes. Light scatter spectra (arbitrary units) indicated that relative cell sizes were SYN<CYANO≤EUK. Cell counts were converted to cell concentrations from measurement times and weight-calibrated flow rates (Veldhuis and Kraay 2000).

Bacteria were also counted on a FACSort flow cytometer. One milliliter of formalin-fixed (1% final concentration) sample was incubated for 30 min at 37°C with 0.1 g l^{-1} RNAse (1:1 mix of RNAse A and B) before staining with SYBR Green I (10^{-5} dilution of commercial stock) in the presence of 30 mM potassium citrate (Marie et al. 1997). Cells were counted for 60 s and converted to bacterial abundance based on measurement time and weight calibration of flow rate (0.2 μl s^{-1}; Jochem 2001).

Bacterial biomass production (BP) was measured by ^{3}H-leucine incorporation. Triplicate 10-ml samples and one formalin-fixed control were incubated with 90.9 nM ^{3}H-leucine for 2 or 2.5 h at 21°C. Incubations were stopped by formalin addition (1% final concentration). Samples were filtered onto 0.2-μm polycarbonate filters, rinsed three times with 2 ml of ice-cold 5% trichloroacetic acid, and analyzed by liquid scintillation counting (Giesenhagen et al. 1999; Kirchman 2001). Cell-specific production (fg C $cell^{-1}$ day^{-1}) was calculated from BP (μg C l^{-1} day^{-1}) and bacterial abundance (BAC) using a standard conversion factor of 10 fg C $cell^{-1}$ (Kirchman 2001).

All data were ln-transformed to conform to the assumptions of normality and homogeneity of variance. Significant differences ($p \leq 0.05$) were assessed by analysis of variance; station, month, and canal discharge period were included in the model. Significant factors were examined post hoc by Student–Newman–Keuls to discern how the levels within each factor differed. Pearson's bivariate correlation was used to find significant relationships ($p \leq 0.05$) between variables across stations.

Results

The 2004 hurricane series brought needed moisture upstream of and into the wetland–estuary transition area, which allowed continued freshwater discharge and relieved static drought conditions (Fig. 2). In 2003, South Florida was not affected by a tropical event, and climate patterns were influenced by a moderate El Niño-Southern Oscillation event (Childers et al. 2006). Water temperatures were similar among years, with lowest temperatures (17.1±2.1°C) from December–January and highest temperatures (29.9±1.1°C) from June–September (data not shown). Winds were generally moderate across the study period, but a marked lull in wind stress commenced at the beginning of the 2004 wet season (Fig. 2). Hurricane Charley (8/13/2004) did not disrupt this pattern, but the subsequent storms (Hurricane Frances, 9/04/2004, and Jeanne, 9/26/2004) produced tropical storm force winds across the Taylor Slough/C-111 canal basin. Annual rainfall of 126 cm was higher during 2003 compared to 103 cm in 2004. However, rainfall was well distributed throughout the 2003 wet season but condensed around the tropical activity in 2004, which was otherwise a drought year (Fig. 2). The hurricane series caused 19–72 cm of precipitation within a 6-week span over the south-central Florida peninsula (www.nhc.noaa.gov). This upstream rainfall caused intense inland flooding and increased flow through the SFWMD canal system, which ultimately increased freshwater delivery to the coastal oceans. Combined canal discharge from S332D and S18C reflected temporal rainfall patterns: Near-constant discharge throughout 2003 ceased during the dry season, and discharge was not resumed until 3 weeks before Hurricane Charley (Fig. 2). These freshwater discharge patterns, which followed rainfall, influenced salinity patterns and the spatiotemporal location of the freshwater-marine mixing zone within the study transect.

Salinity along the Taylor Slough to Florida Bay transect fluctuated from fresh or brackish conditions during times of southerly freshwater flow to normal or hypersalinity when marine waters encroached upon the wetlands (Fig. 2). TS3 is unique to the study transect because it is a short-hydroperiod site that dries down completely in the absence of freshwater discharge. When TS3 is dry, marine water penetrates TS6 and TS/FB7a, which creates a biogeochemically active brackish-marine zone within the wetland mangrove ecotone (Childers et al. 2006). During 2003, the period of negative estuarine flow was brief (2 months) and FB and TS stations remained brackish and fresh, respectively, for the remainder of the year (Fig. 2). During 2004, TS3 dry down and negative estuarine flow were more extensive, lasting 4–6 months. Negative estuarine flow and drought conditions equalized salinities between FB and TS stations, which reached hypersalinty of 41.4±1 in July. Hypersalinity at TS stations was reversed rapidly to fresh or brackish conditions with the onset of freshwater discharge (Fig. 2). When freshwater flow was terminated after the hurricane series, salinities returned to normal marine levels at FB23–TS6, and TS3 went dry.

NH_4^+ and SRP were more available during the hurricane series than the preceding dry season (Fig. 3). NH_4^+ concentrations tended to be higher at FB than at TS

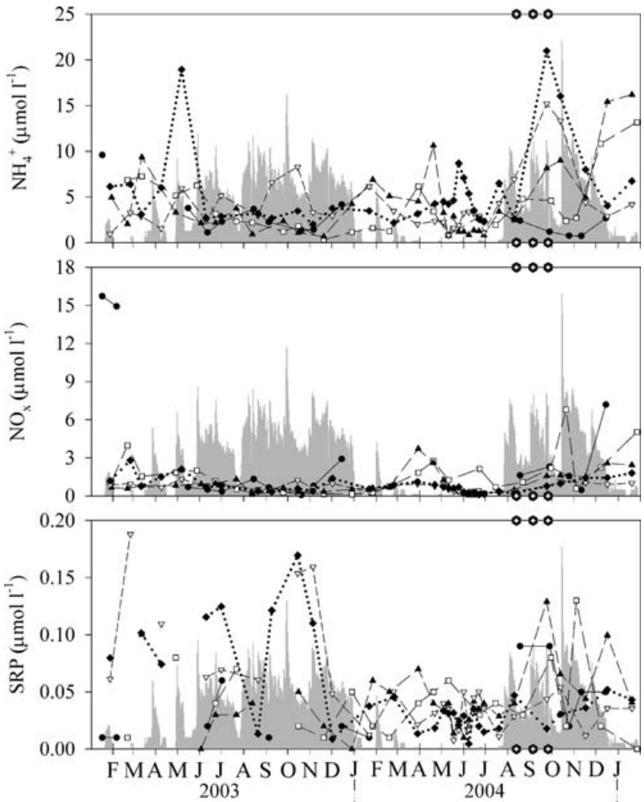

Fig. 3 Time-series of ammonium (NH_4^+), nitrate + nitrite (NO_x), and soluble reactive phosphorus (*SRP*) concentrations. See Fig. 2 for legend

stations, although not statistically significantly (p=0.073). NH_4^+ concentrations lacked a clear temporal pattern but increased significantly during the hurricane series at FB stations ($p<0.001$). These changes were followed by a similar increase in NH_4^+ concentrations within the mangrove ecotone once freshwater discharge was decreased. NO_x concentrations were highest at TS stations during the 2003 dry and late 2004 wet seasons ($p<0.001$), but high NO_x concentrations during the 2004 wet season were unrelated to the hurricane series and freshwater discharge (Fig. 3). NO_x concentration in Florida Bay did not vary much over time. SRP concentrations varied between 2003 and 2004 (Fig. 3). During 2003, relatively high SRP concentrations at FB11 and FB23 contrasted more typical, low concentrations at TS stations. From the beginning of the 2004 dry season, SRP concentrations remained low across the study area until shortly after Hurricane Charley when they increased at TS stations (Fig. 3). The spatial distribution of SRP was opposite to that of NH_4^+ during the hurricane series, i.e., higher SRP concentration at TS than FB stations. These patterns suggest that freshwater discharge after drought conditions and during the hurricane series affected nutrient cycles at TS and FB stations differently, whereas the intermediate station, TS/FB7a, experienced both increased SRP and NH_4^+ availability.

TOC concentrations were significantly higher at TS than FB stations and during the wet than the dry season at all stations ($p<0.001$; Fig. 4). During the hurricane series, TOC concentrations were significantly higher ($p<0.001$) than during pre- or post-hurricane conditions. In fact, TOC concentrations were the highest recorded at TS3–TS/FB7a among the 4-year LTER dataset (May 2001–May 2005; D. L. Childers unpublished data). TOC increases were less pronounced at FB11 and not evident at FB23 (Fig. 4). Changes in TOC concentration were short-lived, and concentrations were typical of late wet season values 3 months after the hurricane series.

Within the mangrove ecotone, increased TOP concentrations were evident during the late dry seasons of 2003 and 2004. TOP concentrations were highest at TS6 and TS/FB7a and lowest at TS3 ($p<0.001$) where seasonal TOP enrichments were not observed (Fig. 4). In 2003, TOP concentrations declined in the mangrove ecotone when freshwater was discharged, but TOP did not increase downstream at FB11 and 23. However, in conjunction with the hurricane series, subtle increases in TOP were observed at FB11 and FB23, suggesting that P was released from the ecotone into Florida Bay. In concert with changes in inorganic nutrients, hurricane-related and drought-ending freshwater discharges led to an overall increase in C, N, and

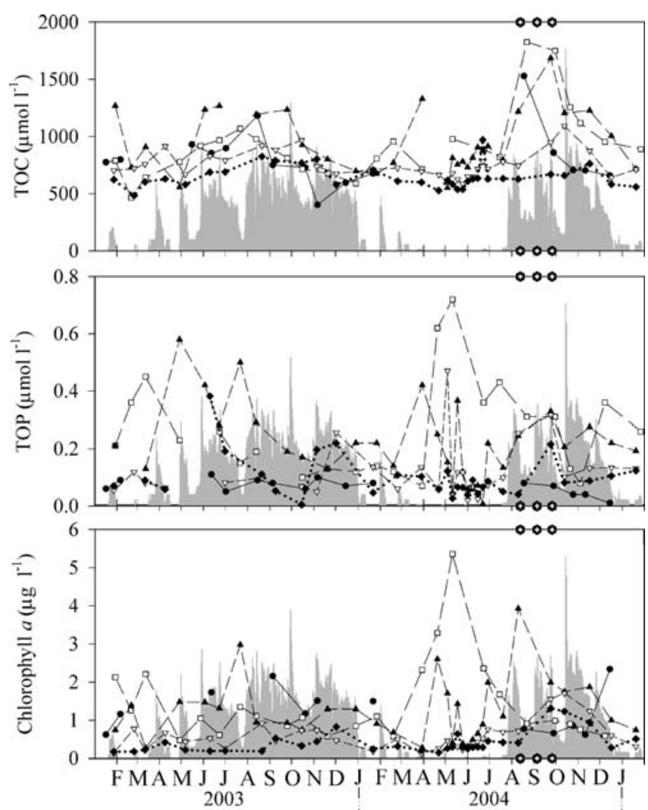

Fig. 4 Time-series of total organic carbon (*TOC*), total organic phosphorus (*TOP*), and chlorophyll *a* concentrations. See Fig. 2 for legend

P availability across the study area, although the sources of these enrichments differed.

The transition from higher P concentrations in the mangrove ecotone to higher P concentrations in Florida Bay was accompanied by increased phytoplankton biomass and changes in phytoplankton community composition at FB stations (Figs. 4 and 5). Chl *a* concentrations were higher at TS3–TS/FB7a than at FB11 and FB23 ($p<0.001$). Chl *a* correlated significantly ($p\leq0.05$) with TOP ($r=0.57$),

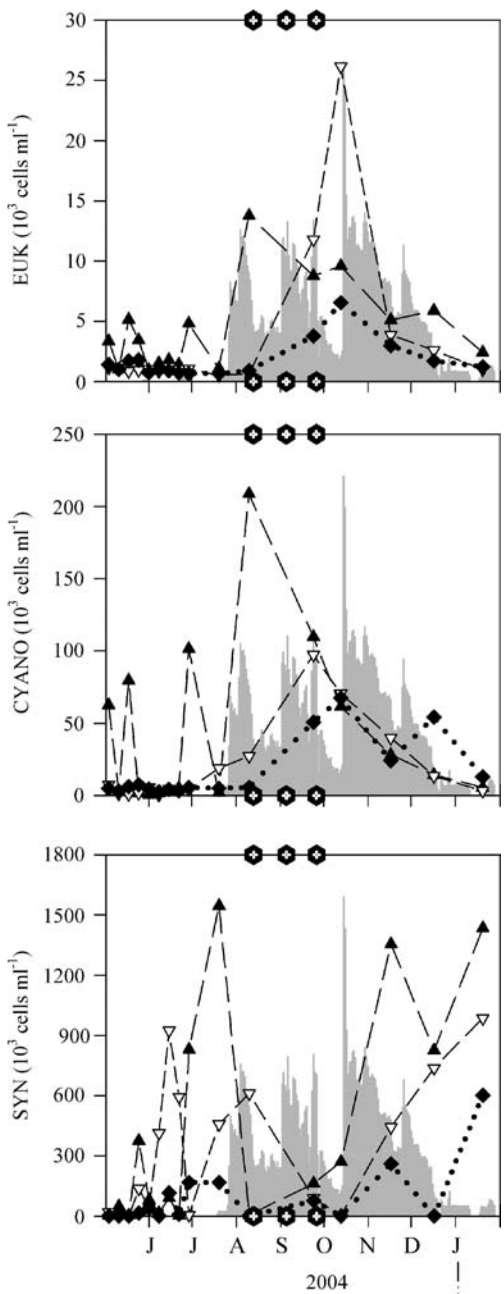

Fig. 5 Time-series of flow cytometry-determined phytoplankton populations of eukaryotic algae (*EUK*), phycocyanin-type cyanobacteria (*CYANO*), and phycoerythrin-type cyanobacteria (*SYN*). See Fig. 2 for legend

but not with SRP ($r=-0.06$). In 2003, the regional peak in Chl *a* concentrations formed only weakly within the mangrove ecotone and declined with increased freshwater discharge without impacting Chl *a* concentrations downstream. During the prolonged 2004 dry season, a distinct phytoplankton bloom occurred at TS6. The bloom was short-lived and had mostly declined by the end of the drought period. With the onset of freshwater discharge, another phytoplankton bloom occurred at TS/FB7a. With continued discharge during the hurricane series, Chl *a* subsequently increased at FB11 and FB23 (Fig. 4). These biomass increases corresponded to a shift in phytoplankton community structure towards larger cells within the pico- and nanophytoplankton size fractions analyzed by flow cytometry at FB stations (TS/FB7a–FB23). EUK and CYANO abundances increased significantly during the hurricane series ($p<0.001$), whereas smaller-sized SYN abundance was low (Fig. 5). Phytoplankton community composition correlated significantly ($p\leq0.05$) with TOP ($r=0.35$ for EUK and 0.53 for CYANO) and SRP ($r=0.38$ for EUK and 0.32 for CYANO). These results suggest that phytoplankton biomass and composition were at least partly regulated by P availability.

BP and bacterial cell-specific production more than doubled in Florida Bay with the onset of freshwater discharge and the end of the drought period, but BAC did not increase accordingly (Fig. 6). BAC and BP were highest at TS/FB7a and decreased significantly ($p<0.001$) away from the wetlands. However, bacterial cell-specific production was comparable among all FB stations. In 2004, during freshwater discharge into the Taylor Slough/C-111 basin, BAC decreased significantly at TS/FB7a and FB11 ($p=0.005$). At FB23, BAC remained unaffected by freshwater discharge and the associated hydrochemical changes. Before freshwater release, BP and cell-specific production increased with ambient water temperature, which peaked in July. When freshwater was discharged into Florida Bay, BP and cell-specific production increased significantly ($p<0.001$) and remained increased at bayward stations throughout the study period (Fig. 5). Given these temporal trends, BAC did not correlate with inorganic and organic nutrient increases associated with the hurricane-related freshwater discharges. BAC was only weakly related to Chl *a*. However, BP correlated positively and significantly ($p\leq0.05$) with resource increases ($r=0.29$ for NH_4^+, 0.50 for NO_x, 0.35 for SRP, 0.58 for TOC, and 0.44 for TOP). Similarly, BP and cell-specific production were significantly related to changes in phytoplankton biomass and composition. These results support distinct increases in autotrophic and heterotrophic activity and shifts in pico- and nanoplankton community structure during drought-ending freshwater discharges, which corresponded to changes in resource availability.

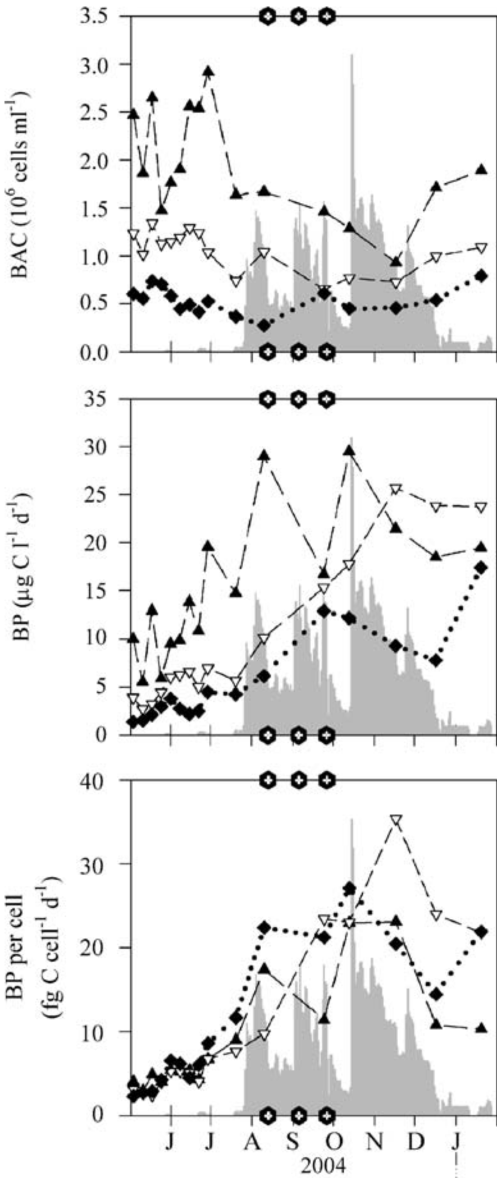

Fig. 6 Time-series of bacterial abundance (*BAC*), bacterial production (*BP*), and BP per cell. See Fig. 2 for legend

Discussion

In 2004, three sequential hurricanes made landfall north of the Everglades/Florida Bay wetland–estuary transition area where they relieved preceding drought conditions and caused inland flooding. Along the study transect in the Everglades–Florida Bay ecotone area, though, only light rains and moderate wind stress were recorded. Hurricane-related freshwater import was, therefore, not so much the result of local rainfall over the study area but of upstream water management practices involving drainage of flood mitigation canals before and during the hurricane events. The timing, rather than the magnitude, of the storm events and of SFWMD canal system-dependent freshwater discharge initiated observed biogeochemical responses across the Taylor Slough to Florida Bay transect.

Drought conditions persisted in the study area, which did not receive a significant rain event until 2 weeks before the hurricane series (Fig. 2). Under drought conditions, marine hypersaline water encroached upon the wetlands, helping to form a pronounced area of increased total P and phytoplankton biomass within the wetland mangrove ecotone. With the onset of freshwater discharge and hurricane activity, these high levels of P and production within the ecotone were forced south into northeastern Florida Bay. During the hurricane series, resource availability, predominantly in terms of C and P, increased and nutrient cycles seemed altered. Changes in resource availability were associated with a trophic shift within the northeastern Florida Bay microbial community. Nanophytoplankton populations increased significantly with increased P (the assumed limiting nutrient), whereas picophytoplankton and heterotrophic bacteria abundances declined. The biogeochemical response to freshwater discharge within the wetland–estuary transition area is discussed in relation to drought conditions and hurricane activity, which, together, caused an atypical biogeochemical response to freshwater discharge within the mangrove ecotone and northeastern Florida Bay as compared to typical wet seasons with evenly distributed freshwater flow.

Hurricanes are associated with strong winds (≥33 m s^{-1}) around their center of circulation, which diminish outwardly. Over the study area, maximum sustained wind speeds for Hurricane Frances, the strongest of the three 2004 storms, reached 22 m s^{-1}, comparable to Topical Storm Gordon (1994; Pitts 2001) and Hurricane Irene (Cat 1, 1999; Davis et al. 2004) with maximum sustained winds of 20 m s^{-1} and ≤27 m s^{-1}, respectively. During these tropical events, water clarity was not affected at TS6 through FB11, a pattern apparently typical of hurricane impacts and freshwater discharges to the Everglades–Florida Bay ecosystem (Roman et al. 1994; Tilmant et al. 1994; Davis et al. 2004; J. N. Boyer unpublished data). Similar to wind stress, freshwater discharge rates and precipitation were low to moderate during the 2004 hurricane series. Total freshwater discharge into the Taylor Slough/C-111 canal basin was comparable in 2003 and 2004. Discharge rates were approximately half the average daily rates recorded for Hurricane Irene (1999) and Hurricane Katrina (2005), which caused direct precipitation over the study area. Still, the 2004 hurricane series impacted the wetland–estuary transition area indirectly by disrupting drought and hypersaline conditions across the transition area and promoting the release of greater than historical freshwater discharge volumes during drought.

The Everglades and Florida Bay are rain-fed systems, although natural freshwater sheet flow has been replaced by a point source delivery system regulated by SFWMD canal discharge and annual rainfall amount. Little freshwater is released by SFWMD canal control stations into the Taylor Slough/C-111 canal basin when rainfall is ≤100 cm (Rudnick et al. 1999). The year 2004 was a dry year (103 cm of rainfall), although annual freshwater discharge was higher than discharge volumes reported for years with similar annual precipitation (100–110 cm; Rudnick et al. 1999). The timing and continued release of freshwater discharge by SFWMD management in preparation and response to hurricane activity changed the temporal distribution and volume of annual freshwater discharge in 2004. Eighty-three percent of annual discharge was released from August–November 2004, as compared to 57% for the same time period in 2003 (Fig. 2). Beginning with the initial 2004 wet season rainfall and freshwater discharge, prolonged negative estuarine flow reversed. During the hurricane series, hypersalinity was relieved across the study area, and the wetland–marine mixing zone shifted southwards, creating a distinct salinity gradient (Fig. 2). Together, drought conditions and hurricane activity heightened the impact of freshwater discharge on biogeochemical cycles within the wetland–estuary study area.

In contrast to 2003, initial freshwater discharges in 2004 enhanced resource availability along the Taylor Slough–Florida Bay transect (Figs. 3 and 4). OM and nutrient concentrations at LTER monitoring stations located immediately south of SFWMD canal control structures S332D and S18C remained unchanged during the 2004 hurricane series and did not increase with freshwater discharge (D. L. Childers unpublished data). This indicates that OM and P were produced locally and/or regenerated in Taylor Slough and the mangrove ecotone during the drought period. With the onset of freshwater discharge and positive estuary flow, these resources were transported towards Florida Bay. This downstream transfer of resources from the ecotone is unexpected in the study area. In most years, including 2003, resource enhancements evident during the dry season are retained within the ecotone when freshwater flow is restored (Childers et al. 2006). Close examination of the SERC long-term data set revealed that spatiotemporal nutrient, OM, and Chl *a* increases are generally not observed at FB11 and FB23 during the dry-wet season transition and initial freshwater discharges. Generally, the stochastic processes associated with the formation, maintenance, and dissolution of the productive and P-enriched zone within the mangrove ecotone are not transferable to Florida Bay, but 1999 and 2004 were exceptions to this rule.

Hurricane Irene (1999) caused increases in SRP and OM concentrations at TS stations and a two to fourfold increase in NH_4^+ and SRP concentrations at FB11 (Davis et al. 2004; Boyer and Briceño 2006). During the 2004 hurricane series, TOC, NH_4^+, and SRP concentrations were two to five times higher than long-term median concentrations for eastern Florida Bay (Boyer et al. 1999). Freshwater discharge during both hurricane series forced the OM and nutrient enrichments associated with the mangrove ecotone southwards into Florida Bay, and NH_4^+ cycles were altered. Interpretation of the 2004 hurricane series, however, is complicated by the preceding drought conditions. The prolonged dry period in 2004 delayed the normal dry–wet season transition. This delay alone could be sufficient to alter biogeochemical cycles associated with freshwater release into the wetland–estuary transition area. However, without the increased moisture associated with the high tropical activity of 2004, rainfall levels would not have been sufficient to relieve drought conditions, as freshwater discharge would have been low. Thus, late and temporarily concentrated wet season freshwater discharge caused by the hurricanes triggered enhanced biogeochemical responses in the wetland–estuary study area.

The prolonged drought conditions preceding freshwater discharge created conditions that facilitated the accumulation of detrital OM. When the wetland and mangrove forest are dry, OM decomposition is slowed, and OM builds on the forest floor. Once inundated, senesced dwarf red mangrove (*Rhizophora mangle*) leaves leached approximately 1.9 and 39 mmol TOC per gram dry weight leaf tissue within the first day and 21 days, respectively (Davis et al. 2006). Hurricane Irene (1999), which caused similar wind forcing as Hurricane Frances, doubled leaf litter production in the mangrove ecotone (Davis et al. 2004). Fresh red mangrove leaves leach significant amounts of C, N, and P into the water during the first 30 days of leaf fall (Davis et al. 2003a; Scully et al. 2004). The 2004 hurricane series likely produced new leaf liter and contributed to the already high OM load that amassed during the preceding drought. Hence, leaching can explain the historically high TOC concentrations observed in Taylor Slough, of which >90% were dissolved organic carbon, and in part increased P availability (Fig. 4). In addition, surface sediments in the mangrove ecotone contain a higher fraction of OM and non-refractory P than Florida Bay sediments (Koch et al. 2001). Rapid salinity decreases, and enhanced OM production during initial freshwater discharge can alter physical and chemical interactions in the carbonate sediments, which facilitate benthic release of OM and P into the water column (Froelich 1988; Davis et al. 2003b).

Contrary to OM and P, NH_4^+ originated from Florida Bay and was transported northwards up the estuary/wetland transition as freshwater flow ceased and salinity recovered (Figs. 2 and 3). After sequential hurricane disturbance, elevated NH_4^+ concentrations in Pamlico Sound did not correlate with salinity and were attributed to hypoxic conditions and mineralization of organic nitrogen inputs (Peierls et al. 2003). Significantly increased water column NH_4^+ concentrations across Florida Bay in 1998 were attributed to wind-driven resuspension by Hurricane Georges (J. N. Boyer unpublished data). However, neither of these mechanisms fit the 2004 hurricane series, which was not associated with hypoxia nor significantly increased suspended sediments. Mangrove communities surrounding the study area have been suggested as an important source of NH_4^+ to the water column (Fourqurean et al. 1993), but hydrological and nutrient conditions during the 2004 hurricane series were more favorable for mangrove sediment net uptake of NH_4^+ from the water column than net export of NH_4^+ into the water column (Davis et al. 2003b).

Observed increases in NH_4^+ concentrations during the hurricane period appear more linked to microbial NH_4^+ regeneration because of the activity of and structural changes within the pelagic microbial food web. Microbial regeneration of NH_4^+ was not measured directly, and little is currently known about the importance of this mechanism to N cycling in Florida Bay. However, microbial water column NH_4^+ regeneration balanced water column NH_4^+ uptake rates in five out of eight experiments across Florida Bay in August 2004 and January 2005 (W. S. Gardner and M. J. McCarthy, unpublished data), indicating the significance of microbial NH_4^+ regeneration in the bay. Enhanced bacterial production and high aminopeptidase activities and substrate affinities (Williams and Jochem 2006) point to bacterial NH_4^+ regeneration from allochthonous wetland-derived OM, as has been documented for the upper Mississippi River plume (Jochem et al. 2004). Observed phytoplankton blooms and leachates provided dissolved OM to enhance bacterial NH_4^+ regeneration. These nanophytoplankton blooms likely stimulated increased nano- and microzooplankton grazing (Lavrentyev et al. 1998, F. J. Jochem and P. J. Lavrentyev, unpublished data), which, in turn, contributed to enhanced water column NH_4^+ regeneration.

In conjunction with resource enhancements, increased phytoplankton biomass is reported frequently after episodic events (Tilmant et al. 1994; Paerl et al. 2001; McKinnon et al. 2003). However, effects on pelagic heterotrophic bacterial communities, aside from nuisance forms, have been largely overlooked (Fogel et al. 1999; Mallin et al. 1999; Burkholder et al. 2004). In Pamlico Sound, Chl *a* increased three to five fold from pre-storm concentrations after a hurricane series (Paerl et al. 2001). These increases in phytoplankton biomass were caused by relieved nutrient limitation imposed by N, but impacts on heterotrophic bacteria were not assessed (Peierls et al. 2003). In the present study, Chl *a* and BP increased significantly at FB sites in association with the hurricane-related freshwater inflow, but BAC decreased (Figs. 4 and 6). These patterns indicate that changes in resource availability altered the pelagic microbial food web. Previously, an episodic wind event in Florida Bay introduced benthic resources (C, N, and P) into the water column, which initially stimulated pelagic heterotrophy followed by autotrophy once light limitation caused by resuspended solids was removed (Lawrence et al. 2004). During the initial freshwater discharge of 2004, the water column remained optically clear, which would have allowed phytoplankton to compete successfully with bacteria for introduced nutrients.

Nanophytoplankton (CYANO and EUK) were able to outcompete picophytoplankton (SYN) and possibly heterotrophic bacteria for introduced nutrients when freshwater was initially released in 2004 (Figs. 3, 5 and 6). In oligotrophic systems, nutrient increase can shift phytoplankton community composition towards larger phytoplankton (Jacquet et al. 2002; Samuelsson et al. 2002). For example, in a coastal Baltic Sea mesocosom study, N and P addition caused diatoms to dominate over heterotrophic and autotrophic bacteria, which prevailed in control treatments (Samuelsson et al. 2002). Severe flooding of south Jamaica enriched the Hellshire coastal ocean with N and P, which caused significant increases in nanophytoplankton and a suppression of picophytoplankton (Webber et al. 1992). Similarly, CYANO and EUK nanophytoplankton populations were favored with freshwater discharge when resources were more abundant during the 2004 hurricane series.

The change towards larger phytoplankton (within the pico- and nanoplankton size range) and reduction of SYN during initial freshwater discharge and hurricane events support a trophic shift towards increased bacterivory. Bacteria and cyanobacteria abundances were highly correlated with those of heterotrophic nanoflagellates and oligotrich ciliates in Florida Bay (Lavrentyev et al. 1998). Competitive reduction of *Synechococcus* spp. abundance could increase the relative predation on heterotrophic bacteria (Jacquet et al. 2002). In the present study, bacteria increased production in response to newly available resources with freshwater discharge, but abundance decreased concurrently with SYN. Increased nano- and microzooplankton grazing on bacteria in response to decreased SYN availability and dominance of larger phytoplankton under higher nutrient availability can explain the observed dynamics. Bacterivory rates in Florida Bay exceeded or matched bacterial growth rates when P was more available (C. J. Williams, unpublished data). These results indicate that bacteria can maintain high production rates when stimulated by resource enrichments, whereas bacterial abundance is controlled by top-down grazing pressure. The hypothesized trophic shift towards increased bacterivory and larger phytoplankton when OM and P were more available during the initial freshwater discharge was, however, short-lived (Figs. 4, 5 and 6). With continued freshwater discharge, microbial community structure returned to pre-discharge patterns.

Hurricane activity is predicted to increase over the next decade, and climate patterns are currently in flux. Studying the short- and long-term biogeochemical impacts of these pulse and press forces will allow a better understanding of the conditions that cause boundary ecosystems (ecotone areas) to retain or release their characteristic resource and production enrichments. In this study, pulsed freshwater discharge after drought conditions and during the hurricane series forced nutrient and organic matter enrichments in the mangrove ecotone southwards into northeastern Florida Bay. These enrichments stimulated nanoplankton and increased bacterivory, which enhanced NH_4^+ cycling in the bay. Under normal dry–wet season transitions, similar enrichment releases from the ecotone and biogeochemical responses are not observed with freshwater discharge. In 2004, drought conditions preceding the pulsed freshwater inflow enhanced biogeochemical cycles within the mangrove ecotone and the OM and P release into Florida Bay upon hurricane-related freshwater discharge. Current long-term environmental monitoring programs in the Everglades and Florida Bay should allow for the observation of multiple episodic events of varying intensities and under different climatic presses. This will enable the mechanisms and meteorological conditions that govern retention or release of resource enrichments within and from the ecotone area to be resolved.

Acknowledgments We thank Daniel L. Childers, Evelyn E. Gaiser, the NSF-FCE-LTER, SERC, and SFWMD for long-term data and logistical and laboratory assistance. We also thank the Florida Institute of Oceanography's Florida Keys Marine Lab for boat transport. This research was funded by NOAA COP grant NA04NOS4780020 and by the NSF LTER under NSF grant 9910514. This is contribution 370 of the Southeast Environmental Research Center at Florida International University.

References

Boyer, J.N. and H.O. Briceño. 2006. FY2005 Annual report of the water quality monitoring project for the Florida Keys national marine sanctuary. EPA Agreement #X994621-94-0. SERC Tech. Report T-327. http://serc.fiu.edu/wqmnetwork/Report%20Archive/2005CWQMN.pdf.

Boyer, J.N., J.W. Fourqurean, and R.D. Jones. 1999. Seasonal and long-term trends in the water quality of Florida Bay (1989–1997). *Estuaries* 22:417–430.

Burkholder, J., D. Eggleston, H. Glasgow, C. Brownie, R. Reed, G. Janowitz, M. Posey, G. Melia, C. Kinder, R. Corbett, D. Toms, T. Alphin, N. Deamer, and J. Springer. 2004. Comparative impacts of two major hurricane seasons on the Neuse River and western Pamlico Sound ecosystems. *Proceedings of the National Academy of Sciences* 101:9291–9296.

Childers, D.L., J.N. Boyer, S.E. Davis, C.J. Madden, D.T. Rudnick, and F.H. Sklar. 2006. Relating precipitation and water management to nutrient concentrations in the oligotrophic "upside-down" estuaries of the Florida Everglades. *Limnology and Oceanography* 51:602–616.

Davis, S.E., C. Coronado-Molina, D.L. Childers, and J.W. Day. 2003a. Temporally dependent C, N, and P dynamics associated with decay of *Rhizophora mangle* L. leaf litter in oligotrophic mangrove wetlands of the southern Everglades. *Aquatic Botany* 75:199–215.

Davis, S.E., D.L. Childers, J.W. Day, D.T. Rudnick, and F.H. Sklar. 2003b. Factors affecting the concentration and flux of materials in two southern Everglades mangrove wetlands. *Marine Ecology Progress Series* 253:85–96.

Davis, S.E., J.E. Cable, D.L. Childers, C. Coronado-Molina, J.W. Day, C.D. Hittle, C.J. Madden, E. Reyes, D. Rudnick, and F. Sklar. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida gulf coast estuary. *Journal of Coastal Research* 20:1198–1208.

Davis, S.E., D.L. Childers, and G.B. Noe. 2006. The contribution of leaching to the rapid release of nutrients and carbon in the early decay of wetland vegetation. *Hydrobiologia* 569:87–97.

Fogel, M.L., C. Aguilar, R. Cuhel, D.J. Hollander, J.D. Willey, and H.W. Paerl. 1999. Biological and isotopic changes in coastal waters induced by Hurricane Gordon. *Limnology and Oceanography* 44:1359–1369.

Fourqurean, J.W., R.D. Jones, and J.C. Zieman. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA—inferences from spatial distributions. *Estuarine Coastal and Shelf Science* 36:295–314.

Froelich P.N. 1988. Kinetic control of dissolved phosphate in natural rivers and estuaries: A primer on the phosphate buffer mechanism. *Limnology and Oceanography* 33:649–668.

Giesenhagen, J.C., A.E. Detner, J. de Wall, A. Weber, R.R. Gradinger, and F.J. Jochem. 1999. How are Antarctic planktonic microbial food webs and algal blooms affected by melting of sea ice? Microcosm studies. *Aquatic Microbial Ecology* 20:183–201.

Houston, S.H. and M.D. Powell. 2003. Surface wind fields for Florida Bay hurricanes. *Journal of Coastal Research* 19:503–513.

Jacquet, S., H. Havskum, T.F. Thingstad, and D. Vaulot. 2002. Effects of inorganic and organic nutrient addition on a coastal microbial community (Isefjord, Denmark). *Marine Ecology Progress Series* 228:3–14.

Jochem, F.J. 2001. Morphology and DNA content of bacterioplankton in the northern Gulf of Mexico: analysis by epifluorescence microscopy and flow cytometry. *Aquatic Microbial Ecology* 25:179–194.

Jochem, F.J., M.J. McCarthy, and W.S. Gardner. 2004. Microbial ammonium cycling in the Mississippi River plume during the drought spring of 2000. *Journal of Plankton Research* 26:1265–1275.

Kirchman, D.L. 2001. Measuring bacterial biomass production and growth rates from leucine incorporation in natural aquatic environments. In *Methods in microbiology, volume 30*, ed. J.H. Paul, 227–237. London: Academic.

Koch, M.S., R.E. Benz, and D.T. Rudnick. 2001. Solid-phase phosphorus pools in highly organic carbonate sediments of northeastern Florida Bay. *Estuaries, Coastal and Shelf Science* 52:279–291.

Lavrentyev, P.J., H.A. Bootsma, T.H. Johengen, J.F. Cavaletto, and W.S. Gardner. 1998. Microbial plankton response to resource limitation: Insight from the community structure and seston stoichiometry in Florida Bay, USA. *Marine Ecology Progress Series* 165:45–57.

Lawrence, D., M.J. Dagg, H. Liu, S.R. Cummings, P.B. Ortner, and C. Kelble. 2004. Wind events and benthic-pelagic coupling in a shallow subtropical bay in Florida. *Marine Ecology Progress Series* 266:1–13.

Mallin, M.A., M.H. Posey, G.C. Shank, M.R. McIver, S.H. Ensign, and T.D. Alphin. 1999. Hurricane effects on water quality and benthos in the Cape Fear Watershed: Natural and anthropogenic impacts. *Ecological Applications* 9:350–362.

Marie, D., F. Partensky, S. Jacquet, and D. Vaulot. 1997. Enumeration and cell cycle analysis of natural populations of marine picoplankton by flow cytometry using nucleic acid stain SYBR Green I. *Applied and Environmental Microbiology* 63:186–193.

McKinnon, A.D., M.G. Meekan, J.H. Carleton, M.J. Furnas, S. Duggan, and W. Skirving. 2003. Rapid changes in shelf waters and pelagic communities on the southern Northwest Shelf, Australia, following a tropical cyclone. *Continental Shelf Research* 23:93–111.

Noe, G.B., L.J. Scinto, J. Taylor, D.L. Childers, and R.D. Jones. 2003. Phosphorus cycling and partitioning in an oligotrophic Everglades wetland ecosystem: A radioisotope tracing study. *Freshwater Biology* 48:1993–2008.

Paerl, H.W., J.D. Bales, L.W. Ausley, C.O. Buzzelli, L.B. Cowder, L. A. Eby, J.M. Fear, M. Go, B.L. Peierls, T.L. Richardson, and J.S. Ramus. 2001. Ecosystem impacts of three sequential hurricanes (Dennis, Floyd, and Irene) on the United States' largest lagoonal estuary, Pamlico Sound, NC. *Proceedings of the National Academy of Sciences* 98:5655–5660.

Peierls, B.L., R.R. Christian, and H.W. Paerl. 2003. Water quality and phytoplankton as indicators of hurricane impacts on a large estuarine ecosystem. *Estuaries* 26:1329–1343.

Pitts, P.A. 2001. Interactions between Florida Bay and Atlantic shelf waters in response to Tropical Storm Gordon. *Estuarine, Coastal and Shelf Science* 52:225–235.

Price, R.M., P.K. Swart, and J.W. Fourqurean. 2006. Coastal groundwater discharge—An additional source of phosphorus for the oligotrophic wetlands of the Everglades. *Hydrobiologia* 569:23–36.

Roman, C.T., N.G. Aumen, J.C. Trexler, R.J. Rennema, W.F. Loftus, and M.A. Soukup. 1994. Hurricane Andrew's impact on freshwater resources. *Bioscience* 44:247–255.

Rudnick, D.T., Z. Chen, D.L. Childers, J.N. Boyer, and T.D. Fontaine. 1999. Phosphorus and nitrogen inputs to Florida Bay: The importance of the Everglades watershed. *Estuaries* 22:398–416.

Samuelsson, K., J. Berglund, P. Haecky, and A. Andersson. 2002. Structural changes in an aquatic microbial food web caused by inorganic nutrient addition. *Aquatic Microbial Ecology* 29: 29–38.

Scully, N.M., N. Maie, S.K. Dailey, J.N. Boyer, R.D. Jones, and R. Jaffé. 2004. Early diagenesis of plant-derived dissolved organic matter along a wetland, mangrove, estuary ecotone. *Limnology and Oceanographgy* 49:1667–1678.

Solorzano, L. and J.H. Sharp. 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. *Limnology and Oceanography* 25:754–758.

Sutula, M., J.W. Day, J. Cable, and D. Rudnick. 2001. Hydrological and nutrient budgets of freshwater and estuarine wetlands of Taylor Slough in southern Everglades, Florida (U.S.A.). *Biogeochemisrty* 56:287–310.

Tilmant, J.T., M.B. Robblee, D. Smith, R.W. Snow, and H. Wanless. 1994. Hurricane Andrew's effects on marine resources. *Bioscience* 44:230–237.

Veldhuis, M.J.W. and G.W. Kraay. 2000. Application of flow cytometry in marine phytoplankton research: Current applications and future perspectives. *Scientia Marina* 64:121–134.

Webber, D.F., M.K. Webber, and J.C. Roff. 1992. Effects of flood waters on the planktonic community of the Hellshire Coast, southeastern Jamaica. *Biotropica* 24:362–374.

Williams, C.J. and F.J. Jochem. 2006. Ectoenzyme kinetics in Florida Bay: Implications for bacterial carbon source and nutrient status. *Hydrobiologia* 569:113–127.