1 **Seasonal differences and response to a tropical storm reflected in diatom assemblage changes in a**
2 **southwest Florida watershed**

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25
26 **Abstract**

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28 Because estuaries are dynamic on many temporal scales, it is difficult to differentiate
29 long-term shifts from those resulting from erratic pulse events like severe storms. Diatoms are
30 abundant and diverse in estuaries, and may characterize these dynamics across relevant time
31 scales. The climate of south Florida is subtropical, with dry winters and wet summers that may
32 also harbor tropical storms and cyclones. We investigated whether these repeated seasonal
33 drivers of change in estuaries differ from the influence of tropical cyclones on planktonic and
34 benthic diatom assemblages. Diatom assemblages and environmental parameters were measured
35 in the Charlotte Harbor watershed of southwest Florida to identify differences between the wet

and dry seasons and changes that occurred following Tropical Storm Debby in 2012. Indicator taxa that were significantly affiliated with each season and post-storm conditions were identified. Diatom assemblages across the watershed were similar in wet and dry seasons, but differences increased following the tropical storm. The reduction in community dispersion following the storm was pronounced in each of the major drainages of the estuary. There were spatially-distinct responses of diatoms to environmental changes driven by the storm. These results suggest that past storm activity could be detected using diatoms preserved in estuarine sediments using both single indicator-species as well as community approaches.

Keywords: diatom assemblages; disturbance; seasonal dynamics; tropical cyclones; dispersion

1. Introduction

Estuaries are highly dynamic on many spatial and temporal scales, changing in response to tides, seasonal hydrological and biological patterns, multidecadal climate and land use changes, as well as erratic storms and other pulse events. Distinguishing effects of unpredictable events from cyclical patterns in such dynamic systems can be challenging but important in order to predict the influence of altered press and pulse drivers in the face of climate change (Angeler and Moreno, 2007; Glasby and Underwood, 1996). Estuarine algal communities respond to and influence estuarine dynamics on all scales, but because they respond relatively quickly to fluctuating drivers, their communities may be useful sentinels of event-based ecosystem impacts on a changing backdrop of drivers. In aquatic systems, diatom assemblages generally have

strong relationships with environmental conditions and rapidly respond to change due to their short generation times (Battarbee, 1986). Different diatom assemblages may therefore characterize changes driven by large-scale cycles such as the El Niño Southern Oscillation (Bull et al., 2000; Lange et al., 1987), seasonal changes such as the onset and intensity of monsoon season (Zong et al., 2006), and pulse events like tsunamis and hurricanes (Hemphill-Haley 1996; Parsons 1998).

Competitive dynamics among diatom taxa are expected to be relatively stable during times of little environmental change, given the homogeneity of the habitat and expected similarity in resource requirements (Hutchinson, 1961). However, environmental homogeneity is dynamic both spatially and temporally, which allows taxa to coexist in diverse assemblages (Descamps-Julien and Gonzalez, 2005; Hutchinson, 1961; Powell and Richerson, 1985). As environmental conditions fluctuate, the tolerance ranges and optima of different taxa can be exceeded or shift, causing changes to the relative abundance of diatom taxa present. In this study, we examine diatom assemblages in a coastal southwest Florida watershed during different seasons and following a tropical storm to investigate the magnitude and direction of change in the assemblages and their relationships with changing environmental conditions.

The climate of south Florida is subject to a strong and regular seasonal contrast in rainfall and runoff; wet summers receive approximately 60% of yearly precipitation, resulting in large changes in the quantity of freshwater flow to coastal estuaries throughout the year (Flannery et al., 2002). Estuarine organisms, including diatoms, are sensitive to the changing quantity of freshwater inflow, which occurs naturally with the seasons in south Florida but has also been strongly influenced by anthropogenic alteration during early efforts to drain Everglades wetlands for agricultural and urban development (summarized in Grunwald, 2006; McVoy et al., 2011).

Habitat alterations can reduce ecosystem resilience and hinder recovery from other disturbances by compounding pressures related to pollution, climate change, and reductions in biodiversity (Folke et al., 2004; Gunderson, 2001, 2000). In south Florida, interactions between anthropogenic alteration of nutrient cycles and hydrological regimes appear to have contributed to state shifts in Everglades wetlands and Florida Bay, possibly as a result of eroding ecosystem resilience (Fourqurean and Robblee, 1999; Gunderson 2001).

Tropical storms and hurricanes (tropical cyclones) also affect Florida during almost every summer season, and occasionally in other months. Accompanying increases in precipitation, nutrient influx from runoff, and mixing due to wind and storm surges all cause changes to biogeochemical variables that affect phytoplankton communities at varying time scales (Briceño and Boyer, 2010; Williams et al., 2008). These extreme events often result in regional flooding and coastal hypoxia in response to the nutrient loading and stratification caused by increased freshwater flow to the estuaries (Kim et al., 2010; Stevens et al., 2006; Tomasko et al., 2006). Tropical cyclones are a natural and important component of global heat distribution, and can be locally important in redistributing nutrients in estuarine habitats (Castañeda-Moya et al., 2010; Kang and Trefry 2003); however, other ecosystem stresses such as pollution and coastal land use can compound the effects of the natural disturbance and alter resilience regimes of ecosystem components (Greening et al., 2006; Mallin et al., 1999).

Documenting changes in diatom assemblages related to regular seasonal cycles and in response to a tropical cyclone in south Florida will help to distinguish patterns of seasonal variability from extreme events, potentially providing a tool for interpretation of change on broad temporal scales. The frequency, intensity, and spatial landfall patterns of tropical cyclones tend to vary with global climate cycles that operate on various time scales (Goldenberg et al., 2001;

Kerr, 2000; Landsea et al., 1999) and are expected to change with increasing levels of greenhouse gases in the atmosphere (Bender et al., 2010; Landsea et al., 1999). Understanding long-term trends will become increasingly difficult in a time of unprecedented climate change (Schiermeier, 2011), as changing conditions may disguise or accentuate poorly understood natural cycles (Enfield and Cid-Serrano, 2010). If sensitivity to events can be distinguished from other dynamics, then diatom assemblages preserved in sediments may provide records of past event frequencies to improve future forecasts.

To better understand patterns of change through the seasons and following a tropical cyclone in a south Florida watershed, we examined diatom assemblages collected at four different times during 2012: at the height of the dry season, at the end of the wet season, within a few days of a tropical storm's passage, and a few weeks after the storm had passed. With these diatom samples, we investigated three key questions: 1) are there differences between diatom assemblages between the wet and dry seasons in a coastal, hydrologically-dynamic watershed?; 2) do tropical cyclones alter community composition, and if so, on what time scale?; and 3) what are the key environmental drivers of these changes?

2. Materials and Methods

2.1. Study site

Charlotte Harbor, on southwest Florida's Gulf Coast, has a spatially extensive and heterogeneous watershed. The harbor has an estuary surface area of approximately 700 km² (Hammett, 1988), and it receives freshwater from three major rivers, the Caloosahatchee, Peace,

and Myakka, as well as numerous small creeks and streams. The Caloosahatchee River was channelized and connected to Lake Okeechobee as part of an effort to drain the Everglades in the late nineteenth century, and its freshwater flow is now strictly managed through a series of lock and dam structures. The lock that is farthest downstream provides a barrier to tidal action and mixing with marine waters except when it is occasionally breached during severe events, where historically marine influence extended farther upstream (Chamberlain and Doering, 1998; Lane, 1990). Its drainage basin is dominated by agriculture upstream and coastal urban development downstream. The Peace River is naturally enriched in phosphorus, and its drainage area includes extensive phosphate mining and extraction, as well as agriculture (Pierce et al., 2004). In contrast, the Myakka River is relatively pristine with much of its watershed in permanent conservation land, including expansive freshwater and tidal wetlands (Dorsey and Barry, 1990). A previous study of diatom assemblages and environmental features of this estuary during the dry season revealed compositional, salinity, and nutrient gradients in the harbor and each river (Nodine and Gaiser, 2014). In order to evaluate assemblage patterns and environmental dynamics at different times throughout the watershed, the present study used a subset of 16 sample sites that capture the full environmental gradient. Sites extend from Charlotte Harbor upstream through the Caloosahatchee, Myakka, and Peace Rivers (Fig. 1).

2.2. Sample collection, preparation, and laboratory analysis

To represent seasonal variability in diatom assemblages, we sampled during the height of the dry season in March 2012 and at the end of the wet season in November 2012, in order to capture maximal differences in base freshwater flow. On June 20, a low pressure system formed

Fig. 1. Map showing location of sampling sites across the Charlotte Harbor watershed.

in the Gulf of Mexico as a result of the confluence of the Inter-Tropical Convergence Zone, an anomalous low-level flow from the Pacific, and a tropical wave (Stewart, 2013). It remained in the southeastern portion of the Gulf of Mexico for several days, causing large amounts of rainfall across the Charlotte Harbor watershed. On June 23, the storm developed into Tropical Storm Debby and slowly intensified and moved northeastward, making landfall well north of Charlotte Harbor late on June 26. Although rainfall and flooding were not as severe as in other parts of the state, Tropical Storm Debby generated approximately 5-10 inches of precipitation over parts of the Charlotte Harbor watershed (Kimberlain, 2013), and caused minor regional flooding. To evaluate changes that occur quickly following a severe rainfall event, we collected samples between June 28 and July 1 and then sampled again approximately two weeks later, between July

12 and 14, to evaluate changes that occur in response to changing water chemistry conditions following a storm. During the June 28 to July 1 sampling event, there were difficulties with accessibility at four of the 16 sites, three in the Myakka River and one in the Caloosahatchee River, so sampling was not done; those four sites were sampled at the other three times and the remaining 12 sites were sampled on all four occasions. We attempted to collect samples at approximately the same tidal period, but the large spatial distribution of the sites precluded exact coordination; seasonal variability in freshwater flow and currents is expected to have a larger relative effect on environmental gradients and diatom distribution than diurnal changes at the few sites where inter-tidal variability may have been a factor (He and Weisberg, 2002; Weisberg et al., 1996). In some of the subsequent analysis, the two sampling times following the storm are considered “storm-effect” times, and the March (dry season) and November (wet season) sampling times are considered “no storm-effect” times.

Diatoms were collected by towing a 20-micron plankton net through the water column after tossing it from the shoreline three times at each site. Water depths were very shallow (< 1m), so the net made contact with the substrate on each tow, disturbing the sediment. Diatom samples therefore included planktonic, tychoplanktonic, and benthic taxa, as well as many for which life the habit is not known; all taxa were analyzed together as a single assemblage from each site. Surface water samples were collected for nutrient analysis using a clean bottle rinsed thoroughly and then filled at each site. Salinity and conductivity were measured at approximately 30 cm depth in the water column using a YSI multiparameter Sonde.

In the laboratory, diatom samples were cleaned using a series of acid baths following the oxidation technique described by Battarbee (1986) and then diluted until a neutral pH was achieved. A measured aliquot of 0.01 to 1.0 ml (depending on diatom concentration) of the

resulting mixture was removed by calibrated pipette, placed on a coverslip, and dried. Coverslips were then permanently mounted onto glass slides using Naphrax®. A minimum of 500 diatom valves were identified from each sample along measured, random transects using a Nikon E4000 light microscope at x1000 magnification. Identification of diatoms was based on regional and standard diatom taxonomic literature (e.g., Foged, 1984; Hein et al., 2008; Hendey, 1964; Peragallo and Peragallo, 1908; Witkowski et al., 2000). Water samples were analyzed for total phosphorus (TP) with a UV-2101PC Scanning Spectrophotometer, total nitrogen (TN) with an ANTEK 9000 N Nitrogen Analyzer, and total organic carbon (TOC) with a SHIMADZU TOC-L Analyzer by the Southeast Environmental Research Center Nutrient Analysis Laboratory following EPA methods.

2.3. Data analysis

The abundance of all taxa in each sample was calculated relative to total abundance of diatom valves counted. Taxa occurring in at least three samples with a relative abundance of at least 0.5% in at least one sample were included for statistical analyses, because inclusion of potentially undersampled taxa can increase noise in the dataset (McCune et al., 2002). Relative abundances were fourth-root transformed to more closely approximate a normal distribution and to downweight the relative importance of very abundant taxa. Indicator species analysis (ISA) was used to identify taxa that were strongly associated with post-storm sampling periods or the wet or dry season based on taxon persistence in the group (in most samples from that group) and exclusivity to that group (not found in most other groups) (McCune et al., 2002). Similarity matrices were created using Bray-Curtis similarity to evaluate diatom assemblage differences

among sites. A similarity percentages (SIMPER) analysis was used to identify species that contributed most to the differences among sampling periods; for this analysis, only taxa that accounted for at least four percent of the total abundance in a single sample were included because similarities among rare species have little meaning and confound clustering patterns, particularly when large numbers of taxa are present (Clarke and Warwick 2001).

Environmental variables were transformed using the method that best reduced the skewness for each variable. Conductivity and salinity values were arcsine transformed, TN concentrations were inverse transformed, TP concentrations were inverse square-root transformed, and TOC concentrations were square-root transformed. All environmental data were normalized (mean subtracted and divided by standard deviation) to equalize values to a common scale (Clarke and Warwick, 2001). Similarity matrices were created using Euclidean distance to evaluate environmental relationships among sites.

Nonmetric multi-dimensional scaling (NMDS) ordination (Kruskal and Wish, 1978) was used to visualize assemblage and environmental patterns among sites at different sampling times. After evaluating the stress of ordinations with up to five axes, two-dimensional NMDS was selected to ease interpretability of results, given that stress values did not decrease greatly with additional axes. Stress is a measure of the departure from fit of the sample dissimilarity to distance in the ordination; it tends to decrease with additional axes, as more of the sample variance is represented, but additional dimensions make interpretation increasingly difficult (McCune et al., 2002). Multi-response permutation procedures (MRPP) were used to test for differences among groups observed in the ordination (McCune et al., 2002), and visually-estimated convex hulls were superimposed around groups to ease interpretability. MRPP analysis provides both a statistical metric ($p < 0.05$ was considered significantly different), and

an ecological effect size (A), or group homogeneity as compared to random expectation (McCune et al., 2002). Environmental vectors representing the direction and strength of each variable's correlation with sample differences were also overlaid on the ordinations.

An index of multivariate dispersion (IMD) was calculated to examine the relative variability among assemblages from each sampling event and in each sub-basin. IMD values contrast the average rank of similarities within groups to provide a metric of dispersion, but do not provide a statistical framework appropriate for testing (Clarke and Warwick, 2001). Differences among sampling events were assessed with analysis of similarity (ANOSIM) to determine the relative similarity of diatom assemblages and environmental conditions at each time period. R values reported represent the difference of mean ranks of variables and ranges from 0 to 1 with increasing dissimilarity (Clarke and Warwick, 2001), and comparisons having a $p < 0.05$ were considered statistically significant.

Kendall's tau correlation coefficients were calculated representing the rank relationships between each variable and the differences among diatom assemblages for each sampling event in each sub-basin. Kendall's tau represents a probability of dependence between non-normally distributed variables (Bolboaca and Jäntschi, 2006). These correlations are strictly descriptive, as ordination scores are not independent of one another, violating one of the assumptions that validate a p-value (McCune et al., 2002). Correlations with variables therefore represent relative and interacting effect sizes related to the diatom assemblages, and these range from 1 to -1, with 0 representing no correlation. The above analyses were all conducted using the software Primer version 6 (Clarke and Gorley, 2006) and PC-ORD version 5 (McCune and Mefford, 1999).

3. Results

3.1. Diatom assemblage differences

A total of 254 taxa were identified from all samples, with 176 present in the dry season (March), 169 in the wet season (November), 152 in the days after Tropical Storm Debby (June), and 166 two weeks after the storm passed (July). Species richness and diversity were not significantly different among sampling times. Many of the dominant taxa were prevalent at all sampling times, including benthic taxa *Staurosirella martyi* (Héribaud) Morales and Manoylov, *Staurosirella leptostauron* var. *dubia* (Grunow) Edlund, *Fragilaria sopotensis* Witkowski & Lange-Bertalot, *Planothidium delicatulum* (Kützing) Round and Bukhtiyarova, *Catenula adhaerens* Mereschkowsky, and the likely planktonic *Cyclotella* cf. *meneghiniana* F.T. Kützing, all of which were in the top ten most abundant taxa at every sampling time.

NMDS ordinations reflect this taxonomic overlap among sampling times (Fig. 2). While environmental variables showed a distinction between post-storm sampling times and the wet/dry seasons (a storm-effect vs. no storm-effect dichotomy), diatom assemblages showed a convergence in similarity following the storm and wider dispersion with intermixing among wet and dry season sampling. These differences were quantified using MRPP analysis, which revealed that diatom assemblages were not significantly different between the wet and dry seasons ($p = 0.11$; $A = 0.01$), but were different between storm-effect and no storm-effect periods ($p < 0.02$; $A = 0.01$). The SIMPER test identified some of the most common and abundant taxa as the predominant drivers of assemblage dissimilarity across sampling times

Fig. 2. NMDS ordination biplots showing differences in diatom assemblage composition (a and b) and environmental variables (c and d) for all sites (plotted points) over time. The same ordination is shown in a and b with two overlays: a) solid line surrounding samples from wet and dry seasons and dotted line surrounding samples from the two post-storm sampling events, and b) vectors showing the magnitude and direction of correlations of environmental variables with diatom assemblage dissimilarity. The ordination of environmental variables is shown with the same two overlays: c) solid line surrounding wet and dry season sampling events and dotted line surrounding the two post-storm sampling events, and d) correlations of environmental variables with the sample dissimilarity among sites.

(Table 1), as well as *Pseudostaurosira brevistriata* (Grunow) Williams and Round, which occurs both in benthic and plankton assemblages (Morales, 2010). MRPP of environmental characteristics were significantly different between both wet vs. dry season ($p < 0.01$; $A = 0.11$) and between storm-effect and no storm-effect periods ($p < 0.01$; $A = -0.05$).

Table 1. Taxa that are the strongest contributors to assemblage differences among sampling times.

	Taxon	Percent dissimilarity contributed
Dry vs. wet season	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams and Round	2.7
	<i>Cyclotella</i> cf. <i>meneghiniana</i> F.T. Kützing	2.6
	<i>Staurosirella martyi</i> (Héribaud) Morales and Manoylov	1.8
	<i>Staurosira construens</i> var. <i>venter</i> (Ehrenberg) Hamilton 1992	1.8
Dry season vs. post-storm	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams and Round	2.6
	<i>Cyclotella</i> cf. <i>meneghiniana</i> F.T. Kützing	2.1
	<i>Staurosirella martyi</i> (Héribaud) Morales and Manoylov	1.8
	<i>Opephora pacifica</i> (Grunow) Petit	1.7
Wet season vs. post-storm	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams and Round	2.7
	<i>Cyclotella</i> cf. <i>meneghiniana</i> F.T. Kützing	2.6
	<i>Staurosirella martyi</i> (Héribaud) Morales and Manoylov	1.8
	<i>Staurosira construens</i> var. <i>venter</i> (Ehrenberg) Hamilton 1992	1.8

Dispersion analysis showed that dissimilarity among diatom assemblages was lower following the storm compared to the seasons with no storm effect, in the whole watershed as well as in each sub-basin (Fig. 3). The biggest differences were in the Myakka River and the Harbor, with index differences of 0.67 and 0.61, respectively, and the smallest difference occurred when all sites in the watershed were included (difference of 0.19). There was also a

Fig. 3. Bar graph showing the index of multivariate dispersion (IMD) for diatom assemblages in all sites and each sub-basin during the seasons not affected by the storm (light gray) and the sampling period following the storm (dark gray).

relatively small difference in the Caloosahatchee River (0.27) compared to other sub-basins. The IMD for each of the four sampling times shows slightly more complex patterns across the sub-basins (Table 2). All sub-basins had the highest dispersion index values in the wet and dry seasons, with lower values following the storm; however, Harbor sites had the lowest dispersion immediately after the storm, and dispersion increased two weeks later, while in the Caloosahatchee and Peace Rivers, dispersion decreased immediately after the storm and was further reduced two weeks later. When all sites in the watershed were included, differences in dispersion following the storm and in the wet season were negligible.

ANOSIM showed that diatom assemblages were significantly different across the watershed between the dry season and the wet season and between the dry season and two weeks following the storm, but not between other sample periods (Table 3). Environmental conditions differed between the dry season and all other sample periods, but there were no significant differences among post-storm samples and the wet season. Indicator species were identified for the wet and dry seasons, as well as for the post-storm sampling events for each sub-basin and in

Table 2. IMD values quantifying dispersion among diatom assemblages within each region at each sampling time: June (within 4 days after TS Debby), July (2 weeks following TS Debby), March (dry season), and November (wet season).

Region	Storm-effect		No storm-effect	
	June	July	March	November
All sites	0.88	0.94	1.15	0.93
Harbor	0.42	1.08	1.1	1.19
Caloosahatchee River	0.98	0.69	1.03	1.29
Myakka River	-	0.5	1.42	0.83
Peace River	0.91	0.55	1.44	1.11

the watershed as a whole; 13 taxa were significant indicators across all sites in the watershed, as well as within at least one of the sub-basins (Table 4).

Table 3. ANOSIM of diatom assemblage composition (a) and environmental variables (b) between the dry season (March), the days following TS Debby (June), two weeks following TS Debby (July), and the wet season (November). * indicates statistically significant at $p < 0.05$.

a. Assemblage composition	March	June	July
June	0.05		
July	0.12*	0.02	
November	0.12*	0.06	0.06
b. Environmental variables			
June	0.19*		
July	0.14*	-0.03	
November	0.09*	0.08	0

Table 4. Indicator species for dry season, wet season, and period following storm that are significant indicators ($p < 0.05$) in all sites taken together and at least one sub-basin. * indicates a p -value < 0.01 .

Indicators for dry season	Significant in sub-basin(s)
<i>Cocconeis peltoides</i> Hustedt	Harbor, Caloosahatchee, Peace
<i>Navicula hagelsteinii</i> Hustedt	Harbor*
<i>Nitzschia lanceola</i> Grunow	Harbor
<i>Staurosirella</i> cf. <i>subrobusta</i> Morales	Caloosahatchee, Peace*
Indicators for wet season	
<i>Bacteriastrum</i> cf. <i>elongatum</i> Cleve	Harbor*
<i>Cocconeis placentula</i> var. <i>placentula</i> Ehrenberg	Myakka
<i>Cyclotella</i> cf. <i>striata</i> (Kützing) Grunow	Harbor*
<i>Nitzschia grossestriata</i> Hustedt	Harbor, Caloosahatchee, Myakka
Indicators for post-tropical storm	
<i>Achnanthes exigua</i> Grunow	Peace
<i>Cocconeis speciosa</i> Gregory	Peace*
<i>Navicula phylleptosoma</i> Lange-Bertalot	Harbor
<i>Nitzschia angularis</i> W.Smith	Harbor
<i>Tabularia gaillonii</i> (Bory de Saint-Vincent) Bukhtiyarova	Peace

3.2. Relationships with environment

Environmental changes in the watershed through the sampling periods showed different patterns in the sub-basins (Fig. 4). Salinity changes were as expected across the watershed; salinity decreased from the highest values in the dry season to lower values following the storm that were maintained into the wet season. One site in the mid-Peace River had extremely high concentrations of TN in the dry and wet season and showed a dramatic reduction following the storm that persisted for the two weeks after the storm. Other sites across the watershed had highly variable patterns of TN concentration; some TN concentrations decreased from higher dry season values following the storm and then increased again in the wet season, and other sites saw

Fig. 4. Plots of environmental changes at each sampling time by region. Each line depicts the values measured at a different site within that region.

TN concentrations as much as double from dry season levels after the storm and then decrease again in the wet season. Most sites across the watershed had elevated TP concentrations following the storm and maintained comparatively low levels in the dry and wet seasons. The Peace River, which is naturally enriched in TP, had a flashier TP response pattern, with concentrations that increased in the days following the storm but dropped dramatically two weeks later and returned to elevated concentrations in the wet season. Most sites across the watershed showed increases in TOC following the storm with relatively low levels in the dry and wet seasons, with the exception of the Caloosahatchee River sites. Most of the Caloosahatchee River sites showed slight decreases in TOC from dry season levels following the storm and highest concentrations in the wet season.

The relative strength of the relationships between the diatom assemblages and environmental variables shifted among the different sampling times (Fig. 5). Salinity and conductivity maintained a relatively high and stable correlation with the diatom assemblage at each sampling time, but relationships with nutrient concentrations changed. The correlation with TP concentrations increased dramatically in the days following the storm compared to the dry season, quickly declined two weeks later, and fell to near zero (no relationship) in the wet season. The correlation between diatom assemblages and TN concentrations was highest two weeks after the storm.

Relationships with nutrient concentrations through time also differed among sub-basins (Fig. 6). In the Harbor sites, the relationship of the diatom assemblages with TN concentrations was opposite that of salinity and conductivity in the dry season, but similar to them at all other times. In the Caloosahatchee River sites, the correlation of assemblages with TN concentration

Fig. 5. Kendall's tau correlations of diatom assemblage dissimilarity with environmental variables through the seasons. Greater distance from the zero line (no correlation) represents a stronger relationship with diatom assemblage composition.

Fig. 6. Kendall's tau correlations of diatom assemblage composition with environmental variables through the seasons in each sub-basin: Harbor sites (a), Caloosahatchee River (b), Myakka River (c), and Peace River (d). Greater distance from the zero line (no correlation) represents a stronger relationship with diatom assemblage composition.

was elevated in the dry season, increased slightly in the days following the storm, and declined to near zero in the wet season, while the relationship with TP concentrations declined to zero following the storm and was relatively strong in the dry and wet seasons. In the Myakka River, the correlation of the assemblages with TN concentrations changed direction following the storm and then increased in the wet seasons, while the opposite pattern occurred in the relationship with TP concentrations. The Peace River site assemblages had very low correlations with TN concentrations during the dry season and two weeks after the storm, with relatively high correlations in the days after the storm and during the wet season; correlations of diatom assemblages with TP concentrations were strongest following the storm.

4. Discussion

Given the strong natural seasonality of south Florida's freshwater flow, we expected compositional differences between the wet and dry seasons; however most of the dominant taxa were equally abundant across seasons. Many of the most abundant taxa have been documented to have relatively broad salinity tolerances (Nodine and Gaiser, 2014), appearing in Florida rivers (Morales, 2005, 2002) and eastern USA estuaries like the Chesapeake Bay (Cooper, 1995) and the Pamlico and Neuse estuaries of North Carolina (Cooper, 2000). The persistence of dominant taxa reduced the clarity of assemblage differences between the dry and wet seasons; the difference was significant in ANOSIM, which analyzes rank dissimilarity, but not significant in MRPP, which evaluates average dissimilarity. The persistent and dominant taxa were generally also the ones driving differences among sample times, suggesting that shifts in relative abundance rather than species turnover are critical changes. Analysis using rank rather than

average is particularly sensitive to distributional differences (i.e., the groups differ in skewness or dispersion), so changes among common taxa may result in a significant result because of shifts among the largest numbers (Anderson and Walsh, 2013).

Indicator species for the periods following the storm were relatively rare (among them, the highest average relative abundance was 2.5%) and only one, *A. exigua*, was also detected during both the dry and wet seasons. Other indicators for the periods following the storm included *Cocconeis speciosa*, *Navicula phylleptosoma*, *Nitzschia angularis*, and *Tabularia gaillonii*, which are generally considered cosmopolitan in marine to brackish habitats in the Atlantic, Mediterranean, and Baltic Seas (Witkowski et al., 2000). It is therefore likely that they are also present in the Charlotte Harbor watershed during the dry and wet seasons, but in such small numbers that they were not sampled at those times. If the passage of the storm caused an increase in their abundance, these taxa may provide evidence of past storm activity in sediment records where they are relatively abundant. That these are predominantly benthic taxa may also be an indication that habit is important to post-storm assemblages; diatoms attached to a substrate may be better able to persist following disturbance relative to planktonic taxa (Townsend et al., 1997).

Dry season indicators *Nitzschia lanceola* and *Navicula hagelsteinii* are generally associated with strictly marine environments on warmer coasts, but *N. lanceola* also occurs in freshwaters with high ion content (Witkowski et al., 2000). In this study it was a significant dry season indicator for the whole watershed, as well as for the Harbor sub-basin. *N. hagelsteinii* has previously been reported in Cuba and other parts of the Caribbean (Foged, 1984; Navarro, 1983), and was also an indicator for the watershed and the Harbor but not for the river sub-basins, likely because these two taxa occur less frequently at the river sites. Wet season indicators include

both planktonic and benthic, and marine and freshwater, taxa that are generally associated with pollution or high nutrient content. *Cocconeis placentula* is an epilithic taxon associated with high nutrients in streams (Jones, 1978; Kelly et al., 1995), and members of the planktonic *Cyclotella striata* complex have been associated with pollution from agriculture in the Mediterranean (Ismael and Dorgham, 2003).

Tropical cyclones can be important mechanisms of dispersal and distribution of phytoplankton in shallow subtropical ecosystems (McKinnon et al., 2003). In this study, diatom assemblages across the watershed generally became more similar to one another following the tropical storm, but patterns of recovery were site specific. For example, the NMDS shows that some sites have a similar wet and dry season composition that changes following the storm, while others shift following the storm and continue to diverge into the wet season. There were no consistent regional patterns. Previous studies have documented increased diatom dominance (Delesalle et al., 1993; Son et al., 2007) and diversity (McKinnon et al., 2003) following a tropical cyclone, which suggests that changes in diatom diversity and assemblage composition can provide a reliable signal of tropical cyclone occurrence in some ecosystems.

Diatom assemblage dispersion was lower across the watershed following the storm, and differences were greater when constrained by sub-basin. Evaluating all of the sites in the watershed together therefore dampened the observable effects on dispersion, and interpreting changes on a sub-basin spatial scale may be more relevant for understanding patterns of assemblage change following disturbance. The diminished contrast when all sites were analyzed together was consistent when evaluating storm-effect (June and July sampling) vs. no storm-effect (dry and wet season, or March and November, sampling) periods or comparing all four sample times individually, which provides evidence that the sub-basins recover from such a

disturbance on different time scales. For example, the Harbor sites returned to pre-storm assemblage dispersion within a couple weeks of the storm; their lowest dispersion values occurred after the storm and were relatively constant at the other three sampling times. In contrast, dispersion in the Caloosahatchee River sites decreased only very slightly in the few days following the storm but continued to decrease and reached their lowest values two weeks following the storm, which may be influenced by the greater physical distance and transport that affect change across those sites, or by management of water flow.

The smallest overall changes in dispersion occurred in the Caloosahatchee River sites, where water flow is highly managed, and were highest in the relatively pristine Myakka River, which raises interesting questions about how management has influenced ecosystem resilience in the Caloosahatchee River watershed. It appears that a reduction in assemblage dissimilarity following a major storm and comparatively high dispersion during normal seasonal periods, regardless of the hydrological state, is a normal pattern in the estuary watershed. If management practices in sub-basin watersheds have dampened the expected response to disturbance, it could have broader impacts for resilience of the greater ecosystem. Effects on trophic systems, for example, have been documented in other studies; an increase in pelagic diatom diversity found following a tropical cyclone off the coast of Australia was coincident with a decrease in copepod diversity and overall increases in zooplankton and larval fish diversity (McKinnon et al., 2003). A change in the response of diatom assemblages, which occur on time scales of a few days, may further affect responses in zooplankton and fish assemblages, which occur on longer time scales, thus having cascading effects on the system.

Relationships between the diatom assemblages and the measured suite of potential environmental drivers were complex, both spatially and temporally. Based on rank similarity of

the measured environmental variables (ANOSIM), conditions during the dry season were significantly different from the three other sampling times, which is not surprising because of the increase in freshwater flow during the other periods. However, NMDS ordination showed that wet and dry season measurements are more similar to each other than to post-storm conditions at almost all sites, whereas diatom assemblages become more similar following the storm. By evaluating the correlation of environmental variables with the diatom assemblages in each sub-basin, it is clear that assemblages relate to different variables at different times, and that these controls vary across the watershed. An examination of the diatom assemblages of the Three Gorge Reservoir in China similarly showed that relationships with nutrient concentrations varied by season and by location within the system, including proximity to the anthropogenically modified portion (Zeng et al., 2006).

The different sub-basins of the Charlotte Harbor watershed provided an excellent opportunity to characterize the variations in environmental controls on diatom assemblages and their relevance to spatial characteristics. Kendall's tau correlation coefficients indicate that the strength of the dependence of diatom assemblages on nutrient concentrations varies in relation to season and freshwater flow. TP, for example, has been shown to have a significant relationship with diatom assemblage differences in the watershed (Nodine and Gaiser, 2014), but this study demonstrates that the time and spatial scale of this relationship is important. Throughout the watershed, diatom assemblages had a relatively high correlation (~ 0.6) with TP immediately following the storm, but in the wet season there was almost no correlation, suggesting that the relative influence of TP on assemblage composition across the watershed increases under flashier conditions and other factors are more important during base flow times. However subsets of each sub-basin analyzed separately show different trends. The smaller sample size of each of the

sub-basins (3 to 5 sites each) reduces the power of the correlations, but interesting patterns are suggested nonetheless. Among the Harbor and Caloosahatchee River sites, the assemblage relationship with TP is low following the storm compared to the dry and wet seasons, exhibiting almost the opposite pattern of the watershed as a whole. Instead, the strongest correlation (~ 0.9) following the storm in these sub-basins is with TN, which may indicate that differences in nutrient limitation related to terrestrial runoff patterns in the watershed cause differing relationships with drivers. In the Peace River sites, for example, the N to P ratio was lowest immediately after the storm and highest two weeks later, which is opposite the pattern of their correlation between the diatom assemblages and TP. The N to P ratio was highest in the Harbor in the dry season and lowest in the wet season, while in the Caloosahatchee and Myakka Rivers it was lowest following the storm, which matches the pattern of correlation with TP in the Myakka but not in the Caloosahatchee River.

It is possible that unassessed habitat differences among the sub-basins also contribute to changing relationships with nutrient concentrations, as benthic assemblages associated with different substrate types (such as epilithic, epipsammic, epiphytic, etc.) can respond differently to environmental controls (Soininen and Eloranta, 2004). Our samples included entrained benthic diatoms from a variety of shallow water habitats, so variable responses to nutrients by functional groups were not detected. Habitat characteristics may also affect ecosystem resistance and resilience, because diatoms affixed to substrates may persist following disturbance in greater proportion than planktonic taxa (Townsend et al., 1997), which could explain some of the differences in the magnitude of the change across the sampling times in each sub-basin. We did not sample benthic and planktonic diatoms separately, so it is also possible that some assemblages contained higher proportions of benthic taxa coincident with greater sediment

disturbance during sample collection; however, all assemblages were composed of a mixture of planktonic and benthic taxa, so representatives from each microhabitat were included at each site at each sample time.

Conclusions

Results from this study provide evidence of the resilience of aquatic ecosystems in this watershed. This hydrologically dynamic system that exhibits considerable spatio-temporal variation in salinity and nutrient concentrations supports relatively stable diatom assemblages. Flooding following a tropical cyclone reduces assemblage dispersion on regional scales. As changes in freshwater flow and nutrient influx result from climate change and/or anthropogenic effects, it is important to understand how response regimes are affected by management so that we can make informed decisions that may help to mitigate negative impacts on the ecosystem. Our results suggest that the reduction in dispersion of diatom assemblages following the disturbance of a tropical cyclone is a natural occurrence in the watershed that may be dampened with intensive management. The changes in dispersion may therefore provide a tool for interpreting changes on longer time scales, through analysis of diatom assemblages in sediment cores. By identifying periods of lower dispersion that occurred prior to anthropogenic impacts in the watershed, we may be able to identify times of intense storm activity that pre-date modern records, thus providing information that can be used to identify long-term patterns and climate cycles that can improve predictions of future changes. Care should be taken to consider different patterns displayed across sub-basins when selecting the relevant spatial scale, as watershed

characteristics including geomorphic setting and other factors influence the applicability of a given depositional basin for representation of larger catchments.

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References

- Anderson, M.J. and D.C.I. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* 83:557–574.
- Angeler, D.G. and J.M. Moreno. 2007. Zooplankton Community Resilience after Press-type Anthropogenic Stress in Temporary Ponds. *Ecological Applications* 17:1105–1115.
- Battarbee, R.W. 1986. Diatom analysis. In B.E. Berglund (Editor), *Handbook of Holocene palaeoecology and palaeohydrology*. Caldwell: Blackburn, 527-570.
- Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T. Garner and I.M. Held. 2010. Modeled Impact of Anthropogenic Warming on the Frequency of Intense Atlantic Hurricanes. *Science* 327: 454-458.
- Bolboaca, S.D. and L. Jäntschi. 2006. Pearson versus Spearman, Kendall's tau correlation analysis on structure-activity relationships of biologic active compounds. *Leonardo Journal of Sciences* 9: 179-200.
- Briceño, H., and J. Boyer. 2010. Climatic Controls on Phytoplankton Biomass in a Sub-tropical Estuary, Florida Bay, USA. *Estuaries and Coasts* 33: 541-553.
- Bull, D., A.E.S. Kemp, and G.P. Weedon. 2000. A 160-k.y.-old record of El Nino-Southern Oscillation in marine production and coastal runoff from Santa Barbara Basin, California, USA. *Geology* 28: 1007-1010.

- Castañeda-Moya, E., R.R. Twilley, V.H. Rivera-Monroy, K. Zhang, S.E. Davis III, and M. Ross. 2010. Sediment and Nutrient Deposition Associated with Hurricane Wilma in Mangroves of the Florida Coastal Everglades. *Estuaries and Coasts* 33: 45-58.
- Chamberlain, R.H. and P.H. Doering. 1998. Freshwater inflow to the Caloosahatchee Estuary and the resource-based method for evaluation. Charlotte Harbor National Estuary Program Technical Report No. 98-02. Punta Gorda: Proceedings of the Charlotte Harbor Public Conference and Technical Symposium.
- Clarke, K.R., and R.N. Gorley. 2006. *Primer v6: user manual/tutorial*. Plymouth: Primer-E Ltd.
- Clarke, K.R., and W.M. Warwick. 2001. *Change in marine communities: An approach to statistical analysis and interpretation*. Plymouth: Primer-E Ltd.
- Cooper, S.R. 1995. Diatoms in sediment cores from the mesohaline Chesapeake Bay, U.S.A. *Diatom Research* 10: 39-89.
- Cooper, S.R. 2000. The History of Water Quality in North Carolina Estuarine Waters as Documented in the Stratigraphic Record. Report 2000-327. Raleigh: University of North Carolina Water Resources Research Institute.
- Delesalle B., M. Pichon, M. Frankignoulle, and J.P. Gattuso. 1993. Effects of a cyclone on coral reef phytoplankton biomass, primary production and composition (Moorea Island, French Polynesia). *Journal of Plankton Research* 15:1413–1423.
- Descamps-Julien, B., and A. Gonzalez. 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology* 86:2815–2824.
- Dorsey, T., and R. Barry. 1990. Myakka River. In D. Marth and M. Marth (Editors), *The Rivers of Florida*. Sarasota: Pineapple Press, Inc., pp.83-86.
- Enfield, D.B., and L. Cid-Serrano. 2010. Secular and multidecadal warmings in the North Atlantic and their relationships with major hurricane activity. *International Journal of Climatology* 30: 174-184.
- Flannery, M.S., E.B. Peebles, and R.T. Montgomery. 2002. A percent-of-flow approach for managing reductions of freshwater inflows from unimpounded rivers to Southwest Florida estuaries. *Estuaries* 25: 1318-1332.
- Foged, N. 1984. Freshwater and littoral diatoms from Cuba. *Bibliotheca Diatomologica* 5: 1–243.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C.S. Holling. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review*

- of Ecology, Evolution, and Systematics 35: 557-581.
- Fourqurean, James W. and Michael B. Robblee. 1999. Florida Bay: A history of recent ecological changes. *Estuaries* 22: 345-357.
- Glasby, T.M. and A.J. Underwood. 1996. Sampling to differentiate between pulse and press perturbations. *Environmental Monitoring and Assessment* 42: 241-252.
- Goldenberg, S.B., C.W. Landsea, A.M. Mestas-Núñez, and W.M. Gray. 2001. The Recent Increase in Atlantic Hurricane Activity: Causes and Implications. *Science* 293: 474-479.
- Greening, H., P. Doering, and C. Corbett. 2006. Hurricane impacts on coastal ecosystems. *Estuaries and Coasts* 29: 877-879.
- Grunwald, M. 2006. *The Swamp: The Everglades, Florida, and the Politics of Paradise*. New York: Simon & Schuster.
- Gunderson, L.H. 2000. Ecological Resilience in Theory and Application. *Annual Review of Ecological Systems* 31: 425-439.
- Gunderson, L.H. 2001. South Florida: The Reality of Change and the Prospects for Sustainability: Managing surprising ecosystems in southern Florida. *Ecological Economics* 37: 371-378.
- Hammett, K.M. 1988. Land use, water use, streamflow and water-quality characteristics of the Charlotte Harbor inflow area, Florida. Record Number QH 541 U526. Tampa: Southwest Florida Water Management District.
- He, R., and R.H. Weisberg. 2002. Tides on the West Florida Shelf. *Journal of Physical Oceanography* 32: 3455-3473.
- Hemphill-Haley, E. 1996. Diatoms as an aid in identifying late-Holocene tsunami deposits. *The Holocene* 6: 439-448.
- Hein, M.K., B.M. Winsborough, and M.J. Sullivan. 2008. Bacillariophyta (Diatoms) of the Bahamas. *Iconographia Diatomologica* 19: 1-300.
- Hendey, N.I. 1964. An introductory account of the smaller algae of British coastal waters, Part V. Bacillariophyceae. In *Fisheries Investigations (Series IV)*. London: Great Britain Ministry of Agriculture.
- Hutchinson, G. E. 1961. The Paradox of the Plankton. *The American Naturalist* 95: 137-145.

- Ismael, A.A. and M.M. Dorgham. 2003. Ecological indices as a tool for assessing pollution in El-Dekhaila Harbour (Alexandria, Egypt). *Oceanologia* 45: 121-131.
- Jones, J.G. 1978. Spatial variation in epilithic algae in a stony stream (Wilfin Beck) with particular reference to *Cocconeis placentula*. *Freshwater Biology* 8: 539-546.
- Kang, W.-J. and J.H. Trefry. 2003. Retrospective analysis of the impacts of major hurricanes on sediments in the lower Everglades and Florida Bay. *Environmental Geology* 44: 771-780.
- Kelly, M.G., C.J. Penny, and B.A. Whitton. 1995. Comparative performance of benthic diatom indices used to assess river water quality. *Hydrobiologia* 302: 179-188.
- Kerr, R. A. 2000. A North Atlantic Climate Pacemaker for the Centuries. *Science* 288: 1984-1985.
- Kim, T., Y.P. Sheng, and K. Park. 2010. Modeling water quality and hypoxia dynamics in Upper Charlotte Harbor, Florida, U.S.A. during 2000. *Estuarine, Coastal and Shelf Science* 90: 250–263.
- Kimberlain, T. 2013. Tropical Cyclone Report: Tropical Storm Debby (AL042012) 23-27 June 2012. National Hurricane Center. Miami, Florida. <http://consejo.bz/weather/2012/pdf/debby.pdf>.
- Kruskal, J.B., and M. Wish. 1978. Multidimensional scaling. In J.L. Sullivan and R.G. Niemi (Editors), *Quantitative applications in social sciences series 11*, Sage University Series, vol. 92. Beverly Hills: Sage, 1-91.
- Landsea, C. W., R. A. Pielke, A. M. Mestas-Nuñez, and J. A. Knaff. 1999. Atlantic Basin Hurricanes: Indices of Climatic Changes. *Climatic Change* 42: 89-129.
- Lane, G. Jr. 1990. Caloosahatchee River. In D. Marth and M. Marth (Editors), *The Rivers of Florida*. Sarasota: Pineapple Press, Inc., pp. 41-44.
- Lange, C.B., W.H. Berger, S.K. Burke, R.E. Casey, A. Schimmelmman, A. Soutar, and A.L. Weinheimer. 1987. El Nino in Santa Barbara Basin: Diatom, radiolarian, and foraminiferan responses to the "1983 El Nino" Event. *Marine Geology* 78: 153-160.
- Mallin, M.A., M.H. Posey, G.C. Shank, M.R. McIver, S.H. Ensign, and T.D. Alphin. 1999. Hurrican Effects on Water Quality and Benthos in the Cape Fear Watershed: natural and anthropogenic impacts. *Ecological Applications* 9:350–362.
- McCune, B., and J.B. Grace, with a contribution from D.L. Urban. 2002. *Analysis of ecological communities*. Gleneden Beach: MjM Software Design.

- McCune, B., and M.J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. Gleneden Beach: MJM Software Design.
- 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.
- McVoy, C.W., W.P. Said, J. Obeysekera, J. Van Arman, and T. Dreschel. 2011. *Landscapes and Hydrology of the Predrainage Everglades*. Gainesville: University Press of Florida.
- Morales, E.A. 2002. Studies in selected fragilarioid diatoms of potential indicator value from Florida (USA) with notes on the genus *Opephora* Petit (Bacillariophyceae). *Limnologia – Ecology and Management of Inland Waters* 32: 102-113.
- Morales, E.A. 2005. Observations of the morphology of some known and new fragilarioid diatoms (Bacillariophyceae) from rivers in the USA. *Phycological Research* 53: 113-133.
- Morales, E. 2010. *Pseudostaurosira brevistriata*. In *Diatoms of the United States*. Retrieved March 30, 2015, from http://westerndiatoms.colorado.edu/taxa/species/pseudostaurosira_brevistriata.
- Navarro, J.N. 1983. A Survey of the Marine Diatoms of Puerto Rico VI. Suborder Raphidineae: Family Naviculaceae (Genera *Haslea*, *Mastogloia* and *Navicula*). *Botanica Marina* 26: 119–136.
- Nodine, E.R. and E.E. Gaiser. 2014. Distribution of diatoms along environmental gradients in the Charlotte Harbor, Florida (USA), estuary and its watershed: implications for bioassessment of salinity and nutrient concentrations. *Estuaries and Coasts* 37: 864-879.
- Parsons, M. L. 1998. Salt Marsh Sedimentary Record of the Landfall of Hurricane Andrew on the Louisiana Coast: Diatoms and Other Paleoindicators. *Journal of Coastal Research* 14: 939-950.
- Peragallo, H., and M. Peragallo. 1908. In M.J. Tempere (Editor), *Diatomees de France*, 2. Grez-sur-Loing: Micrographe-Editeur.
- Pierce, R.H., D.L. Wetzel, and E.D. Estevez. 2004. Charlotte Harbor Initiative: Assessing the ecological health of Southwest Florida's Charlotte Harbor estuary. *Ecotoxicology* 13: 275-284.
- Powell, T., and P.J. Richerson. 1985. Temporal Variation, Spatial Heterogeneity, and Competition for Resources in Plankton Systems: A Theoretical Model. *The American Naturalist* 125: 431-464.
- Schiermeier, Q. 2011. Can violent hurricanes, floods and droughts be pinned on climate change? Scientists are beginning to say yes. *Nature* 477: 148-149.

- Siqueiros-Beltrones, D., F.O. López-Fuerte, and I. Gárate-Lizárraga. 2005. Structure of Diatom Assemblages Living on Prop Roots of the Red Mangrove (*Rhizophora mangle*) from the West Coast of Baja California Sur, México. *Pacific Science* 59: 79-96.
- Soininen, J. and P. Eloranta. 2004. Seasonal persistence and stability of diatom communities in rivers: are there habitat specific differences? *European Journal of Phycology* 39: 153-160.
- Son, S., T. Platt, C. Fuentes-Yaco, H. Bouman, E. Devred, Y. Wu, and S. Sathyendranath. 2007. Possible biogeochemical response to the passage of Hurricane Fabian observed by satellites. *Journal of Plankton Research* 29: 687-697.
- Stevens, P.W, D.A. Blewett, and J.P. Casey. 2006. Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of hurricane Charley. *Estuaries and Coasts* 29: 997-1003.
- Stewart, S.R. 2013. Atlantic Hurricanes 2012: Northeastern United States Devastated by Sandy. *Weatherwise* 66: 28-39.
- Tomasko, D.A., C. Anastasiou, and C. Kovach. 2006. Dissolved oxygen dynamics in Charlotte Harbor and its contributing watershed, in response to Hurricanes Charley, Frances, and Jeanne – Impacts and recovery. *Estuaries and Coasts* 29: 932-938.
- Townsend, C., S. Doledec, and M. Scarsbrook. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology* 37: 367–387.
- Weisberg, R.H., B.D. Black, and H. Yang. 1996. Seasonal modulation of the West Florida Continental Shelf Circulation. *Geophysical Research Letters* 23: 2247-2250.
- Williams, C., J. Boyer and F. Jochem. 2008. Indirect Hurricane Effects on Resource Availability and Microbial Communities in a Subtropical Wetland-Estuary Transition Zone. *Estuaries and Coasts* 31: 204-214.
- Witkowski, A., H. Lange-Bertalot, and D. Metzeltin. 2000. Diatom flora of marine coasts. I. *Iconographia Diatomologica* 7: 1-925.
- Zeng, H., S. Lirong, Y. Zhigang, and C. Hongtao. 2006. Distribution of phytoplankton in the Three-Gorge Reservoir during rainy and dry seasons. *Science of the Total Environment* 367: 999-1009.
- Zong, Y., J.M. Lloyd, M.J. Leng, W.W.S. Yim, and G. Huang. 2006. Reconstruction of Holocene monsoon history from the Pearl River Estuary, southern China, using diatoms and carbon isotope ratios. *The Holocene* 16: 251-263.