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research paper

Shift in baseline chlorophyll *a* concentration following a three-year *Synechococcus* bloom in southeastern Florida

NC Millette [1, 2, 3] *
C Kelble [3]
A Linhoss [4]
S Ashby [2]
L Visser [3, 5]

[1] *Mississippi State University, Starkville, Mississippi 39762.*

[2] *Northern Gulf Institute, Mississippi State University, Stennis Space Center, Mississippi 39529.*

[3] *National Oceanic and Atmospheric Administration, Atlantic Oceanographic and Meteorological Laboratory, Miami, Florida 33149.*

[4] *Agricultural and Biological Engineering, Mississippi State University, Starkville, Mississippi 39762.*

[5] *Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Miami, Florida 33149.*

* *Corresponding author email: <nicole.millette@noaa.gov>.*

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ABSTRACT.—A picophytoplankton bloom dominated by *Synechococcus* formed in September 2005 in a series of shallow lagoons between Florida Bay and Biscayne Bay and lasted until May 2008. Chlorophyll *a* concentrations peaked at >20 μg L^{-1}. The bloom coincided with a massive mortality of sponges and caused massive mortality of the seagrass. However, follow-up analysis to determine if there were any long-term impacts from the bloom on the system is lacking. We used long-term water quality data (chlorophyll *a* and nutrient concentrations) collected at 13 stations in the affected region over a 20-yr period to compare environmental conditions before (1995–2004) and after (2009–2014) the bloom. We found that after the bloom, baseline chlorophyll *a* concentration significantly increased 45%, from 0.42 (SE 0.02) to 0.77 (SE 0.04) μg chl *a* L^{-1}, at the stations most impacted by the bloom. Before-After Control-Impact paired analysis suggested these changes were related to the 3-yr bloom and not a larger, regional scale shift. The increase in chlorophyll *a* does not appear to be associated with additional changes in water quality, but is potentially due to a reduction in the epibenthic community (e.g., SAV and sponges). Now that the bloom has terminated and the causes of the bloom abated, the system has not returned to its original status, suggesting a lasting impact from the bloom on the ecosystem.

In September 2005, a cyanobacteria bloom of *Synechococcus* formed in the Manatee Bay and Barnes Sound region of south Florida (Rudnick et al. 2007, Glibert et al. 2009). The bloom, dominated by three clades of *Synechococcus*—WH8101, CB0201, and RS9708—lasted 3 yrs, and spanned from Duck Key in Florida Bay to Card Sound in southern Biscayne Bay (Fig. 1) (Rudnick et al. 2007, Glibert et al. 2009). A combination of three hurricanes over a 3-mo period (Katrina, Rita, and Wilma) and major construction on an adjacent causeway connecting the mainland to the Florida Keys is hypothesized to have triggered the initiation of the bloom (Rudnick et al. 2007, Glibert et al. 2009). The main factor limiting phytoplankton growth in this region

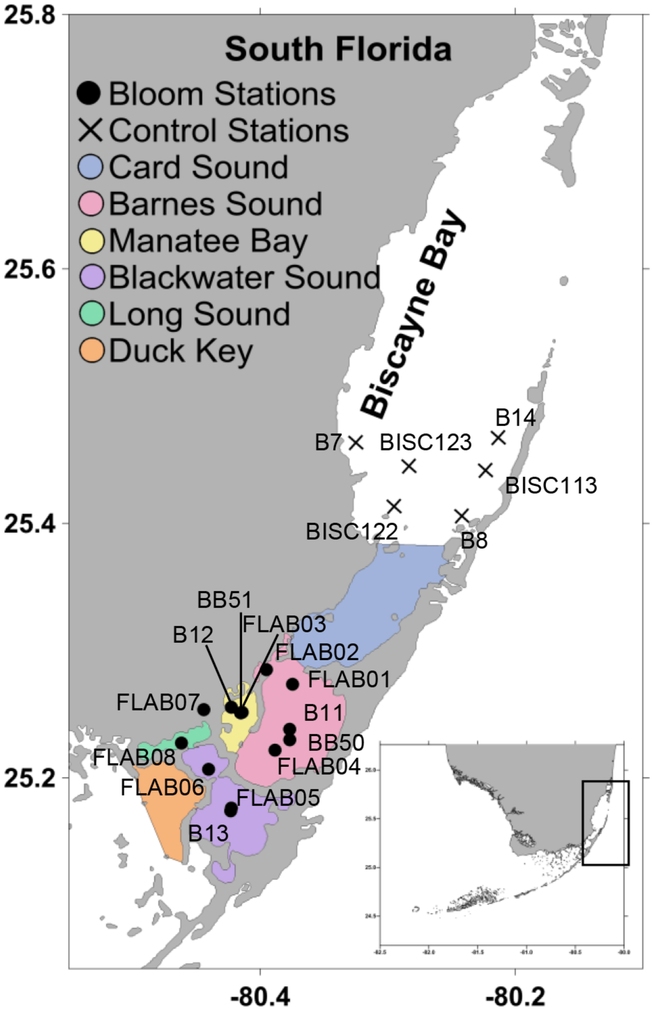

Figure 1. Location of water quality stations in Manatee Bay, Barnes Sound, Blackwater Sound, Long Sound, and Biscayne Bay. Stations in Biscayne Bay were used as controls for some analysis.

is phosphorus (Koch et al. 2001, Nielsen et al. 2006) and the three hurricanes and construction likely released a large concentration of phosphorus through increased run-off from land and disturbance of the sediment, stimulating rapid phytoplankton growth (Glibert et al. 2009). For a full description on the initiation, duration, and termination of this *Synechococcus* bloom, see Glibert et al. (2009).

The region of Manatee Bay, Blackwater Sound, Barnes Sound, and Long Sound (Fig. 1) is where the cyanobacteria bloom had the largest and longest impact (Glibert et al. 2009). The bloom was a dramatic deviation from the normal characteristics of this region. Typically, this region has lower mean chlorophyll *a* concentrations (<2 μg chl *a* L^{-1}) than the adjacent ecosystem of Florida Bay (Phlips et al. 1999). Diatoms and dinoflagellates were the dominant phytoplankton groups in this region in the 1990s (Phlips et al. 1999); however, phytoplankton species data just prior to the bloom were not available. The highest peak in chlorophyll *a* concentrations (>20 µg chl *a* L^{-1}) occurred in Blackwater and Barnes Sound, an order of magnitude higher than average concentrations (Glibert et al. 2009). It is conceivable that following persistent bloom conditions for 3 yrs, the study region never fully recovered.

The bloom was eventually terminated around May 2008 (Glibert et al. 2009), but the lasting impacts of the bloom have never been investigated. There is some evidence that *Synechococcus* is toxic, but its toxicity is poorly understood (Cox et al. 2005, Martins et al. 2007, Hamilton et al. 2014). However, there are many ways a large phytoplankton bloom can negatively impact an ecosystem, regardless of its toxicity, as synthesized by Paerl et al. (2001). During the initiation of the bloom, there was a mass mortality of sponges and following the initiation, high mortality of seagrass and benthic macroalgae were recorded (Rudnick et al. 2008). Such mortality can help to shift the main source of primary production in an ecosystem from the benthic community to the pelagic community and further fuel the bloom (Glibert et al. 2009). It was unknown if the system fully shifted back to being dominated by benthic production after the bloom.

Regime shifts from one stable state to another can occur when an environment experiences a loss of resilience (Folke et al. 2004). The more external stressors added to a system, the more resilience that is lost and the easier it is to exceed a tipping point into a new stable state (Folke et al. 2004). The shift from a benthic submersed aquatic vegetation (SAV) dominant state to a pelagic phytoplankton dominant state is known to occur in shallow lagoons (Gunderson 2001). Large phytoplankton blooms cause light limitation for SAV communities, which can result in SAV mortality (Kleppel et al. 1996, Glibert et al. 2014). Thus, a phytoplankton bloom can cause a tipping point to be exceeded and result in hysteresis. Hysteresis occurs when an ecosystem does not return to its initial stable state after one or more environmental stressors are reduced, and enters into an alternative stable state. The 3-yr bloom caused massive SAV mortality (Rudnick et al. 2008), but prior to our study, it was unknown whether phytoplankton abundances returned to prebloom conditions or a potential regime shift occurred.

We hypothesized that mean phytoplankton abundances increased following the bloom, signaling a shift towards a more phytoplankton-dominant state. We investigated whether water quality returned to prebloom conditions in the 5 yrs following the bloom. Here, we use water quality to refer to nutrient concentrations, specifically nitrate + nitrite (NO_x) and phosphate, NO_x:PO_4^{3-} ratio, and chlorophyll *a* concentrations. Additionally, we looked for any baseline shifts in temperature and salinity. For shifts detected, we determined if they were related to the bloom or to regional processes. Lastly, we explored potential mechanistic causes of any shifts; specifically examining if they were related to other changes in the ecosystem, either in the water column or benthos.

Methods

Location.—Manatee Bay, Blackwater Sound, Barnes Sound, and Long Sound are shallow (<3 m detph) oligotrophic lagoons located between Biscayne Bay and Florida Bay (Fig. 1). The influence of the C-111 canal on this region results in higher inorganic nitrogen and lower inorganic phosphorus concentrations compared to Florida Bay

Table 1. The name, location in Florida Bay, agency in charge of collecting data, and the range of years for which data was available at each station used in the analysis. AOML = Atlantic Oceanographic and Meteorological Laboratory, NOAA = National Oceanic and Atmospheric Administration, DERM = Miami-Dade County's Department of Environmental Resource Management, SFWMD = South Florida Water Management District. See Figure 1 for station locations.

Station name	Region	Collection agency	Years of data
B11	Barnes Sound	AOML/NOAA	2002–2014
B12	Manatee Bay	AOML/NOAA	2002–2014
B13	Blackwater Sound	AOML/NOAA	2002–2014
BB50	Barnes Sound	DERM	1995–2014
BB51	Manatee Bay	DERM	1995–2014
FLAB01	Barnes Sound	SFWMD	1995–2014
FLAB02	Barnes Sound	SFWMD	1995–2014
FLAB03	Manatee Bay	SFWMD	1995–2014
FLAB04	Barnes Sound	SFWMD	1995–2014
FLAB05	Blackwater Sound	SFWMD	1995–2014
FLAB06	Little Blackwater Sound	SFWMD	1995–2014
FLAB07	Long Sound	SFWMD	1995–2014
FLAB08	Long Sound	SFWMD	1995–2014

(Boyer et al. 1997). The low phosphorus concentrations limit phytoplankton growth and, therefore, chlorophyll *a* concentrations (Boyer et al. 1997, Glibert et al. 2009).

Stations.—There are 16 water quality stations throughout Manatee Bay, Blackwater Sound, Barnes Sound, and Long Sound that are sampled by three different agencies, the National Oceanic and Atmospheric Administration (NOAA), Miami-Dade County's Department of Environmental Resources Management (DERM), and the South Florida Water Management District (SFWMD). For the purpose of our study, we selected 13 stations to analyze based on the availability of sufficient chlorophyll *a* data before and after the 2005–2008 bloom (Table 1). The parameters collected and methods used to collect data at each station varied based on which agency sampled the station; therefore, we analyzed only parameters consistently collected at most

Table 2. A list of the instruments and laboratory methods used to collect and analyze the data collected by Atlantic Oceanographic and Meteorological Laboratory (AOML), South Florida Water Management District (SFWMD), and Department of Environmental Resources Management of Miami-Dade County, Florida (DERM) and used in the present study. Temperature and salinity were both measured in situ with various instruments. Chlorophyll *a* (Chl *a*), NO_x, and PO_4^{3-} concentrations were collected in situ and analyzed in the laboratory with a range of methods.

Agency	Temperature	Salinity	Chl *a*	NO_x	PO_4^{3-}
AOML	Seabird SBE 21 TSG	Seabird SBE 21 TSG	Filtration extraction using a 60:40 mixture of acetone and dimethyl sulfide (Shoaf and Lium 1976)	EPA Methods 353.4	EPA Methods 365.5
SFWMD	Hydrolab multiparameter sonde	Hydrolab multiparameter sonde	Filtration extraction using a 90% acetone (Strickland and Parson 1972)	Alpkem model RFA 300 (Caccia and Boyer 2007)	Alpkem model RFA 300 (Caccia and Boyer 2007)
DERM	Hydrolab Sonde Model 3 and 4 (until 2006) YSI 600 xlm (after 2006)	Hydrolab Sonde Model 3 and 4 (until 2006) YSI 600 xlm (after 2006)	Filtration extraction using a 90% acetone (EPA Methods 445.0)	N/A	N/A

stations with no apparent bias between different methods: temperature, salinity, chlorophyll *a*, nitrate + nitrite, and soluble reactive phosphate (Table 2). Additionally, for each sampling point we calculated a NO_x:PO_4^{3-} ratio using nitrate +nitrite and soluble reactive phosphate concentrations. DERM did not report nutrient data for stations BB50 and BB51, but these stations were included because they are near stations FLAB04 and FLAB03, respectively (Fig. 1), which did report nutrient data.

Pre- and Postbloom.—For our analysis, we defined prebloom as January 1995 to December 2004 and postbloom as January 2009 to December 2014. We began our analysis in 1995 because there was a shift in the Atlantic multi-decadal oscillation around 1995 that significantly shifted chlorophyll *a* in south Florida coastal waters, including our study domain (Briceño and Boyer 2010). Ten of the 13 stations had data starting in 1995; the remaining three stations (B11, B12, and B13) had data starting in 2002 (Table 1). The bloom started in mid–late 2005, and continued until early-mid 2008 (Glibert et al. 2009). We defined the bloom period as January 2005–December 2008 to ensure the prebloom period was before the system experienced any changes leading up to the 3-yr bloom and that the postbloom period was after the region had sufficient time to recover following termination of the bloom.

Analysis.—Initially, the data from each month for all stations were averaged together for preliminary analysis. We then broke the stations into two groups based on whether chlorophyll *a* at the individual stations returned to prebloom concentrations or not following the termination of the bloom. Environmental parameters can be highly variable over space and time, especially in coastal systems. Averaging data from multiple stations over space and time helps to reduce the variability and identify the dominant changes throughout the entire sample area. Analyzing each station individually acknowledges that not every station is responding the same to changes in the system. Then, through grouping stations together based on whether chlorophyll *a* concentrations returned to prebloom concentrations or not, we were able to compare changes to other environmental factors between the two station groups.

Unequal variance *t*-tests were used to compare the average pre- and postbloom values for each environmental factor. A 12-mo moving average was used to transform the data before estimating the rate of change via linear regression for each factor pre- and postbloom. The moving average was calculated by averaging the 6 mo prior and 6 mo following each time point. A 12-mo moving average helps remove seasonal cycles and random components of a data set to facilitate analysis of overall trends (OECD 2007). The rate of change was estimated using the slope from linear regression analyses. While postbloom rates of change could be compared between altered stations and unaltered stations, there were insufficient years of data to detect an accurate long-term trend (Meals et al. 2011).

Before-After Control-Impact (BACI) analysis was employed to examine whether changes observed in the region affected by the 3-yr bloom could be attributed to the bloom vs regional scale changes (Smith 2002). The control group for this analysis was six water quality stations in southern Biscayne Bay (Fig. 1; SFWMD: BISC113, BISC122, and BISC123; and NOAA: B7, B8, and B14). Manatee Bay and Barnes Sound connect with southern Biscayne Bay through Card Sound (Wang et al. 2003) (Fig. 1). These stations are north of the study region and were selected because they were close to Manatee Bay and Barnes Sound, had enough data before and after the bloom, and showed no indication of having been affected by the bloom. The monthly data at each station were averaged, as described above, to create a single control group.

Results

Mean Chlorophyll *a*.—Before we transformed the data using a 12-mo moving average, we compared the chlorophyll *a* concentrations prebloom and postbloom at each station. Chlorophyll *a* concentrations at stations B11, B13, BB50, BB51, FLAB01, FLAB02, FLAB03, FLAB04, and FLAB05 were all significantly higher postbloom compared to prebloom ($P < 0.05$, Fig. 2). Chlorophyll *a* concentrations at stations B12, FLAB06, FLAB07, and FLAB08 were not significantly different postbloom compared to prebloom ($P > 0.05$, Fig. 2). Thus, for all further analyses we combined the stations into two different groups, stations where there was a significant increase in chlorophyll *a* concentrations postbloom (altered group) and stations where there was not a significant change (unaltered group).

The mean chlorophyll *a* concentrations for the altered group were 0.42 (SE 0.02) μg chl *a* L^{-1} prebloom compared to 0.77 (SE 0.04) μg chl *a* L^{-1} postbloom (Table 3). The mean chlorophyll *a* concentrations for the unaltered group 0.63 (SE 0.03) μg chl *a* L^{-1} per-bloom compared to 0.67 (SE 0.04) μg chl *a* L^{-1} postbloom (Table 3). Before the bloom, chlorophyll *a* concentration for the unaltered group was significantly higher than that for the altered group (unequal variance *t*-test: $P < 0.001$, $n = 108$). Following the bloom, there was no significant difference in the chlorophyll *a* concentrations between the two groups (unequal variance *t*-test: $P = 0.10$, $n = 60$).

Before the bloom, chlorophyll *a* concentrations at altered and unaltered stations were stable over the 10-yr period (Fig. 3A, B). After the bloom, chlorophyll *a* at unaltered stations continued to be stable (Fig. 3B). At altered stations, there was a weak significant increase in chlorophyll *a* over the 5-yr period (Fig. 4A).

The BACI analysis indicated that the difference between chlorophyll *a* concentrations at altered stations and the control group was significantly higher after the bloom [+0.31 (SE 0.06) μg chl *a* L^{-1}] compared to before the bloom [+0.13 (SE 0.01) μg chl *a* L^{-1}] (unequal variance *t*-test: $P = 0.004$, $n = 108$, Fig. 4). However, the difference between chlorophyll *a* concentrations at unaltered stations and the control group was not significantly different after the bloom [+0.21 (SE 0.06) μg chl *a* L^{-1}] compared to before the bloom [+0.34 (SE 0.03) μg chl *a* L^{-1}] (unequal variance *t*-test: $P = 0.07$, $n = 60$, Fig. 4).

Changes in Water Quality.—As with the chlorophyll *a* data, we averaged selected environmental parameters among all stations in the altered group and unaltered group for each month from 1995 to 2004 and from 2009 to 2014. We examined temperature (°C), salinity, nitrate + nitrite (NO_x, μmol L^{-1}), phosphate (PO_4^{3-}, μmol L^{-1}), and the ratio of NO_x:PO_4^{3-}.

Temperature was not significantly different between altered and unaltered stations, and pre- and postbloom (Table 3). At both the unaltered and altered stations, salinity was significantly higher postbloom compared to prebloom (Table 3). Moreover, salinity at altered stations was significantly higher both pre- and postbloom compared to the unaltered stations (Table 3). However, salinity increased 28% at unaltered stations, but only increased 9% at altered stations postbloom compared to prebloom.

NO_x concentrations significantly decreased after the bloom at both unaltered and altered stations (Table 3). After the bloom, NO_x concentrations were significantly higher at altered stations compared to unaltered stations; whereas prior to the bloom there was no difference (Table 3). There was no significant change in

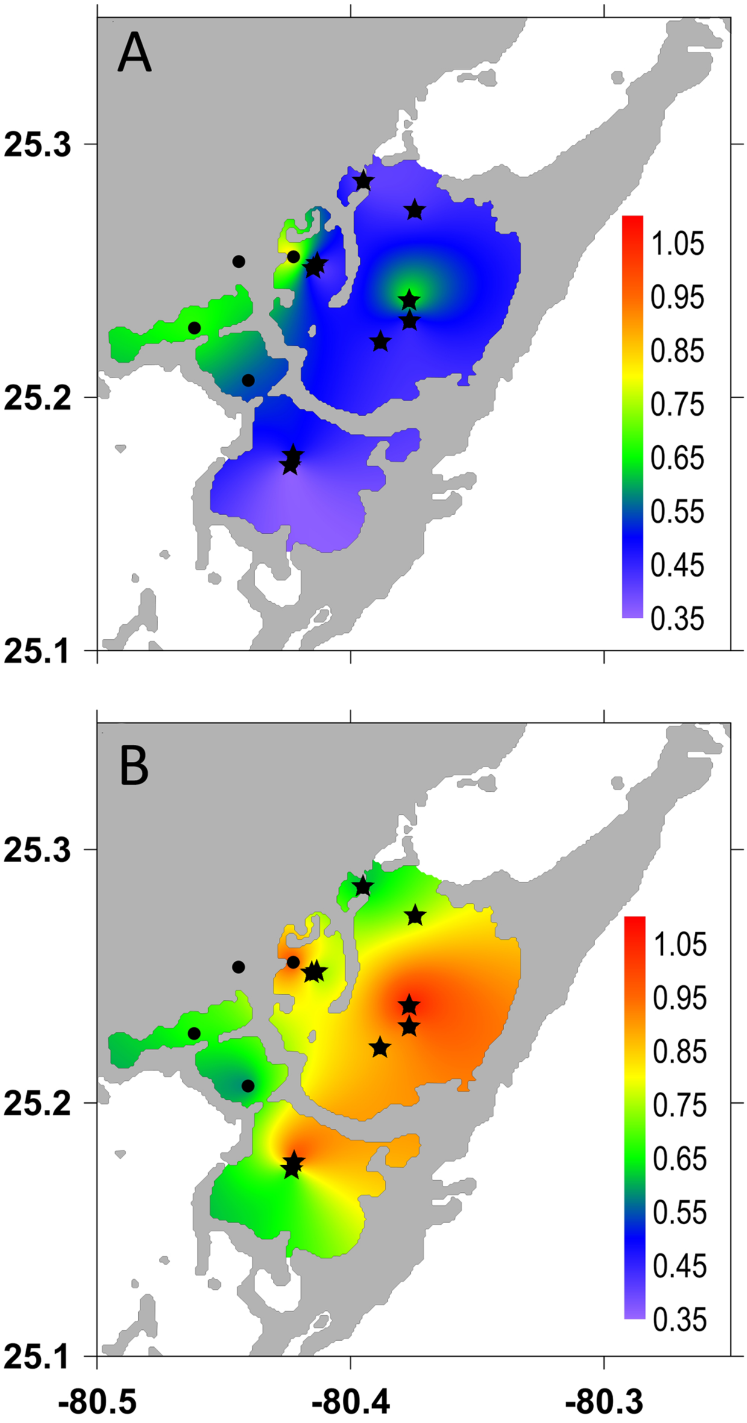

Figure 2. A spatial map of interpolated mean chlorophyll *a* ($\mu g\ L^{-1}$) concentrations at each station (A) prebloom (1995–2004) and (B) postbloom (2009–2014). The black stars are stations where chlorophyll *a* concentrations were significantly higher ($P < 0.05$) postbloom compared to prebloom and the black circles are where there was no significant difference ($P > 0.05$).

Table 3. A comparison of mean values (SE) for water quality factors before the three-year bloom (1995–2004) to after the bloom (2009–2014) at stations where chlorophyll *a* was not significantly different after the bloom (unaltered) and significantly different after the bloom (altered). * When the mean value of a factor within the same group was significantly different ($P < 0.05$) after the bloom compared to before the bloom. ¥ When the mean value of a factor between groups at the same time point was significantly different ($P > 0.05$).

Group and time	*n*	Temp (°C)	Salinity	Chl *a* (µg L^{-1})	NO_x (µmol L^{-1})	PO_4^{3-} (µmol L^{-1})	NO_x:PO_4^{3-}
Unaltered							
Prebloom	108	26.01 (0.36)	16.57 (0.87)	0.63 (0.03)	1.22 (0.07)	0.06 (0.01)	39.84 (6.32)
Postbloom	60	25.86 (0.59)	23.08 (1.06)*	0.67 (0.04)	0.61 (0.06)*	0.05 (0.01)	14.29 (1.42)*
Altered							
Prebloom	108	25.84 (0.34)	26.96 (0.50)¥	0.42 (0.02)¥	1.20 (0.10)	0.04 (0.00)¥	139.62 (48.50)¥
Postbloom	60	25.46 (0.48)	29.69 (0.53)*¥	0.77 (0.04)*	0.87 (0.10) *¥	0.05 (0.00)	24.54 (3.91)*¥

PO_4^{3-} concentrations following the bloom at unaltered and altered stations, but before the bloom, PO_4^{3-} concentrations were significantly higher at unaltered stations, and following the bloom there was no significant difference between the two groups of stations (Table 3). At both the unaltered and altered stations, the NO_x:PO_4^{3-} ratio significantly decreased postbloom compared to prebloom. NO_x:PO_4^{3-} was always significantly higher at the altered stations compared to the unaltered stations (Table 3).

We analyzed the pre- and postbloom rate of change for water quality parameters that were significantly different after the 3-yr bloom (Fig. 3). Prebloom, salinity was significantly increasing at unaltered stations and altered stations (Fig. 3). Postbloom, salinity was still significantly increasing at unaltered stations, but was not significantly changing at altered stations (Fig. 3). At unaltered and altered stations, NO_x and NO_x:PO_4^{3-} were significantly decreasing pre- and postbloom (Fig. 3).

Using a Pearson's correlation analysis, we determined whether any of the changes in salinity, NO_x, and, NO_x:PO_4^{3-} were correlated for each group of factors (Table 4). Prebloom, changes in NO_x concentrations were significantly negatively correlated to salinity at both altered and unaltered stations (Table 4). Postbloom, changes in NO_x concentrations were significantly negatively correlated to salinity at unaltered stations (Table 4), but not altered stations (Table 4). Both pre- and postbloom, changes in NO_x: PO_4^{3-} ratios were significantly positively correlated with NO_x concentrations at both altered and unaltered sites, but with much higher *r*-values postbloom (Table 4).

DISCUSSION

Following the 3-yr bloom, chlorophyll *a* concentrations in Manatee Bay, Blackwater Sound, and Barnes Sound did not recover to prebloom concentrations. The mean chlorophyll *a* concentration in these three systems was 45% higher in the 5 yrs (2009–2014) following the bloom compared to the 10 yrs (1995–2004) before the bloom. In Long Sound chlorophyll *a* completely recovered to prebloom concentrations, although this region was less affected during the 3-yr bloom compared to the other three lagoons (Glibert et al. 2009). Based on the environmental factors analyzed, we found no connection between the changes in environmental parameters and the increase in mean chlorophyll *a* concentrations.

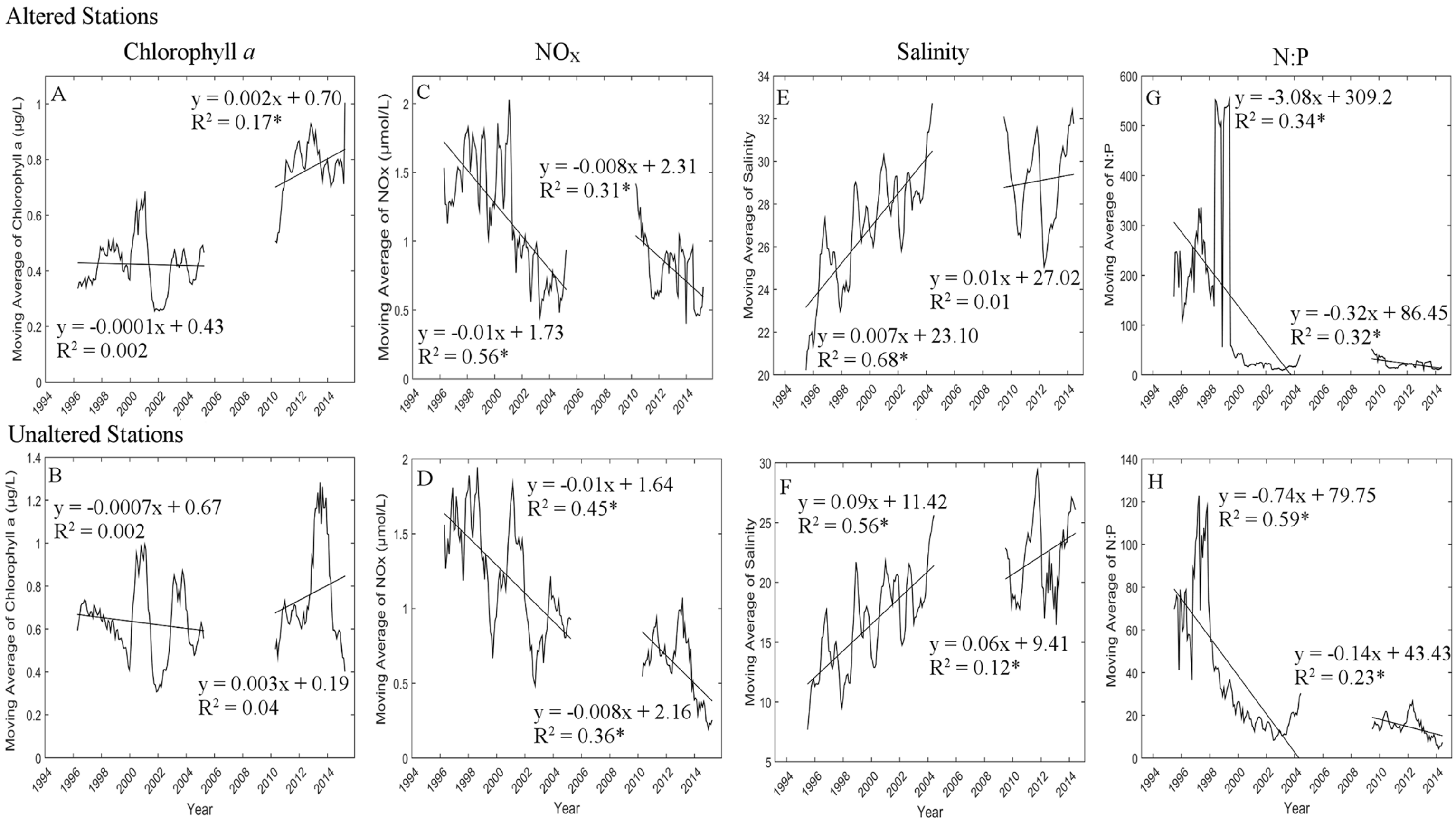

Figure 3. The 12 month moving averages of chlorophyll *a* (µg L^{-1}) concentrations (A,B), NO_x (µmol L^{-1}) concentrations (C,D), salinity (E,F), and NO_x:PO_4^{3-} (G,H) from altered stations (top) and unaltered stations (bottom) prebloom (1995–2004) and postbloom (2009–2014). *Refers to a slope in the linear regression that is significantly different than zero ($P > 0.05$).

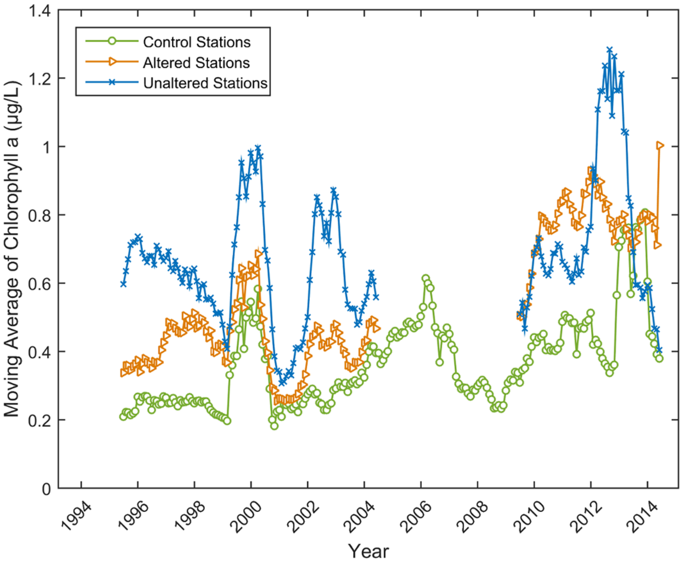

Figure 4. The 12-mo moving average of chlorophyll *a* concentrations (μg L^{-1}) at control stations (green circles), altered stations (orange triangles), and unaltered stations (blue ×'s). For altered and unaltered stations data from 2005 to 2008 during the bloom was removed but data during this range were retained for the control stations.

Shift in Mean Chlorophyll *a* Baseline.—In the study region, there is no evidence that chlorophyll *a* concentrations were increasing over time prior to the bloom, but following the bloom there was a clear shift in the baseline with the mean chlorophyll *a* concentration increased by 45% at altered stations. The altered stations were located in the region most affected by the 3-yr bloom, while the unaltered stations were in a region less impacted by the bloom (Glibert et al. 2009). This is consistent with our conclusion that the shift in baseline chlorophyll *a* concentrations were related to the 2005–2008 bloom. If the increase in chlorophyll *a* concentrations were unrelated to the bloom, we would have expected chlorophyll *a* concentrations to begin to change before the bloom or to see a baseline shift occur at a larger regional scale, such as in the control group. However, we found no evidence of either occurring in our analysis.

Following the bloom, a weak significant increasing trend in chlorophyll *a* concentrations at altered stations was detected. However, the postbloom time-series only covers 5 yrs of data and appears to be overly influenced by the beginning and ending time points. Therefore, we have low confidence that this represents a real increasing trend. This suggests that chlorophyll *a* concentrations should not continue to shift away from the new baseline.

Currently, there are no data on phytoplankton species composition following the bloom. In the 1990s, diatoms and dinoflagellates dominated the phytoplankton biovolume throughout the year (Phlips et al. 1999). During the bloom, the phytoplankton species composition was altered and cyanobacteria (*Synechococcus*) dominated the phytoplankton biovolume (Glibert et al. 2009). While we have shown that the mean chlorophyll *a* concentration at altered stations increased following the bloom, it is unknown if diatoms and dinoflagellates returned as the dominant groups,

Table 4. Results from Pearson correlation analysis that compared the correlations between salinity, nitrate + nitrite, and NO_x:PO_4^{3-}. The analysis was run for each set of factors, at altered and unaltered stations, prebloom ($n = 108$) and postbloom ($n = 60$). We used the moving mean transformed data for this analysis. * Significant correlation ($P < 0.05$).

	Altered stations		Unaltered stations	
	NO_x	NO_x:PO_4^{3-}	NO_x	NO_x:PO_4^{3-}
Prebloom				
Salinity	−0.60*	−0.41*	−0.68*	−0.62*
NO_x		0.53*		0.69*
Postbloom				
Salinity	0.05	0.08	−0.50*	−0.55*
NO_x		0.95*		0.97*

cyanobacteria continues to dominate, or a new assemblage of phytoplankton has become the most abundant group. Collection of water samples to analyze phytoplankton species composition is needed to fully understand whether there was just a shift in the baseline of phytoplankton abundances, or a shift in the species composition occurred as well.

The shift in mean chlorophyll *a* concentrations throughout Manatee Bay, Blackwater Sound, and Barnes Sound signals that the 3-yr bloom had a lasting effect on these systems, but additional data on how phytoplankton species composition was affected may help determine the full impact. The population dynamics of phytoplankton are directly linked to large-scale oceanographic phenomena, such as biogeochemical cycling, fisheries sustainability, and shifts in global climate. Changes in the phytoplankton population dynamics and community will ultimately affect top trophic levels (Fredericksen et al. 2006). Protists, the primary grazers of phytoplankton, can be highly selective, choosing their prey based on a range of factors including, size, shape, and chemical composition (Tillmann 2004). If there were a shift in the phytoplankton species composition in addition to an increase in abundance, then the lasting impact of the 2005–2008 bloom would affect the zooplankton population and higher trophic levels.

CHANGES IN WATER QUALITY.—There was no evidence that changes in water quality parameters following the bloom caused the shift in chlorophyll *a* at altered stations. While certain water quality parameters were significantly different postbloom, these parameters were already trending significantly upward or downward during the 10 yrs prior to the bloom. If the change in chlorophyll *a* was related to any of the water quality factors we analyzed, then we would have expected chlorophyll *a* concentrations to be significantly increasing over the 10-yr period before the bloom. Chlorophyll *a* concentrations and water quality changed from 1995 to 2014, although it appears the changes were due to separate reasons.

The changes in salinity, NO_x concentrations, and the NO_x:PO_4^{3-} ratio from 1995 to 2004 were likely related to efforts taken by SFWMD to redirect the water flow from the C-111 canal (WRDA 2000). The C-111 canal, the largest source of freshwater into this region, was built in 1966 to divert water away from the Everglades into Manatee Bay (McIvor et al. 1994). However, the stated goals of the Comprehensive Everglades Restoration Plan are to increase freshwater flow back toward the Everglades and away from the C-111 canal (WRDA 2000). This reduction in freshwater flow out of

C-111 began shortly after 2000, and was likely the cause of increasing salinity and decreasing NO_x. Freshwater river flow is the primary source of NO_x (Caccia and Boyer 2007); therefore, a reduction of freshwater inflow from C-111 would simultaneously increase salinity and decrease NO_x concentrations. It appears that the decrease in NO_x:PO_4^{3-} was caused primarily by the decrease in NO_x concentrations. Thus, it is likely that the changes in the water quality parameters we analyzed were caused by redirecting the flow of C-111, and not the 2005–2008 bloom.

Possible Causes for a Baseline Shift.—We hypothesize that the shift in the baseline chlorophyll *a* concentrations after the 2005–2008 *Synechococcus* bloom was the result of a reduction in the epibenthic community, specifically SAV and sponges. Loss of SAV may have increased the concentration of nutrients available to phytoplankton (Hunt and Nuttle 2007), and decreased the abundance of epifaunal suspension-feeders, such as bryozans and amphipods, that can consume high quantities of phytoplankton (Lemmens et al. 1996, Lisbjerg and Peterson 2000). The loss of sponges would also have reduced grazing pressure on phytoplankton (Peterson et al. 2006).

Before the 3-yr bloom, the majority of primary production was produced by epibenthic plants, and as a result, pelagic productivity was low (Fourqurean et al. 2002, Nielsen et al. 2006). Phosphorus is considered the primary limiting nutrient in the study region, with most of the phosphorus found in the sediment, available to the benthic community, but not the pelagic community (Koch et al. 2001). After the initiation of the *Synechococcus* bloom, massive mortality of the SAV community was recorded (Rudnick et al. 2008). The large reduction in SAV cover likely caused an increase in pelagic phosphorus concentrations, further sustaining the bloom (Hunt and Nuttle 2007, Glibert et al. 2009). This created a feedback loop between the bloom and SAV, with SAV mortality fueling the bloom by releasing phosphorus that, in turn, caused additional light limitation and mortality for the SAV population (Glibert et al. 2009).

Preliminary analysis of SAV coverage data by DERM suggest that total SAV coverage in Manatee Bay and Barnes Sound is currently lower compared to 2005 (Avila et al. 2017). This could mean that more phosphorus may continue to be available to the pelagic phytoplankton compared to before the bloom and support higher phytoplankton abundances. Our analysis did not show a significant increase in PO_4^{3-} concentrations following the bloom, but PO_4^{3-} concentrations were no longer significantly different between altered and unaltered stations after the bloom. If SAV coverage was lower near unaltered stations before the bloom compared to altered stations, this could explain why chlorophyll *a* and PO_4^{3-} concentrations were significantly higher at unaltered stations before the bloom. If SAV coverage did not completely recover near altered stations following the bloom and is now similar to SAV coverage near unaltered stations, then that could be why chlorophyll *a* and PO_4^{3-} concentrations are now similar throughout the study area. However, further analysis of SAV coverage data is needed to test this hypothesis.

Almost complete mortality of benthic sponges occurred leading up to the initiation of the *Synechococcus* bloom, between July and October 2005 (Alleman et al. 2009). The mortality was likely caused by high sedimentation related to the series of hurricanes—Katrina (August 2005), Rita (September 2005), and Wilma (October 2005)—that passed through southern Florida, and the sponges did not recover by the end of the bloom (Alleman et al. 2009). Sponge mortality was likely not caused by the

Synechococcus bloom because the bloom initiated in September 2005 (Glibert et al. 2009), after most of the mortality occurred (Alleman et al. 2009). Sponges graze on a range of phytoplankton (Peterson et al. 2006); therefore, a large loss of sponges would reduce grazing pressure on phytoplankton and could have contributed to the initial increase in chlorophyll *a* concentrations. As with SAV, there is no analysis on how sponge populations have recovered following the bloom. If benthic sponge coverage remains near zero, then the continued reduced grazing pressure would allow for an increase in mean phytoplankton abundance.

Benthic coverage data is collected by DERM (Avila et al. 2017) and Florida's Fish and Wildlife Research Institute (Hall and Durako 2016), but further study is needed to address the current status of SAV and sponge coverage compared to before the bloom. This is necessary to confirm whether a continued loss or reduction of SAV and sponge populations caused the increase in mean chlorophyll *a* concentrations following the bloom. Additionally, if data are available, a comparison of benthic sponge and SAV coverage at altered and unaltered stations before and after the bloom is needed to help understand why chlorophyll *a* concentrations were higher at unaltered stations before the bloom, but not significantly different after the bloom. Loss of benthic communities, typically SAV, has led to alternative stable states in other coastal systems that have shifted towards a more phytoplankton-dominant state (Burkholder et al. 2007, Glibert et al. 2014).

Typically, when coastal ecological communities exceed a tipping point into a new stable state, it is caused by sustained eutrophication over an extended period of time (Duarte et al. 2009, Wang et al. 2012, Glibert et al. 2014). We suggest, in the present study region, a tipping point at altered stations apparently was surpassed at some point over the 3-yr bloom, as compared to a decade or more in typical eutrophied systems (e.g., Tampa Bay, Maryland and Virginia coastal lagoons, and the Black Sea). The study region had no symptoms of eutrophication before the bloom, in fact, inorganic N was decreasing. It is possible the 3-yr bloom was such an extreme event that it sped up a process which normally takes much longer. Typically, one of the first symptoms of eutrophication is the increase in chlorophyll *a* concentrations (Bricker et al. 1999, Chislock et al. 2013), but before a tipping point occurs, there is a loss of resilience in a system caused by a range of factors, such as reduction in SAV coverage (Zhang et al. 2003, Barbier et al. 2011).

The rapid and sustained increase in chlorophyll *a* concentrations by an order of magnitude was caused by a large increase in phosphorus concentrations (Glibert et al. 2009) and could have reduced the resilience through massive mortality of SAV beds (Rudnick et al. 2008). Once external stressors (here, high inputs of nutrients) are removed from an ecosystem, it is possible it will fail to return to its original state because changes that occurred still remain (Duarte et al. 2009, Burkholder and Glibert 2013). In the case of the 3-yr bloom, once the large increase of phosphorus that initiated and sustained the bloom returned to normal concentrations, chlorophyll *a* concentrations decreased, but did not completely return to prebloom levels. This finding suggests that some of the changes to the system caused by the extreme eutrophication event, such as the loss of SAV, remain. It is possible that by identifying and restoring these lingering alterations, the system could completely recover to its prebloom state.

Summary.—Before the 2005–2008 bloom, the system was in a state of benthic dominance, and then during the bloom the system shifted towards a state of phytoplankton dominance (Glibert et al. 2009). After the bloom, chlorophyll *a* concentrations in the most affected area did not return to prebloom conditions and formed a new baseline, suggesting that the phytoplankton community is now relatively more productive compared to before the bloom. During the bloom, there was a large loss of SAV and sponges (Rudnick et al. 2008, Alleman et al. 2009, Glibert et al. 2009) and preliminary analysis suggests some of these communities have not completely recovered (Avila et al. 2017). A reduction in SAV would have made more phosphorus available for pelagic phytoplankton growth, and a reduction of sponges would reduce removal of phytoplankton. We hypothesize that this resulted in a hysteresis that did not allow the system to return to prebloom conditions, even 5 yrs after the bloom terminated and nutrient concentrations returned to normal. The 3-yr bloom appears to have had a lasting impact on a majority of the study area, with an increase in the baseline of mean chlorophyll *a* concentrations, but more research is needed to understand how this change impacts higher trophic levels.

A combination of multiple, extreme stressors started the *Synechococcus* bloom that lasted for 3 yrs. While it is unlikely that this combination of events, three hurricanes over a 3-mo period and major road construction, will occur again, the higher baseline chlorophyll *a* concentrations at altered stations indicate that the ecosystem may be more susceptible to large phytoplankton blooms caused by smaller disturbances. It is hypothesized that the benthic communities have not fully recovered, and that the loss of SAV and sponge populations has persisted. Thus, a minor disturbance to the environment that favored growth of any phytoplankton species could result in another large phytoplankton bloom.

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