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REPORT

A high-latitude coral community with an uncertain future: Stetson Bank, northwestern Gulf of Mexico

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Abstract Limited data exist that detail trends in benthic community composition of high-latitude coral communities. As anthropogenic stressors are projected to increase in number and intensity, long-term monitoring datasets are essential to understanding community stability and ecosystem resilience. In 1993, a long-term monitoring program was initiated at Stetson Bank, in the Gulf of Mexico. Over the course of this monitoring, a major shift in community structure occurred, in which the coral-sponge community was replaced by an algal-dominated community. During the initial years of this study, the coral community at Stetson Bank was relatively stable. Beginning in the late 1990s, sponge cover began a steady decline from over 30 % to less than 25 %. Then, in 2005, the benthic community underwent a further significant change when living coral cover declined from 30 % to less than 8 % and sponges declined to less than 20 % benthic cover. This abrupt shift corresponded with a Caribbean-wide bleaching event in 2005 that caused major mortality of Stetson Bank corals. Previous bleaching events at Stetson Bank did not result in wide-scale coral mortality. Several environmental parameters may have contributed to the rapid decline in this benthic community. We suggest that the combined effects of coastal runoff and elevated temperatures contributed to the observed shift. We present an analysis of 15 years of monitoring data spanning from 1993 to 2008; this dataset provides both a biological baseline and a multiyear trend analysis of the community structure for a high-latitude coral-sponge community in the face of changing climatic conditions.

Keywords High-latitude reef · *Millepora* · Coral bleaching · Phase shift · Stetson Bank · Gulf of Mexico

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Introduction

High-latitude coral communities exist at the northern and southern limits of their ranges and are thus considered 'marginal' environments. This marginality pivots on temperature and light availability, both of which limit coral growth and productivity; these parameters are in turn associated with latitude and water clarity (Kleypas et al. 1999). Further, coral reefs in general evolved under a regime of intermittent disturbances, including temperature and salinity anomalies, coastal runoff and sedimentation, and hurricane impacts (Hughes and Connell 1999). With the predicted effects of climate change—elevated temperatures, ocean acidification, oxygen depletion, decreasing calcification rates, rising sea levels, changes in ocean currents, and increasing likelihood of hypoxic events (Hoegh-Guldberg 1999; Reid et al. 2009; Hoegh-Guldberg and Bruno 2010), high-latitude reef communities, since they are already exposed to marginal environmental conditions,

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can provide insight into how reef communities might respond to changing conditions.

High-latitude reefs, considered to reside between 25 and 32° latitude (e.g., Johannes et al. 1983; Babcock et al. 1994; Moyer et al. 2003; Riegl 2003), are subject to quite variable environmental and local pressures, which drive their community responses. There are a few studies which have detailed the divergent community paths, and alternate hypotheses given the environmental predictors, using long-term data from these reef systems (e.g., Cook et al. 1990; Celliers and Schleyer 2002; Riegl 2003; Schleyer et al. 2008; Lugo-Fernandez and Gravois 2010; Eakin et al. 2010). For example, increased water clarity and solar radiation, along with prior bleaching and high sea temperatures, may have acted cumulatively to induce a massive bleaching event of the reefs of Sodwana Bay in 2000 (Celliers and Schleyer 2002). However, Cook et al. (1990) suggested that the distribution of bleaching they observed in Bermuda in 1988, where the shallow inner reef *Millepora alcicornis* colonies bleached less frequently than deeper outer reef colonies, may in part be due to local adaptation, where corals may be less sensitive to thermal stress if they developed in areas with widely ranging temperatures. Alternatively, Schleyer et al. (2008) found that increasing temperatures in the Greater St Lucia Wetland Park in South Africa are correlated with a reduction in alcyonacea corals and an increase in scleractinian coral cover. Clearly, we still have much to learn about the specific and variable ecology of high-latitude reef systems.

The reefs in the northwestern Gulf of Mexico are largely neglected when it comes to long-term monitoring of their biological communities (Asch and Turgeon 2003; but see Robbart et al. 2008). The reefs supported by the numerous hard-bottom banks in the northwestern Gulf of Mexico provide the opportunity to gain much needed insight into the community dynamics of high-latitude reefs and regional reef stability. An exception to the general lack of long-term understanding is the ongoing monitoring of the Flower Garden Banks coral reefs (Precht et al. 2008; Robbart et al. 2008) and Stetson Bank, all within the Flower Garden Banks National Marine Sanctuary. Stetson Bank is located on the mid-continental shelf in the northwestern Gulf of Mexico, where it is relatively removed from immediate coastal impacts. However, it has been suggested that these areas can be impacted by runoff from major river discharges in the region, such as the Atchafalaya (Dodge and Lang 1983). Additionally, there are several documented anthropogenic threats that may affect Stetson's coral-sponge community, including fishing activity and marine debris (Hickerson et al. 2008; Schmahl et al. 2008). Further, the northwestern Gulf of Mexico is repeatedly impacted by hurricanes and associated high-energy waves (see Doyle 2009; Lugo-Fernandez and Gravois 2010). The physical impacts from hurricanes are often coupled with coastal freshwater runoff (see review by Fabricius 2005; Hickerson et al. 2008; Robbart et al. 2008; Schmahl et al. 2008; Lugo-Fernandez and Gravois 2010). Here, we examine 15 years of photographic and environmental data on the biological community of a high-latitude reef system in the northwestern Gulf of Mexico, with particular investigation into the massive bleaching event in 2005. This dataset provides both a biological baseline and a trend analysis of the community structure for a unique high-latitude coral-sponge community.

Materials and methods

Study site

Stetson Bank is a submerged topographic peak in the northwestern Gulf of Mexico (28.2°N, 94.3°W), 110 km offshore of Galveston, Texas (Fig. 1a). The main feature of Stetson Bank is a series of claystone and siltstone pinnacle formations that harbor a diverse coral-sponge community (Fig. 1c). Rising from surrounding water depths of over 55 meters, the pinnacles of Stetson Bank crest to within 15 m of the sea surface. Surrounded by a clay-mud bottom, the pinnacles provide hard-bottom structure above the depths into relatively clear, warm surface waters. Rezak et al. (1985) characterized the benthic habitat at Stetson Bank as a "*Millepora*-Sponge" community. More generally, the habitat is described as a coral community (Schmahl et al. 2008), meaning that although hermatypic corals are not abundant enough to build reef structure, they are important components of the benthic community, along with a variety of other reef-associated species. A predominant benthic species found at Stetson Bank is the hydrozoan *M. alcicornis* (fire coral), and eleven other species of hermatypic corals have been documented (e.g., *Diploria strigosa*, *Stephanocoenia intersepta*, *Madracis mirabilis*, *M. decactis*, and *Agaricia fragilis*). Sponges, primarily *Chondrilla caribensis f. hermatypica* (Rutzler et al. 2007), *Ircinia strobilina*, and *Agelas clathrodes*, comprise up to 30 % of the benthic biota. A running total of 180 species of fish, including several species of sharks and rays (Pattengill 1998), 644 species of invertebrates, including mollusks and echinoderms, and 2 species of sea turtle (loggerhead *Caretta caretta* and hawksbill *Eretmochelys imbricata*) also inhabit this unique coral-sponge community (see http://flowergarden.noaa.gov for a full species list).

Stetson was first described in the 1950s (Carsey 1950; Stetson 1953; Neumann 1958) due to increasing interest of the oil and gas industry in offshore oil exploration along the continental shelf. Beginning in 1993, a volunteer organization, the Gulf Reef Environmental Action Team

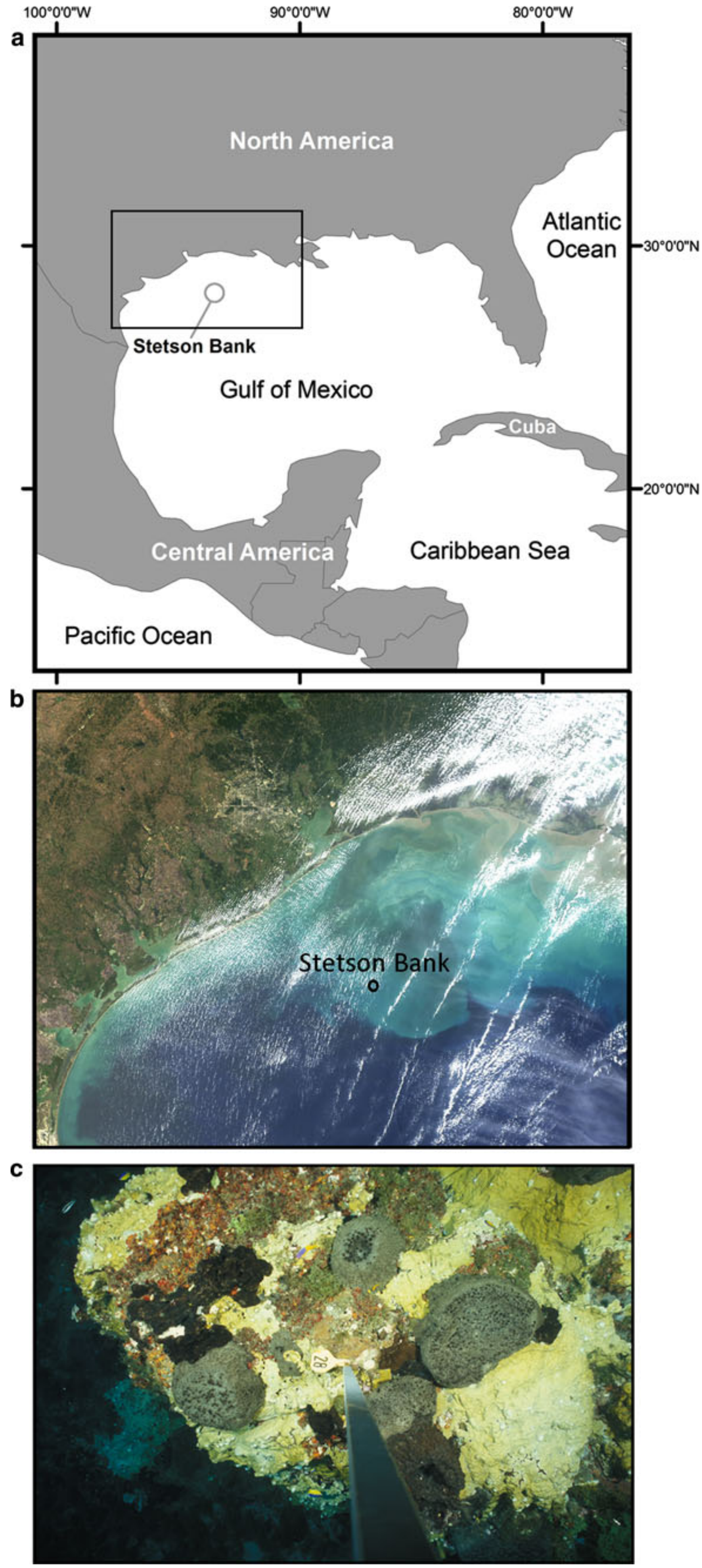

Fig. 1 **a** Location of Stetson Bank, in the northwestern Gulf of Mexico. **b** *Inset* of Texas/Louisiana continental shelf showing satellite imagery of a plume of coastal runoff elicited by Hurricanes Katrina and Rita. The plume moved over 200 km south into the Gulf of Mexico, directly over Stetson Bank. This image is dated September 25, 2005, 1 day after Hurricane Rita's landfall. Data are courtesy of NASA/FSFC MODIS, processed by NOAA Coast Watch. **c** Example of permanent photostation coverage (Pin #28) in 2004

(GREAT), comprised of recreational divers, researchers from Texas A&M University, and the United States Department of the Interior—Bureau of Ocean Energy Management (formerly Minerals Management Service), initiated a monitoring program at Stetson Bank, utilizing permanent photographic stations, fish count methods, and random transect surveys. Over the years, up to 75 photographic stations were established, of which 45 stations are still in existence. Long-term monitoring cruises occur every summer, usually in June or July, weather permitting. In 1996, Stetson Bank was incorporated into the Flower Garden Banks National Marine Sanctuary (FGBNMS) under revisions to the Marine Research and Sanctuaries Act of 1972 (now the Marine Sanctuaries Act), and the monitoring program was supported by the National Oceanic and Atmospheric Administration (NOAA). As part of the FGBNMS, Stetson Bank is afforded protection from most activities that may damage the seafloor (i.e., anchoring, drilling, explosive use) and many types of fishing, other than conventional hook and line.

Repetitive photographic stations

Long-term monitoring cruises were conducted yearly since 1993 (for dates, see Table 1). Permanently marked stations were photographed in the same orientation annually, utilizing a camera and strobes mounted on a 1-meter-high "T-frame" with a bubble leveler and compass. The photographs provided documentation of an approximate area of coverage of 1.6 m^2 each. Originally, a Nikonos V film camera with 15-mm lens was used, and the slides were commercially developed and digitized by scanning at 1,200 pixels per inch (Nikon LS1000). In 2008, a Nikon Coolpix P5000 digital camera, housed in an Ikelite underwater housing with a wide-angle adapter, replaced the Nikonos V film camera. The digital camera was mounted on a modified T-frame (1.25 m high), which provided a slightly larger coverage area than the Nikonos. After downloading digital images, image distortion was removed using Adobe Photoshop CS2 software (Adobe Systems Inc., V9.0.2), and the image was cropped to maintain 1.6 m^2 coverage. Percent benthic cover for species categories (i.e., Coral, Sponge, Algae, Coralline Algae, Other) and individual species (when possible) was determined by a trained observer, from an overlay of 30 random points using Coral Point Count with Excel extensions software (CPCe V3.5; National Coral Reef Institute (NCRI), Florida; Kohler and Gill 2006).

Temperature and salinity measurements

Sea surface temperature (SST) data were obtained from a National Data Buoy Center (NDBC) 3-m discus buoy (Station 42019, 27.91°N, 95.36°W), located 60 nautical miles (111 km) south of Freeport, Texas, and 58 nautical miles (107 km) west-southwest of Stetson Bank. The NDBC buoy reads the water temperature once per hour, at 0.6 m below the water surface, and is positioned over a water depth of 82.3 m. Yearly SST averages, highs, and lows were calculated from measurements of the year preceding the monitoring event (e.g., from May 14, 1997 to July 11, 1998; see Table 1). Hourly temperatures on the reef surface at Stetson Bank were obtained from HOBO® data loggers (1993–1995, 2002–2008; HOBO® Water Temp Pro [H20-001]), data sondes (2004–2008; YSI® 6600 Series), and Sea-Bird instruments (2008; SBE 37, Sea-Bird Electronics, Inc.) placed on the crest of Stetson Bank, at 23.5 m depth. For further analysis, degree heating week (DHW) data from 2001 to 2008 were obtained from NOAA's Coral Reef Watch Program. DHW data provide a measure of the amount of accumulated thermal stress a reef experiences (e.g., 1 DHW is equivalent to 1 week of SSTs 1 °C greater than the expected summertime maximum; for description of DHW methods, see http://www.osdpd.noaa.gov/ml/ocean/cb/dhw.html).

Atchafalaya River discharge

Atchafalaya River discharge (ARD) rates from January 1, 1993 to June 18, 2008, were downloaded from http://www.mvn.usace.army.mil/cgi-bin/watercontrol.pl?03045 (January 10, 2011). Total discharge, daily maximum, and average daily discharge rates were calculated in keeping with the year-prior methodology explained under the temperature measurements methodology above. For this reason, some 'years' have more days of discharge than others.

Tropical storms

Tropical storm tracks in the northwestern Gulf of Mexico, which passed within 200 km of Stetson Bank, between January 1993 and July 2008, were obtained from NOAA's Coastal Services Center (http://csc-s-maps-q.csc.noaa.gov/hurricanes/download.jsp). Tropical hurricanes vary in intensity, strength, and size (Merrill 1984), and very little is known about the degree of impact of various storms on deep underwater features (greater than 20 m depth). The average storm has a radius of 3° latitude (333 km; Merrill 1984) and so, a conservative radius of 200 km around Stetson Bank was delineated to provide a focus on particular storms which may have impacted the biological community of Stetson Bank. Additionally, a recent climatology study conducted on a 200 km buffer around the nearby Flower Garden Banks (WFGB 27°52.5′N, 93°49.0′W; EFGB 27°54.5′N, 93°36.0′W, approximately 48 km southeast of Stetson; Lugo-Fernandez and Gravois 2010) provides an important piece to our understanding of how tropical storms impact

Table 1 Stetson Bank long-term monitoring information, including cruise number, date, number of pins photographed during each cruise, and type of instrumental data collected from the reef crest for that year

Cruise number	Cruise dates	Number of pins photographed	Instrumental data collected (HOBO—temp; YSI, SBE—temp/salinity)
1	October 11–13, 1993	36	HOBO
2	May 15–17, 1994	64	
3	September 26–27, 1994	66	HOBO
4	May 15–16, 1995	65	
5	October 9–11, 1995	57	HOBO
6	June 27–28, 1996	56	
7	May 12–13, 1997	51	
8	July 12–15, 1998	45	
9	June 6–9, 1999	41	
10	June 28–30, 2000	46	
11	August 28–29, 2001	46	
12	June 10–12, 2002	45	HOBO
13	September 2–4, 2003	47	HOBO
14	June 14–16, 2004	46	HOBO/YSI
15	June 13–15, 2005	46	HOBO/YSI
16	June 19–21, 2006	43	HOBO/YSI
17	July 22–25, 2007	45	HOBO/YSI
18	June 15–18, 2008	45	HOBO/YSI/SBE

Pin number varied depending on how many pins were located each year

mid-shelf and shelf-edge reefs in the northwestern Gulf of Mexico. Their findings directly inform our study on the possible impacts of tropical storms on Stetson Bank.

Statistical analyses

Percent cover values for major species categories (i.e., Coral, Sponge, Algae, Coralline Algae, Other) could not be transformed to conform to a normal distribution. Therefore, we analyzed the change in percent cover data for each major species category using nonparametric Friedman's ANOVA. Only photographic stations that were consistently photographed for all years between 1994 and 2008, or were only missing non-consecutive years, were included in the analysis (35 out of a maximum 75 stations). Short, for example, yearly, data gaps were filled using linear interpolation. Photostations from 1993 were excluded from the analysis since only 10 of the 35 consistently photographed stations were in place at that time. In 1994 and 1995, two monitoring cruises were conducted each year. In 1994, cruises occurred in May and September, and in 1995, cruises occurred in May and October. For our analysis, benthic cover data collected during the later cruises (September and October) were used, with the exception of two stations, which were only photographed in May.

Since the dataset included here consists of environmental and percent cover data, both of which are non-normally distributed and are rampant with no-data cells, multivariate classification and regression tree (mCART) analysis was used as the primary methodology to determine variables that might be responsible for influencing the benthic community cover of Stetson Bank. These variables included depth, year, average yearly SST (°C), yearly low temperature (°C), yearly high temperature (°C), maximum degree heating weeks, daily maximum ARD rates (CFS × 1,000), and passage of a tropical storm or hurricane within 200 km in the previous year (yes or no). Analysis was conducted using CART software (DTREG, Sherrod 2003; and *TREES*, S-PLUS 2000, MathSoft, Cambridge, MA, USA).

CART analysis provides statistically robust and ecologically relevant means of analyzing datasets that have nonlinear relationships, contain many missing values, and comprise both continuous and categorical predictors (Breiman et al. 1984; De'ath and Fabricius 2000; Baker and Sheaves 2005). The size of the tree was determined by tenfold cross-validation, and the final tree model selected was the 1-SE tree. Relative importance of the 1-SE tree variables was also determined to investigate whether any variable which did not best predict splits in the final tree might still provide insight into the processes underlying trends in benthic community structure. Variable importance (%) was calculated to determine the overall importance of each of the predictor variables in explaining variance in the final tree. Some variables may explain almost as much variance as the primary splitters (the variables that form splits in the final tree) but do not themselves form splits in the final tree. So, 'importance' measures are more conclusive of the actual values of a predictor. The predictor with the best overall explanatory power is scaled to 100 % importance (Sherrod 2003).

Results

Biological community—repetitive photographic stations

Percent cover of coral at Stetson Bank has changed significantly between 1993 and 2008 (ANOVA, $F_{(1,14)} = 7.5$, $P < 0.05$; Fig. 2a), with the most dramatic decrease in coral occurring after 2005 (Table 2; Electronic Supplemental Material). Benthic cover of coral species ranged between 23 and 32 % from 1993 to 2005 (average ± SEM 28.6 % ± 0.6), peaking at 32 % in 1994 and 1999. In 2006, coral cover fell to 7.4 % (Fig. 2a). Of the coral species present, the fire coral, *M. alcicornis*, showed the most dramatic reduction in percent cover, falling from 27 % in 2005 to 6 % in 2006. Other hermatypic coral species have shown minor fluctuations in percent cover between 1993 and 2008, but were generally stable. In any year, these other species together made up a maximum of 3 % of the overall cover; taken individually, these species' colonies are relatively rare at Stetson Bank and so, inhibit statistical trend analysis.

Algal cover has played a significant role in overall change in benthic cover ($F_{(1,14)} = 47.6, P < 0.001$). Macroalgae, as a general group, increased from 13 % cover in 1993 to a peak of 62 % in 2007. Percent cover of *Dictyota* was variable, peaking above 20 % cover beginning in 2002, but in 2003 accounted for only 1 % cover. Turf-algal matrix peaked in 2005 and 2006 at 30 and 35 %, respectively. Coralline algae (Corallinaceae) averaged 3 % over the 14 years preceding 2008, when it peaked at 10 %.

Sponge cover changed significantly over time ($F_{(1,14)} = 61.4$, $P < 0.001$), decreasing from 39 % in 1993 to a low of 16 % in 2007. Sponge cover first dipped below 30 % in 1997 and again in 1999. From 1999 onward, overall sponge cover decreased, staying below 30 %, while macroalgae steadily increased. The 19 reported sponge species showed differing trends in cover. *Chondrilla caribensis f. hermatypica* decreased from a high of almost 17 % in 1993 to 0.1 % cover in 2008. In contrast, *I. strobilina* remained between 6 and 12 % cover, and *A. clathrodes* between 1 and 2 % cover between 1993 and 2008. An encrusting sponge, *Spirastrella cunctatrix*, ranged between 1.3 and 3.8 % from 1993 until reaching a peak of 6.0 % in 2008.

Physical environment

Temperature and salinity regime

Sea surface temperatures reached a 16 year high in 2005, with water temperatures spiking to 30 °C or greater for 30 days of the year, and for a maximum of 17 consecutive days (21 August to 6 September; Fig. 2b). Temperatures above 30 °C are considered above the bleaching threshold for most tropical corals, depending on the latitude and seasonal maximum SSTs (Manzello et al. 2007a). This high was further apparent in the degree heating weeks (DHW, °C-weeks) analysis (Fig. 3) for years 2001 to 2008, where Stetson Bank was subjected to 6.05 °C-weeks from September to October 2005; degree heating weeks greater than 4 °C-weeks typically result in significant bleaching, while 8 °C-weeks typically result in coral mortality (Eakin et al. 2010). Winter SSTs were also considerably milder in 2005 than in other years, with only 14 days falling below 20 °C and for only 7 consecutive days (14–20 March).

Sea surface and HOBO temperatures showed seasonal fluctuations over the mid-shelf area and Stetson Bank, respectively (Fig. 4). HOBO probes reported lower summer temperatures on the crest of Stetson than nearby, mid-shelf SSTs obtained from the NDBC surface buoy (e.g., August 7, 2005 31.3 °C SST; 29.3 °C HOBO). Further, there were several sudden drops in temperature evidenced by the HOBO dataset, which were not reflected in the SST dataset (e.g., July 15, 2005 29.8 °C SST; 24.6 °C HOBO). These discrepancies could be explained by the occurrence of cold water thermoclines over Stetson Bank during the summer months (see Deslarzes and Lugo-Fernandez 2007). Contrary to summer temperature differences, winter temperatures recorded on the crest of Stetson tended to be warmer than those obtained from the surface buoy (e.g., February 22, 2004 16.2 °C SST; 19.6 °C HOBO).

A particular salinity regime emerged from the limited datasonde measurements acquired from 2002 to 2008. There were repeated freshwater influxes to Stetson Bank during these years (e.g., between November 2002 and January 2004, salinity range observed 25.8–36.9 ppt). However, freshwater influxes in 2005 seemed to be of greater duration and extent than in the other years. In 2006, the average yearly salinity was 35.3 ppt (hourly range from YSI 27.6–38.6 ppt), compared to 32.9 ppt in 2005 (hourly range from YSI 24.2–39.0 ppt). Throughout the end of July and August 2005, daily average salinity measurements were as low as 27 ppt, and with the passage of Hurricane Rita in September, salinity again decreased from an average of 35 ppt to an average daily low of 32 ppt on 2 October (Fig. 5).

Tropical storm track analysis

Twelve tropical storms approached within 200 km of Stetson Bank between 1993 and July 2008 (Table 3). These storms occurred in 10 of the 15 years of the monitoring program. The largest storm during this time period, Hurricane Rita (Category 3), approached within 130 km of Stetson Bank on September 24, 2005. In addition, this storm also impacted the nearby reefs of the Flower Garden Banks (Precht et al. 2008; Robbart et al. 2008). Coastal runoff from Hurricane Rita extended over 161 km

Fig. 2 Long-term data trends at Stetson Bank. **a** Changes in benthic percent cover of Stetson Bank between 1993 and 2008. **b** Average daily sea surface temperatures (*SST*) recorded by National Data Center Buoy 42019, from January 1993 to December 2008. **c** Atchafalaya River discharge rates (CFS × 1,000) from January 1993 to December 2008

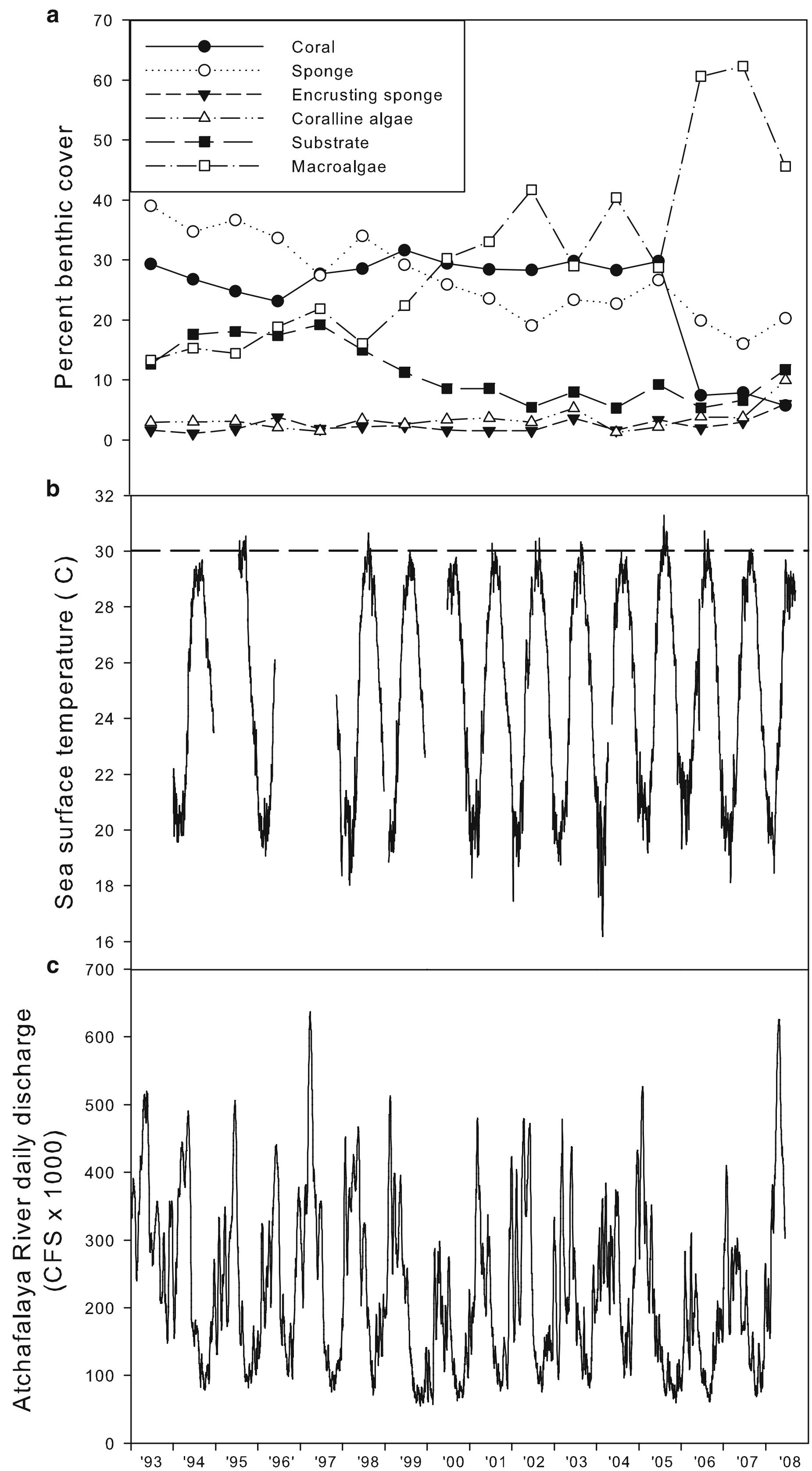

Table 2 Percent benthic cover, averaged over all photostations from 1993 to 2008

Cruise Number/Year Major category	1 1993	2 1994	3 1994	4 1995	5 1995	6 1996	7 1997	8 1998	9 1999	10 2000	11 2001	12 2002	13 2003	14 2004	15 2005	16 2006	17 2007	18 2008
Coral	29.35	32.11	27.56	29.61	24.74	23.13	27.69	28.56	31.63	29.42	28.43	28.34	29.82	28.29	29.80	7.43	7.88	5.73
Sponge	39.04	30.99	35.65	34.61	37.32	33.65	27.43	34.01	29.20	25.90	23.57	19.09	23.38	22.70	26.64	19.89	16.03	20.31
Encrusting sponge	1.60	0.44	1.18	1.34	1.85	3.80	1.85	2.24	2.35	1.63	1.52	1.52	3.61	1.61	3.31	1.96	2.97	6.06
Macroalgae	13.30	23.34	12.65	9.76	14.57	18.82	21.88	16.05	22.42	30.23	33.07	41.67	29.01	40.37	28.74	60.62	62.28	45.61
Unknown	1.03	1.50	0.47	0.21	0.34	0.18	0.13	0.48	0.02	0.11	0.25	0.17	0.10	0.11	0.00	0.00	0.00	0.00
Coralline algae	2.96	2.54	2.95	1.68	3.31	2.01	1.41	3.39	2.58	3.39	3.67	2.93	5.26	1.26	2.15	3.84	3.68	9.95
Other	0.07	0.48	0.91	0.57	0.73	0.95	0.39	0.27	0.55	0.76	0.90	0.83	0.83	0.33	0.12	0.92	0.53	0.60
Substrate	12.65	8.61	18.64	22.21	17.14	17.45	19.21	15.00	11.26	8.56	8.61	5.45	7.98	5.33	9.24	5.34	6.63	11.74

At least one severe bleaching event occurred during the summer of 2005. Species are grouped under major categories: *Coral, Sponge, Encrusting sponge, Macroalgae, Unknown, Coralline algae, Other,* and *Substrate*. Category *Other* represents urchins, fish, and other organisms observed under the random point generated by CPCe software. In 1994 and 1995, two cruises were conducted per year (see Table 1)

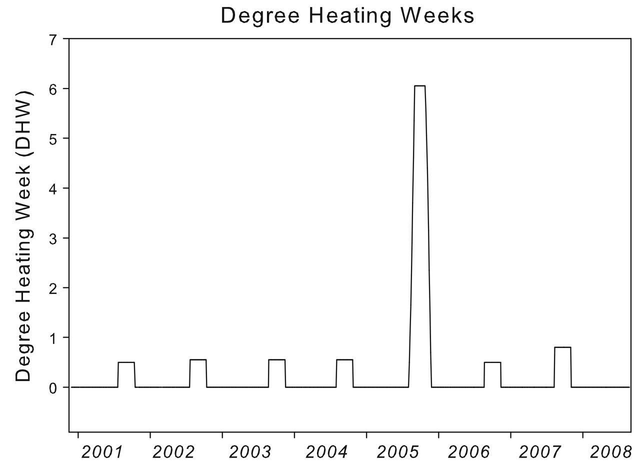

Fig. 3 Degree heating weeks (DHW, °C-weeks) over Stetson Bank, from 2001 to 2008. Data courtesy of NOAA's Coral Reef Watch Program

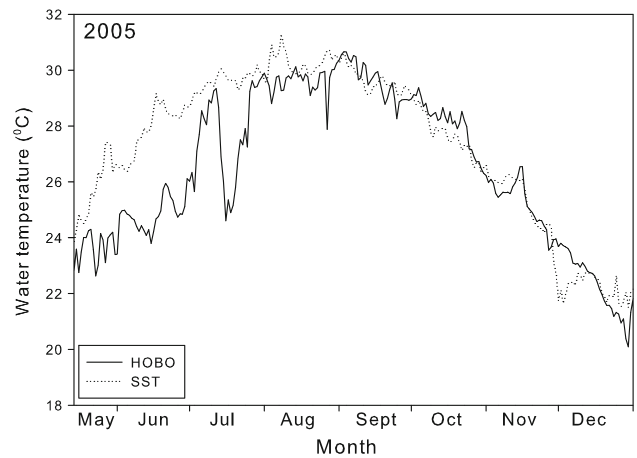

Fig. 4 Comparison of 'bottom' (HOBO) and sea surface temperatures (*SST*) during 2005. Bottom temperatures were recorded by a HOBO® data logger, and sea surface temperatures (*SST*) were recorded by the NDBC buoy 42019, located 60 nm south of Freeport, Texas. Average daily temperatures from both sources, ranging from May 13 to December 31, 2005, are shown

offshore, surrounding Stetson Bank in a plume of turbid water for many weeks before dissipating (Fig. 1b).

Atchafalaya River discharge

Over the 16-year dataset, from January 1, 1993 to June 18, 2008, maximum daily ARD rates ranged between 298 and 637 cubic feet per second (CFS) × 1,000 (Fig. 2c). Minimum daily discharge rates ranged between 55 and 207 CFS × 1,000, with an average minimum of 83 CFS × 1,000. Average daily flow (ADF) rates ranged between 136 and 351 CFS × 1,000. River discharge peaked above 600 CFS × 1,000 in March and April 1997 and in April 2008, and peaked at 527 CFS × 1,000 in February 2005.

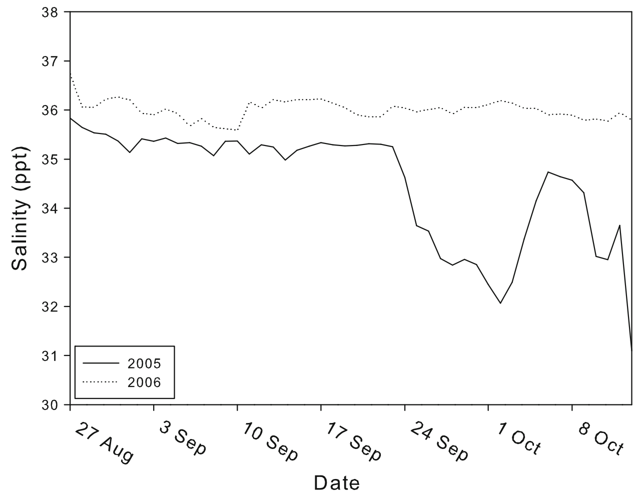

Fig. 5 Average daily salinity measured between August 27 and October 13, 2005 and 2006. Salinity was measured with a datasonde/YSI on the surface of Stetson Bank (23.5 m depth). Hurricane Katrina passed through the Gulf of Mexico on August 28, 2005, while Hurricane Rita passed through the Gulf on September 23, 2005

Table 3 Tropical cyclone activity occurring within 200 km of Stetson Bank, between May 1993 and July 2008

Name	Date	Max category (Saffir-Simpson Scale)	Max wind speed (mph/kph)
Dean	July 30, 1995	Tropical storm	45/72
Danny	July 16, 1997	Tropical depression	35/56
Charley	August 21, 1998	Tropical storm	50/80
Frances	September 10, 1998	Tropical storm	65/105
Allison	June 5, 2001	Tropical storm	60/97
Bertha	August 7, 2002	Tropical depression	30/48
Fay	September 5, 2002	Tropical storm	60/97
Claudette	July 14, 2003	Hurricane Cat. 1	85/137
Grace	August 31, 2003	Tropical storm	40/65
Ivan	September 23, 2004	Tropical storm	60/97
Rita	September 23, 2005	Hurricane Cat. 3	125/201
Humberto	September 12, 2007	Hurricane Cat. 1	90/145

Maximum wind speed (MWS) and maximum category in the Saffir-Simpson Scale obtained by each cyclone while within 200 km of Stetson

Classification and regression tree analysis

At the community level, mCART analysis highlighted the shift in community composition from a coral-sponge-dominated community (pre-1999) to an algae-dominated community (post-2005), with 2005 standing out as when the major shift occurred (Figs. 2a, 6a). Between 2000 and 2005, coral cover remained relatively stable, whereas sponges and macroalgae appeared to swap dominance, with macroalgae dominating percent cover over both corals and sponges. The tree further split 2008 from 2006 and 2007, where macroalgae cover was reduced and bare substrate and coralline algae increased in cover.

By removing year as an explanatory variable from the analysis, we were able to investigate which other variables may have contributed to, or correlated with, the observed shifts in the community structure. Yearly high temperature of greater or less than 30.7 °C explained most of the variability in benthic community, with yearly low temperature of greater or less than 17.7 °C as the secondary explanatory variable (Fig. 6b). Maximum daily ARD (<576.5 CFS × 1,000), average yearly SST, and tropical storm activity the year prior also accounted for variability in the dataset. For both trees (with and without year included), total percent variance explained was 27 %. Relative importance analysis for the second tree (year removed) showed maximum daily ARD to be the most important variable (100 %), followed by high temperature (20 %), average SST (12 %), low temperature (8.2 %), prior-year tropical storm (7.8 %), and prior-year hurricane activity (3 %).

Discussion

Prior to 1999, the benthic community of Stetson Bank exhibited a general level of resiliency (Bernhardt 2000), as evidenced by percent coral cover consistently between 23 and 32 % and sponge cover ranging between 27 and 39 %. There are two specific years where shifts in community composition occurred at Stetson Bank—1999 and 2005. This is consistent with observations from other reefs in the region. Long-term monitoring at the nearby Flower Garden Banks over 1998 and 1999 reported a decrease in *Montastraea* spp. coral cover, bleaching of *M. alcicornis*, and an increase in turf algae in 1999 (Dokken et al. 2001). Stetson Bank, as a mid-shelf coral-sponge community, fared slightly differently, with an increase in macroalgae, but without a precipitous decrease in coral and sponge cover. However, as of 2000, the sponge population, mostly driven by *C. caribensis*, *Ircinia felix,* and an unidentified species, began a decline from 29 % to a minimum of 19 % in 2002, coral cover fell below 30 % and macroalgae became the dominant cover. After 2005, the year of the severe Caribbean-wide bleaching event (Eakin et al. 2010), *Millepora* declined dramatically from 27 to 3 % in 2008 and *C. caribensis* further declined from 4 to 0.1 %.

The declining trend in the sponge community after 1999 warrants further inquiry. Univariate analysis of the sponge cover data and environmental predictors failed to reveal any clear relationships that could explain the commencement of the decline after 1999. The worldwide bleaching event of 1998 may have affected Stetson's population of *C. caribensis;* this species harbors symbiotic

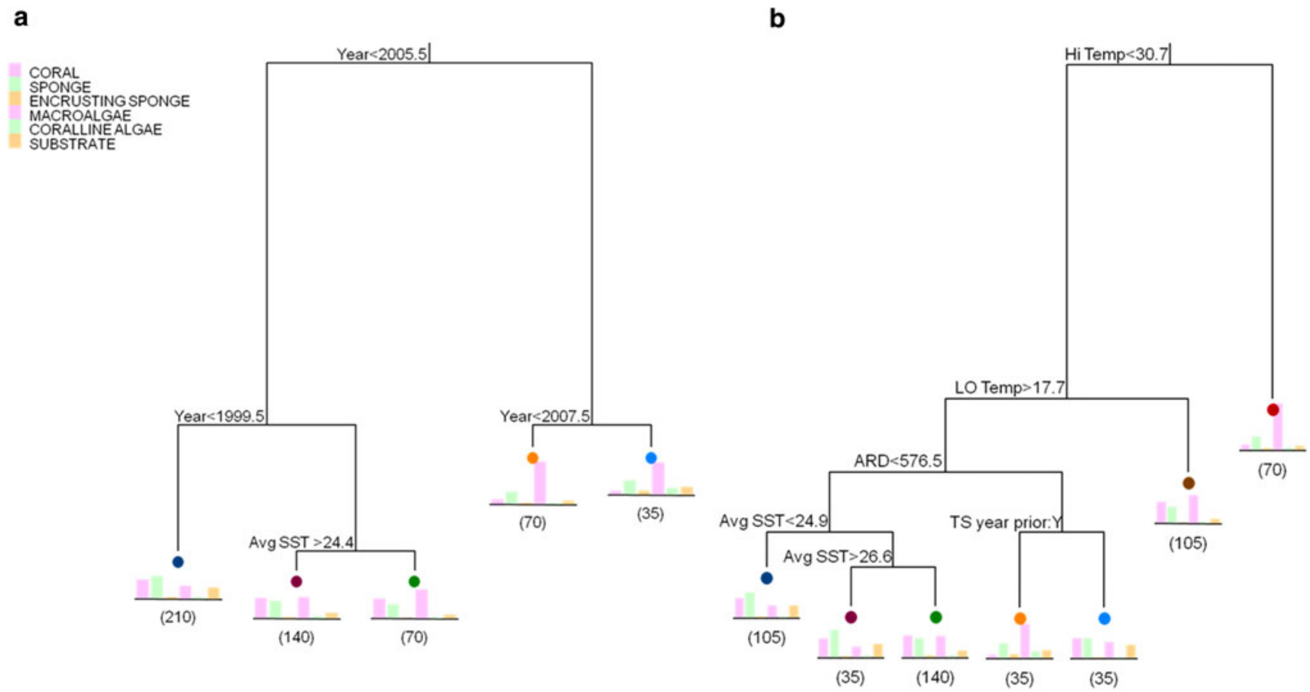

Fig. 6 Decision tree analysis of long-term monitoring data of Stetson Bank's benthic community and coinciding environmental data from 1993 to 2008. **a** Primary analysis included year, average yearly SST ('Avg SST'), yearly high SST ('HI temp'), yearly low SST ('LO temp'), Atchafalaya River discharge (maximum daily per year; 'ARD'), and prior-year tropical storm activity (yes or no, 'TS year prior'). **b** Year was removed, and the analysis run on the remaining correlates. Labels are for left branches, right branches follow the opposite direction in values

cyanobacteria, and a similar species, *C. australiensis,* in Australia is subject to bleaching impacts (Fromont and Garson 1999). *C. caribensis* is also particularly susceptible to 'stress' in the form of water pollution (e.g., Muricy 1989; Gochfeld et al. 2007). In the future, more specific and intensive monitoring of the sponge community and water quality might reveal causative links.

Millepora are typically some of the first coral species to bleach (Goreau 1964; Cook et al. 1990; Hagman and Gittings 1992) but are also the first to recover (Cook et al. 1990). Some bleaching was documented in the photographic station images every year between 1994 and 2007 (range 0.3–9.6 %), and yet, *Millepora* exhibited either resilience or resistance by maintaining an average 28 % cover until after 2005. Interestingly, the coral community at Stetson appeared resilient following an earlier bleaching event in the northwestern Gulf of Mexico in 1991 (Hagman and Gittings 1992), and the worldwide bleaching event in 1998 (Aronson et al. 2002). In contrast, the shift in community structure in 2005 was associated with high SSTs coupled with the close pass of Hurricane Rita and the resulting terrestrial runoff. A second year of high SSTs in 2006 may then have contributed to the precipitous decline in *Millepora* and *Chondrilla* and the near total dominance of macroalgae after 2005.

Tropical storm activity

Tropical storm activity has multiple negative impacts on Stetson Bank, ranging from mechanical damage by wave energy and projectiles to water quality—specifically relating to decreases in salinity, and increases in turbidity and land-based nutrients and pollutants (see Lugo-Fernandez and Gravois 2010 and references therein). Positive impacts of storm activity, which have not been specifically documented at Stetson Bank, might be decreased temperature and an increase in larval distribution and settlement (Manzello et al. 2007b). Lugo-Fernandez and Gravois (2010) conducted a climatology study on the region (200 km radius) surrounding the Flower Garden Banks coral reefs, and this radius encompassed Stetson Bank. Their study explicitly and quite thoroughly investigated the storm cycle occurring from 1900 to 2006 and the possible impacts from storms on these shelf-edge banks. However, Stetson Bank is a mid-shelf bank, with markedly different topography, water quality parameters, and biological community than the nearby Flower Garden Banks (48 km southeast of Stetson). For example, a post-hurricane assessment conducted after Hurricane Rita, in November 2005, found that the East Flower Garden Bank reef suffered physical damage (i.e., missing corals, scoured, and damaged coral heads) as well as unprecedented bleaching at ~10 %, but seemed to recover by June 2006 (Robbart et al. 2008). At Stetson Bank, significant declines in the populations of *M. alcicornis* and *C. caribensis* corresponded with the passage of Hurricane Rita, though the relative impacts from specific mechanisms of abrasion, destabilization, coastal water influences, thermal stress, and sedimentation are unknown, and may be coincidental. The discolored coastal water that extended out over Stetson and the Flower Garden Banks most likely contained pollutants, herbicides, pesticides, and nutrients from the Mississippi and Atchafalaya Rivers and industrial sites (Deslarzes and Lugo-Fernandez 2007; Robbart et al. 2008), which would exacerbate the already thermally stressed coral-sponge community and reduce light penetration during that period. Reduction in light penetration may inhibit the ability of corals and sponges to recover at a critical time (see review by Fabricius 2005). Later tropical storm activity, such as Hurricane Ike, which passed over Stetson Bank on September 12, 2008, might have further delayed the recovery of the coral-sponge community. Gardner et al. (2005) found a minimum 8-year cycle of recovery following hurricane-induced coral loss. Considering the number of tropical storms which pass over the northwestern Gulf of Mexico (Lugo-Fernandez and Gravois 2010), the recovery of Stetson Bank may hinge upon the release of other concurrent stressors which are impacting the reef (e.g., coastal pollution, fishing pressure).

Atchafalaya River discharge

Previous research investigated the possible impacts of ARD on the East Flower Garden Bank reef and found a negative correlation between discharge rate and coral growth (Dodge and Lang 1983). The Atchafalaya River empties into the northern Gulf of Mexico, farther west than the Mississippi River, and the western flowing Central Gulf Current can transport this lower salinity, nutrient-rich water over the Texas–Louisiana continental shelf (see Dodge and Lang 1983; Rabalais et al. 1996). Over the 15-year period of this study, ARD rates showed an annual periodic cycle, with spring peak discharges. Maximum daily discharge rates peaked during 3 years 1997, 2005, and 2008. Higher than average ARD rates occur during the first half of the year, usually between February and May. These peak flows are due to the timing of spring flood events and coincide with the western flow of the inner-continental shelf currents presiding during this time (Deslarzes and Lugo-Fernandez 2007). During May through August, the prevailing wind and shelf currents switch direction and turn eastward along the shelf (Lugo-Fernandez et al. 2001). These prevailing currents account for bands of lower salinity, mixed river–seawater which have been documented as far south as the Flower Garden Banks (Deslarzes and Lugo-Fernandez 2007) and adds an element of uncertainty as to how annual pulses of terrigenous runoff may impact the Stetson Bank community (see Rabalais et al. 1996). From the long-term dataset presented here, CART analysis pinpointed maximum discharge (splitting at 576.5 CFS × 1,000), after high (30.7 °C) and low (17.7 °C) temperature splits in the dataset, as an important factor in the composition of the benthic community. Further, maximum daily discharge was the most important variable in the final tree. In 2005, peak spring flow coincided with the later passing of Hurricane Rita, which pushed a terrigenous plume of water out over Stetson Bank (see Fig. 1b). Though we do not have the data required to separate the effects of these terrigenous sources of water, these factors likely played a pivotal role in the cumulation of events which led to the collapse of Stetson's *Millepora* and *Chondrilla* populations after 2005.

Long-term monitoring program

There are limitations inherent in the particular monitoring program established at Stetson Bank. Loss of photostations over time due to storms and other factors limit the usable size of the dataset. Further, the monitoring stations were not initially set up in a stratified design, but sites were chosen based on coral and sponge pinnacle formations, and consistent long-term temperature and salinity measurements at reef depth have been difficult to maintain. From comparisons of HOBO and NDBC Buoy SST measurements, it is clear that using surface buoy SST measurements for the reef crest of Stetson is not an accurate representation of the actual temperatures the benthic community experiences, but for this dataset, the NDBC Buoy SST data do provide an important long-term approximation of the temperature regime over Stetson and nearby mid-shelf banks.

Though this dataset is limited, it offers a unique baseline for a high-latitude, marginal reef in the northwestern Gulf of Mexico, and this is especially important as global climate change threatens to further alter Stetson Bank's environment and as other anthropogenic impacts (e.g., Deep Horizon oil spill in April 2010) increase in severity and proximity. There are approximately 35 reefs and banks lying along the continental shelf in the northern Gulf of Mexico (Rezak et al. 1990). These banks have been documented and studied in varying, limited degrees (Rezak et al. 1985, 1990), but the benthic monitoring of Stetson and the Flower Garden Banks is the longest running monitoring program that currently exists for these reef communities. Stetson Bank might thus be used as a proxy for understanding community trends at other similar mid-shelf reefs in the northwestern Gulf of Mexico. For example, Sonnier Bank, located at a similar latitude as Stetson (28.30°N, 92.45°W) and once harboring a thriving sponge reef and fish community (Rezak et al.

1985), has undergone a scouring event and shows similar changes in benthic community structure as Stetson (see Kraus et al. 2007).

From the community trends presented here and observations as recent as 2011, Stetson's benthic community appears to have undergone a moderate-to-severe phase shift from a coral-sponge-dominated community to an algae-dominated community (see Bruno et al. 2009). Monitoring efforts are ongoing, and further analysis will help determine whether this community shift is a permanent or reversible one (for review, see McManus and Polsenberg 2004; Norström et al. 2009). This study indicates the potential influence of a combination of environmental factors on the composition of Stetson Bank's benthic community, for example, surface and at-depth water temperatures, river discharge regimes, and salinity and solar radiation fluctuations. However, due to lack of direct, encompassing measurements of water quality and other site-specific variables (e.g., UV radiation), it is difficult to draw more specific conclusions as to how and why the reef, and specifically, the sponges and coral, responded to the environmental conditions we observed. Future monitoring programs should include more direct monitoring of these parameters.

The overall variance explained by the decision tree model (27 %) highlights the limitations in dealing with a complex natural system and a community level analysis incorporating a range of physical variables which serve as proxies for conditions likely to regulate the benthic community. However, such models provide a clear foundation for generating hypotheses about causation and for understanding long-term trends which can be otherwise difficult to follow. Due to the long-term monitoring program already in place at Stetson Bank, this reef community is situated to be an important sentinel site for monitoring climate change and direct impacts from anthropogenic activities on a high-latitude coral-sponge community in the Gulf of Mexico.

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