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National Oceanic and Atmospheric Administration
National Marine Sanctuaries Conservation Science Series

Stetson Bank Long-Term Monitoring: 2015-2018 Synthesis Report

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Cover photo: A diver swimming over a high-relief pinnacle at Stetson Bank. Photo: G.P. Schmahl/NOAA

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Abstract

This report documents methods, analyses, and results from annual long-term monitoring of fish and benthic communities at Stetson Bank over a period of four years, 2015–2018. Stetson Bank is an uplifted claystone/siltstone feature, located within Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico, that supports a well-developed coral community of tropical marine sponges and coral. Due to a wide range of temperatures and variable light availability, Stetson Bank has marginal environmental conditions for coral reef development and growth. The fish community is similar to other Caribbean reefs, but has comparatively reduced diversity.

Monitoring has occurred on the bank crest (17-34 m) of the site since 1993. In 2015, monitoring efforts were expanded to include the deeper mesophotic habitat (34–64 m) surrounding the bank crest. The bank crest benthic community at Stetson Bank has undergone several significant shifts, changing from a habitat of predominantly hydrocoral and sponges to one of macroalgae and sponges. The fish community on the bank crest has been highly variable each year. Fluctuations in oceanic conditions, fluctuations in macroalgae cover, and continued annual variation in fish communities were documented. Additionally, an exotic species arrived and a baseline characterization of mesophotic communities was established.

Key Words

benthic community, fish community, Flower Garden Banks National Marine Sanctuary, long-term monitoring, mesophotic coral ecosystem, Stetson Bank, water quality

Chapter 1: Background and Monitoring Objectives

Stetson Bank (28° 09.931' N, -94° 17.861' W), located approximately 130 km southeast of Galveston, Texas, is an uplifted mid-Tertiary (Miocene epoch) claystone feature associated with an underlying salt dome. It supports a coral community located near the northern limit of coral reef growth in the Gulf of Mexico. Environmental conditions at Stetson Bank are considered "marginal" for coral reef development and growth due to low winter temperature and variable light availability. Despite the variable environmental conditions, Stetson Bank supports a well-developed benthic community comprised of tropical marine sponges, corals, and other sessile marine invertebrates (such as hydroids and zoanthids).

Sponges, primarily *Neofibularia nolitangere*, *Ircinia strobilina*, and *Agelas clathrodes*, compose a large portion of the benthic biota, but have been in steady decline since 1999 (DeBose et al. 2012). The sponge *Chondrilla nucula* was historically prevalent on the bank, but underwent a dramatic decline after 2005, following a coral bleaching event, and is now almost absent. Similarly, the hydrozoan *Millepora alcicornis* (fire coral) was historically the most prominent coral at Stetson Bank with approximately 30% cover, but underwent a rapid decline in 2005 due to bleaching and has not recovered (Figure 1.1) (DeBose et al. 2012).

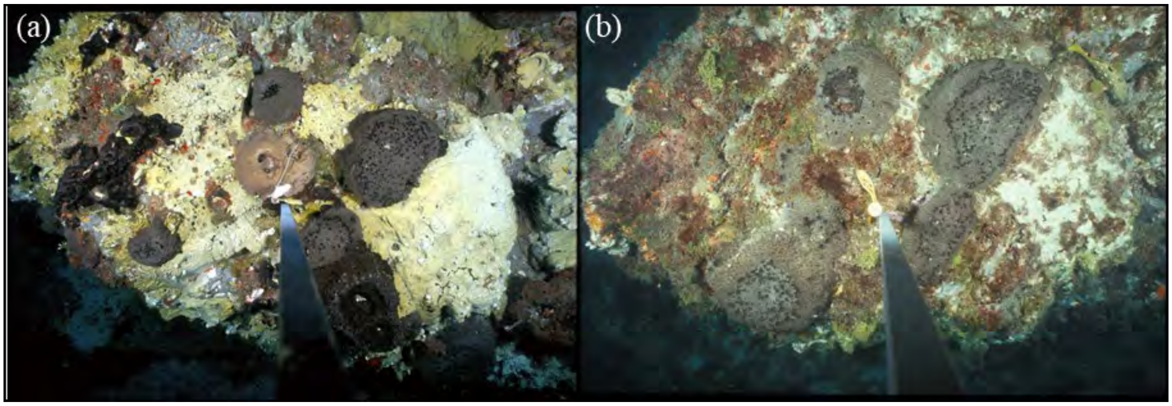

Figure 1.1. Repetitive photostation benthic images. Images (a) from 2000 and (b) from 2007 show the change from a *Millepora*-sponge community to an algae-sponge community. Photo: NOAA

Twelve species of hermatypic coral have been documented at Stetson Bank, including *Pseudodiploria strigosa*, *Stephanocoenia intersepta*, *Madracis brueggemani*, *Madracis decactis*, and *Agaricia fragilis*, which have maintained low but stable cover over time (Figure 1.2). Benthic algae cover, primarily *Dictyota* sp. and turf algae, varies between years. Since the initiation of monitoring at Stetson Bank, significant changes have occurred in the benthic community, where a community characterized by *Millepora* and sponges has become an algae-dominated community (DeBose et al. 2012).

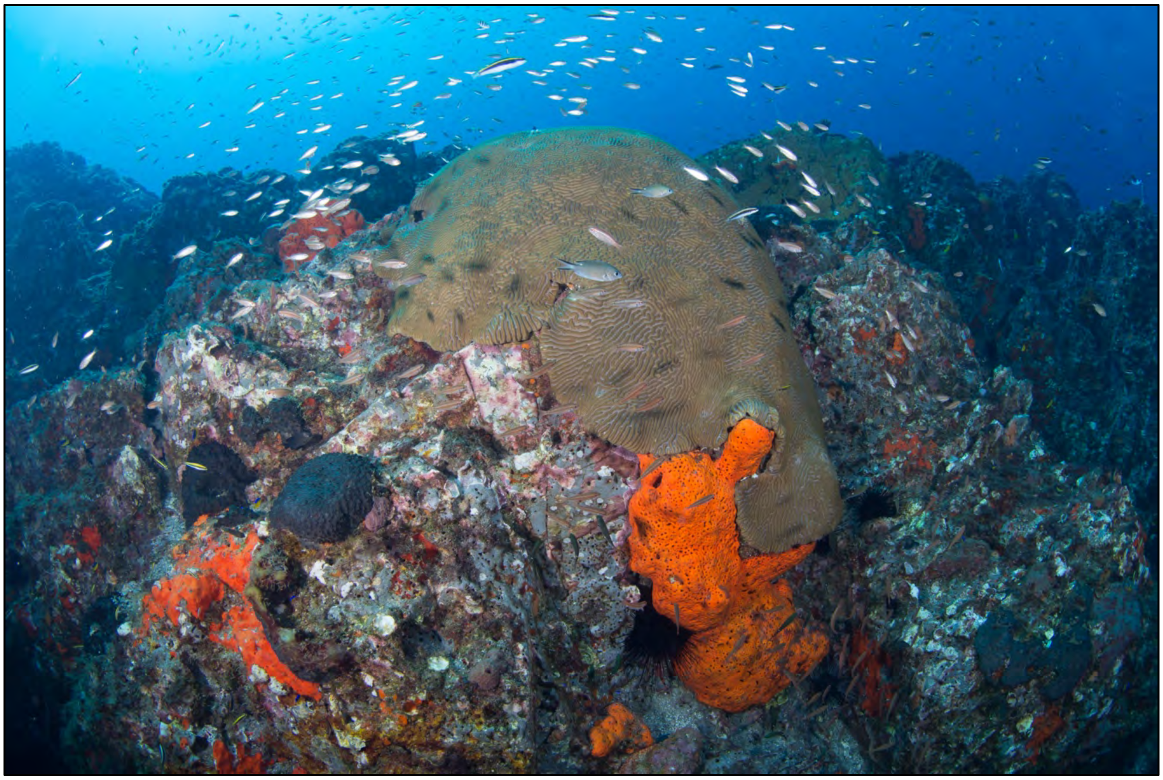

Figure 1.2. *Pseudodiploria strigosa* at Stetson Bank. This species is one of twelve species of Scleractinia documented. Photo: G.P. Schmahl/NOAA

While the fish community at Stetson Bank is temporally variable, with sporadic recruitment events, mean biomass has remained high. Overall, the community is comprised of similar species to other Caribbean reefs, but with low species diversity for hamlets (*Hypoplectrus* sp.), grunts (Haemulidae), and snapper (Lutjanidae).

In 1993, an annual long-term monitoring program was initiated at Stetson Bank by the Gulf Reef Environmental Action Team (GREAT) and was later conducted by Flower Garden Banks National Marine Sanctuary (FGBNMS). The monitoring program was initially focused on the bank crest, within non-decompression scuba diving limits (16.8 - 33.5 m), and provided data to support the addition of Stetson Bank to FGBNMS in 1996. In 2015, the Bureau of Safety and Environmental Enforcement (BSEE) and FGBNMS expanded monitoring at Stetson Bank to include both the historically monitored bank crest and the surrounding mesophotic reef habitat (>33.5 – 64.0 m). A technical report documenting detailed field methods, observations, and notes was published for each year (Nuttall et al. 2017, Nuttall et al. 2018, Nuttall et al. 2019a, Nuttall et al. 2019b, Nuttall et al. 2020).

While the boundaries of Stetson Bank were designated based on the best available data at that time, subsequent mapping and exploration led to the discovery of mesophotic reefs surrounding the bank crest. They occur both inside and outside of the current sanctuary boundary (Figure 1.3). Current sanctuary expansion efforts propose to modify the boundaries to include the associated mesophotic reefs explored in this study (ONMS 2016).

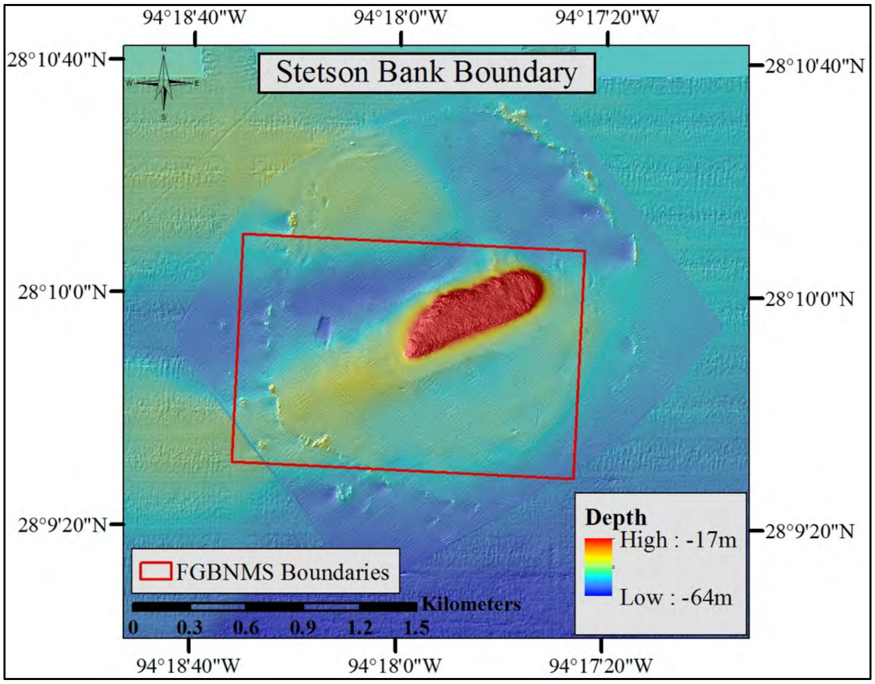

Figure 1.3. Stetson Bank boundary as described in 65 FR 81175. Image: NOAA

To date, 26 years of coral community monitoring efforts have occurred at Stetson Bank, representing one of the longest ongoing monitoring programs of a northern latitude coral community. As stressors to marine environments are projected to increase in frequency and duration, long-term monitoring datasets are essential for understanding community stability, ecosystem resilience, and responses to a changing environment. Additionally, as exotic species invade and become established, these long-term data sets are critical for documenting and tracking impacts of these species on natural populations. Results from this dataset help guide research and management in the region.

Monitoring Objectives

This monitoring program is a partnership between FGBNMS and BSEE. It was established through interagency agreement E14PG00052 to assess the health of the bank through the evaluation of changes in living coral and other benthic community cover, reef fish population dynamics, water quality, and other indices of reef vitality. It will enable detection of changes in reef communities, including detection of anthropogenic influences (namely oil and gas impacts). The specific objectives of this monitoring program included:

- monitoring community health at Stetson Bank
- monitoring environmental conditions at Stetson Bank
- detecting any significant effects from natural and human activities that could potentially endanger the reef community
- supporting analysis of the long-term monitoring dataset for Stetson Bank

Monitoring Components

The interagency agreement between FGBNMS and BSEE established a financial partnership to support the Stetson Bank long-term monitoring program and was based on the extensive institutional knowledge, monitoring experience, and research equipment housed at the sanctuary.

The monitoring protocol was consistent with past NOAA monitoring of Stetson Bank, but included the addition of methods to address the outlined objectives and expansion to monitor all habitats at Stetson Bank (i.e. shallow and mesophotic reefs). Observations were made to evaluate species cover, vitality, and general community health.

The following methods are used to evaluate the benthic and fish community, as well as water quality, at Stetson Bank:

- benthic community
    - random diver and remotely operated vehicle (ROV) photographic transects to document benthic cover
    - repetitive diver and ROV photostations to detect and evaluate benthic cover changes while controlling for spatial variation
    - repetitive diver video transects to document general observations of site conditions
    - repetitive diver sea urchin and lobster transects to evaluate population densities
- fish community
    - random diver stationary fish census to assess community structure, density, and biomass
    - random ROV fish belt transects to assess community structure, density, and biomass
- water quality
    - continuous temperature and salinity recordings on the bank crest to track environmental changes
    - continuous temperature recordings at 30 m and in the mesophotic zone to track environmental changes
    - nutrient sampling to track trends in water quality
    - ocean acidification sampling to track ocean carbonate trends

Field Operations and Data Collection

Field operations were conducted on multiple cruises from 2015–2018 (Table 1.1).

Table 1.1. Cruises and tasks completed as part of Stetson Bank monitoring from 2015 to 2018.

Date	Cruise Name and Monitoring Task
11/9/2014–11/10/2014	2014 November water quality • download and change out water instruments • water sample collection (nutrients and ocean carbonate)
2/9/2015–2/11/2015	2015 February water quality • download and change out water instruments • water sample collection (nutrients and ocean carbonate)

Date	Cruise Name and Monitoring Task
4/29/2015–5/1/2015	2015 April water quality • download and change out water instruments • water sample collection (nutrients and ocean carbonate)
6/21/2015–6/26/2015	2015 bank crest monitoring • diver repetitive and random benthic surveys • diver random and buoy stationary visual fish census • diver urchin and lobster transects • diver repetitive video transects • download and change out water instruments
7/12/2015–7/16/2015	2015 mesophotic monitoring: benthic and fish community monitoring • ROV repetitive and random benthic surveys • ROV random fish belt transects • ROV video transects • deploy thermistor
10/7/2015–10/8/2015	2015 October water quality: • new water instruments test deployment • water column profile • water sample collection (ocean carbonate)
11/2/2015–11/5/2015	2015 November water quality: • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
11/2/2015–11/5/2015	2015 November water quality: • download and change out water instruments • diver repetitive benthic surveys
2/17/2016–2/18/2016	2016 February water quality I: • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
2/28/2016–2/29/2016	2016 February water quality II: • download and change out water instruments • water column profile • diver repetitive benthic surveys
5/19/2016	2016 May water quality: • water sample collection (nutrients and ocean carbonate) • water column profile
6/7/2016–6/10/2016	2016 reef crest monitoring: • diver repetitive and random benthic surveys • diver random and permanent stationary visual fish census • diver urchin and lobster transects • diver repetitive video transects

Date	Cruise Name and Monitoring Task
9/11/2016–9/15/2016	2016 mesophotic monitoring: • ROV repetitive and random benthic surveys • ROV random fish belt transects
11/13/2016–11/15/2016	2016 November water quality • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
2/2/2017	2017 February water quality: • water column profile • water sample collection (nutrients and ocean carbonate)
2/17/2017	2017 February water quality II: • download and change out water instruments
5/6/2017–5/8/2017	2017 May water quality: • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
7/17/207–7/21/2017	2017 reef crest monitoring: • diver repetitive and random benthic surveys • diver random and permanent stationary visual fish census • diver urchin and lobster transects • diver repetitive video transects
8/23/2017	2017 WFGB LTM cruise: water sample collection
9/17/2017	2017 post-Hurricane Harvey assessment
10/13/2017–10/15/2017	2017 mesophotic monitoring: • ROV repetitive and random benthic surveys • ROV random fish belt transects
11/1/2017	2017 November water quality I: • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
11/8/2017	2017 November water quality II: • Diver repetitive benthic surveys
4/24/2018	2018 April water quality (M/V *Hull Raiser*): • water sample collection (nutrients and ocean carbonate)
6/26/2018–6/29/2018	2018 June water quality: • download and change out water instruments

Date	Cruise Name and Monitoring Task
7/15/2018–7/19/2018	2018 reef crest monitoring: • diver repetitive and random benthic surveys • diver random and repetitive stationary visual fish census • diver repetitive video transects
7/28/2018–7/31/2018	2018 mesophotic monitoring: • ROV repetitive and random benthic surveys • ROV random fish belt transects • install new thermistor
8/2/2018–8/4/2018	2018 mooring buoy installation: • diver random benthic surveys • diver random stationary visual fish census
8/21/2018–8/24/2018	2018 East Flower Garden Bank long-term monitoring and water quality: • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
10/30/2018	2018 October water quality: • download and change out water instruments • water column profile • water sample collection (nutrients and ocean carbonate)
11/7/2018–11/8/2018	2018 November reef crest monitoring: • diver random benthic surveys • diver random stationary visual fish census

Chapter 2: Sessile Benthic Community

Introduction

Stetson Bank harbors a high-latitude coral community featuring mesophotic coral ecosystems that exist along the northern limit of conditions that foster coral development and growth. In 1985, the reef was characterized as a "*Millepora*-Sponge" community (Rezak et al. 1985), similar to the community documented at the onset of the monitoring program in 1993. Over the following decades, the bank crest community became algae-dominated; monitoring data documented the gradual but pervasive decline in Porifera and steep, step-wise declines in hydrocoral abundance. Despite existing in marginal and dynamic environmental conditions, Scleractinia coral cover, while low, has remained stable throughout the monitoring program. Similarly, phase-shifts from coral- to algae-dominated reefs have been documented throughout the Caribbean in the past decade, but it is unknown whether algal communities represent an alternative stable state or a reversible phase change (Côté et al. 2005, Rogers & Miller 2006, Mumby et al. 2007, Somerfield et al. 2008, Mumby 2009, Norström et al. 2009).

Historical observations at Stetson Bank were based primarily on permanent photostations installed on the bank crest in 1993 (Figure 2.1). These stations were concentrated on the northwestern edge of the bank and selected and marked by scuba divers along a series of ultra-high-relief hard bottom outcroppings with a diverse benthic community. This area was referred to as the "pinnacles" due to the unique high-relief outcroppings and interesting topography of the site, which is not found elsewhere on the bank crest. Initially, 36 permanent photostations were installed, but over time many of these stations have been lost (due to tag breakage, biotic overgrowth, or substrate loss) and new stations were established. Today, 59 stations exist, of which 18 are original, installed in 1993. These photostations have been critical in documenting and characterizing major shifts in community structure at Stetson Bank by enabling a repeated analysis of the same location and controlling for small-scale environmental heterogeneity (Côté et al. 2005). However, as they are located on high-relief features on the bank crest, they are not representative of the community as a whole. In order to capture spatial and temporal variations representative of the entire bank, annual random benthic transects were added to the survey techniques at Stetson Bank in 2013.

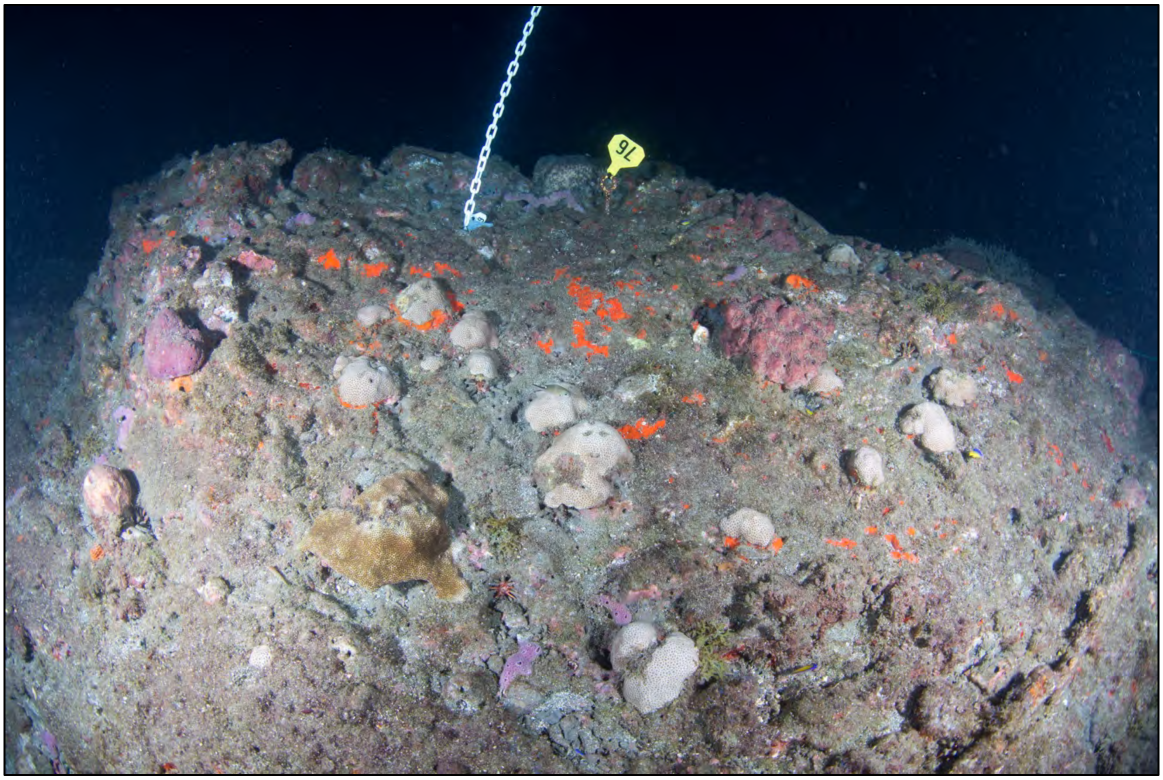

Figure 2.1. Repetitive photostation located on a high-relief outcropping on the bank crest. Photo: G.P. Schmahl/NOAA

In 1998, high-resolution multibeam bathymetry of Stetson Bank by Gardner et al. (1998) revealed a ring of hard bottom outcroppings surrounding the bank (Figure 1.3). Exploratory remotely operated vehicle (ROV) surveys confirmed that these outcroppings were mesophotic reefs, supporting multiple species of Porifera, black corals, and octocorals in a persistent nepheloid layer (see Rezak & Bright 1981, Rezak et al. 1985). In addition, marine debris, primarily in the form of longline and trawl nets, were commonly found among these features. In 2015, repetitive photostations and random transects similar to those previously established for the bank crest were added in mesophotic habitats to track changes among this community (Figure 2.2).

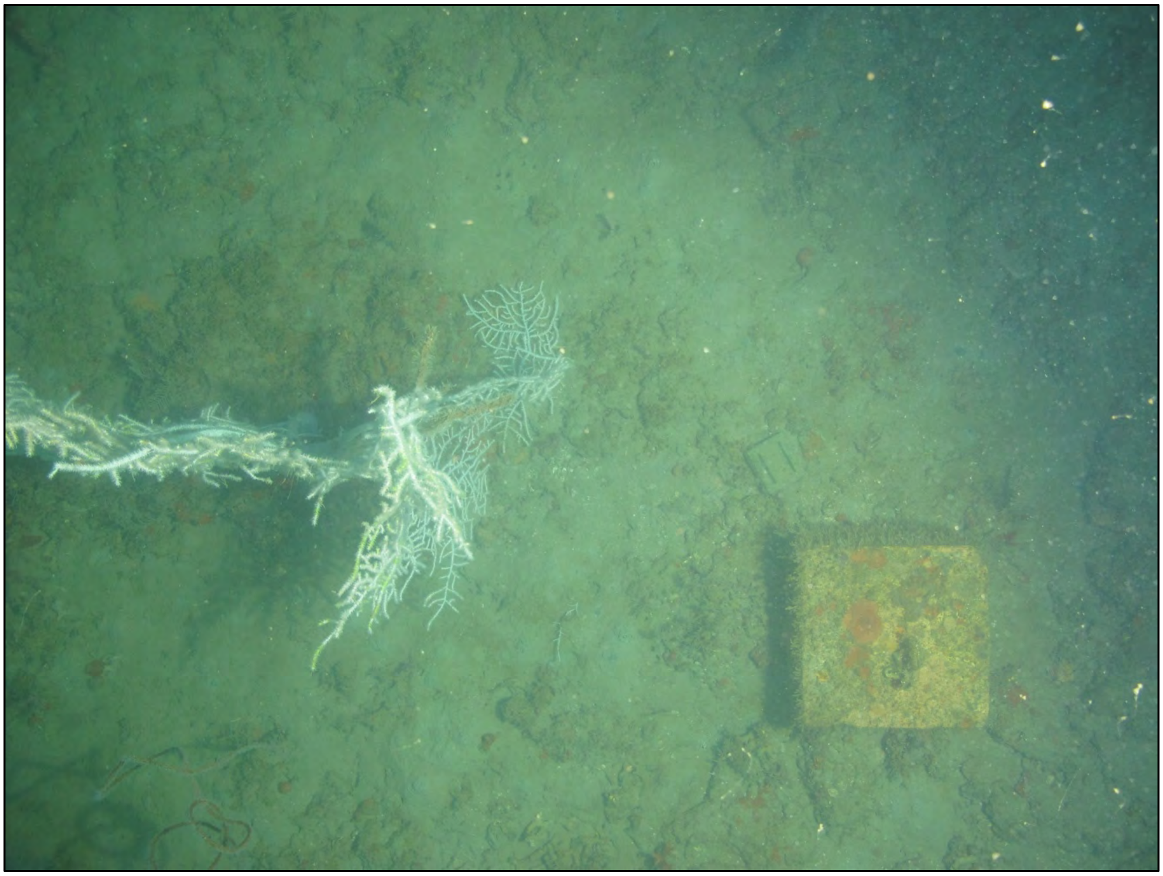

Figure 2.2. Repetitive photostation in mesophotic habitat. Photo: UNCW-UVP/NOAA

Benthic communities were monitored to compare community composition and diversity among years, track community changes, and quantify the presence of disease and bleaching. Additionally, the effectiveness of repetitive benthic photostations was evaluated for mesophotic communities.

Methods

Field Methods

Repetitive Benthic Photostations

Permanent photostations were installed on the bank crest at Stetson Bank in 1993, concentrated along the northwestern edge of the bank, on or near outcrops ranging from 16.8 to 29.6 m depth. Locations were selected by scuba divers along a series of high-relief hard bottom features with a diverse benthic community and marked using nails or eyebolts and numbered tags. Initially, 36 permanent photostations were installed in 1993. However, over time, many of these stations have been lost due to overgrowth or damage, and new stations were established. All of these photostations were installed on hard bottom habitat that are accessible from permanent mooring buoys 1, 2, or 3 (Table 2.1, Figure 2.3). Each station was located by scuba divers using detailed maps (Figure 2.4, Figure 2.5) and photographed annually.

Table 2.1. Buoy locations. Coordinates and depths of buoys used to access repetitive photostations at Stetson Bank.

Buoy No.	Latitude (DDM)	Longitude (DDM)	Depth (m)
1	28 09.931	94 17.861	22.6
2	28 09.981	94 17.834	23.8
3	28 09.986	94 17.766	22.3

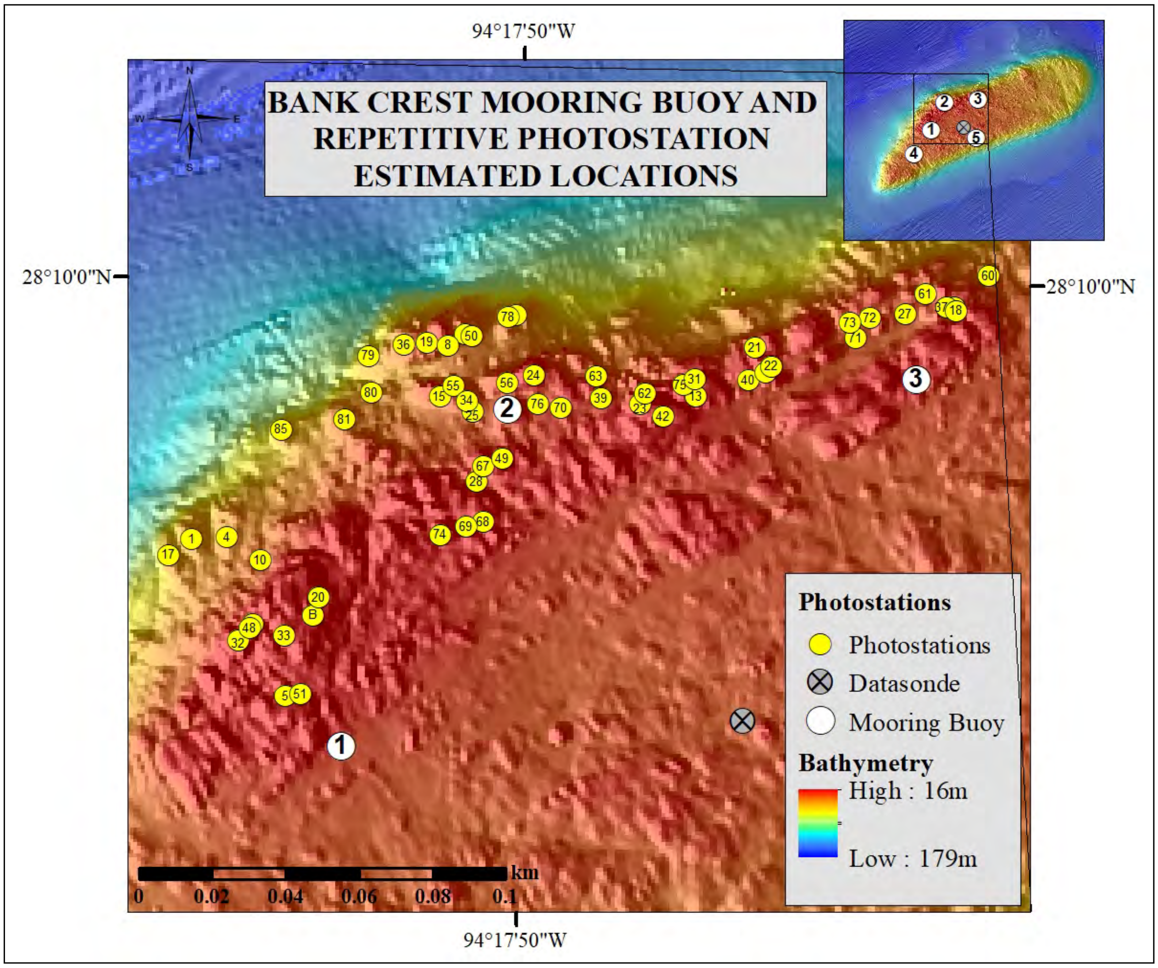

Figure 2.3. Stetson bank study site map. Seafloor topography with mooring buoy locations and approximate repetitive photostation locations. Image: NOAA

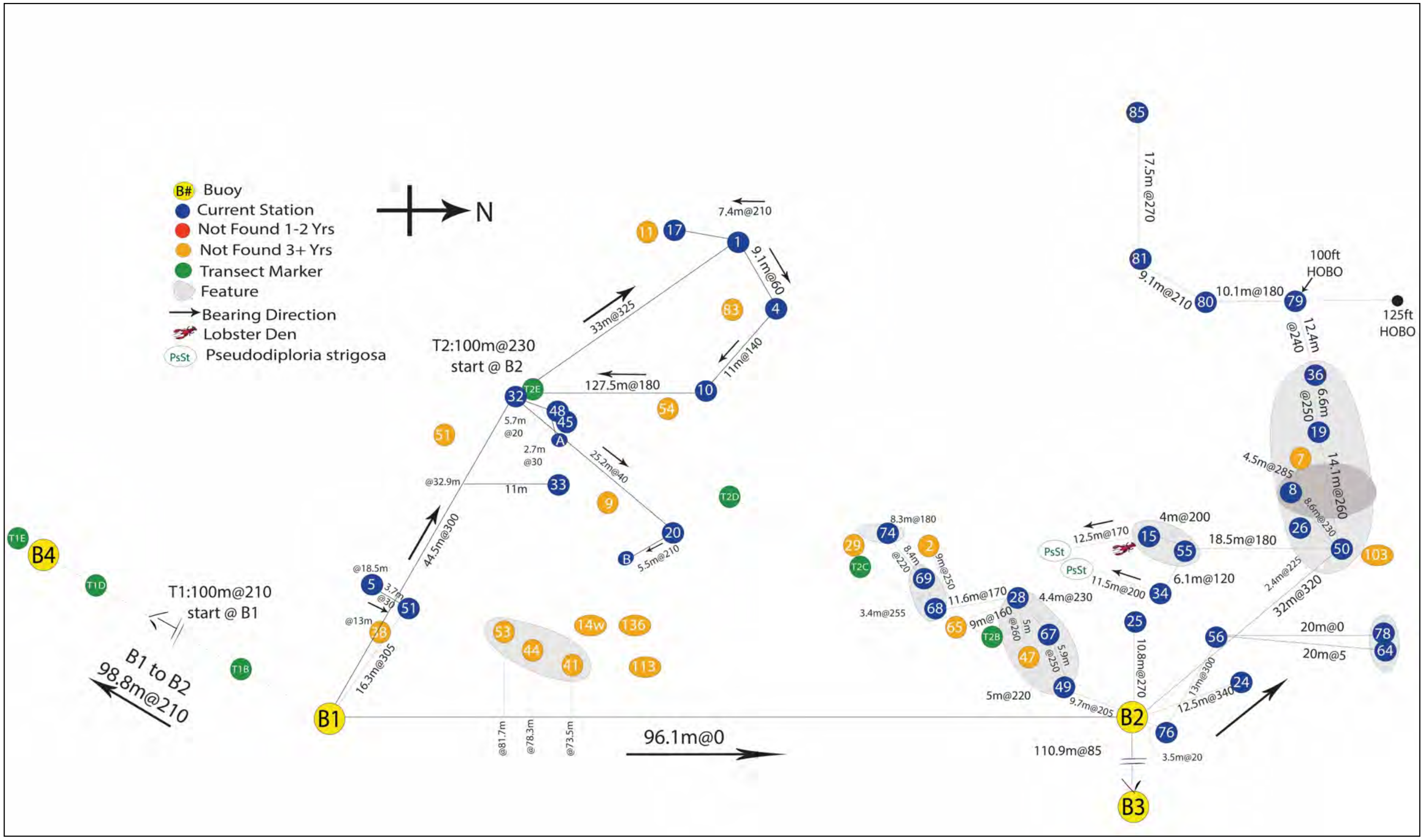

Figure 2.4. West Stetson map used by divers to locate the repetitive photostations in the study site. Image: NOAA

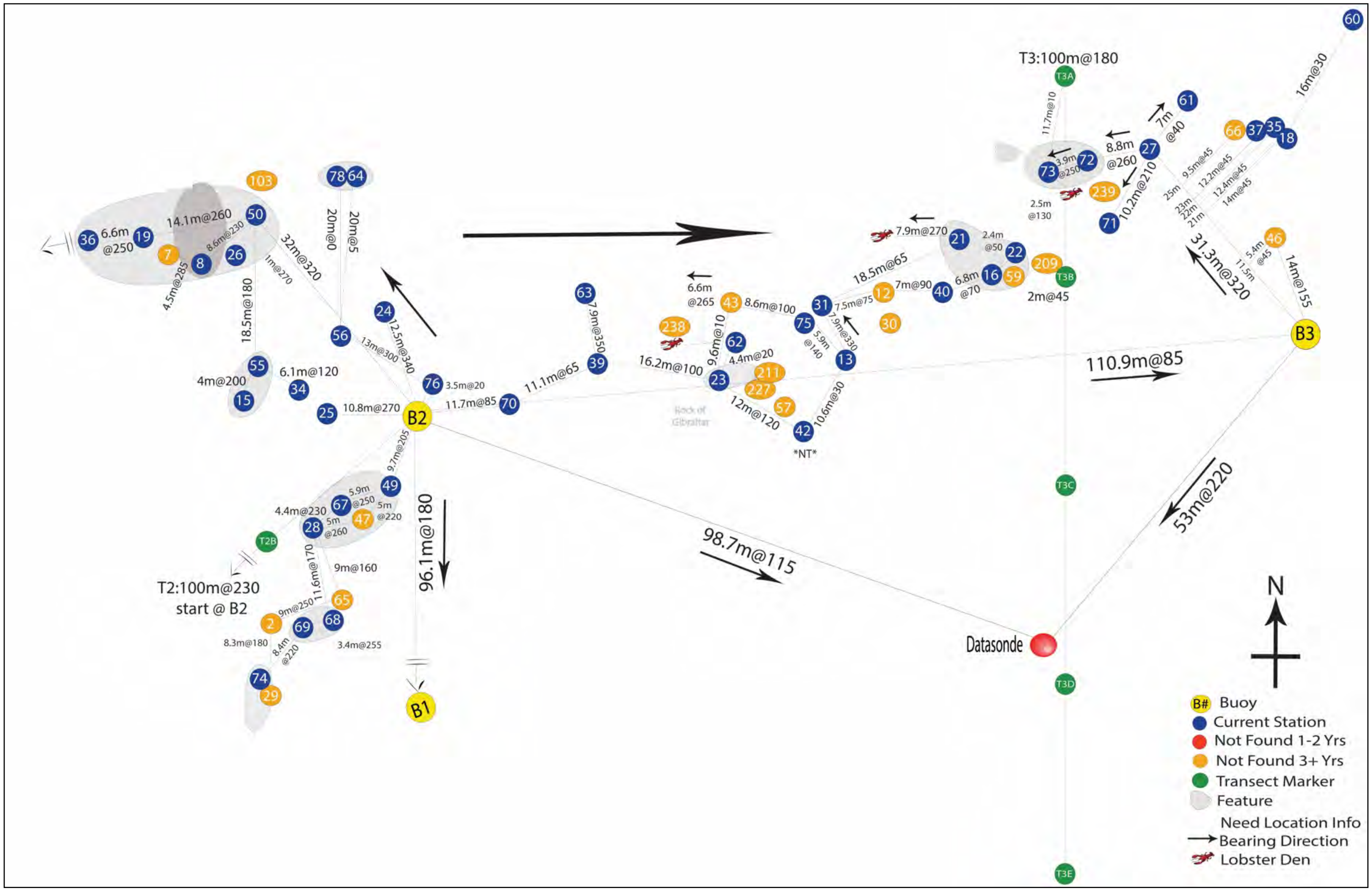

Figure 2.5. East Stetson map used by divers to locate the repetitive photostations in the study site. Image: NOAA

Bank crest repetitive photostations were located and marked with weighted floating plastic chains by scuba divers. A second dive team then photographed each station and removed the chains. In 2015–2017, images were captured using a Canon Power Shot G11 digital camera in a G11 Fisheye FIX® housing with a wide-angle dome port. In 2018, images were captured using a Sony® A6500 digital camera in a Nauticam® NA-A6500 housing with a Nikkor Nikonos® 15 mm underwater lens. Both camera systems were mounted to a T-frame set at 1.5 m and 1.75 m (2015–2017 and 2018, respectively) from the substrate, with two Inon® Z240 strobes set 1.2 m apart (Figure 2.6). A set of lasers was mounted to the pole of the T-frame, fixed at 30 cm, for spatial scale reference. To ensure repeatability of the area captured in each image, a compass and bubble level were mounted to the center of the T-frame to allow images to be taken in a vertical and northward orientation.

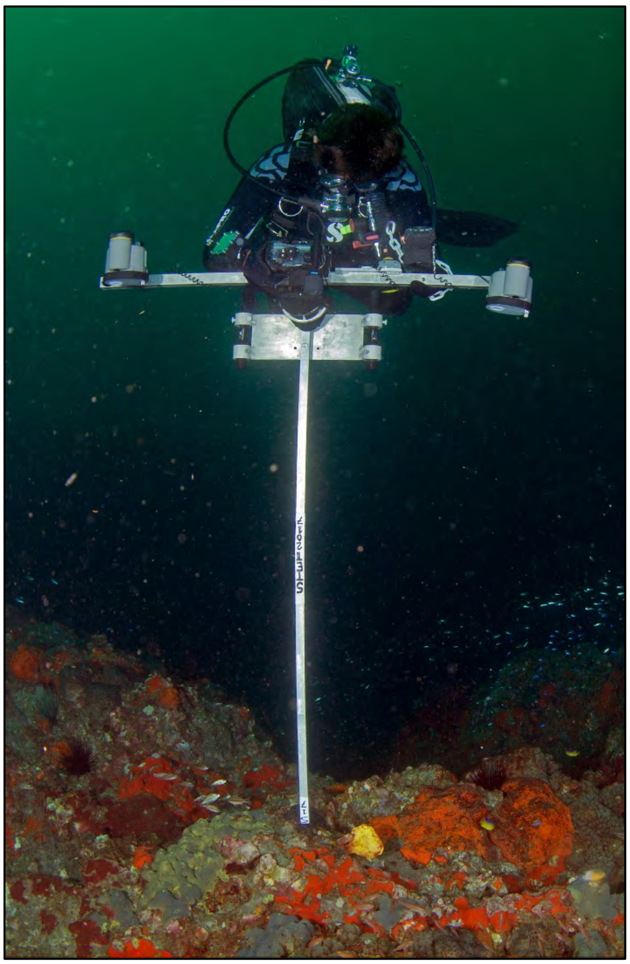

Figure 2.6. T-frame configuration. Photo: Schmahl/NOAA

Mesophotic permanent repetitive photostations were installed by ROV in 2015 at biologically-interesting sites ranging from 35.8 to 54.7 m depth. Locations were selected along hard bottom features in both coralline algae and deep reef habitat using historical ROV data. Photostations were physically marked with concrete blocks (25.4 cm x 25.4 cm x 15.2 cm) weighing 25 kg in air (9 kg in saltwater). An eyebolt was embedded into the concrete block, and a cattle tag with a station number and 1.8 m of wire rope was attached via a shackle and thimble. A small 20 cm hard trawl float (3.15 kg buoyancy) was attached to the wire rope using crimping sleeves. The latitude and longitude of each site were recorded using the ROV's navigation system. Subsequently, the recorded latitude and longitude were used to locate each station. To create repeatable images annually, each station was assigned a heading from which the ROV oriented itself to collect high-definition video imagery of the site, with the marker in view and the original site images used for reference. Still frames were extracted from this video for each repetitive station. Starting in 2016, a downward-facing photograph of each station was also captured, with the ROV positioned directly above the station marker, approximately 1 m above the bottom. The SubAtlantic Mohawk® 18 ROV, owned by the National Marine Sanctuary Foundation (NMSF) and FGBNMS, and operated by University of North Carolina at Wilmington - Undersea Vehicle Program (UNCW-UVP), was used. The ROV was equipped with a Kongsberg® Maritime OE14-408 10 mp digital still camera, Insite Pacific® Mini Zeus II high definition (HD), OE11-442 strobe, two Sidus® SS501 50 mW green spot lasers (set at 10 cm in the still camera frame for scale), and an ORE® transponder with ORE TrackPoint® II (Figure 2.7).

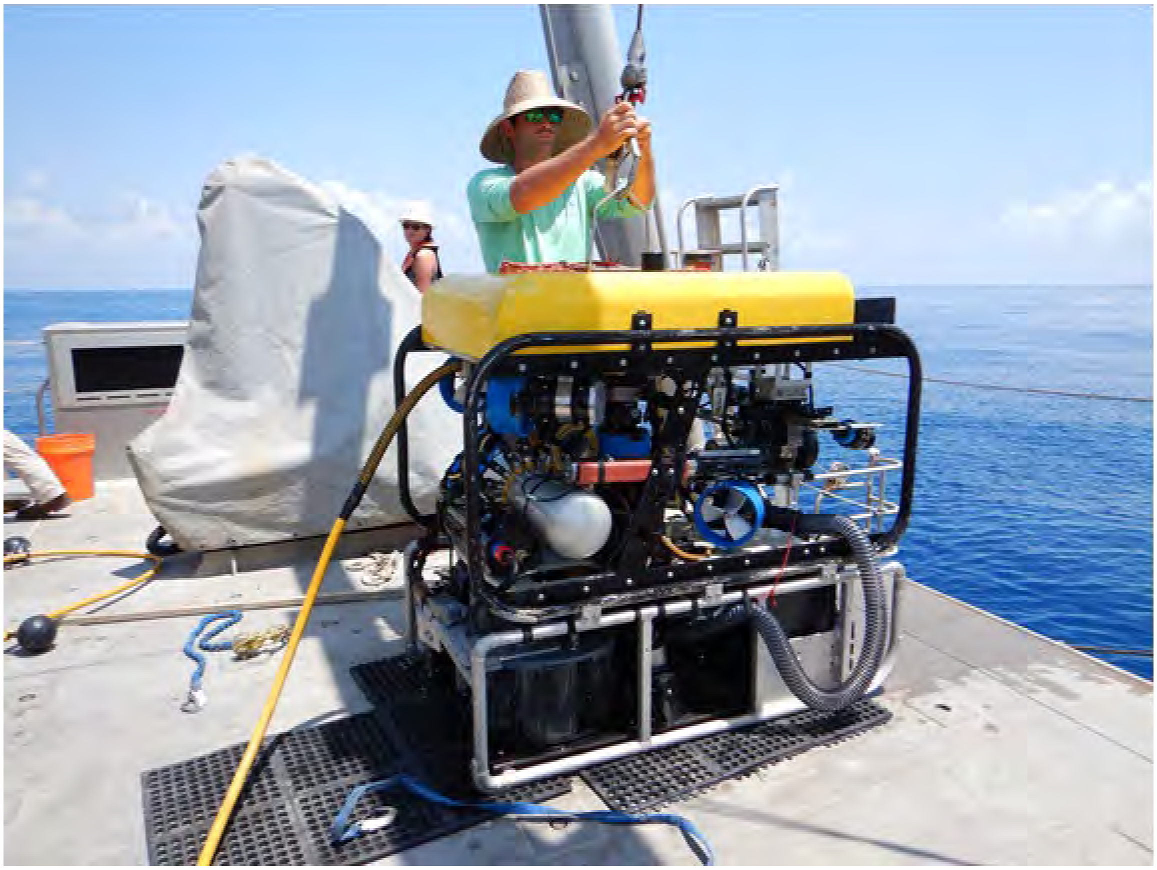

Figure 2.7. SubAtlantic Mohawk 18 ROV for mesophotic surveys. Owned by NMSF and operated by UNCW-UVP. Photo: Drinnen/NOAA

Random Benthic Transects

Stratified random benthic transects were conducted from 2015–2018 on both the bank crest (17.9 to 32.8 m) and mesophotic reefs (33.5 to 58.3 m). On the bank crest, transect sites were selected within high- and low-relief habitat, defined using 1 m^2 resolution bathymetric data. Depth range was calculated with a 5 m x 5 m rectangular window, and reclassified to define low-relief habitat (<1 m range) and high-relief habitat (>1.1 m range). A 33.5 m contour was used to restrict the extent of the layer, limiting surveys to depths that would allow scuba divers sufficient time to conduct surveys and avoid decompression. Annually, 30 survey sites were randomly generated on the bank crest. Sites were distributed proportionally, by area, between habitats, resulting in 20 low-relief sites and 10 high-relief sites. A still camera mounted on a 0.65 m T-frame with strobes was used to capture non-overlapping images of the reef, where each image captured approximately 0.8 x 0.6 m (0.48 m^2). Each transect was designed to capture 8.16 m^2 of benthic habitat, consistent with methods used to monitor East and West Flower Garden Banks (EFGB and WFGB), therefore requiring 17 images (Johnston et al. 2015). Spooled fiberglass 15 m measuring tapes with 17 pre-marked intervals (every 0.8 m) were used as guides, providing a 0.2 m buffer between each image to prevent overlap. A Canon Power Shot® G11 digital camera in an Ikelite® housing with a 28 mm equivalent wet mount lens adapter, with two Inon® Z240 strobes set 1 m apart on the T-frame, was used (Figure 2.8).

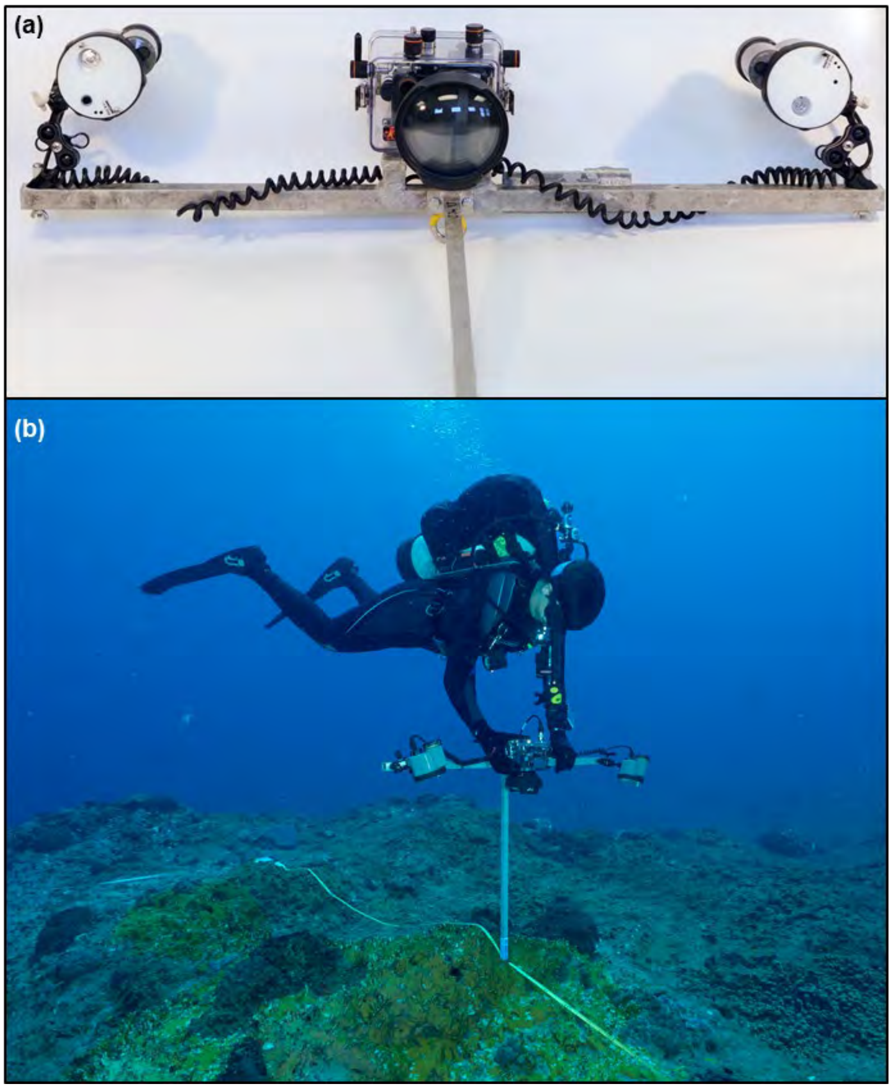

Figure 2.8. Random transect setup for bank crest surveys. (a) T-frame, camera, and strobe configuration and (b) diver using the equipment to conduct the transect along a pre-marked tape measure. Photos: (a) Eckert/NOAA and (b) Schmahl/NOAA

In mesophotic habitat, transect sites were selected within potential hard bottom habitat to exclude soft bottom habitat. Habitat was defined using 2 m resolution bathymetry raster with focal statistics calculated for range (minimum to maximum depth) within a 5 m x 5 m rectangle. Cells with a depth range >1 m were identified as potential habitat. A 33.5 m contour was used to restrict the extent of the layer, limiting surveys to depths greater than those conducted by scuba divers on the bank crest. Annually, 30 survey sites were randomly generated within mesophotic habitat, distributed proportionally by area between habitats: 15 in coralline algae reef and 15 in deep reef. The same SubAtlantic Mohawk 18 ROV described in Field Methods for repetitive photostations was used. Images were collected with the ROV still camera facing downward, perpendicular to the substrate. Transects started at each of the random drop sites and continued for 10 minutes along hard bottom habitat while the ROV traveled at one meter above the bottom, at a speed of approximately 1 knot per hour, taking downward-facing images every 30 seconds.

Bathymetric data processing and random site selection was conducted using ESRI ArcGIS® 10.3. If generated transects were anticipated to overlap or be unsuccessful due to poor environmental conditions (high current and low visibility), they were removed as a target site in the field.

Data Processing

Repetitive Benthic Photostations

On the bank crest, different image processing was required for each camera system used. From 2015–2017 (Canon Power Shot® G11 digital camera in a G11 Fisheye FIX® housing with a wide-angle dome port), the resulting image covered 7.68 m^2. These images were cropped using a scaled template to maintain the historically captured 1.6 m^2 area. In 2018 (Sony A6500 digital camera in a Nauticam NA-A6500 housing with a Nikkor Nikonos 15 mm underwater lens), the resulting image covered 1.6 m^2 and required no cropping. In mesophotic habitat, forward-facing still images of repetitive photostations were extracted from high-definition video obtained by ROV using VLC Media Player (1920 x 1080 dpi). All cropping and color and brightness corrections were made, as necessary, using Adobe Photoshop® CS2.

Percent cover was calculated for bank crest repetitive photostations using Coral Point Count® with Excel® extensions (CPCe; Kohler & Gill 2006). Thirty points were randomly overlaid on each image, and the benthos lying directly under each point was identified as follows: all Cnidaria, Porifera, and macroalgae to the lowest possible taxonomic group (macroalgae included algae longer than approximately 3 mm and thick algal turfs); other organisms were identified to the phylum level; and substrate was characterized as rubble, soft bottom, fine turf, and bare rock. Summary data were organized into major groups: substrate, phylum, or order, where crustose coralline algae, fine turf, and bare rock were combined into a group denoted as colonizable substrate, formerly called "CTB" (Aronson & Precht 2000, Aronson et al. 2005), other live components (ascidians, fish, serpulids, etc.) and unknown species were recorded as "other biota," and rubble was recorded in its own category. Bleaching, paling, fish biting, and other disease or damage were recorded as "notes," providing additional information for each random point. Excel spreadsheets were created automatically via CPCe using custom coral code files.

For mesophotic repetitive photostations, key features were identified in each image from 2015 and outlined using a color-coded key in Adobe Illustrator. If markers moved between years, new key features were identified. These key features were assigned a code using the first two letters of the genus and species name, along with a unique number (for example, StIn_1 = *Stephanocoenia intersepta* colony 1). Measurements of key features were made in ImageJ based on the 10 cm reference lasers.

All repetitive photostation images were qualitatively compared to the image from the previous year. The loss, reduction, expansion, or gain of species of interest and key features, in addition to changes in general conditions, were noted in Microsoft® Excel®.

Random Benthic Transects

Bank crest transects were processed to remove transects with poor quality images (dark, silted, or out-of-focus). Of the remaining transects, all 17 images were processed using CPCe. Mesophotic transect images were processed to remove silted, shadowed, out-of-focus, or soft bottom images (images with <50% hard bottom). From the remaining images in each transect, 11 images were randomly selected for processing. If a transect did not have at least nine useable images, it was removed from the analysis. Table 2.2 shows the number of samples processed by year.

Table 2.2. Number of random transect samples per year. Values represent transects that met data processing requirements. Number of high-relief or deep reef surveys are shown with low-relief or coralline algae reef surveys in parentheses.

Year	Bank Crest Samples High Relief (Low Relief)	Mesophotic Samples Deep Reef (Coralline Algae Reef)
2015	8 (12)	10 (10)
2016	10 (21)	12 (13)
2017	8 (15)	14 (12)
2018	7 (13)	9 (11)

Percent cover was calculated using CPCe with 500 points per transect, evenly distributed among the number of images but randomly overlaid on an image. The species lying under each point was identified as described in *Repetitive Benthic Photostations*.

Bank crest data are presented as percent cover by transect, with each sample site treated as one sample. In 2015, two transects were completed at each sample site, so data were averaged. In subsequent years, one transect was completed at each site.

Mesophotic data are presented as weighted cover, as transects differed in area. Weight was calculated for each sample by dividing the goal area (8.16 m^2) by the actual transect area. Transect area was obtained with ImageJ by calculating the area captured in each processed image, using the scale lasers, and summing over the transect. In addition, mesophotic transect images were processed to determine density of cnidarian species of interest (stony corals, octocorals, black corals, and soft corals) using colony counts. Colony counts for each species were summed across transects and converted to density per 100 m^2.

Statistical Analysis

Data were analyzed by survey method (repetitive photostation and random transect) and habitat (bank crest and mesophotic) (Table 2.3). Corals (Scleractinia and hydrocoral) and Porifera were analyzed to the species level, then summed and analyzed by major groups: Scleractinia, hydrocoral, Antipatharia, Octocorallia, Alcyonacea, Porifera (encrusting and erect), macroalgae (algae > 3 mm and thick algal turfs), colonizable substrate, and other biota. Rubble was removed from analyses. Data were tested for benthic community differences using non-parametric distance-based analyses. Non-binomial percent cover data were square root transformed to meet the assumption of normality. Permutational multivariate analysis of variance (PERMANOVA; Anderson 2017b) was based on Bray-Curtis similarity matrices. PERMANOVA is a better alternative to ANOVA or MANOVA for ecological data, as it does not assume Euclidean distance or a normal distribution. When significant differences were detected, specific contrasts were conducted within PERMANOVA to examine factors of particular interest, including consecutive years, while reducing error rates. In addition, beta diversity was examinged among years by transforming species composition data to presence/absence, generating Jaccard's similarity matrices, and using a distance-based test for homogeneity of multivariate dispersion based on deviations from centroids (permutational analysis of multivariate dispersions [PERMDISP]; Anderson et al. 2006). The contribution of variables to significant dissimilarities was examined using similarity percentages (SIMPER; Clarke 1993, Clarke et al. 2014) on square root-transformed Bray-Curtis similarity matrices.

Table 2.3. PERMANOVA designs for benthic community data.

Data	Factors (# of Levels)	Fixed/Random	Sum of Squares	Number of Permutations	Permutation Method
Bank crest repetitive benthic photostation	Station (59) Year (4)	Random Fixed	Type III	9999	Reduced model [crossed]
Bank crest random benthic transect	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]
Bank crest random benthic transect by habitat	Year (4)	Fixed	Type I	9999	Unrestricted permutation of raw data
Bank crest random benthic transect by year	Habitat (2)	Fixed	Type I	9999	Unrestricted permutation of raw data
Mesophotic random benthic transect	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]

Data	Factors (# of Levels)	Fixed/Random	Sum of Squares	Number of Permutations	Permutation Method
Mesophotic benthic random transect by habitat	Year (4)	Fixed	Type I	9999	Unrestricted permutation of raw data
Mesophotic random benthic transect by year	Habitat (2)	Fixed	Type I	9999	Unrestricted permutation of raw data

Diversity measures (total species, Shannon diversity [log base e], Pielou's evenness, and Margalef species richness) were calculated for each sample. These measures were analyzed in concert as Euclidean distance similarity matrices, based on untransformed data, and tested for significant differences using PERMANOVA and SIMPER.

Historical analyses of repetitive photostation data used bank crest data averaged by year (1993–2018) to reduce within year variability. Significant year groupings were determined using cluster and similarity profile analysis (SIMPROF; Clarke et al. 2008, Clarke et al. 2014), based on square root-transformed data and Bray-Curtis similarity matrices. Principal component ordination (PCO; Anderson et al. 2008) was used to visualize the data, with percent variability explained in each canonical axis. Correlation vectors with correlation > 0.6 and temporal trajectory were overlaid on the plot. Where significant clusters were found with SIMPROF, variables contributing to observed differences were examined using SIMPER on square root-transformed Bray-Curtis similarity matrices. Monotonic trends were examined with the non-parametric Mann-Kendall trend test.

PERMANOVA, SIMPER, CLUSTER, SIMPROF, and PCO were performed in PRIMER version 7 (Clarke & Gorley 2015). Mann-Kendall trend tests were performed in R version 3.6.0 (R Core Team 2015).

Spatial interpolation of percent cover data was mapped using inverse distance weighting (IDW). Interpolations were created without separating data by habitat, using a variable search radius and 4 points. Analyses were performed in ESRI's ArcMap version 10.4.

Results

Repetitive Benthic Photostations

On the bank crest, 59 stations were located and photographed annually from 2015–2018 (Appendix 1). No significant differences in beta diversity (based on species composition) were found among years. Diversity measures were significantly different among stations and between years, with pairwise significant differences between 2015–2016 and 2017–2018, primarily due to changes in total species (Table 2.4).

Table 2.4. Bank crest repetitive benthic photostation PERMANOVA and SIMPER results for diversity measures. The measure contributing predominantly to the dissimilarity between the groups, mean value, and percent contribution are reported for each comparison.

		PERMANOVA			SIMPER			
		Pseudo-F	P	Unique Perms	Functional Group	Mean Group 1	Mean Group 2	% Cont
Station		2.66	**<0.001**	9881	No analyses			
Year		12.06	**<0.001**	9949	No analyses			
	2015-2016	10.17	**0.002**	9900	Total species	5.19	5.92	90.32
					Pielou's evenness	1.28	1.43	4.80
	2016-2017	1.52	0.225	9908	No analyses			
	2017-2018	12.56	**<0.001**	9902	Total species	5.61	6.58	91.97
					Margalef species richness	1.01	1.25	4.66

In repetitive photostations on the bank crest, *M. decactis* and *M. alcicornis* had the greatest mean cover of all coral species (Figure 2.9). When examining these corals at the species level, the community was significantly different among stations and between years, with only 2017–2018 exhibiting significant differences between consecutive years, primarily due to a reduction in the cover of *M. alcicornis* and *Siderastrea radians* (Table 2.5). No coral bleaching was documented during this study period at Stetson Bank.

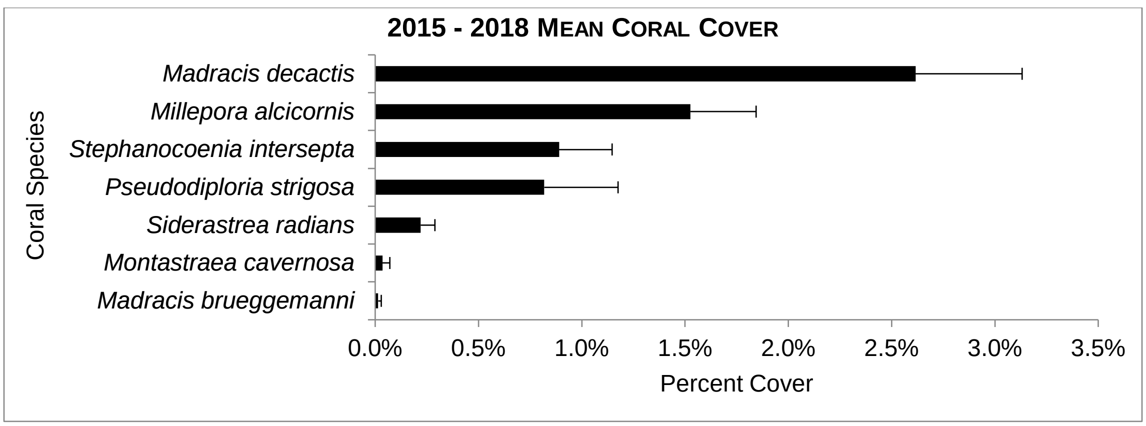

Figure 2.9. Mean coral cover 2015–2018. Error bars represent standard error.

Table 2.5. Bank crest repetitive benthic photostation PERMANOVA and SIMPER results for coral species. The coral species contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison.

Test	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Station	11.37	**<0.001**	9743	No analyses			
Year	2.41	**0.0117**	9933	No analyses			
2015-2016	0.24	0.8998	9952	No analyses			
2016-2017	1.82	0.1334	9960	No analyses			
2017-2018	2.81	**0.0309**	9942	*M. alcicornis*	1.45	1.13	30.91
				S. radians	0.52	0.24	24.13
Station x Year	No analyses – insufficient replication						

Ircinia strobilina and *Ircinia felix* had the greatest mean cover of all Porifera species on the bank crest in repetitive photostations (Figure 2.10). The community was significantly different among stations and between years, with both 2015–2016 and 2017–2018 exhibiting significant differences between consecutive years (Table 2.6). In 2015–2016, a decline in *I. strobilina* and increase in *Spirastrelle cunctatrix* cover were the primary contributors to the dissimilarity. In 2017–2018, an increase in *I. felix* and decrease in *I. strobilina* cover were the primary contributors to the dissimilarity.

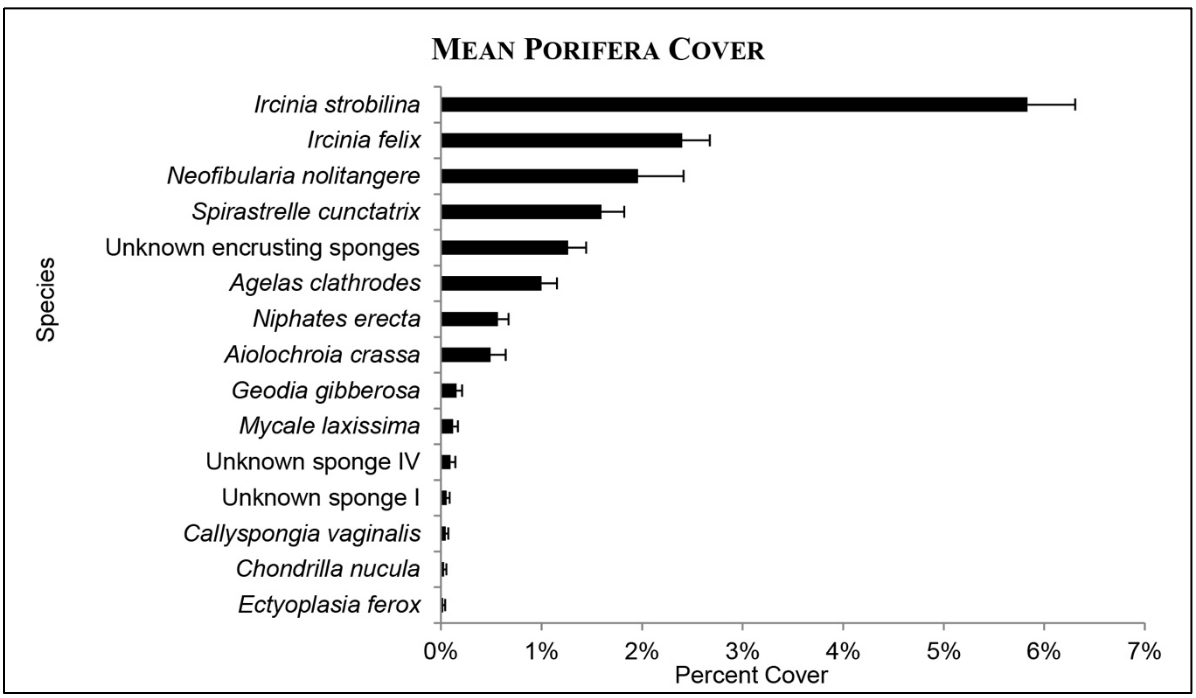

Figure 2.10. Mean Porifera cover 2015–2018. Error bars represent standard error. Numbered unknown sponges represent morphospecies that can be visually differentiated.

Table 2.6. Bank crest repetitive benthic photostation PERMANOVA and SIMPER results for Porifera species. The species contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison.

Test		PERMANOVA			SIMPER			
		Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Station		4.00	**<0.001**	9725	No analyses			
Year		6.56	**<0.001**	9916	No analyses			
	2015-2016	12.13	**<0.001**	9946	*I. strobilina*	6.60	5.40	20.02
					S. cunctatrix	0.00	3.03	16.99
	2016-2017	2.04	0.097	9970	No analyses			
	2017-2018	4.17	**0.002**	9961	*I. felix*	2.28	2.55	17.49
					I. strobilina	6.07	5.24	14.70
Station x Year		No analyses – insufficient replication						

These findings were supported in qualitative comparisons of bank crest repetitive photostations between years (Appendix 2). An additional observation of note that was not captured in random point analysis was the recruitment of additional colonies of the exotic species *Tubastraea coccinea* in 2018.

When examined by major categories, the bank crest community was significantly different among stations and all consecutive years, with dissimilarities primarily due to variable cover of macroalgae (Table 2.7); macroalgae cover increased annually from 2015–2017 and declined in 2018.

Table 2.7. Bank crest repetitive benthic photostation PERMANOVA and SIMPER results for major categories. The major category contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison.

Test		PERMANOVA			SIMPER			
		Pseudo-F	P	Unique Perms.	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Station		6.41	**<0.001**	9778	No analyses			
Year		16.04	**<0.001**	9953	No analyses			
	2015-2016	4.33	**<0.018**	9975	Macroalgae	27.31	30.74	28.63
					Porifera	14.27	16.17	23.90
	2016-2017	19.99	**<0.001**	9960	Colonizable substrate	43.04	27.91	27.43
					Macroalgae	30.74	44.89	26.79
	2017-2018	24.10	**<0.001**	9976	Macroalgae	44.89	28.62	28.76
					Colonizable substrate	27.91	42.24	26.05
Station x Year		No analyses – insufficient replication						

From 1993–2018, the number of bank crest repetitive photostations photographed annually varied. When analyzed by annual mean cover of major groups, six year clusters were found (A: 1993–1998; B: 1999–2005; C: 2006–2010; D: 2011–2013; E: 2014 and 2017; and F: 2015–2016 and 2018) (Figure 2.11). Primary contributors to the dissimilarities among clusters were hydrocoral, macroalgae, and colonizable substrate cover (Table 2.8).

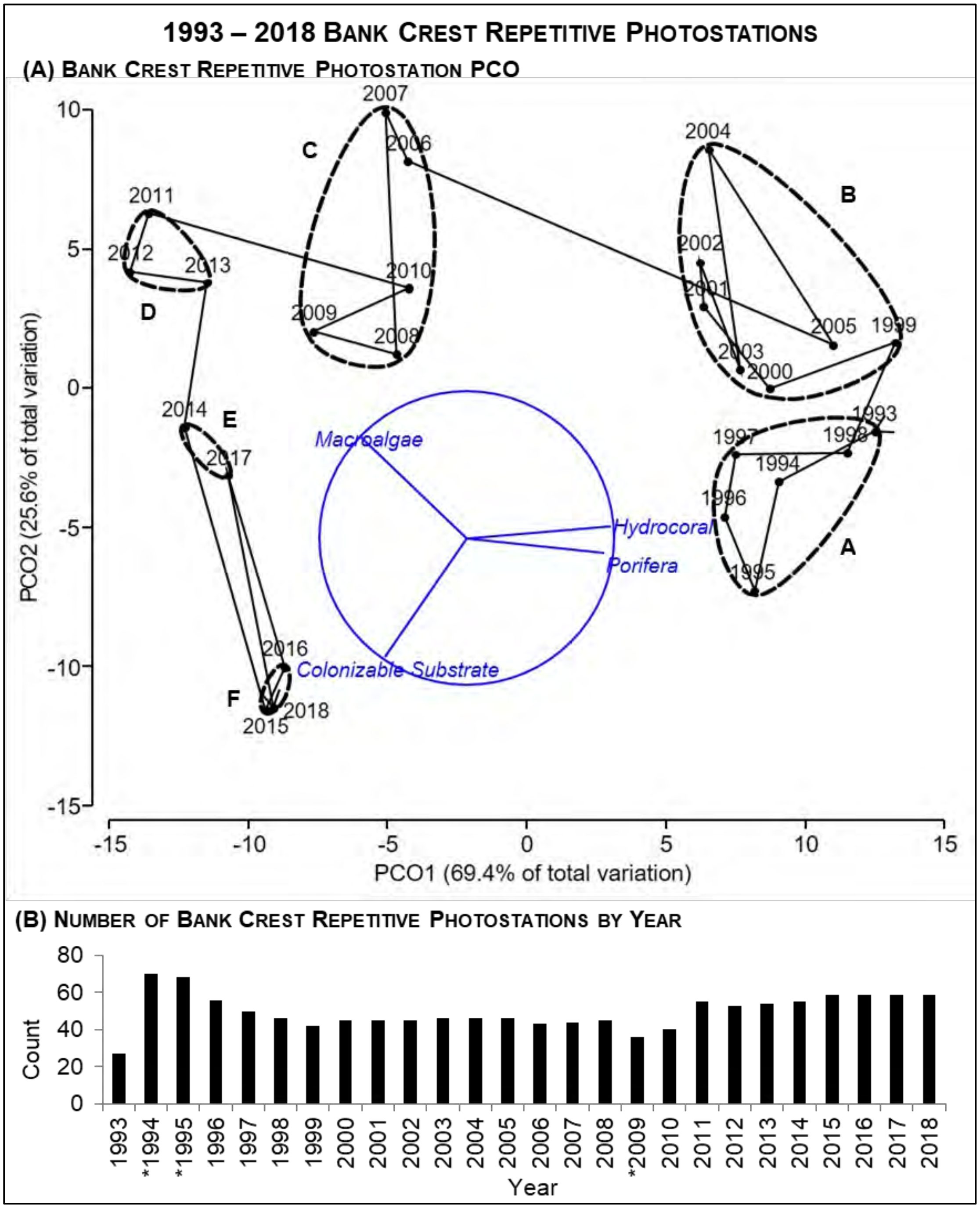

Figure 2.11. 1993–2018 bank crest repetitive benthic photostations. (A) Bank crest repetitive benthic photostation PCO, where the solid black line represents year trajectory, dashed black line represents significant SIMPROF clusters, and blue text and graphics represent vector overlays with >0.8 Pearson correlation. (B) Number of bank crest repetitive benthic photostation by year, where * denotes years where the mean of two sampling events were taken.

Table 2.8. Bank crest repetitive benthic photostation SIMPROF clusters SIMPER results. The major group contributing to the dissimilarity between the groups and the percent contribution are reported for each comparison.

Cluster	A	B	C	D	E
B	Macroalgae: 30.5%	-	-	-	-
C	Hydrocoral: 38.1%	Hydrocoral: 38.2%	-	-	-
D	Hydrocoral: 37.5%	Hydrocoral: 42.9%	Macroalgae: 40.1%	-	-
E	Hydrocoral: 39.7%	Hydrocoral: 46.7%	Macroalgae: 38.0%	Colonizable substrate: 29.3%	-
F	Macroalgae: 35.4%	Hydrocoral: 41.1%	Colonizable substrate: 39.6%	Colonizable substrate: 33.3%	Hydrocoral: 43.6%

In historical bank crest data, Mann-Kendall trend tests identified significant negative monotonic trends in hydrocoral and Porifera, and significant positive trends in macroalgae and colonizable substrate (Figure 2.12 and Table 2.9).

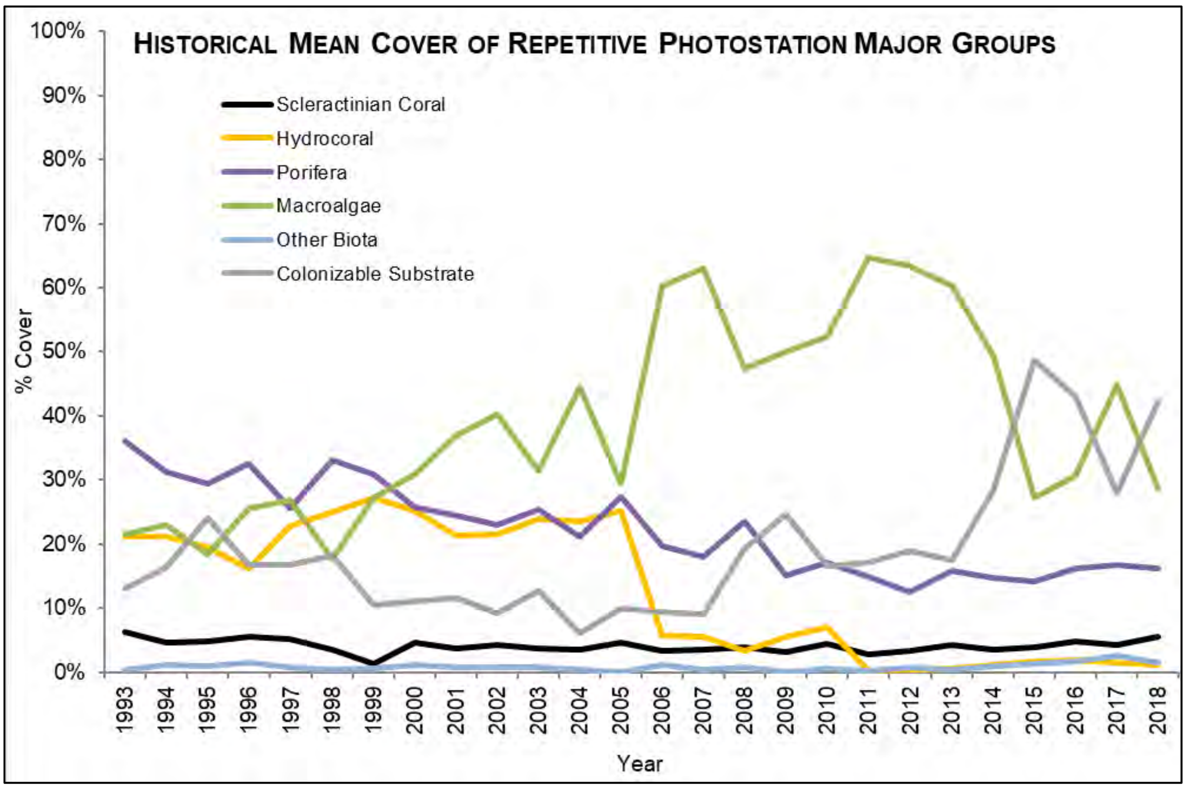

Figure 2.12. Historical mean cover of repetitive benthic photostation major groups.

Table 2.9. Historical mean cover Mann-Kendall monotonic trend test results. Bold indicates significant values.

Major Group	τ	p
Scleractinia	-0.17	0.234
Hydrocoral	-0.49	**<0.001**
Porifera	-0.71	**<0.001**
Macroalgae	0.47	**<0.001**
Other Biota	0.17	0.234
Colonizable Substrate	0.34	**0.015**

Mesophotic repetitive photostations were evaluated for feasibility during this study period. All floating markers were lost within a year of installation due to a material failure, leaving only cement blocks as site markers, which, due to their low profile and quick overgrowth, made the site difficult to find. Float loss combined with variable visibility on mesophotic habitat meant that excessive ROV dive time was spent searching for sites and not all sites were photographed annually (Table 2.10). Forward-facing images were difficult to recreate due to changes with the ROV setup (sampling skid on/off) and the heavily silted environment making fine-scale movements problematic due to resuspension of sediments. Data collection protocols were changed to capture imagery of key features instead of creating repeatable images. Downward-facing images were added to support the protocol.

Table 2.10. Mesophotic repetitive benthic photostation annual effort.

Year	Percent of Stations Found	Search Time (mins)
2015	100	-
2016	100	134
2017	71	183
2018	100	164

Due to consistent challenges finding and imaging mesophotic repetitive photostations, only qualitative comparisons were feasible. This revealed that three of seven cement blocks marking the stations moved from their original site over the four-year period. In addition, changes in key features were observed; these included bleaching and recovery of scleractinian corals, reduction and growth of black corals, and breakage of octocorallian branches (Appendix 3).

Random Benthic Transects

Following processing, 94 random transects were analyzed from the bank crest for 2015–2018 (Figure 2.13, Appendix 4). No significant differences in beta diversity (based on species composition) were found between habitats or years. Diversity measures were significantly different between habitats and years, with no significant interactions. Between habitats, the difference was primarily due to greater total species in high-relief habitats than in low-relief habitats. Between years, significant differences were found between 2016–2017, primarily due to a reduction in total species (Table 2.11).

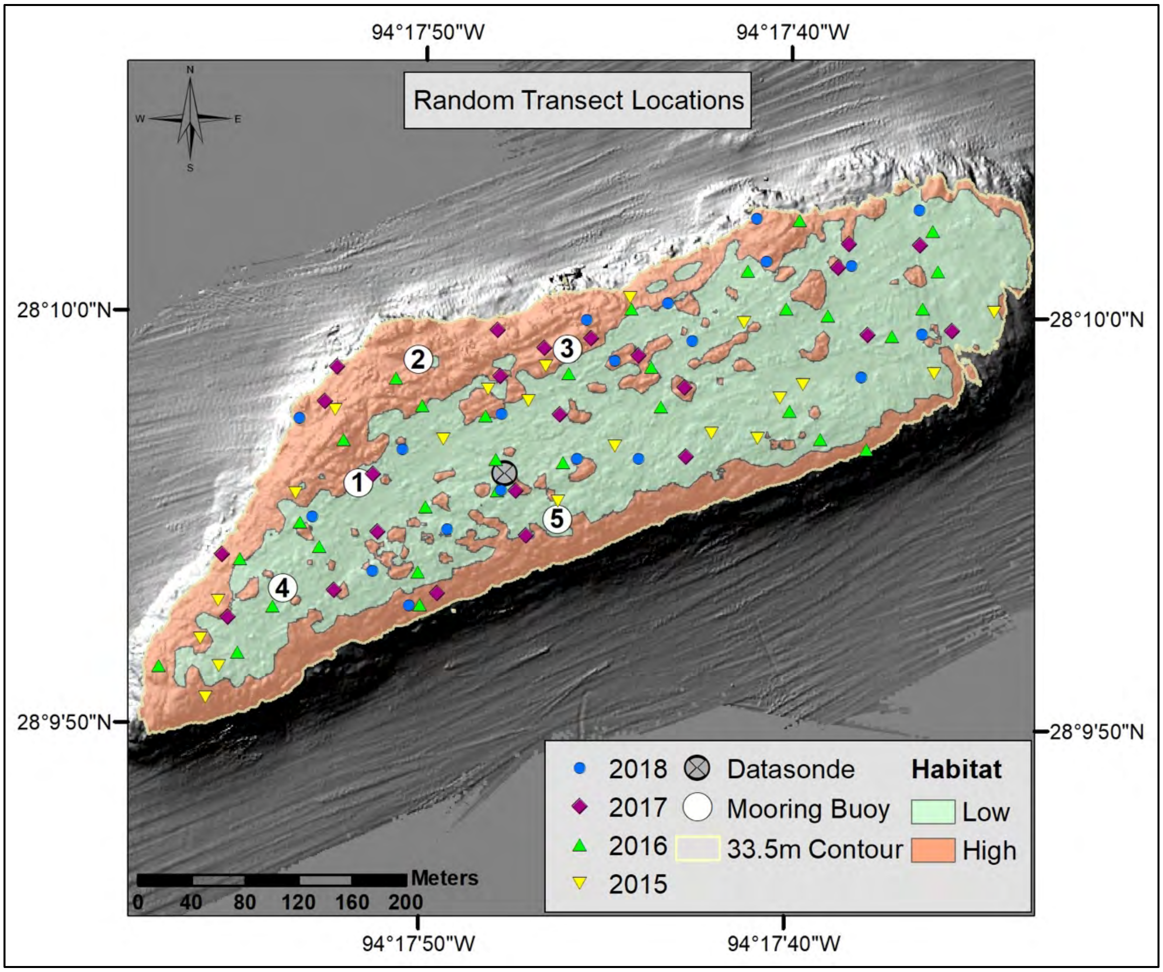

Figure 2.13. Bank crest random transect locations. Surveys are grouped by year, from 2015 through 2018. Mooring buoys and are labeled with their respective buoy number. The location of the monitoring datasonde, in 25 m of water, is also indicated. Image: NOAA

Table 2.11. Bank crest random benthic transects PERMANOVA and SIMPER results for diversity measures. The measures contributing most to the dissimilarity between the groups, mean value, and percent contribution are reported for each comparison.

	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean Group 1	Mean Group 2	% Cont
Habitat (Low: High)	15.63	**<0.001**	9896	Total species	14.21	16.36	95.01
				Margalef species richness	3.01	3.44	4.43
Year	3.53	**0.020**	9947	No analyses			
2015-2016	0.08	0.793	9895	No analyses			
2016-2017	4.31	**0.042**	9898	Total species	15.61	14.22	94.41
				Margalef species richness	3.31	2.97	4.88
2017-2018	0.10978	0.744	9910	No analyses			
Habitat x Year	0.25981	0.859	9943	No analyses			

Mean coral cover from 2015–2018 highlights that different species had greater cover in low- and high-relief habitats (Figure 2.14). In low-relief habitat, *S. intersepta* had the greatest coral cover, while in high-relief habitat, *M. alcicornis* had the greatest coral cover. *Madracis brueggemanni* and *M. auretenra* were only present in low-relief habitats. When examining corals at the species level, the bank crest coral community had a significant interaction between habitat and year. When separated by habitat, both low- and high-relief habitat had no significant difference in coral community among years. When separated by year, high- and low-relief habitats were significantly different in 2016 and 2018, primarily due to greater cover of *M. alcicornis* and *S. radians* in high-relief habitat compared to low-relief habitat (Table 2.12). No coral bleaching was documented during this study period at Stetson Bank.

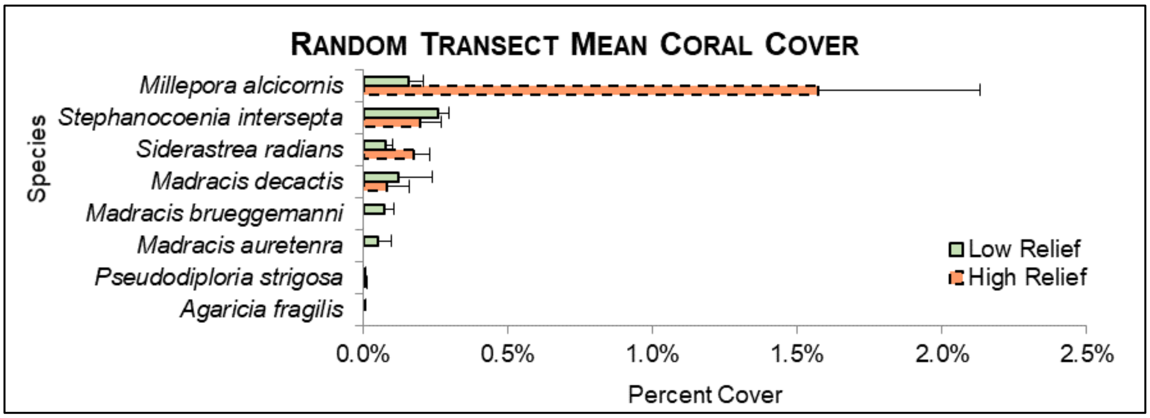

Figure 2.14. Bank crest random benthic transect mean coral species cover, 2015-2018. Error bars represent standard error.

Table 2.12. Bank crest random benthic transects PERMANOVA and SIMPER results for coral species. The coral species contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison.

Test	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat x Year	2.04	**0.030**	9926	No analyses			
Low Relief, Year	1.47	0.160	9944	No analyses			
High Relief, Year	1.91	0.085	9943	No analyses			
2015, Habitat (Low: High)	2.46	0.069	9570	No analyses			
2016, Habitat (Low: High)	5.90	**0.002**	9915	*Millepora alcicornis*	0.34	3.04	49.48
				Siderastrea radians	0.03	0.15	49.36
2017, Habitat (Low: High)	0.93	0.460	9717	No analyses			
2018, Habitat (Low: High)	3.96	**0.009**	3461	*Siderastrea radians*	0.03	0.28	52.95
				Millepora alcicornis	0.00	1.09	47.05

On the bank crest, *N. nolitangere* was the sponge species with the greatest cover in both habitats (Figure 2.15). When examining Porifera on the bank crest at the species level, the community was significantly different among stations and years, with no significant interaction. Between habitats, the difference was primarily due to greater cover of *N. nolitangere* and lower cover of *I. strobilina* in low-relief habitats compared to high-relief habitats. Between years, the variable cover of *N. nolitangere* was the primary cause of the dissimilarities (Table 2.13).

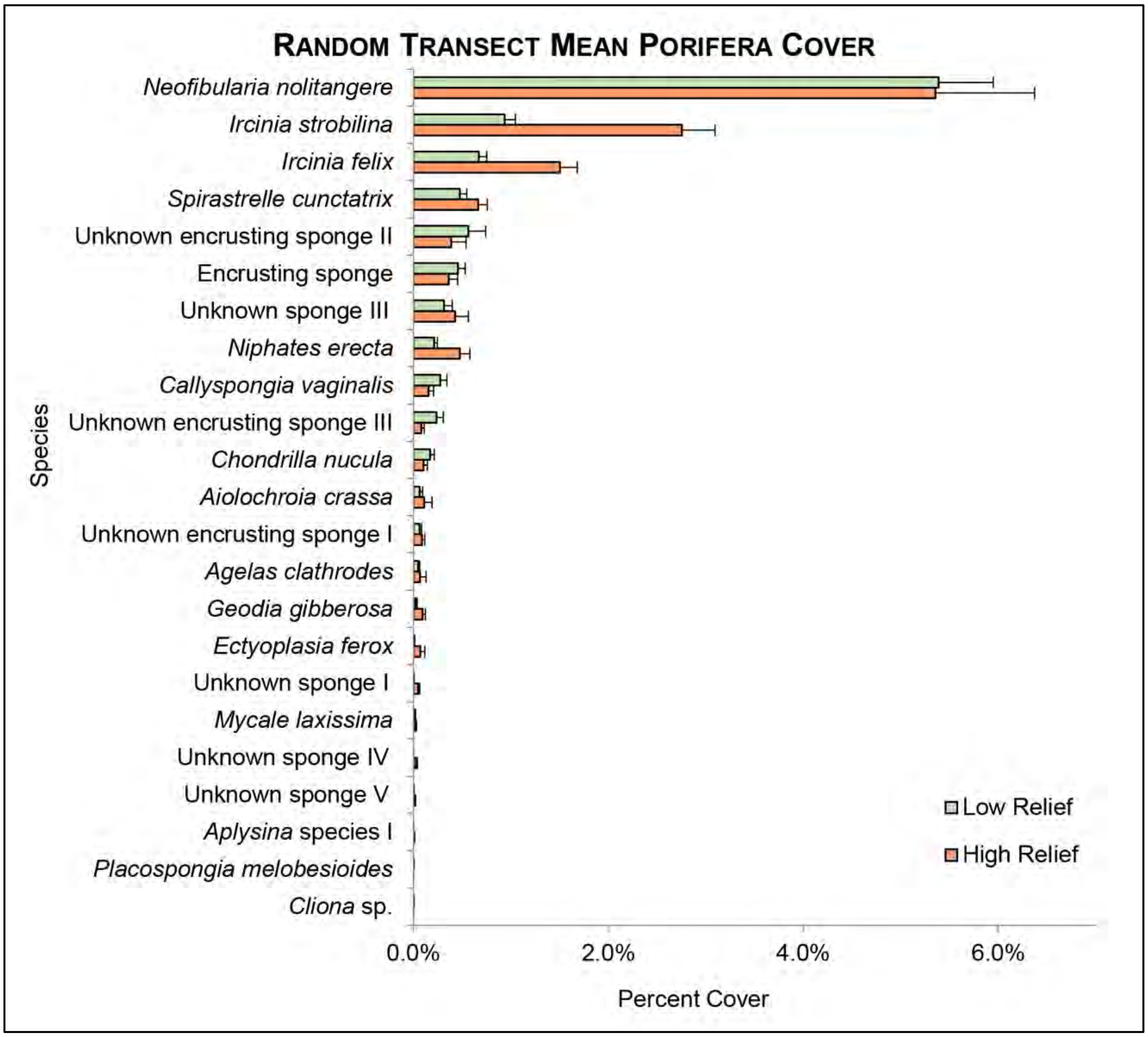

Figure 2.15. Bank crest random benthic transect mean Porifera cover. Error bars represent standard error. Numbered unknown sponges represent morphospecies that can be visually differentiated.

Table 2.13. Bank crest random benthic transects PERMANOVA and SIMPER results for Porifera species. The species contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison.

Test		PERMANOVA			SIMPER			
		Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat (Low: High)		5.73	**<0.001**	9948	*Neofibularia nolitangere*	5.39	5.36	20.57
					Ircinia strobilina	0.94	2.76	14.20
Year		7.61	**<0.001**	9919	No analyses			
	2015-2016	3.69	**<0.001**	9938	*Neofibularia nolitangere*	6.08	6.14	20.63
					Ircinia strobilina	1.71	1.63	10.99
	2016-2017	9.16	**<0.001**	9943	*Neofibularia nolitangere*	6.14	4.64	17.10
					Unknown encrusting sponge II	0.11	1.13	10.77
	2017-2018	3.01	**0.013**	9952	*Neofibularia nolitangere*	4.64	4.34	20.96
					Unknown encrusting sponge II	1.13	0.86	12.14
Habitat x Year		0.81	0.690	9914	No analyses			

There was a significant interaction between habitat and year when the bank crest community was examined by major groups. When separated by habitat, both low- and high-relief habitats were significantly different, with pairwise analyses finding significant differences in low-relief habitat between 2015–2016 and in high-relief habitat between 2015–2016 and 2016–2017. In both habitats, these differences were primarily due to reduced macroalgae cover in 2016 and a subsequent increase in 2017. When separated by year, high- and low-relief habitats were significantly different in 2016 and 2018. In 2016, these differences were primarily due to a lower cover of colonizable substrate and a greater cover of hydrocoral in high-relief habitat compared to low-relief habitat. In 2018, these differences were primarily due to lower cover of macroalgae and greater cover of Porifera in high-relief habitat compared to low-relief habitat (Table 2.14).

Table 2.14. Bank crest random benthic transects PERMANOVA and SIMPER results for major categories. The category contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison.

Test	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat x Year	2.29	**0.021**	9923	No analyses			
Low Relief, Year	3.06	**0.006**	9943	No analyses			
2015-2016	5.76	**0.003**	9958	Colonizable substrate	38.68	27.04	27.95
				Macroalgae	34.27	46.06	25.83
2016-2017	0.95	0.4117	9963	No analyses			
2017-2018	1.72	0.172	9957	No analyses			
High Relief, Year	3.68	**<0.001**	9931	No analyses			
2015-2016	4.15	**0.010**	8900	Colonizable substrate	36.85	20.58	27.63
				Macroalgae	38.15	53.02	20.61
2016-2017	5.76	**0.003**	8901	Colonizable substrate	20.58	34.41	26.17
				Macroalgae	53.02	39.18	19.87
2017-2018	1.74	0.1646	5084	No analyses			
2015, Habitat (Low: High)	1.90	0.129	9517	No analyses			
2016, Habitat (Low: High)	3.68	**0.015**	9945	Colonizable substrate	27.04	20.58	22.27
				Hydrocoral	0.34	3.04	19.86
2017, Habitat (Low: High)	2.58	0.067	9847	No analyses			
2018, Habitat (Low: High)	2.97	**0.048**	9364	Macroalgae	41.04	34.11	27.53
				Porifera	8.31	16.57	23.05

In mesophotic habitat, 100 random transects were used for analysis following data processing (Figure 2.16 and Appendix 5 and 6). Significant differences in beta diversity (based on species composition) were found among years (F=3.62, p=0.030), with pairwise analysis finding significant differences between 2016–2017 and 2017–2018 (t=3.22, p=0.002 and t=2.37, p=0.025, respectively). Analysis of diversity measures revealed a significant interaction between habitat and year. When separated by habitat, significant differences by year were only found in deep reef habitat, with pairwise analyses finding significant differences between 2015 and 2016, primarily due to reduced total species in 2016. When separated by year, the two habitats were significantly different in 2016, 2017, and 2018. In all years, the differences were primarily due to greater total species in coralline algae reef compared to deep reef (Table 2.15).

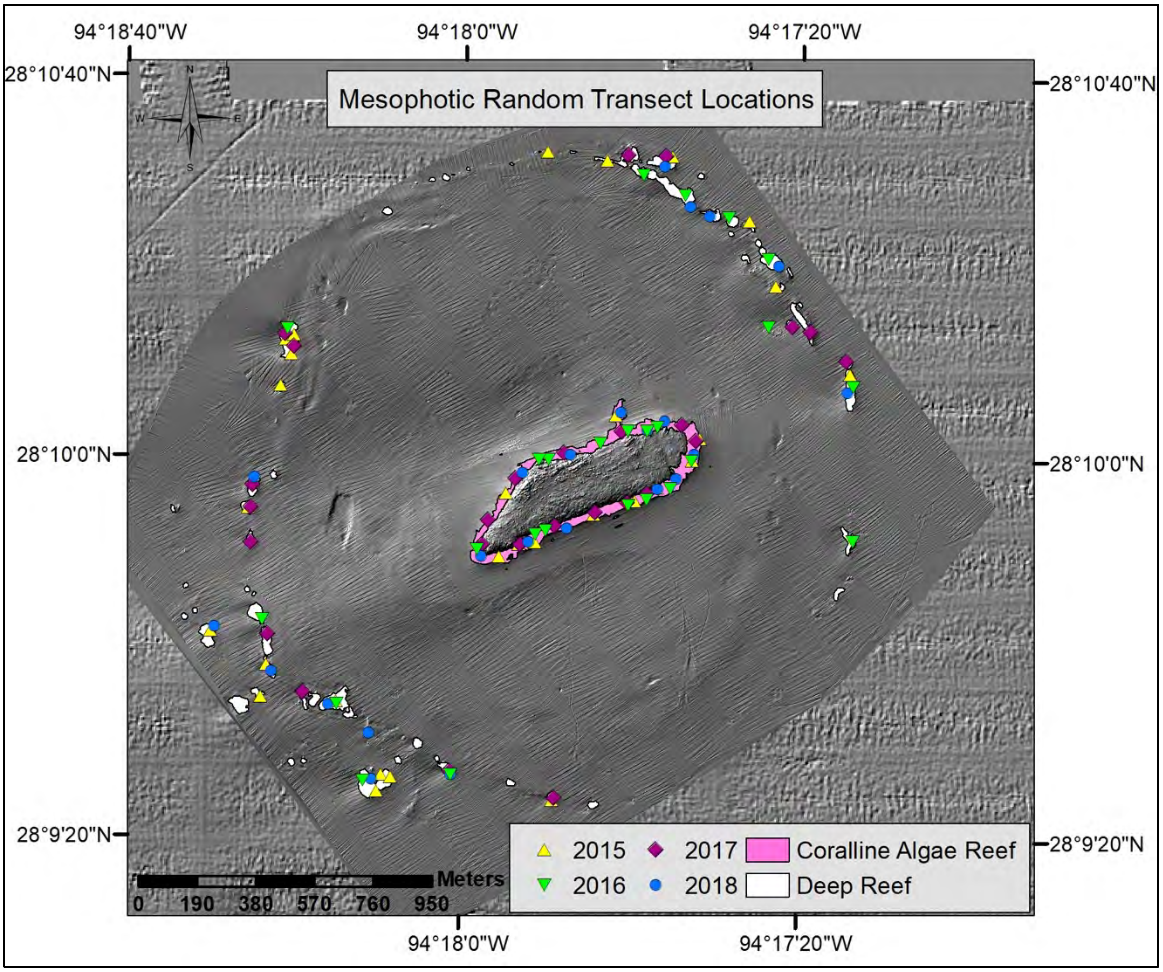

Figure 2.16. Mesophotic random benthic transect locations. Surveys are grouped by year, from 2015 through 2018. Image: NOAA

Table 2.15. Mesophotic random benthic transects PERMANOVA and SIMPER results for diversity measures. The measures contributing most to the dissimilarity between the groups, mean value, and percent contribution are reported for each comparison. CR represents coralline algae reef and DR represents deep reef.

Test	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean Group 1	Mean Group 2	% Cont
Habitat x Year	2.88	**0.042**	9950	No analyses			
Coralline Algae, Year	0.64	0.609	9952	No analyses			
2015-2016	0.80	0.419	9848	No analyses			
2016-2017	0.75	0.406	9883	No analyses			
2017-2018	0.09	0.792	9856	No analyses			
Deep Reef, Year	3.21	**0.028**	9949	No analyses			
2015-2016	4.96	**0.035**	9831	Total species	14.50	11.33	89.57
				Margalef species richness	4.20	3.22	9.80
2016-2017	0.20	0.706	9930	No analyses			
2017-2018	0.63	0.427	9827	No analyses			
2015, Habitat (CR: DR)	0.06	0.853	9345	No analyses			
2016, Habitat (CR: DR)	18.43	**<0.001**	9867	Total species	14.92	11.33	96.50
				Margalef species richness	3.40	3.22	2.82
2017, Habitat (CR: DR)	15.16	**0.001**	9898	Total species	15..25	11.07	92.07
				Margalef species richness	4.09	2.86	7.55
2018, Habitat (CR: DR)	7.56	**0.013**	9581	Total species	15.64	11.89	93.12
				Margalef species richness	4.06	3.20	6.58

The species with the highest coral cover were *S. intersepta* in coralline algae reef habitat was and black coral sea fans (possibly *Antipathes atlantica/gracilis*) in deep reef habitat (Figure 2.17). Little overlap in coral species (Alcyonacea, Antipatharia, Octocorallia, Scleractinia, and hydrocoral) was observed between these two mesophotic habitats. The mesophotic coral community was found to be significantly different between habitats and among years, with no significant interaction. Between habitats, the difference was primarily due to greater cover of black coral sea fans and *Stichopathe*s sp. in deep reef communities compared to coralline algae reef communities. No significant differences were found between consecutive years (Table 2.16).

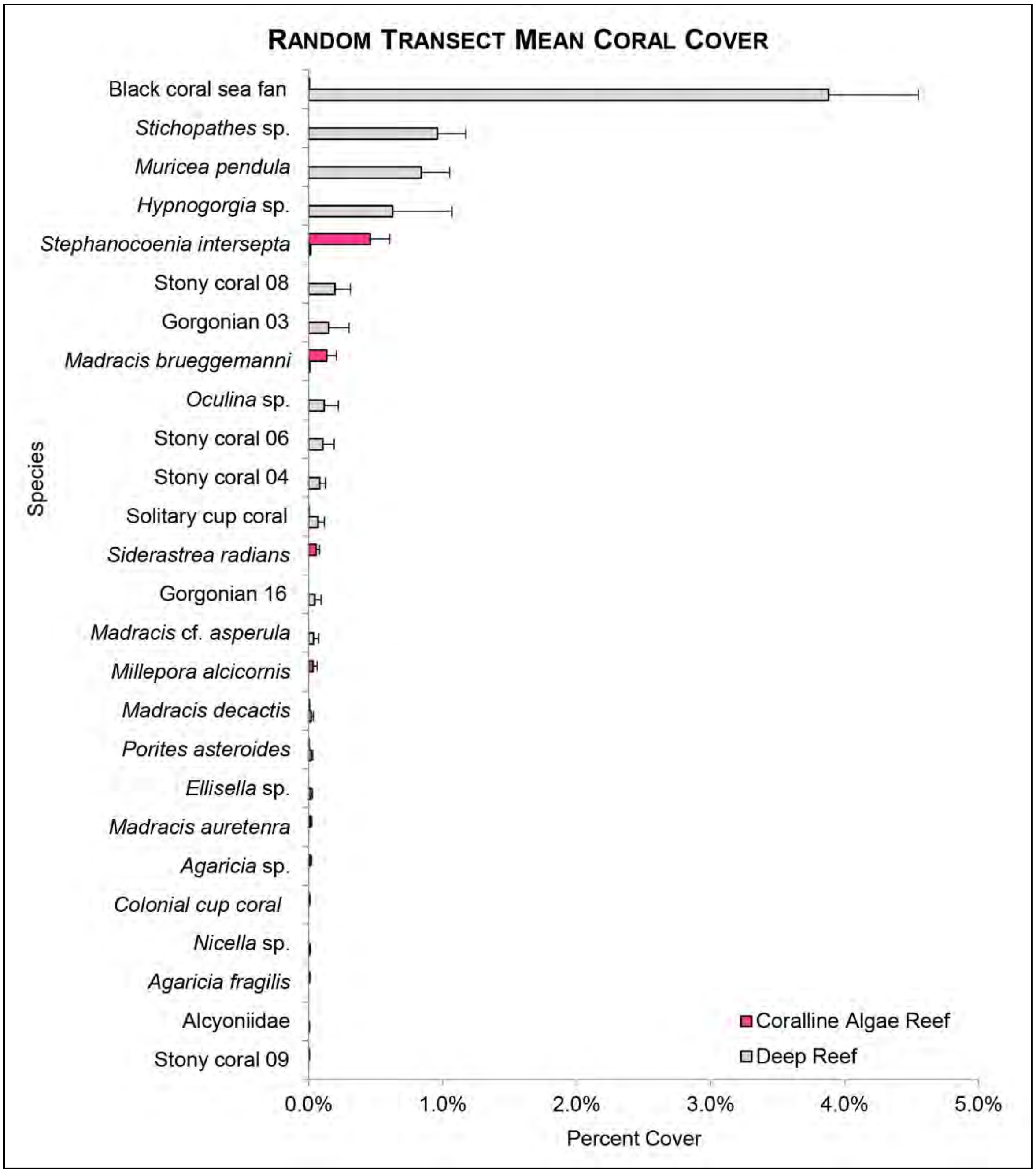

Figure 2.17. Mesophotic random benthic transect mean coral species cover. Error bars represent standard error. Numbered species represent morphospecies that can be visually differentiated.

Table 2.16. Mesophotic random benthic transects PERMANOVA and SIMPER results for coral species. The coral species contributing to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison. CR represents coralline algae reef and DR represents deep reef.

Test		PERMANOVA			SIMPER			
		Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat (CR: DR)		88.85	**<0.001**	9942	Black coral sea fan	<0.01	3.88	38.62
					Stichopathes sp.	0.00	0.96	17.55
Year		1.71	**0.029**	9901	No analyses			
	2015-2016	1.76	0.094	9944	No analyses			
	2016-2017	1.69	0.111	9935	No analyses			
	2017-2018	1.62	0.127	9939	No analyses			
Habitat x Year		1.48	0.078	9916	No analyses			

The mesophotic coral community was also examined using colony density (individuals per m^2). While there was still little overlap in species between the two mesophotic habitats, *M. brueggemanni* and solitary cup corals were the predominant species in coralline algae reef and deep reef habitats, respectively (Figure 2.18). Similar to percent cover data at the species level, the community was significantly different between habitats and among years, with no significant interaction. Between habitats, the difference was primarily due to greater density of black coral sea fans and *Stichopathe*s sp. in deep reef communities compared to coralline algae reef communities. No significant differences were found between consecutive years (Table 2.17).

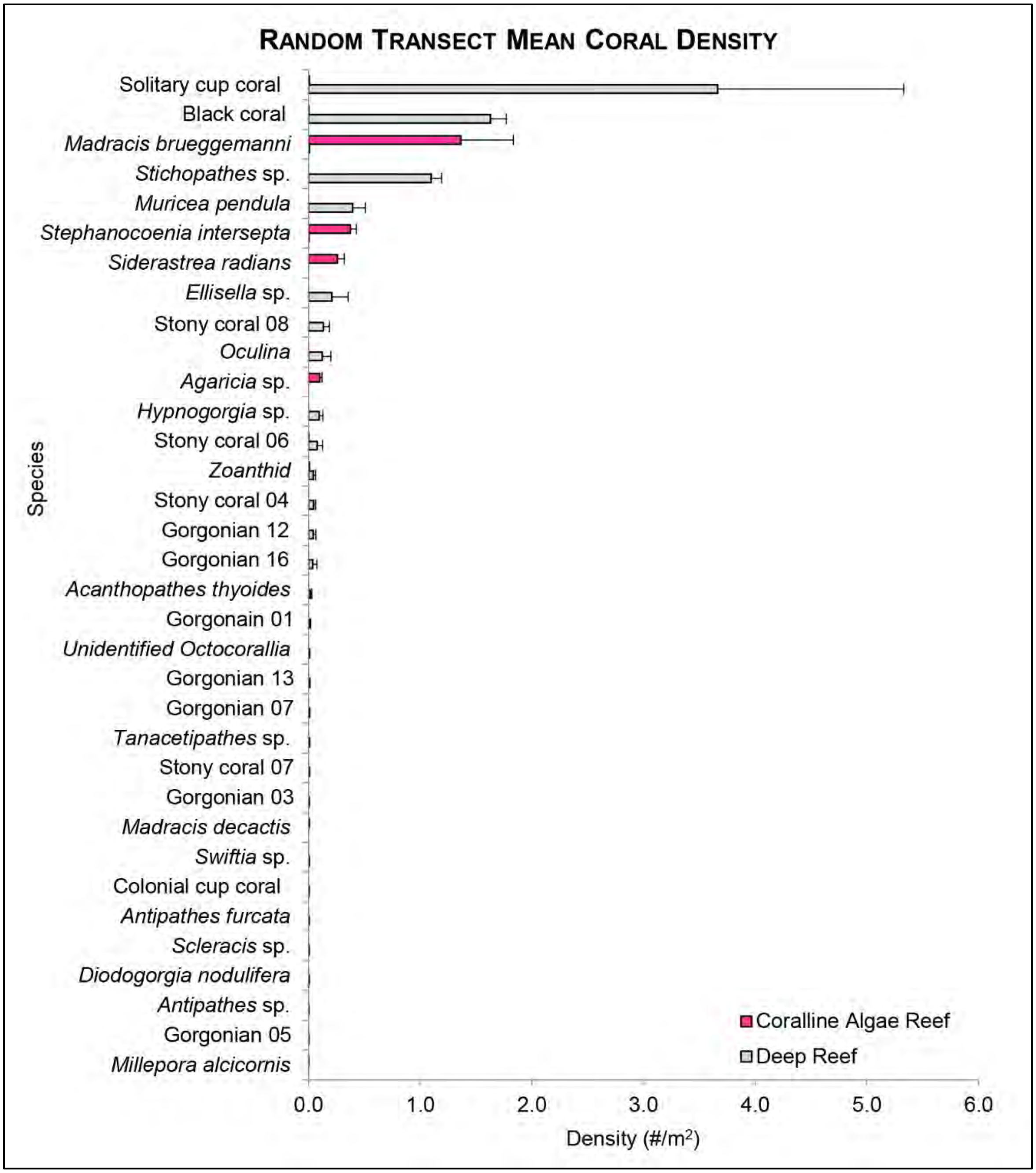

Figure 2.18. Mesophotic random benthic transect mean coral species density. Error bars represent standard error. Numbered species represent morphospecies that can be visually differentiated.

Table 2.17. Mesophotic random benthic transects PERMANOVA and SIMPER results for coral species density. The coral species contributing to the dissimilarity between the groups, mean density per m2, and percent contribution are reported for each comparison. CR represents coralline algae reef and DR represents deep reef.

Test		PERMANOVA			SIMPER			
		Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat (CR: DR)		98.80	**<0.001**	9932	Black coral sea fan	<0.01	1.63	20.07
					Stichopathes sp.	0.00	1.10	16.81
Year		1.7339	**0.030**	9914	No analyses			
	2015-2016	1.74	0.110	9932	No analyses			
	2016-2017	1.42	0.195	9935	No analyses			
	2017-2018	1.65	0.115	9939	No analyses			
Habitat x Year		1.44	0.101	9909	No analyses			

Porifera cover in mesophotic habitat was mostly comprised of an unidentified orange encrusting sponge. *N. nolitangere* had the second highest cover in coralline algae reef habitat but was absent from deep reef habitat; *Niphates erecta* had the second highest cover in deep reef habitat (Figure 2.19). At the species level, there was a significant interaction between habitat and year. When separated by habitat, both coralline algae reef and deep reef had significant differences in Porifera communities among years. The coralline algae reef Porifera community was significantly different between all consecutive years (2015–2016, 2016–2017, and 2017–2018), primarily due to variable cover of *N. nolitangere* and encrusting sponges. In deep reef habitat, the Porifera community was significantly different between 2015–2016 and 2017–2018 due to variable cover of encrusting sponges. When separated by year, coralline algae reef and deep reef Porifera communities were significantly different in all years (2015, 2016, 2017, and 2018) due to greater cover of *N. nolitangere*, *N. erecta*, and various encrusting sponges in coralline algae reef habitat (Table 2.18).

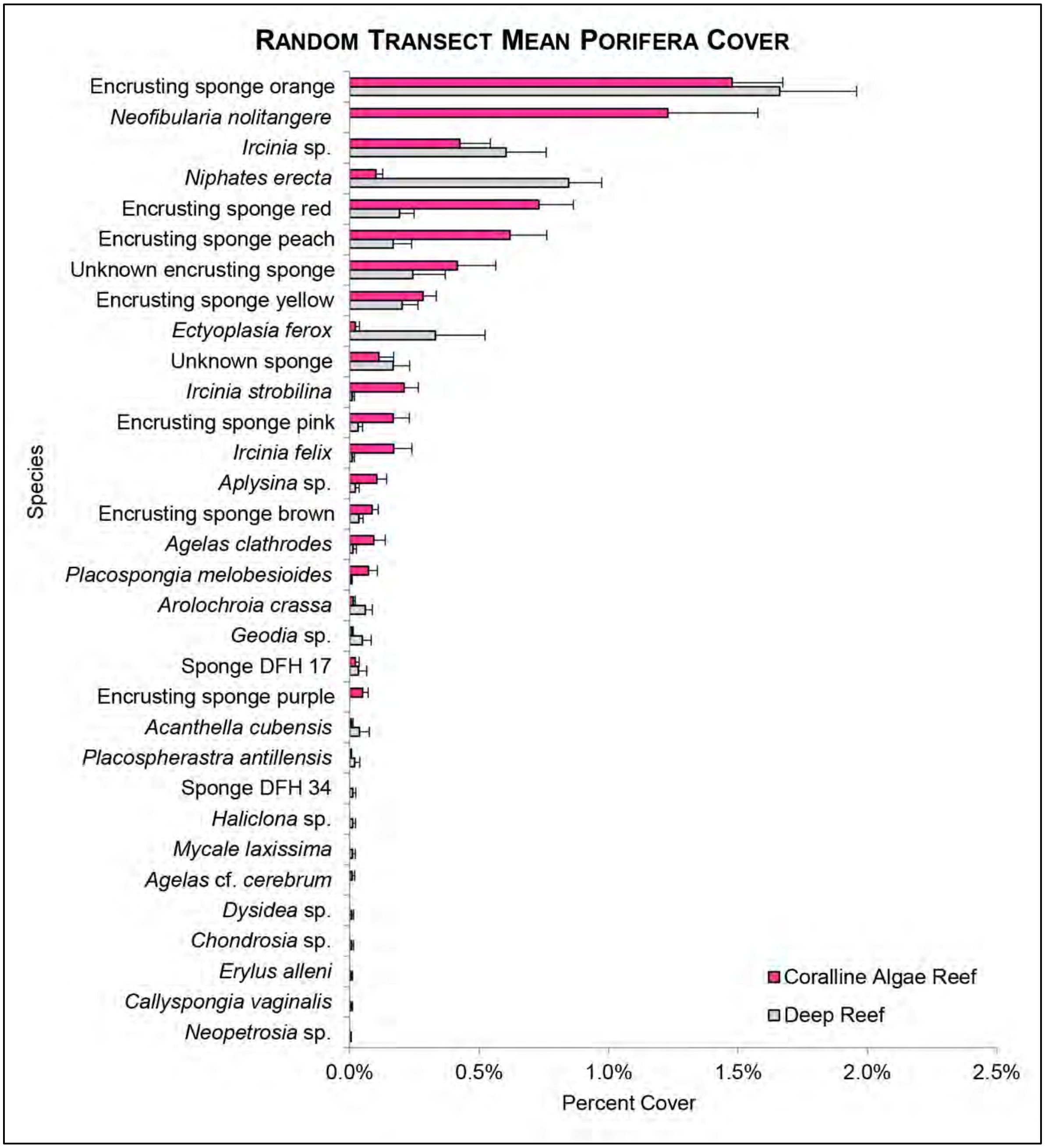

Figure 2.19. Mesophotic random benthic transect mean Porifera cover. Error bars represent standard error. Numbered species represent morphospecies that can be visually differentiated.

Table 2.18. Mesophotic random benthic transects PERMANOVA and SIMPER results for Porifera. The species contributing most to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison. CR represents coralline algae reef and DR represents deep reef.

Test	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat x Year	3.12	**<0.001**	9903	No analyses			
Coralline Algae, Year	14.83	**<0.001**	9918	No analyses			
2015-2016	4.79	**<0.001**	9914	*Neofibularia nolitangere*	1.56	2.59	17.4
				Encrusting - peach	0.11	1.23	12.58
2016-2017	2.33	**0.023**	9942	*Neofibularia nolitangere*	2.59	0.53	19.09
				Encrusting - peach	1.23	0.87	13.59
2017-2018	23.35	**<0.001**	9914	Encrusting sponge	0.00	1.74	15.39
				Encrusting - red	1.07	0.12	10.66
Deep Reef, Year	9.60	**<0.001**	9928	No analyses			
2015-2016	6.94	**<0.001**	9860	*Ectyoplasia ferox*	1.49	0.00	13.54
				Encrusting - red	0.69	0.06	13.39
2016-2017	1.76	0.127	9953	No analyses			
2017-2018	15.65	**<0.001**	9895	Encrusting - orange	2.78	0.00	25.71
				Encrusting sponge	0.00	1.22	15.05
2015, Habitat (CR: DR)	3.56	**<0.001**	9402	*Ircinia* sp.	1.29	0.89	12.59
				Neofibularia nolitangere	1.56	0.00	11.76
2016, Habitat (CR: DR)	10.71	**<0.001**	9937	*Neofibularia nolitangere*	2.59	0.00	17.69
				Encrusting - peach	1.23	0.35	13.56
2017, Habitat (CR: DR)	11.03	**<0.001**	9945	Encrusting - red	1.07	0.07	15.10
				Niphates erecta	0.11	0.98	13.56
2018, Habitat (CR: DR)	6.93	**<0.001**	9623	Encrusting sponge	1.74	1.22	13.96
				Niphates erecta	0.06	1.02	13.40

A significant interaction between habitat and year was present when major mesophotic community groups were analyzed. When separated by habitat, both coralline algae and deep reef communities were significantly different, with pairwise analyses finding significant differences in coralline algae reef in all consecutive years (2015–2016, 2016–2017, 2017–2018) and in deep reef between 2015–2016 and 2016–2017. In both habitats, these differences were primarily driven by variable macroalgae cover. When separated by year, coralline algae reef and deep reef communities were significantly different every year. In all years, these differences were due to higher cover of colonizable substrate in coralline algae reef habitat (Table 2.19).

Table 2.19. Mesophotic random benthic transects PERMANOVA and SIMPER results for major groups. The group contributing most to the dissimilarity between the groups, mean percent cover, and percent contribution are reported for each comparison. CR represents coralline algae reef and DR represents deep reef.

Test	PERMANOVA			SIMPER			
	Pseudo-F	P	Unique Perms	Functional Group	Mean % Cover Group 1	Mean % Cover Group 2	% Cont
Habitat x Year	4.00	**<0.001**	9923	No analyses			
Coralline Algae, Year	19.95	**<0.001**	9939	No analyses			
2015-2016	25.48	**<0.001**	9917	Macroalgae	4.28	30.73	47.33
				Colonizable substrate	39.12	21.87	22
2016-2017	15.60	**<0.001**	9947	Macroalgae	30.73	9.92	44.72
				Porifera	8.50	4.74	16.85
2017-2018	12.54	**<0.001**	9912	Macroalgae	9.92	25.04	41.35
				Colonizable substrate	19.40	9.55	28.64
Deep Reef, Year	3.36	**<0.001**	9932	No analyses			
2015-2016	8.97	**<0.001**	9876	Macroalgae	4.47	12.99	23.80
				Colonizable substrate	7.42	2.20	19.85
2016-2017	5.09	**0.003**	9939	Other biotic	4.78	18.04	21.06
				Macroalgae	12.99	8.81	19.95
2017-2018	1.74	0.140	9877	No analyses			
2015, Habitat (CR: DR)	19.97	**0.001**	995	Colonizable substrate	39.12	7.42	34.25
				Antipatharia	0.00	4.79	17.72
2016, Habitat (CR: DR)	39.63	**<0.001**	9941	Colonizable substrate	21.87	2.20	30.91
				Macroalgae	30.73	12.99	17.83
2017, Habitat (CR: DR)	22.98	**<0.001**	9950	Other biotic	0.23	18.04	25.08
				Colonizable substrate	19.40	9.20	22.7
2018, Habitat (CR: DR)	28.54	**<0.001**	9639	Other biotic	0.48	9.98	22.62
				Colonizable substrate	9.55	2.29	21.41

When examining mean cover of major groups from 2015–2018 by habitat, Scleractinia had similar percent cover in all habitats. However, Antipatharia and Octocorallia were only present in mesophotic deep reef habitat and hydrocoral had the greatest mean cover in bank crest high-relief habitat. Overall, Porifera had greater cover in bank crest habitats than in mesophotic habitats. Macroalgae and colonizable substrate made up the predominant cover in all habitats (Figure 2.20).

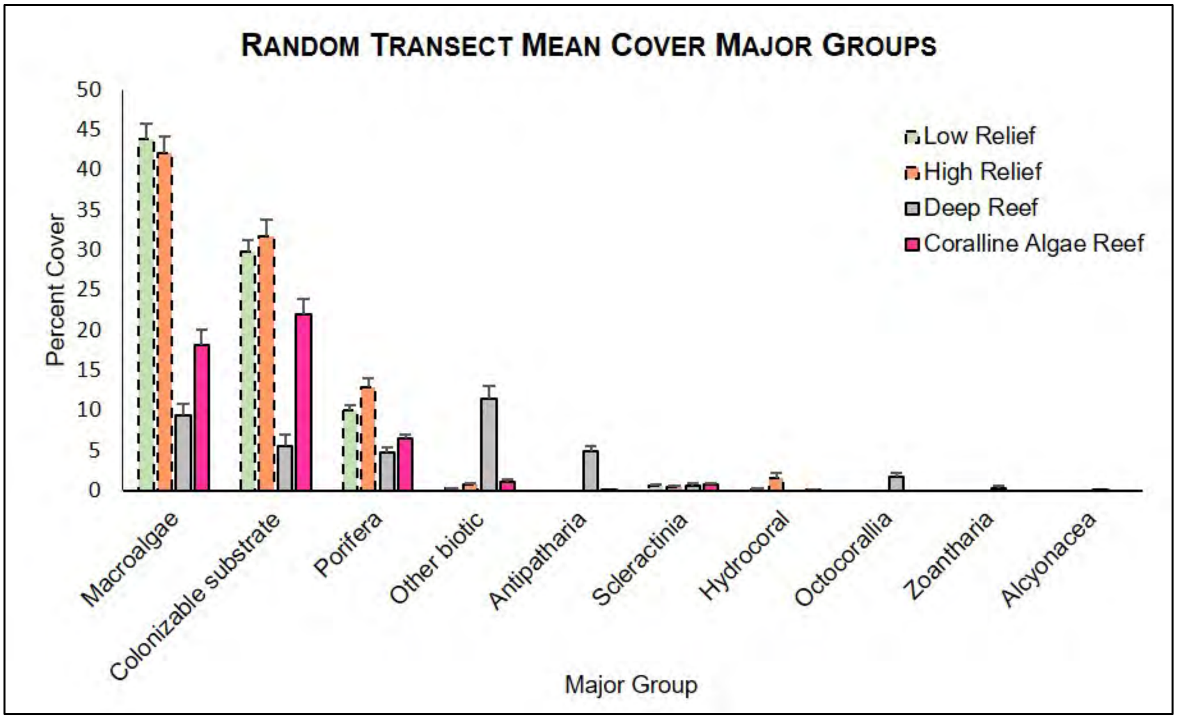

Figure 2.20. Mean cover of random benthic transect major groups. Bank crest data have dashed outlines while mesophotic data has solid outlines.

When projected spatially, additional patterns were observed. Alcyonacea were only found in the deep patch reefs to the north-northwest of the bank crest. Antipatharia were almost entirely restricted to the deep patch reef ring around Stetson Bank. Colonizable substrate had highest cover on the central bank feature, including the bank crest and coralline algae reefs. Hydrocoral cover was limited to the bank crest habitats, with particularly high cover on the northwest bank crest, in the pinnacles area. Similar to colonizable substrate, macroalgae had highest cover located on the central bank feature. Octocorallia were predominantly observed in the northwestern deep patch reefs. Porifera were distributed throughout the study area, with highest cover on the bank crest. Scleractinia were found in all habitats at Stetson Bank, but had the highest cover in coralline algae reef habitat, on the slopes of the central bank feature. Zoantharia were only found in the deep patch reef ring, with the highest cover in the south (Figure 2.21).

Spatial Projection of Random Transect Major Groups

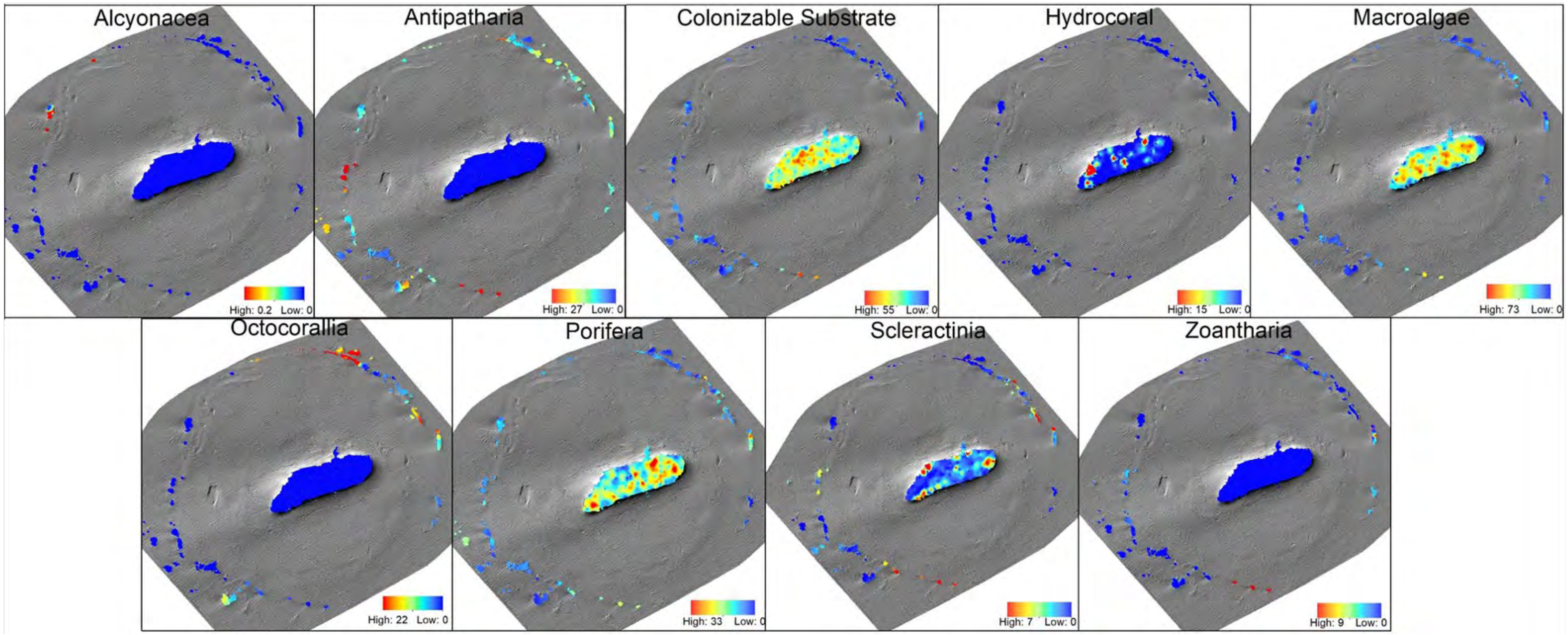

Figure 2.21. Inverse distance weighted cover maps for random benthic transect major groups across all habitats. Red represents highest cover and blue represents lowest cover. Maps are oriented so that the top of the image represents north. Image: NOAA

Discussion

Random transects were added to the annual monitoring protocol to provide a comprehensive assessment of the benthic communities in all habitats at Stetson Bank. Based on these surveys, on the bank crest, *M. alcicornis* corals and *N. nolitangere* sponges comprised the greatest mean benthic cover in high-relief habitats, while *S. intersepta* corals and *N. nolitangere* sponges comprised the greatest cover in low-relief habitats. In the mesophotic zone, *S. intersepta* corals and encrusting sponges were the predominant cover in coralline algae reef habitat while black coral sea fans (possibly *A. atlantica/gracilis*) and encrusting sponges were the predominant coral and Porifera cover, respectively, in deep reef habitat. While these species comprised the greatest benthic cover, they were not the most abundant species based on density; *M. brueggemanni* had the greatest density in coralline algae reef habitat and solitary cup corals had the greatest density in deep reef habitat. This community is very different from that of EFGB and WFGB, where the stony coral *Orbicella* spp. are the major contributor to benthic cover (Johnston et al. 2019a). However, Sonnier Bank, located approximately 97 nautical miles east-northeast of Stetson Bank, possesses a similar *Millepora*–sponge community from 18–40 m and a nepheloid layer from 50–62 m with turbidity-tolerant species (Rezak et al. 1985), analogous to the community at Stetson Bank.

Four habitats were examined in this study: bank crest low relief, bank crest high relief, mesophotic coralline algae reef, and mesophotic deep reef. While the mesophotic habitats were consistently significantly different, on the bank crest, significant differences between habitats (based on major groups and coral species) did not occur every year, suggesting that high- and low-relief habitats share similar major group and coral communities. However, despite these similarities, the Porifera community between these two habitats was significantly different throughout the period of this study, supporting the continued separation of these bank crest habitats for analysis. Spatial analysis also indicated how major groups are distributed over Stetson Bank differently. Antipatharia and Octocorallia were restricted to turbid mesophotic habitats and were entirely absent from the bank crest. Antipatharia abundance is known to increase with depth, potentially to reduce competition with obligate photosynthetic biota (Wagner et al. 2012). The turbid waters in the mesophotic habitat at Stetson Bank would have a similar effect on light availability with increasing depth, providing suitable habitat for several Antipatharia species. Several species of shallow water Octocorallia are known throughout the Gulf of Mexico, but are not found at Stetson Bank, potentially due to environmental conditions, location, and reduced ecological connectivity due to larval duration (Jordán-Dahlgren 2002, Schmahl et al. 2008). Additionally, the primary known cause of mortality in Octocorallia is from detachment of a colony's singular holdfast, making them particularly vulnerable to physical damage in high-energy environments (Yoshioka & Yoshioka 1991). While the impact of daily wave energy at Stetson Bank is not well-understood, periodic impacts from high energy waves have been documented in association with tropical weather systems (Nuttall et al. 2020).

While significant differences were found in comparisons of major groups between years, these differences were primarily attributed to variable cover of macroalgae and colonizable substrate in all habitats. Colonizable substrate includes crustose coralline algae, fine turf algae, and bare substrate, and most frequently varies inversely with macroalgal cover. This finding highlights the important role of variable cover of macroalgae in shaping community structure at Stetson

Bank and indicates that further analysis of species of interest, including corals and Porifera, could reveal more detailed community changes. In most comparisons, coral community analyses did not find many differences between years in all habitats, indicating that cover and density of corals, including Alcyonacea, Antipatharia, Octocorallia, Scleractinia, and hydrocoral, was stable throughout this study period. However, multiple significant differences between consecutive years were found in Porifera community analyses in all habitats, and while not detected as a significant difference in community from 2016–2017, qualitative analysis documented the loss of multiple colonies of *Ircinia* spp. from repetitive photostations (Nuttall et al. 2018). Several species of Porifera were involved in these differences, and while no cause for these changes was documented, variations in Porifera abundance can be caused by many factors, including physical damage, environmental conditions, and seasonal water temperature variations (Reiswig 1973, Elvin 1976). Porifera are strong competitors, often overgrowing other benthic organisms, and, while not supported by data presented in this report, have been reported to have a positive feedback loop with macroalgae cover, in which increased macroalgae cover supports Porifera growth and vice versa (Pawlik et al. 2007, Pawlik et al. 2016).

Analysis of historical repetitive photostation data found one new significant cluster from this study period, including all years from 2015–2018, except 2017 (Nuttall et al. 2020). The community in 2017, based on major groups, was more similar to the community in 2014, primarily due to relatively high macoralgae cover. While historical trends were similar to those reported in Nuttall et al. (2020), with significant declining trends in hydrocoral and Porifera and increasing trends in macroalgae and colonizable substrate, the additional data on Scleractinia cover from this study period contradicts the previous finding of a significant declining trend in Scleractinia cover.

Overall, methods employed to monitor the benthic communities at Stetson Bank during the study period, including an update to the camera systems used for bank crest repetitive photostations in 2018, were successful. However, obtaining usable imagery from repetitive photostations in mesophotic habitat was difficult, primarily due to poor water clarity, marker movement, and heavily silted environments. All of these factors prevented the collection of repetitive images of the sites for quantitative analyses. However, qualitative analysis of these images was possible and interesting observations were made, including the growth or loss of Porifera and breakage of corals. This information will serve as a baseline for future studies and impact assessments. To improve the method, floating markers should be reinstalled using braided rope instead of wire at each site and the photo collection technique should be reassessed.

Chapter 3: Sea Urchin and Lobster Density

Introduction

Motile benthic marine invertebrates serve important roles in the marine community as grazers, predators, cleaners, coral associates, and prey (Carpenter 1981, Liddell & Ohlhorst 1986, Hartney & Grorud 2002, Harborne et al. 2009, Pratchett et al. 2009). Of particular note at Stetson Bank are long-spined sea urchins (*Diadema antillarum*), a major grazer (Ogden et al. 1973, Carpenter 1981, Carpenter 1986, Macia et al. 2007), and lobster, a commercially important crustacean (Figure 3.1). *Diadema antillarum* is considered a critical component of the benthic community, supporting the survival of other species in the ecosystem. When removed, impacts can be seen throughout the environment (Liddell & Ohlhorst 1986, Mumby et al. 2006). As an important grazer, *D. antillarum* serves a critical role in top-down control of macroalgae cover, supporting the settlement and growth of other sessile benthic organisms, including corals. However, in the mid-1980s, an unknown pathogen decimated populations throughout the Caribbean and Gulf of Mexico, including at Stetson Bank. Following this mass die-off, irregular, limited recovery has been documented in the region (Edmunds & Carpenter 2001), while numerous studies documented increases in fleshy and filamentous algae among reefs where urchin density was reduced (Hughes et al. 1985, Liddell & Ohlhorst 1986, Hughes et al. 1987, Hughes 1994).

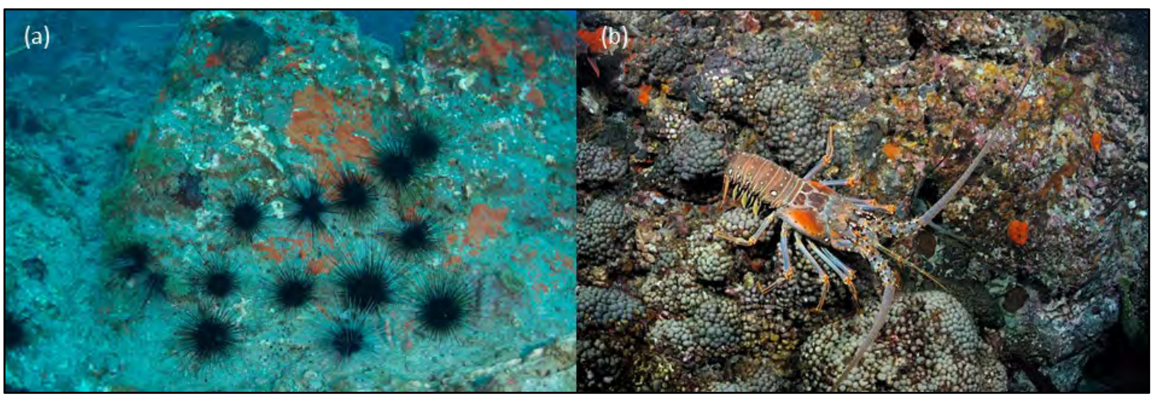

Figure 3.1. Common motile benthic marine invertebrates at Stetson Bank. (a) D. antillarum and (b) Panulirus argus. Photo: Schmahl/NOAA

Modeling studies by Mumby et al. (2006, 2007) suggested that reef systems with sea urchin densities >1 per m^2, in addition to a robust grazing fish community, were more resilient than reef systems with lower urchin densities. Limited recovery of long-spined sea urchin populations has been observed following the 1983-1984 die-off throughout the Caribbean (Kramer 2003, Nimrod et al. 2017). Studies have documented single observation local densities ranging from 0–8.9 per m^2 throughout the Caribbean (Carpenter & Edmunds 2006), with a high of 12.5 per m^2 in Grenada (Nimrod et al. 2017), while EFGB and WFGB in the Gulf of Mexico have documented post-mortality average densities from 0–0.23 per m^2 (Johnston et al. 2018). Long-spined sea urchin density at Stetson Bank peaked at 2.72 individuals per m^2 in 2014, which is higher than the regional average for the Caribbean but lower than observed regional maxima (Nuttall et al. 2020).

Lobster, including the Caribbean spiny lobster (*Panulirus argus*) and spotted lobster (*Panulirus guttatus*), are commercially important crustaceans in the Caribbean and Gulf of Mexico. Under current regulations, they are protected from harvest within FGBNMS (National Marine Sanctuaries Preservation Act [P.L. 104-283]). In 2006, *P. argus* sampled from Stetson Bank were large in size compared to other marine protected areas in the Caribbean (Bertelsen et al. 2004, Nuttall et al. 2020), suggesting infrequent recruitment and low fishing pressure (John Hunt, personal communication, June 2, 2015, Davis 1977, Bertelsen & Matthews 2002).

Diadema antillarum and lobster density were obtained for comparison between years as a measure of ecosystem vitality.

Methods

Field Methods

Long-spined sea urchins were counted on bank crest repetitive photostation and random transect images annually.

Due to the nocturnal nature of *D. antillarum* and lobsters, visual surveys were also conducted at night, when abundance was estimated by scuba divers. Transects started 1.5 hours after sunset and consisted of two repetitive belt transects, 2 m x 100 m, between permanent mooring buoys (from buoy #1 to #2 and #2 to #3) and one 2 m x 50 m transect from buoy #3 to repetitive photostation 27. A total of 500 m^2 were surveyed annually, except in 2018 when no nocturnal transects were completed (Figure 2.4 and Figure 2.5).

Data Processing

Repetitive Urchin Photostations

Diadema antillarum counts were conducted on each photostation image. The area of the image (1.6 m^2) was then used to calculate density per m^2. Historical analyses were based on data from 14 repetitive photostations that were located and processed for *D. antillarum* density annually from 1994–2018 (Pins 8, 16, 19, 20, 21, 22, 25, 26, 28, 31, 40, 49, 55, and 70).

Random Urchin Transects

Diadema antillarum counts were summed across all images in a transect. Transect area (8.16 m^2) was then used to calculate density per m^2. As two transects were conducted at each random site location in 2015, density was averaged between the two surveys.

Repetitive Nocturnal Urchin Transects

Counts for each species were converted to number per m^2 for each transect.

Statistical Analysis

Repetitive photostation, random transect, and nocturnal survey data were analyzed independently using PERMANOVA (Anderson et al. 2008). Density was compared between years and habitats, when applicable. When significant differences were found, density was compared between consecutive years in PERMANOVA to reduce error rate.

Correlations between macroalgae cover on the bank crest and *D. antillarum* density, habitat/station, and year were assessed using Bray-Curtis resemblance matrices on untransformed data. PERMANOVA was used to determine whether correlations were significant. *Diadema antillarum* density and benthic cover of all major groups were examined for covariance using coherence plots in PRIMER.

Long-term historical trends in *D. antillarum* density were examined using CLUSTER analysis and SIMPROF (Clarke et al. 2008, Clarke et al. 2014), based on square root-transformed data and Bray-Curtis similarity matrices. PCO (Anderson et al. 2008) was used to visualize the data, with percent variability explained in each canonical axis. This analysis expanded on data presented in Nuttall et al. (2020).

PERMANOVA, CLUSTER, SIMPROF and PCO were performed in PRIMER version 7 with PERMANOVA+ add-in (Anderson et al. 2008, Clarke & Gorley 2015). Mean densities are presented as the value ± standard error.

Spatial interpolation of random transect density data was mapped using IDW. Interpolations were created using a variable search radius and four points. Analyses were performed in ESRI's ArcMap version 10.4.

Results

Mean density of *D. antillarum* was >1/m^2 in most surveys and years, except in nocturnal surveys and low-relief random transects (Figure 3.2, Appendix 7, 8, and 9). In random transects, density was significantly different between habitats, with greater mean density in high-relief compared to low-relief habitats. *Diadema antillarum* density was significantly different by year in repetitive photostations (2016–2017, significant decline) and random transects (2015–2016 and 2016–2017, significant declines).

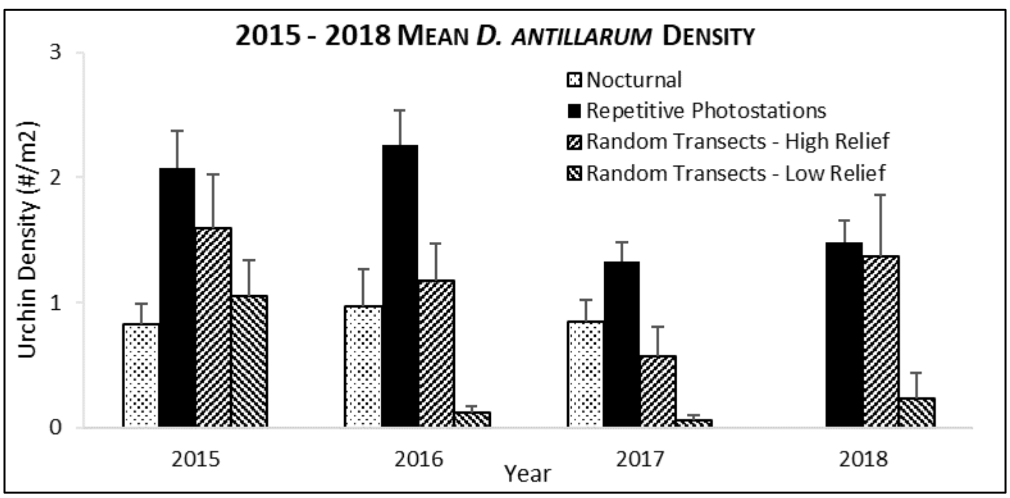

Figure 3.2. 2015–2018 mean D. antillarum density. Densities are presented per m2, by survey type, with standard error bars.

Macroalgae cover was found to be significantly correlated with *D. antillarum* density, and was significantly different between years (as documented in Chapter 2). Sum of squares values indicated that year had a greater effect than *D. antillarum* density on macroalgae cover (Table

3.1). Additionally, *D. antillarum* density covaried with colonizable substrate in repetitive photostations.

Table 3.1. PERMANOVA results examining variation in macroalgae cover between habitats and years and correlation of macroalgae cover with *D. antillarum* density in repetitive photostations. Bold text represents significant values.

Test	PERMANOVA					
	DF	SS	MS	Pseudo-F	P	Unique Perms
Random Transect						
D. antillarum Density	1	1467.40	1467.40	5.2701	**0.017**	9935
Habitat	1	272.86	272.86	0.97995	0.337	9937
Year	3	2681.60	893.87	3.2103	**0.013**	9927
2015–2016	1	1529.00	1529.00	8.4042	**0.002**	9932
2016–2017	1	131.94	131.94	0.69743	0.423	9932
2017–2018	1	898.26	898.26	2.2386	0.115	9948
Habitat x Year	3	1632.60	544.21	1.9545	0.102	9948
Residuals	85	23667.00	278.44			
Total	93	29722.00				
Repetitive Photostation						
D. antillarum Density	1	4124.10	4124.10	5.0337	**0.009**	9950
Pin	60	61364.00	1022.70	1.9568	**<0.001**	9828
Year	3	15266.00	5088.50	9.7356	**<0.001**	9940
2015–2016	1	1140.50	1140.50	2.1631	0.103	9954
2016–2017	1	4989.70	4989.70	11.25	**<0.001**	9928
2017–2018	1	11446.00	11446.00	24.34	**<0.001**	9952
Residuals	171	89376.00	522.67			
Total	235	170130.00				

Historically, *D. antillarum* density has fluctuated inversely with macroalgae cover at Stetson Bank, with a slight temporal offset (Figure 3.3). At the onset of monitoring, mean *D. antillarum* density was ~1 per m^2, but declined to approximately 0.5 per m^2 in 1997. Density remained below 0.5 per m^2 for ten years while macroalgae cover increased from ~20% to 60%. Following the increase in macroalgae cover, sea urchin density began to increase in 2009 to ~2 per m^2, followed by a decline in macroalgae cover. While no significant year clusters were found, a shift in the balance of *D. antillarum* density and macroalgae cover was documented; the balance of *D. antillarum* density and macroalgae cover in 2018 was more similar to that observed at the onset of monitoring (Figure 3.3).

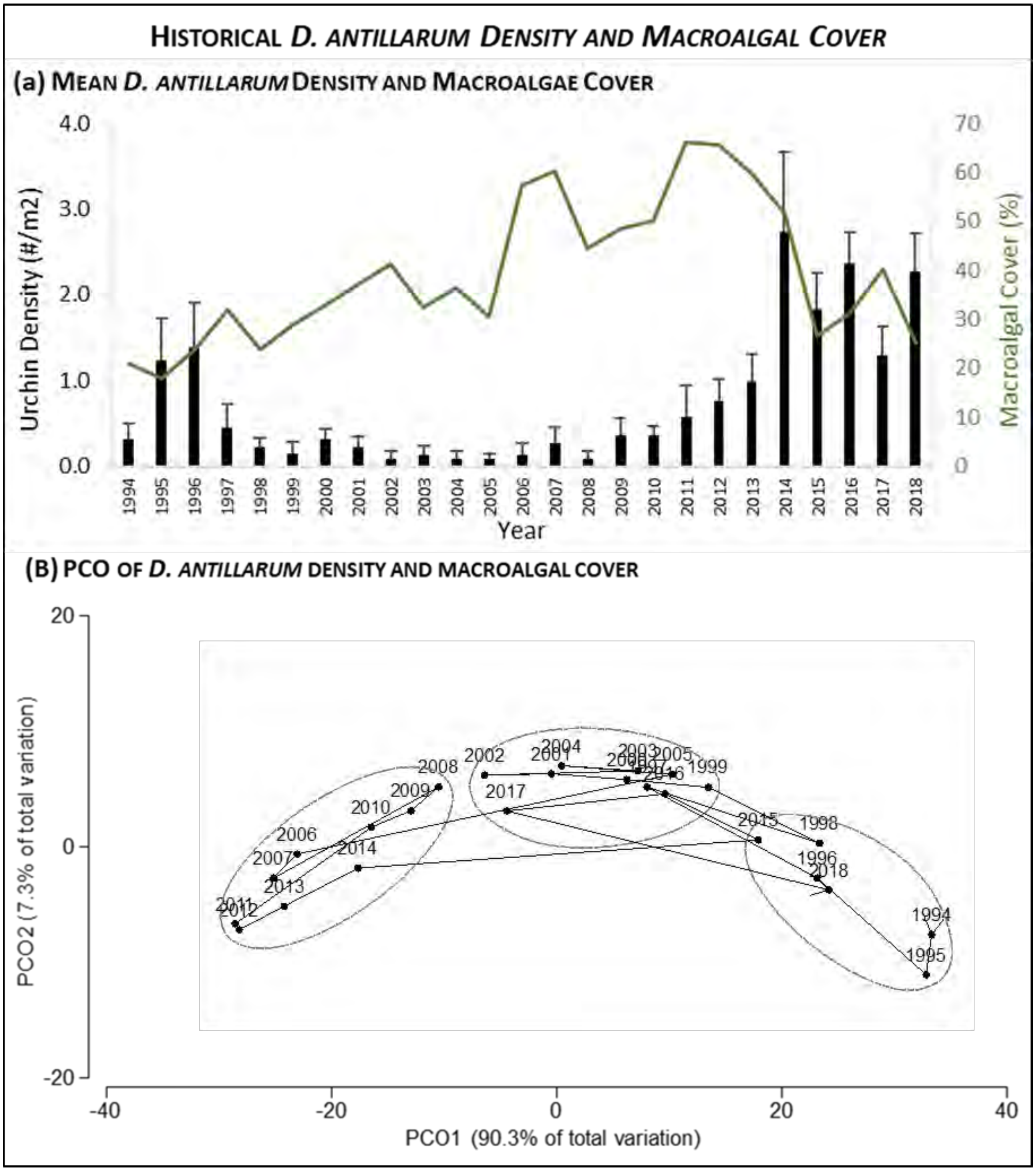

Figure 3.3. Historical *D. antillarum* density and macroalgae cover. Data represents 14 continuously imaged repetitive photostations. (A) Mean density and macroalgae cover from 1994 through 2018, where line represents macroalgae cover and bars represent *D. antillarum* density with standard error bars. (B) PCO plot of *D. antillarum* density and macroalgae cover, where the solid black line represents year trajectory and the dashed grey ellipses represents 80% similarity clusters.

When random transect data are projected spatially, patterns were apparent. *Diadema antillarum* had a clumped distribution, with highest densities focused around high-relief features (Figure 3.4).

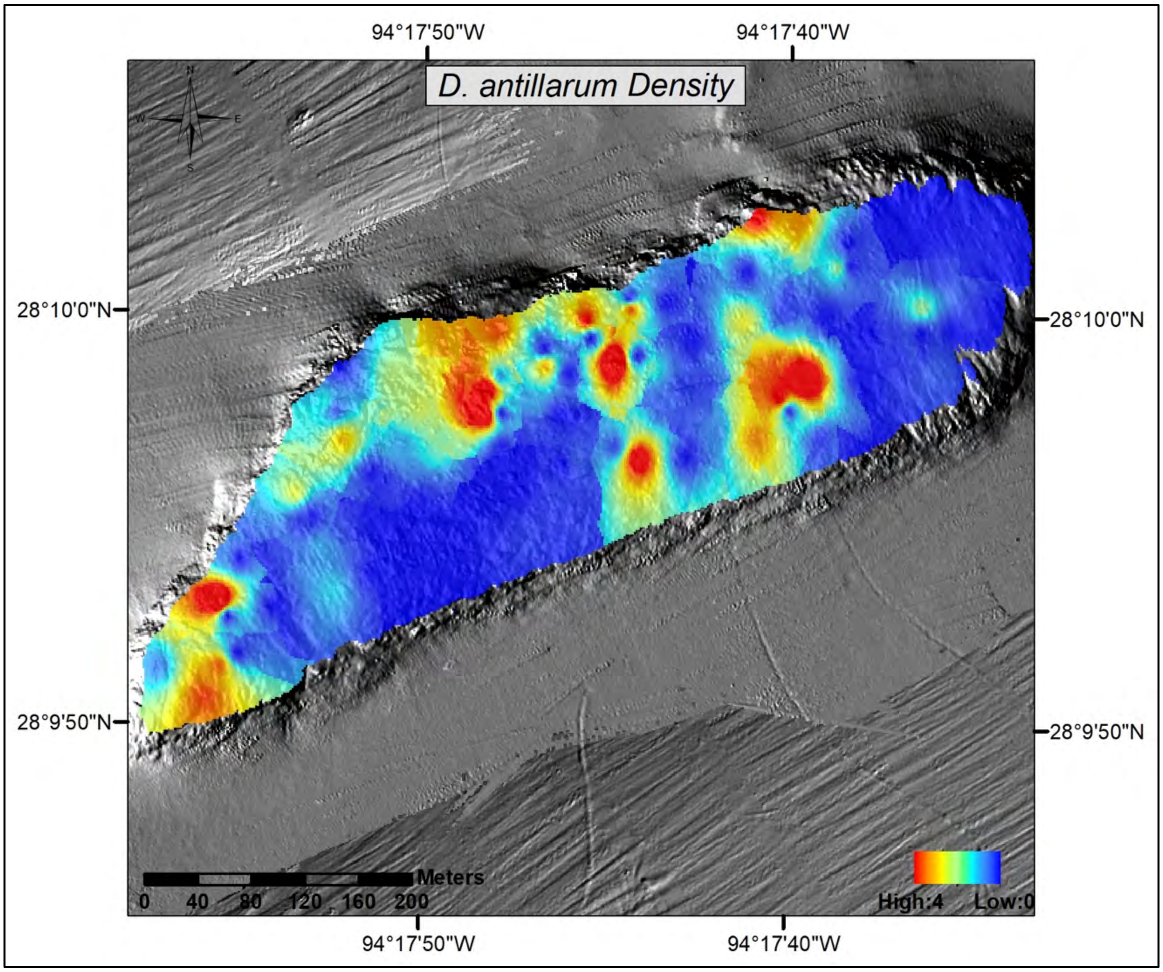

Figure 3.4. Random transect *D. antillarum* density inverse distance weighted cover map. Color ramp indicates high to low density. Image: NOAA

No lobster were observed in surveys for the duration of this study period. Therefore, no analyses were conducted.

Discussion

The density of *D. antillarum* was different between surveys, likely due to differences in time of day and habitat types. The greatest densities were in ultra-high-relief features and diverse benthic communities at repetitive photostations, which may be attractive to *D. antillarum* due to the shelter they provide. Similarly, high-relief habitat (>1m relief) had greater densities than low-relief (<1m relief) habitats in random transects. This was expected, as *D. antillarum* have been found to exhibit greater population densities with increasing habitat complexity (Tuohy et al. 2020). Nocturnal surveys included both high- and low-relief habitat and were located in the vicinity of ultra-high-relief repetitive photostations, but had the lowest mean densities (with the exception of low-relief random transects). *Diadema antillarum* occur in clusters and are inactive during daylight, but increase activity and grazing behavior at night (Ogden et al. 1973), becoming more dispersed through their environment. A change in dispersal pattern may have contributed to the lower densities documented in nocturnal surveys. For this reason, continued monitoring using both image analysis and nocturnal surveys is needed.

As *D. antillarum* are important grazers, their density was significantly negatively correlated with macroalgae cover at Stetson Bank. However, a significant decline in *D. antillarum* density was documented in 2015–2017, while macroalgae cover fluctuated.

While data are not available for *D. antillarum* density prior to the mass die-off in the mid-1980s, a robust *D. antillarum* population was documented in recent years (2015–2018), despite recent declines in 2015–2017, with densities >1 per m^2 (Mumby et al. 2006, Mumby et al. 2007). However, historical data indicated a potential pattern of *D. antillarum* density with robust populations documented from 1995–1996 followed by low densities from 1997–2013, followed by robust populations again from 2014–2018. Macroalgae cover appeared to fluctuate similarly, with a slight temporal offset. Further monitoring will elucidate if this is a cyclic pattern of fluctuation around carrying capacity or influenced by factors related to reproduction or survival as the species struggles to recover to pre-die-off abundance.

In addition to their role as important grazers, *D. antillarum* provide refugia for fish and invertebrates (Townsend & Bologna 2007). While reef-building corals are a major source of biogenic structure on coral reefs, Stetson Bank exhibits low coral cover and, thus, is limited in this type of refuge. However, *D. antillarum* can provide protective biogenic structure and impact the survival and recruitment of juvenile fish and, therefore, local fish abundance at Stetson Bank (Hartney & Grorud 2002).

As no lobsters were observed during the study period, no analyses were conducted to evaluate changes between years. While lobster density was also low throughout historical surveys, divers, including authors on this report, observed large *P. argus* while conducting other monitoring activities during this study period.

While nighttime surveys were effective for documenting density of *D. antillarum*, they were logistically challenging due to the large amount of time required to schedule and conduct them. In 2018, these surveys were not completed due to time constraints. Throughout the course of this study, photographic analyses of urchin density were added to data processing methods to improve density estimates without requiring additional field work. Due to the lack of refugia for *D. antillarum* at Stetson Bank, post processing of daytime images produced a robust, comparable dataset for urchin density. Further, nighttime surveys did not document any lobster, supporting re-examination of field methods for lobster density to ensure appropriate survey techniques are being used.

Chapter 4:
Fish Community

Introduction

Fish community composition at Stetson Bank is similar to other Caribbean reefs, although overall diversity is lower and abundance is higher (Pattengill 1998). On other Caribbean reefs, hamlets (*Hypoplectrus* sp.), grunts (Haemulidae), and snapper (Lutjanidae) are prevalent and diverse; however, these families are either absent or represented by low diversity at Stetson Bank (Pattengill et al. 1997).

Fish populations within coral reef environments are critical to ecosystem function (Holmlund & Hammer 1999, Kennedy et al. 2013). Since the late 1990s, reef fish density throughout the Caribbean has declined (Paddack et al. 2009), potentially due to habitat complexity loss (Alvarez-Filip et al. 2015) and overexploitation (Jackson 1997, Pandolfi et al. 2003, Jackson et al. 2014). Within the designated boundaries of the FGBNMS, which encompasses the bank crest at Stetson Bank (Figure 1.3), only hook and line fishing activities are permitted (National Marine Sanctuaries Preservation Act [P.L. 104-283] 1996, 15 C.F.R. § 922, 65 FR 81175).

Reef fish populations on EFGB and WFGB, approximately 30 miles southeast of Stetson Bank, have been monitored since the late 1980s and have been relatively stable. However, consistent temporal variation in local reef fish populations has been observed (Zimmer et al. 2010, Johnston et al. 2013, Johnston et al. 2015, Johnston et al. 2018). On the crest of Stetson Bank, a variety of fish surveys have been conducted since the initiation of the monitoring program, but were limited to < 33.5 m (110 ft) prior to 2015. Temporal variation similar to that observed at EFGB and WFGB was documented in the Stetson Bank fish community, in addition to sporadic recruitment events and the maintenance of an inverted trophic biomass pyramid (Nuttall et al. 2020).

Piscivore dominance and an inverted biomass pyramid have been associated with healthy reef systems with high coral cover and minimal detrimental environmental impacts, particularly from fishing (Friedlander & DeMartini 2002, DeMartini et al. 2008, Knowlton & Jackson 2008, Sandin et al. 2008, Singh et al. 2012). While coral cover at Stetson Bank is low compared to other Caribbean reefs (Jackson et al. 2014), the high-relief environment at Stetson Bank is composed of moderately complex geologically- and biologically-structured habitat that supports schooling behavior and concentrates many species in particular areas (Figure 4.1).

Figure 4.1. Fish schooling around a pinnacle feature at Stetson Bank. Photo: Schmahl/NOAA

Continued and expanded monitoring of the fish population to assess composition and temporal change occurred from 2015 onwards, with the addition of monitoring of the fish population in mesophotic habitat.

The fish community was monitored to compare and track composition, diversity, biomass, and abundance (density) between years and habitats, and to quantify invasive species and species of particular interest.

Methods

Field Methods

Bank Crest Random Fish Surveys

Scuba divers used the modified Bohnsack and Bannerot (1986) stationary visual fish census technique, restricting observations to an imaginary cylinder with a radius of 7.5 m, extending from the benthos to the surface (Figure 4.2). All fish species observed within the first five minutes of the survey were recorded as the diver slowly rotated in place above the bottom. Immediately following this five-minute observation period, one rotation was conducted for each species noted in the original five-minute period to record abundance (number of individuals per species) and fork length (within size bins). Size was binned into eight groups: <5 cm, ≥5 to <10 cm, ≥10 to <15 cm, ≥15 to <20 cm, ≥20 to <25 cm, ≥25 to <30 cm, and ≥30 to <35 cm. If fish were >35 cm, individual size was estimated. Divers carried a 1 m PVC pole marked in 10 cm increments to provide a reference for size estimation. Each survey required at least 15 minutes to complete. Transitory or schooling species were counted and measured at the time they moved through the cylinder during the initial five-minute period. Notes were made on the habitat within each survey area, including information on benthic relief (Figure 4.3). Surveys began after sunrise and were repeated throughout the day until dusk. Survey start location was selected using a stratified random sampling design (see Chapter 2: Methods: Field Methods: Random Benthic Transects).

Figure 4.2. Diver conducting modified Bohnsack and Bannerot (1986) stationary visual fish census. Tape measures were used to establish cylinder radius and a 1 m PVC pole, marked in 10 cm increments, was used to provide a reference for fish size estimation. Photo: Schmahl/NOAA

Station ID:______________ Date:__________ Visibility:______ft

Diver:________________ Start Time:________ Water Temp:______F

Buddy:______________ End Time:________ Current:

Station Depth:______ft None Mild

Bearing:________ Moderate High

Hard Substrate Relief Coverage	
<0.2m	%
0.2-0.5m	%
0.5-1.0m	%
1.0-1.5m	%
>1.5m	%
Max Relief	m

Abiotic Footprint	
SAND	%
HARD-B	%
RUBBLE	%
Total	100%

Comments

	Fish ID	<5	5-10	10-15	15-20	20-25	25-30	30-35	>35
1									
2									
3									
4									
5									
6									
7									
8									
9									
10									
11									
12									
13									
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Figure 4.3. Fish data entry sheet used in the present study.

Bank Crest Repetitive Fish Surveys

Scuba divers conducted the modified Bohnsack and Bannerot (1986) stationary visual fish census technique described above (see Chapter 4: Methods: Field Methods: Bank Crest Random Fish Surveys) to quantify fish abundance near permanent benthic photostations. Survey start point was determined using repetitive photostations, where the pin marked the center of the survey area (see Chapter 2: Methods: Field Methods: Repetitive Benthic Photostations). Six photostations were used: 19, 20, 27, 45, 50, and 73. All surveys occurred on high-relief habitat.

Bank Crest Buoy Fish Surveys

Scuba divers used the modified Bohnsack and Bannerot (1986) stationary visual fish census technique described above (Methods: Field Methods: Bank Crest Random Fish Surveys) to quantify fish observed near mooring buoys. Survey start points were determined using permanent mooring buoys 1, 2, and 3 (Table 2.1Table 2.1), with at least four surveys originating from each. Mooring buoys were selectively located in flat habitat, near high-relief habitat. Starting locations for these surveys were determined by the use of a random heading, from the mooring, of 0–360°, and a random number of kick cycles, from 0–40 kicks, to arrive at the survey start location. It was estimated that 40 kick cycles moved a diver approximately 50 m, with no current (Figure 4.4). A third number was generated to provide a random heading, from 0–360°, along which the tape was laid to mark the 7.5 m radius of the survey. Habitat relief was recorded in survey metadata and used to assign habitat, where maximum relief >1 m was considered high relief and <1 m was considered low relief.

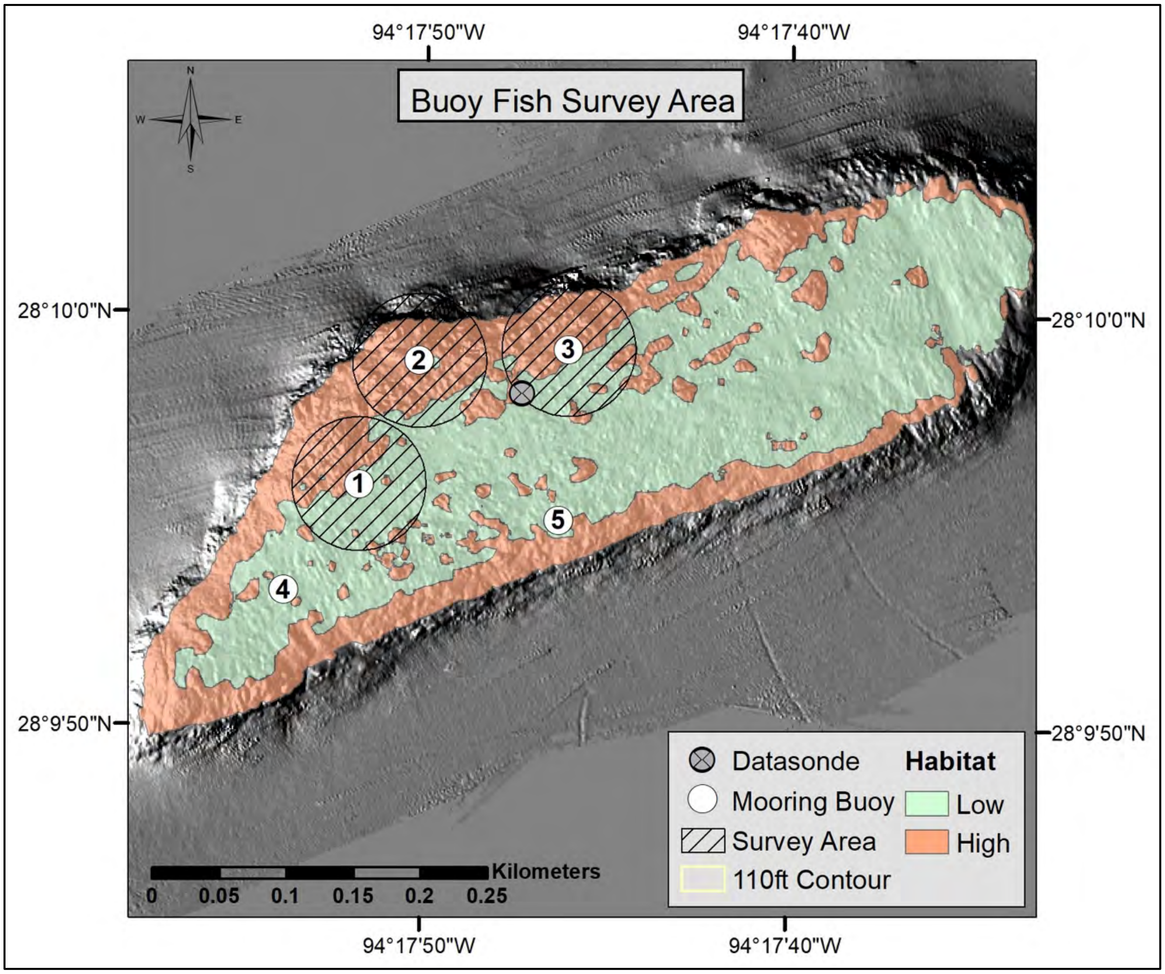

Figure 4.4. Potential survey area for bank crest buoy fish surveys. Image: NOAA

Mesophotic Random Fish Transects

Fish were visually assessed by ROV using forward-facing video footage obtained from belt transects discussed in Chapter 2 (Methods: Field Methods: Random Benthic Transects) (Figure 4.5). Observations of fish were restricted to the field of view of the ROV's forward-facing, high-definition video camera. All fish species observed were recorded, counted, and sized using parallel lasers, 10 cm apart. Fork length was binned as described above (Chapter 3: Methods: Field Methods: Bank Crest Random Fish Surveys). Each survey was 10 minutes in duration and occurred from the early morning (after sunrise) until dusk.

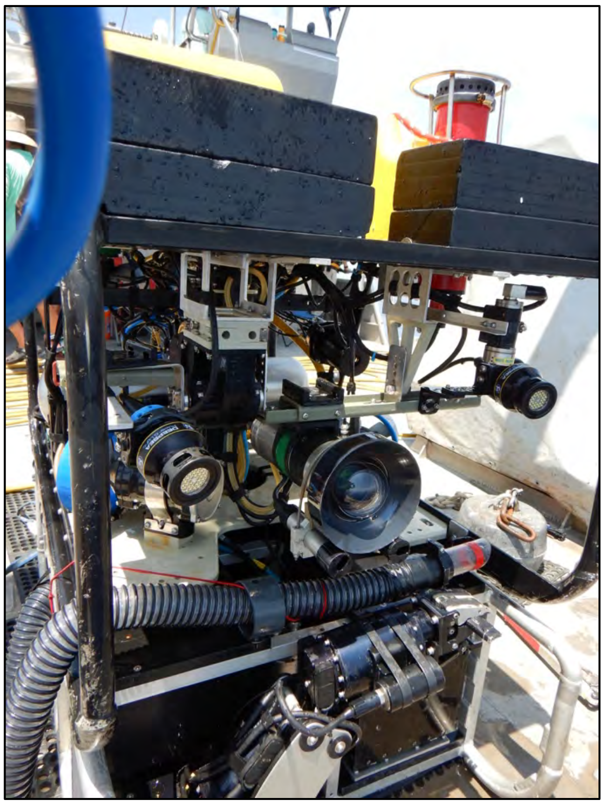

Figure 4.5. Camera and light systems aboard the SubAtlantic Mohawk ROV. Photo: Drinnen/NOAA

Surveys were conducted in conjunction with random benthic transects in mesophotic habitat, where the survey starting location was selected using a stratified random sampling design (Chapter 2: Methods: Random Benthic Transects). Throughout the study period, the same ROV system described in Chapter 2: Methods: Random Benthic Transects was used. This ROV was also equipped with an ORE transponder to collect ROV position information with ORE TrackPoint II and an independent set of paired, parallel lasers, 10 cm apart.

Data Processing

Fish survey data were entered into a Microsoft® Excel® database by the surveyor. Entered data were checked for quality and accuracy prior to processing. For each entry, family and trophic guild were recorded. Species were classified by primary trophic guilds: herbivores (H), piscivores (P), invertivores (I), and planktivores (PL), based on information provided from FishBase (Froese & Pauly 2016). Biomass was calculated using the allometric length-weight conversion formula (Bohnsack & Harper 1988) based on information provided from FishBase (Froese & Pauly 2016). Fish biomass was expressed as grams per 100 m^2. Observations of rays and sharks were removed from all biomass analyses due to their rare nature and large size. Each survey represented one sample. Sample numbers varied by year and survey type (Table 4.1).

Table 4.1. Number of fish samples per year. Values represent surveys that cleared data processing requirements.

Year	Bank Crest Random Fish Survey High Relief (Low Relief)	Bank Crest Repetitive Fish Survey	Bank Crest Buoy Fish Survey	Mesophotic Random Fish Transect Coralline Algae (Deep Reef)
2015	8 (13)	-	18	10 (7)
2016	11 (20)	6	-	11 (8)
2017	12 (13)	6	-	12 (9)
2018	7 (13)	2	-	11 (12)

In mesophotic surveys, transects where visibility was restricted to <3.5 m in the lateral field of view were removed from analysis. These transects exhibited low species richness and may not be representative of the habitat due to the limited visibility preventing observations and species identifications. Mesophotic benthic transects with >50% soft bottom habitat were also removed from analyses. Area of each survey was calculated by importing ROV track data, recorded every two seconds, into ArcMap. The line data were smoothed using the polynomial approximation with exponential kernel (PAEK) algorithm and a smoothing tolerance of 10 m. Line length was then calculated in WGS83 UTM15 for the 10-minute transect. Distance was multiplied by the maximum horizontal distance in the field of view, where field of view was determined using forward-facing dual lasers, measured at the farthest point in the field of view. Measurements were performed using ImageJ.

Density was calculated for each species and expressed as the number of fish per 100 m^2. Sighting frequency was determined as the percentage of surveys in which a species was recorded. Diversity measures (Shannon diversity [log base e], Pielou's evenness, and Margalef species richness) were calculated for each sample.

Based on species abundance and biomass, dominance plots (k-dominance or abundance-biomass curves) were generated using PRIMER. W-values (difference between the abundance curve and biomass curve) were calculated for each survey (Clarke 1990). This value can range between -1 and 1, where w=1 indicates that the population is dominated by a few large species, and w=-1 indicates that the population is dominated by many small species.

Statistical Analysis

Due to different survey techniques, bank crest random fish surveys and mesophotic random fish transects were analyzed independently. There were no significant differences between buoy fish surveys and random transect fish surveys in high-relief habitat in terms of species presence/absence and density data, therefore, bank crest buoy fish surveys were pooled with high-relief random transect surveys for statistical analyses (Appendix 10).

Beta diversity was examined between years and habitats using PERMDISP based on presence/absence-transformed data and Jaccard similarity matrices.

Using non-parametric distance-based analyses, density, biomass, trophic richness, trophic biomass, and size frequency were compared between years, habitats, and survey types (bank crest only: random vs. repetitive) (Table 4.2). Species density and biomass data were dispersion weighted to reduce the impact of large schooling species on the analysis. Trophic richness, trophic biomass, and size frequency data were square root transformed. PERMANOVA analyses (Anderson et al. 2008) were based on Bray-Curtis similarity matrices for density, biomass, trophic richness, trophic biomass, and size frequency. When significant differences between groups were found with PERMANOVA, variables contributing to observed differences were examined using SIMPER (Clarke 1993, Clarke et al. 2014). SIMPER analyses in species-level data were based on the same transformations and similarity matrices used in PERMANOVA. Further evaluation of species contributions to observed differences were conducted through Type III SIMPROF (Clarke et al. 2008, Clarke et al. 2014) and presented as shade plots.

Diversity measures were analyzed together using a Euclidean distance matrix, based on untransformed data, and tested for significant differences using PERMANOVA (fixed factors, type III sum of squares, 9999 permutations, and reduced model [crossed]).

Abundance-biomass curve *w* values were tested for differences between years and habitats with parametric ANOVA and pairwise Student's t-tests on untransformed data.

Coherent species curves (Somerfield & Clarke 2013) were used to conduct r-mode analyses (an analysis of patterns among variables) and examine if factors varied in significantly similar patterns through samples ordered naturally as a time series. Data were averaged by year to reduce noise.

Community density was tested for correlation with lionfish density using Bray-Curtis resemblance matrices on dispersion weighted data. Size frequency was tested for correlation with lionfish density using Bray-Curtis resemblance matrices on square root-transformed data. All analyses were conducted by testing matched resemblance matrices (Clarke & Gorley 2015) to determine significance.

Historical analyses were only conducted on bank crest data, as mesophotic data collections began in 2015. Summary data, including trophic richness, total density, total biomass, *w* values, and diversity measures (Shannon diversity [log base e], Pielou's evenness, and Margalef species richness), were averaged by year (2012–2018) to reduce inter-annual variance. Significant year groupings were examined using cluster analysis and SIMPROF, based on normalized, untransformed data and Euclidean distance similarity matrices. PCO was used to visualize the data, with percent variability explained in each canonical axis. Temporal trajectories were overlaid on the plot. Where significant clusters were found with SIMPROF, variables contributing to observed differences were examined using SIMPER on normalized, untransformed, Euclidean distance similarity matrices. Monotonic trends were tested with the non-parametric Mann-Kendall trend test.

PERMANOVA, cluster, SIMPROF, and PCO were performed in PRIMER version 7 with PERMANOVA+ add-in (Anderson et al. 2008, Clarke & Gorley 2015). ANOVA and Student's t-test were performed in R version 3.6 (R Core Team 2015). Mean values are presented as the value ± standard error.

Table 4.2. PERMANOVA fish community analysis settings.

Data	Transformation/ Resemblance	Factors (# of Levels)	Fixed/ Random	Sum of Squares	Number of Permutations	Permutation Method
Bank crest density	Dispersion weighted/ Bray Curtis	Habitat (2) Year (4) Survey Type (2)	Fixed Fixed Random	Type III	9999	Reduced model [crossed]
Bank crest biomass	Dispersion weighted/ Bray Curtis	Habitat (2) Year (4) Survey Type (2)	Fixed Fixed Random	Type III	9999	Reduced model [crossed]
Bank crest trophic richness	Square root/ Bray Curtis	Habitat (2) Year (4) Survey Type (2)	Fixed Fixed Random	Type III	9999	Reduced model [crossed]
Bank crest trophic biomass	Square root/ Bray Curtis	Habitat (2) Year (4) Survey Type (2)	Fixed Fixed Random	Type III	9999	Reduced model [crossed]
Bank crest size frequency	Square root/ Bray Curtis	Habitat (2) Year (4) Survey Type (2)	Fixed Fixed Random	Type III	9999	Reduced model [crossed]
Mesophotic density	Dispersion weighted/ Bray Curtis	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]
Mesophotic density by year (2015, 2016, 2017, 2018)	Dispersion weighted/ Bray Curtis	Habitat (2)	Fixed	Type I	9999	Unrestricted
Mesophotic density by habitat (coralline algae reef, deep reef)	Dispersion weighted/ Bray Curtis	Year (4)	Fixed	Type I	9999	Unrestricted
Mesophotic biomass	Dispersion weighted/ Bray Curtis	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]
Mesophotic biomass by year (2015, 2016, 2017, 2018)	Dispersion weighted/ Bray Curtis	Habitat (2)	Fixed	Type I	9999	Unrestricted
Mesophotic biomass by habitat (coralline algae reef, deep reef)	Dispersion weighted/ Bray Curtis	Year (4)	Fixed	Type I	9999	Unrestricted
Mesophotic trophic richness	Square root/ Bray Curtis	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]

Data	Transformation/ Resemblance	Factors (# of Levels)	Fixed/ Random	Sum of Squares	Number of Permutations	Permutation Method
Mesophotic trophic richness by year (2015, 2016, 2017, 2018)	Square root/ Bray Curtis	Habitat (2)	Fixed	Type I	9999	Unrestricted
Mesophotic trophic richness by habitat (coralline algae reef, deep reef)	Square root/ Bray Curtis	Year (4)	Fixed	Type I	9999	Unrestricted
Mesophotic trophic biomass	Square root/ Bray Curtis	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]
Mesophotic trophic biomass by year (2015, 2016, 2017, 2018)	Dispersion weighted/ Bray Curtis	Habitat (2)	Fixed	Type I	9999	Unrestricted
Mesophotic trophic biomass by habitat (coralline algae reef, deep reef)	Dispersion weighted/ Bray Curtis	Year (4)	Fixed	Type I	9999	Unrestricted
Mesophotic size frequency	Square root/ Bray Curtis	Habitat (2) Year (4)	Fixed Fixed	Type III	9999	Reduced model [crossed]
Mesophotic size frequency by year (2015, 2016, 2017, 2018)	Square root/ Bray Curtis	Habitat (2)	Fixed	Type I	9999	Unrestricted
Mesophotic size frequency by habitat (coralline algae reef, deep reef)	Square root/ Bray Curtis	Year (4)	Fixed	Type I	9999	Unrestricted

Spatial interpolation of richness, biomass, and density data from bank crest and mesophotic stratified random transects were mapped using IDW. Interpolations were created without separating data by habitat, using a variable search radius of four points. Analyses were performed in ESRI's ArcMap version 10.4.

Results

Occurrence and Beta Diversity

The twenty most important species, based on occurrence, were examined using shade plots (Figure 4.6). On the bank crest, species present in more than 80% of surveys included seaweed blenny, doctorfish, sharpnose puffer, bluehead, cocoa damselfish, and bicolor damselfish. In mesophotic habitat, species presence was highly differentiated between habitats. In mesophotic habitats combined, spotfin hogfish, sunshinefish, French angelfish, and reef butterflyfish were present in more than 50% of surveys.

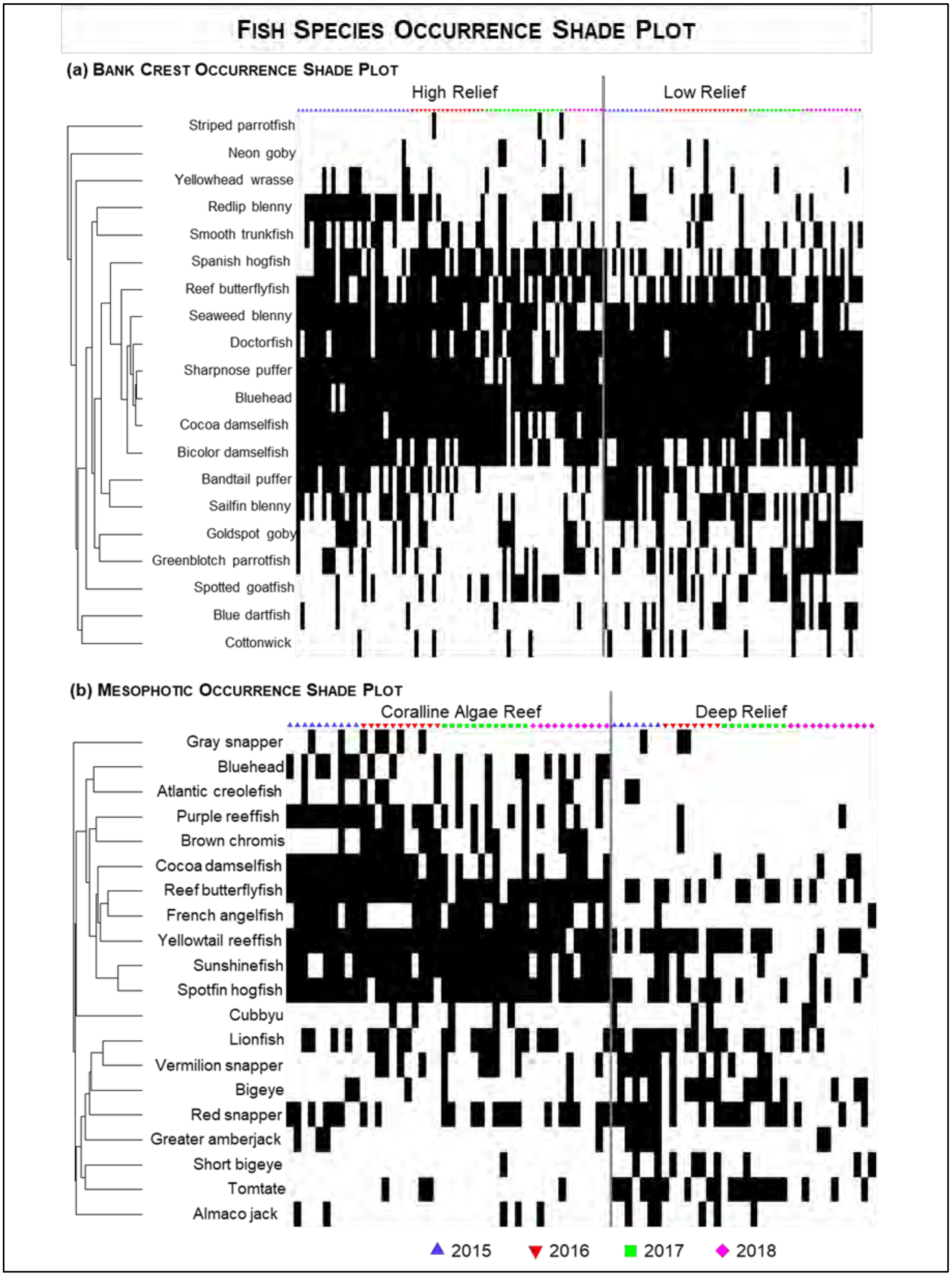

Figure 4.6. Fish species occurrence shade plots, where black denotes species presence and white denotes absence, for (a) the bank crest community and (b) the mesophotic community.

On the bank crest, a significant difference in beta diversity was found between years (F=7.57, p=<0.001), with significant differences in consecutive years 2016–2017 and 2017–2018. In mesophotic habitat, a significant difference in beta diversity was found between habitats and years, with pairwise comparisons showing a significant difference in beta diversity from 2017–2018 (Table 4.3). Overall, fish community composition at Stetson Bank was significantly different between most years, but only differed between habitats in deep coral and coralline algae reef.

Table 4.3. PERMDISP results for fish occurrence. Bold numbers represent significant differences.

Test	PERMDISP					
	F	DF1	DF2	t	P	Number of Perms
Bank Crest Habitat						
Habitat	1.94	1	127		0.186	9999
Year	7.57	3	125		**<0.001**	9999
2015–2016				1.88	0.077	
2016–2017				2.80	**0.010**	
2017–2018				2.26	**0.037**	
Mesophotic Habitat						
Habitat	28.96	1	78		**<0.001**	9999
Year	11.06	3	76		**<0.001**	9999
2015–2016				0.76	0.513	
2016–2017				1.03	0.339	
2017–2018				3.71	**0.001**	

SIMPER results for occurrence data showed that sighting frequency of multiple species contributed to the significant dissimilarities in beta diversity between years on the bank crest (2016–2017 and 2017–2018) and in mesophotic habitat (2017–2018), and between habitats. On the bank crest the dissimilarities between 2017 and 2018 were primarily due to the exotic regal demoiselle (*Neopomacentrus cyanomos*) becoming abundant in 2018 and a reduction in blue angelfish sighting frequency. However, in mesophotic habitat the significant dissimilarity between 2017 and 2018 was primarily due to an increase in blue angelfish sighting frequency in 2018. The significant dissimilarity between mesophotic habitats was primarily due to greater sunshinefish and rock hind sighting frequency in coralline algae reef habitat (Table 4.4).

Table 4.4. SIMPER results for fish occurrence.

Test		SIMPER			
		Functional Group	% Sighting Frequency Group 1	% Sighting Frequency Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015–2016	No analyses			
	2016–2017	Tomtate	10.81	58.06	2.81
		Bandtail puffer	54.05	0.00	2.70
	2017–2018	Regal demoiselle	0.00	72.73	3.46
		Blue angelfish	35.48	59.09	2.67
Habitat (HR: LR)		No analyses			
Mesophotic Habitat					
Year		No analyses			
	2015–2016	No analyses			
	2016–2017	No analyses			
	2017–2018	Red snapper	71.43	39.13	6.40
		Blue angelfish	66.67	30.43	6.03
Habitat (DR: CR)		Sunshinefish	19.44	84.09	3.98
		Rock hind	13.89	81.82	3.80

Trophic richness was significantly different between bank crest habitats and changed significantly from 2016–2017. In mesophotic habitat, a significant interaction was found between year and habitat (pseudo-F=3.14, p=0.002), so each habitat and year was analyzed independently. Coralline algae reef habitat was not significantly different between years. Deep reef habitat was significantly different between years, with each consecutive year significantly different except 2017–2018. In all years, a significant difference was found between habitats. Overall, trophic richness at Stetson Bank differed significantly between all habitats but not between all years (Table 4.5).

Table 4.5. PERMANOVA results for fish occurrence. Bold numbers represent significant differences.

Test		PERMANOVA					
		DF	SS	MS	Pseudo-F	P	Number of Perms
Bank Crest Habitat							
Habitat		1	464.3	464.3	4.11	**0.011**	9963
Year		3	796.9	265.6	2.35	**0.024**	9938
	2015–2016	1	234.2	234.2	1.96	0.138	9968
	2016–2017	1	474	474	3.38	**0.026**	9960
	2017–2018	1	130.6	130.6	1.27	0.288	9962
Survey type		2	131.5	65.74	0.58	0.712	9945
Mesophotic Habitat							
Coralline algae, Year		3	715.5	238.5	1.22	0.274	9934
	2015–2016	1	-5.333	-5.333	Negative		
	2016–2017	1	214.2	214.2	2.24	0.107	9922
	2017–2018	1	323.3	323.3	1.03	0.411	9916
Deep reef, Year		3	6910	2303	4.96	**<0.001**	9948
	2015–2016	1	521.3	521.3	2.94	**0.046**	4031
	2016–2017	1	833.6	833.6	5.04	**0.015**	6573
	2017–2018	1	1803	1803	2.73	0.079	9459
2015, Habitat (CR: DR)		1	2648	2648	17.05	**<0.001**	7808
2016, Habitat (CR: DR)		1	2119	2119	30.98	**<0.001**	9022
2017, Habitat (CR: DR)		1	4115	4115	23.52	**<0.001**	9693
2018, Habitat (CR: DR)		1	9124	9124	12.10	**<0.001**	9924

Multiple trophic guilds contributed to the observed PERMANOVA results (Table 4.6). In bank crest habitats, a significant difference in trophic richness occurred from 2016–2017, primarily due to increasing richness of piscivores and planktivores. Significant differences between high- and low-relief habitats on the bank crest were primarily due to greater richness of piscivores and lower richness of planktivores in high-relief habitat. In mesophotic habitats, invertivore richness was typically greater in coralline algae reef than deep reef habitat.

Table 4.6. SIMPER results for trophic richness.

Test		SIMPER			
		Functional Group	Mean Richness Group 1	Mean Richness Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015–2016	No analyses			
	2016–2017	Piscivore	1.00	1.65	31.95
		Planktivore	1.84	2.03	26.25
	2017–2018	No analyses			
Habitat (HR: LR)		Piscivore	1.66	1.02	32.37
		Planktivore	2.19	2.05	23.58
Type		No analyses			
Mesophotic Habitat					
Coralline algae, Year		No analyses			
	2015–2016	No analyses			
	2016–2017	No analyses			
	2017–2018	No analyses			
Deep reef, Year		No analyses			
	2015–2016	Piscivore	2.25	1.65	37.8
		Planktivore	0.83	1.63	23.03
	2016–2017	Planktivore	1.63	0.60	37.1
		Invertivore	3.24	1.88	30.54
	2017–2018	No analyses			
2015, Habitat (DR: CR)		Herbivore	0.29	1.45	30.18
		Invertivore	2.41	3.44	27.90
2016, Habitat (DR: CR)		Herbivore	1.49	0.25	40.64
		Invertivore	3.24	2.36	28.71
2017, Habitat (DR: CR)		Invertivore	1.88	3.14	36.05
		Planktivore	0.60	1.47	26.19
2018, Habitat (DR: CR)		Invertivore	1.23	3.09	36.56
		Herbivore	0.25	1.54	25.53

Diversity

No significant differences were found between years, habitats, or survey types on the bank crest. However, a significant interaction was found between year and habitat for mesophotic surveys (pseudo-F=4.27, p=0.013), and therefore each level was independently examined for the differences between years and habitats (Table 4.7). A significant difference between years was only found in coralline algae reef habitat, between 2015 and 2016. Significant differences were only found between habitats in 2015 and 2017.

Table 4.7. PERMANOVA results for fish diversity measures. Bold numbers represent significant differences.

Test		PERMANOVA					
		DF	SS	MS	Psuedo-F	P	Number of Perms.
Bank Crest Habitat							
Habitat		1	1.14	1.14	1.55	0.201	9937
Year		3	1.54	0.51	0.70	0.577	9939
Survey type		2	0.94	0.47	0.64	0.556	9954
Mesophotic Habitat							
Coralline algae, Year		3	54.17	18.06	10.31	**<0.001**	9953
	2015–2016	1	44.65	44.65	23.134	**<0.001**	9793
	2016–2017	1	1.32	1.32	1.7759	0.181	9918
	2017–2018	1	0.766	0.766	0.48124	0.536	9891
Deep reef, Year		3	3.117	1.039	0.16	0.689	9981
	2015–2016	1	No analyses				
	2016–2017	1	No analyses				
	2017–2018	1	No analyses				
2015, Habitat (CR: DR)		1	40.9	40.9	14.28	**0.001**	7722
2016, Habitat (CR: DR)		1	28.21	28.21	2.67	0.059	9295
2017, Habitat (CR: DR)		1	12.51	12.51	14.66	**0.001**	9772
2018, Habitat (CR: DR)		1	1.84	1.84	1.12	0.383	9923

SIMPER results showed Margalef's species richness (d) was the primary driver of significant differences observed with PERMANOVA, contributing >85% to the dissimilarity (Table 4.8). In coralline algae reef habitat, richness increased from 2015 to 2016. In both 2015 and 2017, coralline algae reef had greater richness than deep reef habitat.

Table 4.8. SIMPER results for diversity measures.

Test		SIMPER			
		Functional Group	Mean Abundance Group 1	Mean Abundance Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015–2016	No analyses			
	2016–2017	No analyses			
	2017–2018	No analyses			
Habitat (HR: LR)		No analyses			
Type		No analyses			
Mesophotic Habitat					
Coralline algae, Year		No analyses			
	2015–2016	d	6.81	4.01	91.19
		H'($\log_e$)	2.16	1.36	7.97
	2016–2017	No analyses			
	2017–2018	No analyses			
Deep reef, Year		No analyses			
	2015–2016	No analyses			
	2016–2017	No analyses			
	2017–2018	No analyses			
2015, Habitat (DR: CR)		d	3.80	6.81	91.51
		H'($\log_e$)	1.24	2.16	7.77
2016, Habitat (DR: CR)		No analyses			
2017, Habitat (DR: CR)		d	2.82	4.33	87.94
		H'($\log_e$)	1.31	1.69	10.63
2018, Habitat (DR: CR)		No analyses			

Density

The twenty densest species were examined using shade plots (Figure 4.7 and Appendix 11 and 12). Overall mean density was greater on the bank crest than in mesophotic habitat. While the 20 most important species between these two survey areas were different, six similar species were found: tomtate, French angelfish, reef butterflyfish, sharpnose puffer, cocoa damselfish, and brown chromis. On the bank crest, most species had greater densities in high-relief habitat. In mesophotic habitat, species density was highly differentiated between deep reef and coralline algae reef habitat.

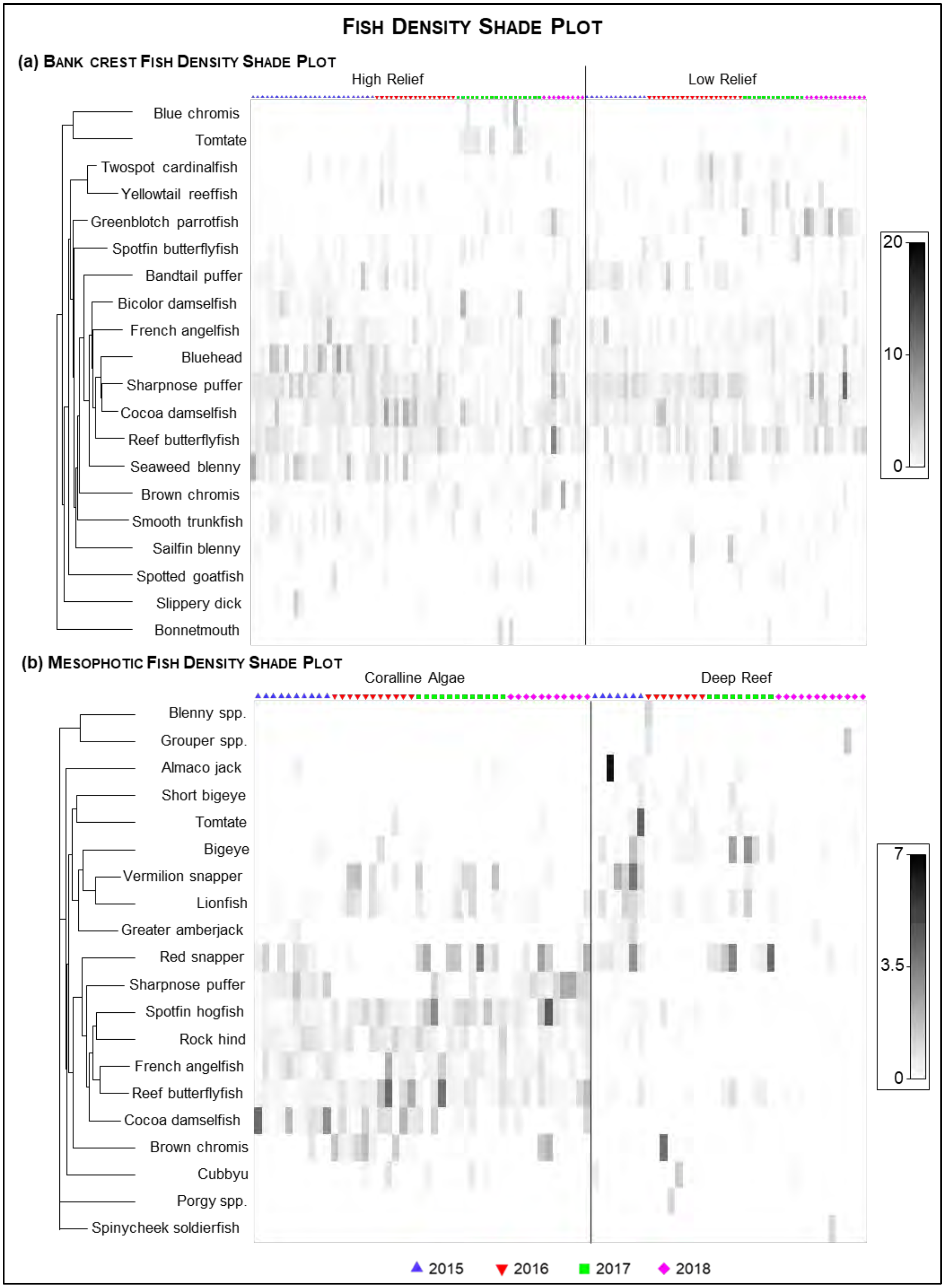

Figure 4.7. Fish species density shade plots, where gray scale values represent dispersion weighted density, for (a) the bank crest community and (b) the mesophotic community.

On the bank crest, a significant difference in community density was found between years (pseudo-F=2.73, p<0.001), habitats (pseudo-F=3.46, p<0.001), and survey types (pseudo-

F=1.47, p=0.014), with significant differences in consecutive years 2015–2016 and 2016–2017. In mesophotic habitat, a significant interaction was found between year and habitat (pseudo-F=2.30, p<0.001), so each habitat and year was analyzed independently. Community density in coralline algae reef habitat differed significantly among years, with each consecutive year also differing significantly. Community density in deep reef habitat also differed significantly among years, with each consecutive year differing significantly. In all years, a significant difference in community density was found between habitats. Overall, the fish community density at Stetson Bank was significantly different between all habitats and years (Table 4.9).

Table 4.9. PERMANOVA results for fish density. Bold numbers represent significant differences

Test		PERMANOVA					
		DF	SS	MS	Pseudo-F	P	Number of Perms
Bank Crest Habitat							
Habitat		1	7714	7714	3.46	**<0.001**	9895
Year		3	18248	6083	2.73	**<0.001**	9835
	2015–2016	1	4415	4415	2.29	**0.001**	9913
	2016–2017	1	6170	6170	2.50	**<0.001**	9899
	2017–2018	1	3799	3799	1.42	0.068	9890
Survey type		2	6541	3270	1.47	**0.014**	9846
Mesophotic Habitat							
Coralline algae, Year		3	23425	7809	3.09	**<0.001**	9814
	2015–2016	1	11826	11826	4.99	**<0.001**	9749
	2016–2017	1	8893	8893	3.54	**<0.001**	9862
	2017–2018	1	4948	4948	1.85	**0.010**	9856
Deep reef, Year		3	24606	8202	2.28	**<0.001**	9832
	2015–2016	1	7892	7892	2.43	**0.002**	5036
	2016–2017	1	8616	8616	2.72	**0.003**	8138
	2017–2018	1	10996	10996	2.86	**<0.001**	9741
2015, Habitat (CR: DR)		1	13068	13068	5.01	**<0.001**	7822
2016, Habitat (CR: DR)		1	15599	15599	5.51	**<0.001**	9303
2017, Habitat (CR: DR)		1	12761	12761	4.65	**<0.001**	9745
2018, Habitat (CR: DR)		1	16447	16447	4.48	**<0.001**	9851

SIMPER results for density data showed that multiple species influenced PERMANOVA results (Table 4.10). Cocoa damselfish frequently contributed to the observed differences in both bank crest and mesophotic habitat, with density varying over time and greater in bank crest high-relief habitat. Red snapper density increased between 2016 and 2017 and decreased between 2017 and 2018. Dense schools of vermilion snapper were only documented in deep reef habitat in 2015.

Table 4.10. SIMPER results for fish density.

Test		SIMPER			
		Functional Group	Mean Density Group 1	Mean Density Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015–2016	Cocoa damselfish	20.00	28.76	6.95
		Seaweed blenny	35.71	24.95	5.85
	2016–2017	Cocoa damselfish	28.76	11.68	6.86
		Sharpnose puffer	6.41	1.55	6.58
	2017–2018	No analyses			
Habitat (HR: LR)		Cocoa damselfish	24.30	16.14	5.65
		Reef butterflyfish	1.20	1.17	5.35
Type		No analyses			
Mesophotic Habitat					
Coralline algae, Year		No analyses			
	2015–2016	Yellowtail reeffish	4.86	68.84	8.12
		Cocoa damselfish	2.05	1.12	6.19
	2016–2017	Yellowtail reeffish	68.84	18.99	6.54
		Red snapper	0.07	2.36	5.78
	2017–2018	Red snapper	2.36	1.56	7.85
		Sharpnose puffer	0.21	0.94	6.06
Deep reef, Year		No analyses			
	2015–2016	Vermilion snapper	20.21	0.14	13.04
		Almaco jack	0.99	0.06	11.03
	2016–2017	Red snapper	0.05	2.99	20.56
		Bigeye	0.16	0.80	12.97
	2017–2018	Red snapper	2.99	0.12	28.71
		Bigeye	0.80	0.04	15.16
2015, Habitat (DR: CR)		Cocoa damselfish	-	20.21	9.00
		Vermilion snapper	2.05	-	7.63
2016, Habitat (DR: CR)		Yellowtail reeffish	2.86	68.84	10.14
		Brown chromis	2.29	3.17	6.56
2017, Habitat (DR: CR)		Red snapper	2.99	2.36	10.88
		Spotfin hogfish	0.07	2.08	7.77
2018, Habitat (DR: CR)		Sharpnose puffer	0.00	0.94	11.10
		Spotfin hogfish	0.04	1.88	8.27

Biomass

The biomass of the twenty densest species was examined using shade plots (Figure 4.8 and Appendix 13 and 14). Overall mean biomass was greater on the bank crest than in mesophotic habitat. While the 20 most important species between these two survey areas were different, five similar species were found: reef butterflyfish, graysby, French angelfish, sharpnose puffer, and red snapper. On the bank crest, most species had greater biomass in high-relief habitat. In mesophotic habitat, biomass was higher in coralline algae reefs.

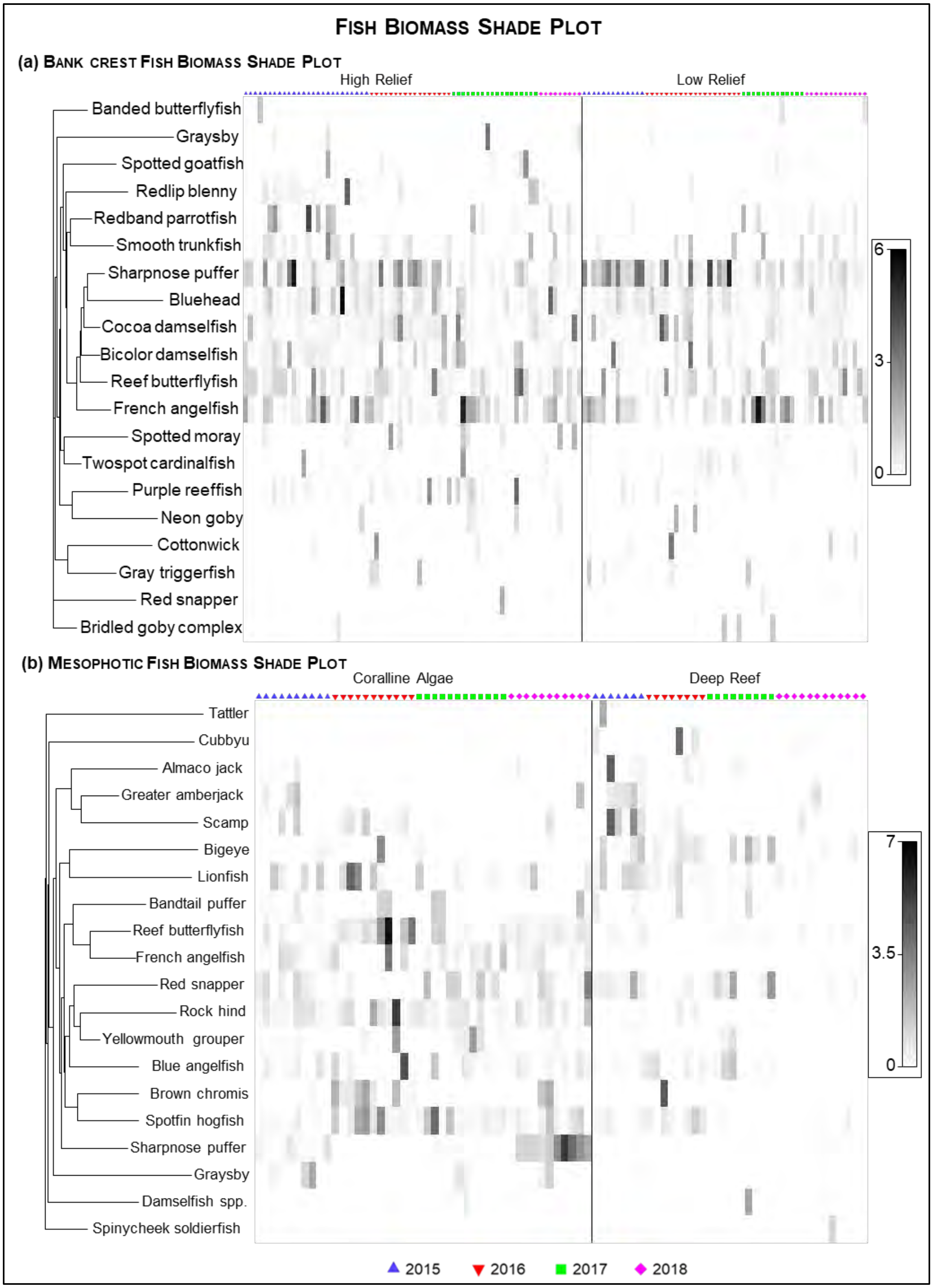

Figure 4.8. Fish species biomass shade plots, where gray scale values represent dispersion weighted biomass, for (a) the bank crest community and (b) the mesophotic community

On the bank crest, a significant difference in community biomass was found between years and habitats, with significant differences in consecutive years 2015–2016 and 2016–2017. In mesophotic habitat, a significant interaction was found between year and habitat (pseudo-F=2.28, $p<0.001$), so each habitat and year was analyzed independently. Community biomass in coralline algae and deep reef habitat differed significantly among years, with each consecutive year significantly different. In all years, a significant difference in community biomass was found between habitats. Overall, the fish community based on biomass at Stetson Bank was significantly different between all habitats and years (Table 4.11).

Table 4.11. PERMANOVA results for fish biomass. Bold numbers represent significant differences

Test		PERMANOVA					
		DF	SS	MS	Pseudo-F	P	Number of Perms
Bank Crest Habitat							
Habitat		1	6742	6742	2.09	**<0.001**	9869
Year		3	16436	5479	1.70	**<0.001**	9780
	2015–2016	1	4570	4570	1.51	**0.043**	9891
	2016–2017	1	6084	6084	1.80	**0.004**	9893
	2017–2018	1	3841	3841	1.09	0.320	9872
Survey type		2	8198	4099	1.27	0.063	9810
Mesophotic Habitat							
Coralline algae, Year		3	29642	9881	3.29	**<0.001**	9826
	2015–2016	1	13523	13523	4.66	**<0.001**	9753
	2016–2017	1	10902	10902	3.53	**<0.001**	9853
	2017–2018	1	8466	8466	2.74	**<0.001**	9844
Deep reef, Year		3	25453	8485	2.30	**<0.001**	9784
	2015–2016	1	7966	7966	2.55	**0.001**	5029
	2016–2017	1	8726	8726	2.63	**0.001**	8130
	2017–2018	1	8273	8273	2.04	**0.004**	9730
2015, Habitat (CR: DR)		1	9661	9661	3.29	**<0.001**	7742
2016, Habitat (CR: DR)		1	12389	12389	4.07	**<0.001**	9293
2017, Habitat (CR: DR)		1	10992	10992	3.33	**<0.001**	9737
2018, Habitat (CR: DR)		1	15004	15004	3.97	**<0.001**	9852

SIMPER results for density data showed that multiple species influenced PERMANOVA results (Table 4.12). French angelfish frequently contributed to the observed differences in the bank crest while reef butterflyfish, vermilion snapper, and red snapper frequently contributed to differences in mesophotic habitat. French angelfish biomass varied annually. A dense school of vermilion snapper was only documented in deep reef habitat in 2015.

Table 4.12. SIMPER results for fish biomass.

Test		SIMPER			
		Functional Group	Mean Biomass Group 1	Mean Biomass Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015–2016	Sharpnose puffer	15.47	16.08	10.01
		French angelfish	777.23	227.60	5.79
	2016–2017	French angelfish	227.60	1054.29	8.16
		Sharpnose puffer	16.08	4.09	7.44
	2017–2018	French angelfish	1054.29	510.55	8.59
		Reef butterflyfish	32.89	43.41	4.48
Habitat (HR: LR)		Sharpnose puffer	9.10	13.09	7.82
		French angelfish	627.08	656.83	6.15
Type		No analyses			
Mesophotic Habitat					
Coralline algae, Year		No analyses			
	2015–2016	Reef butterflyfish	8.20	1.00	7.08
		Squirrelfish	11.81	20.97	6.65
	2016–2017	Reef butterflyfish	1.00	18.01	6.69
		Squirrelfish	20.97	14.94	6.44
	2017–2018	Sharpnose puffer	0.06	4.07	12.51
		Yellowtail reeffish	6.21	28.22	6.23
Deep reef, Year		No analyses			
	2015–2016	Vermilion snapper	1315.37	22.21	13.78
		Scamp	170.06	40.61	9.36
	2016–2017	Red snapper	31.54	670.33	10.39
		Bigeye	17.50	37.91	9.2
	2017–2018	Red snapper	670.33	33.94	24.13
		Bigeye	37.91	3.96	14.96
2015, Habitat (DR: CR)		Vermilion snapper	1315.37	0.00	13.36
		Scamp	170.06	28.75	9.15
2016, Habitat (DR: CR)		Reef butterflyfish	92.96	1.00	7.55
		Squirrelfish	68.72	20.97	6.83
2017, Habitat (DR: CR)		Red snapper	670.33	482.99	10.20
		Spotfin hogfish	1.30	45.08	8.10
2018, Habitat (DR: CR)		Sharpnose puffer	0.00	4.07	16.40
		Yellowtail reeffish	0.06	28.22	10.04

When summed by trophic guild, biomass differed significantly between years and habitats on the bank crest, with no significant interactions. In mesophotic habitat, a significant interaction was found between year and habitat (pseudo-F=3.07, $p<0.001$), so each habitat and year was analyzed independently. Trophic biomass in coralline algae and deep reef habitat differed significantly between years, with each consecutive year significantly different, except for coralline algae habitat from 2017–2018. In all years except 2016, a significant difference was found in trophic biomass between habitats. Overall, the trophic composition at Stetson Bank, based on biomass, was significantly different between habitats and years (Figure 4.9 and Table 4.13).

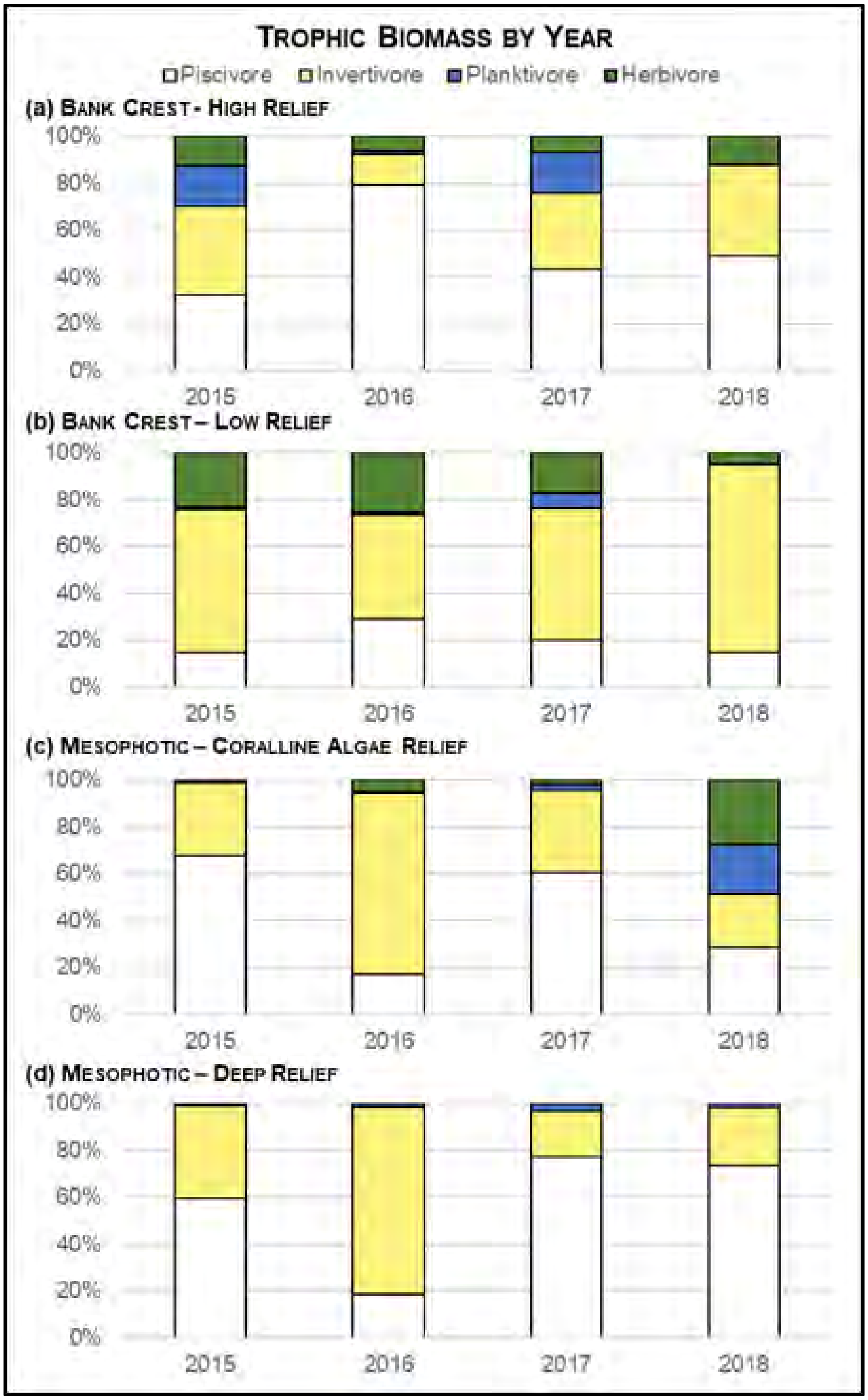

Figure 4.9. Trophic biomass by year.

Table 4.13. PERMANOVA results for trophic biomass. Bold numbers represent significant differences.

Test		PERMANOVA					
		DF	SS	MS	Pseudo-F	P	Number of Perms
Bank Crest Habitat							
Habitat		1	7904	7904	6.66	**<0.001**	9955
Year		3	7615	2538	2.14	**0.018**	9930
	2015–2016	1	1143	1143	1.00	0.375	9954
	2016–2017	1	4665	4665	4.09	**0.003**	9951
	2017–2018	1	861.3	861.3	0.69	0.609	9951
Survey type		2	4263	2131	1.80	0.076	9940
Mesophotic Habitat							
Coralline algae, Year		3	5510	1837	1.91	**0.018**	9918
	2015–2016	1	3193	3193	4.22	**0.007**	9818
	2016–2017	1	2636	2636	3.65	**0.019**	9906
	2017–2018	1	1163	1163	1.01	0.410	9894
Deep reef, Year		3	19274	6425	5.36	**<0.001**	9912
	2015–2016	1	4005	4005	4.39	**0.011**	5087
	2016–2017	1	3286	3286	4.42	**0.007**	8111
	2017–2018	1	6481	6481	4.64	**0.004**	9804
2015, Habitat (CR: DR)		1	2699	2699	3.45	**0.030**	7729
2016, Habitat (CR: DR)		1	2018	2018	2.36	0.091	9327
2017, Habitat (CR: DR)		1	2122	2122	3.41	**0.027**	9805
2018, Habitat (CR: DR)		1	10359	10359	5.61	**0.001**	9920

SIMPER results for trophic biomass showed that piscivores and invertivores contributed to the significant differences found with PERMANOVA (Table 4.14). On the bank crest, greater piscivore biomass and lower invertivore biomass was found in high-relief habitat compared to low-relief habitat. A similar trend was observed in mesophotic habitat, with greater piscivore biomass in deep reef habitat (except for 2018) and greater invertivore biomass in coralline algae reef habitat (except in 2015).

Table 4.14. SIMPER results for fish biomass.

Test		SIMPER			
		Functional Group	Mean Biomass Group 1	Mean Biomass Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015–2016	No analyses			
	2016–2017	Piscivore	6289.14	4736.21	34.84
		Invertivore	1501.11	4220.44	29.13
	2017–2018	No analyses			
Habitat (HR: LR)		Piscivore	7631.68	930.76	35.39
		Invertivore	4446.57	3582.50	30.54
Type		No analyses			
Mesophotic Habitat					
Coralline algae, Year		No analyses			
	2015–2016	Invertivore	390.73	1416.54	50.45
		Piscivore	867.78	333.32	32.73
	2016–2017	Invertivore	1416.54	415.00	48.25
		Piscivore	333.32	716.25	31.5
	2017–2018	No analyses			
Deep reef, Year		No analyses			
	2015–2016	Piscivore	3512.12	627.10	56.75
		Invertivore	2323.72	2864.49	35.97
	2016–2017	Invertivore	2864.49	210.48	49.02
		Piscivore	627.10	839.31	38.29
	2017–2018	Piscivore	839.31	168.47	57.89
		Invertivore	210.48	55.77	29.24
2015, Habitat (DR: CR)		Piscivore	3512.12	867.78	58.65
		Invertivore	2323.72	390.73	29.99
2016, Habitat (DR: CR)		No analyses			
2017, Habitat (DR: CR)		Piscivore	839.31	716.25	44.76
		Invertivore	210.48	415.00	32.37
2018, Habitat (DR: CR)		Piscivore	168.47	808.92	35.34
		Invertivore	55.77	644.33	32.80

Size-Frequency

Shade plots were used to examine community size structure (Figure 4.10 and Appendix 15). Both high- and low-relief habitat on the bank crest were predominantly comprised of <5 cm individuals, with a greater abundance of these individuals in high-relief habitat than low-relief habitat. Additionally, high-relief habitat had greater abundance of individuals in all other size groups. In mesophotic habitat, coralline algae reef habitat was predominantly comprised of <5 cm individuals, but their abundance varied over time. Deep reef was the only habitat not predominantly comprised of <5 cm individuals, and was instead dominated by 15–20 cm individuals.

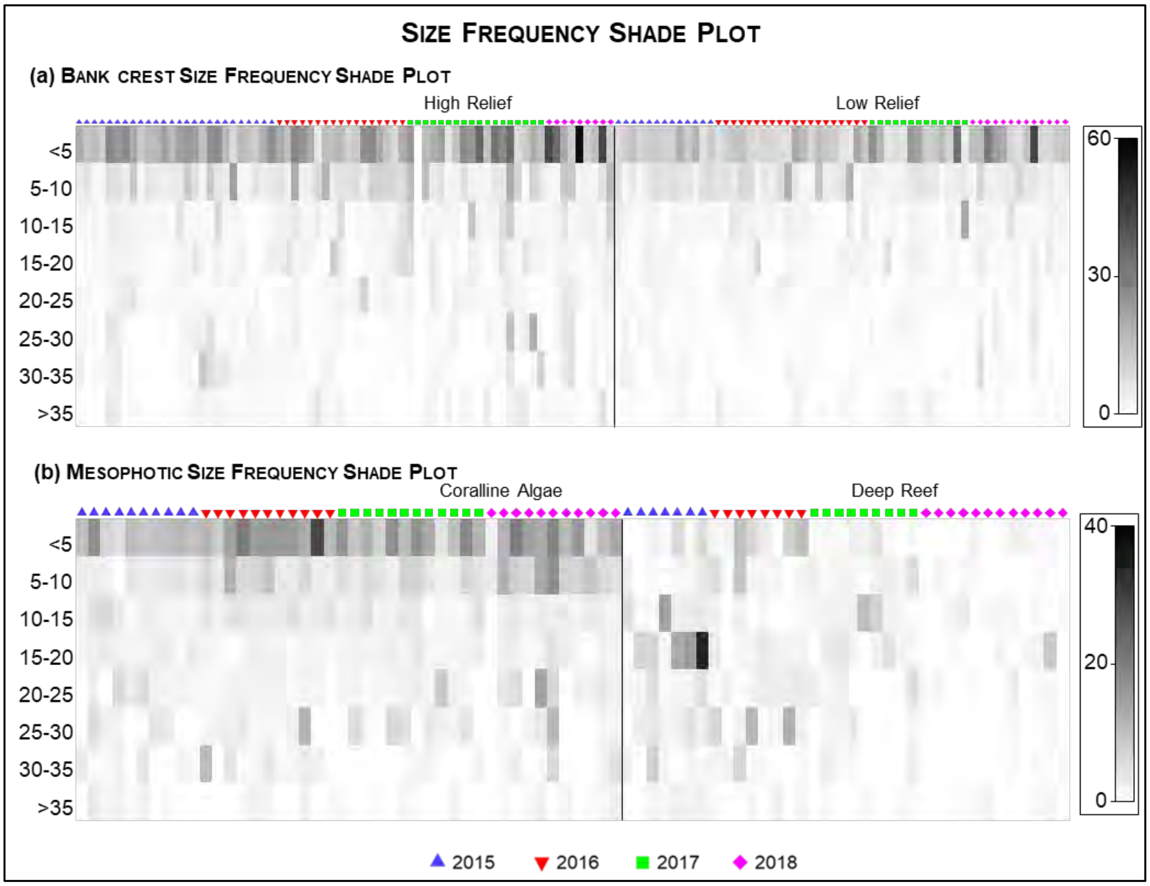

Figure 4.10. Community size frequency shade plots, where gray scale values represent the √abundance, for (a) the bank crest community and (b) the mesophotic community.

On the bank crest, a significant difference in community size structure was found only between habitats. In mesophotic habitat, a significant interaction was found between year and habitat (pseudo-F=3.04, $p<0.001$), so each habitat and year was analyzed independently. Community size structure in coralline algae habitat was significantly different between 2015 and 2016. Community size structure in deep reef habitat was significantly different among years, with each consecutive year significantly different. In all years, a significant difference was found between habitats. Overall, the size structure of the fish community at Stetson Bank was significantly different between years only in the mesophotic zone and significantly different between all habitats (Table 4.15).

Table 4.15. PERMANOVA results for size frequency. Bold numbers represent significant differences.

Test		PERMANOVA					
		DF	SS	MS	Pseudo-F	P	Number of Perms
Bank Crest Habitat							
Habitat		1	4750	4750	6.91	**<0.001**	9932
Year		3	3114	1038	1.51	0.093	9919
	2015-2016	1	1023	1023	2.05	0.070	9947
	2016-2017	1	1337	1337	1.65	0.126	9953
	2017-2018	1	336.9	336.9	0.35	0.891	9932
Survey Type		2	1540	770	1.12	0.334	9939
Mesophotic Habitat							
Coralline algae, Year		3	4030	1343	2.35	**0.002**	9903
	2015-2016	1	1822	1822	3.99	**0.002**	9817
	2016-2017	1	798.2	798.2	1.76	0.112	9914
	2017-2018	1	1264	1264	1.87	0.082	9907
Deep reef, Year		3	18069	6023	3.03	**<0.001**	9904
	2015-2016	1	4232	4232	2.74	**0.002**	5015
	2016-2017	1	4501	4501	3.16	**0.003**	8157
	2017-2018	1	4670	4670	2.04	**0.047**	9781
2015, Habitat (CR: DR)		1	6648	6648	7.01	**<0.001**	7800
2016, Habitat (CR: DR)		1	6101	6101	7.15	**<0.001**	9301
2017, Habitat (CR: DR)		1	9057	9057	10.52	**<0.001**	9759
2018, Habitat (CR: DR)		1	18818	18818	9.55	**<0.001**	9891

SIMPER results for size frequency showed that the size groups <5 cm and 5-10 cm had the greatest influence on PERMANOVA results between habitats. Individuals <5 cm were more abundant in high-relief compared to low-relief habitat and in coralline algae reef compared to deep reef habitat (Table 4.16). In mesophotic habitat, multiple size groupings contributed to the observed differences among years.

Table 4.16. SIMPER results for size frequency.

Test		SIMPER			
		Functional Group	Mean Abundance Group 1	Mean Abundance Group 2	% Cont
Bank Crest Habitat					
Year		No analyses			
	2015-2016	No analyses			
	2016-2017	No analyses			
	2017-2018	No analyses			
Habitat (HR: LR)		<5	478.07	234.34	39.02
		5-10	69.59	41.20	18.10
Type		No analyses			
Mesophotic Habitat					
Coralline algae, Year		No analyses			
	2015-2016	<5	106.10	266.91	33.83
		5-10	9.50	38.73	15.25
	2016-2017	No analyses			
	2017-2018	No analyses			
Deep reef, Year		No analyses			
	2015-2016	15-20	234.14	4.38	30.21
		10-15	36.43	1.63	15.2
	2016-2017	20-25	5.38	4.11	21.21
		<5	37.38	3.44	20.37
	2017-2018	10-15	19.33	1.42	22.33
		15-20	6.00	6.00	18.41
2015, Habitat (DR: CR)		<5	9.43	106.10	29.27
		15-20	234.14	5.00	27.98
2016, Habitat (DR: CR)		<5	37.38	266.91	40.67
		5-10	15.38	38.73	14.72
2017, Habitat (DR: CR)		<5	3.44	167.75	47.40
		5-10	6.22	22.08	11.39
2018, Habitat (DR: CR)		<5	1.08	179.45	38.66
		5-10	0.50	87.00	27.60

Dominance Plots

Dominance plot *w*-values were plotted over time for each habitat (Figure 4.11). On the bank crest, *w*-values for high-relief habitat declined marginally over time, while *w*-values for low-relief habitat were variable over time. Declining *w*-values indicate increasing abundance of small fish, suggesting increased recruitment or removal of large fish (Yemane et al. 2005). Conversely, in mesophotic habitat, coralline algae reef habitat *w*-values were variable among years and deep reef habitat *w*-values increased over time. Increasing *w* -values indicate an increase in abundance of large fish or declining abundance of small fish.

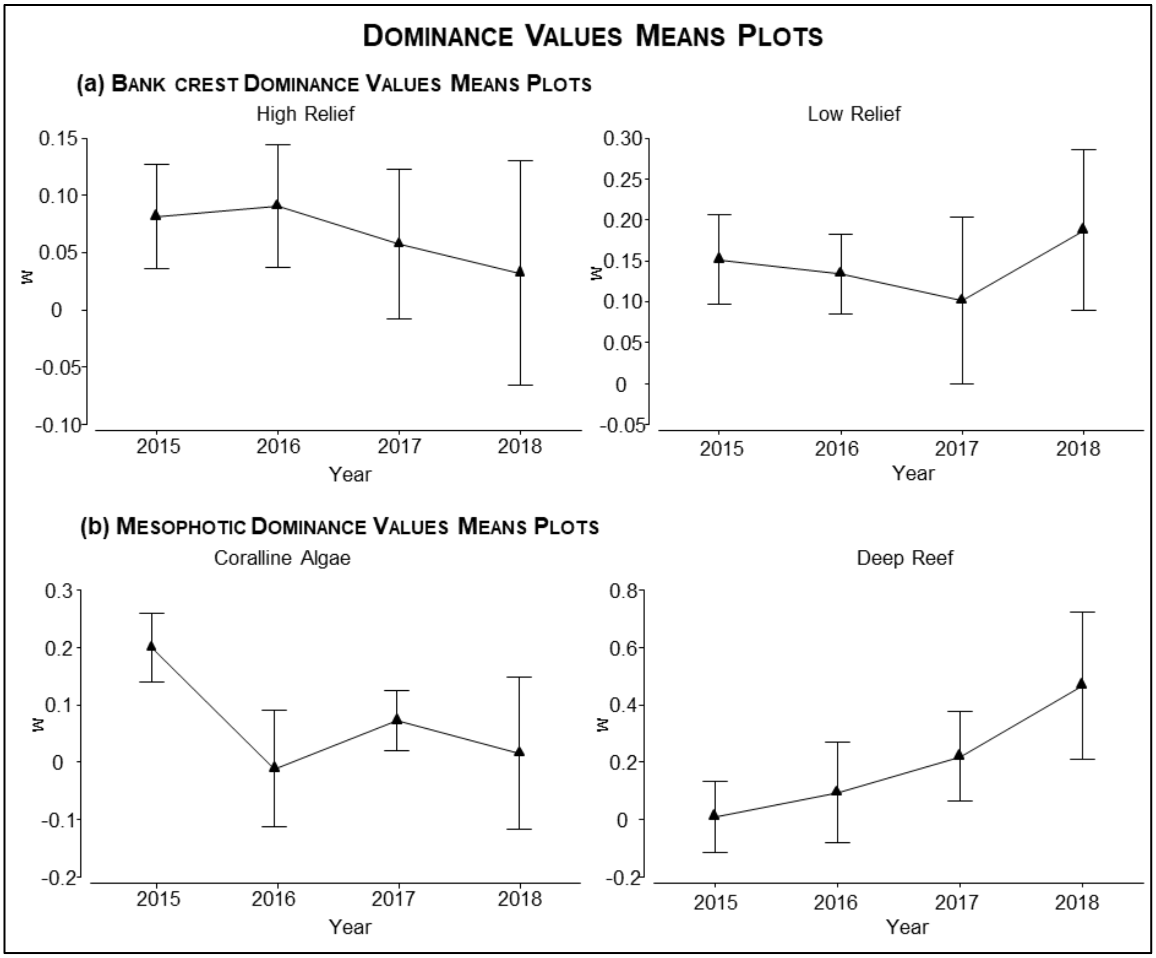

Figure 4.11. Dominance values means plots for (a) bank crest *w*-values and (b) mesophotic community *w*-values. Error bars represent standard deviation.

In the bank crest, dominance plot values did not differ significantly among years, but did differ significantly between habitats. In mesophotic habitat, a significant interaction was found between year and habitat ($F=7.34$, $p<0.001$), so each habitat and year was analyzed independently. Coralline algae habitat was significantly different from 2015–2016. Deep reef habitat was significantly different among years, but not between consecutive years. In all years except 2016, a significant difference was found between habitats. Overall, dominance plot values at Stetson Bank were consistently significantly different among all habitats (Table 4.17).

Table 4.17. ANOVA and Students T-Test results for dominance plot values. Bold numbers represent significant differences.

Test		ANOVA and Students T-Test				
		DF	SS	MS	F value	P
Bank Crest Habitat						
Habitat		1	0.15	0.15	9.77	**0.002**
Year		3	0.04	0.01	0.80	0.497
Survey type		2	0.00	0.00	0.10	0.905
Mesophotic Habitat						
Coralline algae, Year		3	0.27	0.09	4.80	**0.006**
	2015-2016	Pairwise t-test				**0.001**
	2016-2017	Pairwise t-test				0.151
	2017-2018	Pairwise t-test				0.325
Deep reef, Year		3	1.169	0.39	4.90	**0.007**
	2015-2016	Pairwise t-test				0.565
	2016-2017	Pairwise t-test				0.369
	2017-2018	Pairwise t-test				0.054
2015, Habitat (CR: DR)		1	0.149	0.149	13.02	**0.003**
2016, Habitat (CR: DR)		1	0.051	0.051	1.64	0.218
2017, Habitat (CR: DR)		1	0.11	0.11	5.16	**0.035**
2018, Habitat (CR: DR)		1	1.17	1.17	11.22	**0.003**

Spatial Analyses

While methods used to collect data were different between the bank crest (modified Bohnsack and Bannerot [1986] method with scuba divers) and mesophotic habitat (ROV transects), spatial projections highlighted additional patterns (Figure 4.12). Herbivore richness was tied strongly to the bank crest, where algae was the primary type of benthic cover. Piscivore richness was greatest in deep reef habitat. Overall, richness and density were greater on the bank crest and coralline algae reef than in deep reef habitat. Hotspots in biomass were found on the west end of the bank crest.

SPATIAL PROJECTION OF FISH RICHNESS, BIOMASS, AND DENSITY

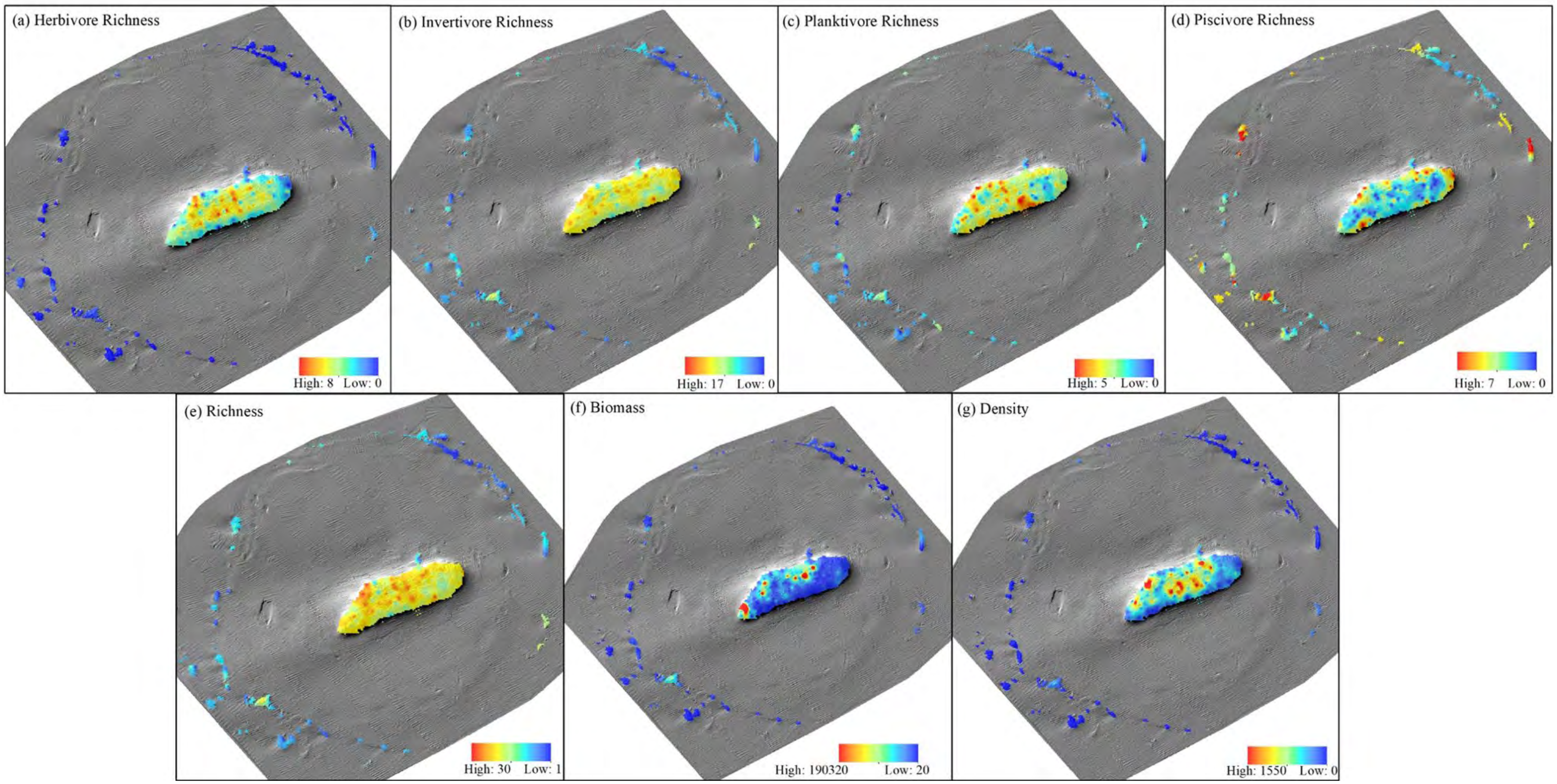

Figure 4.12. Inverse distance weighted fish richness, density, and biomass: (a) herbivore richness, (b) invertivore richness, (c) planktivore richness, (d) piscivore richness, (e) overall richness, (f) overall biomass, and (g) overall density. Red represents highest values and blue represents lowest values. Biomass is reported in g/100m^2 and density is reported in #/100m^2. Image: NOAA

Historical Trends

Historically, the fish community on the bank crest at Stetson Bank varied spatially and temporally (Nuttall et al. 2020). Using summary data, no significant clusters were found from 2012–2018 (Figure 4.13 and Appendix 16).

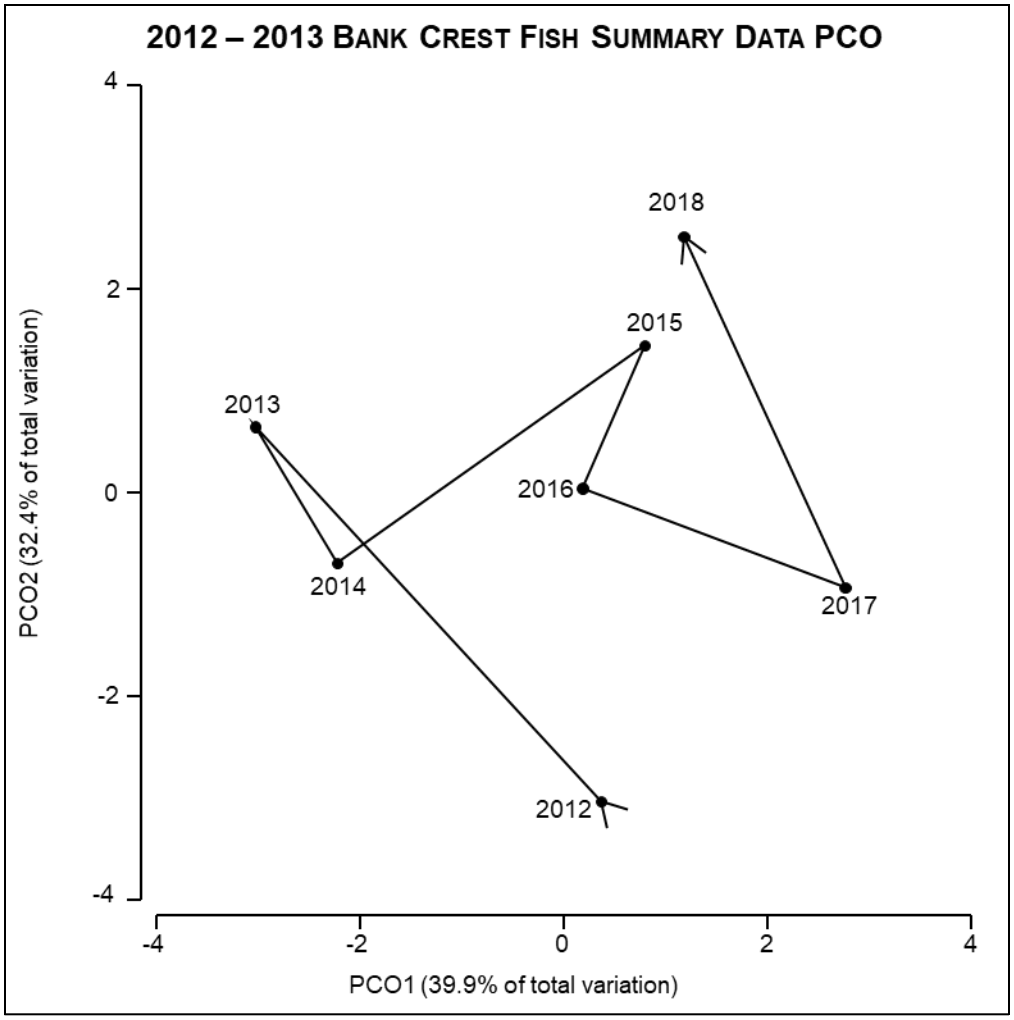

Figure 4.13. PCO plot of 2012–2018 bank crest fish summary data. Black lines represent year trajectory.

Mann-Kendall trend tests revealed no significant monotonic trends in trophic richness, biomass, or diversity measures on the bank crest (Figure 4.14).

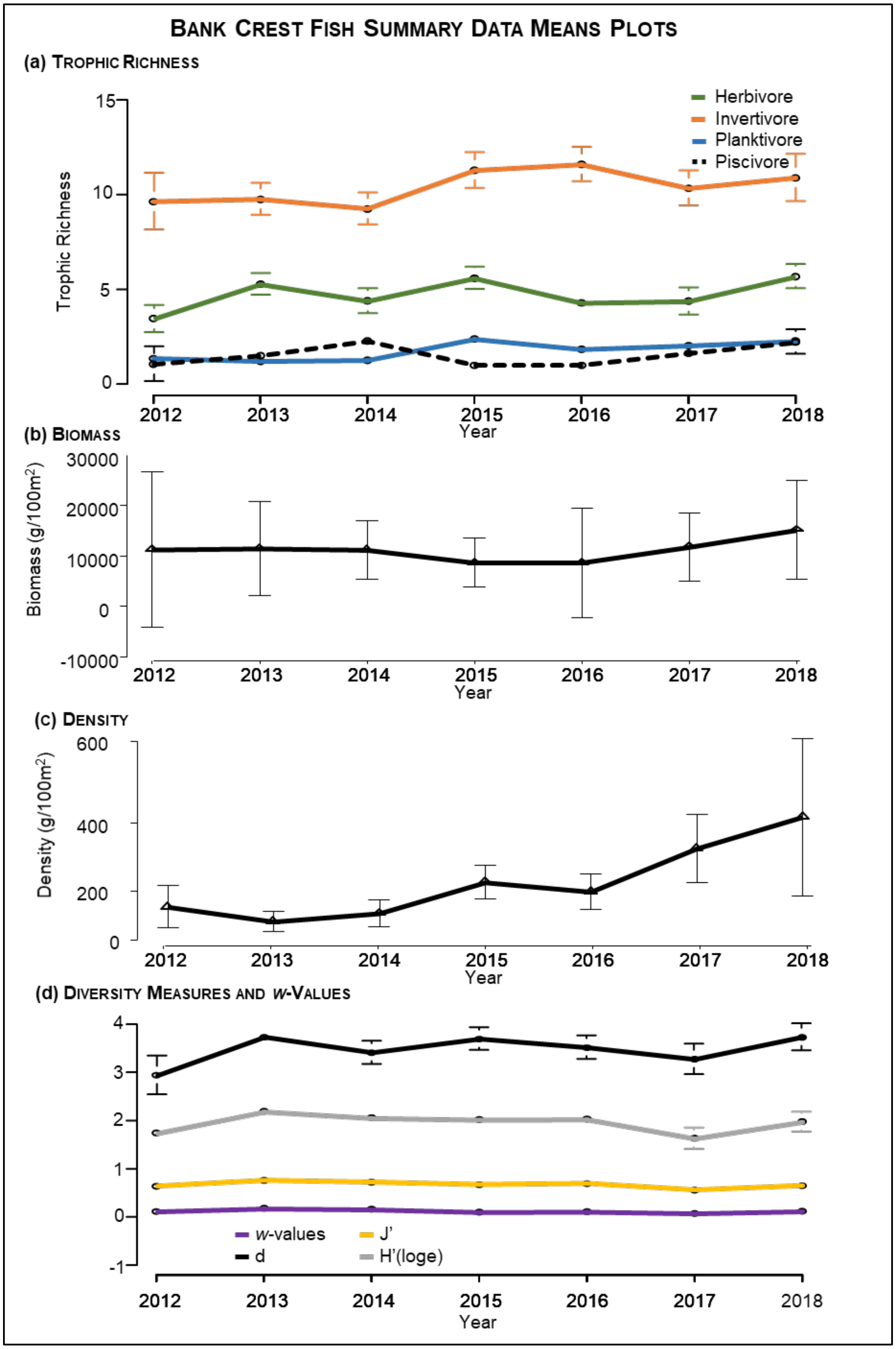

Figure 4.14. Means plots for fish summary data: (a) trophic richness, (b) biomass in g/100m2, (c) density in #/100m2, and (d) diversity measures and w values. Error bars represent standard deviation.

Mann-Kendall trend tests found a significant increasing trend in the abundance of <5 cm individuals (tau=0.71, p=0.035). No other significant trends were found (Figure 4.15).

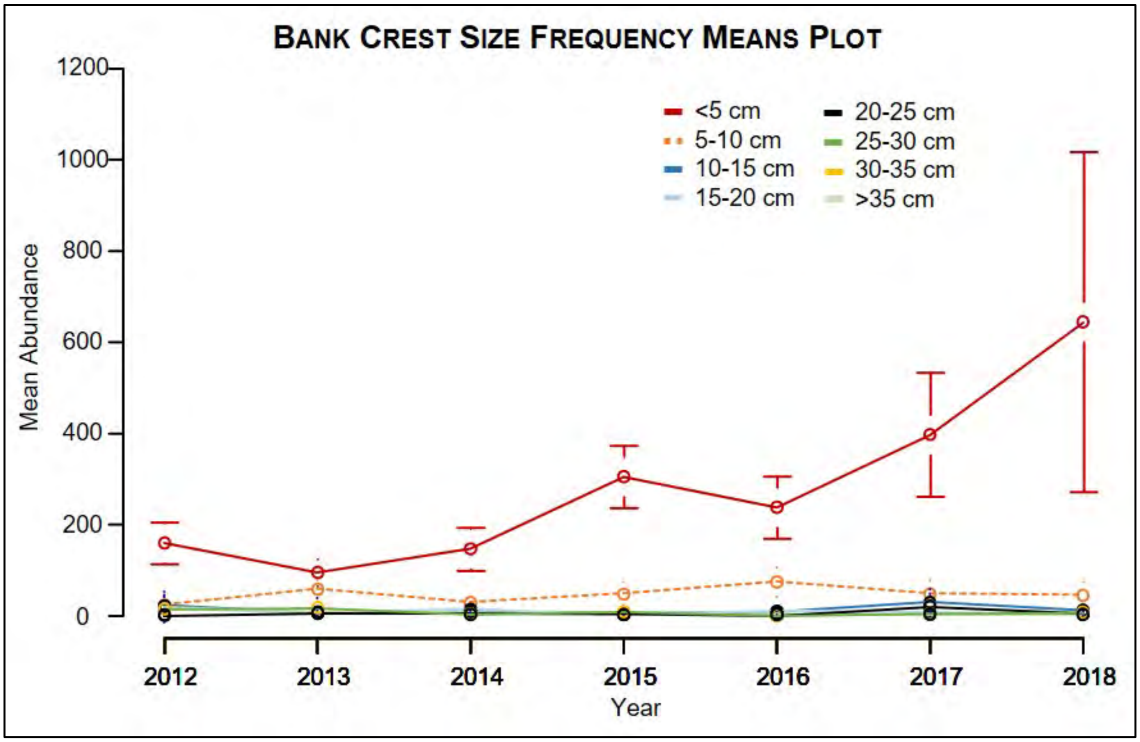

Figure 4.15. Bank crest fish size frequency means plot.

Species of Interest

Due to particular interest in some species groups, including grouper (*Mycteroperca*, *Cephalopholis*, *Epinephelus*, and *Dematolepis* genera only), snapper (*Lutjanidae* genus only), grunt (*Haemulon* genus), parrotfish (*Sparisoma* and *Scarus* genera only), and angelfish (*Holacanthus* and *Pomacanthus* genera only), as well as the non-native red lionfish (*Pterois volitans*) and regal demoiselle, separate analyses were conducted on these groups.

On the bank crest, grouper were comprised of eight species, including graysby (*Cephalopholis cruentata*), rock hind (*Epinephelus adscensionis*), red hind (*Epinephelus guttatus*), yellowmouth grouper (*Mycteroperca interstitialis*), yellowfin grouper (*Mycteroperca venenosa*), scamp (*Mycteroperca phenax*), tiger grouper (*Mycteroperca tigris*), and black grouper (*Mycteroperca bonaci*). In mesophotic habitat, no unique grouper species were found, but graysby, rock hind, yellowmouth grouper, and scamp were observed. Yellowfin grouper, tiger grouper, and black grouper were all solitary sightings and therefore excluded from analyses. Mean density and size frequency of each species varied by year (Figure 4.16 and Figure 4.17). Graysby occurred in greater mean density in high-relief habitat, and their mean size increased over the study period. Conversely, rock hind density in high-relief habitat declined, while mean size increased over time. Red hind were documented on the bank crest from 2012–2014 in increasing size, but have not been documented since 2014. Yellowmouth grouper were documented on the bank crest throughout the study period, but were recorded in higher density in coralline algae reef habitat. Size frequency data indicate potential recruitment events, with increased number of individuals <5 cm documented in 2015 and 2018.

Figure 4.16. Grouper density by habitat and year: (a) graysby, (b) rock hind, (c) red hind, (d) yellowmouth grouper, and (e) scamp.

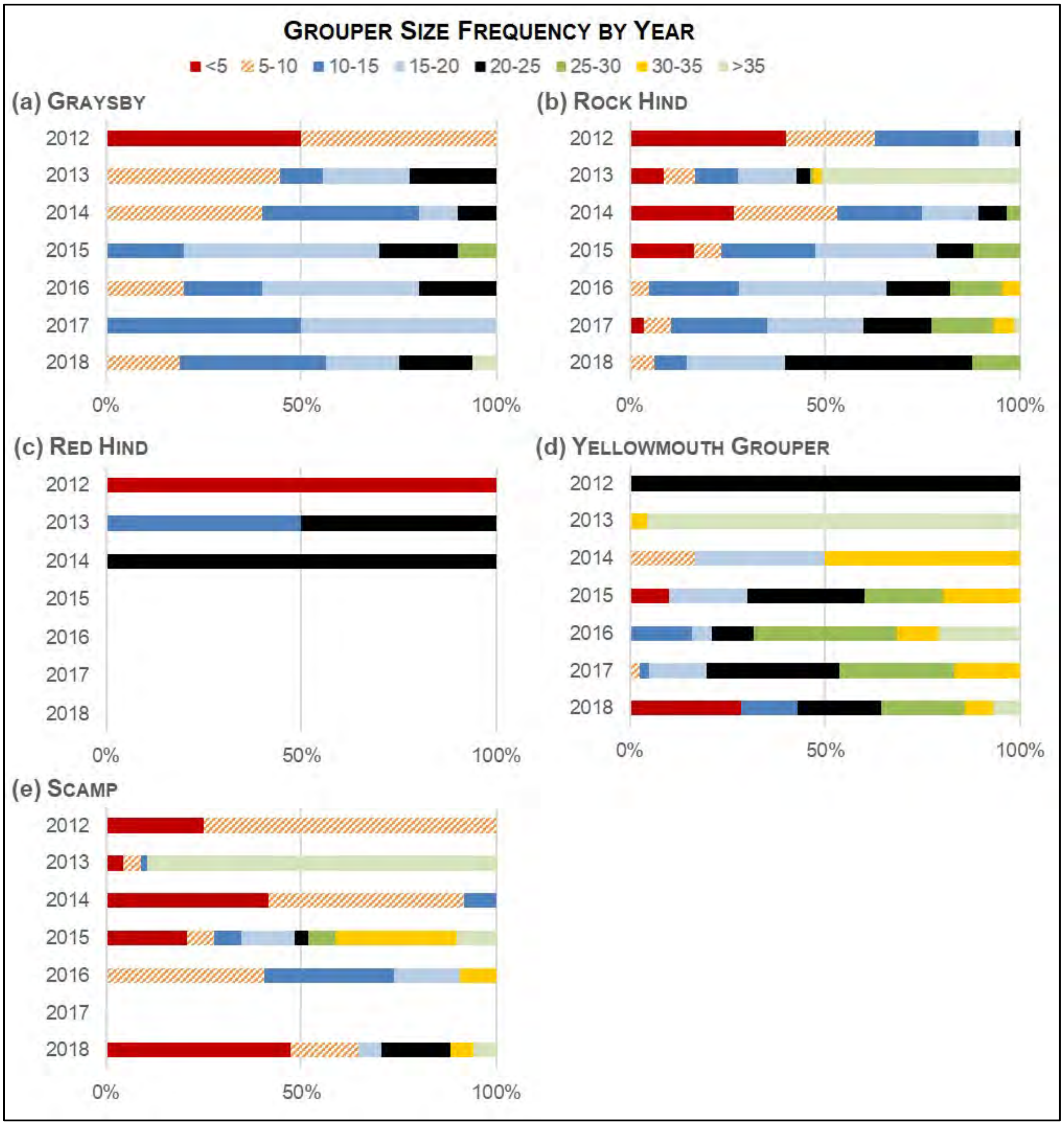

Figure 4.17. Grouper size frequency by year: (a) graysby, (b) rock hind, (c) red hind, (d) yellowmouth grouper, and (e) scamp.

On the bank crest, snapper were comprised of five species, including gray snapper (*Lutjanus griseus*), vermilion snapper (*Rhomboplites aurorubens*), dog snapper (*Lutjanus jocu*), red snapper (*Lutjanus campechanus*), and blackfin snapper (*Lutjanus buccanella*). In mesophotic habitat, no unique snapper species were found, but red snapper, vermilion snapper, and gray snapper were observed. Blackfin snapper was a solitary sighting and therefore excluded from analyses. Density and size frequency of each species varied by year (Figure 4.18 and Figure 4.19). Gray snapper were mostly observed in high-relief habitat on the bank crest, and mostly larger individuals recorded. However, in 2017, a potential recruitment event occurred and > 50% of the gray snapper observed were <5 cm. Vermilion snapper were mostly observed in low-relief and mesophotic habitats, with consistent recruitment of <5 cm individuals from 2016–2018. Dog snapper were only observed in 2014 in high-relief habitat, and most were >35 cm. Red snapper were mostly observed in mesophotic habitat and were typically >20 cm.

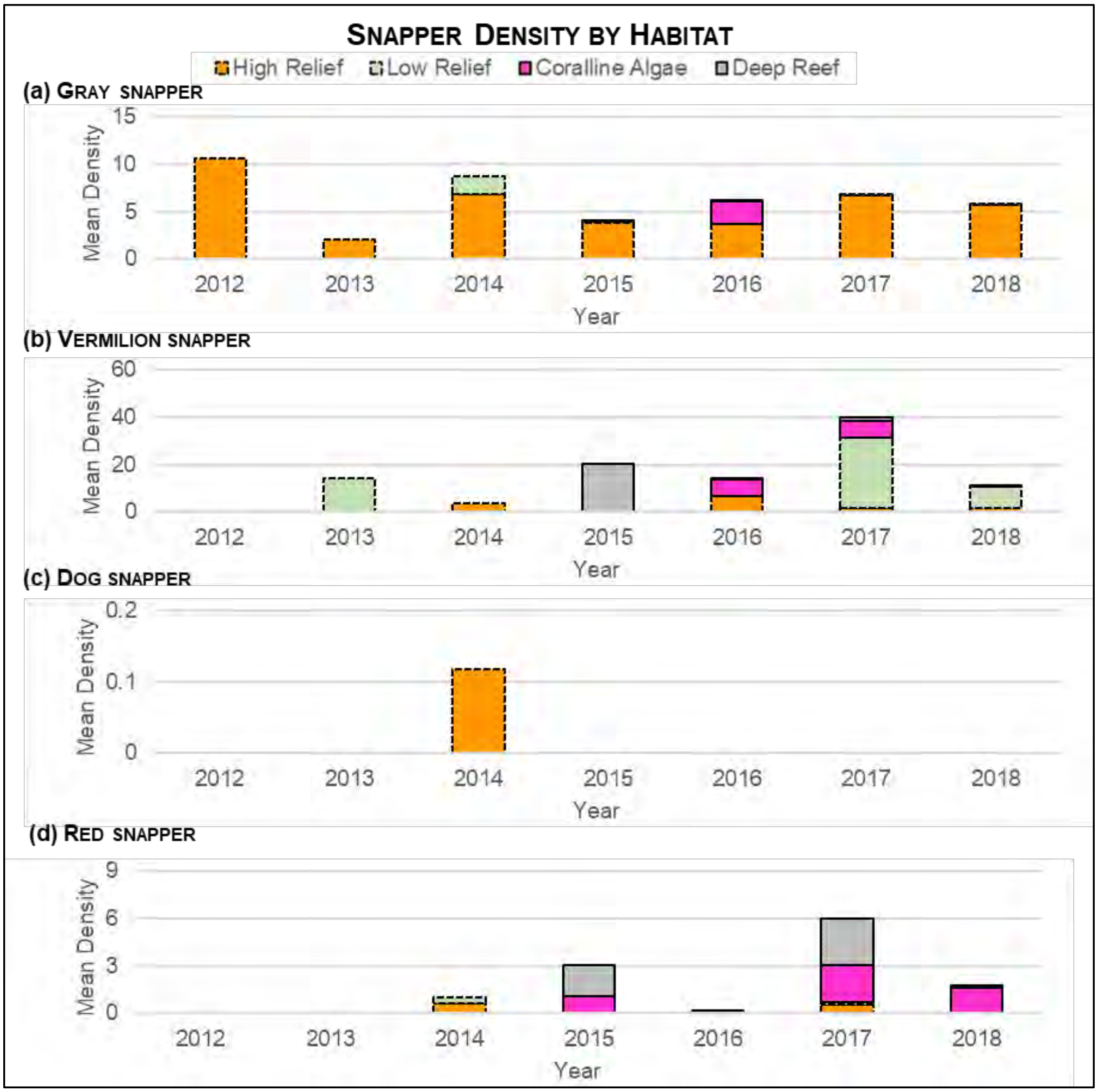

Figure 4.18. Snapper density by habitat and year: (a) gray snapper, (b) vermilion snapper, (c) dog snapper, and (d) red snapper.

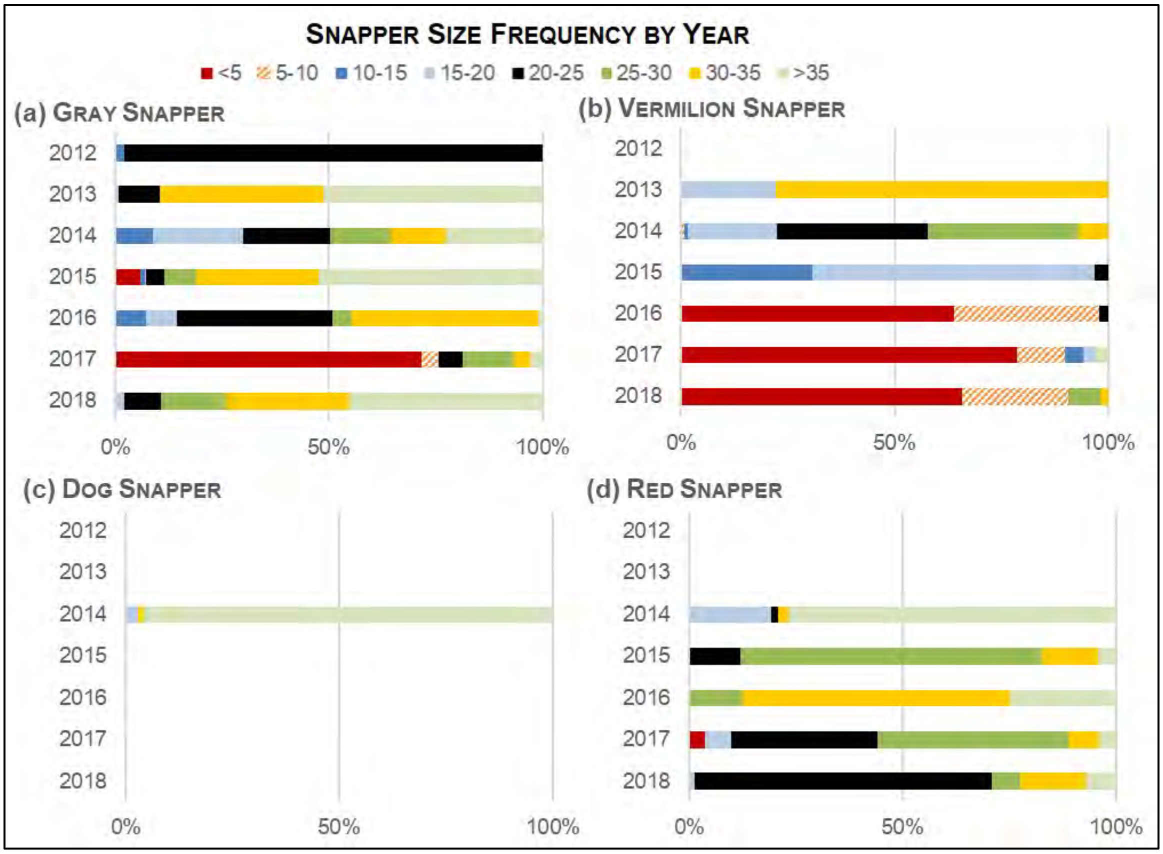

Figure 4.19. Snapper size frequency by year: (a) gray snapper, (b) vermilion snapper, (c) dog snapper, and (d) red snapper.

The grunt family on both the bank crest and in mesophotic habitat was comprised of two species, cottonwick (*Haemulon melanurum*) and tomtate (*Haemulon aurolineatum*). Density and size frequency of each species varied by year (Figure 4.20 and Figure 4.21). Both species were not observed in large numbers until 2015. Cottonwick were absent from deep reef habitat and increased in size over time. Tomtate were found in all habitats and had annual recruitment from 2016–2018.

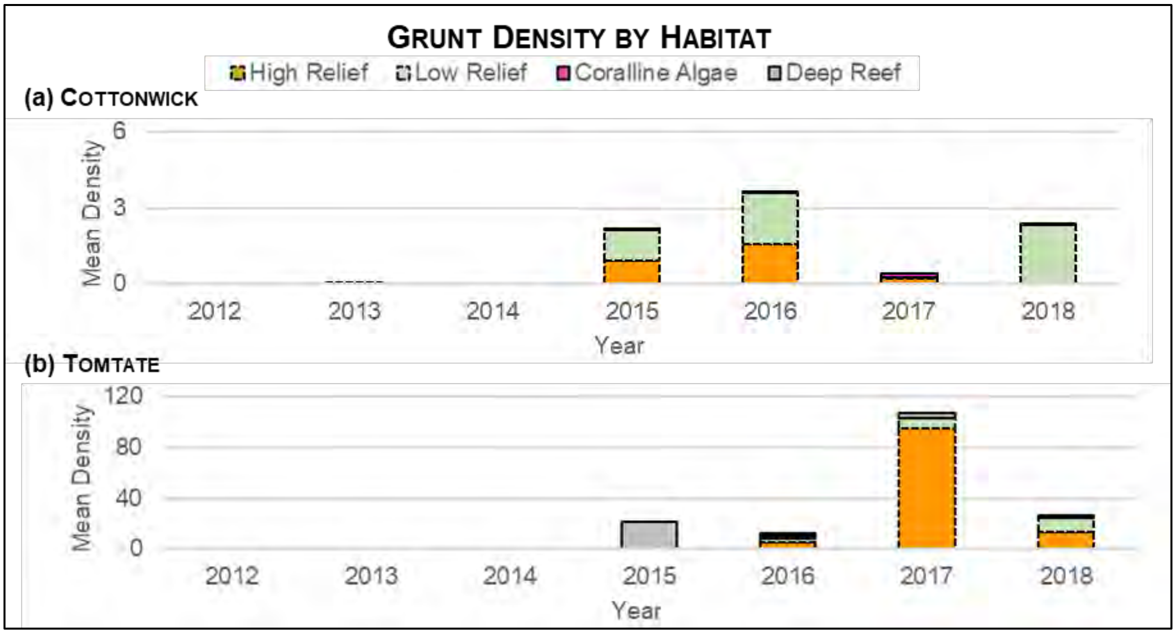

Figure 4.20. Grunt density by habitat and year: (a) cottonwick and (b) tomtate.

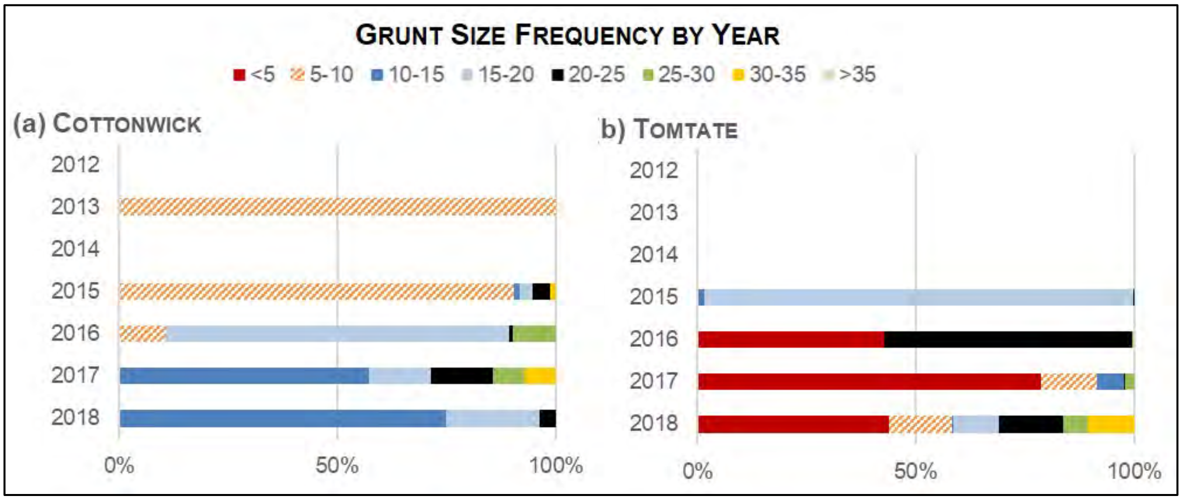

Figure 4.21. Grunt size frequency by year: (a) cottonwick and (b) tomtate.

Parrotfish have been identified as important grazers on coral reefs (Jackson et al. 2014). At Stetson Bank, seven species were documented on the bank crest, including striped parrotfish (*Scarus iseri*), princess parrotfish (*Scarus taeniopterus*), queen parrotfish (*Scarus vetula*), greenblotch parrotfish (*Sparisoma atomarium*), redband parrotfish (*Sparisoma aurofrenatum*), bucktooth parrotfish (*Sparisoma radians*), and stoplight parrotfish (*Sparisoma viride*). In coralline algae reef habitat, no unique parrotfish species were found, but greenblotch parrotfish, redband parrotfish, and striped parrotfish were observed. Parrotfish were not observed in deep reef habitat. Coherence plots did not find any significant covariation between parrotfish density and the benthic community. Total biomass varied by year and habitat with no apparent trend (Figure 4.22) while size frequency remained similar over time, with the community predominantly comprised of individuals <5 cm in size (Figure 4.23).

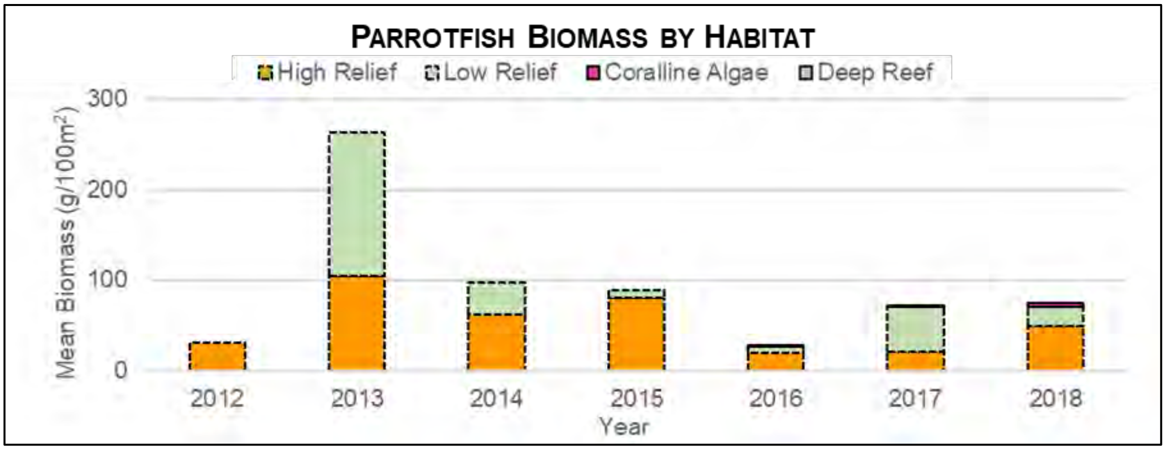

Figure 4.22. Parrotfish biomass by habitat.

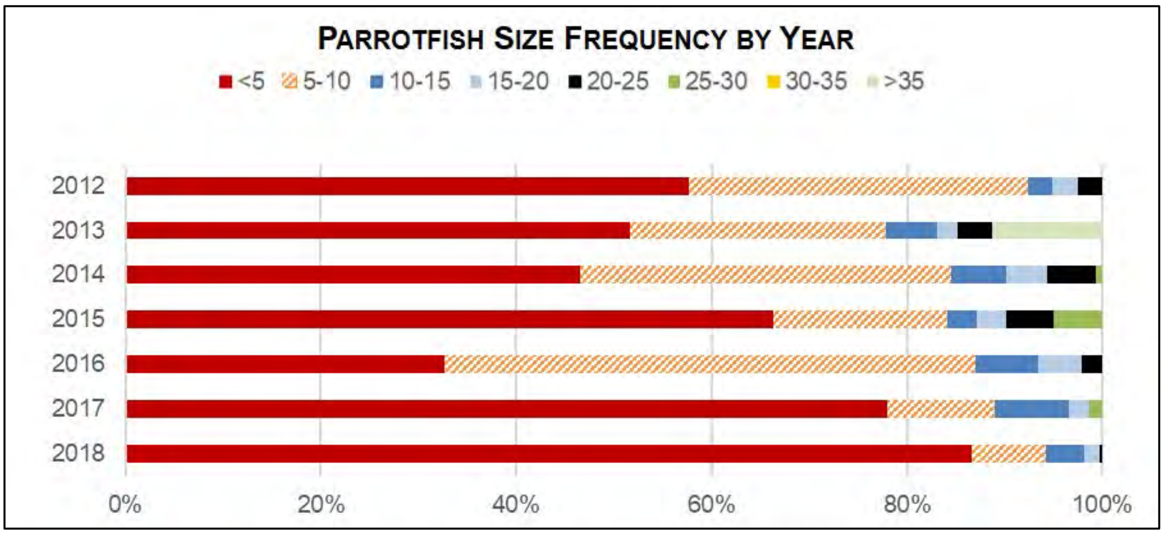

Figure 4.23. Parrotfish size frequency by year.

Spongivorous angelfish are of particular interest in environments where Porifera cover is a major component of the benthic biota, such as Stetson Bank. While not all are spongivores, seven species of angelfish were documented on the bank crest, including blue angelfish (*Holacanthus bermudensis*), queen angelfish (*Holacanthus ciliaris*), Townsend angelfish (*Holacanthus townsendi*), rock beauty (*Holacanthus tricolor*), French angelfish (*Pomacanthus paru*), cherubfish (*Centropyge argi*), and gray angelfish (*Pomacanthus arcuatus*). In mesophotic habitat, no unique angelfish species were found, but blue angelfish, queen angelfish, Townsend angelfish, rock beauty, French angelfish, and cherubfish were observed. All of these species, with the exception of cherubfish, are spongivores. Coherence plots did not find any significant covariation between angelfish density and the benthic community. Angelfish were observed in all habitats and total density varied by year and habitat with no apparent trend (Figure 4.24). Size frequency data show a steep decline in large angelfish over time, while recruits have increased (Figure 4.25).

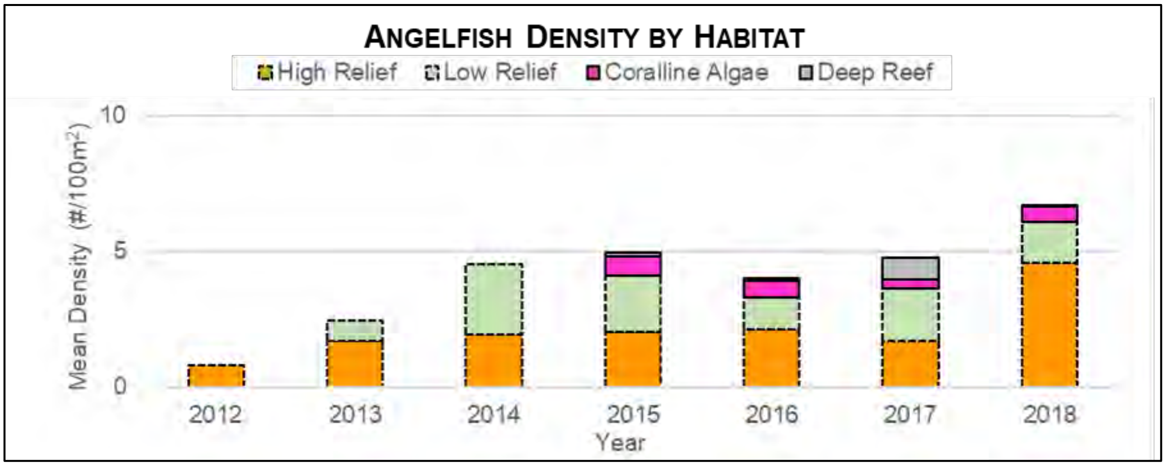

Figure 4.24. Angelfish density by habitat.

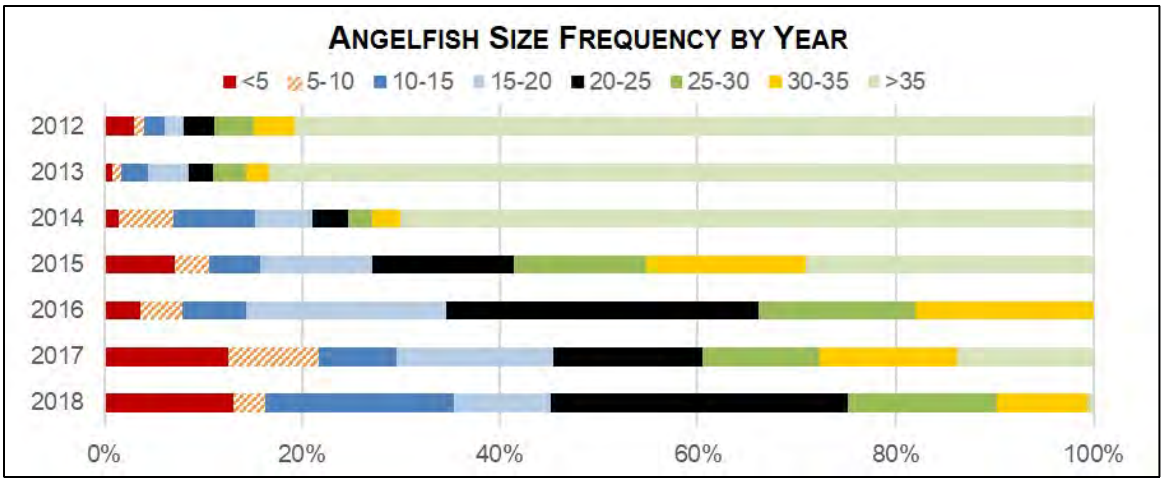

Figure 4.25. Angelfish size frequency by year.

Non-native red lionfish and regal demoiselle were documented during this study period. Red lionfish have been documented at Stetson Bank since 2011 (Johnston et al. 2016b) and their density has varied over time. However, red lionfish were more prevalent in both coralline algae and deep reef habitat than on the bank crest and size frequency shows red lionfish increasing in size from 2013–2016, with recruitment of <5 cm individuals in 2017 and 2018 (Figure 4.26 and Figure 4.27). No significant correlations were found between community density or size frequency and lionfish density in mesophotic habitats. Similar correlation tests were not performed on bank crest lionfish density due to the low sighting frequency (7.75%) of lionfish in all bank crest surveys. Regal demoiselle were first documented at Stetson Bank in 2018 (Nuttall et al. 2019a), when their population of individuals <10 cm in size increased from zero to an average of 120 ± 60 SE/100 m^2 in high-relief habitat and an average of 40 ± 30 SE/100 m^2 in low-relief habitat on the bank crest (Figure 4.26 and Figure 4.27). While not documented in deep reef habitat, regal demoiselle were documented in all other habitats at Stetson Bank.

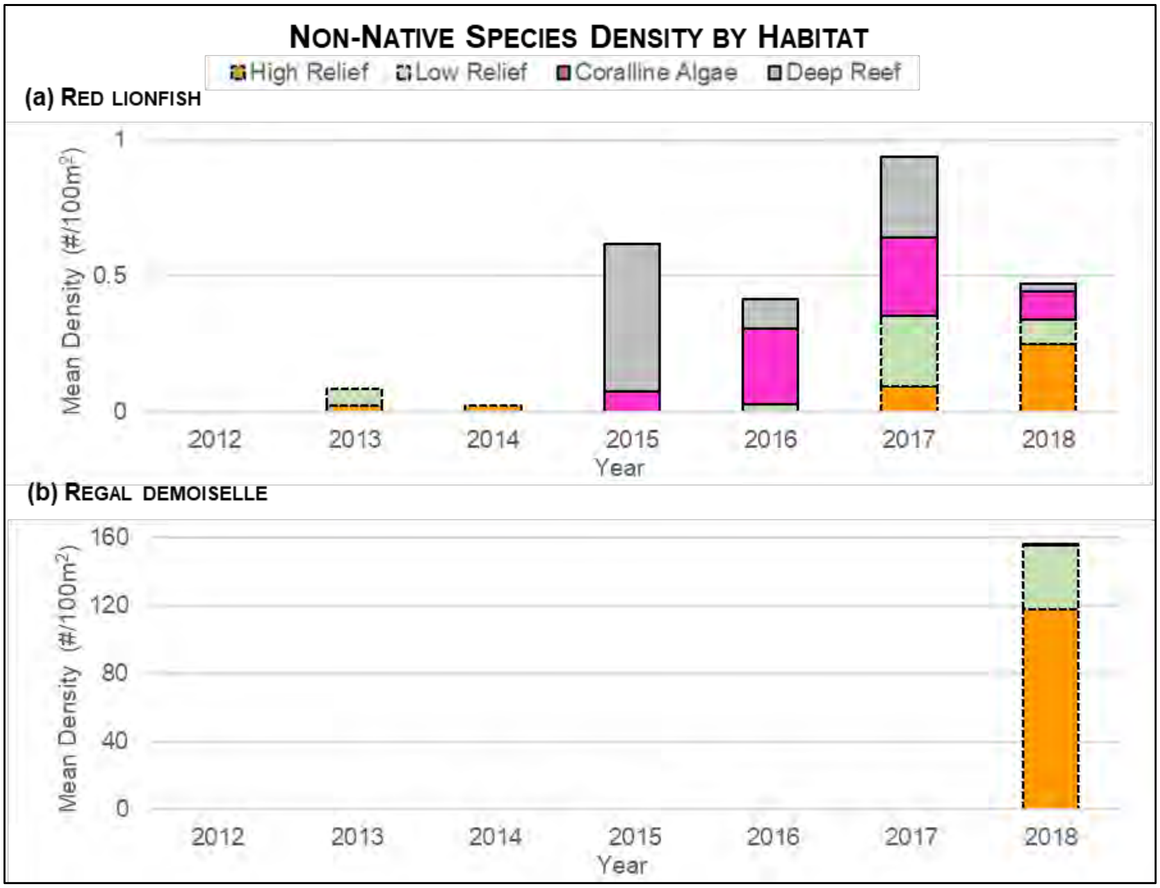

Figure 4.26. Non-native species density by habitat and year: (a) red lionfish and (b) regal demoiselle.

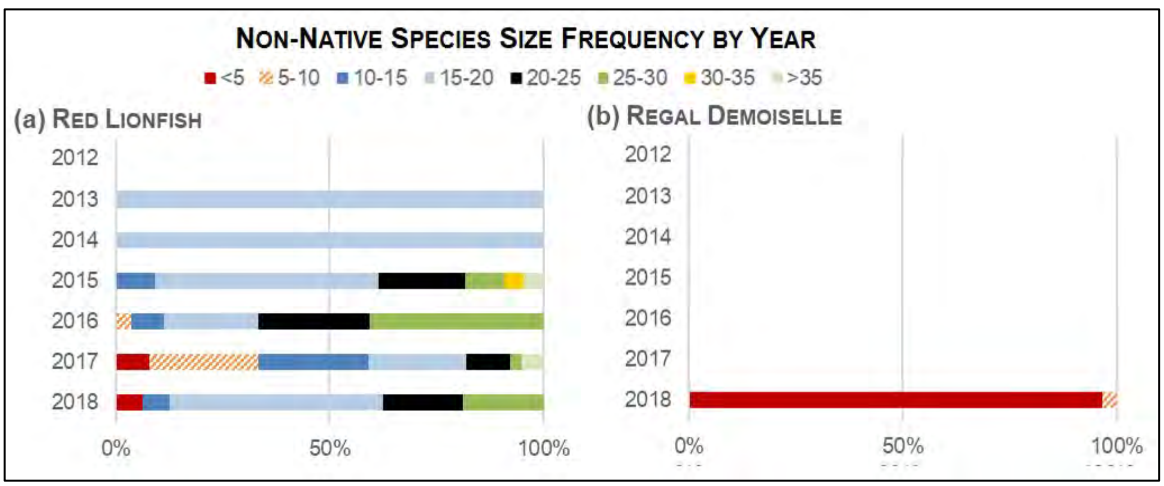

Figure 4.27. Non-native species size frequency by year: (a) red lionfish and (b) regal demoiselle.

Discussion

Fish communities are considered indicators of ecosystem health (Sale 1991) and are therefore an important component in long-term monitoring programs. Monitoring fish community changes over extended periods of time is valuable for detecting changes from normal variations in the community. The fish community at Stetson Bank varied significantly among years and was distinct between habitats, based on multiple measures (occurrence, density, and biomass). However, community metrics (diversity measures, size frequency, *w*-values) varied significantly only between habitats.

In comparison to the Flower Garden Banks and other reefs in the Caribbean region, Stetson Bank mean species richness was lower and mean biomass was greater, with greater variability (Nuttall et al. 2020). Between bank crest habitats, high-relief habitat had higher fish densities, greater biomass, greater piscivore and planktivore richness, and more small fish (<10 cm) than low-relief habitat. While not tested against the bank crest data due to differing sampling techniques, clear differences were also apparent between the bank crest communities and those found in mesophotic habitat. Between mesophotic habitats, coralline algae reef was found to have higher densities, lower herbivore and invertivore richness, and smaller size fish (<5 cm) than deep reef habitat.

Trophic biomass varied significantly by year and habitat, with an inverted biomass pyramid found in most years and habitats. In an inverted biomass pyramid, piscivore dominance is associated with low levels of detrimental environmental impacts, particularly from fishing (Friedlander & DeMartini 2002, DeMartini et al. 2008, Knowlton & Jackson 2008, Sandin et al. 2008, Singh et al. 2012). Typically, inverted biomass pyramids are associated with healthy reef systems with high coral cover. However, coral cover at Stetson Bank throughout the reported timeframe was low compared to other Caribbean reefs (Jackson et al. 2014), comprising less than 3% of the benthic cover. Despite the overall lack of coral cover, the siltstone and sandstone outcroppings at Stetson Bank create moderately complex habitat that provides structure for schooling behavior, but limited potential refuges for prey fish to shelter from predators. Low-relief habitat had fewer occurrences of piscivore biomass dominance, which may be attributed to the lack of refuge available in these habitats. Few herbivores were observed in deep reefs, potentially due to the lack of macroalgae cover found throughout that habitat.

When historical data were analyzed, a significant increasing trend in individuals <5 cm was found. Similarly, among species of interest, increased abundance of small individuals was found for vermilion snapper, tomtate, angelfish, and regal demoiselle. Greater numbers of fish <5 cm suggest an increase in recruitment; however, as surveys were conducted in different months each year (from late May to early July), this finding may also reflect recruitment seasonality (Munro et al. 1973). Additionally, significant differences were not consistently found between years in abundance biomass curve *w*-values, indicating that the community at Stetson Bank remained well balanced between small and large individuals despite increasing abundance of individuals <5 cm.

When examining species of interest, declines in density of two small-bodied groupers, red hind and rock hind, were documented. Both species also experienced increasing size frequency, with an increasing number of sexually mature individuals (>26 and >28 cm, respectively; Farmer et al. 2016). The most abundant large-bodied groupers were immature yellowmouth and scamp, which are recorded to reach maturity at total lengths >45 and >35 cm, respectively (Farmer et al. 2016). Snapper density was variable over time at Stetson Bank, with juvenile (<5 cm) vermilion snapper comprising >50% of the population from 2016–2018. While the number of juvenile vermilion snapper was high, few mature individuals were documented (>32 cm; Farmer et al. 2016). Conversely, the majority of gray and red snapper observed throughout the reported period were mature (>23 cm; Farmer et al. 2016).

Sighting frequency of some spongivorous angelfish has declined along with Porifera cover at Stetson Bank (Nuttall et al. 2020). Additionally, the present study indicates that the size of angelfish at Stetson Bank also declined, with >50% of the population >35 cm in 2012 compared to <5% in 2018. While the proportion of large angelfish declined, the proportion of small angelfish (<10cm) increased.

Red lionfish have been reported at Stetson Bank by recreational scuba divers since 2011 in lower densities than at EFGB and WFGB (Johnston et al. 2016b). While the cause of these lower numbers is likely complex, a contributing factor may be the abundance of moray eels found at Stetson Bank. In their native range, large moray eels not only prey on lionfish, but locations inhabited by these eels are actively avoided by lionfish (Bos et al. 2017). Red lionfish were more frequently observed in mesophotic habitats than on the bank crest, potentially due to buffered thermal variations in deeper water and available refuge. Despite having a wide thermal tolerance, lionfish thermal preference is dependent on typical environmental conditions (Barker 2015). Additionally, removal efforts on the bank crest have been substantial at Stetson Bank; however, removals from habitats deeper than 33.5 m is challenging and has not been conducted to date, allowing the establishment of communities in mesophotic habitats that may serve as source populations for the bank crest. The invasion of this exotic species is of particular concern due to their voracious appetite, high fecundity, and apparent lack of predators. Additionally, the presence of lionfish has been documented to suppress recruitment of other fish (Albins & Hixon 2008). No correlations between community density or size frequency and lionfish density were found in mesophotic habitats.

One new non-native species was documented during this study period, the regal demoiselle. Native to the Indian and western Pacific Oceans, they were first documented in the northern Gulf of Mexico on oil and gas platforms in 2017 (Bennett et al. 2019). They are thought to have been brought to the region in ship ballast water and use oil and gas platforms, as well as natural reefs, as structure for settlement (Sheehy & Vik 2010, González-Gándara & de la Cruz-Francisco 2014). However, the likelihood of long-term viability for regal demoiselle is uncertain, particularly given their narrow thermal tolerance in aquaria (Johansen et al. 2015). At Stetson Bank, the population density of regal demoiselle dramatically increased from zero in 2017 to 120/100m^2 in 2018 in high-relief habitat. Additionally, they were not documented in deep reef habitat, suggesting they use the shallower bank crest habitat for settlement. Further examination of this species over time will provide more information about the likelihood of long-term persistence at Stetson Bank.

The fish community at Stetson Bank is naturally variable, both within the few distinct habitats found at the bank and among years. The community was diverse, comprised of reef-associated and pelagic species, as well as some commercially and recreationally valuable species. Despite having lower total species richness and lower species richness per sample than EFGB and WFGB, biomass at Stetson Bank was greater, but more variable. The fish community as a whole varied from year to year, and most families of interest did not exhibit any trends over time. The abundance of fish <5cm has been increasing at Stetson Bank, with vermilion snapper, tomtate, angelfish, and regal demoiselle all contributing to this trend.

Overall, methods employed to monitor the fish community at Stetson Bank during the study period were successful, especially on the bank crest. However, random transect fish surveys in mesophotic habitat were challenging, primarily due to poor water clarity, heavily silted environments, and fish avoidance behavior. Poor water clarity led to the use of minimum field of view measurements in survey summary data and analyses. To improve the method in the future, the use of stationary fish surveys in mesophotic habitats should be examined.

Chapter 5:
Local Water Quality and Environmental Condtions

Introduction

The physical, biological, and chemical characteristics of the water column at Stetson Bank were assessed using a variety of methods. The bank's location ~130 km offshore provides some separation from turbid, brackish, coastal waters; however, pockets of mixed coastal and oceanic waters have been observed to reach Stetson Bank annually between May–July, increasing turbidity and potentially conveying pollutants and particulates (Deslarzes & Lugo-Fernández 2007).

Anomalously high river discharge combined with ocean currents can transport coastal water toward the outer shelf and to the vicinity of Stetson Bank. Major river outfalls such as the Atchafalaya and Mississippi River basins deliver, on average, upwards of 650,000 ft^3/s of water into the Gulf of Mexico annually. Due to the large volume of water flowing from the Mississippi/Atchafalaya River basin, which drains over 40% of the contiguous United States, increased flow rates from these rivers can alter water conditions on the continental shelf (Rezak et al. 1985, Morey et al. 2003, Bianchi et al. 2010, Kealoha et al. 2020). While proportionally small compared to the major river systems, the net effect of anomalously high discharge from smaller Texas rivers also transports coastally influenced water to the offshore environment (Kealoha et al. 2020).

The periodic impacts of tropical weather systems on the environmental conditions of reefs in the tropical biotope have been documented for decades (Woodley et al. 1981, Scoffin 1993, Harmelin-Vivien 1994, Aronson & Precht 2001, Riegl 2007). However, the impact of these weather systems on habitat greater than 20 m deep, like Stetson Bank, are not well documented. Tropical weather systems can impact habitat in a variety of ways, including mechanical damage from waves, currents, or projectiles, reduced water clarity from sediment resuspension and runoff, and stress from reduced salinity due to rain and runoff. However, these events can also positively influence reefs through sediment transport and removal, reorganization and exposure of new habitat, storm-induced water cooling, and by aiding in larvae dispersal (Hubbard et al. 1991, Lugo-Fernández et al. 2001, Manzello et al. 2007, Lugo-Fernández & Gravois 2010, Rousseau et al. 2010).

Multiple parameters were measured to evaluate environmental conditions throughout the study period. While some data gaps exist, from 2015–2018, a continuous record of water temperature was collected at 24 m, 30 m, and 40 m, and salinity was also continuously collected at 24 m. Other water quality parameters were measured quarterly, including nutrient loading and seawater carbonate chemistry at the bank crest, midwater, and surface.

Water quality and physical parameters were collected to compare among years, investigate extreme observations, examine links between water quality and changes in benthic and fish community, and analyze trends over time. Additionally, water column profiles were collected and examined to identify zones of stratification and compare among years.

Methods

Field Methods

Water temperature and salinity on the crest of Stetson Bank (24 m) were initially collected continuously using a Sea-Bird® Electronics Inc. MicroCAT® 37 logger. In November 2015, a Sea-Bird® Electronics, 16plus V2 conductivity, temperature, and depth (CTD) meter was deployed to replace the MicroCAT® 37, equipped with a WET Labs ECO NTUS turbidity meter. The loggers were installed on a railroad car wheel in the midsection of the bank crest (Figure 5.1 and Figure 5.2). The instrument was downloaded quarterly, and factory service of the instrument was performed annually. Continuous data were collected during the study period with the exception of 7/23/2017–11/7/2017, when instrument failure resulted in a data gap. However, Onset® Computer Corporation HOBO® Pro v2 U22-001 thermisters were used as a backup to the Sea-Bird® instruments and recorded temperature on an hourly basis. These data were substituted for missing temperature data from 7/23/2017–11/7/2017.

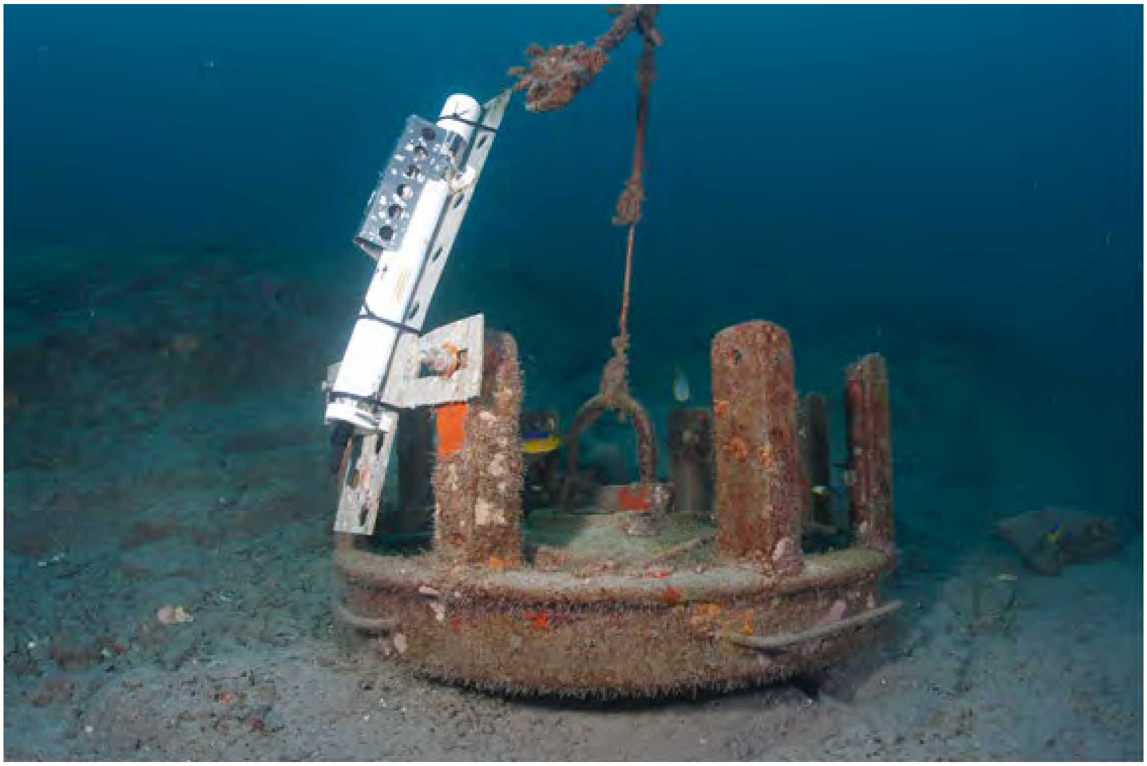

Figure 5.1. Sea-Bird® Electronics Inc. 37 MicroCAT® logger mounted to a railroad car wheel at Stetson Bank. Photo: G.P. Schmahl/NOAA

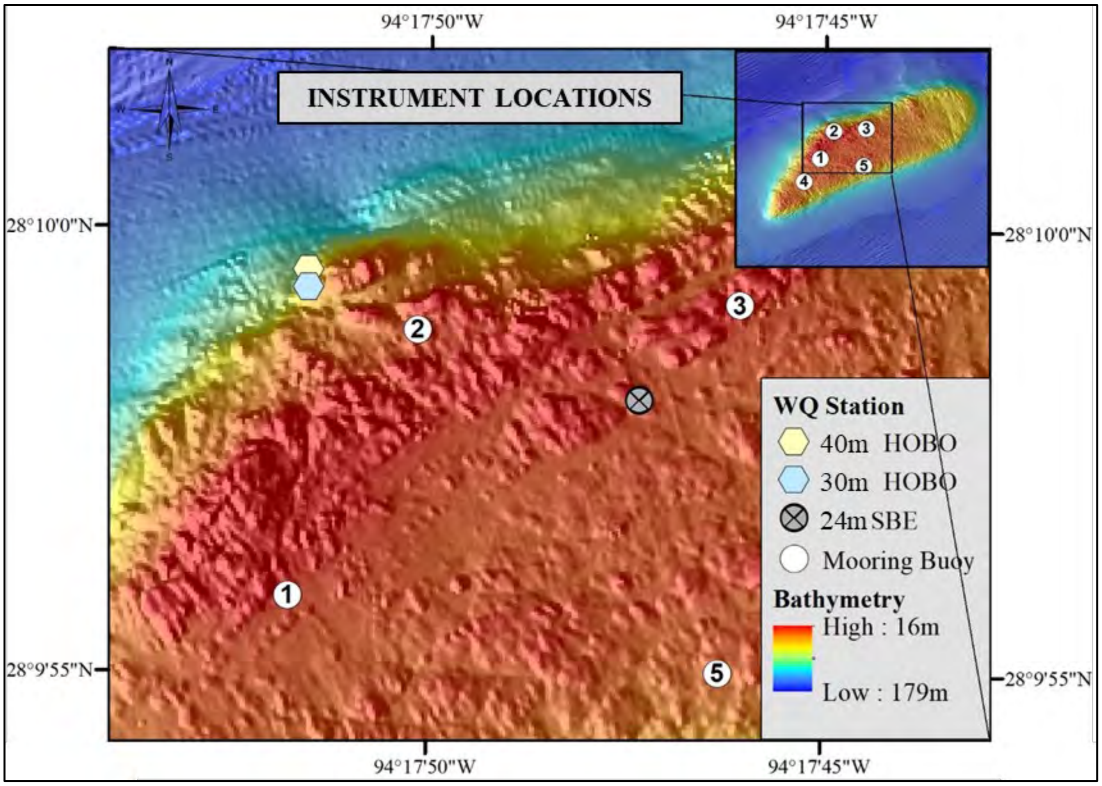

Figure 5.2. Location of bank crest continuous temperature and salinity loggers. Image: NOAA

A HOBO® thermograph deployed at the 30 m station, located on the northern edge of the bank crest, recorded temperature hourly. Continuous data were collected during the study period. On 6/25/2015, another HOBO® thermograph was installed at 40 m, also along the northern edge of the bank crest. The 40 m HOBO® thermistor recorded temperature hourly and collected continuous data from its installation throughout the study period (Figure 5.2). They were downloaded and maintained quarterly and attached to eyebolts embedded in the substrate at the 30 m and 40 m stations. On 7/16/2015, two themistors were deployed in deep reef habitat at 44 m and 54 m using an acoustic release system. However, the acoustic release system failed and the instruments have not been recovered (Figure 5.3).

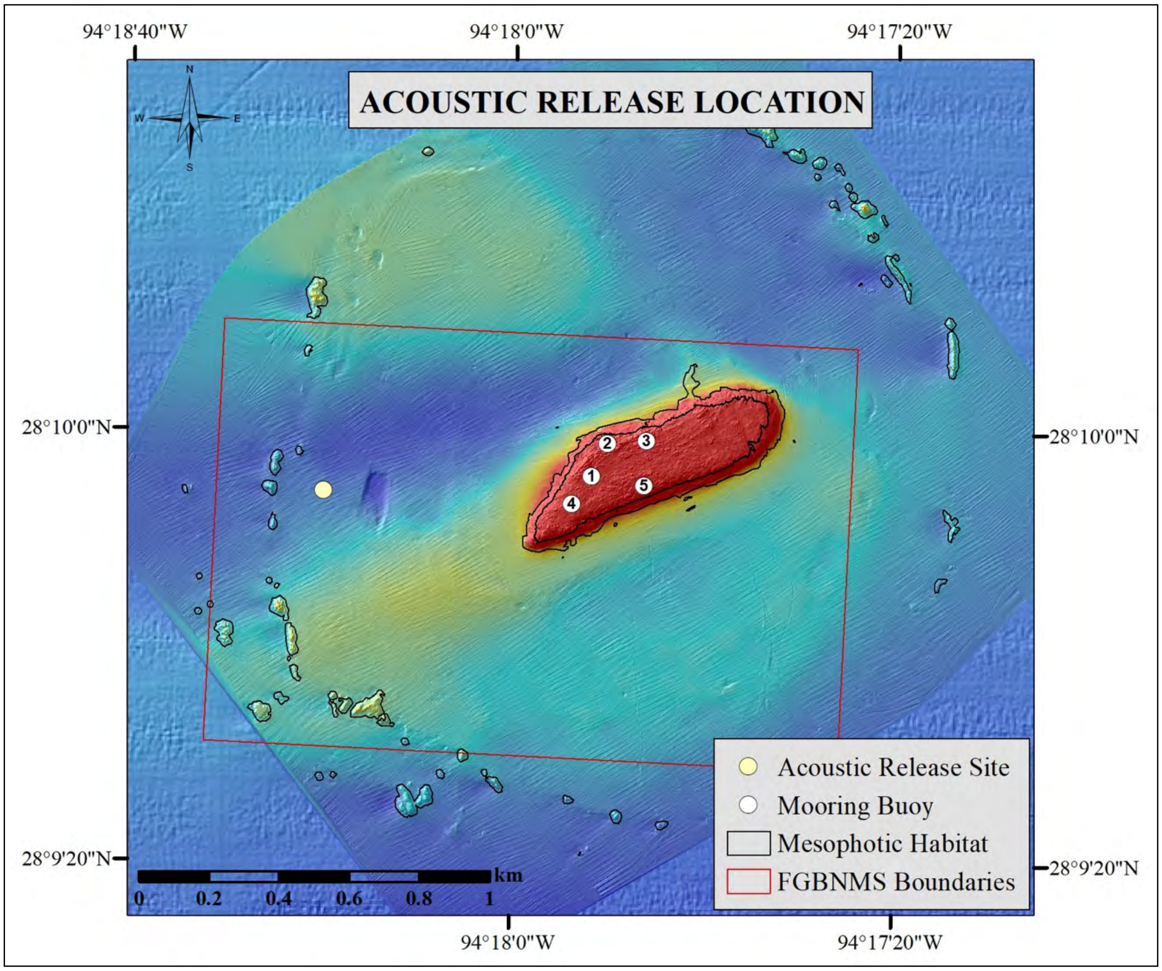

Figure 5.3. Location of mesophotic acoustic release system. The system holds continuous temperature recording instruments at 44 m and 54 m. Image: NOAA

Water samples for nutrient and seawater carbonate chemistry parameters were collected each quarter from 2015–2018. Samples were collected using a sampling carousel equipped with a Sea-Bird® Electronics 19plus V2 CTD and six OceanTest® Corporation 2.5 liter Niskin bottles, with bottles activated at specific depths (Figure 5.4). When this instrument was not available due to maintenance or operational issues, samples were collected using a manually triggered, handheld Niskin bottle, lowered on a measured line. Each quarter, three nutrient samples, with one replicate for each depth, were collected near the seafloor (approximately 20 m depth), midwater (10 m depth) and near the surface (1 m depth). Ocean carbonate samples were collected at identical depth intervals, with one replicate collected with the surface (1 m) sample and no replicates at mid-water and near the seafloor.

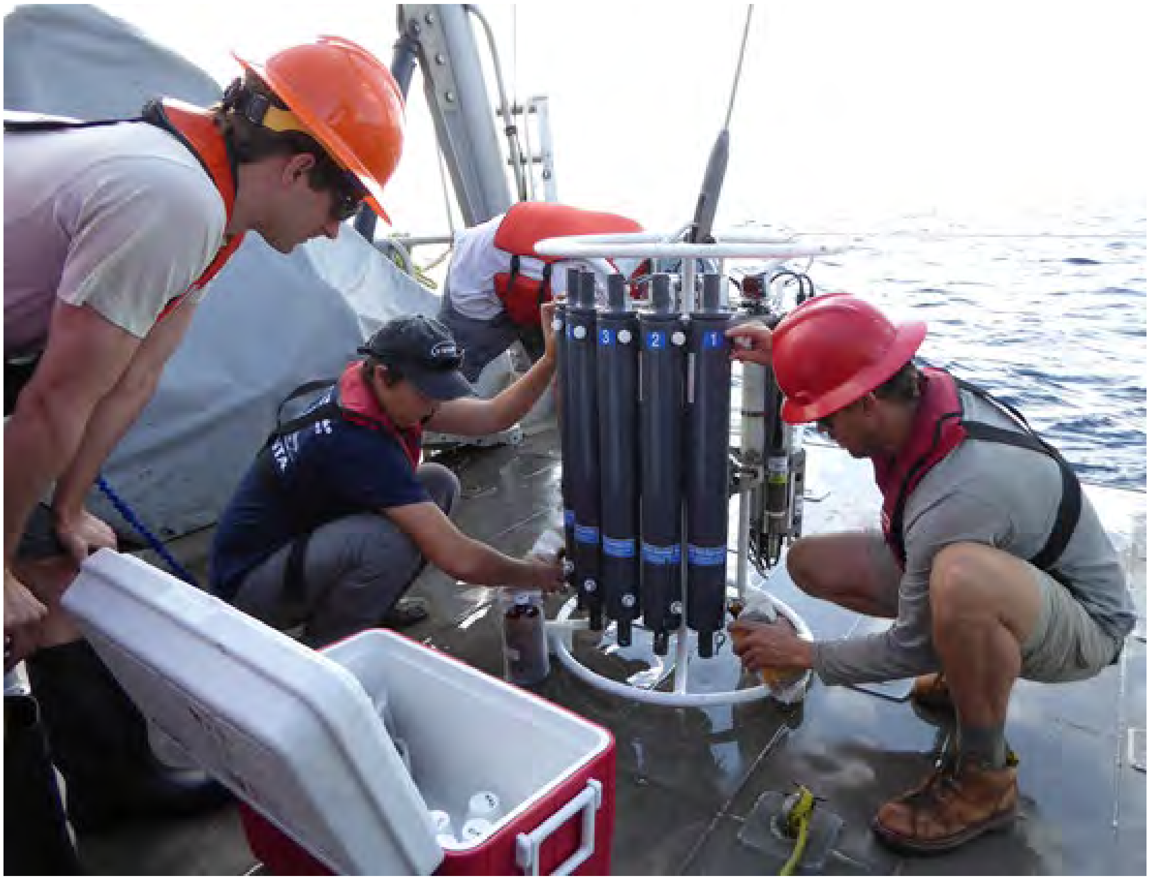

Figure 5.4. Carousel used to collect water samples and vertical profiles. Photo: G.P. Schmahl/NOAA

Once samples were collected, subsamples were transferred as follows: chlorophyll-*a* subsamples were transferred to 1000 ml brown glass containers with no preservatives; reactive soluble phosphorous subsamples were placed in 250 ml white plastic bottles with no preservatives; and ammonia, nitrate, nitrite, and total nitrogen subsamples were transferred to 1000 ml white plastic bottles and preserved with sulfuric acid. Within minutes of sampling, labeled sample containers were stored on ice at 4°C, and a chain of custody was initiated for processing at an EPA-certified laboratory. The samples were transported and delivered to A&B Laboratories in Houston, TX within 24 hours of collection.

Water samples for seawater carbonate chemistry measurements were collected following methods requested by the Carbon Cycle Laboratory (CCL) at Texas A&M University – Corpus Christi (TAMU-CC). Samples were collected in ground neck borsilicate glass bottles. Bottles were filled using a 30 cm plastic tube connected to the filler valve of the Niskin bottle. Bottles were rinsed three times using the sample water, filled carefully to reduce bubble formation, and overflowed by at least 200 ml. A total of100 µl of saturated $HgCl_2$ was added to each bottle, which was then capped. The stopper was sealed with Apiezon® grease and secured with a rubber band. The bottles were then inverted repeatedly to ensure homogeneous distribution of $HgCl_2$. Samples were stored at 4°C and sent to CCL at TAMU-CC, in Corpus Christi, TX. Each sample was analyzed for pH, alkalinity, dissolved inorganic carbon (DIC), saturation state with respect to aragonite ($\Omega_{aragonite}$) following methods in Hu et al. (2018), and pCO_2 was calculated using pH and DIC as the input variables in the MATLAB program developed by Van Heuven et al. (2011).

Periodically, 2 ml of water were subsampled into serum vials and crimp sealed for stable isotope analysis of DIC ($\delta^{13}C$).

Water column profiles were collected quarterly in conjunction with water samples, when possible. When the handheld Niskin system was used to take water samples, no profile data were collected. A Sea-Bird® Electronics 19plus V2 CTD recorded temperature, salinity, pH (on NBS scale), turbidity, fluorescence, and dissolved oxygen (DO) every ¼ second during the column profiles. Following an initial soaking period, data were recorded on the down cast phase of each deployment, while the CTD was lowered to the seafloor at a rate <1 m/sec. Table 5.1 details the instruments used to collect each parameter and Figure 5.5 provides turbidity standards.

Table 5.1. Sensors on the SBE 19plus V2 CTD.

Sensor	Parameter Measured
SBE-18	pH
SBE-43	DO
WET Labs ECO-FLNTUrtd	Fluorescence and turbidity

Figure 5.5. Turbidity standards. Image: Lake Superior Streams 2000

Data Processing

Tropical weather system tracks, sea surface temperature (SST), significant wave height, and degree heating weeks (DHWs) were obtained from external sources and processed.

While each tropical weather system varies extensively in reach and impacts, the following assumptions were made to focus the selection of storm systems to examine in this report. The average storm has a radius of 3° latitude (Merrill 1984) and, following reasoning in Lugo-Fernández & Gravois (2010) and DeBose et al. (2012), storms that passed within 200 km of Stetson Bank had the potential to impact the bank. Type, track, and maximum wind speed of hurricanes and tropical storms that passed within 200 km of Stetson Bank were obtained from NOAA's National Hurricane Center (NOAA National Hurricane Center 2020, updated monthly) for 2015–2018. Storm types were classified using the Saffir-Simpson scale.

SST was obtained from NOAA's Coral Reef Watch Program on a daily basis for 1993–2018 at 5 km resolution (NOAA Coral Reef Watch 2020a).

Salinity, wave height (WVHT), and average wave period data were obtained from the National Data Buoy Center (NDBC) Station 42019, located 107 km west-southwest of Stetson Bank, in a water depth of 82.3 m (Figure 5.6). Data were collected hourly and averaged daily. Anomaly calculations were conducted by subtracting each daily value from the daily average value for all years. Average wave period was converted to wavelength using the deep water wave-relation equation (Dean & Dalrymple 1991), where L_O=wavelength (m) and T=wave period (sec):

$$L_o = \frac{9.8}{2\pi}T^2$$

Figure 5.6. Location of NDBC 42019 and river systems examined in relation to Stetson Bank. Image: NOAA

DHW data were obtained from NOAA's Coral Reef Watch Program from 1993–2018 at 5 km resolution (NOAA Coral Reef Watch 2020b). These data provide a measurement of the accumulated thermal stress based on sea surface temperatures. One DHW is equal to one week of SSTs at least 1^{o}C above the expected summertime maximum (Wellington et al. 2001).

Major Texas and Louisiana River basins draining into the western and northwestern Gulf of Mexico with available discharge data from United States Geological Survey (USGS) were selected (Table 5.2). Discharge, in ft^3/s, of the lower Atchafalaya River USGS station number 07381600, Brazos River USGS station number 08116650, Colorado River USGS station number 08162500, Neches River USGS station number 08041000, Nueces River USGS station number 08211500, Mississippi River USGS station number 07374525, Sabine River USGS station number 08030500, and Trinity River USGS station number 08067000, were obtained from USGS National Water Information System (USGS 2018). Texas Rivers (Brazos, Colorado, Neches, Nueces, Sabine, and Trinity) were summed for analysis. A historical average of data from the previous 10 years (2006–2015) was used for anomaly calculations.

Table 5.2. Major Texas and Louisiana River basins draining into the western and northwestern Gulf of Mexico with discharge data. Source: *Kammerer 1987, ŧTWDB 2019

River	River Length (miles)	Total Drainage Basin Area (square miles)	Annual Discharge (acre-feet/year)
Atchafalaya*	1,420	951,000	41,990,145
Mississippi*	2,340	1,150,000	429,313,000
Brazosŧ	840	45,573	6,074,000
Coloradoŧ	865	42,318	1,904,000
Nechesŧ	476	9,937	4,323,000
Nuecesŧ	315	16,700	539,700
Sabineŧ	360	9,756	5,864,000
Trinityŧ	550	17,913	5,727,000

The diffuse attenuation coefficient for downwelling irradiance at 490 nm (Kd490) in m^{-1} was obtained from the Moderate Resolution Imaging Spectroradiometer aboard NASA's Earth Observing System Aqua satellite, using NASA's KD2M algorithm from 2003–2016 (NASA 2017). From 2017–2018, Kd490 was obtained from the NOAA VIIRS satellite from NOAA's Center for Satellite Applications & Research and the CoastWatch program (NOAA CoastWatch 2020). This coefficient indicates light (at the specified wavelength) attenuation through the water column and is directly related to water clarity and the presence of particles in the water column. Higher coefficients mean shallower attenuation depths and lower water clarity. Data were obtained in 2 km resolution on a weekly basis, resulting in 52 data points per year. A historical average of data from the previous 10 years (2006–2015) was used for anomaly calculations.

Temperature data from SeaBird® Electronics and HOBO® loggers at each station were averaged by day. For SST and temperature at 24 m, a historical average of data from the previous 10 years (2006–2015) was used for anomaly calculations. Salinity from the SeaBird® Electronics instrument was also averaged by day and compared to a historical average of nine years (2010–2018). Turbidity from the SeaBird® Electronics instrument was also averaged by day and compared to a historical average of four years (2015–2018). For temperature and depth comparisons, a four-year average was used for all stations (2015–2018).

Chlorophyll-*a* and nutrient analysis results were processed quarterly by A&B Laboratory in Houston, TX, and the results were compiled. Stable carbon isotope samples were analyzed at Skidaway Institute of Oceanography Stable Isotope Laboratory following methods outlined in Wang et al. (2018), and results were provided to TAMU-CC CCL. The remaining ocean carbonate analyses were performed by TAMU-CC CCL following methods outlined by Hu et al. (2018). Results were compiled into annual reports.

Statistical Analysis

Historical trends in daily SST (1993–2018) and daily temperature at 24 m (2003–2018) were tested for monotonic trends using the seasonal Mann-Kendall trend test. The seasonal Mann-Kendall trend test evaluated daily changes among years over time, accounting for serial correlation in repeating seasonal patterns. Tests were performed using a Microsoft Windows® DOS executable program developed by USGS for water resource data (Hipel & McLeod 1994, Helsel & Hirsch 2002, Helsel et al. 2005).

Results

Tropical Weather Systems

Three tropical weather systems were documented within 200 km of Stetson Bank between 2015 and 2018 (Table 5.3 and Figure 5.7). All were rated as tropical storms; two occurred in June (67%) and one in August (33%).

Table 5.3. Tropical weather systems that passed within 200 km of Stetson Bank between 2015 and 2018.

Name	Date	Max. Saffir-Simpson Scale within 200km of Stetson Bank	Max. Wind Speed within 200 km of Stetson Bank (mph)	Passed within 200 km of NDBC 42019
Bill	Jun 2015	Tropical storm	55	Yes
Cindy	Jun 2017	Tropical storm	45	No
Harvey	Aug 2017	Tropical storm	45	Yes

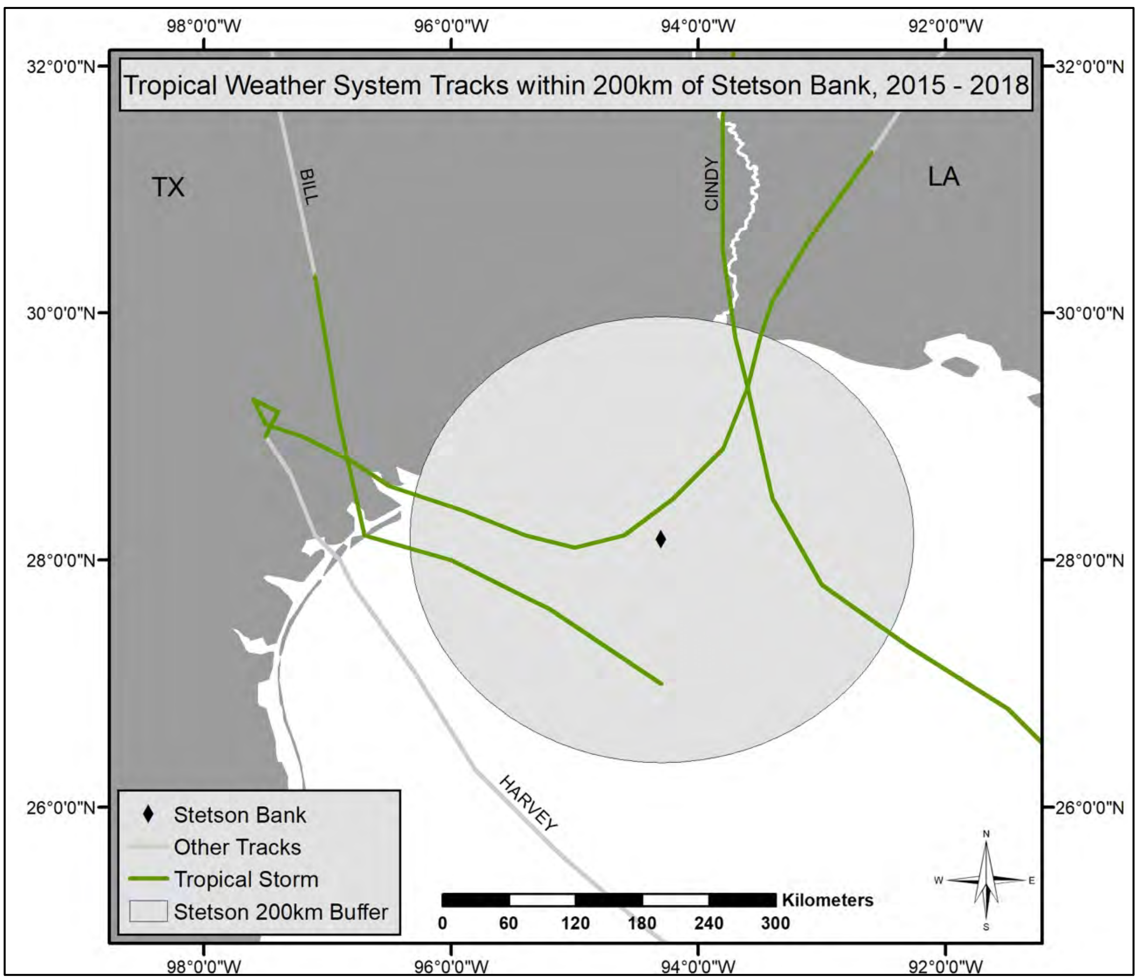

Figure 5.7. Map of tropical weather systems that passed within 200 km of Stetson Bank between 2015 and 2018. Color denotes storm classification based on the Saffir-Simpson scale. Image: NOAA

Wave Impact

Wavelength is indicative of wave impact at depth, where a wavelength of >40 m has the potential energy to impact the crest of Stetson Bank at 20 m. Maximum daily wavelength data indicated that every year there was sufficient wave energy to impact the bank crest, with the maximum wave length recorded in 2018 (104.80 m) and the greatest mean wavelength recorded in 2017 (36.11 m) (Figure 5.8).

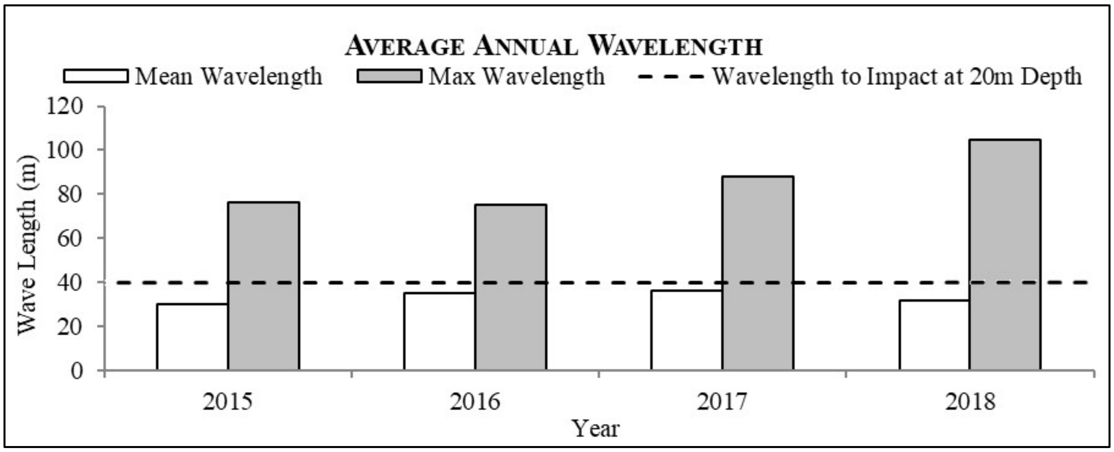

Figure 5.8. Average annual wavelength from NDBC Station 42019.

Temperature

All years in this study period experienced DHWs, with the exception of 2018 (Figure 5.9). DHWs ≥ 4 have resulted in ecologically significant bleaching, and DHWs ≥ 8 have resulted in significant coral mortality (Eakin et al. 2010, Heron et al. 2016). The maximum number of DHWs observed was 6.37 in 2016, followed by 3.15 in 2015. However, no coral bleaching was observed or reported by divers at Stetson Bank between 2015 and 2018.

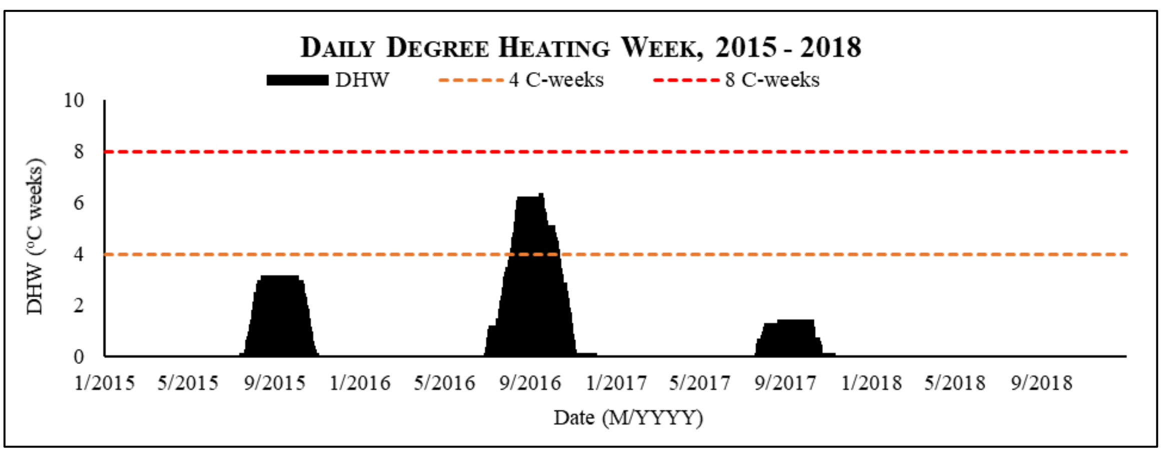

Figure 5.9. Daily degree heating weeks, 2015–2018. Orange line denotes DHW where ecologically significant bleaching is possible and red line denotes DHW where significant coral mortality is possible.

SST was generally higher than average throughout the study period, with SST above 30°C observed in July and August of 2015 and 2017, but not in 2018 (Figure 5.10). In 2015–2018, mean SST maximum anomalies were above average each year, with the maximum anomaly found in 2018 (+2.75°C higher than the average daily temperature). The minimum anomaly was below average only in 2017 (-1.98°C lower than average daily temperature). Temperatures at 24 m were higher than average throughout the study period (Figure 5.11 and Appendix 17). However, temperatures above 30°C were recorded only in September 2016. Similar to SST, maximum anomalies were above average every year, with the maximum anomaly in 2017 (+3.15°C). No years were below the average minimum anomaly, with the minimum anomaly occurring in 2016 (-2.75°C).

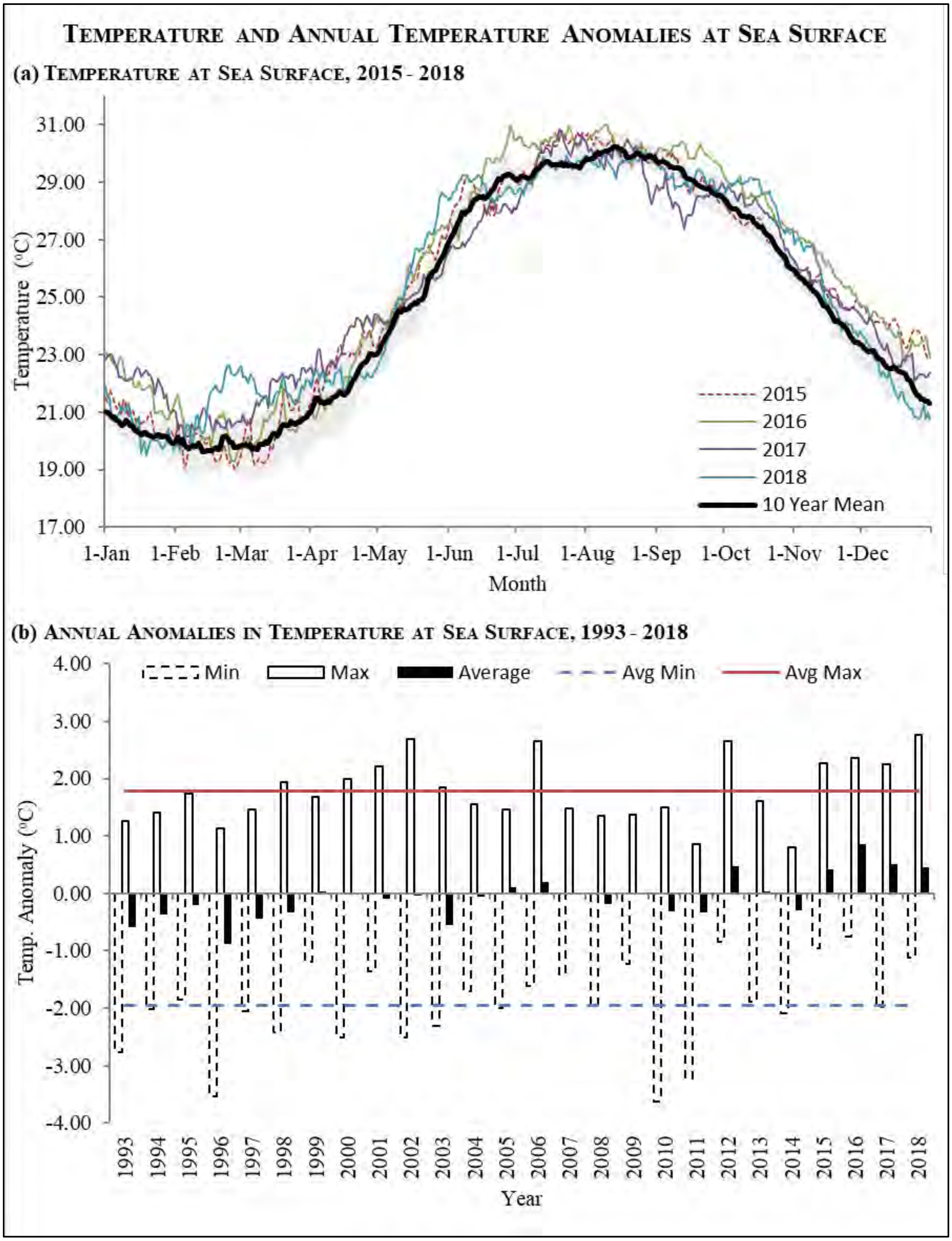

Figure 5.10. Temperature and annual temperature anomalies at sea surface. (a) Temperature at sea surface, 2015–2018. Ten-year mean is black with standard deviation shaded. (b) Annual anomalies in temperature at sea surface, 1993–2018.

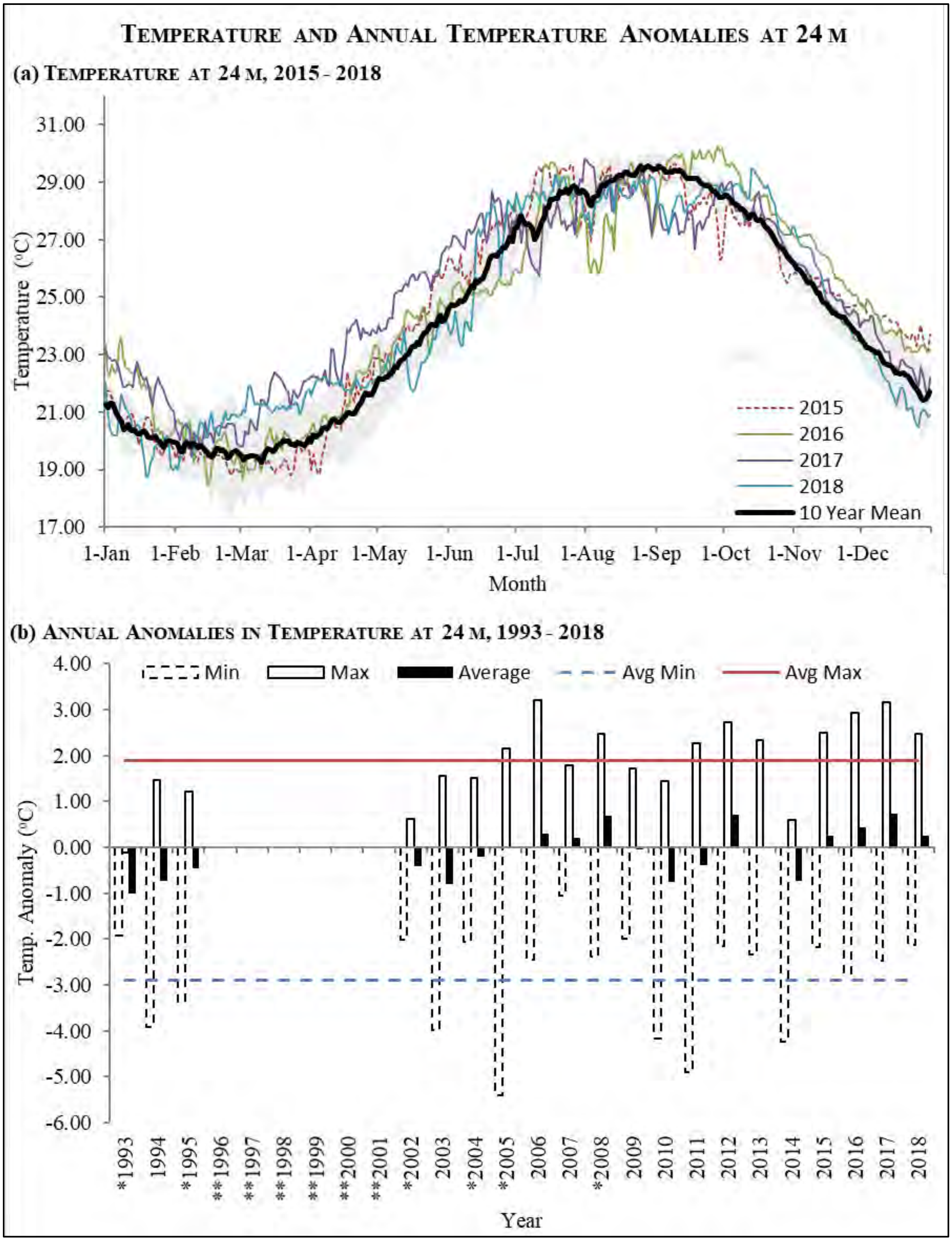

Figure 5.11. Temperature and annual temperature anomalies at 24 m. (a) Temperature at 24 m, 2015–2018. Ten-year mean is black with standard deviation shaded. (b) Annual anomalies in temperature at 24 m, 1993–2018. Years with a single asterisk (*) denote incomplete data and years with double asterisks (**) denote no data.

Temperature at 30 m and 40 m stations varied seasonally and temporally (Figure 5.12 and Appendix 18 and 19). Temperatures above 30°C were documented at 30 m in September of

2016. The two lowest recorded temperatures occurred on February 16th, when values of 18.06°C and 17.97°C were documented at 30 m and 40 m, respectively.

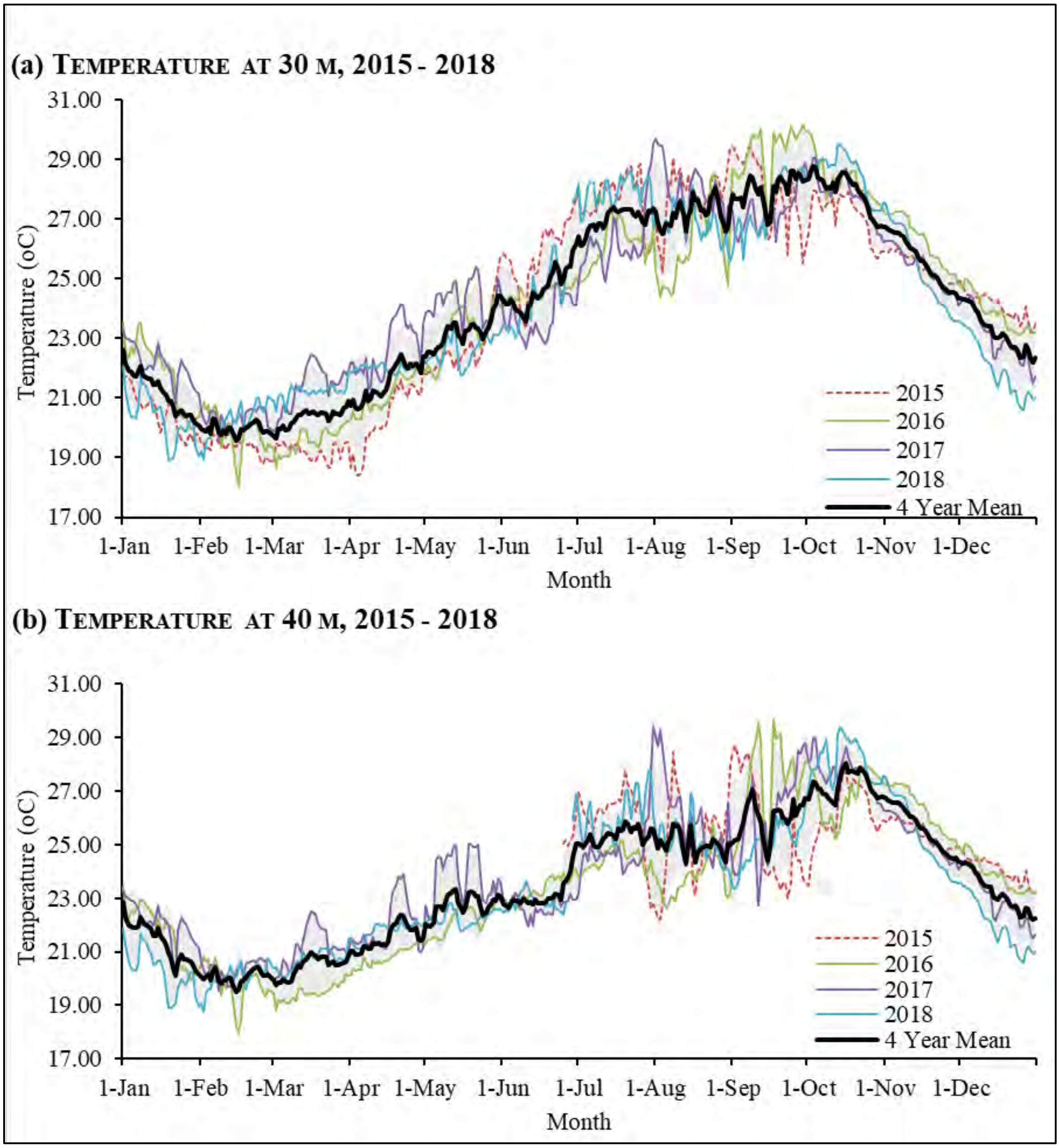

Figure 5.12. Temperature at (a) 30 m, 2015–2018, and (b) 40 m, 2015–2018. Four-year mean is black with standard deviation shaded.

Temperature decreased with depth, with the greatest differences among depths occurring from May through October (Figure 5.13). When averaged over the year, temperature at 24 m was 0.76°C cooler than SST, temperature at 30 m was 0.53°C cooler than 24 m, and temperature at 40 m was 0.69°C cooler than 30 m.

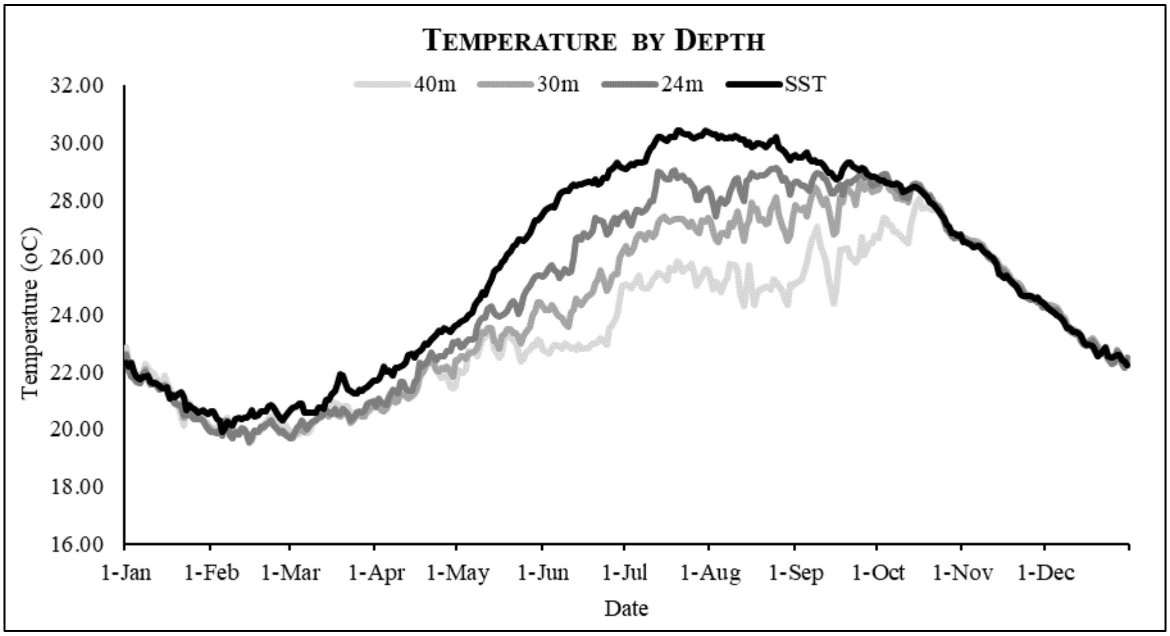

Figure 5.13. Temperature by depth.

Salinity

Salinity was only measured at 24 m (Appendix 20). Mean data demonstrate lower salinity, with greater variation, from late March through mid-August. Salinity was lower than average during this time frame in 2015 and 2016 and higher than average in 2017 and 2018 (Figure 5.14). In 2015–2018, mean salinity anomalies were above average only in 2016 (-2.54 psu lower than average daily salinity).

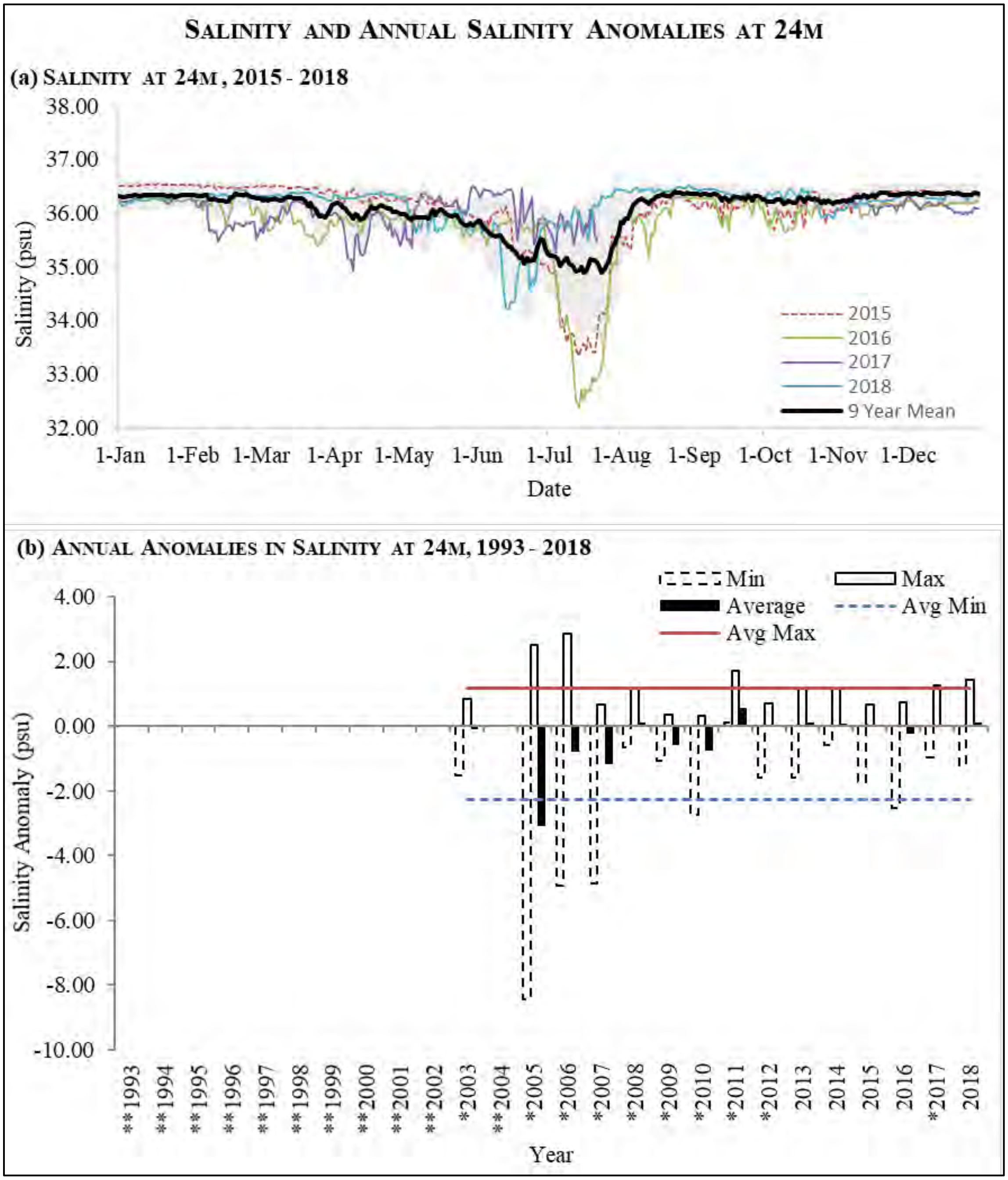

Figure 5.14. Salinity and annual salinity anomalies at 24 m. (a) Salinity at 24 m, 2015–2018. Nine-year mean is black with standard deviation shaded. (b) Annual anomalies in salinity at 24 m, 1993–2018. Years with a single asterisk (*) denote incomplete data and years with double asterisks (**) denote no data.

Turbidity

Turbidity was only measured at 24 m (Appendix 21). Turbidity was near zero for the majority of the study period. However, isolated peaks occurred throughout the year, with no seasonal trend. The highest turbidity values were recorded on January 1, 2017 and April 13, 2017, where turbidity reached 14.73 ntu and 11.09 ntu, respectively. The highest maximum anomaly was observed in 2017 (Figure 5.15).

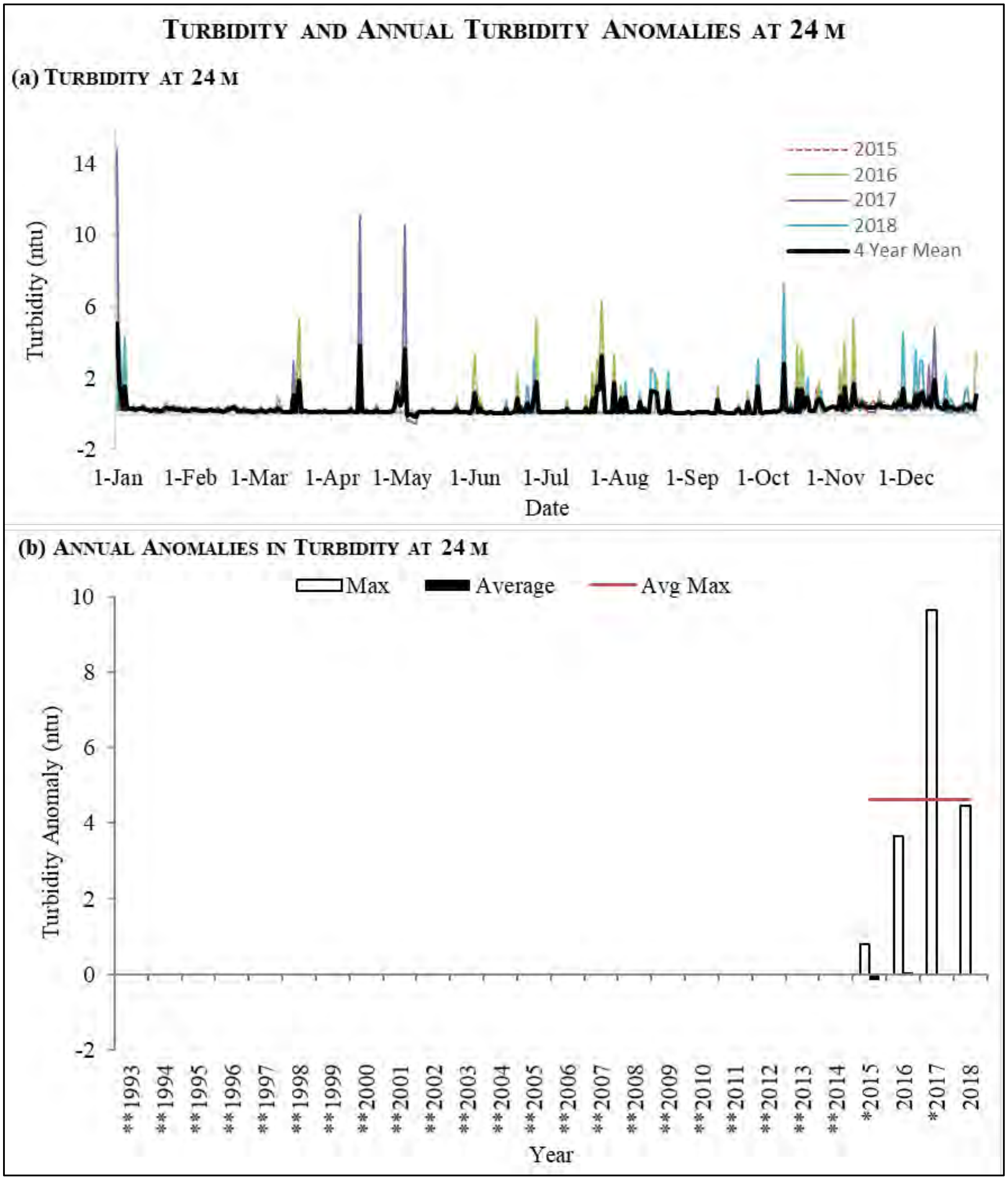

Figure 5.15. Turbidity and annual turbidity anomalies at 24 m. (a) Turbidity at 24 m, 2015–2018. Four-year mean is black. (b) Annual anomalies in turbidity at 24 m, 2015–2018. Years with a single asterisk (*) denote incomplete data and years with double asterisks (**) denote no data.

River Discharge

Anomalously high river discharge must meet with ocean currents in order to convey coastal water offshore toward Stetson Bank. However, river discharge anomalies were considered important and were examined independently of currents during this study period. From 2015–2018, major Texas river discharge was above average (Figure 5.16). In 2017, the highest flow anomaly was observed on September 2nd, in association with Hurricane Harvey, which made landfall along the Texas coastline in late August 2017. For the Mississippi and Atchafalaya Rivers, average discharge peaked between April and June, followed by a gradual decline in discharge through September (Figure 5.17). Anomalies reveal above average discharge from 2015–2018, except in 2017. In all river systems, annual discharge anomalies indicate cyclic higher and lower discharge years, where 2015–2018 was generally higher than average.

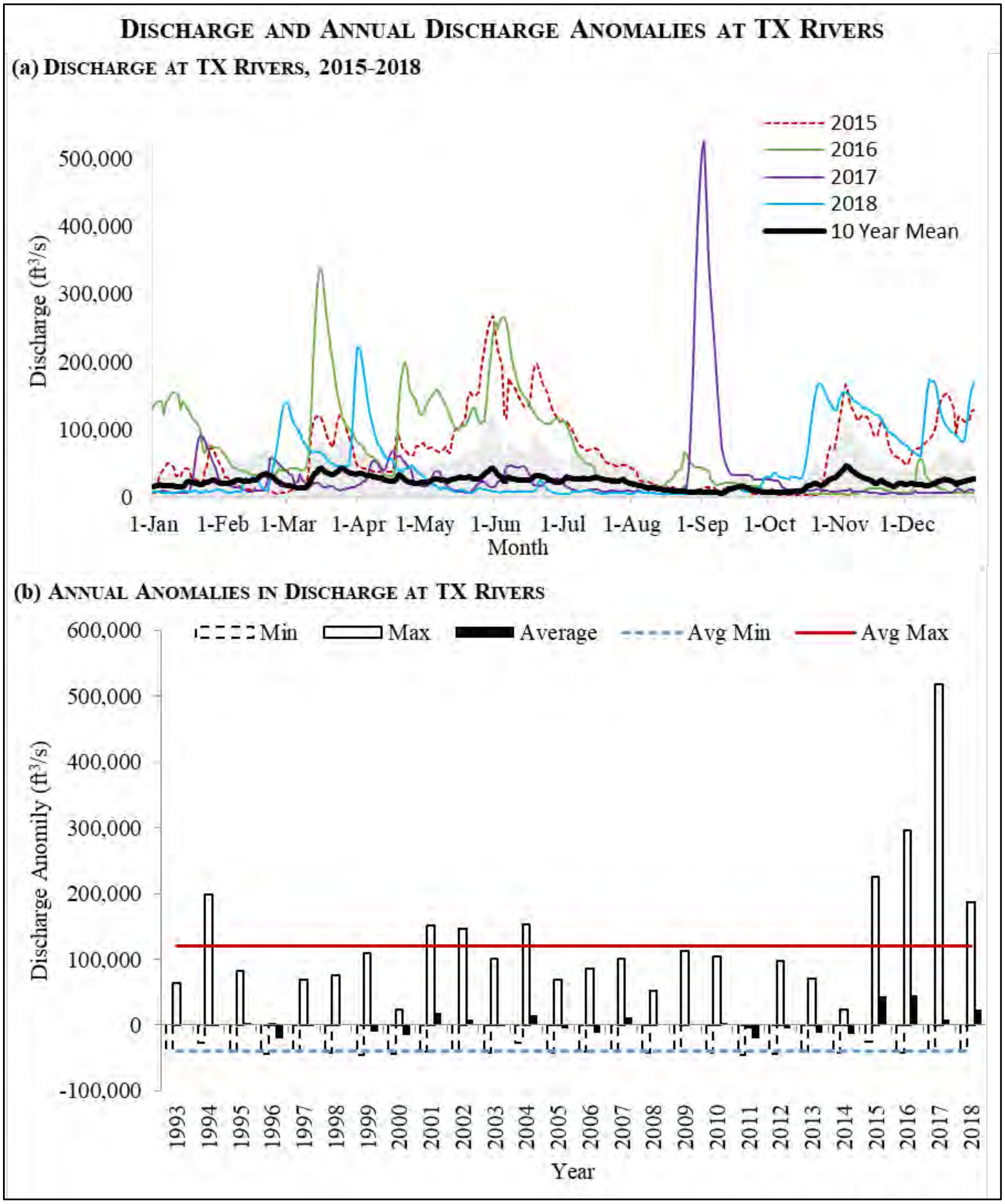

Figure 5.16. (a) Discharge at TX rivers, 2015–2018. Ten-year mean is black with standard deviation shaded. (b) Annual anomalies in discharge at TX rivers, 1993–2018.

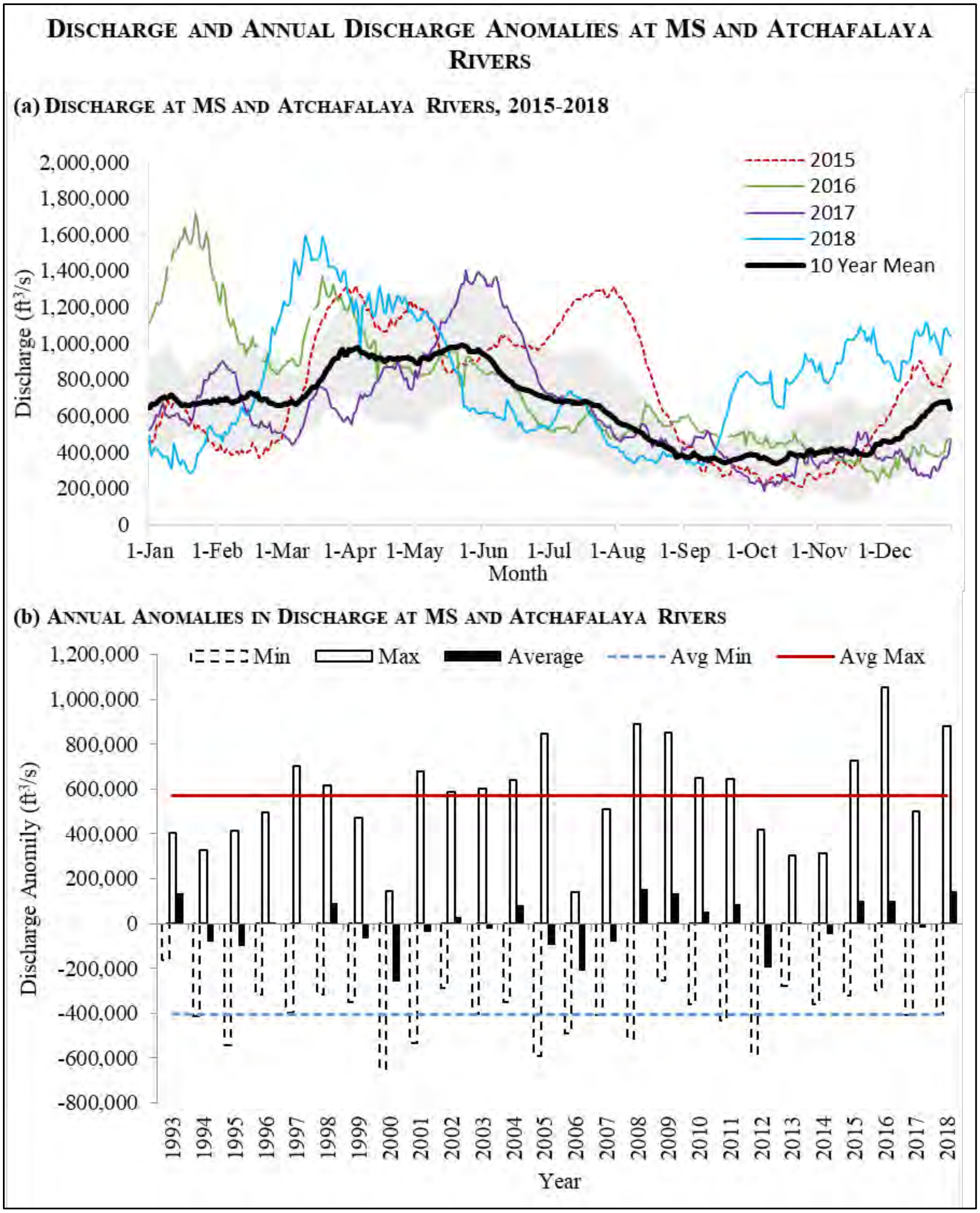

Figure 5.17. (a) Discharge at Mississippi and Atchafalaya Rivers, 2015–2018. Ten-year mean is black with standard deviation shaded. (b) Annual anomalies in discharge at Mississippi and Atchafalaya Rivers, 1993–2018.

Diffuse Attenuation

Kd490 indicated that surface water clarity was lowest between November and March, and greatest between July and October from 2015–2018 (Figure 5.18). All years had higher than average maximum anomalies, with the highest maximum anomaly in 2017 (0.07 m^{-1}).

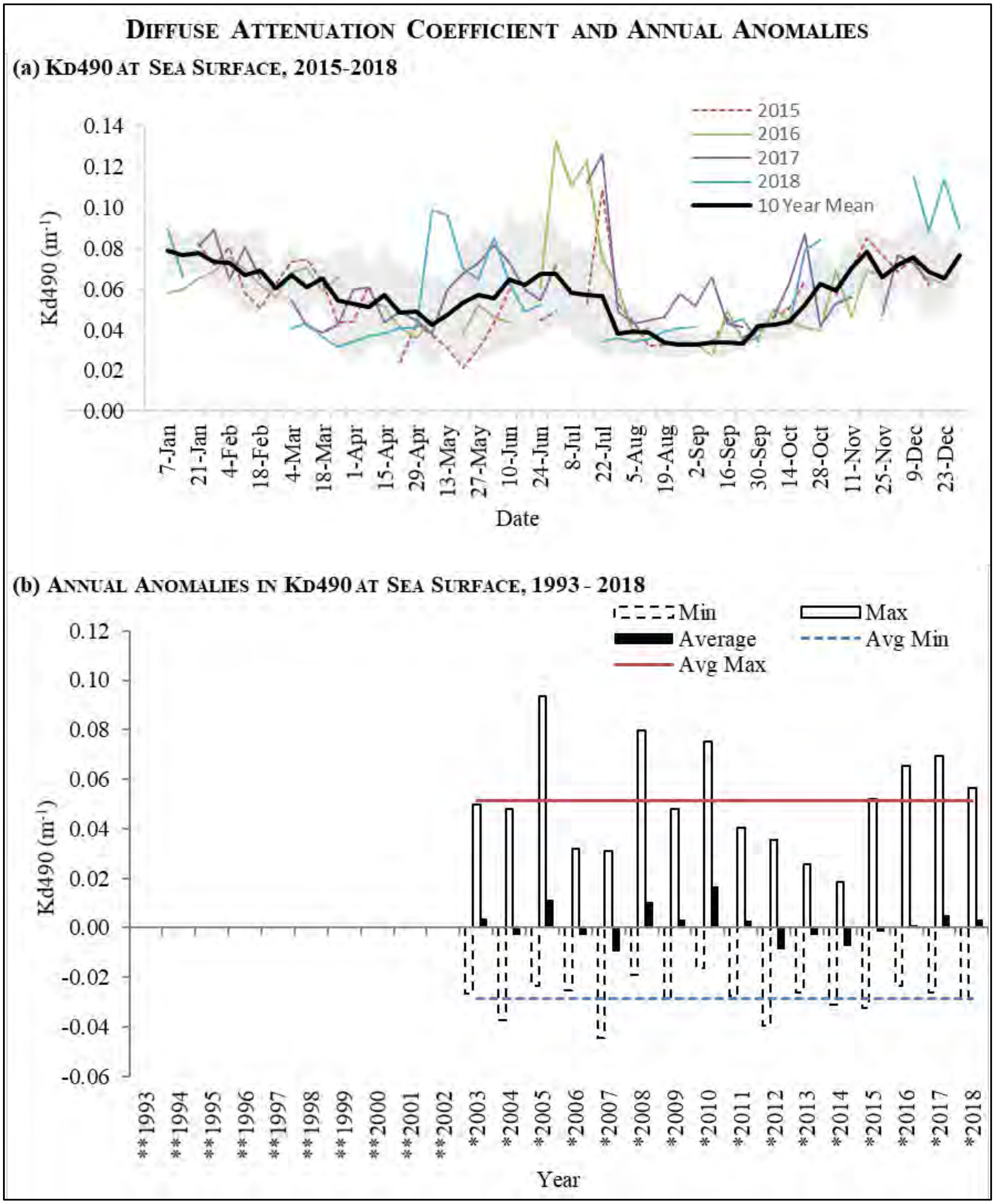

Figure 5.18. Diffuse attenuation coefficient and annual anomalies. (a) Kd490 at sea surface, 2015–2018. Ten-year mean is black with standard deviation shaded. (b) Annual anomalies in Kd490 at sea surface, 1993–2018. Years with single asterisks (*) denote incomplete data and years with double asterisks (**) denote no data.

Water Column Profiles (Physical Parameters, Nutrients, and Carbonate Chemistry)

Samples were collected on a quarterly basis, with approximately four sampling trips per year (Table 5.4).

Table 5.4. Water column profile, nutrient sample, and carbon sample dates. Temp. = temperature, Sal.= salinity, Turb.= turbidity, Fluor.= fluorescence, DO = dissolved oxygen, DIC = dissolved inorganic carbon, and pCO_2 = partial pressure of carbon dioxide.

Date	Profile	Nutrient Samples	Carbon Samples
Feb 2015	Temp., Sal.	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
May 2015	Temp., Sal.	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Sep 2015	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	No data
Oct 2015	Temp., Sal., pH, Turb., Fluor., DO	No data	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Nov 2015	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Feb 2016	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2, $\delta^{13}C$
May 2016	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Aug 2016	Temp., Sal., pH, Turb., Fluor.	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Nov 2016	Temp., Sal., pH, Turb., Fluor.	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Feb 2017	Temp., Sal., pH, Turb., Fluor.	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2, $\delta^{13}C$
May 2017	Temp., Sal., pH, Turb., Fluor.	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Aug 2017	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2, $\delta^{13}C$
Oct 2017	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2
Apr 2018	No data	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen (Handheld Niskin)	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2 (Handheld Niskin)
Aug 2018	Temp., Sal., pH, Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2, $\delta^{13}C$
Oct 2018	Temp., Sal., Turb., Fluor., DO	Ammonia, Chlorophyll-a, Nitrate, Nitrite, Phosphorous, Nitrogen	pH, Alkalinity, DIC, $\Omega_{aragonite}$, pCO_2, $\delta^{13}C$

Physical water column profile parameters are presented in Figure 5.19 (Appendix 22–27). Temperature profiles displayed a seasonal trend; August was generally the warmest month and February was the coolest. Typically, the water column was uniform, with small variations (~1°C). However, in May 2016 and August 2018, the water column was stratified, with ~2°C difference between the surface and 20 m. In May 2016, warmer than average surface water was observed. In August 2018, cooler than average water was observed at 20 m.

Salinity profiles did not exhibit seasonal trends. Typically, the water column remained uniform, with small variations (<0.5 psu). However, May and August 2016 profiles revealed lower than average salinity at the surface, which increased by ~2 psu with depth. Similarly, in September 2015, lower than average salinity was observed at the surface and increased with depth, but the variation was smaller (~1 psu).

No seasonal trends were observed in DO. Profiles varied around the average oceanic DO of 4.5 ml/L. In October 2017, a large variation was observed from the surface to 5 m, after which DO stabilized near the average. Higher DO values were observed throughout the water column in February 2016 and August 2018.

No seasonal trends in pH profiles were found. Average oceanic water pH is 8.2, but can range several decimal points depending on localized conditions. Typically, pH was uniform throughout the water column. However, in February 2017, pH decreased with depth. In October 2017, pH increased from the surface to 4 m, but were average throughout remaining depths.

No seasonal trends were observed in turbidity. Small negative readings are typical of the ECO-NTU turbidity meter and are characteristic of clear, open ocean water that is generally nutrient-deficient. Increased turbidity was found from the surface to 2 m in 2015–2016. While values were still low and indicative of clear, open ocean water, increased turbidity (<1 ntu) was found throughout the water column throughout 2017–2018.

Fluorescence information is directly related to the amount of photosynthetic pigment concentration or chlorophyll, and thereby phytoplankton, in the water column. No seasonal trends were found and fluorescence was stable through the water column. However, in October 2018, high fluorescence was observed from the surface to 4 m, but fluorescence values were average through the remainder of the water column.

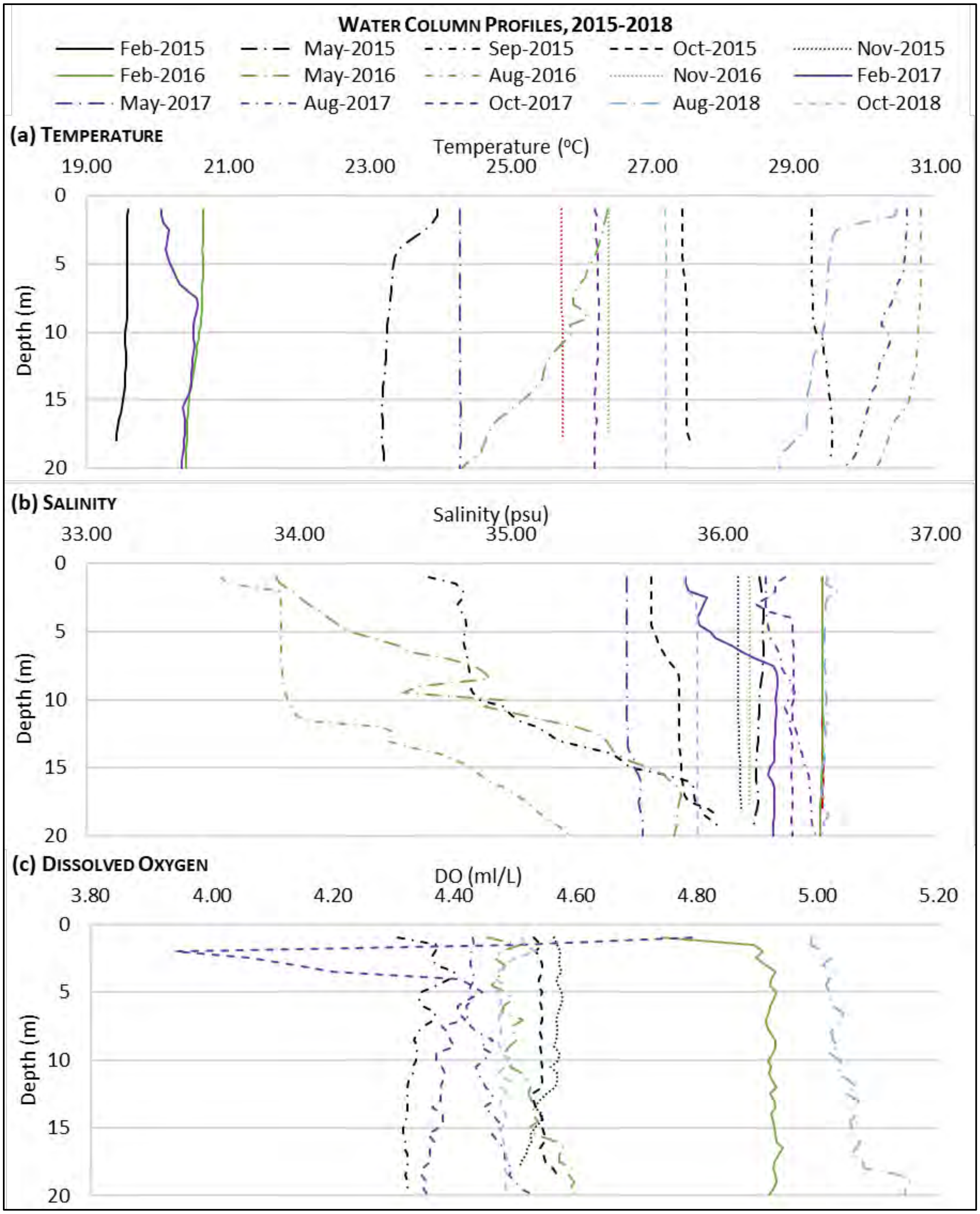

Figure 5.19. Water column profiles, 2015–2018: (a) temperature, (b) salinity, (c) dissolved oxygen, (e) pH, (d) turbidity, and (f) fluorescence. Years are grouped by color and months are groups by line style.

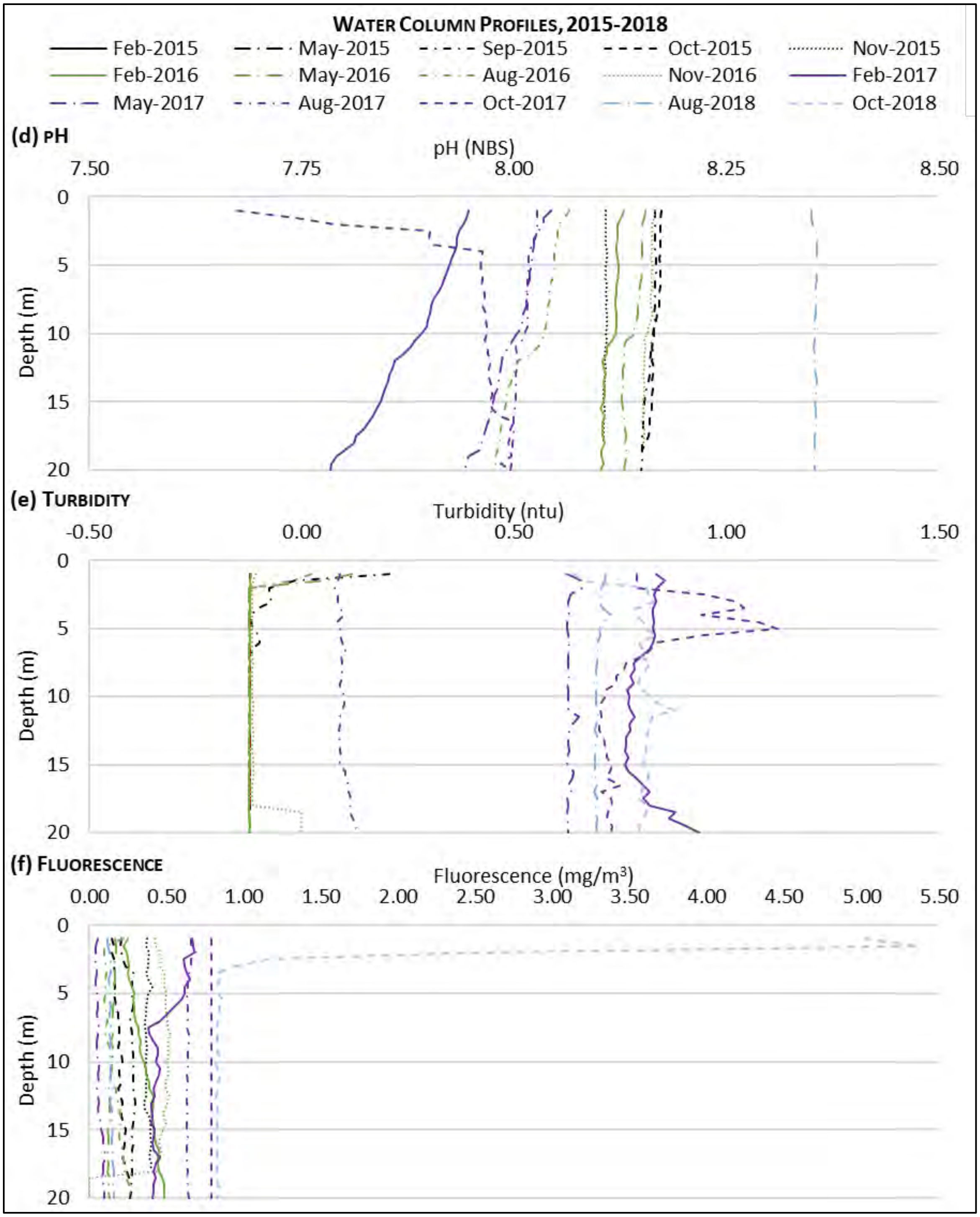

Figure 5.19. Continued

Nutrient samples were below detectable limits for all parameters throughout the study period (Appendix 28), which is indicative of oligotrophic oceanic water.

Ocean carbonate chemistry (pH, $\Omega_{aragonite}$, and pCO_2) showed seasonal cycles (Figure 5.20 and Appendix 29). Among all years, the lowest pH values were recorded in August and the highest were recorded in February. The lowest $\Omega_{aragonite}$ values were observed in the spring, from

February to May, but $\Omega_{aragonite}$ suggested the seawater was well-buffered across all survey times. The lowest pCO_2 value, when the air-sea pCO_2 gradient was greatest, was observed in February for all years sampled. These seasonal variations indicate thermal control on the carbonate systems in this region (Hu et al. 2018).

The water column was nearly uniform in seawater carbonate chemistry, with only small variations. However, alkalinity and DIC were stratified in both May and August 2016, where values increased with depth.

Measurements of $\delta^{13}C$ were uniform through the water column in all samples except in May 2016. May 2016 δC^{13} was comparatively depleted and stratified and also increased with depth compared to other samples.

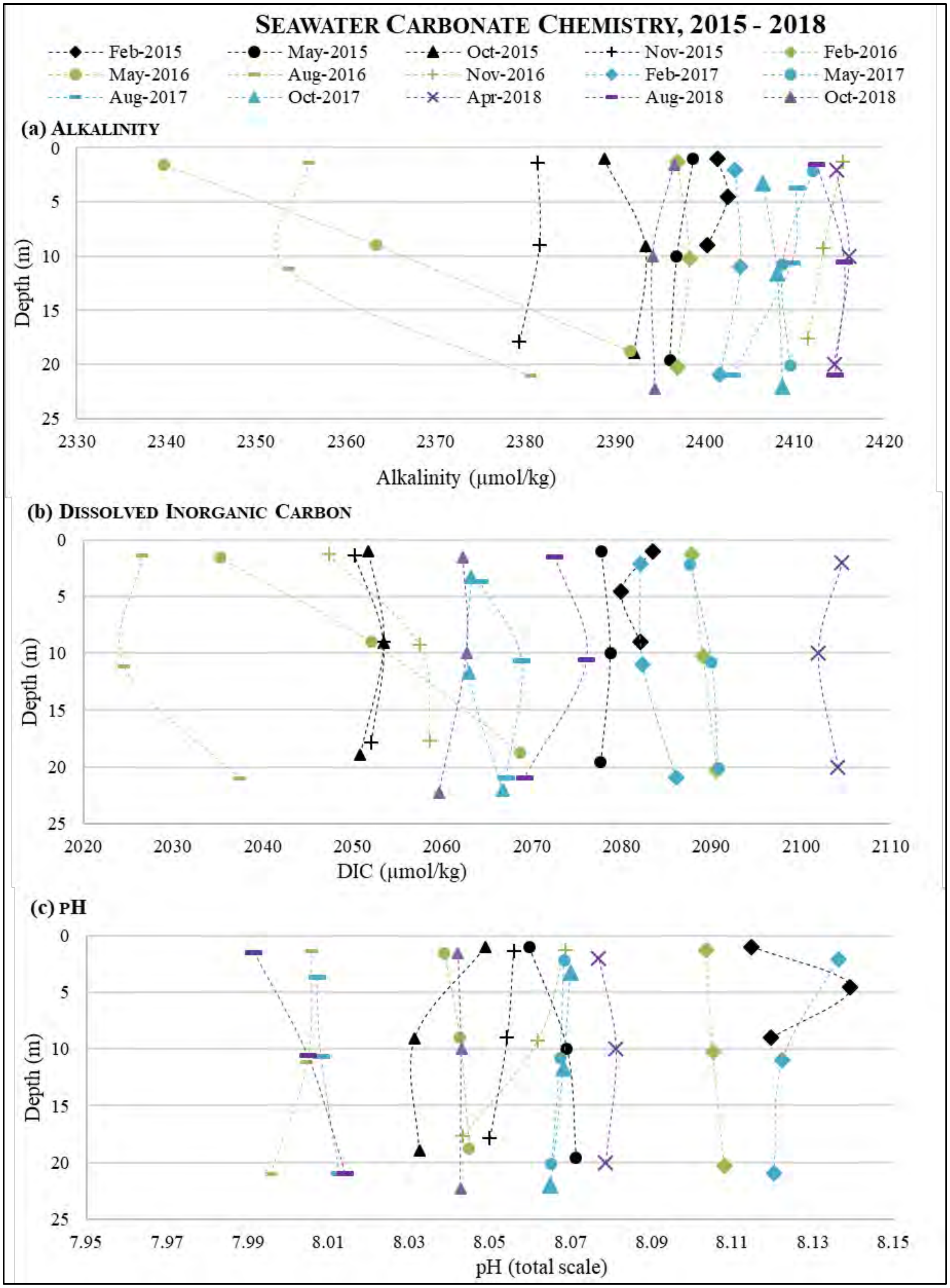

Figure 5.20. Ocean carbonate, 2015–2018: (a) alkalinity, (b) dissolved inorganic carbon, (c) pH, (d) aragonite, (e) partial pressure of CO_2, and (f) $\delta^{13}C$.

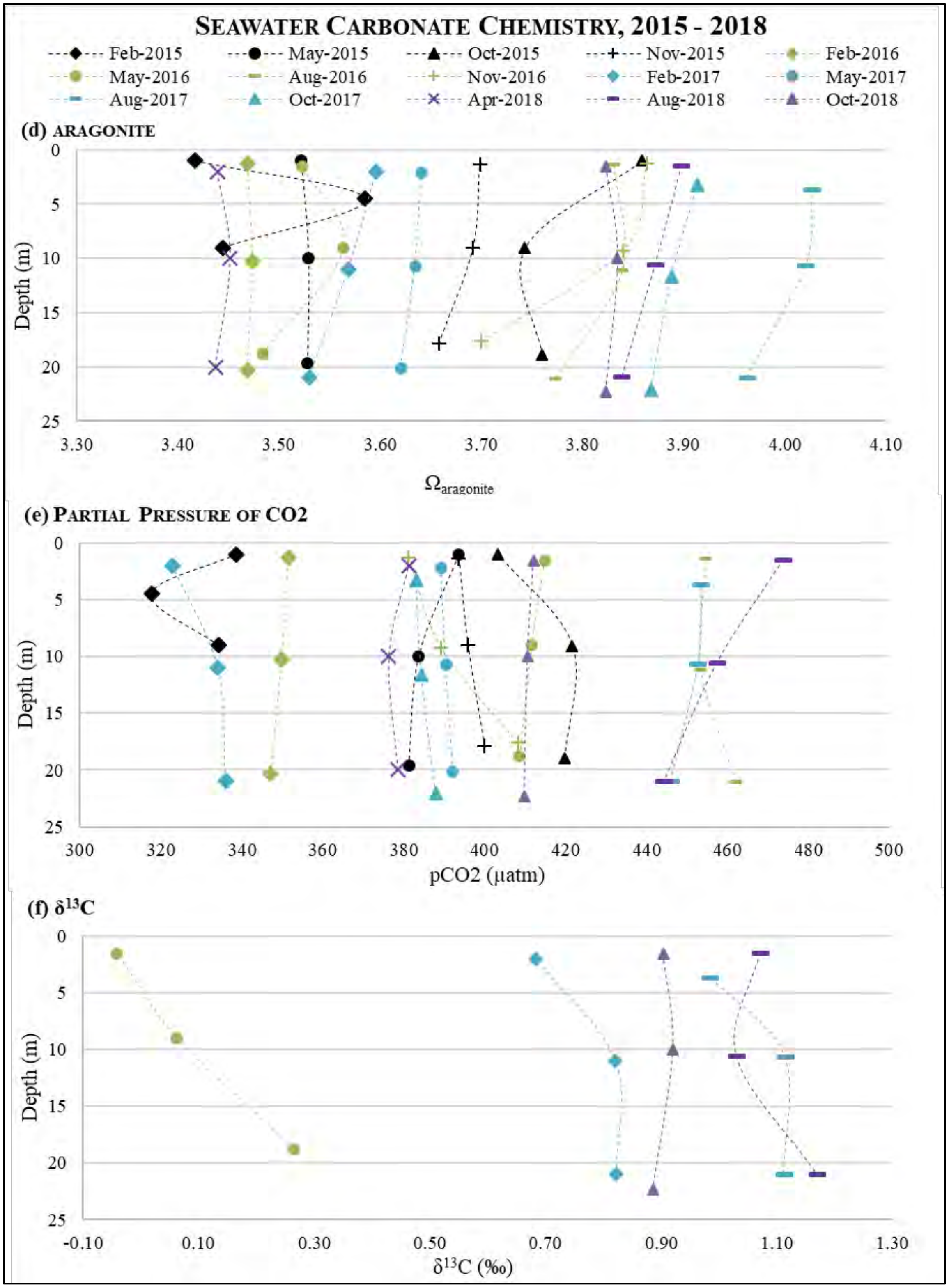

Figure 5.20. Continued

Historical Trends

From 1993–2018, >4 DHWs were observed in 2005, 2010, and 2016 (Figure 5.21).

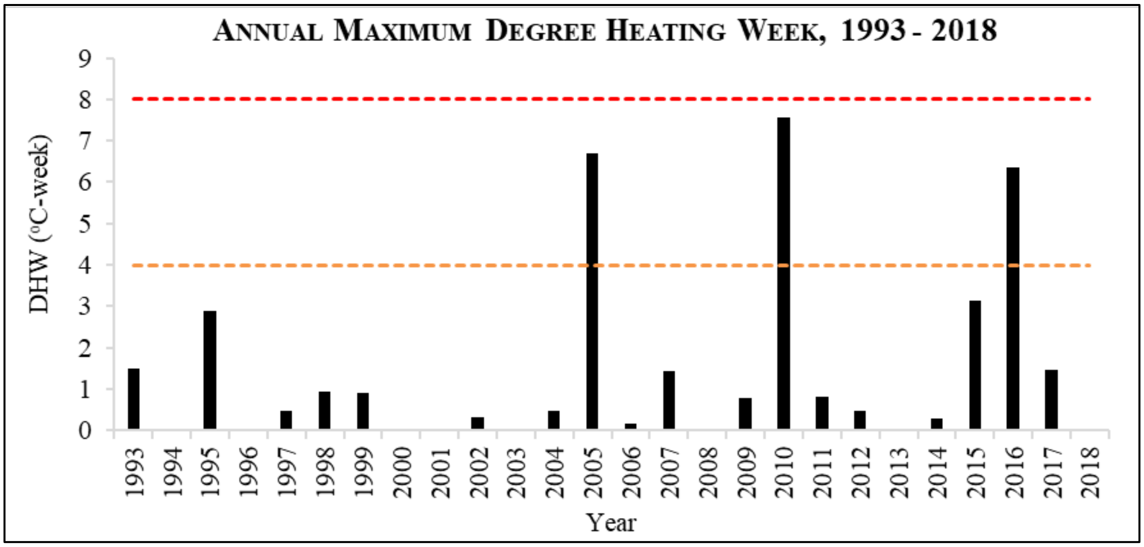

Figure 5.21. Annual maximum degree heating weeks, 1993–2018. Data are provided for the 5 km area surrounding Stetson Bank (28.125N, -94.275W).

Over the 26 year dataset, a significant increasing trend in SST was found from 1993–2018 (τ=0.278, p-value=0.002). However, a similar trend was not found in temperature at 24 m from 2003–2018.

Discussion

Changes in the benthic community have been documented following compounding anomalous oceanographic conditions (Nuttall et al. 2020) (Table 5.5). In 2010, the greatest number of stressors were recorded, including DHWs beyond the threshold known to cause ecologically significant changes. Also during that year, extreme low temperature and salinity anomalies were documented on the bank crest, along with high diffuse attenuation anomalies. In both 2005 and 2016, multiple anomalous conditions were recorded; however, coral bleaching was only documented in 2005.

Table 5.5. Summary of oceanographic events at Stetson Bank. "ND" indicates no data and "X" indicates a year with the listed impact. Years when no events were documented or limited data were available are represented with a dash (-). Data from 1993–2014 are from Nuttall et al. 2020.

Year	Tropical Weather Activity	> 4 DHW	> Avg. High Temp. Anomaly @ 24m	< Avg. Low Temp. Anomaly @ 24m	< Avg. Low Sal. Anomaly @ 24m	> Avg. High Kd490 Anomaly @ Surface	> Avg. High Turbidity Anomaly @ 24m	Total
1993					ND	ND	ND	-
1994				X	ND	ND	ND	1
1995	X			X	ND	ND	ND	2
1996			ND	ND	ND	ND	ND	-
1997			ND	ND	ND	ND	ND	-
1998			ND	ND	ND	ND	ND	-
1999			ND	ND	ND	ND	ND	-

Year	Tropical Weather Activity	> 4 DHW	> Avg. High Temp. Anomaly @ 24m	< Avg. Low Temp. Anomaly @ 24m	< Avg. Low Sal. Anomaly @ 24m	> Avg. High Kd490 Anomaly @ Surface	> Avg. High Turbidity Anomaly @ 24m	Total
2000			ND	ND	ND	ND	ND	-
2001	X		ND	ND	ND	ND	ND	1
2002	X				ND	ND	ND	1
2003	X			X	ND		ND	2
2004	X				ND		ND	1
2005	X	X	X	X	X	X	ND	6
2006			X		X		ND	2
2007	X				X		ND	2
2008	X		X			X	ND	3
2009							ND	0
2010		X		X	X	X	ND	4
2011			X	X			ND	2
2012			X				ND	1
2013			X				ND	1
2014				X			ND	1
2015	X		X			X		3
2016		X	X		X	X		4
2017	X		X			X	X	4
2018			X			X		2

Water temperature both at the sea surface and at the bank crest was above the 10-year average from 2015–2018, with 2016 exhibiting maximum DHWs exceeding the threshold known to cause ecologically significant changes. However, no coral bleaching was documented in this study or reported by recreational divers at Stetson Bank in 2016. In May and August of 2016, the water column was distinctly stratified according to multiple parameters (salinity, alkalinity, DIC, and $\delta^{13}C$), indicating the potential presence of water masses of terrestrial origin.

Typically, the water column over Stetson Bank can be considered oceanic: salinity ~35 psu, low organic nutrient levels, average pCO_2 close to the atmospheric levels, carbonate saturation state favorable for calcifying organisms, and minimal terrestrial input. However, acute impacts from shore-based runoff are observed, primarily between April and August. Coastal runoff can impose short-term changes to the water column at Stetson Bank via anomalous discharge from rivers systems. However, local current conditions at the time of the high flow event are critical in determining the extent of coastal runoff impacts given Stetson Bank's location ~130 km offshore, on the mid-shelf. While both large and small river discharge can significantly influence the water surrounding Stetson Bank, modeling suggests discharge volume plays a critical role in the magnitude of water reaching the bank (Kealoha et al. 2020). During this study period, the Mississippi and Atchafalaya Rivers experienced higher than average discharge and higher than average maximum discharge anomalies in all years except 2017. Similarly, Texas rivers experienced higher than average discharge and higher than average maximum discharge anomalies in all years. However, minimum salinity on the bank crest was only lower than average in 2016, likely due to the prevailing current regimes.

Overall, 2016 varied from historical conditions at Stetson Bank, with increased anomalous river discharge, decreased salinity, and decreased $\delta^{13}C$ suggesting terrestrial water influence (Fry 2002). Following this event, a significant increase in macroalgae cover was documented, but no other significant changes were observed. Conversely, during the summer of 2016, the nearby coral reef of EFGB underwent a localized mass mortality event, and EFGB and WFGB coral reefs exhibited bleaching (Johnston et al. 2019a, 2019b). Unusual water masses were also documented in 2017, in which pH, DO, and turbidity were anomalous. However, salinity and $\delta^{13}C$ remained within typical ranges, suggesting no terrestrial influence. Similar to 2016, declines in macroalgae cover were documented while the rest of the benthic community remained unchanged.

Nutrients remained below detectable limits for all samples during this study period, indicating that nutrient levels remained below levels considered dangerous for marine organisms, and that the water surrounding Stetson Bank was typical of an oligotrophic open ocean setting. High levels of nutrients indicate poor water quality conditions that can impact the organisms on the bank. Ammonia, a natural byproduct of decomposition and protein metabolism (excreted as a waste by animals), can be introduced to a system through anthropogenic sources, including pollution from fertilizers and organic matter. Ammonia serves as a nitrogen source for plant growth; however, in high concentrations, it can be toxic to a variety of marine life (USEPA 1989). Nitrogen and phosphorous are naturally occurring nutrients that can also be introduced through anthropogenic sources such as pollution from fertilizers, and support the growth of algae and plants. However, persistent high levels of these nutrients fuel algal blooms that can smother other benthic organisms and deplete oxygen in the water (Anderson 2017a).

Tropical weather activity was normal during the study period, remaining near the historical annual frequency of ~50% (Lugo-Fernández & Gravois 2010, Nuttall et al. 2020). Stetson Bank, situated deep in the water column (>17 m), can be somewhat insulated from the direct physical impacts of storms; however, the fragile claystone/siltstone substrate of the bank is particularly susceptible to mechanical damage (Hickerson & Schmahl 2005). NDBC Station 42019, located 107 km to the west-southwest of Stetson Bank, recorded sufficient wavelengths to indicate wave energy reached the bank crest annually throughout this study period but no physical damage was documented.

Seasonal and spatial distribution of seawater carbonate chemistry demonstrated that seawater at Stetson Bank, despite its proximity to land, behaved similar to an open ocean setting (such as the Bermuda Atlantic Time-series Study) (Bates et al. 2012) in terms of its annual pCO_2 fluctuation and minimal terrestrial influence. Overall, data continues to indicate a thermal control on carbonate systems (carbonate saturation state and pCO_2) in this region. Surface seawater pCO_2 does not appear to significantly deviate from the atmospheric value, but appears to have a seasonal pattern in which pCO_2 is highest in late winter to early spring (February-March) and lowest in late summer (August-September). The distribution of ΔpCO_2 on an annual basis suggests that the study area had a small net air-sea CO_2 flux.

Long-term analyses show that sea surface temperatures have been significantly increasing. DHW calculations rely on sea surface temperature data, which was typically warmer than the bank crest at 17 m. The water column helps buffer temperature fluctuations, highlighting the value of monitoring temperature at depth. This thermal buffering may explain why, despite significant DHW findings in 2016, no apparent impacts to corals were observed.

While Stetson Bank is typically bathed in oceanic waters with high salinity and low nutrient levels, the water column experienced lower winter temperatures, greater salinity variations, larger turbidity fluctuations, and increased fluorescence compared to EFGB and WFGB (Johnston et al. 2016a, 2017, 2018), supporting previous findings that suggest high-latitude banks undergo variations that make them marginal environments for coral recruitment and growth. However, despite challenging environmental conditions, Stetson Bank supports a benthic community of coral and Porifera that may provide insight on resilience in a changing environment. While the warm tropical waters brought to the area from the Caribbean via the Loop Current and associated spin-off eddies combined with oligotrophic waters maintain sufficient conditions for coral and Porifera community growth and larval transport (Biggs 1992, Schmahl et al. 2008), these dynamics set the stage for the dramatic changes in the benthic community that have been observed at the bank (Coles & Jokiel 1978, Nuttall et al. 2020).

Most methods employed to collect water column information during this study period were successful, except the use of an acoustic release on instruments deployed in mesophotic habitats. All bank crest instruments were accessible by scuba divers, making collection and download straightforward. Mesophotic instruments were not accessible by scuba divers and were therefore deployed on a buoyed line attached to an anchor with an acoustic release system. When recovery was attempted in early 2016, acoustic release system diagnostics indicated that the instrument was lying on the seafloor, presumably due to buoy failure. While extensive searching of the seafloor was conducted was conducted by ROV, the instruments were not found. In 2018, a new thermistor, provided by NOAA’s Deep Sea Coral Research and Technology Program, was deployed using an ROV. This instrument was placed by the ROV at a repetitive photostation site. To further improve and expand the understanding of Stetson Bank water characteristics, a more extensive water column profiling and sampling regime is recommended, including profiles to a maximum depth 50 m and the water surrounding mesophotic habitats. This information would also help answer questions about the persistence of the nepheloid layer and how other environmental conditions may influence it.

Chapter 6
Observations, Notes, and Other Research

Introduction

Repetitive video transects were established to document general conditions at Stetson Bank during annual monitoring. While informative, these videos only provide a snapshot of conditions and can miss interesting observations of the benthic community, fish community, or water column at Stetson Bank throughout the rest of the year. Recreational divers visit Stetson Bank year round and can submit trip or observation reports to FGBNMS researchers, a tool that has proven useful over the years. In addition to recreational trips, other research cruises to Stetson Bank throughout the year documented unique or interesting observations. These observations were compiled throughout the study period.

Methods

Bank crest video transects were conducted along three permanent 100 m transects, installed at Stetson Bank in 2015. Each transect was marked using 30 cm stainless steel eyebolts drilled and epoxied into the reef at 25 m increments along the transect. Each eyebolt was labeled with a cattle tag denoting the transect number and the eyebolt position along the transect. Figure 2.4 and Figure 2.5 show transect start locations. Before recording on video, a line was laid between the eyebolts to mark the transect. Video was recorded using a Sony® Handycam® HDR-CX350 HD video camera in a Light and Motion® Stingray G2® housing. A two-meter-long plumb bob was secured to the front of the camera housing to maintain distance above the bottom. The diver swam along the transect line, following the line with the plumb bob, maintaining the camera at a 45^{o} angle to the seafloor.

Mesophotic video transects were established using latitude and longitude start and end points to create 2500 m lines in north-south and east-west orientations to enable general repeatability of the transects. During the study period, one transect was conducted along a 2500 m north-south line and two were conducted along 2500 m east-west lines (Figure 6.1). An ROV was used to follow the transect line, with the forward-facing video camera set to a 45^{o} angle to the seafloor. Annotations were recorded every five minutes during the ROV dive, documenting habitat, benthic biota, fish community, and general observations.

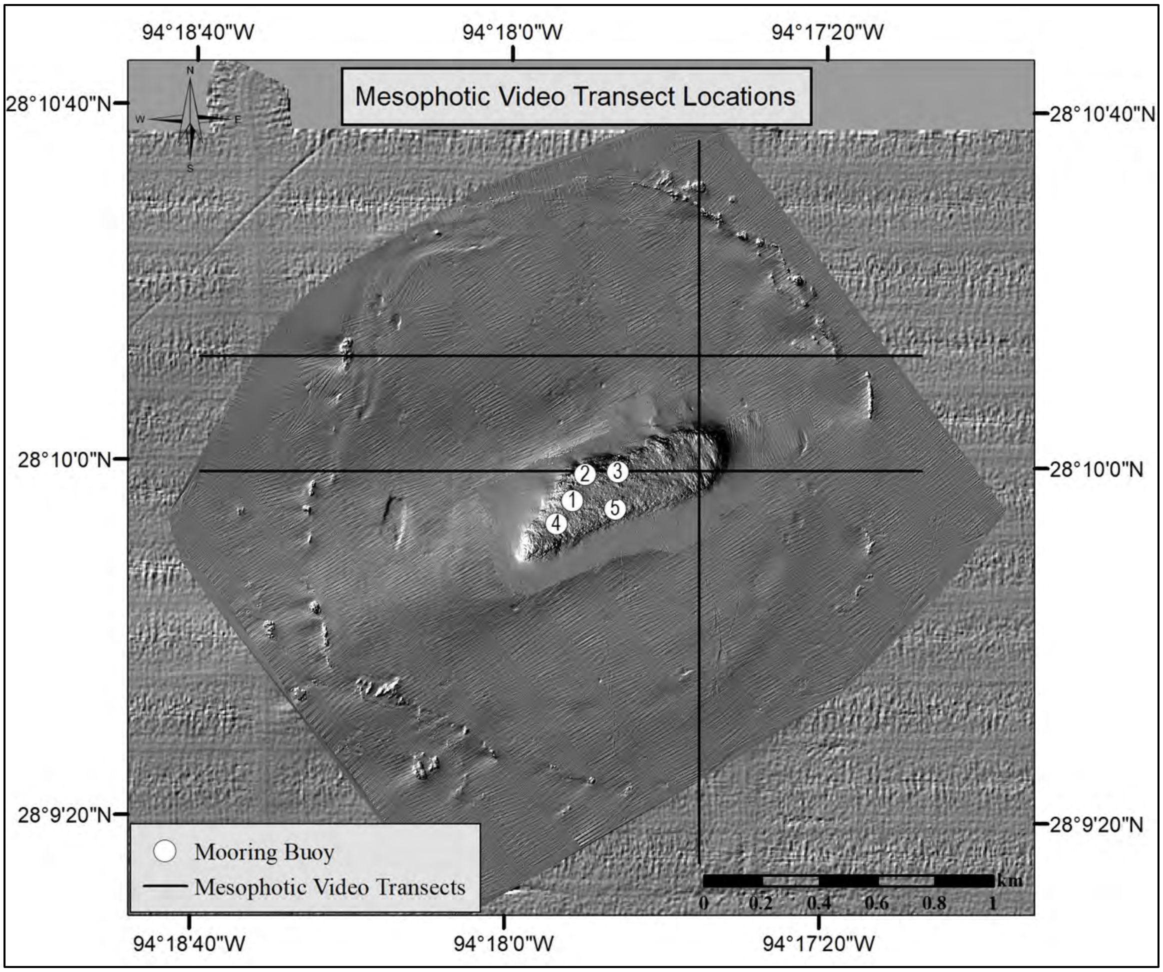

Figure 6.1. Mesophotic video transect locations. Image: NOAA

Other general observations from field work were recorded as notes for each transect or survey and included observations of biology, geology, marine debris, and operations.

Results

Bank crest video transects documented Porifera and coral in good health with no notable changes to the benthic community throughout the study period. Occasional observations of Caribbean spiny lobster (*P. argus*) and queen conch (*Lobatus gigas*) were made. Observations of marine debris, primarily monofilament line, were made; the debris was subsequently removed by scuba divers. In terms of water conditions, a thermocline was documented in 2016 and green water with abundant Atlantic sea nettles (*Chrysaora quinquecirrha*) and few warty sea wasps (*Carybdea marsupialis*) was observed in the upper water column in 2017.

Mesophotic video transects were only completed in 2015. Transects covered a variety of habitats: mesophotic patch reefs, soft bottom pits and burrows, and shallow reefs. Several previously unknown marine debris locations (trawl nets) and low-relief rubble patches with mesophotic and deep-sea corals were observed. Visibility was variable around the bank, with a nepheloid layer near the seafloor in mesophotic habitats. However, this nepheloid layer was noted to shift between morning and afternoon.

Sandbar sharks (*Carcharhinus plumbeus*) were observed annually, while manta rays (*Manta birostris* and *Manta* cf. *birostris*), loggerhead sea turtles (*Caretta caretta*), common octopus (*Octopus vulgaris*), and queen conch (*L. gigas*) were documented sporadically. Uncommon observations at Stetson Bank included the presence of studded sea stars (*Mithrodia clavigera*), unicorn filefish (*Aluterus monoceros*), reticulated cowry helmet (*Cypraecassis testiculus*), non-native regal demoiselle, and a tiger shark (*Galeocerdo cuvier*) with a metal ring entangled around its body forward of the pectoral fins (Figure 6.2).

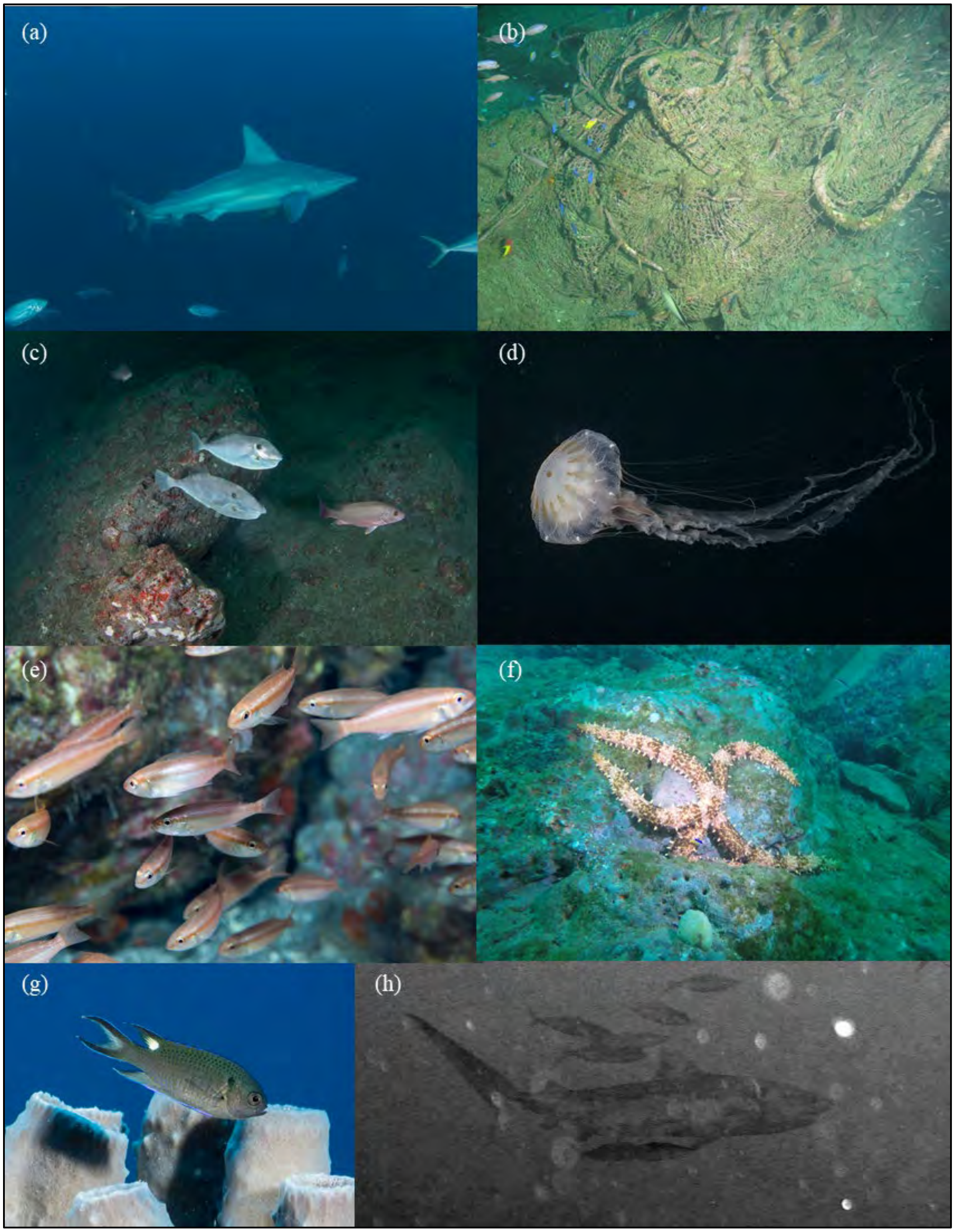

Figure 6.2. Images of interesting observations from 2015–2018. (a) Sandbar shark, Carcharhinus plumbeus, (b) trawl net debris observed in mesophotic video transects, (c) unicorn filefish, Aluterus monoceros, (d) Atlantic sea nettles, Chrysaora quinquecirrha, (e) juvenile vermilion snapper, Rhomboplites aurorubens, (f) studded sea star, Mithrodia clavigera, (g) regal demoiselle, Neopomacentrus cyanomos, and (h) tiger shark, Galeocerdo cuvier, entangled in marine debris. Photos: (a, c–g) G.P. Schmahl/NOAA, (b) UNCW-UVP/NOAA, (h) Marissa Nuttall/CPC

Other Research

1. Dr. Santiago Herrera, of Lehigh University, conducted work in the mesophotic habitats at Stetson Bank in 2017. The team collected samples of *Hypnogorgia/Muricea pendula* for a study entitled "Population connectivity of deep-water coral in the northern Gulf of Mexico," funded by the NOAA RESTORE Act Science Program.

2. Sound trap deployments, led by Dr. Jenni Stanley of Woods Hole Oceanographic Institution in collaboration with NOAA's Office of National Marine Sanctuaries, were conducted on the bank crest in 2016 and 2017.

3. Ron Eytan of Texas A&M University at Galveston collected sailfin blennies (*Emblemaria pandionis*) at Stetson Bank in 2017 for a study entitled "Genetic connectivity of blenny populations, cryptic endemism, and genetics of hybrid breakdown in coral reef fish in the Gulf of Mexico and greater Caribbean."

4. The NOAA Fisheries SEAMAP reef fish project team conducted assessments at Stetson Bank in 2017. Surveys conducted included camera array deployments, bandit reel collections, and CTD profiles. Baited camera arrays and plankton sampling continued in 2018.

5. Thirty samples of the regal demoiselle were collected from Stetson Bank and provided to Dr. Ron Eytan at Texas A&M University at Galveston for further analysis. In addition, a note on the presence of the regal demoiselle was distributed to the Coral-List listserver and observations were submitted to the USGS non-indigenous aquatic species database (https://nas.er.usgs.gov/default.aspx).

6. Ocean carbonate data from FGBNMS were published by Dr. Xinping Hu at TAMU-CC CCL (Hu et al. 2018).

7. Four lionfish removal cruises were completed (Table 6.1).

   Table 6.1. Lionfish removed during lionfish removal cruises, 2015–2018.

Cruise Date	Number Lionfish Removed at Stetson Bank
9-2015	13
9-2016	18
6-2018	83
8-2018	41

8. Historical manta ray observations at FGBNMS were published in the journal *Marine Biology* (Stewart et al. 2018).

Discussion

Additional observations from video transects and diver reports documented species sightings and unique observations that were not present in survey data. Throughout this study period, these data supported findings that no major changes in the benthic community occurred, however changes in water column conditions and unusual fish species were documented. Additionally, marine debris was documented and, when possible, removed.

In 2016, thermoclines on the bank crest were apparent in video transects, indicating the presence of cooler subsurface water that may have contributed to the lack of bleaching observations in 2016, when significant DHWs were documented. In 2017, distinct green water with increased jellyfish abundance was documented, with water column data showing variations in pH and turbidity, while salinity remained within typical ranges.

Methods to collect video transects and observations were successful on the bank crest throughout the study period. However, mesophotic transects were long and took an excessive amount of time to complete. Due to time constraints, these mesophotic transects were only completed in 2015, when additional time was budgeted for establishing the monitoring sites. A reduction in the length of these transects is suggested for future studies to increase success of data collection.

Conclusions

Stetson Bank, an uplifted claystone/siltstone feature, was added to FGBNMS in 1996 due to its unusually diverse and dense benthic and fish assemblages, marking it as a place of national significance. Annual monitoring, focused on the bank crest, has occurred at the site since 1993, with additional methods employed when time permitted. In 2015, BSEE and FGBNMS expanded monitoring at Stetson Bank to include both the historically monitored bank crest and the surrounding mesophotic habitat. This report presents results from this annual research and monitoring of the benthic and fish community and water column at Stetson Bank from 2015–2018, along with comparison to historical trends. In addition to results from annual monitoring, research from federal and state agencies and scientific institutions was summarized, representing a comprehensive summary of research activities at Stetson Bank from 2015–2018. Critical monitoring objectives were met throughout the study period. However, methodological challenges were encountered, particularly in mesophotic habitat, with modifications and resolutions suggested within each chapter.

Four benthic habitats were documented and analyzed in this report, each with significantly different, characteristic communities (high- and low-relief bank crest, coralline algae reef, and deep reef). Since 1993, the high-relief benthic community at Stetson Bank has had periods of stability and periods of significant change, with particularly large declines in coral and sponge cover after 2005 (Nuttall et al. 2020). While Porifera and macroalgae cover varied in all habitats during the recent study period, no significant changes were documented in coral cover.

Although macroalgae cover is highly dynamic and dependent upon location and season (Diaz-Pulido & Garzon-Ferreira 2002, Bruno et al. 2009, Jackson et al. 2014, Bertolino et al. 2016), a significant negative relationship has been found between macroalgae cover and density of the keystone grazer *D. antillarum*, highlighting a top-down control effect on macroalgae cover. Throughout the study period, robust populations (> 1 per m^2) of *D. antillarum* were documented at Stetson Bank. Historical data indicated a potentially cyclic pattern in *D. antillarum* density, with robust populations occurring with a slight temporal offset to high macroalgae cover.

The four distinct benthic habitats each support a diverse and variable fish community. The communities are comprised of reef-associated and pelagic species, as well as some commercially and recreationally valuable species. In most years, an inverted biomass pyramid was found, suggesting minimal detrimental environmental impacts, particularly from fishing (Friedlander & DeMartini 2002, DeMartini et al. 2008, Knowlton & Jackson 2008, Sandin et al. 2008, Singh et al. 2012). Historical data suggest a significantly increasing trend in the abundance of individuals <5 cm. Greater numbers of small fish may indicate an increase in recruitment; however, as surveys were conducted in different months each year (from late May to early July), this finding may also reflect recruitment seasonality. A large increase in <5 cm individuals was documented in 2018, when a new non-native species, the regal demoiselle, was documented in high densities. However, due to a presumed narrow thermal tolerance (based on fish in aquaria), the long-term persistence of this population at Stetson Bank is uncertain (Johansen et al. 2015).

Red lionfish, an invasive species, persisted throughout this study period. This species is of particular concern due to their invasive nature and negative impacts throughout the Caribbean (*P. volitans*) (Arias-González et al. 2011, Albins & Hixon 2013). First documented in 2011 by recreational scuba divers on the bank crest, lionfish were more frequently observed in mesophotic habitats than on the bank crest during this study period. Andradi-Brown et al. (2017) documented that lionfish inhabiting mesophotic habitat in Honduras had greater biomass and higher fecundity than those on shallower reefs, indicating that individuals using deeper habitat may disproportionately contribute to the recruitment of lionfish in shallower habitat. While lionfish were removed annually from the bank crest, it is more difficult to conduct targeted removals below recreational scuba diving limits. It is therefore possible that mesophotic lionfish may serve as a primary source population for the bank crest. While lionfish density has increased throughout this study period, increases in small fish (typically prey items for the red lionfish) and the lack of correlation to changes in the fish community suggest limited impact of lionfish on the native fish population.

Throughout this study period, Stetson Bank experienced multiple stressors annually (such as tropical storm activity, significant DHWs, anomalously high or low water temperatures, anomalously low salinity, or anomalously high diffuse attenuation). Higher than average maximum temperatures at 24 m and higher than average maximum surface turbidity were observed every year. In 2016, anomalously low salinity water of terrestrial origin was documented. In 2017, low DO, low pH, turbidity, and green surface water were documented. Despite multiple stressors, only macroalgae cover varied, while the rest of the benthic community remained stable. Similar to other coral reef ecosystems (Vinebrooke et al. 2004, Yakob & Mumby 2011, Darling et al. 2013), the benthic community at Stetson Bank can be resilient when impacted by a few stressors annually, but the synergistic effect of multiple stressor interactions can result in impaired recovery and significant community changes.

The nearby reefs of EFGB and WFGB, located approximately 30 km south of Stetson Bank, support a very different benthic community to Stetson Bank, with > 50% coral cover and less variable environmental conditions (Johnston et al. 2016a, 2017, 2018). Stetson Bank is located in a high-latitude (above 28° north), marginal environment for coral reef growth. The dynamic pattern of stressors presented in this report highlights that these high-latitude banks may not be suitable for long-term coral reef development, but may experience years of nascent coral reef growth and stable environmental conditions followed by a year of multiple stressors, leading to dramatic changes in the benthic community. However, the variable temperature regimes that corals at these locations experience are thought to increase their thermal tolerance (Oliver & Palumbi 2011), suggesting that high-latitude reefs may be potential coral refugia in the face of climate change. Additional site-specific factors, including larval dispersal, environmental conditions, and geographic location, should be considered in evaluating these communities. Climate experts suggest that the protection of high-latitude reefs, in order to reduce stressors and support resilient communities, is the best current course of action for resource managers (Beger et al. 2014).

The monitoring program at Stetson Bank represents one of the longest-running monitoring efforts of a northern latitude coral community. These historical datasets help document changes in the community, increase our understanding of community change, examine environmental interactions over time, and monitor the drivers of ecosystem change in the northern Gulf of Mexico, thereby guiding research initiatives and management decisions in the region.

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Glossary of Acronyms

BSEE – Bureau of Safety and Environmental Enforcement
CCL – Carbon Cycle Laboratory
CPCe – Coral Point Count® with Excel® extensions
CTD – conductivity, temperature, and depth
DDM – degrees and decimal minutes
DHW – degree heating week
DIC – dissolved inorganic carbon
DO – dissolved oxygen
EFGB – East Flower Garden Bank
FGBNMS – Flower Garden Banks National Marine Sanctuary
GREAT – Gulf Reef Environmental Action Team
HD – high definition
IDW – inverse distance weighting
NASA – National Aeronautics and Space Administration
NDBC – National Data Buoy Center
NMSF – National Marine Sanctuary Foundation
NOAA – National Oceanic and Atmospheric Administration
ONMS – Office of National Marine Sanctuaries
PERMANOVA – permutational multivariate analysis of variance
PERMDISP – permutational analysis of multivariate dispersions
PCO – principal component ordination
pCO_2 – partial pressure of carbon dioxide
ROV – remotely operated vehicle
SIMPER – similarity percentages
SIMPROF – similarity profile analysis
SST – sea surface temperature
TAMU-CC – Texas A&M University – Corpus Christi
TAMUG – Texas A&M University at Galveston
UNCW-UVP – University of North Carolina at Wilmington - Undersea Vehicle Program
USGS – United States Geological Survey
WFGB – West Flower Garden Bank
WVHT – wave height

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