HCNSO Student Theses and Dissertations   HCNSO Student Work

7-10-2018

Spatiotemporal Change in the Benthic Community of Southeast Florida

Nicholas P. Jones

Nova Southeastern University, nj350@nova.edu

Share Feedback About This Item

Thesis of
Nicholas P. Jones

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

July 2018

Approved:
Thesis Committee

Major Professor: Dr David Gilliam

Committee Member: Dr Joana Figueiredo

Committee Member: Dr Matthew Johnston

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Spatiotemporal Change in the Benthic Community of Southeast Florida

By

Nicholas P. Jones

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Biology

Nova Southeastern University

Date

July 2018

Acknowledgements

Table of Contents

List of Tables

List of Figures

Abstract

High-latitude reefs have been postulated as refugia, centers for resilience or the first areas to undergo re-organization under climate change. The Southeast Florida Reef Tract (SEFRT) is a high-latitude reef system (>25 °N) running parallel to the highly urbanized coastline of southeast Florida. With a benthic community comprised of a mixture of coral reef associated assemblages, the SEFRT is towards the northern limit of stony coral cover due to temperature constraints. This study analyzed spatial variations in benthic cover, spatiotemporal changes in the benthic community and the impact of spatial and temporal fluctuations in temperature on benthic cover on the SEFRT, from 2007-2016. Photographic data from two long term monitoring projects was used to calculate the percent cover of taxonomic assemblages in the benthic community. *In situ* temperature data and modelled data from HYCOM were used in combination to assess the impact of temperature fluctuations and thermal stress events. Data was split on a latitudinal gradient into six defined ecosystem regions based on biogeographic boundaries and at major port channels. These accounted for any possible range expansion and spatiotemporal variations on the SEFRT. Statistical analysis via generalized linear models (GLM) identified significant changes in the major benthic taxa, stony coral, octocoral, sponges and macroalgae. Ecosystem regions showed strong clustering by their taxonomic composition and this was in part created by temperature variation. Stony coral cover significantly declined on the SEFRT and a concomitant significant increase in macroalgae cover may create a negative feedback loop which hinders recovery. Spatiotemporal variations in benthic cover were found between ecosystem regions and thermal stress events, both hot and cold, had immediate and latent impacts on benthic cover. This has resulted in biotic homogenization on the SEFRT with a retraction of outlier regions towards the mean. Anthropogenically influenced high-latitude reefs are significantly impacted by thermal stress. As oceans continue to warm, populations expand, coastlines continue to develop and pollutants persist, the benefits of potential thermal refugia are negated.

Keywords: coral reefs, coral, macroalgae, temperature, high-latitude, thermal stress

1. Introduction

Globally, tropical reef ecosystems have changed in benthic composition over the last few decades, with a shift from scleractinian corals (hereafter referred to as stony corals) to turf, macroalgae or sponges (Hughes 1996, Schutte et al. 2010, De Goeij et al. 2013, Jackson et al. 2014, Pawlik et al. 2016). The decline in stony coral cover has been linked to changes in environmental and physical parameters, such as ocean temperature, acidification, storm prevalence and local anthropogenic stressors (Tilmant et al. 1994, Walther et al. 2002) (Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Banks et al. 2008). Functional group change has often followed coral mortality events, shifting from coral to macroalgae dominance throughout the Caribbean (Aronson and Precht 2006) and to octocoral dominance in the Florida Keys (Ruzicka et al. 2013). Concomitant changes in reef structural complexity (Alvarez-Filip et al. 2011), coral recruitment inhibition (Kuffner et al. 2006), reduction in juvenile coral growth and survival (Lirman 2001, Box and Mumby 2007) and biotic homogenization (Burman et al. 2012) can accompany these phase shifts. Species specific changes have also been noted with a significant decrease in the branching species *Acropora cervicornis* and *A. palmata* (Hughes 1994, Gardner et al. 2003) and increases in the encrusting or mounding species *Agaricia* spp*., Porites astreoides, Siderastrea siderea* and *Millepora* spp. (Gardner et al. 2003, Green et al. 2008, Toth et al. 2014). Assessing variation in the marine benthic community, in response to environmental changes, therefore requires a long term understanding of how the ecosystem is responding.

Long term monitoring projects are valuable ways of assessing temporal variation in marine benthic communities (Franklin 1989, Magurran et al. 2010). Repeated surveys can expose temporal fluctuations in benthic composition, cover, and abundance, enabling the detection of localized extinctions and revealing phase shifts within the benthic ecosystem (Gardner et al. 2003, Smol et al. 2005, Magurran et al. 2010). By surveying a spatially extensive area it is possible to understand regional fluctuations in physical parameters and benthic communities. They can then be used to identify how changes may relate to localized anthropogenic impacts, variable benthic habitats and varying degrees of impact from thermal stress events (Moyer et al. 2003, Halpern et al. 2008, Heron et al. 2016).

Climate change has consistently driven global ecological change (Walther et al. 2002, Boucek and Rehage 2014, Suchley et al. 2016) and is predicted to continue to alter ecosystems around the world (Hughes et al. 2003, Hoegh-Guldberg and Bruno 2010, Mokany et al. 2015). Elevated ocean temperatures, hurricane damage, and thermal stress events, defined as periods where temperatures rise above or fall below threshold levels found to have detrimental impacts on organisms, have caused negative changes to coral reef communities (Hughes 1996, Walther et al. 2002, Baker et al. 2008, Heron et al. 2016, Kemp et al. 2016), temperate benthic coastal communities (Garrabou et al. 2009, Vergés et al. 2014) and reef fish assemblages (Roessig et al. 2004). Extreme thermal anomalies often precede mass mortality events, causing functional changes in the benthic ecosystem (Harriott 1985, Glynn 1990, Eakin et al. 2010, Lirman et al. 2011, Ruzicka et al. 2013, Precht et al. 2016, Hughes et al. 2017) and have become more frequent in recent years (Heron et al. 2016, Hughes et al. 2017). Combined, increased water temperature and thermal stress events have caused mortality in gorgonians in the Mediterranean Sea (Cerrano et al. 2000, Linares et al. 2005), in the colonial zoanthid *Palythoa caribaeorum* in the Caribbean (Goldberg and Wilkinson 2004) and in stony corals globally (Hughes et al. 2003, Hughes et al. 2017). Conversely elevated temperatures and disturbance events are predicted to increase the global abundance of cyanobacteria (O'Neil et al. 2012) and macroalgae (Hoegh-Guldberg et al. 2007, Hoegh-Guldberg et al. 2017). Within tropical marine ecosystems thermal stress events and ocean warming have caused changes in benthic composition and coral cover, impacting ecosystem function (Bruno et al. 2007, Eakin et al. 2010, Heron et al. 2016, Kemp et al. 2016, Hughes et al. 2018). Verges et al. (2014) proposed that climate change may drive a shift in reef herbivores poleward, leading to a phase shift from coral to macroalgal dominance in tropical and sub-tropical benthic communities. Changes in the abundance and distribution of benthic species have also been predicted (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010).

One of the major drivers of change in benthic communities, are climate change related increases in ocean temperature, thus this needs to be continuously and accurately measured. *In situ* temperature loggers and satellite data are frequently used to accurately measure and subsequently assess temperature change (Manzello et al. 2007, Muller et al. 2008, Eakin et

al. 2010, Heron et al. 2016). *In situ* monitoring has the advantage of recording the temperature accurately and continuously at a specific point, however has limited spatial range. Satellite measurements allow for the collection of data over wide spatial and temporal spans (Kourafalou and Kang 2012), enabling extensive analysis of continual fluctuations in physical parameters with a high degree of accuracy (Chassignet et al. 2007, Chassignet et al. 2009). They are though, incomplete measurements limited by swath width and satellite orbit. Computer generated models provide a third option to study physical variables in the marine environment. Modelling of environmental variables integrates real-world *in situ* measurements with computer simulations creating real time global and ocean basin scale forecasts and hindcasts. The Hybrid Coordinate Ocean Model (HYCOM) is a comprehensive and widely used three-dimensional ocean prediction system, collating data assimilation techniques to forecast sea surface temperature, sea surface height, salinity, water speed and water direction (Kourafalou et al. 2009). HYCOM provides 1/25th degree resolution in the Western Atlantic and Gulf of Mexico (77.36° W to 98.00° W and from 18.09° N to 30.71° N) enabling spatiotemporal analysis of temperature change across points spaced approximately 4 km apart (Chassignet et al. 2009). Combining modelled data with *in situ* temperature increases confidence in documenting actual temperature change, which can effect growth, recruitment and mortality rates in the benthic community (Glynn 1993, Lopez-Legentil et al. 2008, Manzello et al. 2015).

Aside from climate change a range of local stressors also cause coral reef community structure and ecosystem function to change (Hughes et al. 2003, Harborne et al. 2017). As coastal populations have continued to expand (Small and Nicholls 2003, Neumann et al. 2015), local anthropogenic stressors, such as overfishing (Hughes et al. 2003), sedimentation (Rogers 1990, Storlazzi et al. 2015), nutrient enrichment and pollution have continued to increase (Hoegh-Guldberg et al. 2017). Multiple studies have found decreasing water quality, sedimentation, pollution, fishing, boating activity, coastal development and dredging significantly affect benthic composition and species health (Pastorok and Bilyard 1985, Rogers 1990, D'Angelo and Wiedenmann 2014, Lamb et al. 2015, Stubler et al. 2015, Jones et al. 2016, Zaneveld et al. 2016, Duckworth et al. 2017). Physical actions, such as dredging and ship grounding (Jaap et al. 2006, Walker et al. 2012)

3

can remove large sections of benthic habitat and lead to smothering of coral by sediment (Jones et al. 2016), while chemical pollutants can negatively impact coral survival and growth (Loya and Rinkevich 1980, Shafir et al. 2007, Zaneveld et al. 2016). Therefore, these factors must be taken into consideration when assessing the spatiotemporal causes for benthic community composition variation.

As climate change strengthens, high-latitude reef systems are becoming increasingly valuable study areas to predict the future of coral reefs worldwide. Under global warming, range expansion poleward has been recorded for zooxanthellate corals in Florida, Japan, Australia and the Mediterranean (Precht and Aronson 2004, Yamano et al. 2011, Baird et al. 2012, Serrano et al. 2013). They are predicted to continue (Beger et al. 2014), although with irradiance a limiting factor (Muir et al. 2015). High-latitude reefs have been proposed as refugia (Riegl 2003, Cacciapaglia and Woesik 2016), resilient areas from temperature stress for tropical coral reef species (Pandolfi et al. 2011) and as transition zones between tropical and temperate ecosystems that may function as areas of heightened evolutionary activity (Beger et al. 2014). Elevated sensitivity of high latitudes to climate change has been predicted (Beger et al. 2014, Porter and Schleyer 2017). They may therefore capture the re-organization of benthic communities first and can be used to study a range of globally significant questions with regards to benthic community change. Recent changes to high-latitude reefs have varied with declining stony coral cover in the Florida Keys (Ruzicka et al. 2013, Toth et al. 2014), but increasing hard coral and decreasing soft coral cover in South Africa (Porter and Schleyer 2017). Any potential for high-latitude reefs to act as refugia or centers for resilience may therefore be curtailed by anthropogenic stress. Highly populated areas subject to heightened anthropogenic stress are of interest, enabling comparisons to remote or pristine regions. One such high-latitude reef system, which can be used to understand how and why reefs may change under global and local stress is the Florida Reef Tract (FRT).

The Florida Reef Tract is the world's third largest barrier reef ecosystem (Walker and Gilliam 2013) and is composed of a mixture of coral reef associated assemblages (Collier et al. 2008). Shallow forereef sites off the southern portion of the FRT in the Florida Keys have already transitioned from a stony coral dominated reef community to a non-coral

based benthic community (Ruzicka et al. 2013). The northern region of the Florida Reef Tract, known as the Southeast Florida Reef Tract (SEFRT), covers 170 km extending from Biscayne Bay (24.6333° N, 82.9200° W) to St Lucie Inlet (27.1661° N, 80.1567° W). It has a unique mix of linear limestone ridges and sand channels running parallel to a highly urbanized coastline (Banks et al. 2007, Walker et al. 2008), which includes two large international ports. Anthropogenic impact is ubiquitous on the SEFRT. The benthic community is at the northern limit of the distribution of corals due to low temperature and is comprised predominately of octocoral, zoanthid, macroalgae and sponge assemblages, with localized areas of higher stony coral cover (up to 41%) (Moyer et al. 2003, Collier et al. 2008, Walker and Gilliam 2013, Walker and Klug 2014). The SEFRT covers an extensive latitudinal gradient and distinct ecosystem regions have been defined, based on known biogeographic boundaries (Walker 2012) and major port channels. Latitude, biogeographic boundaries and major divides in the reef have all been identified as delineators for changes in the distribution and diversity of marine organisms (Stevens 1989, Veron 1995, Walker 2012). Assessing benthic community change on the SEFRT by ecosystem regions thus allows spatiotemporal analysis on an ecologically relevant spatial scale.

To assess taxonomic variations in benthic cover spatially and temporally on the SEFRT, data was used from two annual long-term monitoring projects, the Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP) and the Broward County Biological Monitoring Project (BC BIO). 31 sites from these projects, encompassing up to 97 transects per year were analyzed from 2007 to 2016. Photographic *in situ* surveys were conducted for each project to calculate benthic cover, whilst temperature data was collected via *in situ* measurement and hindcast data from HYCOM. Regional variability in temperature has been observed spatially and temporally, with episodic thermal stress events reported, including upwelling events, severe cold fronts (2010), hurricanes and El Niño events (Eakin et al. 2010, Lirman et al. 2011, Johnston and Purkis 2015, van Woesik and McCaffrey 2017). Benthic cover and temperature data were analyzed concurrently to assess the impacts of temperature change and thermal stress over the entire reef tract and on a latitudinal gradient by ecosystem region.

2. Research Questions

- How does benthic community cover vary spatially along the SEFRT?
- Have there been changes in the major benthic taxa cover on the SEFRT over the study period (2007 – 2016)?
- Do spatial and temporal fluctuations in temperature explain observed changes in major benthic taxa cover?

3. Methods

3.1. Monitoring Projects

To evaluate spatial and temporal variations in benthic community cover on the SEFRT, data was used from two monitoring projects. The Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP) conducts annual monitoring of the southeast Florida coastline between May and August. It began in 2003, encompassing sites from Miami-Dade, Broward and Palm Beach counties. Sites in Martin County were introduced in 2006 (Figure 1). SECREMP currently includes 22 sites along the SEFRT (Tables 1 and 3). Each site consists of 4 individual stations, each 22 m long, with video (2007-2012) or overlapping still (2013-2016) photo transect data taken at each station. The change from video to still photographs occurred in 2013, after a quantitative comparison of image acquisition techniques found no significant difference in the percent cover detected (Morrison et al., 2012). All stations at all 22 SECREMP sites were used in this study (Table 3) and except for some sites in Biscayne Bay, sites lie within 3 km of the coastline (Figure 1). Site depths range from 5 m on the inner reef/nearshore ridge complex to 17 m on the outer reef.

The Broward County Biological Monitoring Project (BC BIO) annually monitors Broward County coral reef and hardbottom communities. The project currently consists of 22 sites, surveyed between September and December each year (except 2009), located on each of the 3 linear reefs and the nearshore ridge complex in Broward County. A five-year initial study (2001-2006, with 23 sites) was undertaken to monitor the benthic community

before an extensive nourishment project on Broward County beaches. Monitoring of the sites continued and subsequent nourishment of Broward County beaches also occurred in 2005, 2006 and in 2016. Data from 9 BC BIO sites, surveyed from 2007-2016, were used in this project to enhance statistical power and ensure coverage of all ecosystem regions (Table 2). A single 20 m by 1.5 m transect running north to south was monitored at each site. Non-overlapping photographs of 0.75 m^2 quadrats were taken along each transect using an Olympus c5060 camera, Ikelite housing and two side mounted strobes.
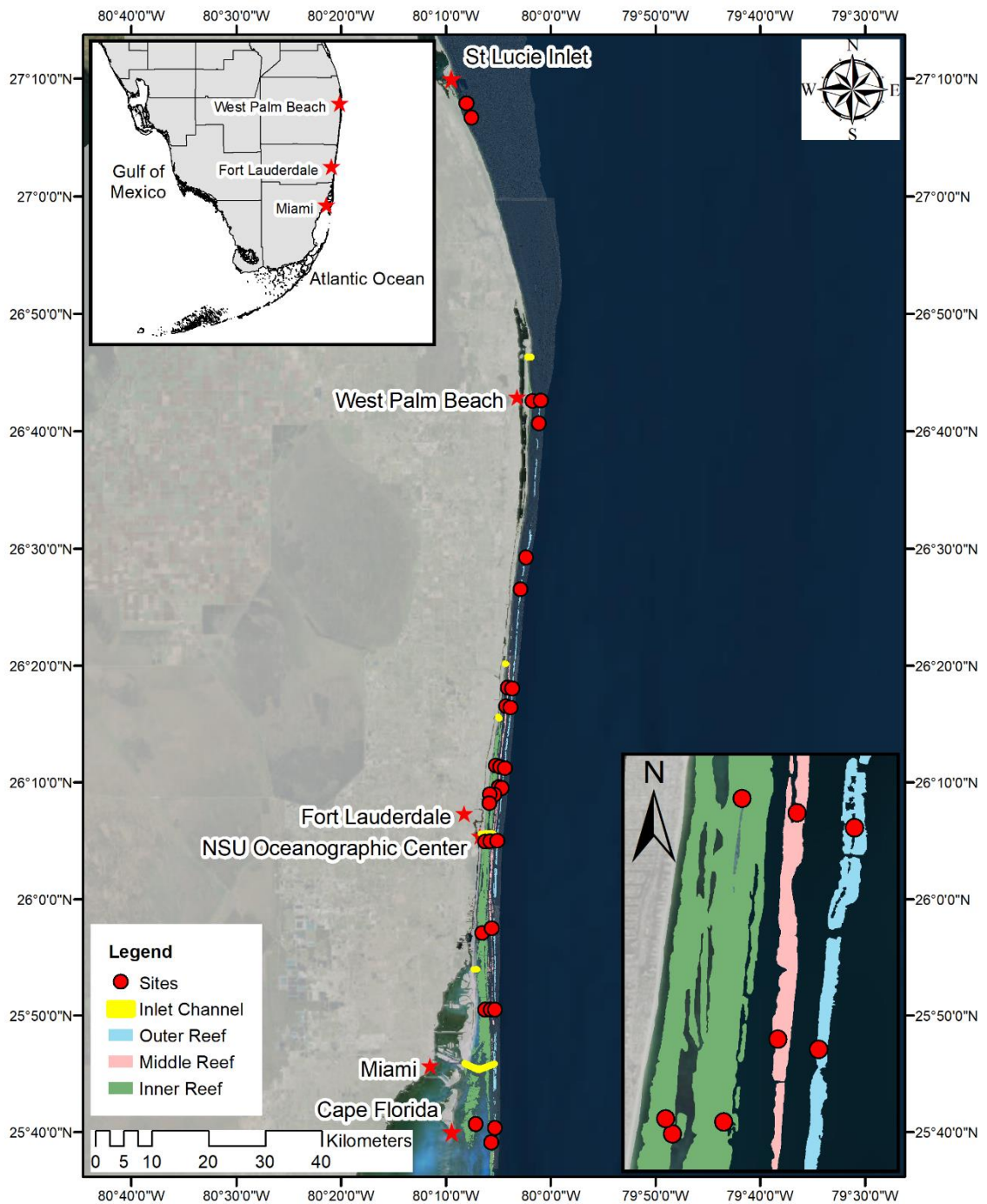
Figure 1. Southeast Florida Reef Tract, with site locations (site names, geographic positions and locations can be found in Tables 1 & 2); inset top left – Southeast Florida, with major cities; inset bottom right – linear reefs (inner, middle and outer) with example site locations on each habitat (for this study sites nearshore ridge complex and inner reef sites, which are at comparable depths, have been grouped).

3.2. Image Analysis

To assess spatial and temporal taxonomic changes in benthic cover, photo transects and photo quadrats were used. These have high precision and statistical power to detect change (Hughes 1996, Aronson and Swanson 1997). Still images taken at SECREMP sites (and those extracted from previous video transects) were 0.4 m wide, giving a total area of 8.8 m^2 photographed per station. Images were analyzed using PointCount '99 (Dustan et al. 1999). The benthic taxa directly underneath 15 randomly placed points per frame were identified, for a total of 900-1000 points per station to determine percentage cover. Photo quadrats for BC Bio sites, which cover 30 m^2 of benthic habitat per site, were analyzed using Coral Point Count with excel extensions (CPCe 4.1) research software (Kohler and Gill 2006). The benthic taxa underneath 25 points per image and 1000 per site were identified to determine the percent cover. Benthic taxa included stony corals (to species level), branching and encrusting gorgonians (Octocoral), Porifera, *Xestospongia muta* (giant barrel sponge), macroalgae (including *Dictyota sp*., *Halimeda spp*. and *Lobophora sp*.), crustose coralline algae, turf algae/substrate, cyanobacteria, *Palythoa caribaeorum*, zoanthids and other biota.

3.3. Power Analysis

To calculate the minimum detectable level of absolute change (for example 3% absolute change in stony coral cover corresponds to a change from 5% cover to 2% cover) a power analysis of the major benthic taxa was performed. This was calculated using the percent cover of the major benthic taxa at every station surveyed during the study. The minimum detectable difference for statistical significance for stony coral cover was 0.7%, octocoral cover 1%, sponge cover 0.6% and macroalgae 2.1%.

A second power analysis of benthic cover data was used to determine the number of points required on each BC Bio image to ensure comparability with SECREMP images. To perform the power analysis a sub-set of 5 images were pointcounted in CPCe 4.1 for 3 BC BIO sites (FTL2, 3 and 5), over 3 years (2014 - 2016), with an overlay of 15, 25, 50, 75 and 100 points per image. The minimum detectable difference between samples was calculated in R (R Core Team 2016) for each set of points using the power.t.test function

in the base package. This function is based upon the equation in Cohen (1988) (see below) and implements a power analysis based on a two-tailed t test to assess whether the mean of two samples are significantly different (Cohen 1988).

$$\delta = d\sqrt{(n/2)} = (t_{(1-\alpha)} + t_{(1-\beta)})$$

Where: n = number of samples

d = standardized mean difference, (calculated from μ1 – μ2 (μ = mean))

δ = minimum detection level

t = 2-tailed t test statistic

α = level of significance

v = degrees of freedom

β = power of the test

Equation 1. Power Analysis calculating minimum detectable difference in cover

The analysis found that 25 points per image were optimum for BC BIO images, as seen by the plateau and lack of dramatic subsequent change in detectability in the loess (locally weighted smoothing) non-parametric curve of best fit (Figure 2). This sample size also ensured comparability in the minimum detectable difference with a subset of images from a subset of SECREMP sites (BC2, BC3 and BC1). It is important to note that the minimum detectable difference calculated in the second power analysis (Figure 2) was used here purely to ensure sample size comparability between the two monitoring projects and is not a true reflection of the overall detectable limit for this thesis.
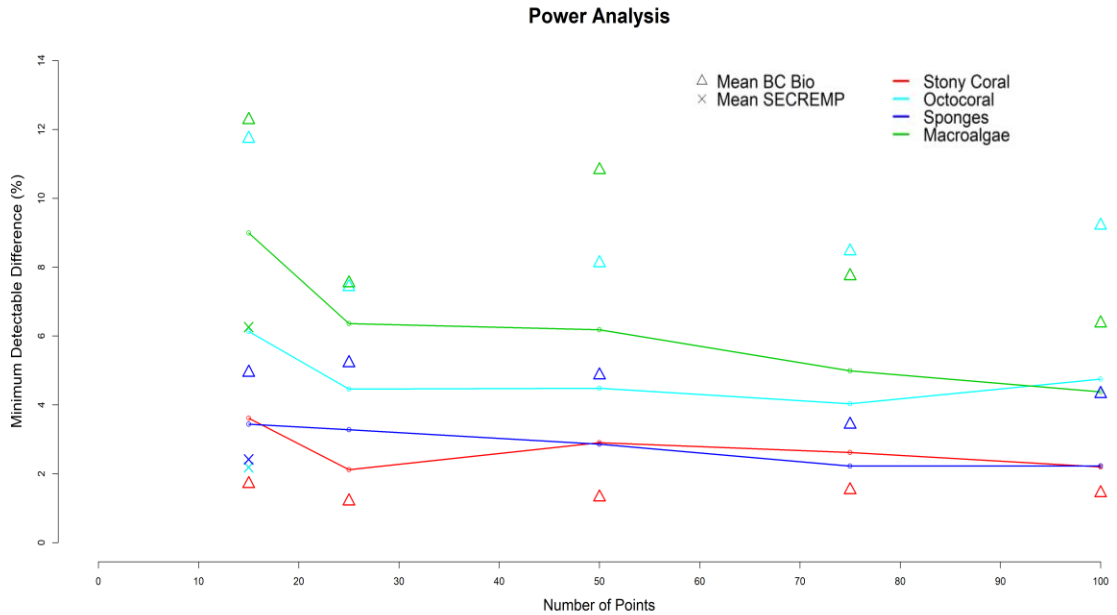
Figure 2. Power analysis of minimum detectable difference in the major benthic taxa vs number of points per image with fitted Loess smoothed curve at BC Bio sites and SECREMP sites.

3.4.   Southeast Florida Ecosystem Regions

To assess spatial changes in the benthic community the SEFRT was split, north to south, into six ecosystem regions (Figure 3). The ecosystem regions were split based on previously identified biogeographical boundaries (Walker et al. 2012, Walker and Gilliam 2013), and by the major port channels, Port Everglades and Port of Miami. The Bahamas Fault Zone, which marks the northern terminus of the outer reef, separates the North Palm Beach-Martin (1) and South Palm Beach (2) regions. The middle reef ends just north of Boca Inlet, which separates the South Palm Beach and Deerfield regions (3). The Deerfield region stretches North from Boca Inlet to Hillsboro Inlet, where the inner reef ends. The Central Broward region (4) stretches from Hillsboro Inlet to Port Everglades and the South Broward-Miami region (5) south to Government Cut at the Port of Miami. The final ecosystem region is the Biscayne Bay region (6) which extends south from Government Cut to central Biscayne Bay.

11
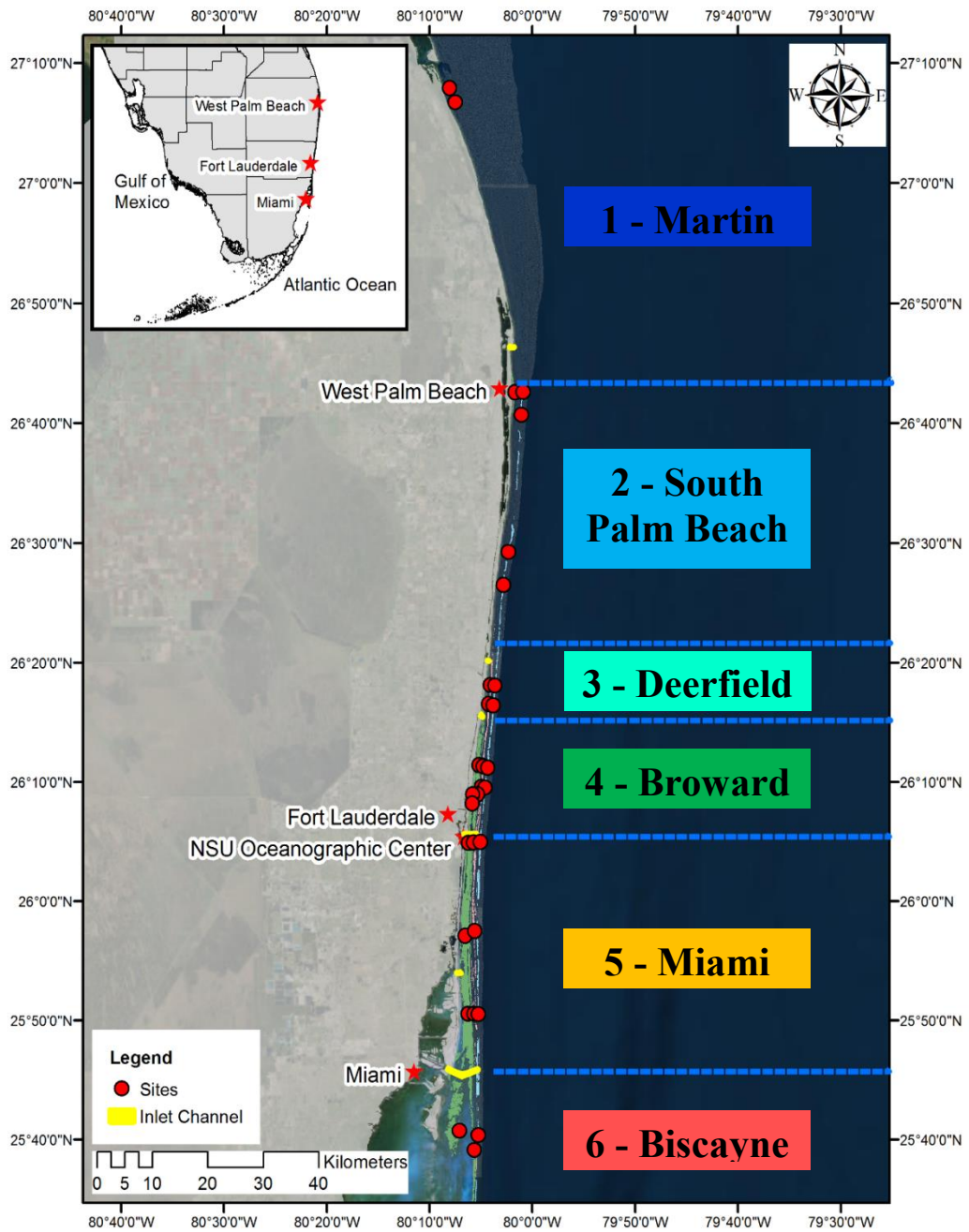
Figure 3. Ecosystem regions of the Southeast Florida Reef Tract. Ecosystem region boundaries represented by dashed blue lines (color codes and number will be consistent for each region throughout the document).

Table 1. SECREMP sites surveyed, county of survey, site depth, ecosystem region, habitat and geographic coordinates.

Habitat: 1 = inner reef, 2 = middle reef, 3 = outer reef

County	Site	Ecosystem Region	Habitat	Depth (m)	Latitude (N)	Longitude (W)
Miami-Dade	DC1	5	1	8	25° 50.540'	80° 06.249'
Miami-Dade	DC2	5	2	14	25° 50.534'	80° 05.698'
Miami-Dade	DC3	5	3	17	25° 50.526'	80° 05.286'
Miami-Dade	DC4	6	3	12	25° 40.357'	80° 05.301'
Miami-Dade	DC5	6	1	7	25° 39.112'	80° 05.676'
Miami-Dade	DC6	5	1	6	25° 57.098'	80° 06.545'
Miami-Dade	DC7	5	2	18	25° 57.511'	80° 05.627'
Miami-Dade	DC8	6	1	8	25° 40.712'	80° 07.117'
Broward	BCA	4	1	8	26° 08.985'	80° 05.810'
Broward	BC1	4	1	8	26° 08.872'	80° 05.758'
Broward	BC2	4	2	12	26° 09.597'	80° 04.950'
Broward	BC3	4	3	17	26° 09.518'	80° 04.641'
Broward	BC4	4	1	9	26° 08.963'	80° 05.364'
Broward	BC5	3	2	12	26° 18.111'	80° 04.090'
Broward	BC6	3	3	18	26° 18.064'	80° 03.654'
Palm Beach	PB1	2	1	8	26° 42.583'	80° 01.714'
Palm Beach	PB2	2	3	17	26° 40.710'	80° 01.095'
Palm Beach	PB3	2	3	17	26° 42.626'	80° 00.949'
Palm Beach	PB4	2	3	17	26° 29.268'	80° 02.345'
Palm Beach	PB5	2	3	17	26° 26.504'	80° 02.846'
Martin	MC1	1	1	5	27° 07.900'	80° 08.042'
Martin	MC2	1	1	5	27° 06.722'	80° 07.525'

Table 2. BC BIO sites surveyed, site depth, ecosystem region, habitat and geographic coordinates

Site	Ecosystem Region	Habitat	Depth (m)	Latitude (N)	Longitude (W)
FTL4	4	1	6	26° 08.2080'	80° 05.8440'
HB2	3	2	11	26° 16.5350'	80° 04.2620'
HB3	3	3	15	26° 16.4255'	80° 03.8189'
JUL6	5	1	4	26° 04.9120'	80° 06.2226'
JUL7	5	2	10	26° 04.9635'	80° 05.7321'
JUL8	5	3	15	26° 04.9957'	80° 05.0990'
POMP1	4	1	6	26° 11.4356'	80° 05.2256'
POMP2	4	2	15	26° 11.3289'	80° 04.8039'
POMP3	4	3	16	26° 11.2141'	80° 04.3650'

Table 3. SECREMP sites and years surveyed; S = surveyed, blank = not surveyed

Year	BCA	BC1	BC2	BC3	BC4	BC5	BC6	DC1	DC2	DC3	DC4	DC5
2007	S	S	S	S				S	S	S		
2008	S	S	S	S				S	S	S		
2009	S	S	S	S				S	S	S		
2010	S	S	S	S				S	S	S	S	S
2011	S	S	S	S				S	S	S	S	S
2012	S	S	S	S				S	S	S	S	S
2013	S	S	S	S	S	S	S	S	S	S	S	S
2014	S	S	S	S	S	S	S	S	S	S	S	S
2015	S	S	S	S	S	S	S	S	S	S	S	S
2016	S	S	S	S	S	S	S	S	S	S	S	S

Year	DC6	DC7	DC8	MC1	MC2	PB1	PB2	PB3	PB4	PB5
2007				S	S	S	S	S		
2008				S	S	S	S	S		
2009				S	S	S	S	S		
2010				S	S	S	S	S	S	S
2011				S	S	S	S	S	S	S
2012				S	S	S	S	S	S	S
2013	S	S	S	S	S	S	S	S	S	S
2014	S	S	S	S	S	S	S	S	S	S
2015	S	S	S	S	S	S	S	S	S	S
2016	S	S	S	S	S	S	S	S	S	S

3.5. Temperature Analysis

Water temperature data were compiled using two methods to cover the entire SEFRT and enable analysis of sea surface temperatures (SST) and temperatures at depth, the latter of which are reflective of *in situ* conditions experienced by the benthic community. Thermal stress events were also investigated in detail. *In situ* temperatures were recorded at SECREMP stations 1 and 2 at all sites between February 2007- June-2016 using HOBO temperature loggers (HOBO Pro V2). Next, HYCOM was used to analyze daily sea surface temperature over the entire SEFRT, by calculating annual mean, maximum and minimum sea surface temperatures over the SEFRT and in each ecosystem region. Thermal stress events were then calculated using a combination of HYCOM SST data and *in situ* temperatures. Thermal highs are considered as 1°C above the maximum of the mean summertime SST and thermal lows 1°C below the minimum of the mean wintertime SST over the study period (2007-2016), defined using NOAA's coral reef watch limits (Liu et al. 2013), which reflect thermal stress found to significantly affect coral health over a prolonged period. The maximum mean summertime temperature was defined as the maximum of the mean SST during summer months (May – September) during the study. The level of thermal heat stress was defined as the number of days where average daily *in situ* temperatures at a specific site are 1°C above the maximum of the mean summer temperatures. The minimum mean wintertime temperature was defined as the minimum of the mean temperature during winter months (December – March) during the study. The level of thermal cold stress was defined as the number of days where *in situ* temperatures at a specific site are 1°C below the minimum of the mean winter temperatures.

3.6. Data Analysis

Statistical data analysis was conducted in R (R Core Team 2016). Principal Component Analysis (PCA; Wold et al. (1987)) was used to evaluate spatial and temporal similarities in percent cover of the major benthic groups over the SEFRT and between ecosystem regions. PCA converts similarities in benthic composition into linear combinations to graphically assess which benthic taxa best explain spatial variation in the benthic community. PCA was conducted using the benthic groups: Stony coral, octocoral, sponge,

macroalgae, zoanthid and "other" fauna (including anemones, corallimorphs, hydroids, tunicates).

Spatiotemporal variation in the taxonomic composition of benthic cover was analyzed using PCA and Generalized Linear Models (GLM). Variation in the benthic taxa determined to cause the greatest amount of spatial variation in PCA was analyzed temporally over the entire SEFRT and spatiotemporally between ecosystem regions and years using GLM. Post hoc analysis was performed on the model to assess in which years significant changes in cover occurred. This was conducted with the sample year as a factor, rather than a continuous variable, using the "ghlt" function in the R package 'multcomp' (Hothorn et al. 2008). GLM's were primarily used because the response variable (in this case the benthic cover) is a percentage. Binomial GLM's also factored in the non-Gaussian distribution of data, potential overdistribution and differences in sample size.

The factors driving spatiotemporal variation in benthic cover were analyzed for each of the major benthic taxa in relation to SST, *in situ* temperature and thermal stress event duration. A stepwise approach was used which starts with the most complex model (Equation 2) and removes insignificant factors before determining a model which appropriately represents the data. Only strongly significant factors were accepted for the final model ($p < 0.01$) as the p-values created by GLM's are approximate (Bolker et al. 2009). Reported p-values were calculated using a Chi-squared ANOVA on the selected model. Eleven temperature related variables (equation 3), were analyzed for their effect on the major benthic taxa. These derived from three main metrics - sea surface temperature, *in situ* temperature and thermal stress - and were selected to reflect current and potential future impacts of climate change and thermal stress. A lag effect of thermal stress on the benthic community the following year (for example the effect of 50 days of heat stress in 2010, on the benthic community in 2011) was included in each model to assess for the latent impact of temperature stress.

$$Temperature\ impact\ on\ benthic\ taxon$$
$$= glm(Taxon \sim SST\ Mean + SST\ Min + SST\ Max + SST\ Range$$
$$+ In\ situ\ Mean + In\ situ\ Max$$
$$+ In\ situ\ \min + Thermal\ heat\ stress + Thermal\ cold\ stress$$
$$+ lag(Thermal\ heat\ stress) + lag(Thermal\ cold\ stress)$$

Equation 2. Model representing variables used to assess the impact of temperature on spatiotemporal change in benthic taxa

The effect of thermal stress duration was also investigated within ecosystem regions to assess temporal change. Non-parametric linear regression was used to assess temporal change in SST maximum, mean, minimum and range during the study period to compare to changes in benthic cover. Kruskal - Wallis one - way analysis of variance was used to assess spatiotemporal change in thermal stress duration. Unless stated all p-values reported here are based upon GLM's.

4. Results

4.1. Spatial Distribution of the Benthic Community

Spatial differences in the taxonomic composition of benthic cover were identified between all ecosystem regions. All six ecosystem regions varied in their principal components (Figure 4 a & b) and GLM's found significant spatial differences in cover for all four taxa, stony corals, octocorals, sponges and macroalgae, which contributed most strongly to variance in PCA ($p < 0.001$). The biplots (Figures 4a & b) show the spatial dissimilarity between ecosystem regions and the importance of each taxa in creating variance. Differentiation between regions was primarily created by macroalgae and octocoral, with principal component 1 (hereafter noted as PC1, PC2, etc.), accounting for 86% of variance (Figure 4a). Macroalgae cover was highest and octocoral cover lowest in the Martin region. Octocoral cover was highest in South Palm Beach. Dissimilarity between the remaining regions was created by octocoral, sponge and stony coral (Figure 4b), with PC2 and PC3 accounting for 9% and 4% of variance respectively. The Broward and Miami regions had relatively higher stony coral cover than South Palm Beach, Deerfield and Biscayne regions which had higher octocoral and sponge cover. The final split in regions is shown by PC3 (Figure 4b), which separated Deerfield where sponge cover was higher and South Palm Beach and Biscayne which had relatively higher octocoral cover.
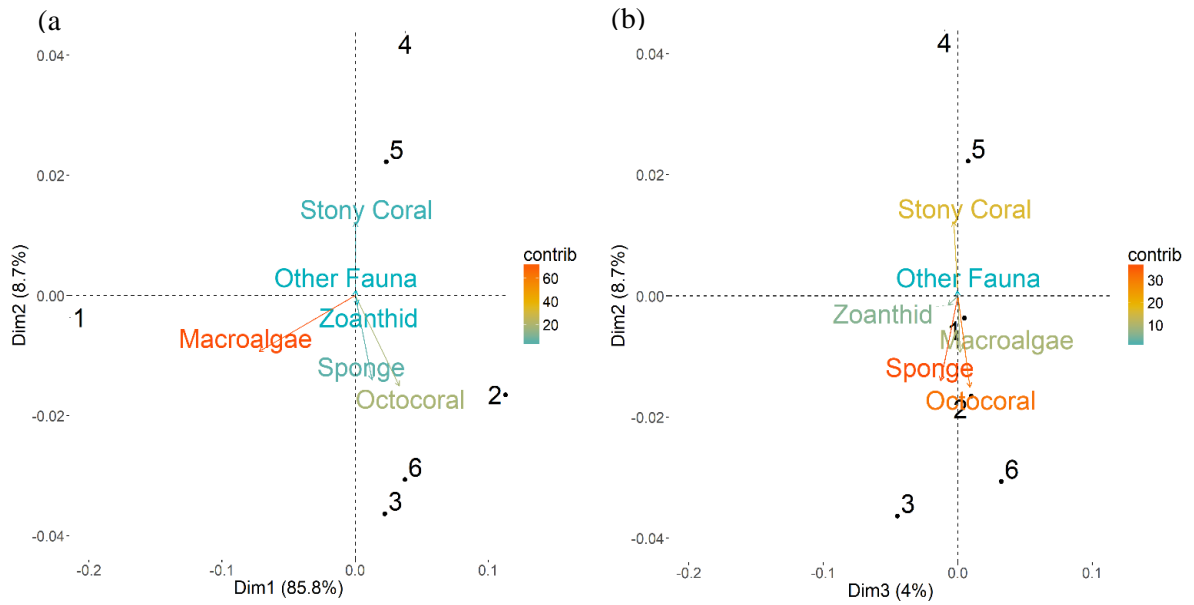
Figure 4. Biplot representing Principal Components Analysis of similarity between ecosystem regions. Numbers represent each ecosystem region 1-6 (1=Martin, 2=South Palm Beach, 3=Deerfield, 4=Broward, 5=Miami, 6=Biscayne), Color coding of variables is reflective of the contribution of that variable (%) to the variance explained by the principal component (contrib); a) PC1 & 2; b) PC2 & 3

4.2. Temporal Change in Benthic Cover on the SEFRT

The taxonomic composition of benthic cover on the SEFRT changed over time (Figure 5). Turf/substrate cover was highest of all benthic categories (maximum 71%, 2009), but decreased significantly in 2016 ($p<0.001$). Stony coral cover significantly declined over the study period ($p<0.001$), with cover in 2016 decreasing by 43% relative to 2015 (Figure 6a). A concomitant significant increase in macroalgae was observed with cover in 2016 significantly greater than all other years ($p<0.001$) (Figure 6b). This included a 94% increase in macroalgae cover in 2016 relative to 2015. A significant decrease in macroalgae cover was seen in 2011, with cover significantly lower than in 2007 ($p<0.05$) and 2008 ($p<0.05$). Octocorals occupied the most cover of any faunal assemblage, peaking at 11% ($\pm$ 1%) in 2011 (Figure 6c). Octocoral did not significantly change overall, but sponge cover in 2011 was significantly higher than in 2008 and 2009 ($p<0.05$) (Figure 6d). Cyanobacteria cover was not recorded in SECREMP images prior to 2011 and therefore statistical analysis was restricted to 2011-2016. During this period no significant changes were seen, but cyanobacteria did contribute over 4% to benthic cover in 2012 ($\pm$ 1%), 2013 ($\pm$ 0.7%) and 2016 ($\pm$ 0.8%). Zoanthid cover was stable over the SEFRT, contributing 0.8-1.5% ($\pm$ 0.2 – 0.4%) cover with no significant changes found.
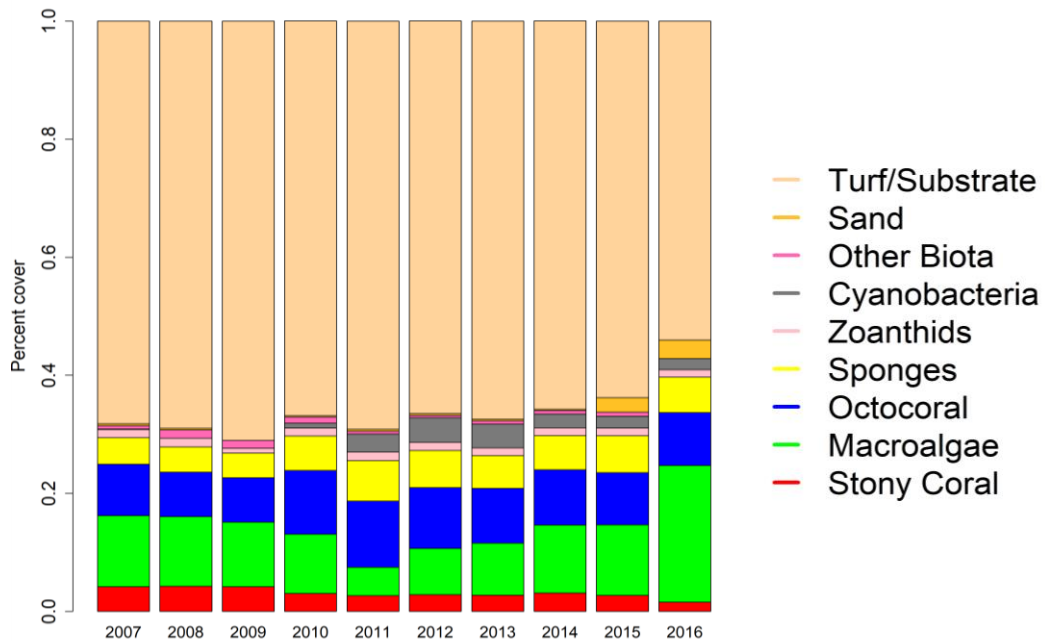
Figure 5. Percent cover of all benthic groups recorded on the SEFRT, from 2007-2016
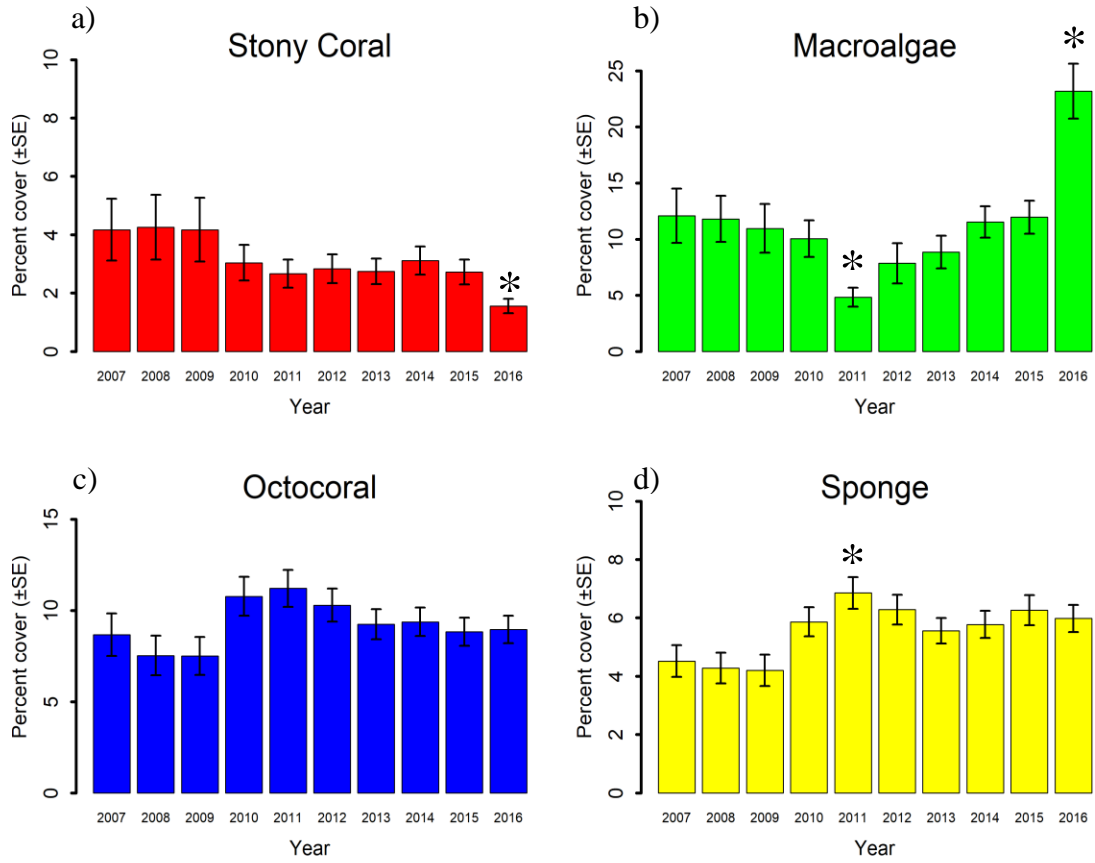
Figure 6. Mean cover of major benthic taxa on the SEFRT; a) Stony coral cover 2007-2016; b) Macroalgae cover 2007-2016; c) Octocoral cover 2007-2016; d) Sponge cover 2007-2016
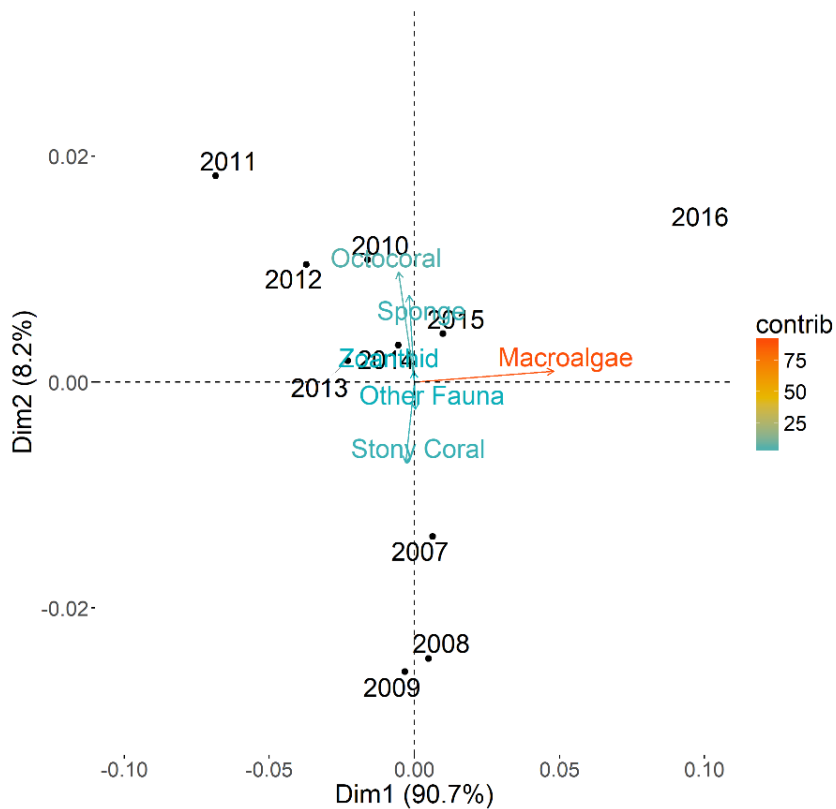
Figure 7. PCA biplot representing taxa creating dissimilarity in sample years. Color coding of variables is reflective of the contribution of that variable (%) to the variance explained by the principal component (contrib).

Macroalgae was the most important contributor to between year differences (Figure 7) followed by octocoral, sponge and stony coral. Macroalgae cover in 2016 was significantly higher than all other years (GLM, p<0.001). The spatial separation in PC1, accounting for 91% of variation, highlights this change. In 2007, 2008 and 2009, stony coral cover was relatively high and octocoral and sponge cover low. Subsequently stony coral cover was comparatively low and sponge and octocoral cover relatively high.

22

4.3. Spatiotemporal Change in the Benthic Community

Spatiotemporal changes on the SEFRT were not ubiquitous (Figure 8). Turf algae/substrate occupied more benthic cover than all other taxa combined in all ecosystem regions, except in Martin in 2007 and 2013, Deerfield in 2014 and 2015 and in Miami in 2016. Macroalgae cover was highest in Martin from 2007-2014, Deerfield in 2015 and Miami in 2016. Octocorals occupied the highest percent cover of any benthic fauna in the South Palm Beach, Miami and Biscayne ecosystem regions throughout the project. Sponges occupied the highest percent cover of faunal assemblages in seven of the ten years in Deerfield, with octocoral cover higher in 2007, 2012 and 2014. Stony coral cover was the highest faunal assemblage in Broward until 2010, with octocoral cover consistently higher subsequently.

Figure 8. Spatiotemporal change in benthic cover in ecosystem regions L – R; Regions 1-6 (No data = Deerfield - 2009, Biscayne - 2007-2009)

23

The spatiotemporal similarity between ecosystem regions and years is shown through PCA (Figures 9 and 10). The results agree with the findings seen in the major benthic taxa (Figures 11-14), with strong structure by ecosystem region predominately seen until 2016. Macroalgae had the largest influence on spatiotemporal similarity, with PC1 accounting for 85% of variance. Macroalgae cover was highest in Martin but decreased over time (Figure 9a and 12). In 2016, macroalgae dominated benthic cover in Broward, Miami and Biscayne with strong inverse relationships to PC1 for the first time (Figure 12). Macroalgae cover was also high in Deerfield during 2014 and 2015.

Octocoral, sponge and stony corals also accounted for a large portion of spatiotemporal variability. Broward and Miami formed distinct clusters with low octocoral and higher stony coral cover until 2016 (Figure 9a, 11, 13). However as stony coral cover declined the relationship with PC2, which had a strong loading of stony coral, octocoral and sponges, became weaker and the spatial uniqueness of the regions decreased (Figure 9a). All ecosystem regions became more positively related to PC2 from 2007 to 2016, highlighting the increased proportion of benthic cover taken up by octocorals and sponges in relation to stony coral. Structure by ecosystem region was weaker for PC2 and PC3 (Figure 10a), but Deerfield consistently had higher sponge cover. While clusters between ecosystem regions are evident up until 2015, particularly for PC1 and PC2, homogenization of the benthic community cover over time was increasingly apparent. Stony coral cover became of decreasing importance to spatiotemporal dissimilarity, with community change towards increased macroalgae, octocoral and sponge cover (Figures 9b and 10b).
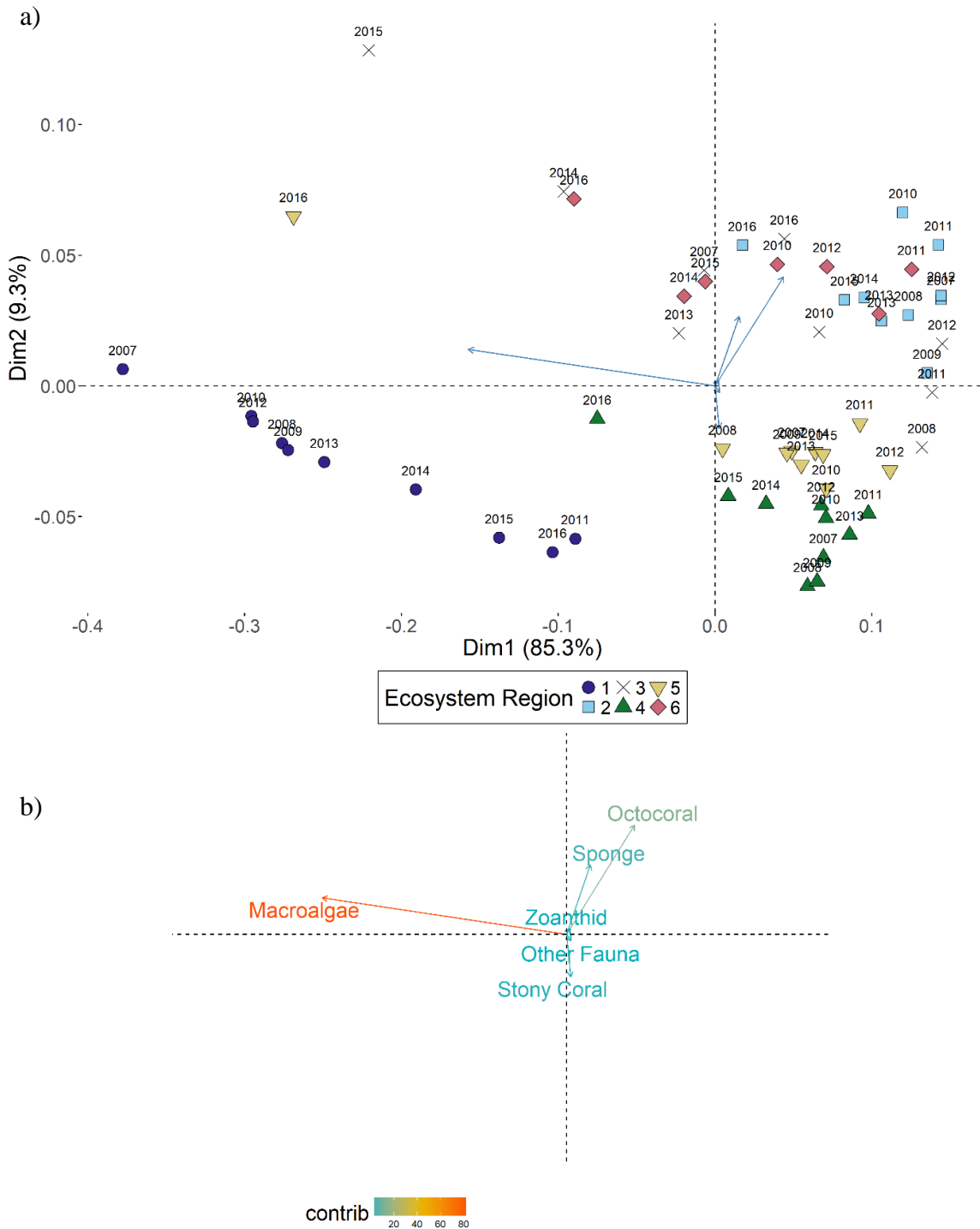
Figure 9. Biplot showing spatiotemporal variability in principal components between ecosystem regions a) PC1 & 2. Colors and shapes are consistent for ecosystem regions, years are labeled; b) Vector loadings. Color coding of variables is reflective of the contribution of that variable (%) to the variance explained by the principal component (contrib).
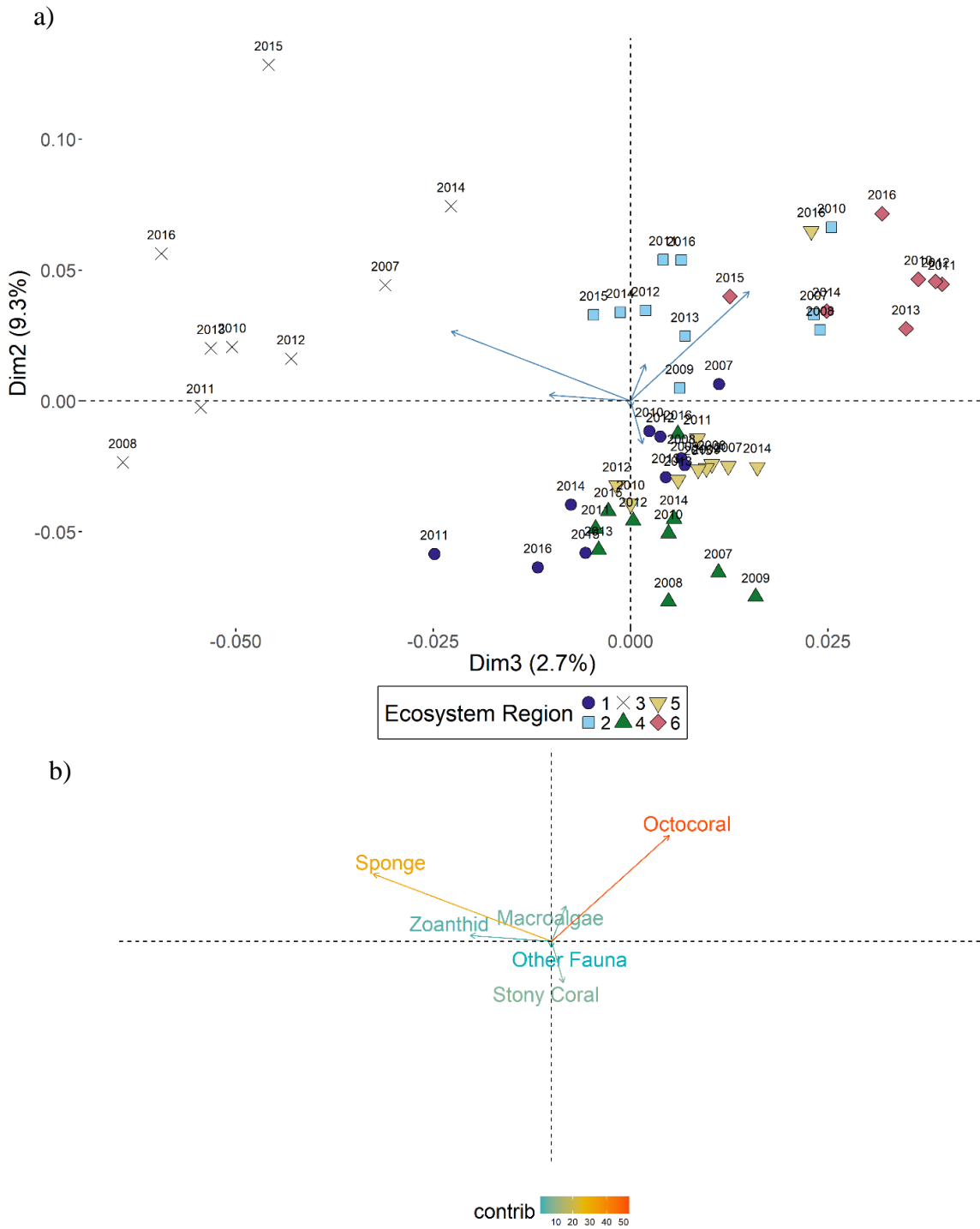
Figure 10. Biplot showing spatiotemporal variability in principal components between ecosystem regions a) PC2 & 3. Colors and shapes are consistent for ecosystem regions, years are labeled; b) Vector loadings. Color coding of variables is reflective of the contribution of that variable (%) to the variance explained by the principal component (contrib).

Stony coral cover was highest in Broward from 2007 to 2016 (max 10% ± 2.8% in 2008 and 2009), but declined significantly in the region (p=0.001) and now only occupies 3% (± 0.7%) (Figure 11). Coral cover also significantly decreased over the study in Deerfield (p<0.001), with cover in 2016 significantly lower than all other years (p<0.05) and occupying less than 1% in 2016 (± 0.05%). In South Palm Beach coral cover was significantly lower in 2016 than in 2013 (p<0.05), 2014 (p<0.01) and 2015 (p<0.05). No change in stony coral cover was found in the Martin, Miami or Biscayne regions, although coral cover in 2016 was lower than all previous years in Biscayne (0.9% ± 0.08%) and at its lowest since 2008 in Miami (1.3% ± 0.3).
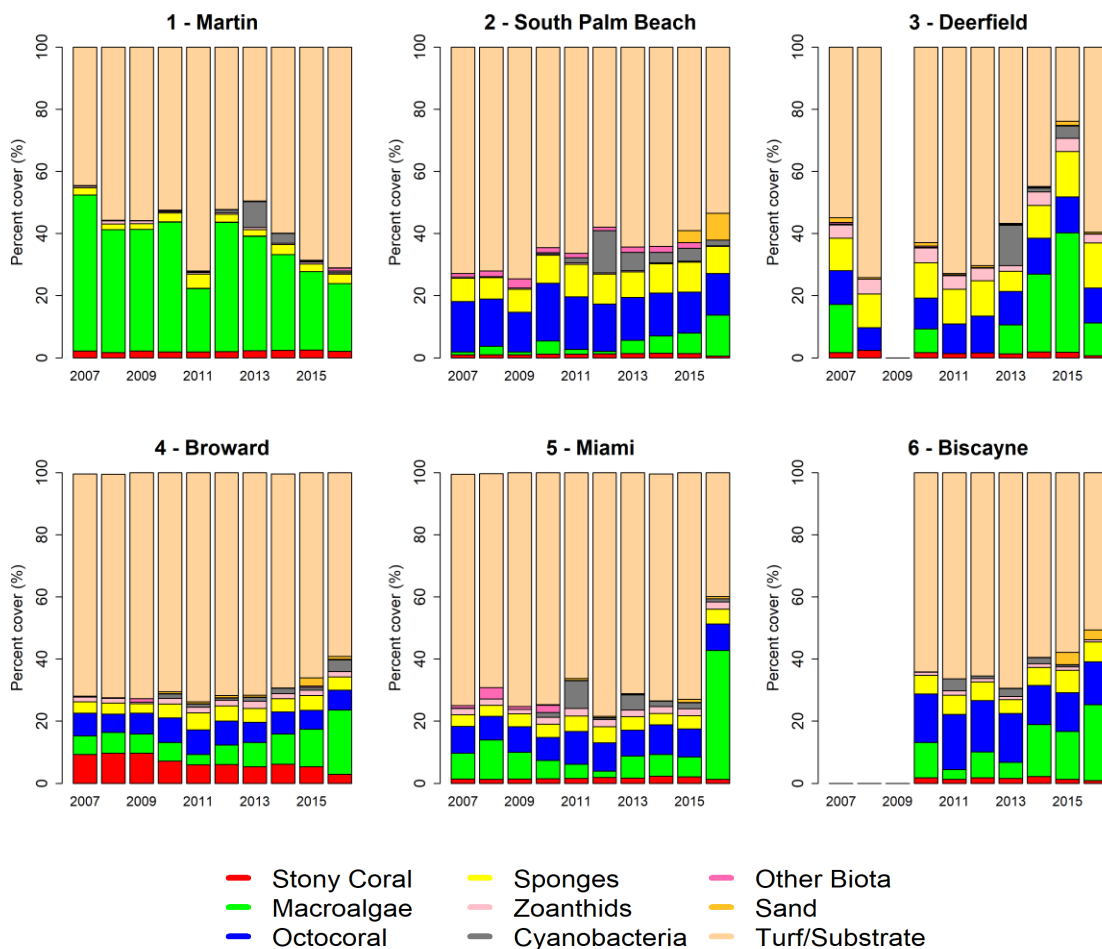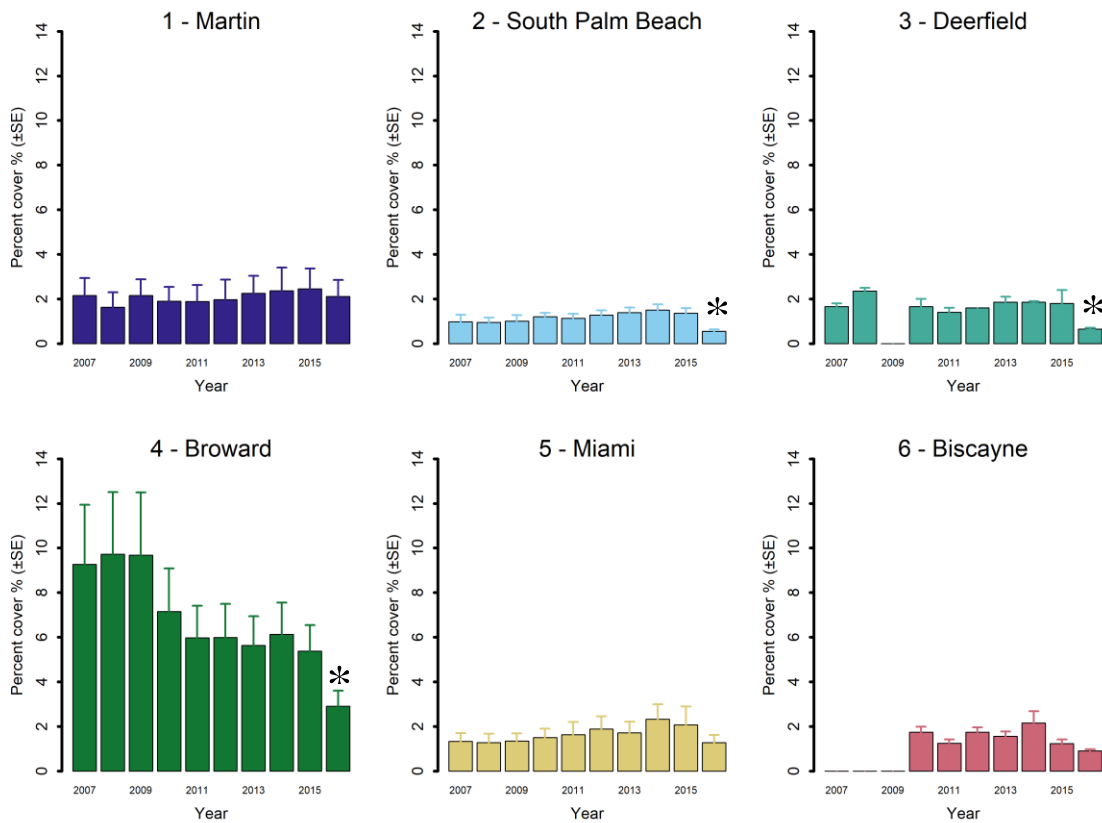

Figure 11. Temporal changes in stony coral cover between ecosystem regions L – R; Regions 1-6 (No data = Deerfield - 2009, Biscayne - 2007-2009)

Macroalgae cover increased significantly in four of the six ecosystem regions (GLM, p<0.001) (Figure 12). The South Palm Beach, Broward, Miami and Biscayne regions all had significant increases in 2016 (p<0.001), with an increase in Miami from 6.4% ($\pm$ 2.2%) in 2015 to 41.5% ($\pm$ 7.6%) in 2016. Macroalgae cover increased in Deerfield in 2015 but decreased significantly in 2016 (p<0.001). Overall, macroalgae cover on the SEFRT was highest in Martin from 2007 to 2014, but decreased significantly (p=0.01) from 2007 (max cover 50.3% $\pm$ 4.6%) to 2016 (max cover 21.8% $\pm$ 7%). A significant decrease in macroalgae cover was also seen from 2010 to 2011 (p=0.02) in Martin. Macroalgae cover was highest in Deerfield in 2015 (38.4% $\pm$ 13.1%) and Miami in 2016 (41.5% $\pm$ 7.6%).
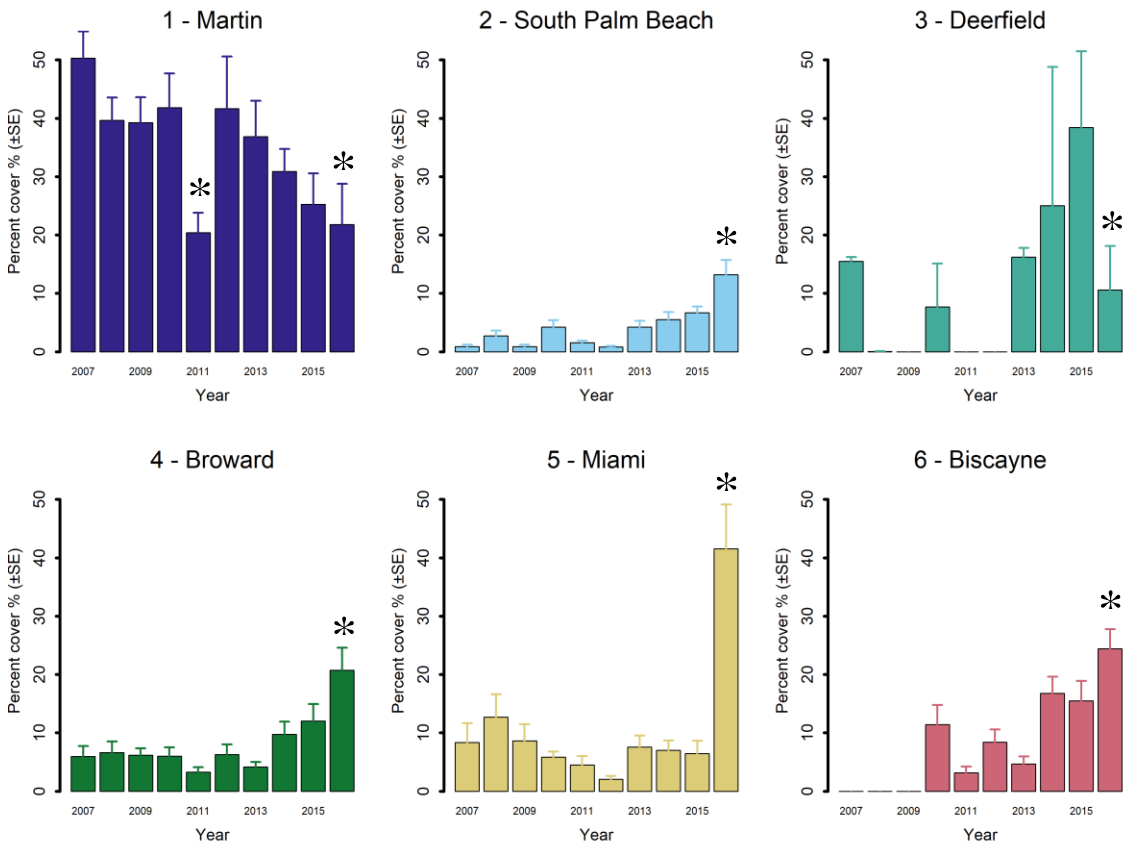
Figure 12. Temporal changes in macroalgae cover between ecosystem regions L – R; Regions 1-6 (No data = Deerfield - 2009, Biscayne - 2007-2009)

Octocoral cover was highest in South Palm Beach in 2010 (18.6% ± 2.6%), while Biscayne had the highest octocoral cover in 2011 (17.8% ± 0.9), 2012 (16.5% ± 1.8%), 2013 (15.6% ± 1.1%) and 2016 (13.8% ± 0.84%) (Figure 13). Octocoral cover declined significantly overall in South Palm Beach (p=0.02), Broward (p=0.002) and Biscayne (p<0.001). The decline in South Palm Beach has seen cover in 2016 at its lowest since 2009 (13.3% ± 1.7%). It has remained stable in all other regions.
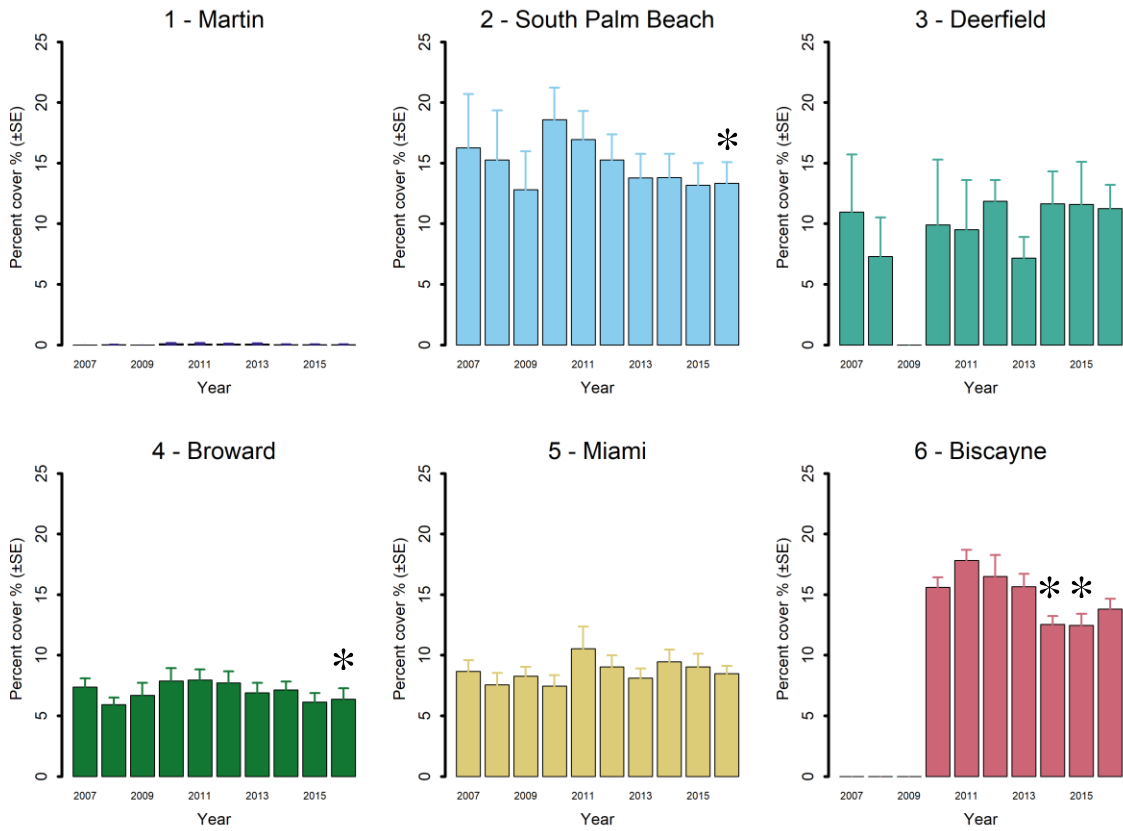
Figure 13. Temporal changes in octocoral cover between ecosystem regions L – R; Regions 1-6 (No data = Deerfield - 2009, Biscayne - 2007-2009)

Sponge cover was highest in the Deerfield region throughout, with a maximum of 14.6% (± 1.7%) in 2015 (Figure 14). Sponge cover in Martin, was significantly higher in 2011 than in 2008 and 2009 (p<0.05), but no other significant changes were found. A phase shift from octocoral to sponge dominance occurred in Deerfield in 2015.
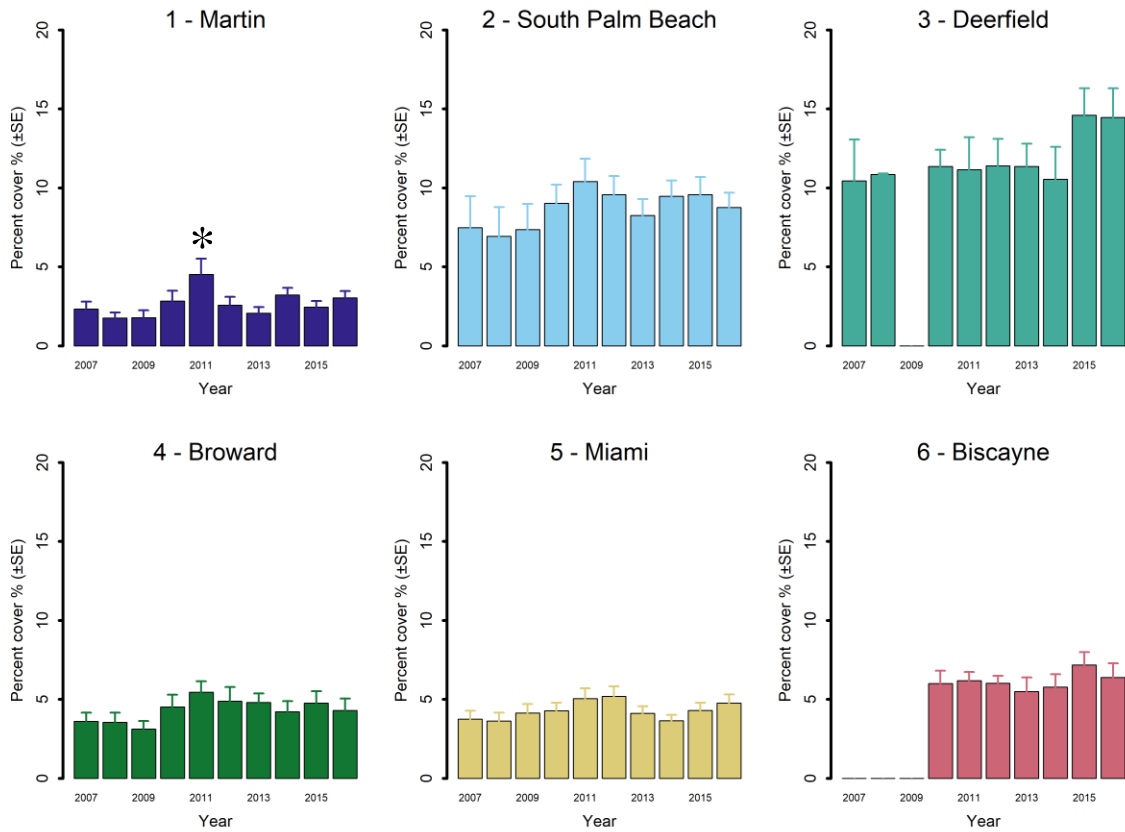
Figure 14. Temporal changes in sponge cover between ecosystem regions L – R; Regions 1-6 (No data = Deerfield - 2009, Biscayne - 2007-2009)

4.4.   Temperature Change on the SEFRT

Mean daily sea surface temperature over the study area was 26.35 °C and ranged from 26.06 °C in 2010 to 26.81 °C in 2015. SST fluctuated seasonally (Figure 15), with a yearly range of 13.19 °C (2011) to 9.19 °C (2013). The maximum daily SST recorded was 31.47 °C (2014) and the minimum daily SST was 14.67 °C (2010), both recorded in the Martin region. Yearly mean and minimum SSTs were significantly different between ecosystem regions (Kruskal-Wallis (KW), $p<0.001$) and the minimum SST in Martin was significantly lower than all others (KW, $p<0.05$). Mean SST in Martin was significantly lower than South Palm Beach, Deerfield, Miami and Biscayne (KW, $p<0.05$). No significant spatial differences were seen in maximum SST between regions (Table 4). In addition to spatial differences in mean and minimum temperature, summer cooling events, likely a result of upwelling, were seen in Martin, South Palm Beach, Deerfield and Broward. Mean and minimum SSTs significantly increased on the SEFRT (Non-parametric regression (NPR), $p<0.001$) (Figure 16a and c), but maximum temperatures decreased significantly (NPR, $p<0.001$) (Figure 16b) over the study period.
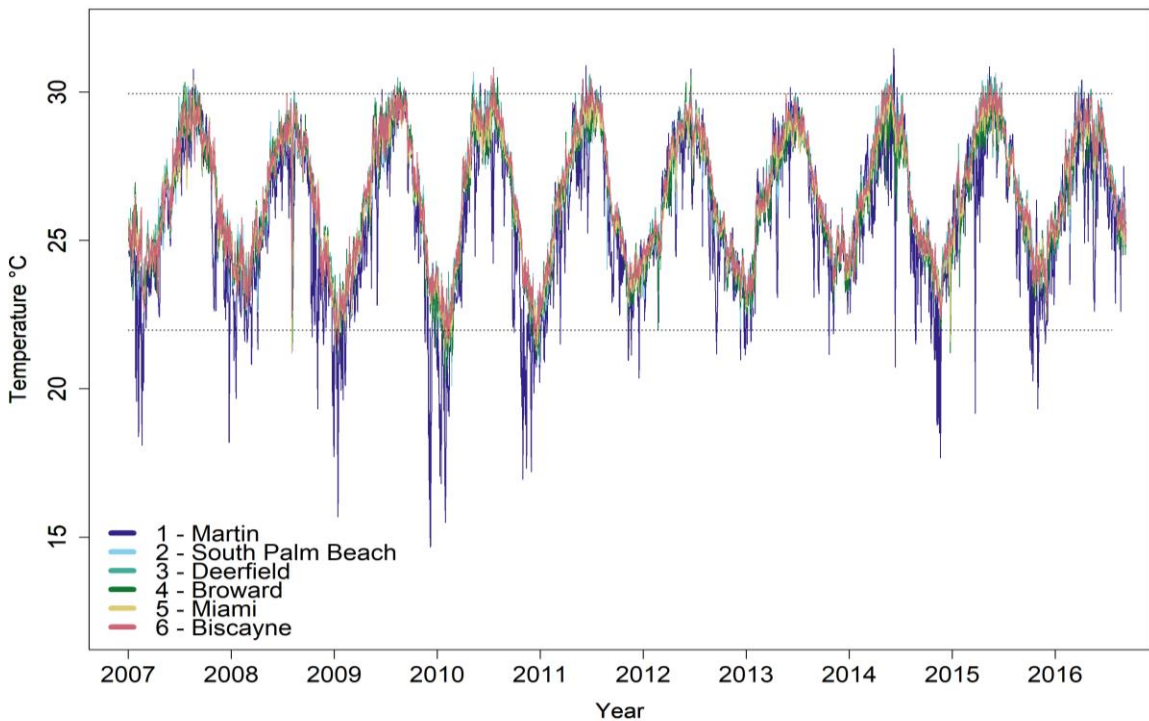
Figure 15. Mean daily sea surface temperature across all regions 2007-2016, top line represents the thermal high threshold (1°c above max mean summertime SST), bottom line represents the thermal low threshold (1°c below min mean wintertime SST)

31

Table 4. Yearly sea surface temperature maximum, mean, minimum and range by ecosystem region, L – R, regions 1-6

1   Martin

Year	Maximum	Mean	Minimum	Range
2007	30.77	25.86	18.10	12.68
2008	29.24	25.19	18.19	11.05
2009	30.09	25.59	15.68	14.41
2010	30.31	24.70	14.67	15.64
2011	30.89	25.57	17.20	13.69
2012	30.79	25.95	20.36	10.43
2013	30.16	26.13	20.97	9.19
2014	31.47	25.96	20.73	10.74
2015	30.86	26.22	17.67	13.19
2016	30.41	25.87	19.32	11.10

2   South Palm Beach

Year	Maximum	Mean	Minimum	Range
2007	30.43	26.63	22.67	7.75
2008	29.71	26.19	21.29	8.42
2009	30.46	26.39	21.02	9.44
2010	30.90	26.10	19.83	11.07
2011	30.74	26.30	20.59	10.15
2012	30.24	26.38	21.62	8.62
2013	29.96	26.41	21.80	8.16
2014	30.65	26.52	22.78	7.87
2015	30.84	26.87	21.82	9.02
2016	30.10	26.68	22.62	7.49

3   Deerfield

Year	Maximum	Mean	Minimum	Range
2007	30.47	26.73	22.59	7.88
2008	30.25	26.33	22.43	7.82
2009	30.63	26.51	21.28	9.35
2010	30.74	26.26	20.48	10.26
2011	30.96	26.46	21.00	9.96
2012	30.52	26.49	22.11	8.41
2013	30.07	26.52	22.30	7.77
2014	30.84	26.64	23.40	7.45
2015	30.82	26.95	22.07	8.75
2016	30.39	26.74	22.41	7.98

4   Broward

Year	Maximum	Mean	Minimum	Range
2007	30.52	26.60	22.77	7.75
2008	29.67	26.23	21.24	8.43
2009	30.36	26.36	21.12	9.24
2010	30.61	25.94	20.03	10.58
2011	30.22	26.25	20.84	9.38
2012	30.69	26.31	21.39	9.30
2013	29.92	26.27	22.17	7.75
2014	30.22	26.26	22.69	7.53
2015	30.15	26.63	21.04	9.11
2016	29.87	26.49	22.32	7.55

5   Miami

Year	Maximum	Mean	Minimum	Range
2007	30.73	26.61	22.68	8.05
2008	29.79	26.26	20.65	9.14
2009	30.49	26.36	21.15	9.34
2010	30.65	26.14	20.88	9.77
2011	30.31	26.35	21.10	9.21
2012	29.90	26.39	22.79	7.11
2013	30.04	26.41	22.39	7.65
2014	30.38	26.53	23.18	7.20
2015	30.23	26.83	21.00	9.23
2016	30.12	26.65	21.62	8.51

6   Biscayne

Year	Maximum	Mean	Minimum	Range
2007	30.13	26.63	22.57	7.56
2008	30.20	26.30	22.39	7.81
2009	30.49	26.46	21.41	9.08
2010	30.89	26.35	21.21	9.68
2011	30.57	26.54	21.36	9.21
2012	30.07	26.59	23.01	7.06
2013	29.96	26.62	22.74	7.22
2014	30.31	26.70	23.14	7.18
2015	30.44	27.00	22.16	8.27
2016	29.93	26.79	22.78	7.15

Maximum SST
y = 54.40 - 0.01201 * Year, p < 0.001

Mean SST
y = -52.72 + 0.03935 * Year, p < 0.001

Minimum SST
y = -143.31 + 0.08215 * Year, p < 0.001
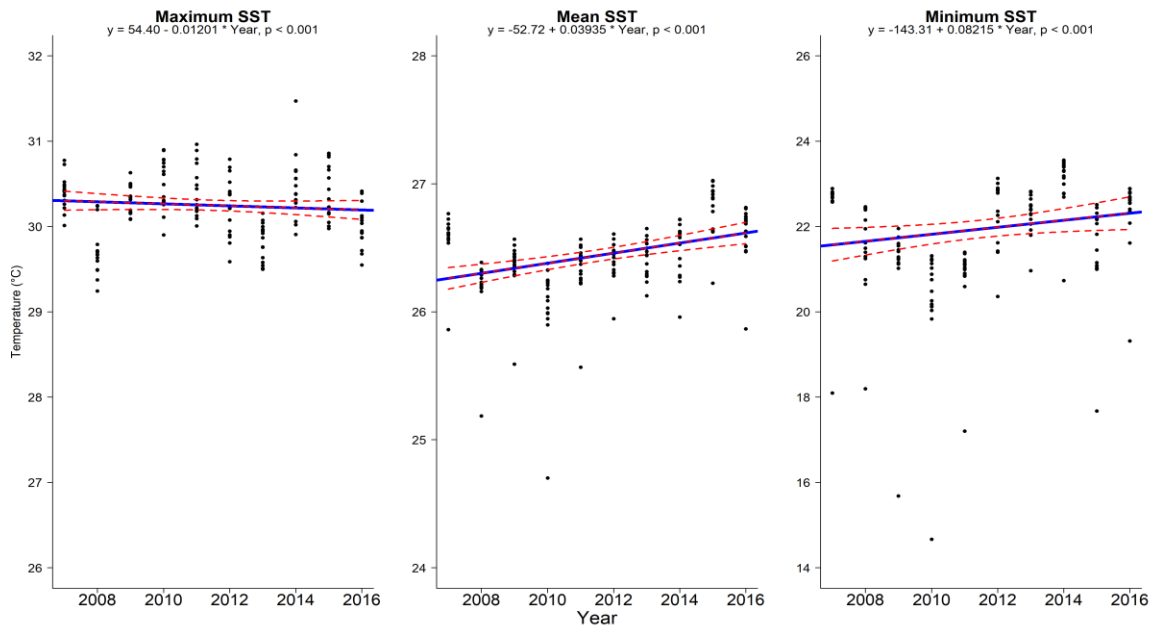
Figure 16. Non-parametric linear regression of sea surface temperature a) Yearly maximum; b) Yearly mean; c) Yearly minimum

Thermal stress duration, i.e. the duration of temperatures 1°C above the maximum mean summer SST (28.95 °C) and 1°C below the minimum mean winter SST (22.97 °C), significantly varied between years (KW, p<0.001) for both heating and cooling duration (Figure 17). Heat stress duration ranged from 0 to 72 days peaking in 2015 (Biscayne) and cold stress duration ranged from 0 to 102 days peaking in 2010 (Martin) (Figure 17). Two El Niño events occurred during the study (2014 and 2015) and heat stress duration was significantly elevated during these years with heat stress in 2015 significantly higher than in 2008, 2010, 2012 and 2013 and 2016 (KW, p<0.05). Heat stress duration in 2014 was significantly higher than in 2008, 2012 and 2013 (KW, p<0.05. Heat stress duration peaked at 72 days (± 11) in Biscayne during 2015. Heat stress significantly varied over the study between ecosystem regions (KW, p<0.001), with heat stress duration significantly higher in Deerfield, Broward and Biscayne, than in the Martin region. Deerfield also had significantly higher duration of heat stress than South Palm Beach. Cold stress significantly varied by year (KW, p<0.001), with cold stress duration in 2009 significantly longer than 2012, 2013, 2014, 2015 and 2016 (KW, p<0.05). Cold stress duration was significantly higher in 2010 and 2011 than all other years, except 2009 and each other (KW, p<0.001).

33

Cold stress duration significantly varied between ecosystem regions (KW, p<0.001) with Martin experiencing significantly higher cold stress duration than all others (KW, p<0.05). Analysis of thermal stress duration identified two periods of significantly increased thermal stress on the SEFRT, the cold winters from 2009-2011 and the two consecutive El Niño years in 2014 and 2015.
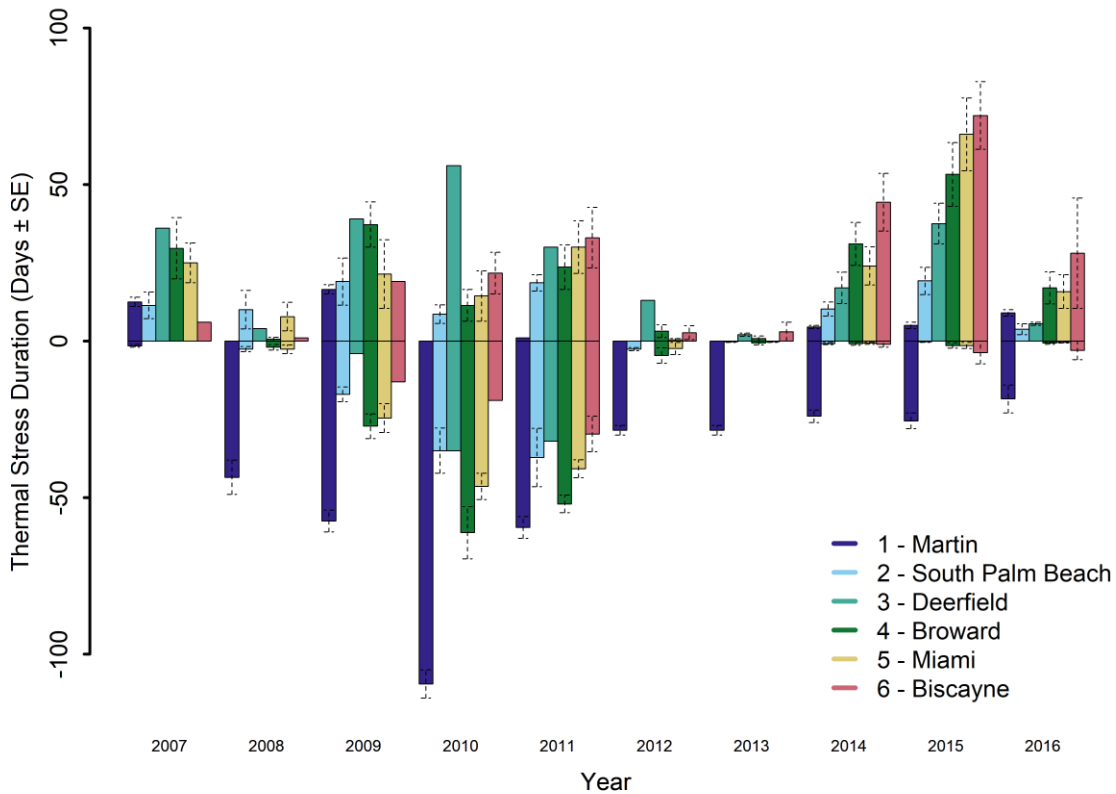
Figure 17. Thermal stress duration (days ± SE) on the SEFRT, thermal highs = above 0, thermal lows = below 0

4.5. Spatiotemporal Relationship of Benthic Cover with Temperature

Multiple temperature related variables had a significant relationship with the spatiotemporal variations in benthic cover over the SEFRT. Stony coral cover had a significant positive relationship to maximum *in situ* temperatures, heat stress duration and cold stress had a significant positive latent effect. Stony coral cover was inversely related

to maximum SST and minimum temperatures (GLM, p<0.01, approx. R^2 = 0.179). Octocoral cover had a significant positive relationship with mean and minimum SST, mean and minimum *in situ* temperature and the cold stress duration. Heat stress duration and maximum *in situ* temperature had significant negative relationships with octocoral cover (GLM, p<0.01, approx. R^2 = 0.182). Sponge cover had a significant positive relationship to mean SST, maximum SST, mean *in situ* temperature and minimum *in situ* temperature. It had a significant inverse relationship to maximum *in situ* temperatures and heat stress duration, with a significant latent effect from heat stress duration (GLM, p<0.001, approx. R^2 = 0.195). Macroalgae cover had a significant negative relationship with cold stress duration, minimum SST and mean SST. The latent effect of heat stress had a significant positive relationship with macroalgae cover (GLM, p<0.001, approx. R^2 = 0.175).

4.6.   Effect of Thermal Stress on Benthic Cover

Ecosystem region responses to thermal stress duration were not uniform. Heat stress duration had a significant positive effect on stony coral cover in Broward (p<0.001) and Miami (p<0.001), but a significant negative latent effect on stony coral cover in South Palm Beach (p=0.006) and Deerfield (p<0.001). Octocoral cover also had a significant negative relationship with heat stress duration in South Palm Beach (p=0.002) and Broward (p<0.001). A significant negative latent effect of heat stress was also seen in Broward (p<0.001) for both octocoral and sponge cover (p<0.001). Heat stress duration had a significant positive lag effect on macroalgae cover in South Palm Beach (p=0.001), Miami (p<0.001) and Biscayne (p<0.001).

Cold stress duration had a significant positive latent effect on sponge cover in Martin (p=0.002), the only region that saw a significant change in sponge cover. Significant negative relationships were seen between cold stress duration and macroalgae cover in South Palm Beach (p<0.001) and Broward (p<0.001). Significant negative latent effects of cold stress duration on macroalgae cover were also seen in South Palm Beach (p<0.001) and Miami (p=0.001). Interestingly, a positive relationship was seen between cold stress duration and macroalgae cover in Miami (p<0.001).

5. Discussion

The Southeast Florida Reef Tract (SEFRT) experienced significant changes in cover of three of the major benthic taxa, stony corals, sponges and macroalgae, from 2007-2016. Phase shifts in the dominant benthic taxonomic assemblage occurred within multiple ecosystem regions, potentially altering ecosystem function. Ecosystem regions showed strong clustering by their taxonomic composition throughout the study, partially driven by temperature variability. Finally, spatiotemporal variations were found in benthic cover on the SEFRT with immediate and latent impacts of thermal stress events related to significant changes recorded. This has resulted in biotic homogenization with the loss of uniqueness between regions. The relationship between thermal stress events and the taxonomic composition of benthic cover is however not uniform across ecosystem regions, suggesting that community composition and local stressors are impacting temporal responses in reef health on the SEFRT.

Stony coral cover significantly declined on the SEFRT in 2016, primarily due to an unprecedented disease outbreak along the FRT (Precht et al. 2016, Gilliam et al. 2017), which coincided with consecutive El Niño years in 2014 and 2015. The duration of temperatures above the bleaching threshold have been found to have a significant effect on coral cover worldwide (Eakin et al. 2010, Heron et al. 2016, Hughes et al. 2017), with thermal stress duration predicted to increase the prevalence and susceptibility of stony corals to disease (Bruno et al. 2007). Cooling in winter months may previously have negated a portion of the impact of heat stress on the SEFRT, but minimum temperatures have significantly increased. Latent thermal heat stress above the bleaching threshold, coupled with a lack of respite from winter cooling, may have exacerbated additional stressors on the SEFRT, resulting in declining cover from disease. This decline is likely to reduce the habitat available for fish and invertebrates (Alvarez-Filip et al. 2011) and decrease shoreline protection (Burke et al. 2004, Sheppard et al. 2005), which combined may have significant effects on the economy in southeast Florida.

As coral cover declined in 2016, macroalgae significantly increased. This appears to have resulted from a combination of the additional space available after the decline

in stony coral cover, as found previously in the Caribbean (Mumby and Steneck 2008), prolonged warm water temperatures and an absence of any major disturbance (hurricane or extreme cold stress) during 2015 and early to mid-2016, which remove macroalgae (Mumby et al. 2005). Macroalgae can reduce coral fecundity, inhibit recruitment, impair growth and cause tissue mortality (Lirman 2001, Box and Mumby 2007, Suchley et al. 2016). The macroalgae increase on the SEFRT may therefore represent a negative feedback loop with coral cover which hinders recovery (Johns et al. 2018). Macroalgae cover declined significantly in 2011, following significant increases in cold stress duration. Thermal heat and cold stress appear to have had both acute and chronic effects on macroalgae cover on the SEFRT, as seen in the Caribbean following disturbance events (Mumby et al. 2005). The impact of thermal stress on changes within the benthic community should continue to be investigated, particularly as it becomes more prevalent with climate change.

The decline in macroalgae in 2011 corresponded to the only significant increase in sponge cover. It is unclear whether sponges benefited from the newly available substrate or whether this may be an artifact of the removal of macroalgae from the image used to calculate cover. Sponges which lack chemical defense have previously been shown to grow rapidly after disturbance when predation pressure is low (Loh and Pawlik 2014, Wooster et al. 2017). Examination of any change in the sponge community during this period may therefore provide evidence of any decline in sponge predators or an increase in specific species lacking chemical defense. Octocoral cover did not change significantly overall on the SEFRT.

The benthic community of the SEFRT differed spatially, with ecosystem regions separating from one another based on the dominant taxa. Spatial differences in benthic composition have been reported previously on the SEFRT (Moyer et al. 2003, Banks et al. 2008, Collier et al. 2008, Walker and Gilliam 2013), but this is one of the first studies where spatiotemporal changes in cover within the benthic community have been investigated using the defined ecosystem regions from Walker (2012). The northernmost region, Martin, was distinctly different to all other regions, characterized by high macroalgae cover and an almost complete absence of octocorals. The high

macroalgae cover may be related to the proximity of this region to the St Lucie Inlet, with the nutrient enrichment it receives from the episodic draining of Lake Okeechobee (Lapointe et al. 2017). In addition, the lower mean annual temperature and shallow depth of the sites surveyed in the region may restrict the growth of other major space occupying benthic taxa, such as reef-building stony coral species and particularly octocorals, which had a significant positive relationship to increasing mean SST.

Octocoral and sponge cover was higher than stony coral cover in half of the ecosystem regions. Whether this results from increased resilience to or an absence of certain stressors that impact those taxa or is a function of higher current flow requires further investigation. Resilience has been posited as a cause of octocoral increase in the Florida Keys (Ruzicka et al. 2013), while current flow has been suggested for the increased abundance of cold water octocoral in temperate regions (Yesson et al. 2012). Deerfield, situated between two inlet channels and two outfalls had highest sponge cover, supporting Moyer et al. (2003). The location may result in an increased influx of nutrients and dissolved organic carbon (DOC) which have been shown to support sponge growth (Ward-Paige et al. 2005, Pawlik et al. 2016).

High stony coral cover regions had a positive association with heat stress duration, reflective of areas where temperatures were generally more conducive to reef-building coral growth. Broward contains the northernmost known thickets of *Acropora cervicornis* (Thomas et al. 2000, Vargas-Ángel et al. 2003), as well as large *Montastraea cavernosa* colonies and these provide the bulk of stony coral cover, as has been found previously in high-latitude and turbid systems (Rogers 1990, Moyer et al. 2003). While thermal stress was predicted to be negatively related to stony coral cover, growth of *A. cervicornis,* which provides high cover in specific areas in Broward and Miami, is highest when temperatures are between 28-30 °C (Shinn 1966). In addition, coral cover in both regions was highest on inner reef sites, suggesting that light attenuation may be impacting coral cover. Calcification rates have previously been found to be elevated in clear sunlit waters (Tomascik and Sander 1987) where irradiance is high. However the close proximity to shore may also increase turbidity,

with coral refugia predicted in other turbid, nearshore areas (Cacciapaglia and Woesik 2016, van Woesik and McCaffrey 2017).

While the overall pattern on the SEFRT of declining stony coral cover and increasing macroalgae cover was seen in most ecosystem regions, the taxonomic composition of benthic cover varied between regions and over time. Stony coral cover significantly decreased in half of the regions in 2016, with a significant negative latent effect of heat stress duration in two of these. A phase shift from stony coral to octocoral dominance occurred in Broward in 2016, the first time over the study period that stony coral was not the dominant faunal taxa of benthic cover there. The Broward region previously exhibited refugia characteristics for stony coral on the SEFRT, but declining cover and the subsequent phase shift suggest that resilience is compromised, particularly from heat stress and disease. Stony coral cover followed a similar trend to the other ecosystem regions and as reported in other studies in the Caribbean and Florida (Bruno et al. 2009, Ruzicka et al. 2013, Precht et al. 2016). It is paramount to understand the impact of declining cover on the composition of the coral community and the impact of phase shifts on the wider ecosystem. The degree to which stony coral cover has declined in relation to heat stress is likely influenced by the composition of the coral community and by local stressors as has been found elsewhere (McClanahan et al. 2012, Zaneveld et al. 2016). Understanding the interactive effect of local and global stress is vital to assess the prospects of resilience for stony corals.

In this study, a significant inverse relationship between octocoral cover and heat stress duration was found, supporting the idea of thermal stress as a cause of octocoral cover decline. Past thermal heat anomalies have caused significant declines in temperate and tropical gorgonians (Garrabou et al. 2009, Prada et al. 2010, Sammarco and Strychar 2013). For example, zooxanthellae symbionts present in alcyonaceans in the Pacific were found to be as susceptible to heat stress as those in scleractinians (Sammarco and Strychar 2013), while colonies of the genus *Muricea* suffered high mortality after thermal bleaching in Puerto Rico (Prada et al. 2010). In addition, periodic storm activity is likely to have reduced cover, with hurricanes and strong tropical storms found to remove octocorals at the holdfast (Woodley et al. 1981,

Yoshioka and Yoshioka 1991). Octocoral density on the SEFRT, like that in the Florida Keys (Ruzicka et al. 2013), is conversely increasing (Gilliam et al. 2017). The declining cover may represent the loss of large colonies, which contribute an increased proportion to canopy, and a concurrent increase in smaller colonies, or an increase in partial mortality from thermal stress or localized anthropogenic impact.

Sponge cover had a significant positive relationship with cold stress duration, with the only significant change following elevated cold stress in 2011. Increased cold stress duration may facilitate increases in sponge cover through space availability, particularly with it linked to a significant decline in macroalgae cover. A phase shift from octocoral to sponge dominance occurred in Deerfield in 2015 and this may give an insight into future change elsewhere if stony coral and octocoral cover continue to decline. Further study examining sponge community change is needed to assess the scale of these changes as phase shifts to sponge dominated reefs have been reported in the Caribbean (Aronson et al. 2002, Maliao et al. 2008, Norström et al. 2009).

Spatiotemporal variability was greatest in macroalgae cover and given the myriad of impacts that macroalgae can have on coral reefs the importance of this should not be overlooked. Significant increases were found in four of the six regions in 2016, with the increase concurrent to declining stony coral cover. Heat stress duration had a significant positive latent effect on macroalgae, while cold stress had a significant negative relationship with macroalgae cover. The lack of winter cooling in regions experiencing the greatest changes (South Palm Beach, Broward, Miami) appears to be enhancing the positive impact of heat stress. The lack of an increase in macroalgae cover in Deerfield in 2016 is likely a direct result of Hurricane Matthew, with two study sites surveyed post hurricane. Hurricanes have been shown to remove large areas of macroalgae in the Caribbean previously (Mumby et al. 2005). The cause of declining cover in Martin is not apparent and as the region is responding differently to all others, may require separating in future studies. Overall many of the regions on the SEFRT are now, like elsewhere in the Western Atlantic and Caribbean (Hughes 1994, Gardner et al. 2003, Jackson et al. 2014), largely dominated by macroalgae, particularly during summer.

At the start of this study ecosystem regions on the SEFRT could be separated by the cover of dominant taxa. While there is still variability between regions and they can still be characterized by these taxa, biotic homogenization is occurring throughout the SEFRT, with declines in stony coral and octocoral cover and replacement by macroalgae. With environmental conditions driving benthic cover to a new state recovery may be difficult and the potential loss of uniqueness of ecosystem regions is a major concern. Understanding the spatiotemporal variability experienced here is increasingly important in the context of local and global stress, particularly with the SEFRT towards the northern limit of reef-building stony coral distribution.

6. Conclusion

From 2007 – 2016 the SEFRT has seen significant changes in cover within the benthic community. Stony coral cover significantly declined in 2016 and hysteresis from elevated heat stress in 2014 and 2015 likely contributed to the decline seen in multiple ecosystem regions. Environmental conditions are facilitating benthic cover changes, while a concurrent increase in macroalgae may represent a negative feedback loop with coral cover which hinders recovery. Ecosystem regions showed strong spatial clustering based on the benthic community cover and spatiotemporal variation was seen on the SEFRT. Regional analysis identified significant changes in the taxonomic composition of benthic cover not seen on a larger scale and it is advised that these regions are used to analyze future changes to the benthic community. However, benthic homogenization is occurring over the SEFRT with outlier regions with higher cover experiencing significant declines. This loss of uniqueness on the SEFRT is a major concern and should be closely monitored globally. Temporal changes in the benthic community were intrinsically linked to temperature change. The impact of thermal stress, both hot and cold, should continue to be investigated, particularly as thermal stress events become more prevalent with climate change. The changes found on the SEFRT are likely to have a significant impact on the ecosystem services and with coral disease still prevalent and a negative feedback loop between stony coral and macroalgae predicted a continued decline in coral cover is expected.

7. References

Alvarez-Filip, L., J. A. Gill, and N. K. Dulvy. 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. Ecosphere **2**:1-17.

Aronson, R., W. Precht, M. Toscano, and K. Koltes. 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. Marine Biology **141**:435-447.

Aronson, R. B., and W. F. Precht. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs **25**:441-450.

Aronson, R. B., and D. W. Swanson. 1997. Video surveys of coral reefs: uni-and multivariate applications. Pages 1441-1446 *in* Proceedings of the 8th International Coral Reef Symposium. Smithsonian Tropical Research Institute.

Baird, A., B. Sommer, and J. Madin. 2012. Pole-ward range expansion of Acropora spp. along the east coast of Australia. Coral Reefs:1-1.

Baker, A. C., P. W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine, coastal and shelf science **80**:435-471.

Banks, K., B. Riegl, E. Shinn, W. Piller, and R. E. Dodge. 2007. Geomorphology of the southeast Florida continental reef tract (Miami-Dade, Broward, and Palm Beach counties, USA). Coral Reefs **26**:617-633.

Banks, K. W., B. M. Riegl, V. P. Richards, B. K. Walker, K. P. Helmle, L. K. Jordan, J. Phipps, M. S. Shivji, R. E. Spieler, and R. E. Dodge. 2008. The reef tract of continental southeast Florida (Miami-Dade, Broward and Palm Beach counties, USA). Pages 175-220 Coral Reefs of the USA. Springer.

Beger, M., B. Sommer, P. L. Harrison, S. D. Smith, and J. M. Pandolfi. 2014. Conserving potential coral reef refuges at high latitudes. Diversity and Distributions **20**:245-257.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in ecology & evolution **24**:127-135.

Boucek, R. E., and J. S. Rehage. 2014. Climate extremes drive changes in functional community structure. Global change biology **20**:1821-1831.

Box, S. J., and P. J. Mumby. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology Progress Series **342**:139-149.

Bruno, J. F., E. R. Selig, K. S. Casey, C. A. Page, B. L. Willis, C. D. Harvell, H. Sweatman, and A. M. Melendy. 2007. Thermal Stress and Coral Cover as Drivers of Coral Disease Outbreaks. PLOS Biology **5**:e124.

Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology **90**:1478-1484.

Burke, L. M., J. Maidens, M. Spalding, P. Kramer, and E. Green. 2004. Reefs at Risk in the Caribbean.

Burman, S. G., R. B. Aronson, and R. van Woesik. 2012. Biotic homogenization of coral assemblages along the Florida reef tract. Marine Ecology Progress Series **467**:89-96.

Cacciapaglia, C., and R. Woesik. 2016. Climate-change refugia: shading reef corals by turbidity. Global change biology **22**:1145-1154.

Cerrano, C., G. Bavestrello, C. N. Bianchi, R. Cattaneo-vietti, S. Bava, C. Morganti, C. Morri, P. Picco, G. Sara, S. Schiaparelli, A. Siccardi, and F. Sponga. 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean), summer 1999. Ecology letters **3**:284-293.

Chassignet, E. P., H. E. Hurlburt, E. J. Metzger, O. M. Smedstad, J. A. Cummings, G. R. Halliwell, R. Bleck, R. Baraille, A. J. Wallcraft, and C. Lozano. 2009. US GODAE: global ocean prediction with the HYbrid Coordinate Ocean Model (HYCOM). DTIC Document.

Chassignet, E. P., H. E. Hurlburt, O. M. Smedstad, G. R. Halliwell, P. J. Hogan, A. J. Wallcraft, R. Baraille, and R. Bleck. 2007. The HYCOM (HYbrid Coordinate Ocean Model) data assimilative system. Journal of Marine Systems **65**:60-83.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences 2nd edn. Erlbaum Associates, Hillsdale.

Collier, C., R. Ruzicka, K. Banks, L. Barbieri, J. Beal, D. Bingham, J. A. Bohnsack, S. Brooke, N. Craig, and L. E. Fisher. 2008. The state of coral reef ecosystems of southeast Florida. The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2008.

D'Angelo, C., and J. Wiedenmann. 2014. Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Current Opinion in Environmental Sustainability **7**:82-93.

De Goeij, J. M., D. Van Oevelen, M. J. Vermeij, R. Osinga, J. J. Middelburg, A. F. de Goeij, and W. Admiraal. 2013. Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science **342**:108-110.

Duckworth, A., N. Giofre, and R. Jones. 2017. Coral morphology and sedimentation. Marine pollution bulletin **125**:289-300.

Dustan, P., J. Leard, O. Meier, M. Brill, and V. Kosmynin. 1999. Point-Count 99 software. University of Charleston, South Carolina.

Eakin, C. M., J. A. Morgan, S. F. Heron, T. B. Smith, G. Liu, L. Alvarez-Filip, B. Baca, E. Bartels, C. Bastidas, C. Bouchon, M. Brandt, A. W. Bruckner, L. Bunkley-Williams, A. Cameron, B. D. Causey, M. Chiappone, T. R. L. Christensen, M. J. C. Crabbe, O. Day, E. de la Guardia, G. Díaz-Pulido, D. DiResta, D. L. Gil-Agudelo, D. S. Gilliam, R. N. Ginsburg, S. Gore, H. M. Guzmán, J. C. Hendee, E. A. Hernández-Delgado, E. Husain, C. F. G. Jeffrey, R. J. Jones, E. Jordán-Dahlgren, L. S. Kaufman, D. I. Kline, P. A. Kramer, J. C. Lang, D. Lirman, J. Mallela, C. Manfrino, J.-P. Maréchal, K. Marks, J. Mihaly, W. J. Miller, E. M. Mueller, E. M. Muller, C. A. Orozco Toro, H. A. Oxenford, D. Ponce-Taylor, N. Quinn, K. B. Ritchie, S. Rodríguez, A. R. Ramírez, S. Romano, J. F. Samhouri, J. A. Sánchez, G. P. Schmahl, B. V. Shank, W. J. Skirving, S. C. C. Steiner, E. Villamizar, S. M. Walsh, C. Walter, E. Weil, E. H. Williams, K. W. Roberson, and Y. Yusuf. 2010. Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. PloS one **5**:e13969.

Franklin, J. F. 1989. Importance and justification of long-term studies in ecology. Pages 3-19 Long-term studies in ecology. Springer.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science **301**:958-960.

Garrabou, J., R. Coma, N. Bensoussan, M. Bally, P. Chevaldonné, M. Cigliano, D. Diaz, J.-G. Harmelin, M. Gambi, and D. Kersting. 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Global change biology **15**:1090-1103.

Gilliam, D. S., C. J. Walton, N. K. Hayes, R. Ruzicka, M. A. Colella, and V. Brinkhuis. 2017. Southeast Florida Coral Reef Evaluation and Monitoring Project 2016 Year 14 Final Report. Florida DEP Report **RM143**.

Glynn, P. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs **12**:1-17.

Glynn, P. W. 1990. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. Elsevier oceanography series **52**:55-126.

Goldberg, J., and C. Wilkinson. 2004. Global threats to coral reefs: coral bleaching, global climate change, disease, predator plagues and invasive species. Status of coral reefs of the world **2004**:67-92.

Green, D. H., P. J. Edmunds, and R. C. Carpenter. 2008. Increasing relative abundance of Porites astreoides on Caribbean reefs mediated by an overall decline in coral cover. Marine Ecology Progress Series **359**:1-10.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'agrosa, J. F. Bruno, K. S. Casey, C. Ebert, and H. E. Fox. 2008. A global map of human impact on marine ecosystems. Science **319**:948-952.

Harborne, A. R., A. Rogers, Y.-M. Bozec, and P. J. Mumby. 2017. Multiple Stressors and the Functioning of Coral Reefs. Annual Review of Marine Science **9**:445-468.

Harley, C. D., A. Randall Hughes, K. M. Hultgren, B. G. Miner, C. J. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology letters **9**:228-241.

Harriott, V. J. 1985. Mortality rates of scleractinian corals before and during a mass bleaching event. Marine ecology progress series. Oldendorf **21**:81-88.

Heron, S. F., J. A. Maynard, R. Van Hooidonk, and C. M. Eakin. 2016. Warming trends and bleaching stress of the world's coral reefs 1985–2012. Scientific Reports **6**:38402.

Hoegh-Guldberg, O., and J. F. Bruno. 2010. The Impact of Climate Change on the World's Marine Ecosystems. Science **328**:1523-1528.

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, and K. Caldeira. 2007. Coral reefs under rapid climate change and ocean acidification. Science **318**:1737-1742.

Hoegh-Guldberg, O., E. S. Poloczanska, W. Skirving, and S. Dove. 2017. Coral Reef Ecosystems under Climate Change and Ocean Acidification. Frontiers in Marine Science **4**.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal **50**:346 - 363.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science-AAAS-Weekly Paper Edition **265**:1547-1551.

Hughes, T. P. 1996. Demographic approaches to community dynamics: a coral reef example. Ecology **77**:2256-2260.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. Jackson, and J. Kleypas. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301**:929-933.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, and R. Berkelmans. 2017. Global warming and recurrent mass bleaching of corals. Nature **543**:373.

Hughes, T. P., J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, and G. Liu. 2018. Global warming transforms coral reef assemblages. Nature **556**:492.

Jaap, W. C., J. H. Hudson, R. E. Dodge, D. S. Gilliam, and R. Shaul. 2006. Coral reef restoration with case studies from Florida.

Jackson, J., M. Donovan, K. Cramer, and V. Lam. 2014. Status and trends of Caribbean coral reefs: 1970-2012. Report, Washington, D.C.

Johns, K. A., M. J. Emslie, A. S. Hoey, K. Osborne, M. J. Jonker, and A. J. Cheal. 2018. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere **9**:e02349.

Johnston, M. W., and S. J. Purkis. 2015. Hurricanes accelerated the Florida–Bahamas lionfish invasion. Global change biology **21**:2249-2260.

Jones, R., P. Bessell-Browne, R. Fisher, W. Klonowski, and M. Slivkoff. 2016. Assessing the impacts of sediments from dredging on corals. Marine pollution bulletin **102**:9-29.

Kemp, D. W., M. A. Colella, L. A. Bartlett, R. R. Ruzicka, J. W. Porter, and W. K. Fitt. 2016. Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. Ecosphere **7**.

Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers & Geosciences **32**:1259-1269.

Kourafalou, V. H., and H. Kang. 2012. Florida Current meandering and evolution of cyclonic eddies along the Florida Keys Reef Tract: Are they interconnected? Journal of Geophysical Research. C. Oceans **117**.

Kourafalou, V. H., G. Peng, H. Kang, P. J. Hogan, O.-M. Smedstad, and R. H. Weisberg. 2009. Evaluation of global ocean data assimilation experiment products on South Florida nested simulations with the Hybrid Coordinate Ocean Model. Ocean Dynamics **59**:47-66.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series **323**:107-117.

Lamb, J. B., D. H. Williamson, G. R. Russ, and B. L. Willis. 2015. Protected areas mitigate diseases of reef-building corals by reducing damage from fishing. Ecology **96**:2555-2567.

Lapointe, B. E., L. W. Herren, and A. L. Paule. 2017. Septic systems contribute to nutrient pollution and harmful algal blooms in the St. Lucie Estuary, Southeast Florida, USA. Harmful Algae **70**:1-22.

Linares, C., R. Coma, D. Diaz, M. Zabala, B. Hereu, and L. Dantart. 2005. Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. Marine Ecology Progress Series **305**:127-137.

Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs **19**:392-399.

Lirman, D., S. Schopmeyer, D. Manzello, L. J. Gramer, W. F. Precht, F. Muller-Karger, K. Banks, B. Barnes, E. Bartels, A. Bourque, J. Byrne, S. Donahue, J. Duquesnel, L. Fisher, D. Gilliam, J. Hendee, M. Johnson, K. Maxwell, E. McDevitt, J. Monty, D. Rueda, R. Ruzicka, and S. Thanner. 2011. Severe 2010 Cold-Water Event Caused Unprecedented Mortality to Corals of the Florida Reef Tract and Reversed Previous Survivorship Patterns. PloS one **6**:e23047.

Liu, G., J. L. Rauenzahn, S. F. Heron, C. M. Eakin, W. J. Skirving, T. Christensen, A. E. Strong, and J. Li. 2013. NOAA coral reef watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management.

Loh, T.-L., and J. R. Pawlik. 2014. Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. Proceedings of the National Academy of Sciences **111**:4151-4156.

Lopez-Legentil, S., B. Song, S. E. Mcmurray, and J. R. Pawlik. 2008. Bleaching and stress in coral reef ecosystems: hsp70 expression by the giant barrel sponge Xestospongia muta. Molecular Ecology **17**:1840-1849.

Loya, Y., and B. Rinkevich. 1980. Effects of oil pollution on coral reef communities. Marine Ecology Progress Series:167-180.

Magurran, A. E., S. R. Baillie, S. T. Buckland, J. M. Dick, D. A. Elston, E. M. Scott, R. I. Smith, P. J. Somerfield, and A. D. Watt. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in ecology & evolution **25**:574-582.

Maliao, R. J., R. G. Turingan, and J. Lin. 2008. Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. Marine Biology **154**:841-853.

Manzello, D. P., R. Berkelmans, and J. C. Hendee. 2007. Coral bleaching indices and thresholds for the Florida Reef Tract, Bahamas, and St. Croix, US Virgin Islands. Marine pollution bulletin **54**:1923-1931.

Manzello, D. P., I. C. Enochs, G. Kolodziej, and R. Carlton. 2015. Coral growth patterns of Montastraea cavernosa and Porites astreoides in the Florida Keys: The importance of thermal stress and inimical waters. Journal of Experimental Marine Biology and Ecology **471**:198-207.

McClanahan, T. R., S. D. Donner, J. A. Maynard, M. A. MacNeil, N. A. Graham, J. Maina, A. C. Baker, M. Beger, S. J. Campbell, and E. S. Darling. 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. PloS one **7**:e42884.

Mokany, K., J. J. Thomson, A. J. J. Lynch, G. J. Jordan, and S. Ferrier. 2015. Linking changes in community composition and function under climate change. Ecological Applications **25**:2132-2141.

Moyer, R. P., B. Riegl, K. Banks, and R. E. Dodge. 2003. Spatial patterns and ecology of benthic communities on a high-latitude South Florida (Broward County, USA) reef system. Coral Reefs **22**:447-464.

Muir, P. R., C. C. Wallace, T. Done, and J. D. Aguirre. 2015. Limited scope for latitudinal extension of reef corals. Science **348**:1135-1138.

Muller, E., C. S. Rogers, A. S. Spitzack, and R. Van Woesik. 2008. Bleaching increases likelihood of disease on Acropora palmata (Lamarck) in Hawksnest Bay, St John, US Virgin Islands. Coral Reefs **27**:191-195.

Mumby, P. J., N. L. Foster, and E. A. G. Fahy. 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs **24**:681-692.

Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends in ecology & evolution **23**:555-563.

Neumann, B., A. T. Vafeidis, J. Zimmermann, and R. J. Nicholls. 2015. Future coastal population growth and exposure to sea-level rise and coastal flooding-a global assessment. PloS one **10**:e0118571.

Norström, A. V., M. Nyström, J. Lokrantz, and C. Folke. 2009. Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Marine Ecology Progress Series **376**:295-306.

O'Neil, J., T. W. Davis, M. A. Burford, and C. Gobler. 2012. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. Harmful Algae **14**:313-334.

Pandolfi, J. M., S. R. Connolly, D. J. Marshall, and A. L. Cohen. 2011. Projecting coral reef futures under global warming and ocean acidification. Science **333**:418-422.

Pastorok, R. A., and G. R. Bilyard. 1985. Effects of sewage pollution on coral-reef communities. Marine Ecology Progress Series:175-189.

Pawlik, J. R., D. E. Burkepile, and R. V. Thurber. 2016. A vicious circle? Altered carbon and nutrient cycling may explain the low resilience of Caribbean coral reefs. BioScience **66**:470-476.

Porter, S., and M. Schleyer. 2017. Long-term dynamics of a high-latitude coral reef community at Sodwana Bay, South Africa. Coral Reefs **36**:369-382.

Prada, C., E. Weil, and P. Yoshioka. 2010. Octocoral bleaching during unusual thermal stress. Coral Reefs **29**:41-45.

Precht, W. F., and R. B. Aronson. 2004. Climate flickers and range shifts of reef corals. Frontiers in Ecology and the Environment **2**:307-314.

Precht, W. F., B. E. Gintert, M. L. Robbart, R. Fura, and R. Van Woesik. 2016. Unprecedented disease-related coral mortality in Southeastern Florida. Scientific Reports **6**:31374.

R Core Team. 2016. R: A language and environment for statistical computing.

Riegl, B. 2003. Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). Coral Reefs **22**:433-446.

Roessig, J. M., C. M. Woodley, J. J. Cech, and L. J. Hansen. 2004. Effects of global climate change on marine and estuarine fishes and fisheries. Reviews in Fish Biology and Fisheries **14**:251-275.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine ecology progress series. Oldendorf **62**:185-202.

Ruzicka, R., M. Colella, J. Porter, J. Morrison, J. Kidney, V. Brinkhuis, K. Lunz, K. Macaulay, L. Bartlett, and M. Meyers. 2013. Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Marine Ecology Progress Series **489**:125-141.

Sammarco, P. W., and K. B. Strychar. 2013. Responses to high seawater temperatures in zooxanthellate octocorals. PloS one **8**:e54989.

Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Marine Ecology Progress Series **402**:115-122.

Serrano, E., R. Coma, M. Ribes, B. Weitzmann, M. García, and E. Ballesteros. 2013. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean. PloS one **8**:e52739.

Shafir, S., J. Van Rijn, and B. Rinkevich. 2007. Short and long term toxicity of crude oil and oil dispersants to two representative coral species. Environmental science & technology **41**:5571-5574.

Sheppard, C., D. J. Dixon, M. Gourlay, A. Sheppard, and R. Payet. 2005. Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. Estuarine, coastal and shelf science **64**:223-234.

Shinn, E. 1966. Coral growth-rate, an environmental indicator. Journal of Paleontology:233-240.

Small, C., and R. J. Nicholls. 2003. A global analysis of human settlement in coastal zones. Journal of Coastal Research:584-599.

Smol, J. P., A. P. Wolfe, H. J. B. Birks, M. S. Douglas, V. J. Jones, A. Korhola, R. Pienitz, K. Rühland, S. Sorvari, and D. Antoniades. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. Proceedings of the National Academy of Sciences of the United States of America **102**:4397-4402.

Stevens, G. C. 1989. The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in the Tropics. The American Naturalist **133**:240-256.

Storlazzi, C. D., B. K. Norris, and K. J. Rosenberger. 2015. The influence of grain size, grain color, and suspended-sediment concentration on light attenuation: Why fine-grained terrestrial sediment is bad for coral reef ecosystems. Coral Reefs **34**:967-975.

Stubler, A. D., A. R. Duckworth, and B. J. Peterson. 2015. The effects of coastal development on sponge abundance, diversity, and community composition on Jamaican coral reefs. Marine pollution bulletin **96**:261-270.

Suchley, A., M. D. McField, and L. Alvarez-Filip. 2016. Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs. PeerJ **4**:e2084.

Thomas, J., R. Dodge, and D. Gilliam. 2000. Occurrence of staghorn coral (Acropora cervicornis) outcrops at high latitudes in nearshore waters of Fort Lauderdale, Florida, USA. Pages 255-258 *in* Proc 9th Int Coral Reef Symp Abstr.

Tilmant, J. T., R. W. Curry, R. Jones, A. Szmant, J. C. Zieman, M. Flora, M. B. Robblee, D. Smith, R. Snow, and H. Wanless. 1994. Hurricane Andrew's effects on marine resources. BioScience **44**:230-237.

Tomascik, T., and F. Sander. 1987. Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Marine biology. Berlin, Heidelberg **94**:53-75.

Toth, L., R. Van Woesik, T. Murdoch, S. Smith, J. Ogden, W. Precht, and R. Aronson. 2014. Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. Coral Reefs **33**:565-577.

van Woesik, R., and K. R. McCaffrey. 2017. Repeated thermal stress, shading, and directional selection in the Florida reef tract. Frontiers in Marine Science **4**:182.

Vargas-Ángel, B., J. D. Thomas, and S. M. Hoke. 2003. High-latitude Acropora cervicornis thickets off Fort Lauderdale, Florida, USA. Coral Reefs **22**:465-473.

Vergés, A., P. D. Steinberg, M. E. Hay, A. G. Poore, A. H. Campbell, E. Ballesteros, K. L. Heck, D. J. Booth, M. A. Coleman, and D. A. Feary. 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Page 20140846 *in* Proc. R. Soc. B. The Royal Society.

Veron, J. E. N. 1995. Corals in space and time: the biogeography and evolution of the Scleractinia. Cornell University Press.

Walker, B. K. 2012. Spatial analyses of benthic habitats to define coral reef ecosystem regions and potential biogeographic boundaries along a latitudinal gradient. PloS one **7**:e30466.

Walker, B. K., and D. S. Gilliam. 2013. Determining the extent and characterizing coral reef habitats of the northern latitudes of the Florida Reef Tract (Martin County). PloS one **8**:e80439.

Walker, B. K., D. S. Gilliam, R. E. Dodge, and J. Walczak. 2012. Dredging and shipping impacts on southeast Florida coral reefs.

Walker, B. K., and K. Klug. 2014. Southeast Florida Shallow-Water Habitat Mapping & Coral Reef Community Characterization.

Walker, B. K., B. Riegl, and R. E. Dodge. 2008. Mapping coral reef habitats in southeast Florida using a combined technique approach. Journal of Coastal Research:1138-1150.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Ward-Paige, C. A., M. J. Risk, O. A. Sherwood, and W. C. Jaap. 2005. Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. Marine pollution bulletin **51**:570-579.

Wold, S., K. Esbensen, and P. Geladi. 1987. Principal component analysis. Chemometrics and intelligent laboratory systems **2**:37-52.

Woodley, J., E. Chornesky, P. Clifford, J. Jackson, L. Kaufman, N. Knowlton, J. Lang, M. Pearson, J. Porter, and M. Rooney. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science **214**:749-755.

Wooster, M. K., M. J. Marty, and J. R. Pawlik. 2017. Defense by association: Sponge-eating fishes alter the small-scale distribution of Caribbean reef sponges. Marine Ecology **38**.

Yamano, H., K. Sugihara, and K. Nomura. 2011. Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. Geophysical Research Letters **38**.

Yesson, C., M. L. Taylor, D. P. Tittensor, A. J. Davies, J. Guinotte, A. Baco, J. Black, J. M. Hall-Spencer, and A. D. Rogers. 2012. Global habitat suitability of cold-water octocorals. Journal of Biogeography **39**:1278-1292.

Yoshioka, P. M., and B. B. Yoshioka. 1991. A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. Marine Ecology Progress Series:253-260.

Zaneveld, J. R., D. E. Burkepile, A. A. Shantz, C. E. Pritchard, R. McMinds, J. P. Payet, R. Welsh, A. M. Correa, N. P. Lemoine, and S. Rosales. 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nature communications **7**:11833.