The Disturbance Response Monitoring within the Florida Reef Resilience Program: data synthesis

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Abstract

The Florida reef Resilience Program (FRRP) implemented a Disturbance Response Monitoring Protocol that was designed in 2005 to determine the status of the coral assemblages in south Florida and determine to what extent the corals were being impacted by thermal stress events. The FRRP used a probabilistic, two stage, stratified randomized survey design to assess the condition of stony corals during peak thermal stress events. At each of 1176 sites, examined over a period of six years, three main parameters were recorded within replicated 10 m^2 belt transects: i) coral species, ii) percentage dead tissue, and iii) colony condition, including disease prevalence and bleaching. This approach provided detailed information on the coral populations' size-frequency distributions, coral cover, and bleaching and disease prevalence. The present study revisited the FRRP sampling framework, which was based on oceanography and reef geomorphology, and examined trends in the sampling strata (i.e., time, depth, subregions, and zones). This study sought to determine (i) whether the defined strata accurately described the coral assemblages and (ii) and whether there was a more optimal approach. We tested the hypothesis that the reef-coral assemblages had become more homogeneous through time, and what such homogenization might mean for reef resilience. There was minimal biological stratification among temporal batches and across depths. Of the nine subregions that were initially allocated by the FRRP, six were found to be redundant in the present study. The coral communities differed in accordance with three main geographic subregions: 1) Martin, 2) Palm Beach and Broward, and 3) Biscayne, Upper Keys, Middle Keys, Lower Keys, Marquesas, and the Dry Tortugas. In recent years, major declines in the primary-reef building corals *Acropora palmata*, *Acropora cervicornis*, and *Montastraea faveolata* have homogenized the Florida reef zones. In their present state the reefs in Florida may be more stable than reefs in the past but there has been a fundamental change in their capacity to maintain key processes and functions (i.e., their capacity to build reefs) because they support fewer reef-building species than in the past.

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Introduction

The coral reefs of southern Florida reefs are at the northern extreme of potential reef-building capacity (Ginsburg and Shinn 1964). As a result, they are subject to frequent temperature stress (Precht & Miller 2007). Over the past three decades, however, the corals on the reefs of south Florida have dramatically declined (Dustan and Halas 1987, Porter and Meier 1992, Gardner et al. 2003, Palandro et al. 2008). The decline has been attributed to coral disease, thermal stress, and *Diadema antillarum* die-off (Jackson 1991; Aronson and Precht 2001; Precht and Miller 2007). Death of the major reef builders lead Jackson (1991) to note that the reef zonation had "changed, and there is little indication of rapid return to the original patterns". Here we investigate the hypothesis that thermal stress and disease has targeted specific corals that delineated reef assemblages, and as a result, the Florida reef tract has become more homogeneous in recent times. We also intend to question what such homogenization may mean for reef resilience. The best means of determining to what extent the Florida reefs have changed and whether they are now more homogenous than in the past is to compare the modern reefs with past assemblages.

In 1885, Agassiz described extensive patches of *Acropora cervicornis* in the Tortugas. He noted that *Porites spp.* clusters covered the shallow sand patches, and abundant colonies of *Meandrina meandrites* grew between the patches of macroalgae (Agassiz 1885). Further from shore, Agassiz described “huge masses” of *Montastraea spp.* and *Meandrina meandrites*, alongside dominating patches of *Acropora palmata* (Agassiz 1885). Agassiz also spoke of the zonation north of the Tortugas, in the Florida Keys reef tract. Hawks channel was characterized by a few large heads of *Meandrina spp. and Montastraea spp.*, and “luxuriant” growth of *Acropora cervicornis* along the sides of the channel (Agassiz 1885). Much of the outer Florida reef appeared similar to that noted in the Tortugas, with masses of *Montastraea spp.* and *Meandrina meandrites,* and dominated by *Acropora palmata* (Agassiz 1885, Marszalek et al. 1977, Ginsburg et al. 2001). In the 1970s, small heads of *Acropora spp.*, *Porites spp.,* and *Siderastrea spp.* were found inshore (Marszalek et al. 1977) (Figure 1).

Through the early transgression (~12,000 years ago) until around 4000 years ago, actively growing reefs extended as far north as Jupiter Inlet (Banks et al. 2007, Shaler 1890). The reefs ceased actively growing around 3,700 years ago, the reason for which is still not perfectly clear (Banks et al. 2007), although coral assemblages still extended to Jupiter Inlet, active reef growth has been evident only south of Miami. The assemblages north of Miami supported *Manicina areolata,* some as large as 0.7 m in diameter (Shaler 1890). Few records exist describing the reefs north of Miami, before the 1970s, although Goldberg (1973) suggested that there were 5 main reef zones, 3 of which were dominated by coral assemblages: i) inshore areas, dominated by *Siderastrea radians,* (ii) the channel, although not well defined, was relatively devoid of coral, (iii) a second reef terrace offshore, with 15 coral species - most abundant were *Oculina diffusa, Solenastrea hyades, Dichocenia stokesii,* and *Montastraea cavernosa,* although most of these colonies were small (< 15 cm), (iv) the outer reef crest, which supported *Acropora cervicornis*, *Meandrina meandrites, Agaricia agaricites,* and all of the back-reef species, except *Oculina diffusa*, (v) the reef slope was dominated by gorgonians, with patches of *Montastraea cavernosa* and *Agaricia lamarcki* (Goldberg 1973). Although *Acropora cervicornis* and *Montastraea annularis* complex were present north of Miami, they were much less abundant than they were south of Miami (Goldberg 1973). The species that clearly separated the north from the south assemblages were *Acropora palmata*, *Porites porites,* and *Diploria strigosa* (Vaughan 1919; Goldberg 1973). *Acropora cervicornis* was far more prolific south of Miami (Goldberg 1973, Agassiz 1885). *Monastraea annularis* complex substantially out-competed the more widely distributed *Montastraea cavernosa* south of Miami as well (Goldberg 1973). These six species play an important part in differentiating different regions of the reef tract.

Beginning in the 1960s, the main reef-building corals suffered extensively from a variety of diseases (Gladfelter 1982, Rutzler et al. 1983, Ginsburg et al. 2001, Patterson et al. 2002, Williams and Miller 2005, Aronson and Precht 2001). It is difficult to determine the prevalence or even the presence of past diseases on corals using proxy paleo-records, and it is unlikely that diseases are new to Florida reefs; yet, white-band disease was first recorded causing problems on *Acropora palmata* populations in the 1960s. Over the course of two decades white-band disease decreased the population of *Acropora palmata* substantially (Gladfelter 1982, Porter and Meier 1992). In the mid-1990s, *Acropora palmata* coverage was about 10% in some locations in the Florida Keys. The outbreak of white pox decimated the population, reducing coral coverage to less than 2% by 1999 (Patterson et al. 2002). Shortly after the infection of white-band disease in *Acropora palmata*, *Acropora* cervicornis was infected with a similar disease (Aronson and Precht 2001). The disease virtually wiped out the *Acropora cervicornis* population from 2002 through 2004 in the Florida Keys (Williams and Miller 2005). Approximately a decade after the 1960s epidemic affected *Acropora palmata*, black-band disease began afflicting other major reef builders (Rutzler et al. 1983). The species most susceptible to black-band disease infection were *Diploria strigosa* and *Montastraea annularis* complex (Rutzler et al. 1983), which previously were instrumental in delineating the assemblages in the north and south systems (Goldberg 1973).

Past cold-water temperature anomalies have caused intermittent and extensive mortality of *Acropora cervicornis* (Shinn 1986, Jaap and Hallock 1990, Precht & Miller 2007). Temperature changes have been recorded as both extreme cold snaps (Burns 1985, Lirman et al. 2011), and more recently as warming events (Wagner et al. 2010), resulting in extensive coral mortality in both cases. Over the course of three decades, the coral species that identified unique zones were nearly eliminated, whereas other species increased in relative abundance. The diseases reduced the biological and habitat diversity of the Florida reef tract (Gladfelter 1982, Patterson et al. 2002, Dustan and Halas 1987, Jackson 1991) and appear to have homogenized the system. In this study we test the hypothesis that the reef-coral assemblages have recently become more homogeneous. And we ask the question: What might homogenization mean for reef resilience? Decreases in species and habitat diversity have been found to diminish resilience (Thrush et al. 2008, Elmqvist et al. 2003) and decrease system stability (Doak et al. 1998, Tilman et al. 1998). We expect that the homogenization across zones and habitats will diminish the system's resilience, or the amount of stress the system can withstand before undergoing a significant loss of system function (Holling 1973). Resilience is imperative for the survival of the Florida reefs.

In order to examine the extent to which the corals were impacted by thermal disturbances the Nature Conservancy developed a sampling design in 2005 to assess the condition of stony corals in south Florida. The sampling strategy was specifically designed to examine stony coral densities (Smith et al. 2011). Sampling also estimated benthic cover, size-frequency distributions, bleaching, and disease. The sampling domain was stratified *a priori* using geological and hydrological features into coral subregions and zones. The working hypothesis was that the recent loss of specialist species, from disease and the frequent thermal stress events, homogenized the Florida reef assemblages. The primary objectives were to: 1) evaluate the value of the organizational structure of the sampling design using biological instead of geological and hydrological data; 2) where appropriate, explore a sampling design which may be more consistent with the demarcations seen in the biological data; 3) compare this holistic framework to early accounts of reef structure; and 4) evaluate the changes to the reef and determine the extent of homogenization.

Methods

Sampling design

In 2005, the Florida Reef Resilience Program (FRRP) developed a probabilistic, two stage, stratified randomized sampling strategy to examine the reef corals in Southern Florida. The sampling domain was stratified into 13 geographic subregions and 14 characteristic reef zones. Within these stratified domains, the primary sampling units were 200 m by 200 m sites, which were assessed at the second tier using two randomly selected 10 m by 1 m wide transects. Within each transect, three main parameters are recorded for each stony coral colony >4cm: (i) coral species, (ii) percent dead tissue (both recent and old mortality), and (iii) coral condition, including disease prevalence and bleaching. This sampling design was employed from 2005 to 2010. During these years, sampling was undertaken at different times throughout the year during thermal stress events, either in summer or winter.

Subregions and reef zones were defined *a priori* by a variety of reef experts. Subregions, from north to south were, Martin (sites, n=29), Palm Beach (n=51), Broward (n=253), Biscayne (n=192), Upper Keys (n=231), Middle Keys (n=122), Lower Keys (n=251), Marquesas (n=6), Marquesas-Tortugas Transition (n=0), Unmapped Tortugas (n=0), Dry Tortugas (n=49), Tortugas Bank (n=2), and Riley's Hump (n=0) (Table 1). For the purposes of analyses, any subregions with no samplings were eliminated. The Tortugas Bank was combined with the Dry Tortugas, yielding a Tortugas subregion (n=51). On the mainland, subregions stretched the coastal length of the respective counties, the Upper Keys extend from Key Largo through Tavernier, the Middle Keys extend from Plantation Key through Marathon, and the Lower Keys extend from Ohio Key through Key West (Figure 2).

The Zones, from North to South, and from nearest to farthest from shore were, Undetermined (n=29), Reef Ridge Complex (n=34), Inner Reef (n=70), Outer Reef (n=55), Inshore Reef (n=210), Midchannel Reef (n=205), Offshore Patch Reef (n=91), Forereef (n=478), Deep Reef (n=6), Intra-island (n=1), Lagoon (n=5), Banks (n=2), New Grounds (n=0), and Back Country Reef (n=0) (Table 1). For analytical purposes zones with no sites were eliminated, as were zones with fewer than 10 sites (Deep Reef, Intra-island, Lagoon, and Banks; Table 1). The four zones off the coast of the Marquesas, Lower Keys, Middle Keys, Upper Keys, and Biscayne subregions were: Inshore (inshore of Hawk's Channel), Mid-channel (in Hawk's Channel), Offshore Patch Reef (Outside of the channel), and Forereef (beyond the patch reefs; Table 1) . North of this area are the Broward and Palm Beach subregions (Table 1). In the Broward subregion, there was no distinct channel, the zones were: Inshore, Inner Reef (the reef between the inshore and the offshore patches, but not specifically defined by any channel), Offshore Patch Reef, Outer Reef (functionally similar to Forereef; Table 1). In the Palm Beach subregion, there were two zones: Inshore and Reef Ridge Complex (the aptly named complex of reefs on the Reef Ridge; Table 1). The reefs in the Martin subregion were allocated to an undefined zone (Table 1).

Data analysis

Mean counts were calculated across transects within the same 200 m x 200 m site (primary sampling unit). Organizational factors, for each site, included sampling period (batch), depth class, subregion, zone, and habitat class. To examine the extent of similarity in species assemblages across subregions and zones, the data were brought into Primer 6©, where Bray-Curtis dissimilarities were computed, and Analysis of Similarities (ANOSIM) were conducted. The resemblance matrix derived from the ANOSIM was plotted using the myImagePlot (http://www.phaget4.org/R/myImagePlot.R) tool in R (R Core Development Team, 2011).

Two dimensional non-metric multidimensional scaling (NMDS) was used to generate plots. An inset 2D NMDS was then generated eliminating one point from the Martin subregion and Undertermined zone. Another inset NMDS was generated, with yet an additional five points eliminated, two were from the Martin subregion and Undetermined zone, two were in the Upper Keys subregion and Inshore zone, and one in the Broward subregion and Inshore zone. The coordinates were matched with their respective subregion and zone designations, and imported into R (R Core Development Team, 2011). The spatstat package (Baddeley and Turner 2005) was used to generate point patterns. A density function was then run on the subsequent points and plotted as density contours.

Results

Across all nine sampling periods (herein batches), there was very little variation in the ANOSIM R-scores, indicating that the batches, regardless of year or time of year, were true replicates through time (Figure 1). Additionally, all three depth classes were about equally dissimilar (Figure 2). There was however consistent stratification between subregions, yielding three distinct sets (Figure 3). The Martin subregion was unique. Palm Beach and Broward were similar in the ANOSIM, and the third subregion incorporated Biscayne, Upper Keys, Middle Keys, Lower Keys, Marquesas, and Tortugas (Figure 4). This amalgamation was reinforced by the NMDS (Figure 5). Zonation patterns were less apparent, except when the least abundant zones were removed and it became apparent that the Undetermined zone, which was found only in the Martin subregion, was unique (Figure 6). The zones found exclusively in the Palm Beach and Broward subregions (Reef Ridge Complex, Inner Reef, and Outer reef) were very similar (Figures 6). Those zones found only from the Biscayne subregion south (Midchannel Reef, Offshore Patch Reef, Forereef) were also very similar (Figure 5). The Inshore zone was found to be similar to both of these amalgamations (Figure 5), whereas the NMDS contours indicated that the Inshore zone was more similar to the zones (Reef Ridge Complex, Inner Reef, Outer Reef) in the Palm Beach and Broward areas (Figure 7). The most abundant species across all subregions and zones was *Siderastrea siderea* (Tables 2, 3); *Montastraea cavernosa* was substantially more abundant than the total of all other species in the *Montastraea annularis* complex (Tables 2, 3).

Discussion

The southern reefs of Florida once supported "luxuriant" growth of *Acropora cervicornis*, dense clusters of *Acropora palmata* on the offshore crests, and clusters of *Montastraea annularis* complex throughout (Agassiz 1885, Marszalek et al. 1977, Vaughan 1919; Figure 7). By contrast, the northern reefs were dominated by *Montastraea cavernosa* (Vaughan 1919), *Siderastrea siderea*, *Oculina diffusa*, *Solenastrea hyades*, and *Dichocenia stokesii* (Goldberg 1973). Over the last century, coral diseases have eliminated many of the vulnerable coral species that were exclusive to the southern regions (Gladfelter 1982, Rutzler et al. 1983, Ginsburg et al. 2001, Patterson et al. 2002, Williams and Miller 2005, Aronson and Precht 2001; Figure 7).

It can be expected that many of the once abundant coral species that delineated the southern Florida reefs in the past, but were vulnerable to diseases, may have been replaced by more tolerant species from the northern reef track. Indeed, *Siderastrea siderea* is now the most abundant species on the Florida reef tract (Table 2). *Montastraea cavernosa*, which was not common on southern reefs in the past, and may have been outcompeted by *Montastrea annularis* complex (Goldberg 1973), is today abundant on contemporary southern reefs (Table 2). While still different from the reefs in the north, the reefs in the south are now substantially less distinct from the northern reefs of the past (Agassiz 1885, Golberg 1973, Marszalek et al. 1977).

Across the shelf, near shore reefs were once (south of Miami) dominated, almost exclusively, by *Acropora cervicornis* (Agassiz 1885). Today, however, *Siderastrea siderea* is more than ten-times as abundant as any other species (Table 3). *Acropora palmata* is exceptionally uncommon – it can no longer really even be considered a meaningful contributor of cross-shelf zonation

(Table 3). The real questions are: (i) will the Florida reefs remain in their current depauperate states? (2) Will the reefs continue to decline further? (3) Will the reefs recover? The Florida reef tract has encountered a number of disturbances, some of which were overcome (Mayer 1903), others which were not (Gladfelter 1982, Rutzler et al. 1983, Ginsburg et al. 2001, Patterson et al. 2002, Williams and Miller 2005, Aronson and Precht 2001, Precht and Miller 2007). It is important to consider what sets the lasting events apart from ephemeral issues.

Red tide events, for example, have in the past caused mass coral mortality (Mayer 1903). The red tide event in 1878 drifted out to the Tortugas reefs, killing the entire population of *Acropora cervicornis* (Mayer 1903). The population still had not recovered 25 years later (Mayer 1903). Remarkably, *Porites spp.*, and *Meandrina spp*. were unaffected (Mayer 1903). Therefore, the red tide event only affected one species. While the reefs have recovered after red-tides, as in 1878 (Mayer 1903), thermal stress affects multiple species (van Woesik et al. 2011; Chapman 2011). This trajectory is emblematic of the larger issue of resilience.

The coral decline throughout the Florida reef tract has not been unilateral, but has instead affected the species that were most significant in delineating the regions of the reef. The corals affected were the ones with the narrowest spatial distributions, or the 'specialists'. Generalists, like the corals that persist on the reefs today are the most resilient (van Woesik and Done 1997). They have withstood a number of disturbances, and will be much more resistant to climate change. Eventually, over time, they may become as pervasive as the specialists once were throughout the Florida reefs. That does not mean, however, that the reefs of Florida will ever look the way they once did. Indeed, in their present state the reefs in Florida may be more stable than reefs in the past but there has been a fundamental change in their capacity to maintain key processes and functions (i.e., their capacity to build reefs) because they support fewer reef-building species than in the past. The diversity of habitat has been lost, and as a result the reefs will remain a homogenized and depauperate system.

Recommendations

The extent and stratified nature of the Florida Reef Resilience Program sampling is laudable and unprecedented in coral-reef ecology. For future sampling we recommend the same experimental design, but during the analysis stage we recommend the use of: 1) three main subregions: i) Martin, ii) Palm Beach and Broward, and iii) the southern subregion, incorporating Biscayne, Upper Keys, Middle Keys, Lower Keys, Marquesas, and Tortugas, and 2) four main zones: i) Undetermined reefs in Martin County, ii) Inner, Outer and Reef-Ridge Complex north of Biscayne Bay, iii) the Inshore zone, and iv) the Mid-channel, Offshore Patch Reef and Forereef zone south of Broward.

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Table 1. Cross-tabulation matrix indicating the zones that were present (shaded) in the respective subregions. Notably, many subregions contained unique zones not found in other subregions. The converse was also true, as many zones were unique to only one or two subregions.

		Subregion								
		Martin	Palm Beach	Broward	Biscayne	Upper Keys	Middle Keys	Lower Keys	Marquesas	Tortugas
Zone	Undetermined	■								
	Reef Ridge Complex		■							
	Inner Reef			■						
	Outer Reef			■						
	Inshore Reef		■	■	■	■	■	■	■	
	Midchannel Reef				■	■	■	■	■	
	Offshore Patch Reef				■	■	■	■	■	
	Forereef				■	■	■	■	■	■

Table 2. The mean (per-site, per-transect) abundance of corals in the Florida Reef Tract defined as amalgamations of subregions, identified in the present study, and sorted in descending order, and where no records indicates that the species was not present or present at densities < 0.01.

Coral species	Martin	Palm Beach Broward	South of Miami
Siderastrea siderea	2.84	1.87	7.84
Millepora alcicornis	0.4	2.39	9.19
Porites astreoides	0.38	2.4	4.6
Stephanocoenia intersepta	0.07	2.09	3.39
Montastraea cavernosa	0.12	2.09	2.04
Siderastrea radians	2.59	0.41	0.96
Porites porites		0.45	1.9
Diploria clivosa	1.88	0.18	0.29
Agaricia agaricites		0.2	2.13
Dichocoenia stokesi	0.07	0.71	1.41
Diploria strigosa	0.53	0.15	0.49
Solenastrea bournoni	0.1	0.53	0.45
Montastraea faveolata		0.11	0.94
Oculina diffusa	1	0.01	0.01
Meandrina meandrites		0.68	0.32
Colpophyllia natans		0.11	0.66
Madracis decactis		0.4	0.17
Porites furcata			0.57
Montastraea franksi		0.02	0.44
Porites divaricata		0.04	0.38
Montastraea annularis		0.04	0.34
Eusmilia fastigiata		0.09	0.28
Millepora complanata	0.17	0.01	0.19
Diploria labyrinthiformis		0.02	0.32
Acropora cervicornis		0.23	0.11
Agaricia lamarcki		0.07	0.21
Isophyllia sinuosa	0.07		0.05
Favia fragum		0.02	0.08
Porites branneri			0.09
Mussa angulosa		0.01	0.07
Manicina areolata			0.06
Solenastrea hyades			0.06
Agaricia fragilis		0.06	
Leptoseris cucullata		0.01	0.03
Madracis mirabilis		0.01	0.03
Madracis formosa			0.03
Acropora palmata			0.02
Cladacora arbuscula			0.02
Isophyllastrea rigida			0.02
Acropora prolifera			0.01
Agaricia humilis			0.01
Mycetophyllia ferox			0.01
Mycetophyllia aliciae		0.01	
Mycetophyllia lamarckiana		0.01	
Scolymia cubensis		0.01	
Agaricia tenuifolia			
Dendrogyra cylindrus			

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Table 3. The mean (per-site, per-transect) abundance of corals in the Florida Reef Tract by zone, sorted in descending order, and where no records indicates that the species was not present or present at densities < 0.01.

Coral species	Undetermined	Ridge Complex	Inner	Outer	Inshore	Mid Channel	Offshore Patch	Forereef
Siderastrea siderea	2.84	2.01	2.19	1.99	3.6	14.27	10.57	4.67
Millepora alcicornis	0.4	3.94	2.71	2.11	2.35	6.58	10.2	10.82
Porites astreoides	0.38	1.32	1.28	2.29	3.3	6.3	5.3	3.95
Stephanocoenia intersepta	0.07	1.74	3.38	2.71	1.62	5.98	5.58	2.04
Montastraea cavernosa	0.12	4.09	2.07	2.91	1.3	3.02	1.93	1.67
Porites porites			0.34	0.24	0.7	3.14	3.01	1.35
Siderastrea radians	2.59	0.99	0.26	0.15	1.02	1.3	0.72	0.7
Agaricia agaricites		0.44	0.13	0.22	0.29	1.88	2.25	2.44
Dichocoenia stokesi	0.07		0.51	0.41	1.09	2.35	1.85	0.93
Meandrina meandrites		0.99	1.06	0.96	0.25	0.28	0.34	0.33
Montastraea faveolata			0.17	0.2	0.38	1.75	0.8	0.61
Solenastrea bournoni	0.1	0.25	0.31	0.18	0.84	0.78	0.55	0.25
Colpophyllia natans		0.07	0.11	0.04	0.32	1.59	0.85	0.23
Diploria clivosa	1.88		0.03		0.37	0.42	0.25	0.24
Diploria strigosa	0.53	0.26	0.11	0.12	0.31	0.81	0.53	0.3
Porites furcata					0.22	0.82	1.13	0.34
Porites divaricata			0.07		0.24	0.34	1.26	0.2
Eusmilia fastigiata		0.07	0.13	0.16	0.08	0.44	0.66	0.15
Montastraea annularis		0.09		0.09	0.19	0.84	0.16	0.14
Montastraea franksi		0.06		0.04	0.09	0.4	0.33	0.47
Diploria labyrinthiformis					0.25	0.6	0.32	0.14
Madracis decactis		0.34	0.44		0.08	0.05	0.13	0.24
Dendrogyra cylindrus		1.09				0.01		
Agaricia lamarcki		0.06	0.07	0.11	0.02	0.17	0.41	0.21
Oculina diffusa	1				0.01	0.04		
Madracis formosa				0.95		0.03		0.04
Acropora cervicornis					0.34	0.18	0.31	0.06
Millepora complanata	0.17				0.01	0.07	0.08	0.27
Mussa angulosa		0.06	0.03		0.01	0.21	0.07	0.01
Favia fragum			0.03		0.07	0.1	0.08	0.07
Solenastrea hyades					0.04	0.07	0.13	0.04
Isophyllia sinuosa	0.07				0.03	0.13		0.01
Agaricia fragilis			0.09	0.12	0.03			
Porites branneri					0.01	0.08	0.02	0.11
Manicina areolata					0.04	0.05	0.08	0.04
Madracis mirabilis		0.09			0.01	0.03	0.03	0.03
Leptoseris cucullata						0.02	0.14	0.02
Cladacora arbuscula					0.01	0.06	0.02	
Mycetophyllia aliciae				0.05				0.01
Scolymia cubensis			0.06					
Agaricia humilis						0.05		
Isophyllastrea rigida						0.02		0.02
Acropora palmata								0.03
Mycetophyllia ferox						0.02		0.01
Acropora prolifera								
Agaricia tenuifolia								
Mycetophyllia lamarckiana								

Figure 1. Grayscale plot of the Analysis of Similarity R-score matrix that compares the sampling periods against each other. The uniformity, regardless of time of sampling, indicates that all sampling periods were useful replicates.

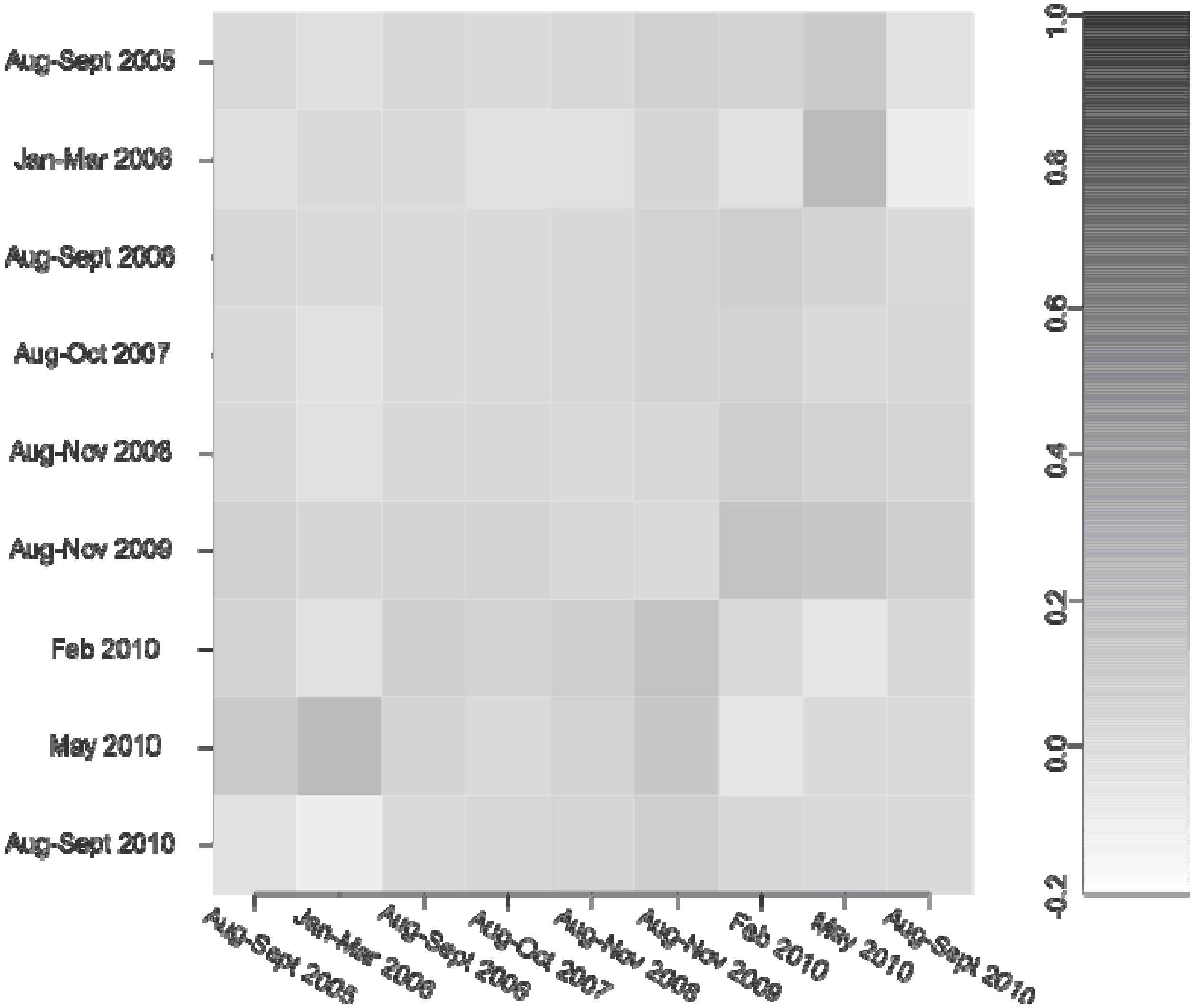

Figure 2. Grayscale plot of the Analysis of Similarity R-score matrix comparing the depth classes against each other. The consistent gray across the plot indicates that there was minimal depth stratification of coral assemblages.

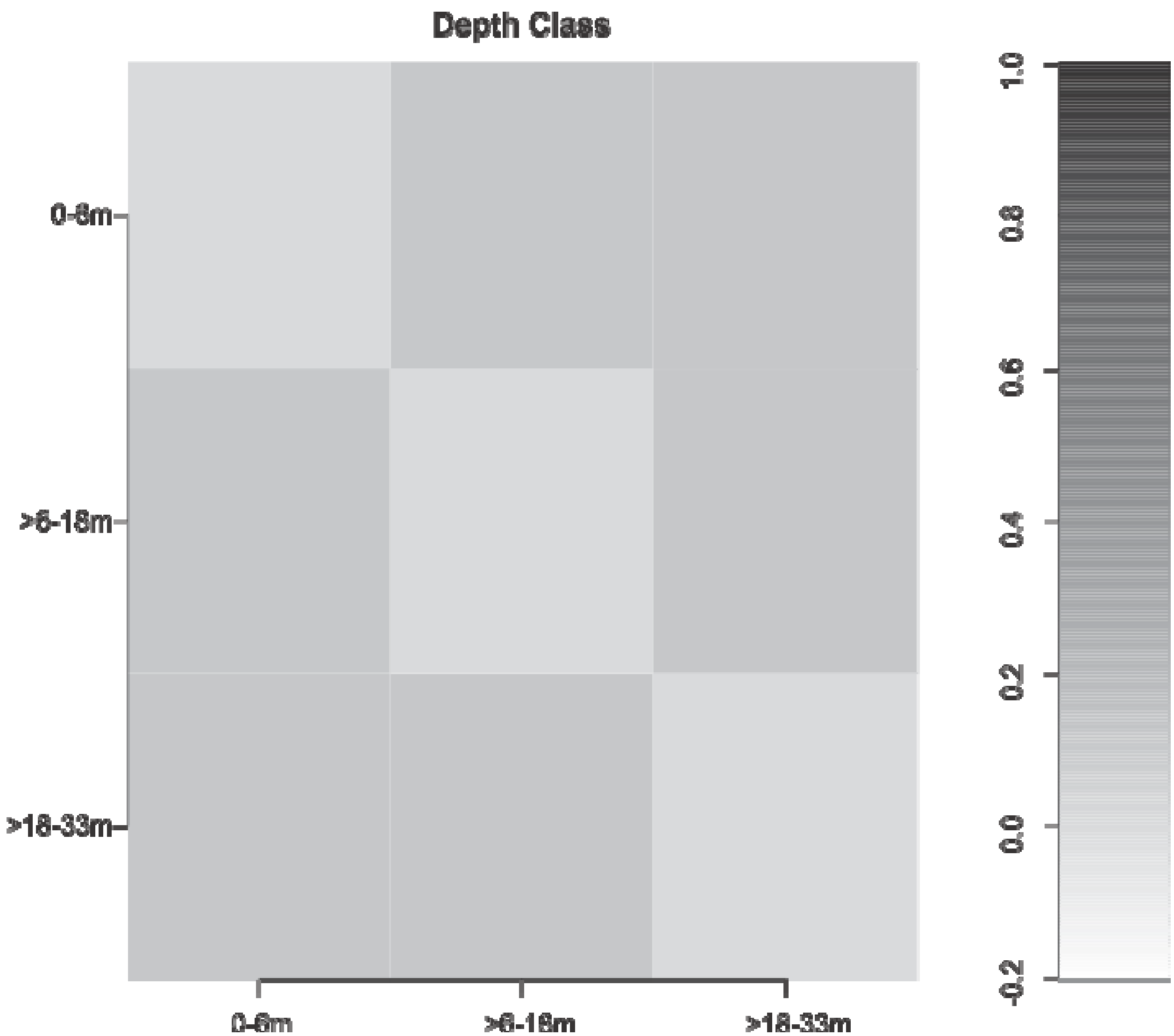

Figure 3. Grayscale plot of the Analysis of Similarity R-score matrix comparing coral assemblages in the different subregions against each other. There were three main subregions: 1) Martin, 2) Palm Beach and Broward, and 3) Biscayne, Upper Keys, Middle Keys, Lower Keys, Marquesas, and Tortugas. The subregions that supported similar coral assemblages are outlined in red.

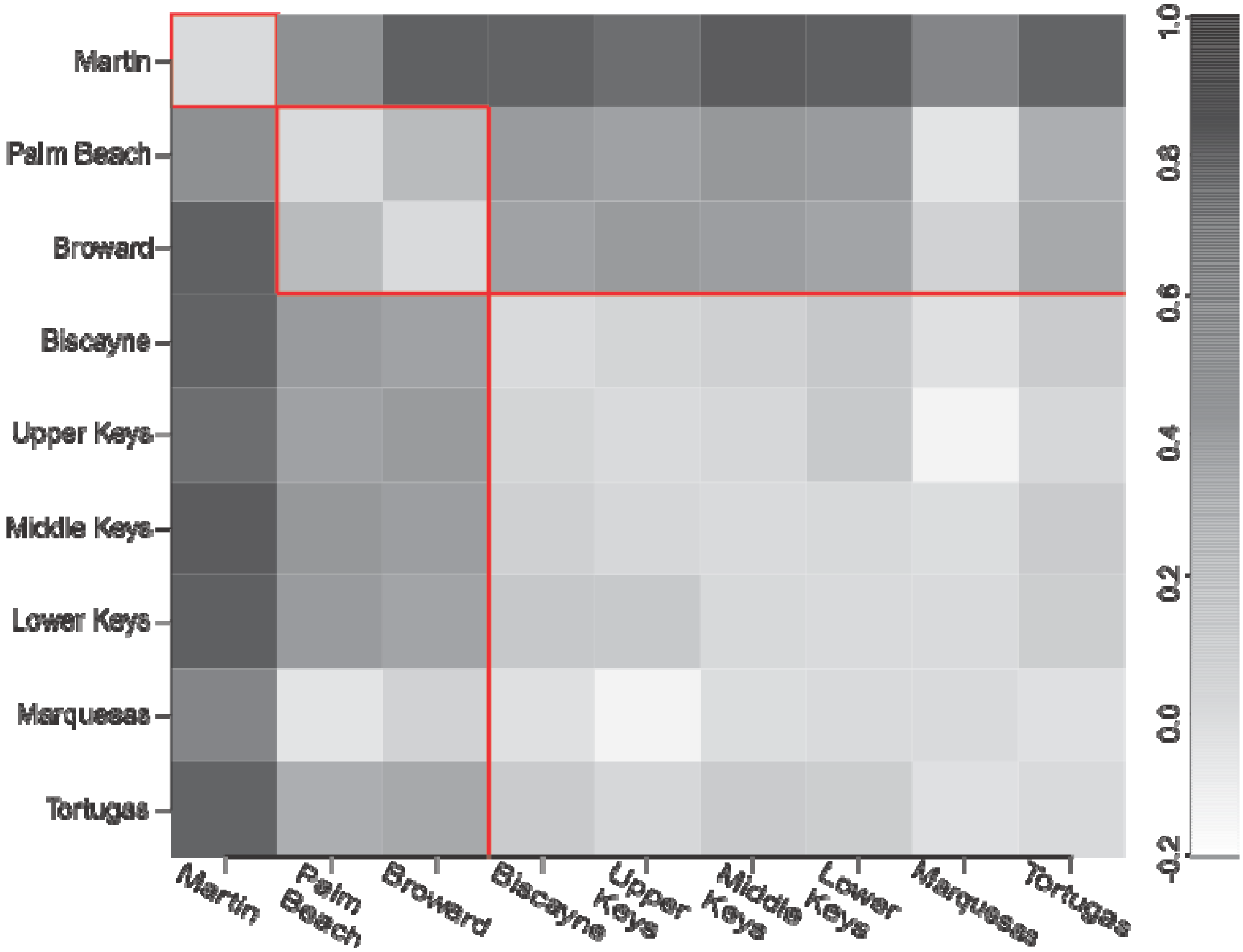

Figure 4. Results of non-metric multidimensional scaling (NMDS) plot outlining site-density contours. Three sets of subregions were apparent: 1) Martin (red points), 2) Palm Beach and Broward (blue contour), and 3) Biscayne, Upper Keys, Middle Keys, Lower Keys, Marquesas, and Tortugas (black contours). This demonstrates the hierarchical subregion 2 nested in subregion 3, and that subregion 1 was considerably- different in coral assemblage composition (NMDS 2D stress=0.23).

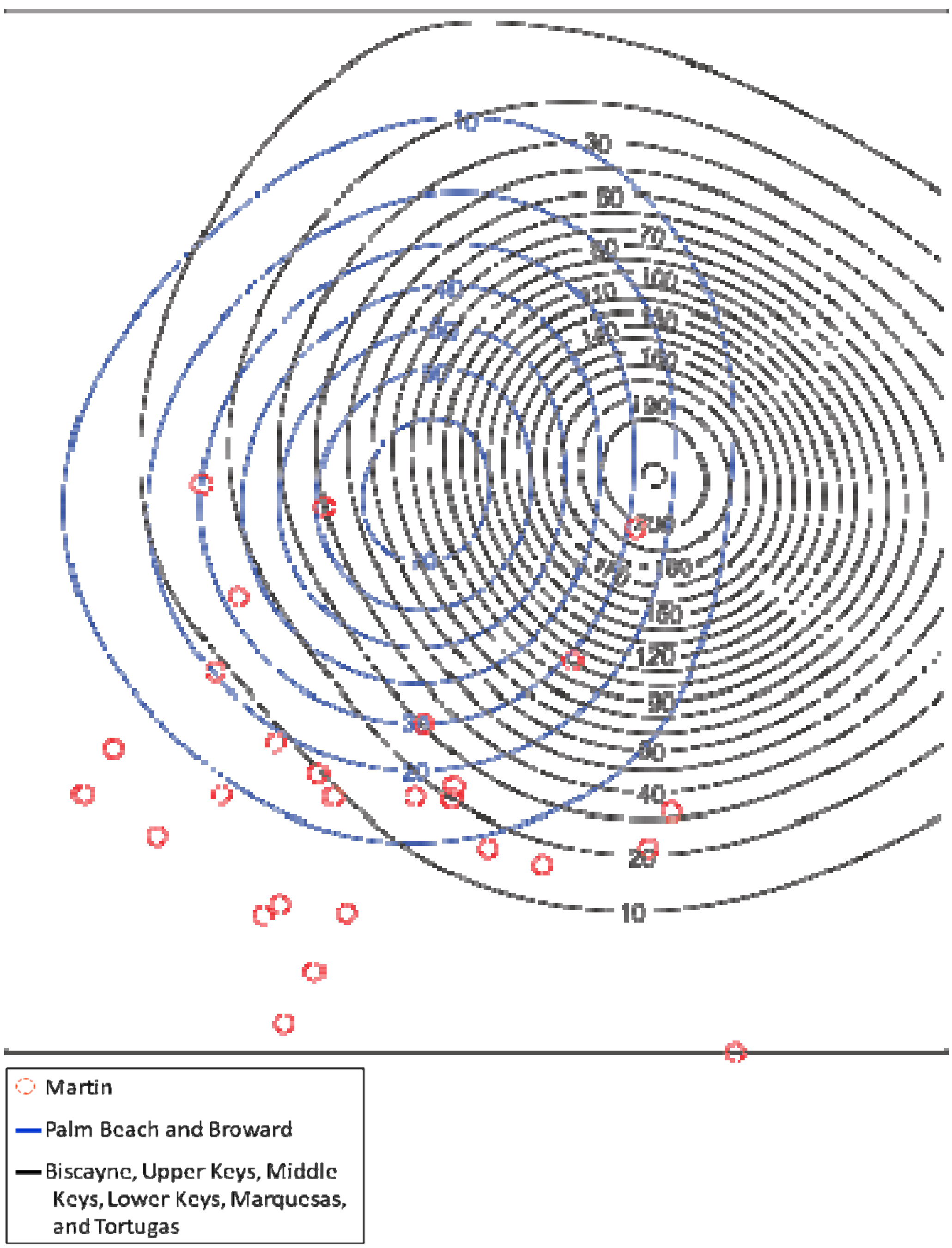

Figure 5. Grayscale plot of the Analysis of Similarity R-score matrix comparing coral assemblages across the zones. The Inshore zone was found from Palm Beach through to the Tortugas, and it was similar to both (i) the Reef Ridge Complex, Inner Reef, and Outer Reef set of zones and (ii) the Midchannel, Offshore Patch Reef, Forereef set of zones.

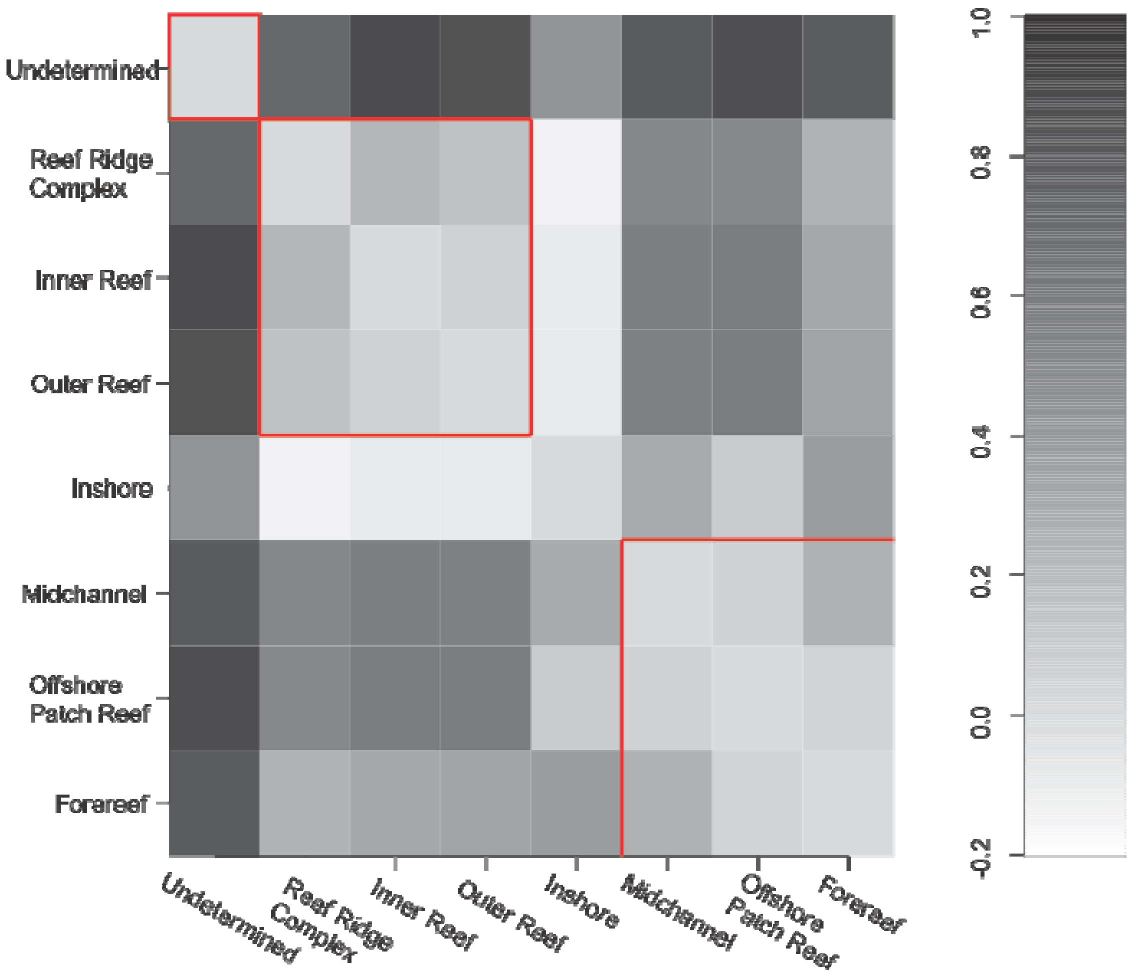

Figure 6. Results of non-metric multidimensional scaling (NMDS) plot outlining site-density contours. Four main zones were apparent: 1) Undetermined reefs (black points), 2) Inner, Outer and Reef-Ridge Complex (red contours), 3) Midchannel, Offshore Patch Reef and Forereef (black contours), and the 4) Inshore zone (blue contours), which was more similar to the Inner, Outer, Reef-Ridge Complex zones than the Midchannel, Offshore Patch Reef, and Forereef zones. NMDS 2D stress=0.23.

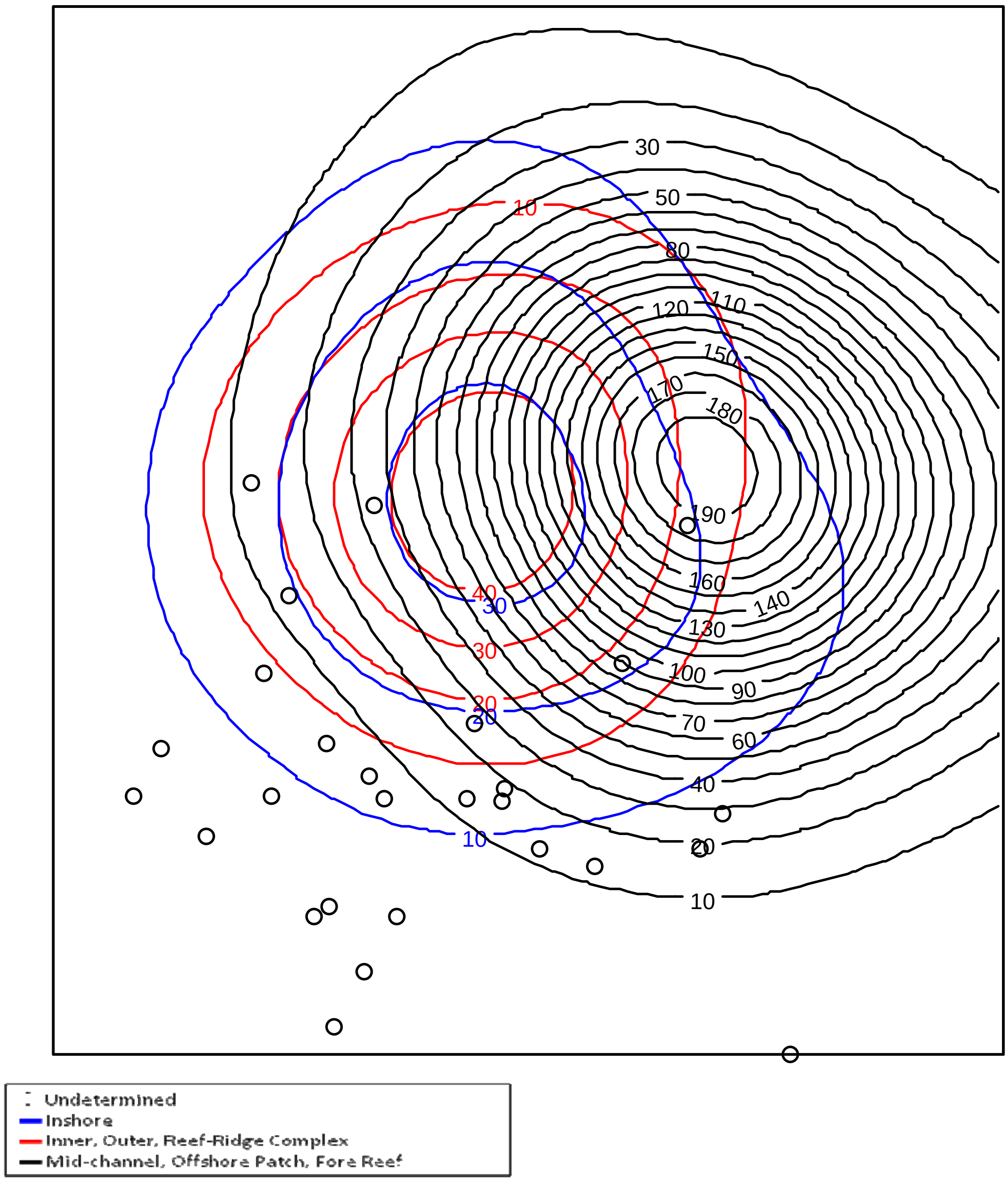

Figure 7. Schematic representation of the dominant coral assemblages across the Florida Keys before the 1970s and on contemporary reefs in 2011.