

Status and Trends of Bonaire's Reefs, 2011 Cause for grave concerns

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Executive Summary: Status and Trends of Bonaire's Reefs: Cause for grave concerns

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Overview and conclusions

Unusually warm ocean temperatures surrounding Bonaire during the late summer and fall of 2010 caused 10 to 20 % of corals to bleach (Fig. 1). Bleaching persisted long enough to kill about 10 % of the corals within six months of the event (Steneck, Phillips and Jekielek Chapters 2A – C). That mortality event resulted in the first significant decline in live coral at sites monitored since 1999 (Fig. 2). Live coral declined from a consistent average of 48 % (from 1999 to 2009) to 38 % in 2011 (Steneck Chapter 1). This increase in non-coral substrate increased the area algae can colonize and the area parrotfish must keep cropped short (Mumby and Steneck 2008). For there to be no change in seaweed abundance would require herbivorous fish biomass and population densities to increase, but they have been steadily declining in recent years. This decline in parrotfish continues despite the establishment of no-take areas (called Fish Protection Areas – FPAs) and the recent law that completely bans the harvesting of parrotfish. The other major herbivore throughout the Caribbean is the black spined sea urchin, Diadema antillarum. However, since 2005 *Diadema* abundance has steadily declined. Damselfishes continue to increase in abundance (except in FPAs) and their aggressive territoriality reduces herbivory where they are present. These declines in herbivory resulted in a marked increase in macroalgae (Steneck Chapter 1). Although patchily distributed, algae on some of Bonaire's reefs are approaching the Caribbean average (Kramer 2003). All research to date indicates that coral health and recruitment declines directly with increases in algal abundance (e.g., Arnold et al 2010).

On the bright side, predatory fishes are increasing in abundance in general but increasing most strongly in FPAs. Typically, responses to closed areas take 3 - 5 years to begin to manifest themselves. Predators of damselfishes have increased significantly in FPA sites and there, damselfish abundances are trending downward. These trends are the first signs of changes in the FPAs, and they are encouraging.

Overall, Bonaire's coral reefs today are more seriously threatened with collapse than at any time since monitoring began in 1999.

The Evidence: 2010 Bleaching Event

The Coral Bleaching/Mortality Rapid Assessment Protocol Bleaching Atlantic and Gulf Reef Rapid Assessment (called BLAGRRA see Chaper 2) is a survey method for quantifying the impact of bleaching events. When corals started to bleach in fall of 2010, STINAPA conducted BLAGRRA surveys at 15 coral reef sites. Surveys were conducted

again at the same sites and depths six months later to determine how serious this bleaching event was.

Bleaching was widespread and many of the observed fully bleached (i.e., white) corals died as a result of this event (Fig. 1).

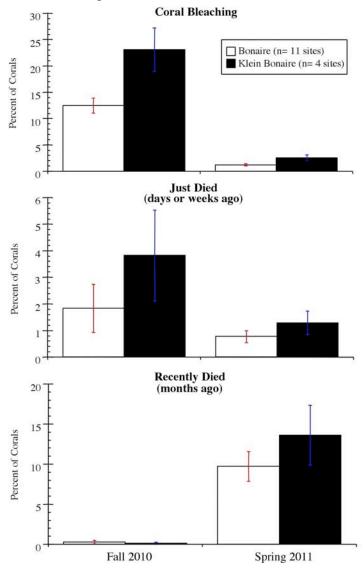


Fig. 1. Percent of corals bleached, those that had just died (days or weeks since death), and those that had died recently (months since death) based on the BLAGRRA protocol.

Monitoring Results

We followed the coral reef monitoring protocol outline in the 2005 Bonaire Report. It is based on monitoring trends among 10 key variables that drive or indicate the health of coral reefs.

The abundance of live coral at the monitoring sites has been remarkably constant since 1999. However, the bleaching related mortality event (Fig. 1) resulted in the first marked decline in live coral (Fig. 2).

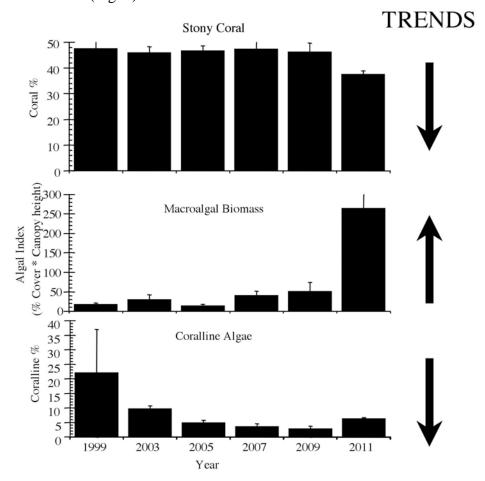


Fig. 2. Monitoring results 1999 – 2011 for coral, macroalgae and coralline algae (details in Chapter 1; Steneck 2011). The trend arrows reflect the departure from historic levels.

Seaweed abundance ("macroalgae") increased sharply in 2011. While the greatest increase in algae occurred at the 18th Palm site where effluent could have increased nutrient levels, most of the other sites showed marked increases in algal abundance (see Steneck Chapter 1). Coralline algae, which has been shown to facilitate coral recruitment, remains at or near unprecedentedly low levels (Fig 2).

Herbivory from parrotfishes and the grazing sea urchin *Diadema antillarum* remains at or near the lowest levels recorded since monitoring began in 1999 (Fig. 3 and see Cleaver Chapter 5). Herbivory from parrotfish is widely thought to be most important (e.g., Steneck and Mumby 2008) but territorial damselfishes can negate parrotfishes' positive effects by attacking grazing herbivores and preventing them from effectively grazing (Arnold et al 2010). Damselfish abundances have trended upward in recent years (Fig.

- 3). However, there is a hint of a reversal to this trend in the FPAs (see Arnold Chapter
- 3). This reversal is consistent with the possibility that areas without fishing have elevated

abundances of damselfish predators such as species of groupers and snappers (Randall 1965).

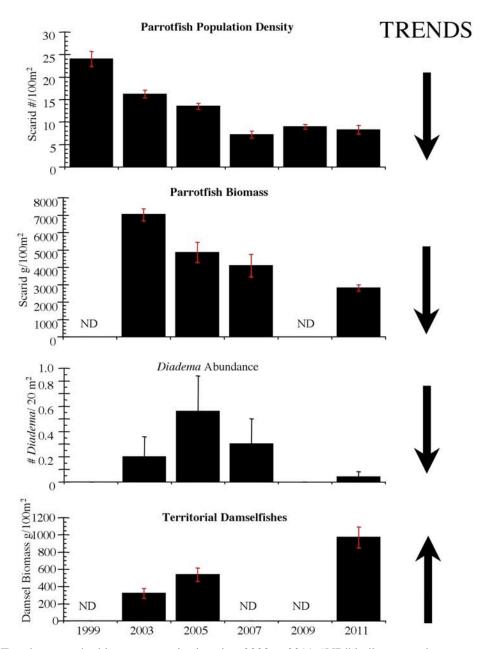


Fig. 3. Trends among herbivores at monitoring sites 2003 to 2011. "ND" indicates no data or no commensurable data. Notations as in Fig. 2. Data from Chapters 1 and 3.

Predatory fishes including snappers, groupers, barracuda, grunts and others increased in abundance at our monitored sites (Fig. 4 and see DeBey Chapter 6a). Specific predators known to eat damselfishes (see Preziosi Chapter 6b) show variable population densities with only a hint of an increase in 2011 (Fig. 4, lower).

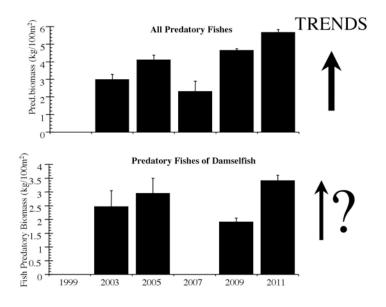


Fig. 4. Abundance trends of predatory fishes and predators of damselfish. Sites and notations as in Figure 2. Data from Chapter 6a.

Predatory fishes increased in abundance in both biomass (most striking) and population densities (Fig. 5). While biomass of predators in FPA and control sites is identical, the population density of predators is slightly greater at FPA sites (Fig. 5).

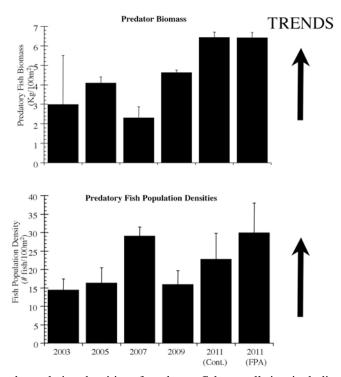


Fig. 5. The biomass and population densities of predatory fishes at all sites including the Control and FPA sites (see DeBey Chapter 6a).

Coral recruitment remained lower than recorded in 2003 and 2005 (Fig. 6). However, the abundance of juvenile corals was higher in 2011 than was quantified in 2009 (see McHenry Chapter 7).

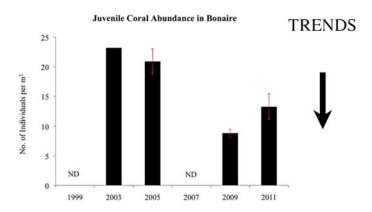


Fig. 6. Trend in abundance of juvenile corals (i.e., less than 4 cm in size). See McHenry Chapter 7.

Interpreting Positive and Negative trends

The monitoring protocol proposed in 2005 was to identify trends in key variables and monitor if they were increasing, decreasing or holding constant (Fig. 7). This rationale has been outlined in previous Bonaire Reports (e.g., 2005, 2007 and 2009). There is strong scientific evidence to support that healthy reefs have the following trends, including most importantly that: coral cover is constant or increasing; seaweed (macroalgae) is low in abundance or declining; herbivory and coral recruitment are high or increasing (see heavy lines and arrows in Fig. 7).

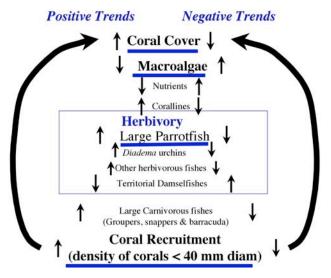


Fig. 7. Variables to monitor positive (arrows on left side) and negative (arrows on right side) trends. Key variables are underlined.

Monitoring results from 2011 indicate that every indicator except for large carnivorous fishes is displaying a negative trend (Fig. 8 and see Figs 2 - 6 above).

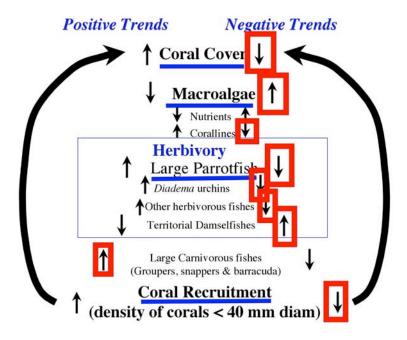


Fig. 8. The interpreted monitoring protocol. The direction of change is indicated by the arrows. The red rectangles indicate trend results revealed in Figs. 2-6).

The positive trend for predatory fishes in FPAs suggests management measures for them are working. There is even a slight increase in herbivores within the FPA sites relative to adjacent control areas.

The trend of greatest concern is the steady decline in parrotfish abundance despite very recent laws banning their harvest. It is possible that the timing of the bleaching event may have increased the area for algal colonization such that existing herbivores were overwhelmed by rapid algal growth which may negatively affect subsequent herbivory (see discussion in McMahan Chapter 4). If so, this would suggest Bonaire's coral reefs could be slipping into a feedback loop that could continue and drive the reef towards a coral depleted state (Mumby and Steneck 2008).

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Chapter 1: Patterns and trends in abundance of corals, seaweeds and sea urchins at monitored sites in Fish Protection and Controls Areas

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Abstract

Surveys of the abundance of live stony coral, seaweed (known as macroalgae), and sea urchins were quantified at four Fish Protection Areas (FPA) sites and at six sites open to fishing (Control sites). All were in 10 m of water and six of the sites have been monitored every other year since 2003. The FPA and Control sites differ in the abundance of these organisms but these differences were similar to the initial state recorded in 2009 (see Bonaire Report 2009). Specifically, live coral and coralline algae were more abundant at Control than FPA sites (38% and 7% vs 34% and 4.7%, cover respectively). In contrast, macroalgae were less abundant at the Control than FPA sites (225 vs 350 Algal Index). Sea urchins were also slightly more abundant at Control sites but still at very low population densities (1.2 vs 0.6 urchins/20 m²). The FPA and Control site baselines established in 2009 are benchmarks against which change is measured. The most dramatic and negative change since 2009 is the decline in coral cover and increase in macroalgae. There were slight increases in sea urchins and slight decline and increase in coralline abundance in the FPA and Control sites, respectively.

Long term trends dating to 1999 (AGRRA data) show the first significant decline in live coral cover and a marked increase in macroalgae. Coralline abundance remains relatively low and Diadema sea urchins remain low but slightly higher than in 2009.

Introduction

Live reef corals define the structure and functioning of coral reef ecosystems. Many coral reefs have become seaweed or algal dominated, and until now the reefs of Bonaire had relatively high coral cover, low algal abundance and relatively high coralline algal abundance (Kramer 2003, see Bonaire Reports for 2003, 2005, 2007, 2009 on file with STINAPA).

Declines in coral abundance is often accompanied with, or possibly caused by, an increase in macroalgae (Hughes 1994, Mumby and Steneck 2008). Conversely, crustose coralline calcareous algae is most abundant on healthy reefs because it facilitates settlement and metamorphosis of some baby corals (Raimondi and Morse 2000, Ritson-Williams et al 2009). Therefore, monitoring inhibitory fleshy algal abundance and facilitating coralline abundance can gauge the health of coral reefs and their ability to recover following a mortality event (Mumby and Steneck 2008).

What controls the abundance of macroalgae and coralline algae has received considerable attention over the past few decades. Most studies have shown that herbivory from scraping herbivores such as parrotfishes and sea urchins controls algal abundance much more strongly than nutrient availablity (McCook 1999, Williams and Polunin 2001, Kramer 2003, and Mumby and Steneck 2008). Other studies have indicated that herbivores facilitate coralline algal abundance (van den Hoek 1969, Steneck 1986, 1988, 1997, Steneck and Dethier 1994, Edmunds and Carpenter 2001).

Thus monitoring trends in coral abundance, macroalgae, coralline algae and scraping herbivores is a good way to guage the relative health of coral reefs. Arguably, increases in macroalgae may be the single best indicator of an unhealthy coral reef. However, to determine reef health requires monitoring patterns of abundance over a long enough period of time to detect significant trends over time.

Overfishing on coral reefs is an everpresent concern. In Bonaire Fish Protection Areas were established in 2008 to be effective oases where fishing pressures are absent and fish stocks can recover. Our long-term monitoring was designed to determine if healthier conditions prevail in FPA areas compared to Control sites.

Materials and Methods

The distribution and abundances of major reef-occupying groups such as stony corals, macroalgae, sea urchins and juvenile corals were quantified using 10 m long line transects placed on reefs (methods of Benayahu and Loya 1977; Kramer 2004) at 10 m depth at each of our nine study sites sites (Listed in Fig. 1). Algae were subdivided into functionally important groups (see Steneck and Dethier 1994) such as crustose coralline, articulated coralline, foliaceous macroalgae (hereafter: "macroalgae") and noncoralline crusts. Transect methods used were modified from the Atlantic and Gulf Rapid Reef Assessment (AGGRA) protocol (Steneck et al. 2003). Specifically, we measured the number of cm occupied by each organism group and all coral species along each transect. Macroalgal biomass is most critical and it was estimated from the calculated algal index as the product of percent cover multiplied by algal canopy height (in mm; Steneck and Dethier 1994, Kramer 2003). We quantified three transects per reef site.

Abundances of four species of sea urchins (*Diadema antillarum*, *Tripneustes ventricosus*, *Echinometra lucunter* and *E. viridis* were quantified in accordance with AGRRA protocols by searching a one-meter path on either side of the 10 m transect tape (i.e. a total of 20 m² were surveyed for each transect).

We present data for the Fish Protection Areas (FPA) and Control sites. However, two of the FPA sites (18th Palm and Scientifico) and three of the Control sites (Windsock, Barkedera, Karpata and Forest) are the sites we have monitored since 2003 (we also draw from comensurable AGRRA data set for 1999 Bonaire surveys). At those sites, ceramic plates mark specific transect areas so all of our monitoring is along nearly fixed transects.

In most cases, the transect falls no more than 0.5 m from the transect locations of previous years.

Results

Live coral remains the single most abundant component of Bonaire's reefs (Fig 1.). Live coral cover at all 10 sites averaged 36.5% which was down from 41.9% in 2009. The coral cover was higher at the Control sites than the FPA sites (Fig. 1). By far, the dominant corals were star corals of the genus *Montastraea* (22.1% ± 3.1 SE). The two most abundant species were, *M. annularis* and *M. faveolata* at 10 and 8.9% cover of the reef, respectively (down from 12.6 and 10% in 2009). The next two most abundant taxa were *M. cavernosa* and *Agaricia agaricites* at 3.0 and 2.5 of the reef surface area, respectively (about the same as 2009).

Turf algae were the second most abundant component of the reef comprising 33.3 % (\pm 1.5 SE) of the reef surface with an average canopy height of 2.5 mm (0.5 mm higher than 2009). This represents an increase in the canopy height of 1.4 mm from the average in 2007 of 1.1 mm (\pm 0.1 SE).

Macroalgal cover for all 10 sites was 17.8 % (± 1.4 SE) up from 10.7% in 2009. The algal index (percent cover x canopy height) reflects algal biomass (Steneck and Deither 1994). The Control sites had significantly lower algal abundance than did the FPA sites (Fig. 1)

Crustose coralline algae were significantly more abundant among the Control than the FPA sites (Fig. 1). However coralline abundance among all 10 sites was only 6.2% (± 0.6 SE) cover.

Herbivorous sea urchins were relatively rare and ecologically unimportant. Among all 10 sites studied, the average population densite of the black long-spined sea urchin, *Diadema antillarum* was 0.3 per 20 m² survey area (or 0.15 per m²). This number was slightly higher than that found in 2009. The most abundant sea urchin was *Echinometra viridis* with a population density averaging 1.93 ± 0.1 SE per 20 m². This represents a large increase in the abundance of this sea urchin but it is still at functionally low population densities (see Cleaver this report for more on sea urchins).

Overall coral cover declined in both FPA and Control sites but did so at a greater rate in the control areas. Most of the other changes were more significant in change over time than changes between FPA and Control with the exception of *Echinometra* urchin populations which increased most dramatically in the Control sites.

The most significant changes since 1999 were the decline in coral cover and the increase in macroalgal biomass (Fig. 2). The overall decline in coralline algae remains (despite its modest increase in 2011). Diadema populations that had peaked in 2005 remain low but have increased slightly in 2011.

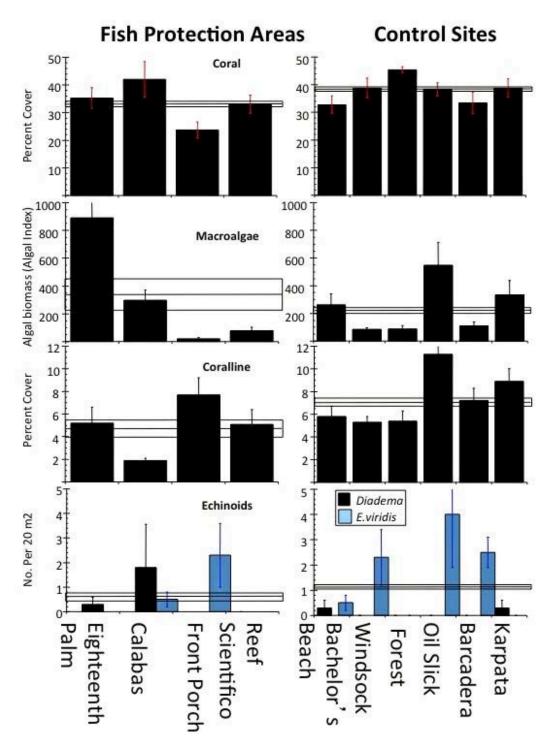


Fig 1. Abundance of key reef organisms in FPA and Control areas. Error bars on histograms represent Standard Error (SE). Horizontal lines represent overall averages (\pm SE).

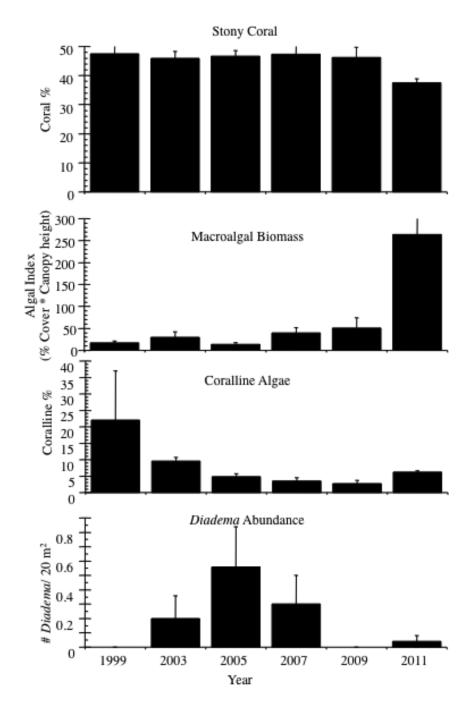


Fig. 2. Temporal trends of key attributes on Bonaire's monitored reefs (Karpata, Baracadera, Reef Scientifico, Forest, 18th Palm and Windsock).

Discussion

The biggest changes in Bonaire's reefs are the decline of live coral and the increase in macroalgae. The coral decline undoubtedly related to the bleaching event in the Fall of 2010 (see chapters 2A & B by Phillips and Jekielek in this report). The algal increases could relate to some degree to the decline in live coral cover but the change is only 4.5

and 9.7% in the FPA and Control sites, respectively. It is tempting to speculate whether the higher coral cover decline relates to the control vs protected conditions of the FPA sites but it is too soon to tell.

The most troubling increase for the health of Bonaire's reefs is the sharp increase in macroalgae (Fig. 2). Healthy reefs were traditionally described as having abundant live coral and little to no macroalgae (Darwin 1909, Steneck 1988, Hughes 1994, Hughes et al 2010). This changed in recent years when most Caribbean reefs "phase-shifted" to macroalgal dominance and now have only about 10% live coral (Gardner et al. 2003). Bonaire's reefs are different since corals remain the most abundant living component of the reef and macroalgae are still relatively rare but rapidly increasing (Figs. 1, 2). Further, only one site, 18th Palm, was overgrown with macroalgae. That site has an average biomass and population density of parrotfishes (See Chapter 3 Arnold). However, because that site is adjacent to one of the largest hotels on the island, it is tempting to speculate that this spike in algal abundance could result from effluent from the hotel. Nearby Bachelor's Beach did not have the same high level of algae. Nevertheless, even when 18th Palm data are removed, the increased algal biomass is significant. Note that juvenile coral surveys that measure algal abundance in quadrats (ie a different method) found the same sharp increase in algal biomass (see Ch. 9, McHenry this report).

There is a clear inverse relationship between macroalgal and coral abundance (Williams and Polunin 2001, Kramer 2003). More troubling is that any increase in algal abundance reduces the success of settling (baby) corals (Arnold et al 2010). Several studies using manipulative experiments concluded that macroalgae competes with, and reduces the fitness of, stony corals with which they are in contact (Lewis 1986, Hughes 1994, McCook 1999, McClanahan et al. 2001). Thus it is possible that the low abundance of macroalgae in the past may have contributed to the high cover of live coral. It also is possible that the relatively high rates of coral recruitment on Bonaire (Arnold et al 2010) may decline as algal abundance increases.

The increasing abundance of macroalgae may be due to the continuing decline in parrotfish abundance (see Arnold chapter in this report). While other studies focused on the sea urchin, *Diadema antillarum*, because their grazing correlates with low algal biomass and higher density of juvenil corals (Edmunds and Carpenter 2001), *Diadema* remains too rare in Bonaire to have a functional impact as an herbivore in this system. Its density should continue to be monitored.

FPA and Control Baseline Data

Fish Protection areas were first established in 2008 and no changes duet to this management action could be found in 2009 because not enough time had lapsed. However, to determine change in highly complex ecosystems, a "before and after controlled impact" (BACI) design is necessary. BACI designs first establish a baseline against which change due to the manipulation is quantified. In this case, the control sites

have higher coral and coralline abundance and lower algal abundance than the FPA sites. It will be against this baseline that future change will be assessed.

The larger picture of reef health in Bonaire is covered in the Executive Summary (Steneck, Arnold, DeBey this report).

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Chapter 2a: Coral Bleaching Creates Mortality on Bonaire's Coral Reefs: A comparative analysis between Fall 2010 and Spring 2011

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Abstract

Unusually warm sea temperatures during the summer and fall of 2010 triggered a coral bleaching event in Bonaire. In September 2010 and March 2011 the Bleaching Atlantic and Gulf Reefs Rapid Assessment (BLAGRRA) technique was used to quantify coral bleaching and mortality at 15 sites and two depths (10 and 20 m but the 20 m surveys were only conducted during the September 2010). Over 30% of all corals were pale (partially bleached) or bleached white by September 2010 on Bonaire and 46% showed those symptoms on Klein Bonaire. Similar patterns were observed at 20 m except fewer corals were pale at that depth. Six months later (March 2011), bleaching had declined at shallow sites from 12.5% to 1.2% and new coral mortality declined from 1.8% to 0.8%. Corals that died in the fall and were colonized by turf algae (called "transitional mortality" increased from 0.3% in the fall to 9.7% in Spring. Klein Bonaire had higher rates of new mortality resulting from the higher rates of bleaching in the fall of 2010 (3.8%) that declined to 1.3% in the spring of 2011. It also had higher rates of transitional mortality. Overall, the measured rates coral mortality resulting from this bleaching event match the decline in live coral cover documented in semiannual reef monitoring.

Introduction

Corals expell their zooxanthellae when they are stressed and turn white in what is known as "coral bleaching". Although bleaching can result from freshwater (salinity stress), sedimentation or cold water anomalies, by far most bleaching occurs as a result of high sea temperatures. While Bonaire was relatively immune to the massive Caribbean wide coral bleaching event in 1998 (Wilkinson 1998; Aronson et al 2000) and the lesser and more aggregated event of 2005, it was not as lucky in 2010. In late summer and fall sea temperatures increased to over 29° C for a long enough period to induce coral bleaching. In fact NOAA issued its "Highest bleaching alert level" for Bonaire during that period based on the estimated 9.9 degree heating weeks (DHW) it had recorded.

To quantify coral bleaching and the possible mortalty conseuquences of this event, the Bleaching Levels of the Atlantic and Gulf Reef Rapid Assessment was applied during and six months following the bleaching event using the web-based standardized methods (http://www.agrra.org/BLAGRRA/). For other specific methods see Philipps 2011 and Jekielek 2011 (chapters 2b and 2c; this report).

Results

Corals were pale and bleached during the Fall of 2010 (September and October) (Fig. 1). Bleached corals were common at shallow sites (10 m or less) along the coast of Bonaire

and Klein Bonaire (12.5% \pm 1.5 SE and 23.1% \pm 23.09 SE, respectively). New mortality which records coral death generally less than a week or two was elevated to 1.8 ± 0.9 SE and 3.8 + 1.7 SE (compared to what was seen in deep water or during the spring of 2011.

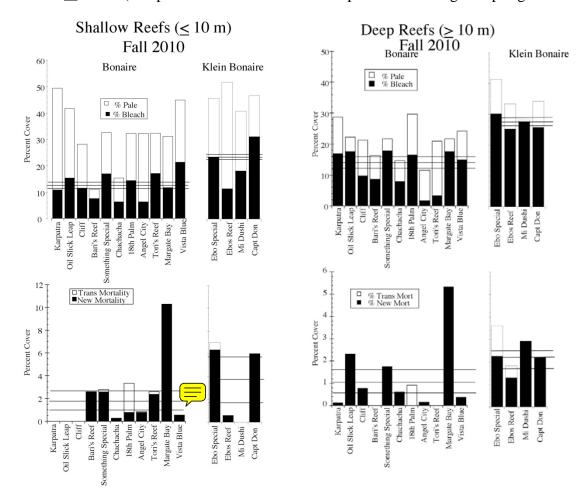
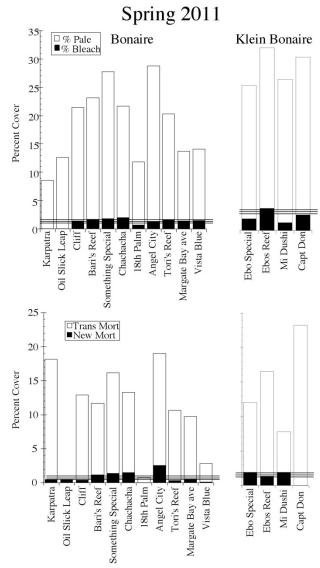


Fig. 1. Fall 2010 BLAGGRA surveys for shallow (left) and deep (right reefs). Horizontal lines represent average \pm SE for bleached and recently dead corals (upper and lower, respectively.

Six months later in the spring of 2011 (27 February to 12 March) BLAGGRA surveys were redone at the same 15 sites studied in the fall of 2010 (other sites were done and reported in Jekielek 2011 (this report). Coral bleaching declined significantly (12.5 % \pm 1.5 SE in fall 2010 to 1.2 % \pm 0.2 SE in spring 2011 imilarly, transitional mortality increased from 0.3% \pm 0.23 SE in fall 2010 to 9.7 \pm 1.8 SE in spring 2011 (Fig. 2).



Shallow Reefs (≤ 10 m)

Fig. 2. BLAGGRA results for Spring 2011. Notations as in Fig. 1.

Discussion

Temperatures exceeding 29 °C for several weeks stimulated NOAA to issue its "Highest bleaching alert level" for Bonaire for late summer and fall of 2010. This triggered a bleaching event (Fig. 1) that was evident in both deep and shallow depths. By the time of the fall BLAGGRA surveys, corals were dying as evident in the higher new mortality however, they had not been dead very long because the proportion of corals in transitional mortality was low at that time. By the spring of 2011 the bleaching event was over but the transitional mortality was high (Fig. 2).

Klein Bonaire had higher rates of bleaching and new mortality in the fall of 2010 and higher rates of transitional mortality in spring of 2011. It is possible that the bleaching

event was more severe at Klein Bonaire than it was on the main island of Bonaire. Several studies over the past decade have observed higher rates of coral bleaching induced mortality on offshore oceanic islands. This was observed in Palau and more recently in the Seyshelle Islands (Graham et al 2006). It is possible that otherwise thermally stable offshore islands may be more susceptiable (ie less adapted) to temperature anomalies. However, this is only speculation at this point. Clearly, Klein Bonaire is more isolated from human activities and pollution so it is unclear what else could explain the conspicuously higher rates of bleaching and mortality at that site.

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Chapter 2b: Assessing bleaching on Bonaire's coral reefs September 2010: Applying "BLAGGRA" during a bleaching event

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Abstract

The Bleaching Atlantic and Gulf Reefs Rapid Assessment (BLAGRRA) technique was used to determing degree of bleaching in Bonaire during an unusually warm period in the fall of 2010. BLAGRRA surveys were taken at 15 sites and two depths on Bonaire during September 2010. Of those sites, five sites were selected for detailed species specific analyses. Coral bleaching (ie they turn white) is most serious and can cause coral mortality if it persists. Bleaching was heterogeneous by species, site and depth. The coral species that bleached most severely (i.e., *Colpophyllia natans* and *Montastrea franksii* also suffered the highest rates of mortality. Likewise by site, about 20% of the corals bleached and while new mortality was relatively rare the site with the most bleaching ("Something Special") and least bleaching ("Tori's Reef") also had the highest and lowest rates of new mortality, respectively. Similarly, the deepest sites at 60 m also had the highest proportion of recent morality. Bonaire's moderate bleaching likely resulted from thermal stress due to higher than average temperatures in the Fall of 2010.

Introduction

Coral bleaching is a phenomenon in which scleractinian corals expel their phytoplankton symbionts, known as zooxanthellae. It can be caused by temperature extremes, fresh water influx, sedimentation, lack of available light, or other stressors. Without the accessory pigments of their photosynthetic endosymbionts the corals will appear white, hence the term "bleached." Bleaching can be fatal, or it can be transient and the coral will fully recover given time. In general, bleaching events that last less than several weeks are considered transient, and the affected corals will likely recover. Bleaching events lasting longer than several weeks are usually fatal. Corals can suffer total mortality, in which the entire colony dies, or partial mortality, in which portions of the colony may die, but the remainder survives and continues to grow and calcify. BLAGRRA is a method developed to rapidly assess the health of corals reefs, and took look at live coral cover, as well as the incidence of bleaching and disease. BLAGRRA can be quickly and easily implemented following a concerning occurrence such as a hurricane or warming event, making it an ideal tool for managers to evaluate the condition of a reef. The BLAGRRA method involves laying down a transect line across a portion of the reef. Each coral that is crossed by the transect line or that falls within a belt on either side of the transect line is measured, and if the coral is pale or bleached the afflicted percentage of the coral is recorded. The percent mortality is noted, as well as whether that mortality is new, transitional, or old. Any evidence of disease is also marked down. These data enable managers and researchers to say something about the state of the reef, and with repeats surveys can start to identify trends over time.

BLAGRRA is a relatively new technique that has only recently begun to be implemented so there is limited information on temporal trends using this method, but comparisons can be drawn between collected BLAGRRA data and past reports on bleaching and disease in Bonaire and throughout the Caribbean.

Methods

BLAGRRA data was collected by Ramón de León of the Bonaire National Marine Park at five sites on the western side of Bonaire in September 2010. The study sites were as follows: Cliff (12°10'25.23"N, 68°17'25.72"W), Something Special (12°9'43.61"N, 68°17'7.22"W), Chachacha Beach (12°8'44.82"N, 68°16'37.84"W), Tori's Reef (12°4'17.41"N, 68°16'55.16"W), and Vista Blue (12°1'57.39"N, 68°15'55.06"W). (Fig. 1) Data were collected using the BLAGRRA methods as described above. A 10m transect line was randomly laid out at two different depths for each site. Transects were laid at 25m and 60m depths for the Cliff and Something Special sites, and at 30m and 60m depths for the Chachacha Beach, Tori's Reef, and Vista Blue sites. The date, time, and temperature when each site was surveyed were recorded on a data sheet. Each coral crossed by the transect line was noted, using a four-letter species code, and the height, length, and width were measured in centimeters. If the coral was pale, (slightly bleached) or bleached, the affected percentage of the coral was recorded. If mortality was noted, the percent mortality was also recorded, as well as whether the mortality was new or old. Transitional mortality was combined with new mortality for this survey. Disease incidence was not noted during these surveys.

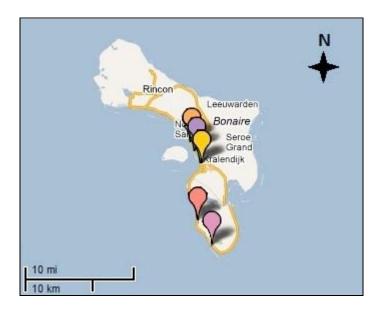


Figure 1. Map of survey sites on Bonaire where BLAGRRA data were taken in September 2010. Sites from north to south are as follows: Cliff, Something Special, Chachacha Beach, Tori's Reef, and Vista Blue.

Results

The most abundant coral by count was *Agaricia agaricites* with 102 colonies recorded between the five survey sites. The next most abundant corals were *Montastraea annularis* and *Porites astreoides*, with 87 colonies and 70 colonies, respectively. (Fig. 2) The most abundant coral by total area was *M. annularis*, which covered a total of 338,130 cm², followed by *Montastraea faveolata* with 147,700 cm², and *Madracis aurentenra* with 97,825 cm². (Fig. 3)

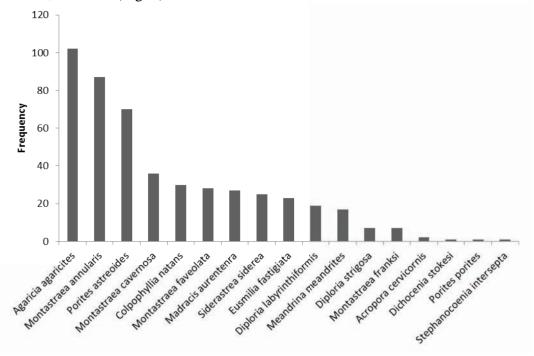


Figure 2. Total coral abundance at all survey sites by number of colonies noted.

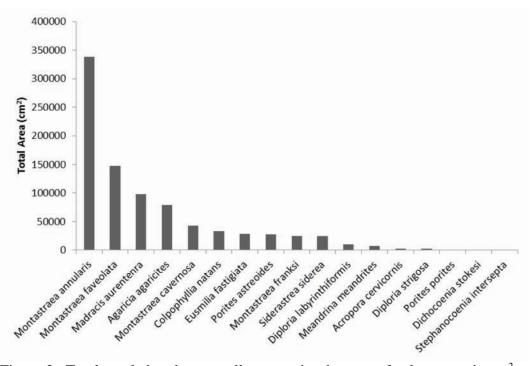


Figure 3. Total coral abundance at all survey sites by sum of colony area in cm². Fifteen out of the 18 species noted had colonies that were bleached white or bleached pale (hereafter referred to simply as "pale"). (Fig. 4) *Stephanocoenia intersepta* exhibited the highest percentage of pale colonies at 100%, followed by *Siderastrea siderea* at 52% pale. *Montastraea franksi* exhibited the highest percentage of bleached colonies at 57%, followed by *Colpophyllia natans* at 47% bleached. The lowest percentages of pale colonies were seen in *Acropora cervicornis*, *Dichocoenia stokesi*, and *Porites porites*, each with 0% pale colonies. The lowest percentages of bleached colonies were seen in *A. cervicornis*, *D. stokesi*, *Montastraea cavernosa*, *P. porites*, and *S. intersepta*, all with 0% bleached colonies. (Fig. 4)

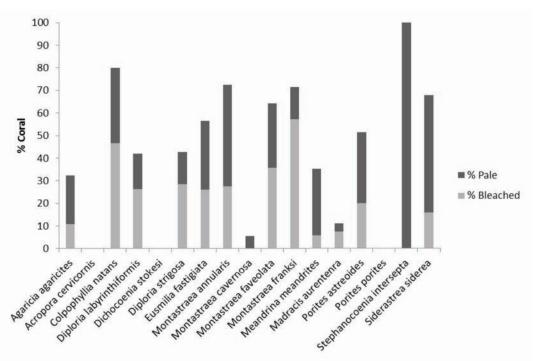


Figure 4. Total percentages of pale and bleached corals from all survey sites. Note that *Colpophyllia* is one of the most bleached of the abundant corals. Six of the 18 species noted showed new mortality. Fourteen of the 18 species showed signs of old mortality. (Fig. 5) The corals with the highest total old and new percentages of mortality were *M. franksi* (100%), *M. faveolata* (93%), and *M. annularis* (82%). *A. cervicornis*, *D. stokesi*, *P. porites*, and *S. intersepta* all exhibited 0% mortality. The highest percentage of new mortality was seen in *Eusmilia fastigiata* at 17%, followed by *M. franksi* at 14%. The highest percentage of old mortality was seen in *M. faveolata* at 93%, followed by *M. franksi* at 86%. (Fig. 5) Of all the mortality observed among all the corals, 9% was new mortality, and 91% was old mortality.

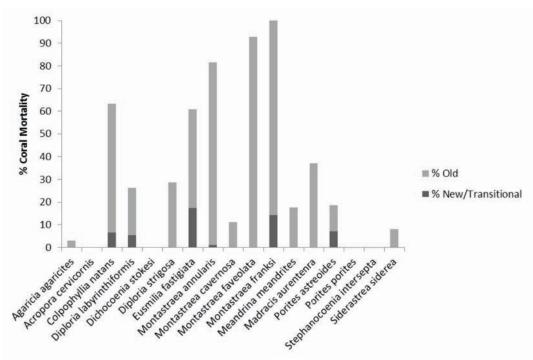


Figure 5. Total percentages of new and old coral mortality from all survey sites in September 2010.

Of the five survey sites, the overall average was Cliff had the highest percentage of pale or bleached coral at 61%. Tori's Reef had the lowest percentage of pale or bleached coral at 38%. The greatest percentage of pale coral was seen at Cliff, with 38% pale. The greatest percentage of bleached coral was seen at Something Special, with 31% bleached. The lowest percentage of pale coral was seen at Chachacha Beach, with 18% pale. The lowest percentage of bleached coral was seen at Tori's Reef, with 11% bleached. (Fig. 6)

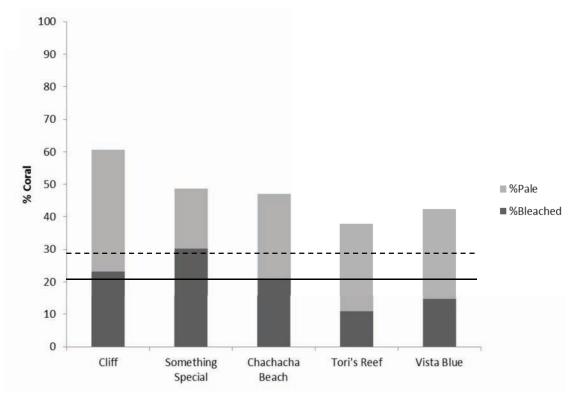


Figure 6. Total percentage of pale and bleached corals by survey site, presented north to south. The solid line represents average bleaching among all five sites, and the dashed line represents average paleness among all five sites.

Three of the five survey sites showed new mortality, and all five sites showed signs of old mortality. (Fig. 7) The site with the highest total mortality was Chachacha Beach, with 52% mortality. The site with the lowest total mortality was Something Special, with 27% mortality. The highest new mortality was seen at Something Special (7%), and the highest old mortality was seen at Chachacha Beach (52%). (Fig. 7) Of the total coral mortality at all five sites, 7% was new mortality and 93% was old mortality.

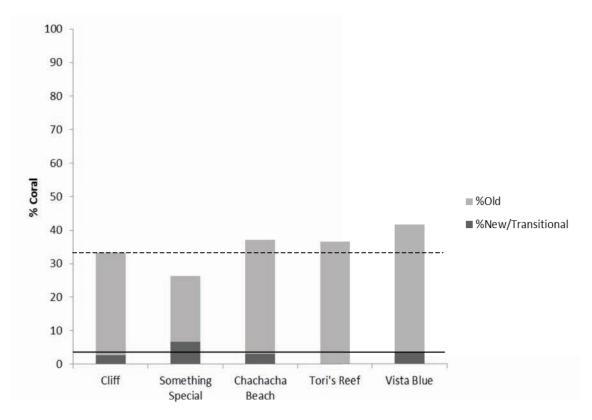


Figure 7. Total percentage of new and old coral mortality by sample site presented north to south. The solid line represents average new/transitional mortality among all five sites, and the dashed line represents average old mortality among all five sites. Pale and bleached corals were seen at all depths (Fig. 8). The highest percentage of pale coral was seen at 25m depth, with 35% pale. The lowest percentage of pale coral was seen at 30m depth, with 22% pale. The highest percentage of bleached coral was seen at 60m depth, with 23% bleached. The lowest percentage of bleached coral was seen at 30m depth, with 14% bleached. (Fig. 8)

New and old mortality was recorded at all depths (Fig. 9). The greatest total mortality was seen at 30m depth, with 48% combined mortality. The depth with the least total mortality was 60m, with 33% combined mortality. The greatest amount of new mortality was seen at 60m, with 4% new mortality. The greatest amount of old mortality was seen at 30m depth, with 47% old mortality. (Fig. 9)

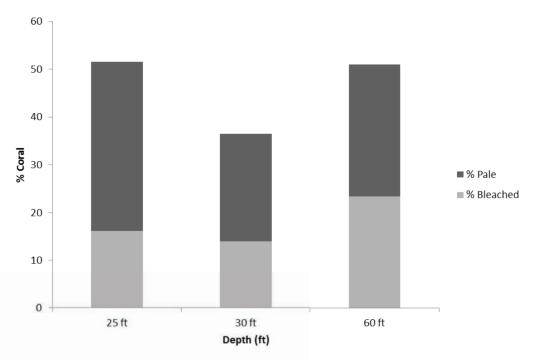


Figure 8. Total percentage of pale and bleached coral recorded at each transect depth.

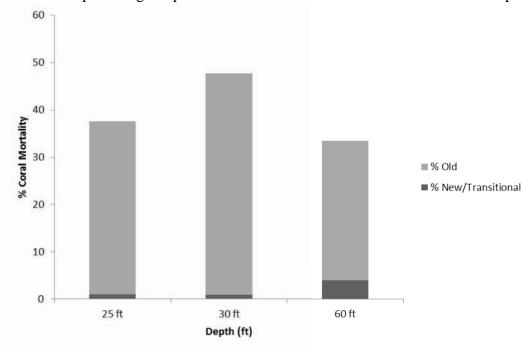


Figure 9. Total percentage of new and old coral mortality at each transect depth.

Discussion

While there was significant coral mortality at all survey sites, transect depths, and in almost all coral species, the majority was old mortality (>90%). This is typical of most corals that can be centuries old, so most of the past growth is dead. New mortality is relatively low (9%) and sporadically distributed, and does not appear to follow any clear geographic trend. While *Montastraea* spp. are by far the most abundant, these corals suffered significant mortality in the past, probably because they are the oldest. In contrast, the plate-like corals have proportionally more live cover than *Montastraea* spp. Acroporids (A. cervicornis, A. palmata) are conspicuously absent from the surveyed sites. These large branching corals were major shallow water reef builders, as they are fast growing and key providers of structural habitat complexity, but only two A. cervicornis and no A. palmata colonies were quantified in the surveys. The few Acroporid colonies that were seen exhibited no paleness, bleaching, or mortality of any kind. The lack of A. cervicornis and A. palmata can be attributed to the fact that these species were decimated by disease in the Caribbean, mainly white band disease (Aronson & Precht, 2001). Acropora spp. are now scarce throughout their previous range. As a result, areas formerly occupied by Acroporids are now dominated by weedy and plate-like corals such as A. agaricites, and P. astreoides (Harvell et al, 1999), as is evident in Bonaire (Fig. 1). These survey sites experienced modest bleaching (about 48% total pale and bleached) in September 2010. At the Cliff reef site over 50% of the corals were pale or fully bleached, and the remaining four sites were between 30% and 50% pale or bleached. Six months later, repeated BLAGRRA could determine if bleaching was transient or fatal. Specifically, BLAGRRA data taken in February and March 2011 show bleaching had dropped more than half (12-15%), and mortality was largely unchanged (7% in September 2010, and 7-10% in March 2011) (Jekielek, Bonaire Report 2011). No one survey site seems to have been particularly vulnerable to paleness, bleaching, or mortality. The survey did find greater new mortality at the 60 ft. transect depth (4%, as opposed to approximately 1% at the other two depths) (Fig. 9). It is difficult to draw major conclusions from these data, as the number of sample sites is small. Overall, BLAGRRA indicates moderate bleaching occurred in September 2010 with about 48% of corals being pale or white. By March there was evidence that the reefs are making a recovery, since by March only 12-15% bleaching was recorded (Jekielek, Bonaire Report 2011). Bleaching was mostly transient. New mortality increased by only about 3% in March 2011, but live coral cover declined over 6% since the 2009 assessment (Steneck, 2009). To see how the paleness, bleaching, and recovery process of Bonaire's reefs measured up to the recovery of other Caribbean reefs, the data and scenarios here were compared to published literature of reefs in Martinique and the Bahamas.

Martinique, along with most of the Caribbean, experienced a significant temperature anomaly from August to October 2005 that resulted in widespread bleaching (Cowan, 2006). When the area was assessed using BLAGRRA in January 2006 the species that had suffered the most mortality were *A. agaricites*, *P. porites*, *M. annularis*, and *M. faveolata*. While the September 2010 BLAGRRA found high amounts of mortality of *Montastraea* spp., the majority was old mortality, as is typical for long-lived species,

with only M. franksi showing a substantial amount of new mortality. Other species in Martinique that experienced high mortality like A. agaricites and P. porites showed very low mortality in Bonaire. The species in Martinique that fared the best following the bleaching event and showed good recovery were M. aurentenra, M. meandrites, and P. astreoides, and in Bonaire these three species also exhibited lower levels of mortality. This study notes that dominant taxa are often the most susceptible ones (Cowan, 2006), using *Montastraea* spp. as an example at this location. *Montastraea* spp. comprises 42.4% to 76.75% of coral at the survey sites in Martinique, and following the bleaching event, *Montastraea* spp. exhibited more partial mortality than other species, and was comparatively less healthy (Cowan, 2006). *Montastraea* spp. are also numerically and spatially dominant corals in Bonaire, and showed the same elevated levels of mortality compared to other less dominant taxa. The recovery of Martinique's reefs following this bleaching event is being inhibited by a disease outbreak causing additional mortality. Corals that survive bleaching events exist in a weakened state for some time after, and this can make them more vulnerable to opportunistic pathogens (Cowan, 2006). New Providence and Rose Island in the Bahamas were surveyed in August 2008. At the time of the survey 12% of corals were pale or bleached, and the authors suggest that this is the result of normal, annual discoloration often seen in this region in late summer due to thermal stress, combined with effects produced by shading from macroalgae (Lang et al, 2008). These surveys found that, of the total coral mortality that was observed, 23-24% was new/transitional (mostly seen in A. palmata and M. faveolata), and the majority of mortality, 80%, was old mortality. This is much higher new/transitional mortality than what was seen in Bonaire. The species showing the greatest amounts of old mortality at New Providence and Rose Island were M. annularis, S. siderea, and M. faveolata. No substantial amounts of new mortality were noted for M. annularis or M. faveolata in Bonaire, and S. siderea did not show high mortality. Recovery of the reef at New Providence and Rose Island is being endangered by the abundance of macroalgae, as the concentrations of herbivores that would normally keep macroalgal cover to a minimum are quite low (Lang et al, 2008). Macroalgal cover is increasing and could inhibit coral recruitment and reef recovery in Bonaire (Steneck et al, 2009).

The combined data present a snapshot of reef conditions during the bleaching event in the fall of 2010, as well as the differential susceptibility of diverse taxa to bleaching and mortality, and species-specific trends for recovery. By looking at obstacles to reef recovery in other reefs that have experienced bleaching, potential threats to future reef recovery can hopefully be identified and prevented in Bonaire.

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Chapter 2c: Assessing bleaching on Bonaire's coral reefs March 2011: Applying "BLAGGRA" six months after a bleaching event

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Abstract

Anomalously high ocean temperatures during fall of 2010 (September – November) resulted in coral bleaching. Six months after that event, corals were assessed for bleaching, paling and death (recent mortality) using the BLAGRRA protocol at 22 sites. Although variable, *Montastrea annularis* the most abundant coral, also had the largest area paling, bleaching or dying (i.e., new mortality). Mean percentages for paling, bleaching and new mortality were higher at Klein Bonaire sites than FPA or Control sites on Bonaire with %22.1, %2.1 and %13.9, respectively. *Montastrea annularis* also had the highest frequency of disease and, across all sites, the most prevalent disease was Yellow Band disease. There were no differences between FPA and Control sites for any of the variables we measured. Comparing 10 m depth BLAGRRA in Fall 2010 with that of Spring 2011 determined bleaching declined (14% to 2%) but new mortality increased (4% to 13.9%). Thus about 10% of the bleaching was lethal and the rest was transient.

Introduction

Coral reef bleaching has dramatically increased worldwide since first recorded in 1911 (Goreau and Hayes 1994). The increase in frequency, intensity and spatial extent often corresponds with large scale temperature disturbances such as El Nino (Goreau and Hayes 1994, Brown 1997, Glynn 1993, Berkelmans et al 2004, Burke et al 2011). Most often, mass bleaching events correlate with high temperature and light levels (Hough-Guldberg 1999). Due to this synergistic interaction, there exist global ocean "hot spots" that may be more susceptible to bleaching (Goreau and Hayes 1994). The Caribbean, an identified hot spot, has experienced major bleaching events in both 1998 and 2005 and, more recently, a less severe but still damaging event in the Fall of 2010 (Goreau and Hayes 1994).

Coral bleaching is the expulsion of symbiotic zooxanthellae algae from coral tissue in response to a stress. Upon expulsion of zooxanthellae, the coral tissue loses its color and becomes completely white, often appearing irregularly on the upper surfaces of coral (Williams et al 1987, Goreau and Macfarlane 1990). "Partial bleaching" is also possible, which results in paled tissue, rather than white, as a result of decreased zooxanthellae activity and may or may not lead to further bleaching (Gates 1990). Although generally attributed to high temperature effects, other environmental stressors can act alone or synergistically, including increased exposure to solar radiation, decreased temperature or salinity and exposure to infections and disease (Brown 1996). Depending upon the duration and intensity of the stress, coral species, colony size, depth, and zooxanthellae

species, responses to these factors may differ (Rowan et al 1997, Marshall and Baird 2000, Brandt 2009). For example, the extent and prevalence of bleaching has been found to be significantly higher in medium-large and large colonies of *Colpophyllia natans* in a mass bleaching event in the Florida Keys (Brandt 2009). Futhermore, Pocilloporid and Acroporid corals have shown higher susceptibilities to bleaching than other families (Marshall and Baird 2000).

Frequency and intensity of bleaching events impact corals biologically and have short-term or long-term effects. Bleaching may allow corals to select for more robust photosynthetic zooxanthellae symbionts that are better suited to handle higher temperatures, making coral more resilient to future bleaching events (Baker 2001). However, non-lethal bleaching might have longer-term negative effects by reducing rates of coral growth and calcification, impairing reproduction and causing tissue necrosis (Glynn 1993). In fact, partially-bleached corals that survived bleaching ceased skeletal growth throughout the recovery period (Goreau and Macfarlane 1989).

Coral disease is also considered one of the greatest threats to the health of coral reef systems. The first reports of coral diseases occurred in the early 1970's and have been on the rise ever since, affecting most common reef building corals (Harvell 1999, Humann 2002). A disproportionate number of records of coral disease have been found in the Caribbean with 76% of coral diseases described world-wide being found here (Green and Bruckner 2000, Miller et al. 2009). Mass mortalities (e.g. white band disease) are well-known but a diversity of diseases are present on most coral reefs (Humann 2002). Generally, disease is not found in isolation on a single colony but, rather, spreads among colonies and tissue that is affected by disease very rarely completely recovers (Green and Bruckner 2000). It is suspected that anomalously high temperatures can also lead to increased outbreaks of disease in corals in addition to bleaching (Bruno et al. 2007).

Synergy of coral disease and bleaching may be one of the greatest global threats to reef health (Miller et al 2009). Recently, outbreaks of disease have been connected with bleaching events and the incidence and number of diseases in marine systems is on the rise (Ward and Lafferty 2004, Miller et al 2009). Bleached colonies of *Acropora palmata* have been shown to be more susceptible to disease, resulting in higher total colony mortality than any other stressor (Muller et al. 2008). In that same study, elevated temperature was also found to increase the prevalence of disease in both bleached and unbleached colonies. Futhermore, the Caribbean basin suffered its greatest total coral loss ever documented due to the synergistic effects of bleaching and disease (Miller et al. 2009).

The goal of this study is to assess the current state of reefs in Bonaire after a high temperature anomaly and bleaching event in November of 2010. For this I used BLAGRRA to quantify the signs and symptoms of bleaching, disease and recovery as indicators of reef health.

Methods

This study was conducted over a period of two weeks from the 28th of February to the 10th of March 2011 on the islands of Bonaire and Klein Bonaire in the Dutch Antilles. The Bleaching Atlantic and Gulf Rapid Reef Assessment (BLAGRRA) protocol was used to assess frequency of mortality, state of bleaching and disease possibly resulting from the November 2010 bleaching event at a total of 22 sites on the island of (Appendix 2c.I). These sites were previously-chosen, all of which had undergone BLAGRRA protocol immediately during and after the bleaching event in the Fall of 2010.

10m² belt transects of fore reef habitat parallel to the coast at 10meters depth were assessed. Due to a lack of time, 10 sites had a single transect assessed while the remaining 12 had 2 transects assessed (Appendix 2c.I). All stony coral greater than or equal to 4cm in maximum length having any part inside the belt was measured to the nearest cm. Corals were identified by a four-letter code made up of the first letter of the genus and the first 3 letters of the species (e.g.; *Favia fragum* = FFRA). If species could not be determined, the first four letters of the genus only were used.

For each coral head, maximum length, width and height were recorded for any measurable colony, solitary coral or clump to the nearest 10cm. A clump is defined as a large group of similar appearing corals of the same species for which individual colony borders are indistinct (BLAGRRA 2010). Disease, if present, was identified, if possible, and noted by disease code. Extent of bleaching, if present, was noted and recorded as percent cover of the live tissue. Bleaching was assessed as either percent pale or percent fully bleached. Mortality was also assessed as percent cover of the entire coral colony and noted as either percent of new, transitional or old mortality, rounded to the nearest 5%. All data was entered into Excel and analyzed using Excel. For analysis, new and transitional mortality were combined and are identified in the analysis as "new mortality".

We present data for the Fish Protection Areas (FPA) and control sites on the island of Bonaire. The control sites include two No Dive Areas (NDA) that are not FPA sites and, therefore, should be grouped with controls.

Results

Bonaire

A total of 28 species of stony coral were identified on Bonaire and Klein Bonaire (Figure 1). *Montastrea annularis* was most abundant with 395 total colonies and contributed the most area in transects with 1,384,342 cm² total (Figure 1 and 2).

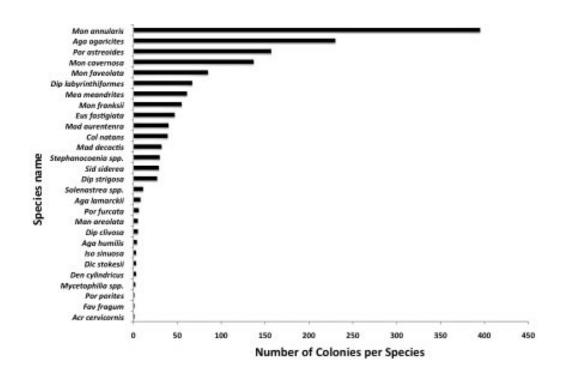


Figure 1. Total number of colonies per species on Bonaire.

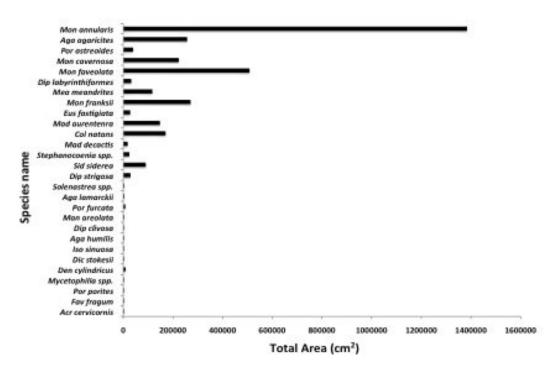


Figure 2. Total combined area of all species.

A total of 25 species, 89%, had pale tissue whereas a total of 19, 68%, had measurable bleached tissue (Figures 3 and 4). New mortality was observed on 20 species, 71% (Figure 5). *Montastrea annularis* was the species with highest area of pale, bleached and new mortality tissue overall (Figures 3,4 &5).

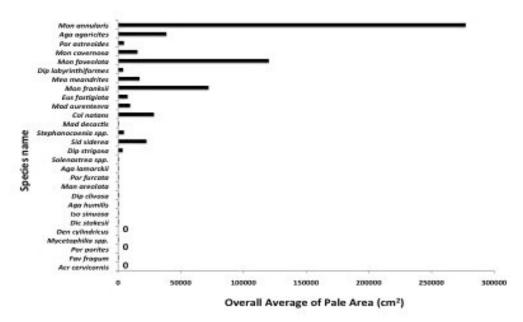


Figure 3. Overall area of average pale tissue per species. Zero's indicate a lack of pale tissue for that species.

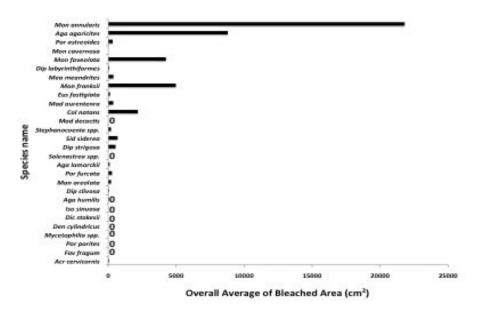


Figure 4. Overall area of average bleached tissue per species.

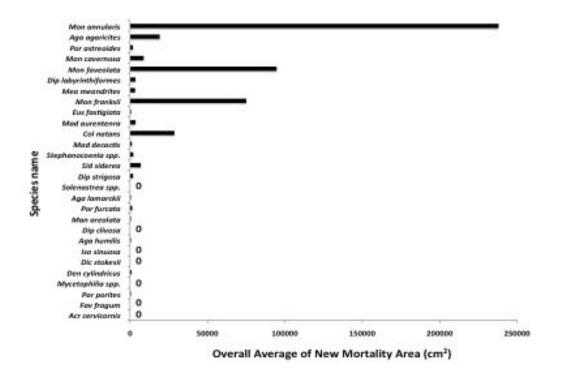


Figure 5. Overall area of average amount of tissue with new mortality per species.

A total of 17 species, %77, were identified as being diseased and the frequency of disease was highest in *Montastrea annularis* (Figure 6). Six diseases were observed throughout the study including Yellow Band disease (YBD), Dark Spot disease (DS), White Plague disease (WP), Red Band disease #2 (RBD2), Black Band disease (BBD), and White Band disease (WBD). Yellow Band disease was the most common disease among corals with a total count of 123 incidences (Figure 7).

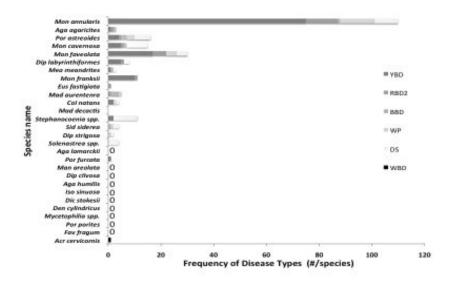


Figure 6. Frequency of disease within species.

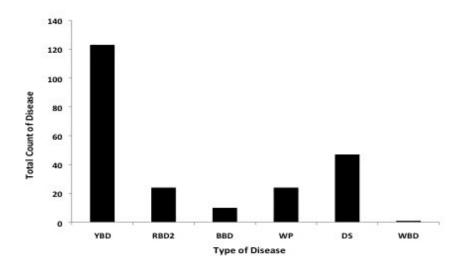


Figure 7. Total count of incidences of disease per disease type.

On the island of Bonaire, FPA and control sites had an average of 15.1% and 14.3% of the live tissue paled, respectively (Figure 8a). FPA and control sites both had an average of 1.1% tissues bleached (Figure 8b). "New" mortality for FPA and control sites was 10.8% and 9.9%, respectively (Figure 8c). For the FPA sites, Chachacha Beach and Calabas had the highest average of "new" mortality. At the control sites, Salt City had the highest average of "new" mortality (Figure 8).

Frequency of disease was highest for Cliff of the FPA sites and for Tori Reef of the control sites with 26 and 21 instances of disease, respectively (Figure 9 A&B). Yellow Band Disease was the most prevalent of diseases across all sites (Figure 10 A&B).

Sites on Klein Bonaire had an average of 22.1%, 2.11% and 13.9% of pale, bleached and "new" mortality, respectively (Figure 11). These values were all considerably higher than found on the island of Bonaire (Figure 8).

Four out of the five sites on Klein Bonaire were observed to have diseased corals, with Ebo's Reef having the highest frequency of disease (Figure 12).

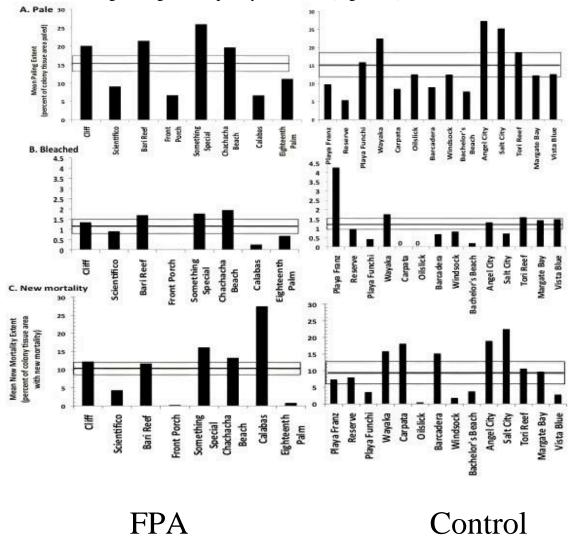


Figure 8. Average tissue (%) at each site of (a) paled, (b) bleached and having (c) "new" mortality. Sites are arranged from North to South (L to R). Horizontal lies indicate the error and the mean of the average paling, bleaching and "new" mortality for FPA and control sites. Note the change in the scale of y-axis among groups.

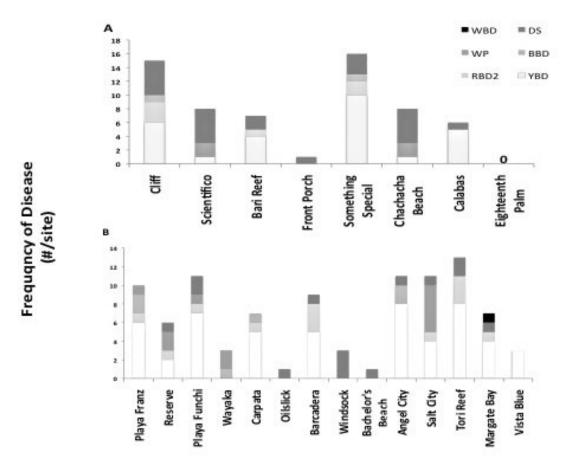


Figure 9. Frequency of disease at A) FPA sites and B) control sites on Bonaire.

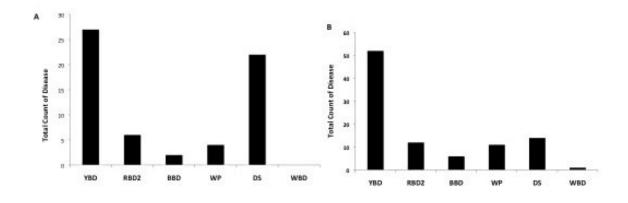


Figure 10. Total count of disease at A)FPA and B) control sites on Bonaire. YBD= Yellow Band disease, RBD2= Red Band disease #2, BBD= Black Band disease, WP= White Plague disease, DS= Dark Spot disease and WBD= White Band disease.

Disease Codes

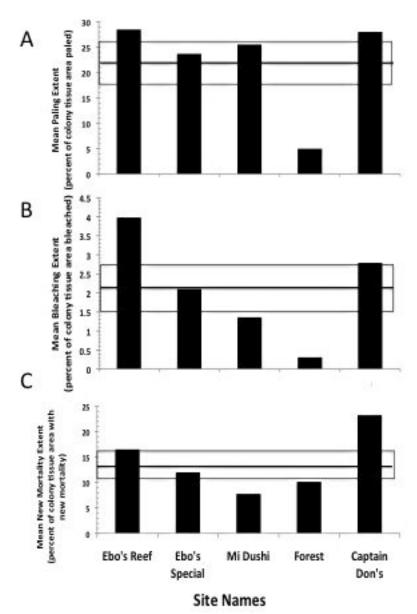


Figure 11. Average tissue (%) at each site of (a) paled, (b) bleached and having (c) "new" mortality. Sites are arranged from North to South (L to R). Horizontal lies indicate the error and the mean of the average paling, bleaching and "new" mortality. Note the change in the scale of y-axis among groups.

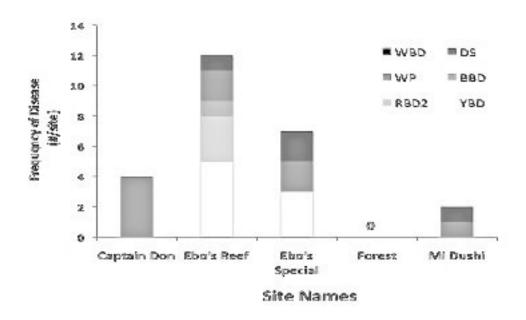


Figure 12. Frequency of disease (#/site) for the island of Klein Bonaire.

Discussion

Four months after a bleaching event in Bonaire, area of tissue paled and area of "new" mortality both increased whereas area of bleaching was decreased compared with assessments done immediately during and after the bleaching event (See Phillips, this report). Increases in new mortality indicate that the coral will have died within the span of a few weeks to months of the recent bleaching event (www.agrra.org/BLAGRRA). The area of tissue that is paled indicates that the reefs may be in a state of recovery or prolonged stress which can have long-term effects such as decreases in growth rate and reproduction, that could hinder the recovery of reef systems (Ward et al 2000,

Different species and morphologies also have different susceptibilities to temperature anomalies and subsequent bleaching (Brandt 2009). Large domal corals, such as *Colpophyllia natans, Montastrea faveolata and Montastrea franksi* showed some of the highest areas of pale tissue, bleaching and new mortality (Figure 8). These species are important members of the coral community because they are the remaining major reefbuilders and are generally resistant to disturbance (Pandolfi and Jackson 2006). Because coral cover and habitat architecture define the carrying capacity of ecosystems, should this continue, we could see declines in the surrounding diversity of reef communities (Jones et al 2004).

Disease in post-bleaching coral communities, especially in the Caribbean, is becoming increasingly common (Miller et al 2005, Muller et al 2008). Although no data are

available on the prevalence of disease prior or during the bleaching event, we suspect that there is a higher incidence of disease in post-bleached colonies compared to unbleached as suggested by Muller et al. (2008). The species that showed high rates of pale and bleached tissue, such as *Montastrea faveolata*, and the most abundant species, *Montastrea annularis*, also showed high frequency of disease. Yellow band disease, the most prevalent disease found in Bonaire, was particularly common on the oldest and largest domal corals in reef systems and has become increasingly abundant in the Caribbean, causing high rates of mortality in the 1990's (Humann 2003). Because this disease is currently so prevalent on reefs in Bonaire, its impact on reef health should continue to be closely monitored.

The incidence of bleaching is increasing in the Caribbean. In the Caribbean, McWilliams et. al (2005) show that bleaching is on an exponential rise and predict increases of up to 45% with even slight temperature increases. Disturbances, events that remove biomass from a given site, such as bleaching can greatly affect the recovery and health of reefs, especially if their frequency and intensity continue to increase (Connell 1997). Disturbance events, such as bleaching and disease, have been on the rise throughout the world and should be closely monitored for short-term and long-term effects (Glynn 1993, Connell 1997, Goreau and Macfarlane 1999).

In conclusion, the effects of the recent bleaching event in Bonaire are apparent with high incidence of disease and increases in pale and "new" mortality tissue. With the majority of paling, bleaching and new mortality affecting the major reef-building domal species, such as those in the *Montastrea* complex, there is concern for a decrease of these species and the structure they provide, which may have cascading effects on other reef-dwelling species (Jones et al. 2004, Bruno et al. 2007). We suggest the continuation of reef health to further assess the recovery after the recent bleaching event, but advise a review of the BLAGRRA protocol to better determine the most salient information to assess recovery.

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Chapter 3: Status and trends of Bonaire's herbivorous fishes

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Abstract

The overall trend of herbivorous fishes on Bonaire is one of decline. All of the six long-term monitoring sites show overall declines since 2003. The February-March 2011 monitoring was too soon after the ban on the take of parrotfishes (instated in 2010) to test the efficacy of this legislation. I recorded an overall increase in biomass of initial and terminal phase parrotfishes since 2009 inside the FPAs, however, this was due to a large spike in terminal phase stoplight parrotfish observed at Front Porch. Excluding this site, parrotfish biomass in the FPAs remained roughly equivalent to 2009. This is not surprising, given that parrotfish were not targeted in these areas prior to protection. With the more recently instated complete ban on the harvest of parrotfishes, we would expect to see increases in parrotfish populations in the future at sites where they were previously targeted.

Introduction

Globally, coral reefs suffer from disturbances, but Caribbean reefs, in particular, are not recovering (Connell et al. 1997, Gardner et al. 2003). Many Caribbean reefs appear to be undergoing a system-wide collapse and are in jeopardy of losing their "resilience" (Hughes et al. 2005). Resilience in this context means a reef ecosystem's ability to resist a phase shift from coral to algal dominance and/or its ability to recover (Holling 1973).

The most important driver of algal community structure on reefs is large denuding and scraping herbivores, including herbivorous fishes and urchins (Steneck 1988). Consensus is now emerging that managing for herbivory is a feasible action reef managers can take to safeguard reef resiliency (Roberts 1995, Rakitin and Kramer 1996, Mumby 2006, Steneck et al. 2009, Mumby and Steneck 2011). Recent studies suggest that scraping herbivores (i.e., sea urchins and parrotfish) reduce algal growth and increase coral abundance. For example, reefs in Jamaica, widely seen as among the world's most degraded, having phase-shifted from coral to macroalgal dominance in the 1980s (Hughes 1994, Kramer 2003), rebounded with an increase in herbivory. With recent increases in the grazing sea urchin Diadema antillarum, macroalgal abundance declined (Aronson and Precht 2000), juvenile coral abundance increased (Edmunds and Carpenter 2001) and, in places, coral cover recovered to levels last seen in the 1970s (Idjadi and Edmunds 2006). However, in most places in the Caribbean, including Bonaire, the scarcity of *D. antillarum* persists (Kramer 2003) leaving parrotfishes as the dominant grazer (Carpenter 1986, Steneck 1994). The positive effect of fish grazing on coral recruitment has also recently been demonstrated (Mumby et al. 2007, Arnold et al. 2010). Specifically, within a Bahamian marine reserve, increased fish grazing was strongly negatively correlated with macroalgal cover and resulted in a 2-fold increase in the

density of coral recruits (Mumby et al. 2007). A later study indicated that increasing fish grazing can actually improve overall coral cover (Mumby and Harborne 2010). If these examples are generally applicable, managers can indeed improve the resilience of reefs by managing for increased herbivory.

Fortunately, Bonaire has a history of a strong conservation ethic and has been proactive in managing their reefs. Continuing with that tradition, two no-take "Fish Protected Areas" (FPAs) were established in January 2008, and legislation to regulate the use of fish traps (which incidentally trap parrotfish; Hawkins and Roberts 2004) and ban the harvest of parrotfish was passed in 2010.

This study quantifies the abundance of algal removing fish in Bonaire, both inside and outside of FPAs, including at 5 sites monitored since 2003.

Methods

Visual surveys of algal removing fish were quantified at ten sites in Bonaire in February and March 2011. Control sites (from south to north) included Bachelor's Beach, Barcadera, Oil Slick Leap, Karpata, the no-dive Reserve, and Forest on Klein Bonaire. FPA sites included Eighteenth Palm, Calabas, Front Porch, and Reef Scientifico. The 5 sites monitored since 2003 include Eighteenth Palm, Reef Scientifico, Barcadera, Karpata, and Forest (herbivorous fish data from Windsock was not obtained in 2011).

Scarids (parrotfishes), acanthurids (surgeonfish, doctorfish and tangs), and yellow tail damselfish inside a $30 \times 4 \text{ m}$ (120 m^2) transect at 10 m depth were identified to species, size (total length to the nearest cm), and life phase (juvenile, initial, or terminal). The 30 m tape was released while swimming, and I swam at a rate that allowed me to complete 8 transects per hour.

Length was converted to biomass using the allometric coefficients of Bohnsack and Harper (1998).

Results

Scarids (parrotfish) are the dominant grazers on Bonaire's reefs, like most Caribbean reefs (Steneck 1988). At the six long-term monitoring sites, scarid biomass overall continues to decline (Fig.1).

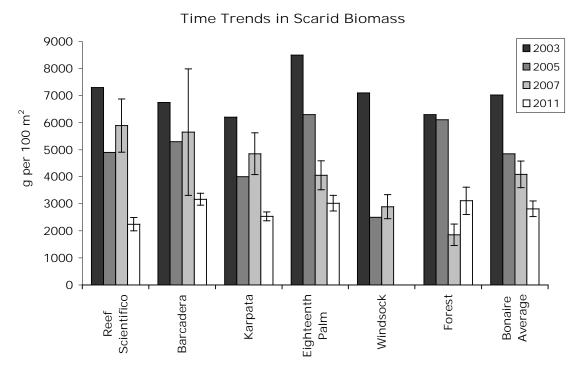


Figure 1. Scarid biomass at six sites from 2003-2011. Windsock data is absent from 2011. Error bars are \pm SE.

Biomass data from 2009 was not included because the 2009 observer did not include juvenile parrotfishes in the survey. However, for the purposes of evaluating the efficacy of the FPAs (established in 2008) in preserving parrotfishes, I compared scarid biomass data from all sites in 2009 to data from 2011, excluding juveniles. Mean biomass for scarids (not including juveniles) in 2009 was approximately 3200 g per 100 m² inside FPAs (Eighteenth Palm, Calabas, Front Porch, and Reef Scientifico) and 3750 g per 100 m² in Controls areas (Windsock, Forest, Barcadera, and Oil Slick). If juveniles were excluded from the 2011 data, for comparisons sake, 2011 scarid biomass would be 4786 \pm 1483 g per 100 m² inside FPAs (same sites as 2009) and 2998 \pm 1308 g per 100 m² in Control areas (same sites as 2009, except no 2011 data for Windsock). This increase in non-juvenile scarid biomass in FPA sites from 2009 to 2011 is largely due to the high density of terminal phase stoplight parrotfish observed at Front Porch. Biomass of scarids (again not including juveniles for the sake of comparison) at Calabas increased by approximately 1000 g per 100 m², whereas cumulative initial and terminal phase scarid biomass remained roughly the same at Reef Scientifico and Eighteenth Palm from 2009 to 2011.

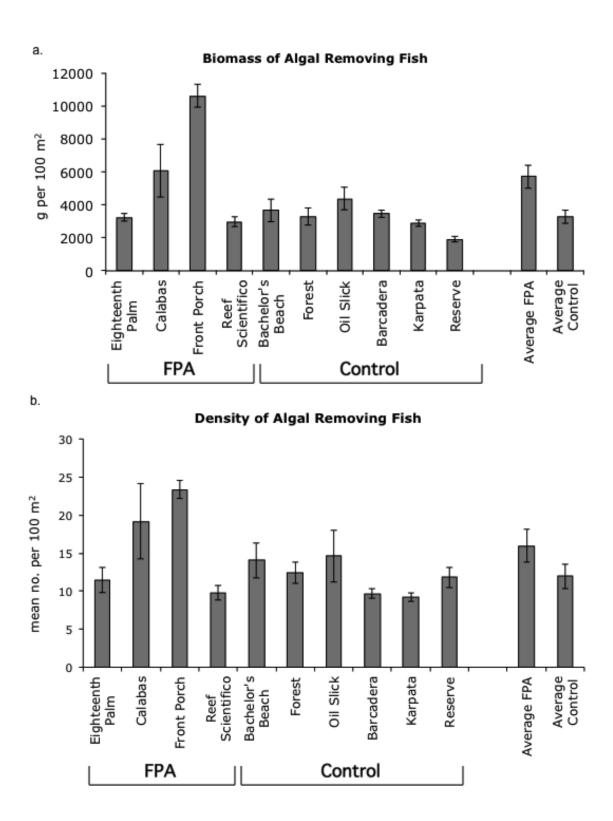


Figure 2. Biomass (a) and density (b) of all algal removing fish (scarids, acanthurids, and yellowtail damsels). Error bars are \pm SE.

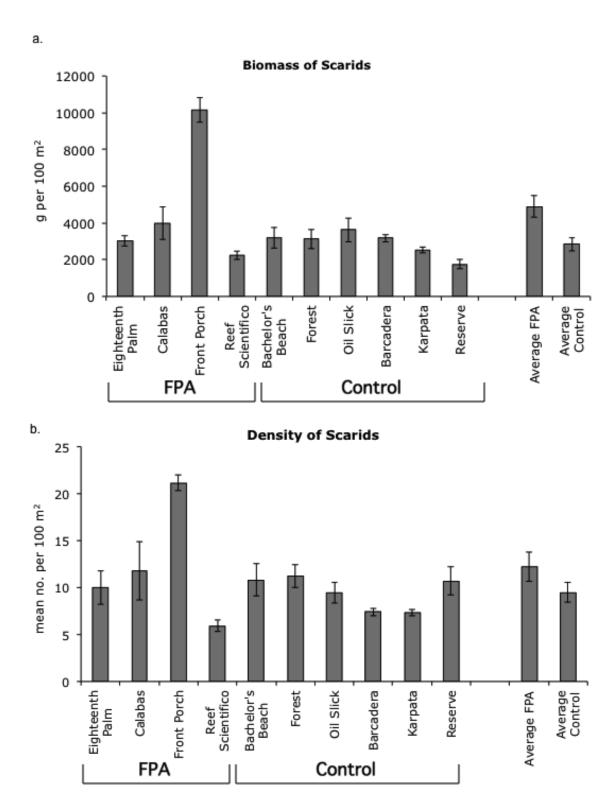
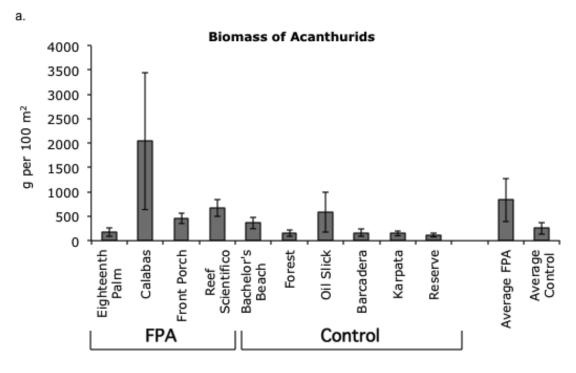


Figure 3. Biomass (a) and density (b) of scarids. Error bars are \pm SE.



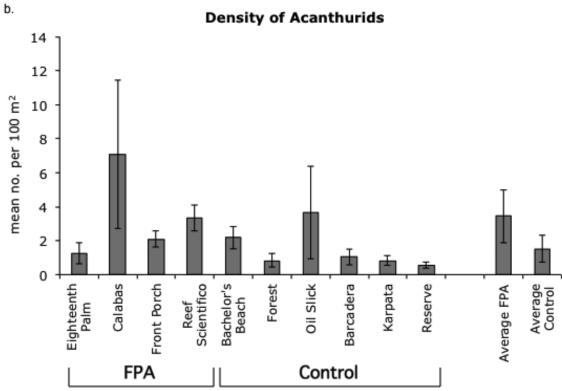


Figure 4. Biomass (a) and density (b) of acanthurids. Error bars are \pm SE.

Territorial damselfish are important herbivores because their aggression reduces herbivory from other fishes. Overall damselfish abundance has been increasing but their

abundance is greater in control sites than in FPA sites (Fig. 5). This is consistent with the observation that fish predators are generally increasing in the FPA areas. It is also possible (but not yet confirmed) that fishes known to be predators of damselfishes are increasing in areas where they are not fished (FPA).

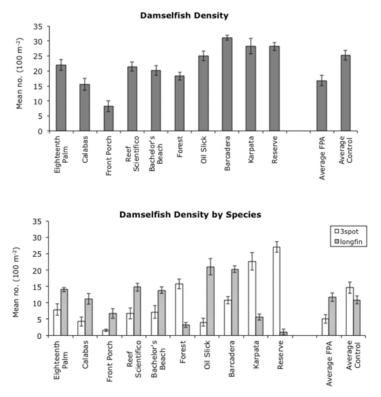


Figure 5. Population densities of territorial damselfishes (three-spot and longfin damselfishes) by species (lower figure) and overall (upper figure).

Discussion

Overall biomass of initial and terminal phase parrotfishes since 2009 increased inside the FPAs and decreased in Control areas. This increase in biomass inside the FPAs, however, was due to the high abundance of terminal phase stoplight parrotfish observed at Front Porch. Excluding this site, parrotfish biomass in the FPAs remained roughly equivalent to 2009. This is not surprising, given that parrotfish were not targeted in these areas prior to protection. With the more recently instated complete ban on the harvest of parrotfishes in 2010, we would expect to see increases in parrotfish populations in the future at sites where they were previously targeted, such as Oil Slick Leap.

More striking, however, was the continuing trend of decline in biomass of algal removing fish on Bonaire since 2003. All of our six long-term monitoring sites show an overall decline since 2003. The February-March 2011 monitoring was too soon after the instated ban on the take of parrotfishes to test the efficacy of this legislation. For example, biomass of targeted fish increased by a factor of 3.1 between 1 and 9 years of protection

in the Philippines, where clear differences in fish biomass between reserve and non-reserve sites were noted after approximately 6 years (Alcala et al. 2005). Similarly, in St. Lucia, after 5 years of protection, no-take reserves encompassing 35 % of the local fishing grounds resulted in 46-90% increases in catch (Roberts et al. 2001).

It is important to note that herbivore biomass is not necessarily a straightforward proxy for grazing because of different bite sizes and rates of various parrotfish species (Mumby 2006). Thus, it is important to consider species composition (see Appendix 3.I) and grazing rates by species (see McMahan, Chp. 4). Furthermore, declining coverage of live coral, as reported in this report (see Steneck, Chp. 1), increases space for the encroachment of macroaglae. Thus, grazers have a greater area of reef to maintain, often reducing rates of grazing per unit area, leading to macroalgal takeover.

Certainly, there is no panacea for reef conservation (Aronson and Precht 2006, Steneck et al. 2009), and managing for herbivores is no exception. However, this strategy can be a tangible, enforceable effort. Ideally, an increase in grazing by herbivorous fish would reduce the abundance of algae, and we would see increase in juvenile corals. However, Bonaire is not tracking in this direction. Since 2003, we have documented a recent decline in live coral cover and an abrupt increase in macroalgae, coincident with a long-term decline in herbivore and juvenile coral abundance. Declining juvenile coral abundance appears to now be as rampant in the southern Caribbean as the rest of the region, with a recent study showing declines of 54.7 % in juvenile coral density in Curacao from 1975 to 2005 (Vermeij et al. 2011). Studies such as this may indicate that Bonaire and Curacao, while slightly more resilient, are following the path of decline common on Caribbean reefs.

Global stressors, such as coral bleaching and ocean acidification, are indeed contributing to the decline of Bonaire's reefs. However, other local measures can be taken to mitigate stress on reefs, including improving land use practices such as restricting coastal development and reducing nutrient input.

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Chapter 4: Grazing rates before and after management to protect parrotfish (Scaridae) and establishing Fish Protection Areas

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Abstract

Herbivorous fish play a major role in overall reef health by reducing algal cover that would otherwise disrupt coral growth and recruitment. Several fish protection areas (FPA) and a ban on fishing of parrotfish were established in 2008 and 2010, respectively, in Bonaire, Netherland Antilles. I quantified bite rates of herbivorous fish at 10m depth within meter square areas on topographic highs at 11 reef sites on the leeward reefs of Bonaire. Four of these sites are inside of FPAs. An average of 10 five minute observations were made at each site. The average bite rate observed was 245 bites/m²/hr. Sites inside FPAs had significantly higher bite rates than sites outside FPAs (T-test, p=0.04). Parrotfish (Scaridae) had the highest average bite rates at each site and most commonly consisted of small-size intermediate phase fish. Bite rates of large parrotfish were higher inside FPAs. There was no correlation between bite rates and herbivorous fish density. In fact, areas with highest parrotfish abundance had the lowest algal cover (Ch. 3) but showed lower bite rates. Territorial damselfish were present in 77% of the quadrats and overall negatively influenced the bite rates on topographic high spots of scrapers (scarids) and denuders (acanthurids and yellowtail damselfish). Average bite rates for 2011 were higher than previous years and significantly differed from the declining trend in bite rates seen in 2005, 2007, and 2009 (T-test, p<0.05). This may relate to the marked increase in algae on Bonaire's reefs (Ch. 1). Herbivores avoid algal patches so they concentrate their grazing on high spots as low spots switch to macroalgae. This may be due to complex feedbacks between macroalgae and herbivores and also between damselfish and herbivores.

Introduction

Herbivory is an important process that promotes the overall health of coral reef systems. Herbivorous grazers reduce algal biomass and in turn positively influence reef resilience (Hughes et al. 2007). This is evident from studies in which areas where grazers are excluded quickly become overgrown by macroalgae and coral recruitment and survival subsequently decline (Hughes et al. 2007, Arnold et al. 2010). In 1983 the Caribbean-wide mass mortality of *Diadema antillarum* led to a reduction in herbivory and subsequent increase in algal abundance (Hughes et al. 1987, Lessios 1988). The loss of *D. antillarum* combined with a reduction in biomass of herbivorous reef fishes due to overfishing caused many Caribbean reefs to shift from coral dominated to macroalgal dominated (Knowlton 1992, Hughes 1994). Areas where herbivorous fish populations are protected or only lightly fished may provide refuge from a phase shift from coral to macroalgal dominance because it has been shown that there is a strong negative correlation between herbivorous fish biomass and macroalgal abundance (Williams & Polunin 2001, Mumby et al. 2006). It is therefore important for managers to consider the health of herbivorous fish populations when assessing overall reef health.

Herbivorous fish can be separated into three functional categories; scrapers (excavators), denuders, and non-denuders (Steneck 1988). These functional groups differ in their impact on algal communities. Scrapers are deep grazing parrotfish that have the greatest impact on algal abundance and are able to feed on the widest range of algal groups (Steneck 1988). This group can be further broken into scrapers and excavators or fish that only remove algae from the substrate when they take a bite and fish that remove both algae and substrate when they take a bite (Bellwood & Choat 1990). For this study scrapers and excavators will be grouped under the single functional group of excavators. Denuders are generally acanthurids (and some damselfish) and can only significantly reduce algal biomass in high densities (Steneck 1988). They are also limited in the types of algae they can consume, generally avoiding tough or thick algae. Non-denuders are territorial damselfish that do not significantly decrease algae abundance, and in many cases increase algal biomass within their territories by defending against excavators and denuders (Steneck 1988, Hixon 1997). It is also important to point out that herbivore size greatly influences grazing. Larger parrotfish tend to leave deeper grazing scars and intake a greater amount of food per bite (Bruggemann et al. 1994a, Bonaldo & Bellwood 2008).

The purpose of this study was to quantify herbivore bite rates on the reefs surrounding Bonaire, Netherland Antilles. There has been on-going monitoring every other year since 2003 at several sites including Eighteenth Palm, Reef Scientifico, Barcadera, and Forest (Klein Bonaire), and also including Windsock and Karpata since 2005. In 2008 Bonaire established fish protection areas (FPAs) including at Reef Scientifico, Front Porch, Calabas, and Eighteenth Palm and in 2010 a management decision was made to ban parrotfish fishing. In order to analyze both spatial and temporal trends several variables were recorded at each site in addition to bite rates. These included herbivore species, size, phase, and presence or absence of territorial damselfish. These data were then compared between sites inside FPAs and outside FPAs (control) and also over time (2003, 2005, 2007, 2009, and 2011).

Materials and Methods

I collected bite rate data from 26 February to 3 March 2011 in Bonaire, Netherland Antilles. At each site I observed meter square quadrats between 5-10 m depth on a topographical high and with at least 75% algal cover for five minute intervals. During this time, I recorded the number of bites taken by herbivorous fish within the quadrat as well as herbivore species, phase (juvenile, intermediate, or terminal), and size (total length). Size categories included small (<7 cm) and large (≥7 cm) for Pomacentridae, small (<15 cm) and large (≥15 cm) for Acanthuridae, and small (<13 cm), medium (13-20 cm), large (21-30cm), and very large (>31 cm) for Scaridae. I laid pieces of PVC pipe, cut to the length of each size category, on the substrate roughly five meters from the quadrat and used them to calibrate sizes of fish taking bites. In addition to this, I recorded the presence or absence of territorial damselfish within each quadrat. I observed an average of 10 quadrats at each site. Sites were either inside FPAs or outside FPAs (control). I used Excel for data entry and analysis.

Results

The average bite rate for Bonaire was 245 bites/m²/hr. Bite rates were significantly higher at FPA sites compared to control sites (T-test, p=0.04, Fig. 1A). The highest bite rates were observed at Reef Scientifico, and the lowest bite rates were observed at Oil Slick Leap (Fig. 1A). Observed herbivorous fish belonged to three families; Scaridae, Acanthuridae, and Pomacentridae, which comprise the three functional groups; excavators, denuders, and non-denuders (a complete list of herbivore species and bite rates can be seen in Appendix 4.I). Excavators (Scaridae) had the highest average bite rate as well as the highest bite rate at each individual site (Fig. 1B) while denuders (Acanthuridae and yellowtail damselfish) and non-denuders (Pomacentridae) both had low average bite rates (Fig. 1C, D). Bite rates for herbivores (scarids and acanthurids combined) and scarids were not significantly density dependent while bite rates for acanthurids showed a significant, but relatively weak, negative relationship with density (density data from Arnold 2011) (Fig. 2). The highest macroalgae abundance was recorded at Eighteenth Palm (Steneck 2011) where bite rates were relatively high, and the lowest macroalgae abundance was recorded at Front Porch (Steneck 2011) where bite rates were relatively low (Fig. 3).

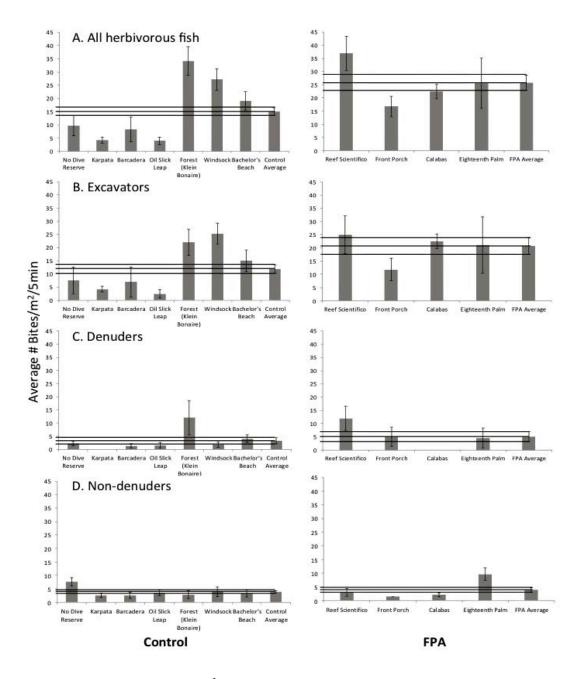


Figure 1. Average bite rates (# bites/m²/5min) for A) All herbivorous fish (excavators and denuders), B) Excavators (Scaridae), C) Denuders (Acanthuridae and yellowtail damselfish) and (D) Non-denuders (Pomacentridae) from 26 February to 3 March 2011. Control (left) and FPA (right) sites arranged from north to south (left to right). Error bars equal \pm standard error, horizontal black lines indicate average bite rates \pm standard error among control and FPA sites.

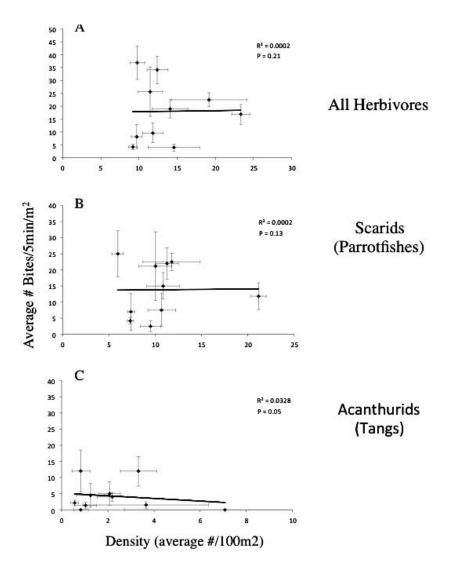


Figure 2. Site specific average bite rates (# bites/m²/5min) as a function of density (average #/100m²) for A) all herbivores (scarids and acanthurids), B) scarids, and C) acanthurids. Best-fit linear relationship given as solid line, as well as r^2 and P values for each group. Error bars equal \pm standard error.

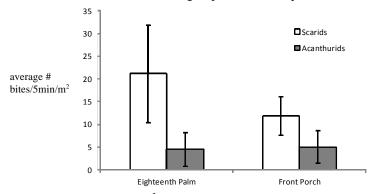


Figure 3. Average bite rates (# bites/ m^2 /5min) for Scarids and Acanthurids at areas with high (Eighteenth Palm) and low (Reef Scientifico) macroalgae abundance (Steneck 2011). Error bars equal \pm standard error.

Scaridae herbivory

The most commonly observed scarid species was the princess parrotfish (Fig. 4B), the most commonly observed phase was intermediate (Fig. 4C), and the most commonly observed size was small (Fig. 4A), though there were differences in these patterns among sites. On average scarids were larger inside FPAs (Fig. 4A), and FPAs had higher abundances of both juvenile and

terminal phase Scarids compared to the control areas (Fig. 4C). FPAs also had higher abundance of both stoplight parrotfish and queen parrotfish (Fig. 5). There was a significant increase in parrotfish bite rates between 2009 and 2011 (T-test, p=0.002).

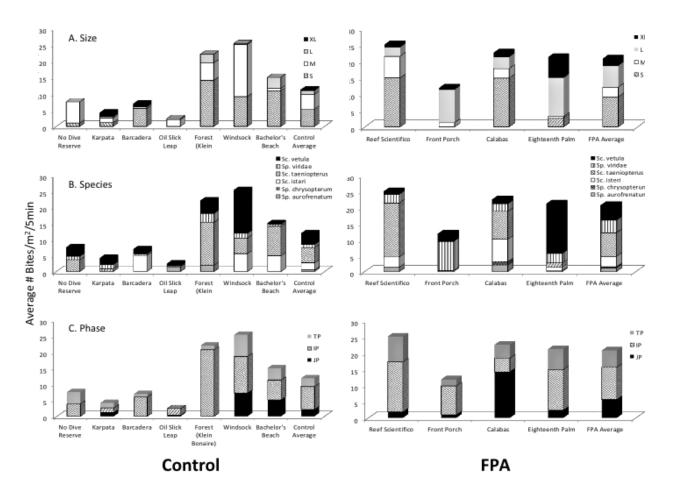


Figure 4. Average scarid bite rates (# bites/m 2 /5min) categorized by A) size (small = S, medium = M, large = L, very large = XL), B) species, and C) phase (terminal phase = TP, intermediate phase = IP, juvenile phase = JP). Control (left) and FPA (right) sites arranged from north to south (left to right).

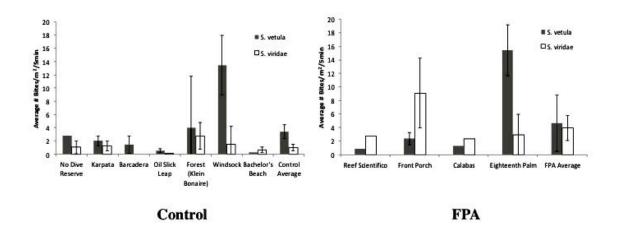


Figure 5. Average bite rates (# bites/m²/5min) for *S. vetula* and *S. viridae*. Control (left) and FPA (right) sites arranged from north to south (left to right). Error bars equal \pm standard error.

Influence of territorial damselfish

Territorial damselfish were present in 89% of the quadrats at control sites and 65% of the quadrats at FPA sites (Fig. 6). When territorial damselfish bite rates were low, excavator (Scarid) and denuder (Acanthurids and yellowtail damselfish) bite rates varied widely, but as territorial damselfish bite rates increased, excavator and denuder bite rates decreased (Fig. 7A). This relationship was stronger for small and medium sized parrotfish and weaker for large and very large parrotfish (Fig. 7B). Overall there were higher bite rates in quadrats were territorial damselfish were not present (Fig. 8), however this relationship was not significant (T-test, p=0.25). There was an overall increase in damselfish presence in 2011 compared to 2009 when they were only present in 60% of sampled quadrats (Jaini 2009).

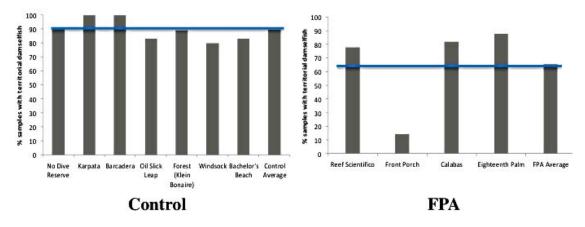


Figure 6. Percent of quadrats containing territorial damselfish at each site. Control (left) and FPA (right) sites arranged from north to south (left to right).

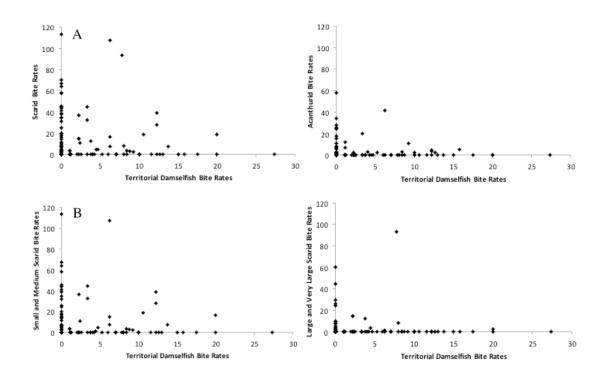


Figure 7. A.) Average bite rate (# bites/m²/5min) of scarids (left) and acanthurids (right) as a function of territorial damselfish bite rates (# bites/m²/5min) at all sites. B.) Average bite rates (# bites/m²/5min) of small and medium (left) size scarids and large and very large (right) size scarids as a function of territorial damselfish bite rates (#bites/m²/5min) at all sites.

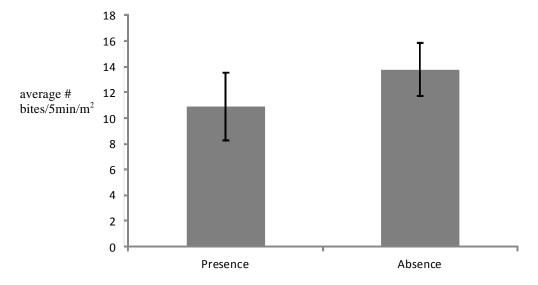


Figure 8. Average herbivore (excavators and denuders) bite rate (# bites/m 2 /5min) in the presence and absence of territorial damselfish. Error bars equal \pm standard error. *Temporal trends: bite rates over time*

Bite rate data have been collected since 2003 at Eighteenth Palm, Reef Scientifico, Barcadera, and Forest (Klein Bonaire) and since 2005 at Windsock and Karpata. There has been a significant decline in average bite rates over this time period (T-test, p<0.05, Fig. 9), however, bite rates from 2011 showed a significant increase from 2009 (T-test, p=0.03, Fig. 9) and the average bite rate for Bonaire was higher in 2011 than in any other year (Fig. 9). Site specific trends of average bite rate show that both Reef Scientifico and Windsock had the highest bite rates recorded in 2011 while Karpata had the lowest bite rates recorded in 2011 (Fig. 9).

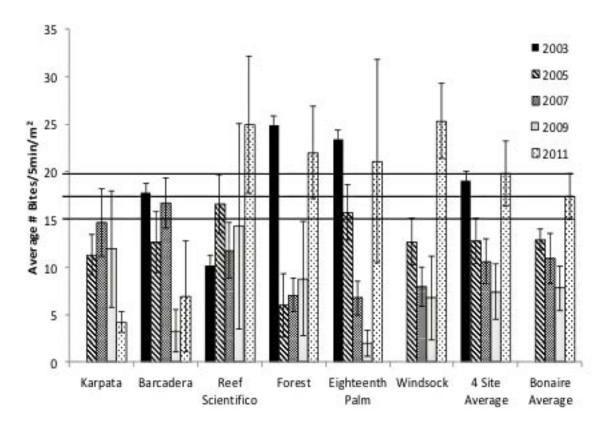


Figure 9. Average bite rates (# bites/m²/5min) at monitored sites in Bonaire from 2003 to 2011. Error bars equal \pm standard error, horizontal black lines indicate average bite rates \pm standard error for 2011. Sites arranged from north to south (left to right). Control sites = Karpata, Barcadera, Forest, and Windsock. FPA sites = Reef Scientifico and Eighteenth Palm. Four site average = Barcadera, Reef Scientifico, Forest, and Eighteenth Palm for all years. Bonaire average = all sites from 2005 to 2011.

Discussion

Average bite rates in Bonaire have increased significantly from previous years. Scarid bite rates in particular showed a significant increase from 2009 (Jaini 2009), and there was a greater frequency of grazing by large scarids. In addition to this, bite rates inside of FPAs in 2011 were significantly greater than in control areas as was grazing by large parrotfish and queen and stoplight parrotfish in particular. The establishment of FPAs occurred only a few months before 2009 observations were made so it is unlikely that we

would have seen any effect on those results, however the 2011 bite rate data suggest that grazing is higher inside FPAs, which may mean that we are seeing the effect of large herbivores being released from fishing pressure. Many studies have shown that FPA establishment is rapidly followed by increased fish abundance and grazing (Rakitin 1996, Abesamis & Russ 2005), which may explain these results, however a decrease in macroalgae abundance is also commonly seen after establishment of FPAs (Mumby et al. 2006, Hughes et al. 2007, Mumby & Steneck 2008) and this was not a pattern that was seen in Bonaire (Steneck 2011). Larger parrotfish, especially queen parrotfish and stoplight parrotfish, should have a greater impact on algal abundance because they intake a greater amount of food per bite (Bruggemann et al. 1994a, Bonaldo & Bellwood 2008) but despite high bite rates inside FPAs (especially by larger parrotfish) an increase in macroalgal abundance was documented (Steneck 2011).

It is important to point out that the increase in bite rates seen in 2011 may not be indicative of population densities. In fact, observations made by Arnold (2011) showed an overall decrease in scarid and acanthurid biomass. These observations coupled with the overall increase in macroalgae abundance (Steneck 2011) strongly suggest that herbivory has decreased despite the increase in observed bite rates. These conflicting patterns may be part of a complex feedback mechanism between macroalgae and grazers. Recently a study by Hoey and Bellwood (2011) showed that herbivorous fish preferred to graze in areas with lower macroalgae cover and that macroalgae displaced turf grazing parrotfish. They speculated that this may have a positive feedback effect on the growth of macroalgae stands which could reinforce phase shifts to macroalgae dominance. In addition to this, other studies have shown that herbivorous fish selectively feed on turfs and avoid macroalgae (Bruggeman et al. 1994b, Williams & Polunin 2001). If this is the case in Bonaire, then we may see herbivores avoiding areas with dense macroalgae and instead choosing to graze in areas where macroalgal abundance is low and turf abundance is high, such as the topographic highs that were surveyed in this study. These high areas are more heavily grazed than surrounding low areas (Jaini 2009) and are kept relatively free of macroalgae. If macroalgae abundance is increasing elsewhere on the reef, these preferred grazing areas would become even more heavily grazed by herbivores. Essentially grazing would be concentrated on topographic highs. This may explain why the 2011 bite rate data appear to indicated an increase in herbivory while herbivorous fish abundance has decreased (Arnold 2011) and macroalgae abundance has increased (Steneck 2011). Grazing concentration may also be the reason why bite rates did not positively correlate with herbivore density and why, counter intuitively, bite rates were high at the site with the highest macroalgae abundance and low at the site with the lowest macroalgae abundance.

The percent abundance of territorial damselfish increased from an average of 60% in 2009 (Jaini 2009) to an average of 77% in 2011, however there were fewer damselfish inside FPAs which may be due to a greater abundance of predators in these areas (Mumby et al. 2006). Territorial damselfish defend their territory by being aggressive towards other herbivores, which tends to result in thick turf carpets within their territories (Steneck 1988, Hixon 1997). The results suggest that as damselfish bite rates increase, scarid and acanthurid bite rates decline and that overall herbivore bite rates were lower in

the presence of territorial damselfish. It is possible that the increase in territorial damselfish is partially responsible for the increased macroalgal abundance (Steneck 2011) and also in concentrating herbivory on topographic highs.

Although it appears that grazing has increased in Bonaire, managers should approach these results with caution. The mobile nature of herbivores and high variability in bite rates increases the likelihood of sampling error. Both the increase in algal biomass (Steneck 2011) and decrease in herbivore abundance (Arnold 2011) suggest herbivory has declined. Because herbivorous fish tend to selectively feed on turfs and avoid macroalgae (Bruggemann et al. 1994b, Williams & Polunin 2001, Hoey & Bellwood 2011), grazing may be intense on well cropped topographical highs where observations for this study were made, but less intense in other areas where macroalgal abundance has increased (Hoey & Bellwood 2011). The increase in damselfish presence may also lead to a concentration of herbivory on topographic highs. Unfortunately, I only sampled areas that were topographical highs, so I cannot conclusively say what is happening elsewhere on the reef, but a situation like this would result in high bite rate observations as well as observations of high macroalgae abundance. Further experimentation on the effects of macroalgae on grazing is warranted. However, the greater amount of grazing, increased bite rates by large scarids, and lesser abundance of territorial damselfish inside FPAs as opposed to outside suggests that FPAs are promoting herbivory. It is also possible that we will see a turnaround in macroalgal abundance in the future as the influence of the management decision to ban parrotfish fishing becomes more apparent.

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Chapter 5: The status and trends of sea urchins *Diadema antillarum* and *Echinometra* species on leeward coral reefs of Bonaire

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Abstract

Sea urchins, *Diadema antillarum* and *Echinometra* species (*E. viridis* and *E. lucunter*), at high densities, control macroalgae abundance and species composition on coral reefs. Surveys conducted in 2011 of *Diadema antillarum*, *Echinometra viridis* and *Echinometra lucunter* population abundance at ten coral reef sites along Bonaire's leeward coast recorded low population densities of less than $0.01/m^2$ to $0.06/m^2$ for *Diadema antillarum* and population densities of less than $0.01/m^2$ to $0.32/m^2$ for *Echinometra* species. Population trends from 1999 to 2011 at five long-termed monitored sites show *Diadema antillarum* population increased to peak abundance in 2005 but increased in 2011 from being absent in 2009. *Echinometra viridis* increased significantly from less than $0.05/m^2$ for 2005 through 2009 to $0.14/m^2$ in 2011. Sea urchins remain rare on leeward reefs in Bonaire.

Introduction

Coral reefs throughout the Caribbean have experienced a shift from a coral-dominated state to a macroalgal-dominated state likely due to the depressed herbivore populations. Decreased herbivore abundance can potentially facilitate the persistence of the macroalgal-dominated state (Done 1992, Hughes 1994). The inverse relationship between herbivore abundance and macroalgae abundance is well documented (e.g. Williams & Polunin 2001). In addition, a shift in algal community composition from turf and coralline algae to macroalgae often occurs (Carpenter 1990). This relationship and subsequent phase shift was particularly evident after the 1983/1984 mass mortality event of the sea urchin, Diadema antillarum. The disease, which was spread rapidly throughout the geographic range of this species, caused morality rates as high as 95-99% of premortality abundance levels of up to 25/m² (Lessios 1984, Carpenter 1988, Miller et al. 2003). Following this event, macroalagae abundance increased on many reefs (Carpenter 1990, Edmunds & Carpenter 2001, Miller et al. 2003). Recovery of *Diadema* populations over the last three decades has been slow and patchy. Some studies suggest increasing rates of recovery at certain Caribbean reefs while others report increase in abundance may have peaked in 2003, but *Diadema* populations may once again be in decline (Miller et al. 2003, Hughes et al. 2010). The slow rate of *Diadema* recovery on many reefs raises questions about the stability and persistence of a macroalgal-dominated state (Mumby 2009).

Sea urchins, both *Diadema* and species of *Echinometra*, when abundant (e.g. with densities > 1.0/m²), play a critical functional role as grazers, controlling algal abundance on coral reefs (Carpenter 1988, McClanahan 1999, Woodley et al. 1999, Aronson & Precht 2000). Urchin grazing can facilitate coral recruitment by reducing competition for space and removing macroalgae that would otherwise inhibit juvenile coral settlement (Edmunds & Carpenter 2001, Miller et al. 2003, Griffin et al. 2003, Mumby et al. 2006).

The objective of this study seeks to monitor population abundance of *Diadema* antillarum, *Echinometra viridis* and *Echinometra lucunter* at 10 m depth on coral reefs in Bonaire and to determine population trends for *Diadema antillarum* and *Echinometra viridis*.

Methods

We surveyed abundance of sea urchins (*Diadema antillarum*, *Echinometra viridis* and *Echinometra lucunter*) at ten sites along the leeward coast of Bonaire. From north to south, the sites included: Karpata, Barcadera, Oil Slick Leap, Reef Scientifico, Front Porch, Forest, Calabas, Eighteenth Palm, Windsock and Bachelor's Beach. We deployed 2 x 10 m belt transects over areas dominated by coral colonies at 10 m depth. We avoided contiguous areas of sand and followed the AGRRA protocol of surveying one meter on either side (i.e. surveying an area of 20 m² for each transect).

Along each transect, we counted and identified individuals to the species level. We surveyed between four and ten transects at each site and averaged the population density of each species for each site based on the number of transects surveyed at that site. We compared Fish Protection Areas (FPA) of Reef Scientifico, Front Porch, Calabas and Eighteenth Palm (listed north to south) to the control sites of Karpata, Barcadera, Oil Slick Leap, Windscock and Bachelor's Beach (listed north to south). For population trends, we compared 2011 survey data to data collected at five monitored sites in past years. The sites, listed from north to south, include Barcadera, Karpata, Reef Scientifico, Forest, Eighteenth Palm, and Windsock. *Diadema antillarum* average population density pooled from these sites was compared to average population densities for the years 1999, 2003, 2005, 2007 and 2009. We also compared 2011 *E. viridis* average population density from the monitored sites to the average population densities for the years 2005, 2007 and 2009. Historical population densities were taken from past Bonaire reports available via STINAPA (Steneck et al. 2003, 2005, 2007, 2009).

Results

Surveys quantified only *Diadema antillarum* and two species of *Echinometra*. *Diadema antillarum* had an average population density for all sites of 0.01 ± 0.006 / m². *Diadema* individuals were found at eight of the ten sites including four of the five control sites and two of the four FPA sites (Fig. 1). Calabas, an FPA, had the highest density.

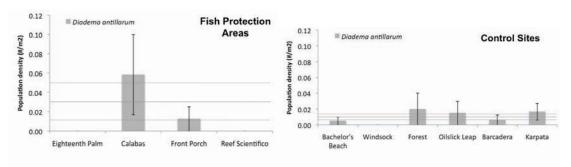


Figure 1. *Diadema antillarum* population densities at Fish Protection Areas and control sites. Lines represent average population densities ± SE for each treatment.

E. viridis was the most abundant sea urchin species with an average population density for all sites of $0.09 (\pm 0.02)/m^2$. Individuals of this species were found at all sites except for Front Porch, an FPA (Fig. 2). The highest population density for *E. viridis* was recorded at Barcadera, a control site.

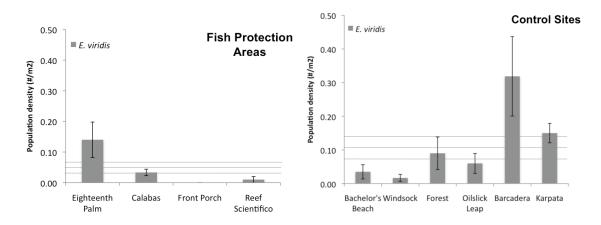


Figure 2. *Echinometra viridis* population densities at Fish Protection Areas and control sites. Lines represent average population densities ± SE for each treatment.

E. lucunter individuals were found at seven of the ten sites with an average population density of $0.01 (\pm 0.003)/\text{m}^2$. E. lucunter was identified at only one of the FPA sites, Eighteenth Palm. The highest population density for this species was recorded at Forest on Klein Bonaire, a control site (Fig. 3).

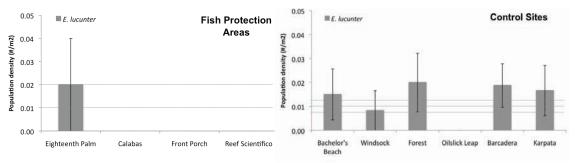


Figure 3. *Echinometra lucunter* population densities at Fish Protection Areas and control sites. Lines represent average population densities ± SE for each treatment.

Comparing population densities for *Diadema antillarum* over time, specifically at monitored sites (Barcadera, Karpata, Reef Scientifico, Forest, Eighteenth Palm, and Windsock), population densities peaked in 2005 with a density of $0.027 (\pm 0.013)/ \text{ m}^2$. Population densities then declined to zero in 2009, but in 2011, there was a slight increase with a density of $0.007 (\pm 0.004)/ \text{ m}^2$ (Fig. 4).

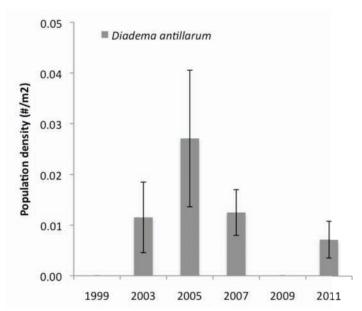


Figure 4. Population densities of *Diadema antillarum* at monitored sites over time.

Comparing population densities of *E. viridis* at the five monitored sites over time, a significant increase in abundance of this species occurred in 2011 with a population density of 0.14 ± 0.034 / m² (Fig. 5).

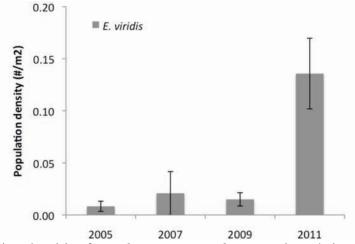


Figure 5. Population densities for *Echinometra viridis* at monitored sites.

Discussion

Sea urchins were rare at all sites surveyed in 2011 and are at such low densities that they likely do not play a functional role in the reef system (Fig. 1, Fig. 2, Fig. 3). *Diadema antillarum*, despite a slight increase from being absent in 2009, appear to be declining since a peak in abundance in 2005 (Fig. 4). Hughes et al. (2010) report similar results from an analysis of *Diadema* density from 35 sites throughout the Caribbean. *Diadema* abundance began increasing in 2000 with a peak around 2003-2004 but a decline since. Average population densities of up to 25/m² were common prior to the 1983/1984 mass mortality event and some recent studies indicate support for widespread *Diadema*

recovery; however, other studies do not support an increase in abundance. In addition, Hughes et al. (2010) report that average densities recorded since 2000 remain less than $0.3/\text{m}^2$.

Current *Diadema* densities on Bonaire reefs remain well below the density determined through ecological modeling as necessary to serve a functional role in terms of controlling macroalgae abundance ($> 1/m^2$) (Mumby et al. 2006). This means that while *Diadema* are present in Bonaire, they may not be playing as much of a functional role as they could at higher densities.

A number of factors can potentially influence *Diadema* recovery including limited larval supply, poor larval survival, interspecific competition and a lack of suitable recruitment sites (Lessios 1988). At some Caribbean reefs, where fish protection areas have been implemented, increases in predator abundance may inhibit *Diadema* recovery. Harborne et al. (2009) found lower sea urchin densities yet higher fish densities within marine reserves showing an inverse relationship between urchin predator abundance and urchin abundance. This may not necessarily be the case in Bonaire. Past monitoring reports have not found a significant increase in predator abundance in fish protection areas or a difference in predator abundance between control sites and fish protection areas (Steneck et al. 2009). In Bonaire specifically, there does not seem to be a strong distinction between *Diadema* densities found at FPA sites compared to densities found at control sites (Fig. 1).

Determining whether or not an increase in *Diadema* abundance is equivalent to a recovery remains a challenge. The patchy nature of this species and the difficulty in sampling the same exact location over multiple survey years can produce a wide variety of population density estimates. Further there is a lack of baseline abundance data prior to the mass mortality event of 1983/84 (Lessios 2005). Woodley et al. (1999) found a slow recovery of *Diadema* at Discovery Bay, Jamaica. Population densities at 8 m depth were $0.1/m^2$. Jamaica's reefs also have few predators present due to overfishing (Hughes et al. 1994). The 2011 Bonaire survey was conducted at 10 m depth and shows quite a significantly lower density than Jamaica (Fig. 1); it is possible that *Diadema* populations are higher at shallower zones on Bonaire's reefs.

E. viridis, one of the most common sea urchins in the Caribbean is often found in shallow zones, but also at deeper reef locations (McClanahan 1999). *E. viridis* are known to live sympatrically with *Diadema*. In Bonaire, *E. viridis* had relatively high, but functionally low population densities at all sites surveyed and has increased significantly in 2011 compared to past years (Fig. 2 and Fig. 5).

Even though abundance of *E. viridis* is increasing, this species is not a functional equivalent to *Diadema antillarum*. *E. viridis* has a smaller body size and a smaller foraging range as well as shorter spines than *Diadema* and so may be more susceptible to predation. *E. viridis*, at moderate predator abundances, tends to find refuge in cryptic locations such as cracks and crevices within coral colonies (McClanahan 1999). This behavior holds true for those *E. viridis* quantified in the 2011 Bonaire survey. All of the

observed *E. viridis* individuals were hidden in the crevices of *Montastrea annularis* or other mounding coral colonies and none were found on exposed surfaces (*pers. observation C. Cleaver*). Due to this adaptive predator avoidance behavior, *E. viridis* tends to graze within the cracks and crevices as well as on drift feed while *Diadema*, being more mobile and of a larger body size, are better able to graze open, exposed surfaces. *E. viridis*, even at high densities, is unable to maintain similar grazing rates on fleshy algae as *Diadema* and is less likely to control macroalagae abundance (McClanahan 1999).

McClanahan (1999) found a positive correlation between increasing abundance of *Echinometra* individuals with an increase fleshy macroalgae at Glovers Reef in Belize and suggests both an increase in urchin abundance, particularly in *Echinometra* species, and fleshy algal abundance may both be indicators of reef degradation. Reef degradation, in this case, being attributed to continued low abundance of *Diadema* and overfishing of predators as urchin densities tend to be inversely correlated with fish abundance (McClanahan 1999, Brown-Saracino et al. 2007, Harborne et al. 2003).

Few individuals of *E. lucunter* and no individuals of any other echinoid species were found in the 2011 Bonaire survey. While populations of *E. viridis* have increased significantly in 2011 and *Diadema* has slightly increased from being absent in 2009, at current abundance levels, these species likely do not play a functional role. Echinoids remain rare on Bonaire's reefs. Continued monitoring of sea urchin abundance in Bonaire is important to understand the dynamics between herbivore populations and macroalgae abundance. Increasing herbivore populations may ultimately improve the resilience of the reef system in response to potentially increasing macroalgae abundance.

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Chapter 6a: Patterns in Predatory Fish Distribution, Abundance and response to Fish Protected Areas

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Abstract

Underwater surveys at 10 meters depth quantified predatory fish abundance at four Fish Protected Areas (FPA) and seven Control sites where fishing is permitted, in Bonaire's National Marine Park. Of the 33 species of predatory fish surveyed, overall predator biomass and density has increased since surveys began in 2003. Of the most common predatory fishes were snapper (*Lutjanidae*) and grunt (*Haemulidae*). Their abundance has been stable or increasing while grouper (*Serranidae*) abundance has remained below 2003 levels. Although still early, predatory fish abundance has increased since the implementation of FPAs in 2008. The strongest FPA response was for snappers, fish that prey upon damselfish and predatory fish targeted by the fishing community.

Introduction

Predators play an important functional role in many ecosystems, including coral reefs (McClanahan 2005). In the context of coral reefs, most ecologically important predators are piscivores (i.e., fish that eat other fish). Piscivorous fish are influential on coral reefs because their feeding behavior directly affects the abundance of their prey. As such, predatory fish are seen as playing an important role in structuring biodiversity of fish on coral reefs.

There is evidence to suggest that predatory fish that prey upon damselfish provide a particularly important service to coral reefs, by indirectly affecting algal abundance on Caribbean reefs. Damselfish in the Caribbean are small but highly territorial fish (of the family *Pomacentridae*) that farm algal patches on reefs that ultimately smother adult and recruiting corals (Arnold and Steneck 2010). Predatory fish that prey upon damselfish, such as species of snappers and groupers, may regulate the abundance of damselfish and indirectly hinder harmful algal growth on reefs.

Predatory fish are most targeted by fishing activity because they are usually the largest fish on the reef. However, most predatory reef fish are also of low productivity, meaning that they do not spawn regularly or as much as their pelagic, offshore counterparts. Management of predatory fish is essential for protecting low productivity predatory reef fish for the purposes of sustainable fishing, marine conservation and for promoting the resilience of coral reefs faced with increasing disturbance through climate change (Bellwood 2004).

This chapter looks at the trends in predatory fish abundance in Bonaire from 2003 up until 2011. This chapter also compares the abundance of predatory reef fish in FPAs (established in 2008) and control sites where fishing is permitted. The ultimate goal of this work is to help elucidate the broader ecological trends occurring on Bonaire's reefs

with respect to predatory fish with the ultimate goal of informing management efforts and strategies.

Methods

Location

Predator abundance was quantified at the 11 sites listed in the table below (Table 6.1). Site names correspond to the dive site names established by the Bonaire National Marine Park. Fishing is permitted in "control sites" but prohibited in "FPAs".

Table 6.1: Survey Sites (from north to south)

Site Name	ite Name Type of Year Surveyed (marked "✔")					# transects	
	Protection	2003	2005	2007	2009	2011	in (2011)
1. No Dive Reserve*	Control site					V	7
2. Karpata	Control site	/	✓	✓	✓	'	8
3. Oil Slick	Control site				✓	'	11
4. Barcadera	Control site	~	~	~	~	~	8
5. Reef Scientifico	FPA	V	~	~	/	V	8
6. Front Porch	FPA				~	~	11
7. Forest	Control site	~	~	~	~	~	8
8. Calabas	FPA				~	~	8
9. Eighteenth Palm* *	FPA	~	~	~	~	~	8
10. Windsock	Control site	V	~	~	'	~	8
11. Bachelor's Beach	Control site				'	/	8

^{*}Data collected for "No Dive Reserve" is listed in Appendix 6a but not included in this chapter because the site was not previously monitored

Survey protocol

Underwater surveys were conducted by SCUBA at 10 meters depth (approximately 33 feet) along consecutive belt transects of 30 meters (length) by 4 meters (width) (total area: 120 square meters). The number of transects conducted at each site is listed in Table 6.1.

Species

Fish densities (i.e. number of individuals) and size of individuals were recorded for 33 predatory fish species during surveys (Table 6.2). The predatory fish species surveyed in 2011 included the same species as previous years as well 3 additional species (Bermuda chub, dog snapper and cero mackerel).

^{**}formerly referred to as "Plaza"

Table 6.2:

	Scientific name	Common name	No Data (2011)	Damselfish Predator*	Target Species**	Non-target species**
1.	Anisotremus surinamensis	black margate			V	
2.	Aulostomus maculatus	trumpetfish				~
3.	Bodianus rufus	spanish hogfish			V	
4.	Bothus lunatus	peacock flounder				V
5.	Caranx latus	horse-eye jack	~			-
6.	Caranx rubber	bar jack		V	✓	
7.	Epinephelus cruentatus	graysby		~	✓	
8.	Epinephelus fulvus	coney			~	
9.	Epinephelus guttatus	red hind				~
10.	Epinephelus adscensionis	rock hind		~	✓	
11.	Gymnothorax sp.	eel sp.				V
12.	Haemulon carbonarium	caesar grunt			~	
13.	Haemulon chrysargyreum	smallmouth grunt				~
14.	Haemulon flavolineatum	french grunt				~
15.	Haemulon plumieri	white grunt	~			-
16.	Haemulon sciurus	bluestriped grunt			V	
17.	Hypoplectrus sp	hamlet sp.				~
18.	Kyphosus sectatrix***	Bermuda chub			V	
19.	Lutjanus apodus	schoolmaster		V	V	
20.	Lutjanus cyanopterus	cubera snapper				-
21.	Lutjanus griseus	mangrove snapper	~			-
22.	Lutjanus jocu***	dog snapper			V	
23.	Lutjanus mahogoni	mohagany snapper		~	✓	
24.	Lutjanus synagris	lane snapper	~			-
25.	Mycteroperca bonaci	black grouper	~			-
26.	Mycteroperca tigris	tiger grouper		~	✓	
27.	Mycteroperca venenosa	yellowfin grouper	~			-
28.	Ocyurus chrysurus	yellowtail snapper		~	✓	
29.	Scomberomorus regalis***	cero mackeral			~	
30.	Scorpaena plumieri	spotted scorpionfish		~		~
31.	Serranus tigrinus	harlequin bass				~
32.	Sphyraena barracuda	great barracuda		~	~	
33.	Synodus intermedius	sand diver				~

^{*}based on Randall, 1965

Analysis

The fork lengths of fish were recorded and later converted into biomass estimates, using length weight relationships from Bohnsack and Harper (1988).

Before-After-Control-Impact (BACI) study

In 2009 four monitoring sites were added to the reef monitoring efforts to establish the baseline for an ongoing Before-After-Control-Impact (BACI) study. A BACI study quantifies the differences in the ecological characteristics of a particular marine reserve (in this case a reserve that only permits bait fishing) before and after its establishment, in order to measure the ecological, economic or social benefits associated with marine protection.

^{**}based on Nenadovic, 2007

^{***}species not previously surveyed

[&]quot;-" indicates species not specified as target species by Nenadovic, 2007.

These four BACI sites are identified in the table 6.1 and include: Reef Scientifico, Front Porch, Calabas and Eighteenth Palm.

Other, similar BACI studies have indicated that the effects of marine reserves such as FPAs on fish populations are manifested after 1-3 years of their establishment. This report is timely in that it includes data from surveys conducted 3 years after the implementation of these FPAs. For this reason the "FPA effects" apparent in the data collected could suggest real changes on Bonaire's coral reefs.

Results

The most common predatory fish families were: *Haemulidae* (grunt), *Lutjanidae* (snapper), and *Serranidae* (grouper & seabass). Appendix 6a, at the end of this report, provides detailed lists of the biomass, density and fork length data for all species at all monitored sites.

Trends

Overall predator densities (number per 100 m²) have remained constant among all sites (Figure 6.1). Predator density was highest at Calabas with an average of 42 predators per 100 m² and lowest at Barcadera with an average of 15 predators per 100 m² (Figure 6.9). Predator Biomass has also remained constant (Figure 6.2). Biomass was highest at Bachelor's Beach with an average of 12 Kg per 100 m² and lowest at Barcadera with an average of 2 Kg per 100 m² (Figure 6.10).

Snappers (Lutjanidae)

Species surveyed belonging to the snapper family included: schoolmaster (*Lutjanus apodus*), mahogany snapper (*Lutjanus mahogoni*), yellowtail snapper (*Ocyurus chrysurus*), cubera snapper (*Lutjanus cyanopterus*), mangrove snapper (*Lutjanus griseus*), dog snapper (*Lutjanus jocu*) and lane snapper (*Lutjanus synagris*). Snapper density and biomass has been declining since monitoring efforts began in 2003 (Figure 6.3 and 6.4). But there is evidence that snapper biomass and density is on the rise, particularly in FPAs (Figure 6.3 and 6.4). Snapper biomass was highest at Reef Scientifico (7 Kg per 100 m²) and lowest at Barcadera (1 Kg per 100 m²) (Figure 6.11). Snapper density was highest at Calabas (22 individuals/ 100 m²) and lowest at Barcadera (2 individuals/ 100 m²) (Figure 6.12).

Groupers (Serranidae)

Grouper species surveyed included black grouper (*Mycteroperca bonaci*), tiger grouper (*Mycteroperca tigris*), yellowfin grouper (*Mycteroperca venenosa*), graysby (*Epinephelus cruentatus*), coney (*Epinephelus fulvus*), red hind (*Epinephelus guttatus*), rock hind (*Epinephelus adscensionis*), and harlequin bass (*Serranus tigrinus*). Since 2003 grouper biomass and density has decreased (Figure 6.5, Fig.6.6). Grouper biomass was highest at Reef Scientifico (1.1 Kg/ 100 m²) and lowest at Barcadera (0.2 Kg/ 100 m²) (Figure 6.13). Grouper density was highest at Reef Scientifico (7 individuals/ 100 m²) and lowest at Barcadera, Calabas and Eighteenth Palm (1 individuals/ 100 m²) (Figure 6.14).

Grunts (Hameulidae)

Grunt species that were surveyed included Caesar grunt (*Haemulon carbonarium*), French grunt (*Haemulon flavolineatum*), Bluestriped Grunt (*Haemulon sciurus*), smallmouth grunt (*Haemulon chrysargyreum*), white grunt (*Heamulon plumieri*). Grunts have largely increased in biomass and density since monitoring of these species began in 2005, (Figure 6.7 and 6.8). Grunt biomass was highest at Bachelor's Beach (6 Kg/ 100 m²) and lowest at Reef Scientifico (0.5 Kg/ 100 m²) (Figure 6.15). Grunt density was highest at Bachelor's Beach (29 individuals/ 100 m²) and lowest at Reef Scientifico (3 individuals/ 100 m²) (Figure 6.16).

Predatory fish targeted by fishing

16 species of predatory fish, of the ones surveyed, are targeted by fishing activities (Table 6.2) (Nenanovic, 2007). The highest biomass of target species was at Bachelor's Beach (10 Kg/ 100 m²) and the lowest was at Barcadera (2 Kg/ 100 m²) (Figure 6.19). The highest density of target species was at Calabas (25 individuals/ 100 m²) and the lowest was at Barcadera (5 individuals/ 100 m²)

Damselfish predators

9 species of predatory fish, of the ones surveyed, are known to be damselfish predators (Randall 1965). The highest biomass of damselfish predator species was at Reef Scientifico (6 Kg/ 100 m²) and the lowest was at Barcadera (1 Kg/ 100 m²) (Figure 6.17). The highest density of damselfish predator species was at Calabas (25 individuals/ 100 m²) and the lowest was at Barcadera (5 individuals/ 100 m²).

Predatory fish not targeted by fishing

Non-target

The highest biomass of non-target species was at Windsock ($1.6 \text{ Kg}/100 \text{ m}^2$) and the lowest was at Eighteenth Palm ($0.4 \text{ Kg}/100 \text{ m}^2$) (Figure 6.21). The highest density of non-target species was at Bachelor's Beach ($25 \text{ individuals}/100 \text{ m}^2$) and the lowest was at Eighteenth Palm ($5 \text{ individuals}/100 \text{ m}^2$)

Predatory fish size classes

Snappers, damselfish predators and targets species were generally larger in FPAs than at control sites. Size classes for these predatory fish are depicted in Figures 6.23, 6.24 and 6.25.

FPA effects

The observed FPA effects on biomass, density and size class of the most common predatory fish is identified in Table 6.3. Notable FPA effects (i.e., a statistically significant difference between the means of the FPAs and control sites) were observed for snapper, damselfish predator and predatory fish targeted by fishing biomass and density.

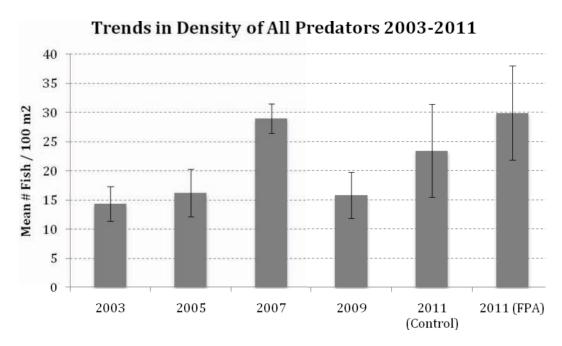
Table 6.3:

Species	FPA effect for	FPA effect for	FPA effect for	
	Biomass: Yes/No	Density: Yes/No	size class:	
	(higher or	(higher or	Yes/No (**)	
	lower?)*	lower?)*		
All Predators	Yes (higher)	No	No	
Snappers	Yes (higher)	Yes (higher)	Yes (higher: 2/4)	
Groupers	No	No	No	
Grunts	Yes (lower)	No	No	
Damselfish	Yes (higher)	Yes (higher)	Yes (higher: 1/4)	
Predators				
Target species	Yes (higher)	Yes (higher)	Yes (higher: 2/4)	
Non-target species	Yes (lower)	Yes (lower)	No	

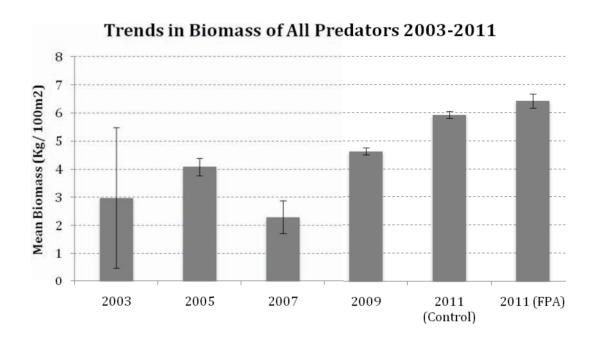
^{*&}quot;Yes" and "No" indicate whether or not there was a statistically significant difference in abundance in FPAs compared to control sites. "Higher" and "Lower" specify whether or not the FPA had higher or lower abundance than the control sites.

Entries in bold highlight the instances in which FPAs had a statistically significant greater abundance of predators or larger-sized predators, compared to control sites.

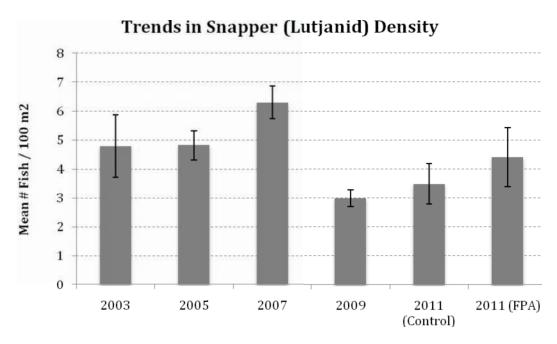
^{**} number of size classes larger out 4 size classes



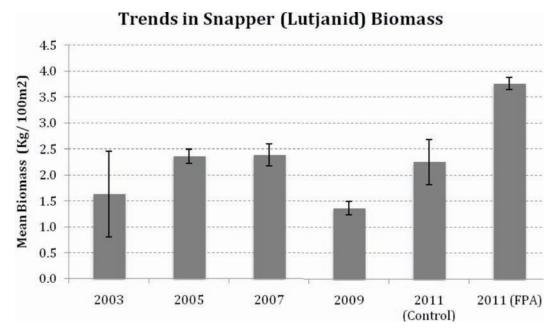
<u>Figure 6.1</u>: Average population density of all predatory species surveyed in 2003, 2005, 2009 and 2011. (Monitoring data from 2007 was not included because not all predatory species were recorded.) Error is represented as \pm one standard error.



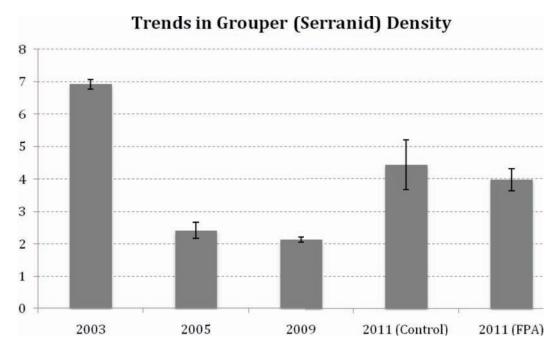
<u>Figure 6.2</u>: Average biomass of all species surveyed in 2003, 2005, 2009 and 2011. (Monitoring data from 2007 was not included because not all predatory species were recorded.) Error is represented as \pm one standard error.



<u>Figure 6.3</u>: Average population density of snapper (*Lutjanidae*) species surveyed in 2003, 2005, 2009 and 2011. Error is represented as \pm one standard error.

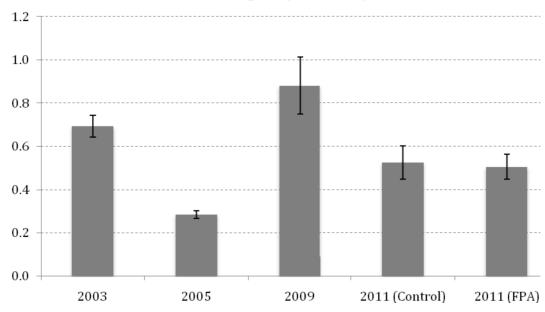


<u>Figure 6.4</u>: Average biomass of snapper (*Lutjanidae*) species surveyed in 2003, 2005, 2009 and 2011. Error is represented as \pm one standard error.

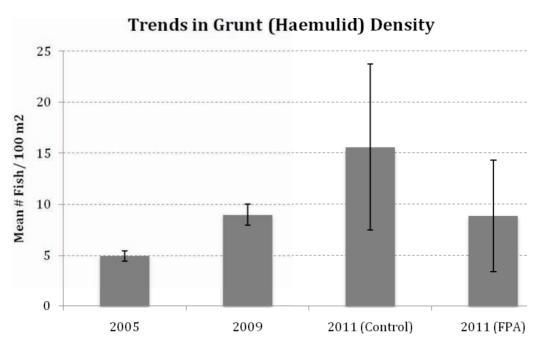


<u>Figure 6.5</u>: Average population density of snapper (*Serranidae*) species surveyed in 2003, 2005, 2009 and 2011. Error is represented as \pm one standard error.

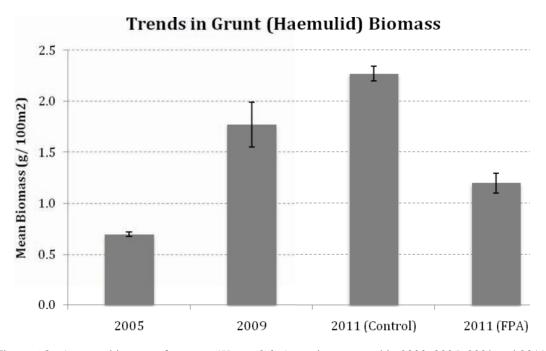
Trends in Grouper (Serranid) Biomass



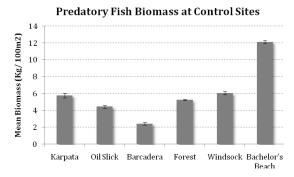
<u>Figure 6.6</u>: Average biomass of grouper (*Serranidae*) species surveyed in 2003, 2005, 2009 and 2011. Error is represented as \pm one standard error.



<u>Figure 6.7</u>: Average population density of grunt (*Haemulidae*) species surveyed in 2003, 2005, 2009 and 2011. (Monitoring data from 2003 and 2007 was not included because these data were incomplete.) Error is represented as \pm one standard error.

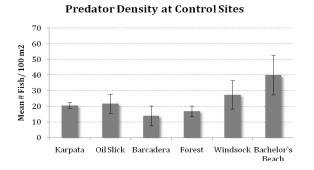


<u>Figure 6.8</u>: Average biomass of grouper (*Haemulidae*) species surveyed in 2003, 2005, 2009 and 2011. (Monitoring data from 2003 and 2007 was not included because these data were incomplete.) Error is represented as \pm one standard error.



Predator Biomass at FPA Sites 14 12 10 8 6 4 2 0 Reef Front Porch Calabas Eighteenth Palm

<u>Figure 6.9:</u> Average biomass of predatory fish at control sites (left) and FPAs (right). Error is represented as \pm one standard error.



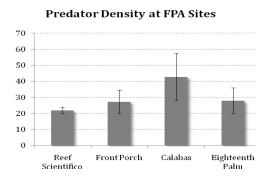
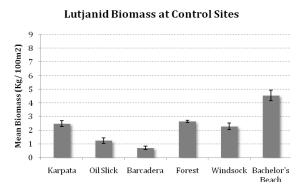


Figure 6.10: Average density of predatory fish at control sites (left) and FPAs (right). Error is represented as \pm one standard error.



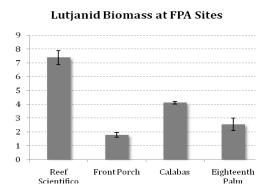
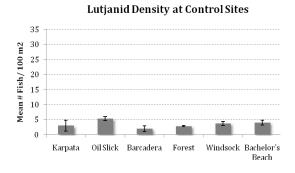
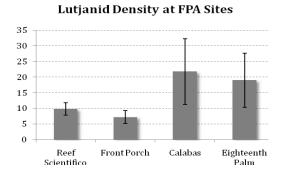
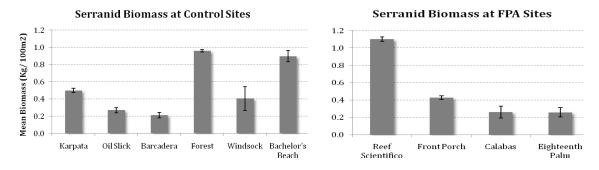


Figure 6.11: Average biomass of snappers at control sites (left) and FPAs (right). Error is represented as \pm one standard error.





<u>Figure 6.12</u>: Average density of snappers at control sites (left) and FPAs (right). Error is represented as \pm one standard error.



<u>Figure 6.13</u>: Average biomass of groupers at control sites (left) and FPAs (right). Error is represented as \pm one standard error.

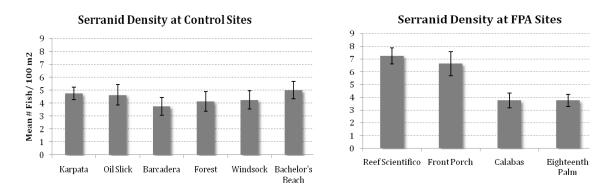
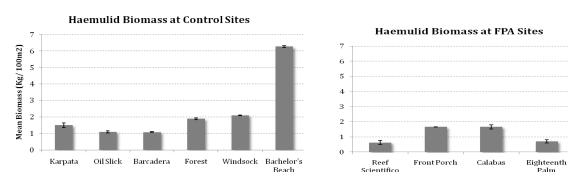


Figure 6.14: Average density of groupers at control sites (left) and FPAs (right). Error is represented as \pm one standard error.



<u>Figure 6.15</u>: Average biomass of grunts at control sites (left) and FPAs (right). Error is represented as \pm one standard error.

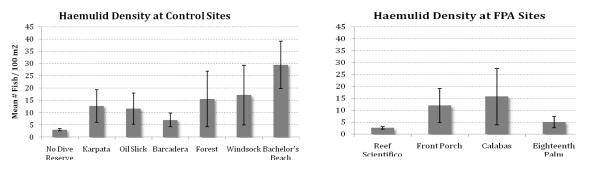
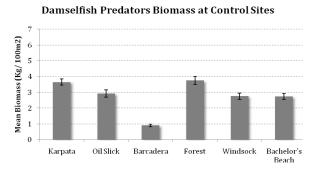


Figure 6.16: Average density of grunts at control sites (left) and FPAs (right). Error is represented as \pm one standard error.



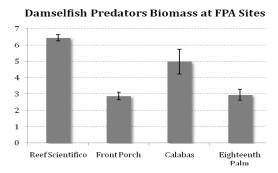
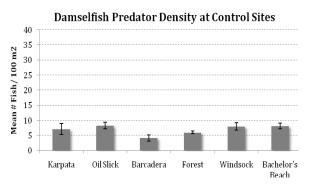


Figure 6.17: Average biomass of damselfish predators at control sites (left) and FPAs (right). Error is represented as \pm one standard error.



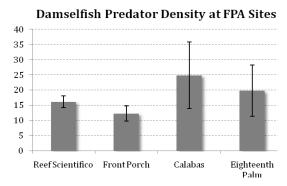
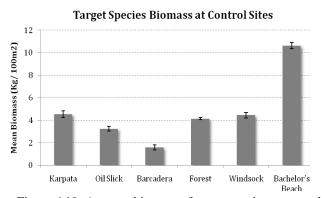
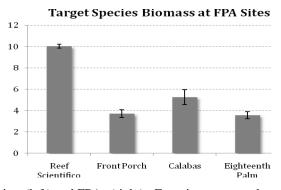
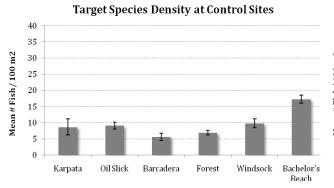


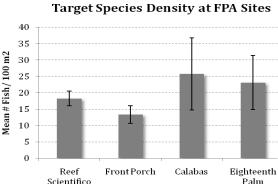
Figure 6.18: Average density of damselfish predators at control sites (left) and FPAs (right). Error is represented as \pm one standard error.





<u>Figure 6.19:</u> Average biomass of target species at control sites (left) and FPAs (right). Error is represented as \pm one standard.error.

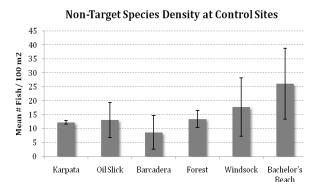


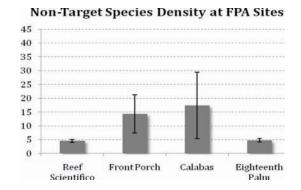


<u>Figure 6.20:</u> Average density of target species at control sites (left) and FPAs (right). Error is represented as \pm one standard error.

Non-Target Species Biomass at FPA Sites 1.8 1.6 1.4 1.2 1.0 0.8 0.6 0.4 0.2 0.0 Reef FrontPorch Calabas Eighteenth Palm

Figure 6.21: Average biomass of non-target species at control sites (left) and FPAs (right). Error is represented as \pm one standard.





<u>Figure 6.22:</u> Average density of non-target species at control sites (left) and FPAs (right). Error is represented as \pm one standard error.

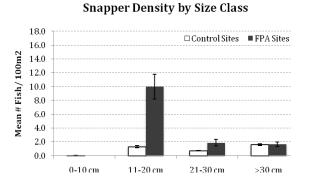


Figure 6.23: Average density of snapper species. Error is represented as \pm one standard error.

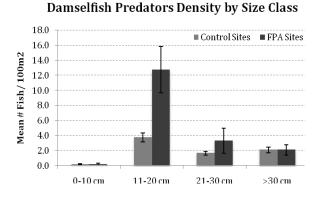


Figure 6.24: Average density of damselfish predator. Error is represented as \pm one standard error.

Target Species Density by Size Class

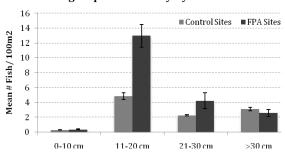


Figure 6.25: Population density of predatory fishes targeted by fishermen.

Discussion

Most of the trends in predatory reef fish abundance are encouraging, considering that overall predator density and biomass is increasing, with a few exceptions (e.g., groupers).

Barcadera appears to have much lower abundance of predatory reef fish than other sites, which is troubling. Fishing at Barcadera may be more popular than other sites because there are fewer divers and less public oversight (i.e., no coastal road but rather rarely-occupied vacation homes).

Reef Scientifico and Bachelor's Beach boasted high biomass and density for a variety of predatory reef fish. The encouraging patterns seen at Reef Scientifico are likely the result of no fishing (because it is an FPA) and good enforcement. The patterns of high predatory fish abundance observed at Bachelor's Beach are less clear. Perhaps the presence of hotels along the coastline, adjacent to Bachelor's Beach, deter fishermen, resulting in higher abundances of reef fish.

The increases in abundance of snappers, damselfish predators and predatory fish targeted by fishing in FPAs are a particularly positive sign for Bonaire's reefs. But it is important to remember that Bonaire's four FPAs cover only a small portion of the leeward reefs (less than ~20%). So while some of the FPA effects are good for Bonaire they should not be construed as wide-ranging. The FPAs are also highly impacted by other anthropogenic impacts (e.g. cruise ships, land based runoff and sedimentation), so abundances in these areas could be even higher if noise or nutrient pollution were reduced. Most importantly, the positive FPA trends could result in a spillover effect benefitting fishing activities adjacent to FPAs. It will be important to disseminate the results of this research in order to consider extending current FPAs or designating additional ones.

Conclusion

Predators are key ecological drivers in coral reefs by influencing diversity of other reef fish and subsequently bolstering resilience to disturbance (Bellwood et al. 2004, McClanahan 2005, Sandin et al. 2008). Trends in Bonaire's predatory fish abundance are encouraging, particularly in Fish Protected Areas (FPAs). Abundance of groupers however is still below data reported in 2003. Efforts should be considered to protect groupers due to their low productivity and to their potential importance in regulating damselfish abundance. It will be essential to track the effectiveness of the FPAs in order to continue to inform and guide management efforts and possibly create new FPAs.

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Chapter 6b: Effects of Predatory Fishes on Damselfish Abundance

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Abstract

The purpose of this review is to assess whether damselfish abundance on coral reefs is controlled by predation. By compiling studies on a variety of genera of damselfish, I concluded that predation is one of if not the greatest factors influencing damselfish abundance. Of the 25 research articles found on damselfish abundance, 14 of them looked at and found predation as a control of damselfish abundance. The other 11 studies were split between food, habitat, competition, and climate as controls on damselfish abundance.

Introduction

Coral reefs are biologically diverse ecosystems (Knowlton 2001). Such great diversity is influenced by a variety of ecosystem drivers. Perhaps the most important ecosystem drivers are the herbivores. Herbivores can limit algal abundance and thus can be particularly influential dynamic on coral reefs because the presence of algae can both reduce the recruitment of corals as well as provide habitat for some species of mobile invertebrates. One of the most influential groups of coral reef herbivores is the damselfishes (Hixon 1997). Their territorial behavior and ability to create suitable habitat for specific species of algae within their "gardens" has enabled them to make a large impact on coral reef ecology. Damselfish are considered to be essential in maintaining species diversity on coral reefs because algae within their territories produce greater biomass and species richness than surrounding areas. To defend their "garden", damselfish repulse most herbivores. The increased algal growth tends to overgrow recruiting corals (Hixon 1997). This is much different than the effect seen from grazing of general foraging herbivores which greatly decrease algal biomass (Ceccarelli et al 2005b). In addition, the species composition of corals and small mobile organisms are also impacted within damselfish territories (Ceccarelli et al 2005a).

The preferred habitat of damselfish is corals with complex architecture to allow shelter from predators. This is essential because damselfishes are generally small in size and therefore prey for numerous large piscovores (Ceccarelli et al 2005a). *Acropora cervicornis* is an example of a coral frequently populated by damselfish. The branching morphology of the coral serves as an exclusion mechanism from large predators (Precht et al 2010). Corals also function as a nesting site for the damselfish's eggs (Cheney 2007). The males will defend both eggs and coral territory with actions ranging from aggressive displays to chasing. This aggression will be shown even against organisms many times larger than the damselfish (Helfman 1988).

There are many damselfish species. *Dischistodus* and *Stegastes* are the best studied genera of damselfish because they are larger damselfish (up to 20cm in length) and aggressive about maintaining their territories. The genus *Plectroglyphidodoni* contains many of the smaller grazer damselfish (Ceccarelli et al 2001). This review will include

studies on damselfish from both groups in order to better support a generalization on what controls damselfish abundance.

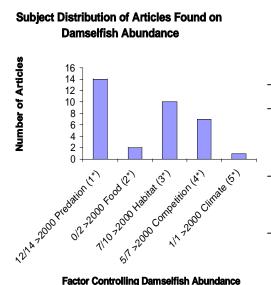
Knowing what controls the abundance of damselfish of coral reefs is imperative given their impact on coral reef ecology. Their impact is great enough to merit them as playing "keystone" role in the coral reef ecosystem (Hixon 1997). Numerous studies have been done to explore the extent of the effects damselfish can have on the organisms within their territories (Ceccarelli et al 2005b; Zeller 1988). The question of what exactly controls damselfish abundance is still being investigated. Predation has been suggested as a possible control as it can occur at different scales and stages of the damselfish lifecycle. Damselfish predators can include larger fish, parasites, and even other damselfish. The scientific literature on damselfish abundance will be collected and reviewed to assess what the most influential factor affecting damselfish abundance is.

Methods

An extensive literature search was done on damselfish abundance. The data from the primary studies found within the literature was compiled and compared so that a majority opinion could be determined on what controls damselfish abundance. All articles were found by searching Google Scholar, Scopus data base, JSTOR, or Coral Reefs journal. All primary studies found include the key words damselfish abundance.

Results

The literature search turned up 25 articles on factors that impact damselfish abundance. The articles found relating to damselfish abundance were then organized based on the subject matter. The five subject categories are predation, food, habitat, competition, and climate. If an article touched on multiple subjects, it was included in all the categories to which it applied.



1* Helfman 1988, Hixon and Beets 1993, Haley and Muller 2002, Holbrook and Schmitt 2003, Almany 2004, Hixon and Jones 2005, Ceccarelli et al 2006, Cheney 2007, Figueira et al 2008a, Figueira et al 2008b, Jones and Grutter 2008, Belmaker et al 2008, Schimitt et al 2009, Holmes and McCormick 2010

2* Tyler III et al 1995, Booth and Hixon 1999

3* Hixon and Beets 1993, Beukers and Jones 1998, Holbrook et al 1999, Holbrook and Schmitt 2003, Almany 2004, Belmaker et al 2008, Wilkes et al 2008, Feary et al 2009, Holbrook et al 2000, Precht et al 2010 4* Roberston 1996, Schmitt and Hollbrook 1999, Almany 2004, Hixon and Jones 2005, Figueira et al 2007, Figueira et al 2008, Schimitt et al 2009

5* Cheal et al 2007

Figure 1. The totals of the articles found in the literature search on damselfish abundance categorized by subject.

The number of articles published in or after the year 2000 is also listed on each category label.

Articles classified under predation relate to the process of an organism either wounding or killing damselfish for nutrition. To qualify as a food article the study needed to include how food availability can affect damselfish populations. The habitat studies needed to include at least one coral feature in relation to damselfish abundance such as coral size or coral surface heterogeneity. The competition studies are about organisms that occupy potential damselfish habitat, thus competing for a common resource. The climate article deals primarily with winds and water temperature (Cheal et al 2007). The distribution of the subject material the articles covered is shown in figure 1.

	Location	Damsel species	Territorial	Negative correlation with predator	Significant demographic effect
Helfman, 1988	Teague Bay, St. Croix, Virgin Islands	Stegastes planifrons	Yes	N/A	N/A
Hixon and Beets 1993	Perseverance Bay, St. Thomas, Virgin Islands	Chromis cyanea C. multilineatus, S. leucostictus, S. mellis, S. partitus, S. planifrons, S. variabilis	Yes although to varying degrees	Yes, but prey was not exclusively damselfish	Yes, predation limits prey species richness and numbers
Holbrook and Schmitt 2003	Moorea, French Polynesia	Dascyllus flavicaudus, D. aruanus	Both yes	Yes	Yes
Almany 2004	Bahamas	S. partitus, S. leucostictus	Both yes, S. partitus only moderate	Yes	Yes
Hixon and Jones 2005	Great Barrier Reef	Pomacentrus ambionensis	No	No	None
Ceccarelli et al 2006	Great Barrier Reef	P. adelus, P. wardi	Both yes	N/A	Yes
Figueira et al 2008a	Great Barrier Reef	D. aruanus, P. moluccensis	Both yes	No	Yes but due to competition
Figueira et al 2008b	Florida Keys	S. partitus	Moderately	Yes	Yes, due to predation and competition
Belmaker et al 2008	Gulf of Aqaba, Israel	D. marginatus	Yes	Yes	Yes
Schimitt et al 2009	Moorea, French Polynesia	D. flavicaudus	Yes	No	None

Table 1- The basic information of 10 damselfish predation studies. The information listed is what was found in the specific study in the left column. N/A indicates that variable was not tested.

The majority of primary literature found was on how predation influences damselfish abundance. Nearly all of these studies were done within the past 5 years. Habitat and competition studies could also be readily found although several of them were published before the year 2000. Studies on climate and food rationing effects were very scarce. All the studies that focused on food rationing were also done before the year 2000 (Fig 1).

To summarize the importance of the predation studies, 10 of them were assembled into a table that includes information about the study subjects and how predation affected them. The studies covered a variety of damselfish species. The majority of them are territorial to some extent. The negative correlation with predator column indicates if the study showed predator populations increase while prey numbers decrease. The significant demographic effects column indicates whether a study found a change in damselfish demographics due to predation as well as any other causes listed in the table entry. Many of the studies found on predation revealed that predation can have substantial demographic effects on damselfish populations (Table 1). These 10 studies examine damselfish being attacked at the juvenile stage and onward. Studies have been done on damselfish egg predation, but very few turned up in the literature search (Haley and Muller 2002; Cheney 2007).

Discussion

The results of this review indicate that the scientific community recognizes predation has a substantial impact on damselfish abundance. I expect these findings to continue to grow because of the significant findings in numerous recent studies (Fig 1; Table 1).

Predators can change damselfish abundance in both indirect and direct ways. Limiting suitable habitat for damselfish is one way predators indirectly reduce damselfish abundance. Both the sight and smell of predators have been shown to trigger avoidance strategies in damselfish (Helfman 1988; Holmes and McCormick 2010). The presence of a predator in a habitat would therefore deter damselfish from settling there. One study demonstrated this by manipulating predator and competitor presence on suitable reef habitat. Damselfish recruitment rates to corals decreased greatly when either predators or other damselfish were present although the recruitment rate calculations included several other reef fish species as well (Almany 2004). As another example, it was found that damselfish of the species Dascyllus marginatus choose smaller corals as habitat when under the predation pressure by the dottyback (Pseudochromis olivaceus). The dottyback prefers to hunt around larger corals and stays close to a single coral. D. marginatus individuals chose smaller corals over large corals in both field and laboratory trials (Belmaker 2008). A variety of damselfish species are used in predation studies (table 1). Before any generalizations are made, predation studies on other damselfish species will be examined.

Predation and competition can also cause directly impact damselfish abundance. When larger fishes were excluded via cages from the habitats of the damselfishes *Pomacentrus adelus* and *P. wardi*, there was a 100% increase in abundance of *P. wardi* adults and recruits. *P. adelus* abundance decreased by 50% within the caged areas. *P. wardi* is a larger species than *P. adelus* so elimination of large predators presumably leads to increased competition between the two species (Ceccarelli et al 2006).

Parasitic isopods are effectively micropredators. They can reduce the growth of damselfish (*Dischistodus perspicillatus*) in the lab and *P. moluccensis* in the field. Although much less common, micropredators can also directly impact damselfish abundance by killing their host (Jones and Grutter 2008). This is can be a factor that should be kept in mind when analyzing damselfish demographics.

By including many of the environmental variables discussed here, one can find how much of an impact each has. The magnitude of the impacts changes with the environments dynamic. A long-term study on prey abundance showed this by manipulating both the habitat structure and predator presence. Numerous damselfish species were included as prey in addition to other reef fishes. On artificial reefs with no holes to hide in, predation did not significantly impact prey abundance. An inverse relationship between predator and prey became apparent however on reefs with more holes (Hixon and Beets 1993). The impact of predation then is linked to the amount of prey habitat available. This concept has also been demonstrated in a more recent study (Hixon and Jones 2005). The complexity of the reef ecosystem makes it unlikely for predation to have a direct impact on damselfish abundance without at least one indirect impact occurring.

No single environmental factor can control damselfish abundance alone. One factor can however have a much a stronger impact on damselfish abundance than any of the others. This seems to be the case with predation. Habitat and competition are also of great importance to damselfish abundance, but are occasionally paired with predation effects (Figueira et al 2007, Belmaker et al 2008, Figueira et al 2008, Schimitt et al 2009). These inclusions of predation into damselfish demographic studies in addition to all the studies found on predation is clear evidence that predation has the greatest impact on damselfish abundance. I expect to see an increase in both habitat and predation studies in the coming years because both of these fields have very recent entries (Holmes and McCormick 2010, Precht et al 2010).

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Chapter 7: Patterns of juvenile coral abundance on Bonaire's reefs: Spatial and temporal trends

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Abstract

I quantified patterns of juvenile coral (≤ 40mm diameter) abundance relative to macroalgal abundance in Bonaire at nine dive sites in 2011 and compared data with past studies in 2003, 2005, 2007 and 2009. Population densities of juvenile corals remain greatly reduced compared to previous monitoring years in Bonaire, while macroalgal abundance continues to rise. There is an inverse relationship between macroalgal abundance and juvenile coral densities, which suggests that macroalgal abundance is reducing the recruitment potential of Bonaire's reefs. This study also compared population densities of juvenile corals within and outside of Fish Protected Areas (FPAs) and found no significant difference between FPAs and the control sites. Declining coral recruitment on Bonaire's reefs is cause for concern. Hence we should work to understand the causes of the increasing algal biomass.

Introduction

In recent decades, many Caribbean reefs have experienced a striking decline in coral cover due to human and natural disturbances (Gardner *et al.* 2003 and Pandolfi *et al.* 2003). Often this decline has been accompanied by an increase in fleshy macroalgae (Hughes 1994, Steneck 1994 and McClanahan *et al.* 1999). To date, the reefs of Bonaire have remained relatively pristine with high coral cover and low macroalgal abundance (Steneck and McClanahan 2003 and Kramer 2003). However coral cover and herbivore populations has begun to decline (Bowdoin and Wilson 2005 and Jaini 2009).

Studies have shown that elevated macroalgal biomass results in the overgrowth and smothering of adult and juvenile corals (Lewis 1986). Furthermore, studies have demonstrated that macroalgal dominance reduces the substrate available for settling corals, thus reducing coral recruitment and the overall resilience of the reef (Birkland 1977 and Hughes *et al.* 2007). To promote coral recruitment and prevent a shift from coral dominated to an algal dominated reefs, Fish Protection Areas (FPA) were established in January 2008 in Bonaire.

The objective of this study was to quantify patterns of juvenile coral abundance relative to macroalgal abundance after the establishment of FPAs on Bonaire's reefs. For this, I gathered data in the spring of 2011 and compared the abundance of juvenile corals in and among FPA and control sites. Assuming that FPAs will increase grazing pressure and thus reduce macroalgal biomass, I tested the hypothesis that juvenile abundance is higher in FPAs. I also examined the relationship between juvenile coral abundance and macroalgal biomass on Bonaire reefs. Finally, I examined temporal patterns by comparing data from 2011 to previous Bonaire Reports from 2003 (Slingsby and Steneck 2003), 2005 (Brown and Arnold 2005), 2007 (Barrett 2007) and 2009 (Steneck and Arnold 2009).

Methods

The methods used in this survey are outlined in Brown and Arnold (2005). Dive surveys were conducted at nine sites on the leeward fringing reefs of the island of Bonaire of the Netherland Antilles in the Southern Caribbean. The sites, from north to south, are No Dive Reserve, Karpata, Barcadera, Oil Slick Leap, Reef Scientifico, Front Porch, Forest (on Klein Bonaire), Calabas and Eighteenth Palm. At each dive site, I placed a 1/16m² (25cm X 25cm) quadrat every 2.5 meters along ten meter transects at a depth of 10m. Quadarts were placed randomly on "available substrate," where coral larvae may settle (i.e.- areas with <25% sand or invertebrate cover). Within each quadrat, I recorded the species and size of all juvenile corals (those ≤40mm in diameter) (Bak & Engel 1979). In addition, I quantified the percent cover of macroalgae, turf algae, coralline algae, sponges, gorgonians and live coral. Finally, I measured the average canopy height for turf, macroalgae and articulated algae; and calculated an algal index as a proxy for algal biomass (percent cover multiplied by canopy height) (Kramer 2003).

Data were analyzed to determine average juvenile population densities and species dominance on the reefs of Bonaire in 2011. I also determined whether there were differences in juvenile coral abundance among dive sites and between the FPAs and the control sites. I employed linear regression analysis to determine whether juvenile abundance relates to macroalgal biomass on Bonaire's reefs and used a square-root transformation to ensure that all assumptions of the linear model were met. Significance was determined using ANOVA for the regression model. Then overall average coral juvenile abundance and macroalgal biomass were examined over time using data from long-term monitoring sites (Eighteenth Palm, Barcadera, Forest, Karpata, Reef Scientifico and Windsock).

Results

Overall, average juvenile coral abundance for the nine dive sites was 18.56 individuals per m² (± 2.11 SE). Of the 11 taxa observed, *Agaricia* spp. and *Porites astreoides* were the most abundant juvenile corals (Fig. 1). Among sites, the highest juvenile population densities were observed at "Oil Slick Leap" and "Front Porch" and the lowest were observed at "Calabas" (Fig. 2). While juvenile abundance greatly varied among sites, there was no significant difference between the average population densities of juvenile corals between the Fish Protected Areas and the control sites (Fig. 2).

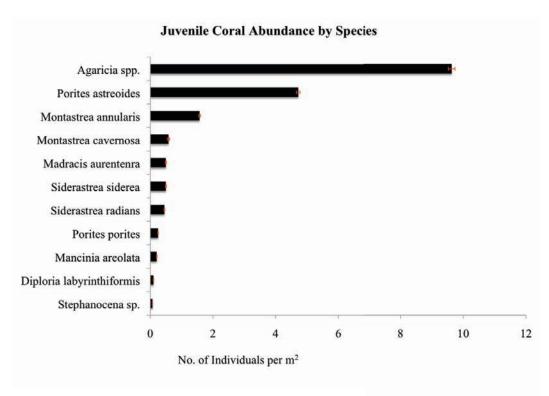


Figure 1: Average population densities of juvenile corals by species on the reefs of Bonaire in 2011 (N=245).

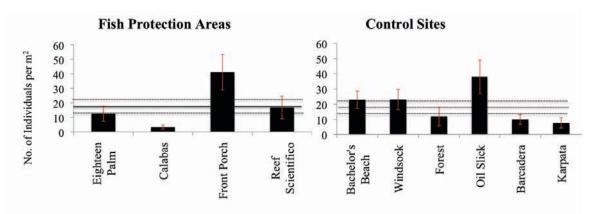


Figure 2: Population densities of juvenile corals in Fish Protected Areas (N=75) and Control sites (N=155) on the reefs of Bonaire in 2011. Error bars denote \pm 1 standard error.

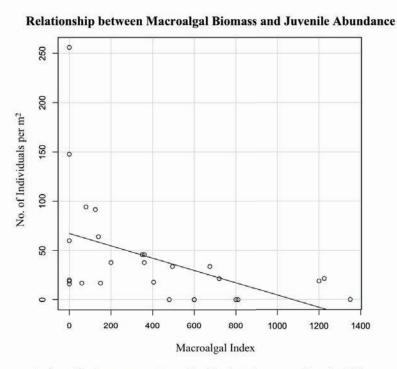


Figure 3: Linear relationship between macroalgal index (a proxy for algal biomass) and average population densities of juvenile corals on the reefs of Bonaire in 2011 (N=25). Y = -0.06X + 67.26; $R^2 = 0.21$.

There was an inverse relationship between the population density of juvenile corals and macroalgal index (the proxy for algal biomass) (p=0.003, R^2 =0.28) (Fig. 3). Among long-term monitored sites, there is also an overall declining temporal trend in juvenile coral abundance and an increasing trend in macroalgae abundance. Overall, juvenile coral abundance on Bonaire in 2011 remains reduced compared to previous monitoring years (Fig. 4). Population densities of juveniles recorded in 2009 were slightly lower than those recorded in 2011 (8.83 individuals per $m^2 \pm 0.67$ SE, 13.24 individuals per $m^2 \pm 2.18$ SE respectively). However this may relate to a storm driven mortality event between 2007 and 2009. Furthermore, overall average macroalgal index was 235.41 (\pm 1.73 SE) and nearly double that of 2007 and quadrupal that of 2005 (Fig. 5).

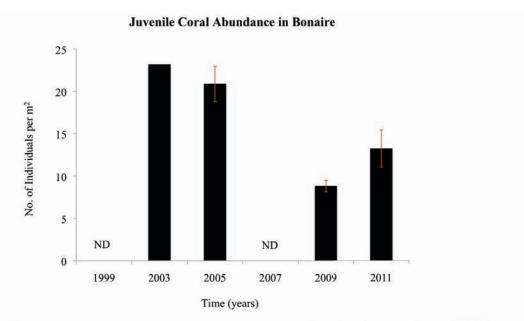


Figure 4: Trends in population densities of juvenile corals in Bonaire. A comparison of 2003 (data from Slingsby and Steneck 2003), 2005 (data from Brown and Arnold 2005), 2009 (Data from Steneck and Arnold 2009) and 2011. Error bars denote \pm 1 standard error.

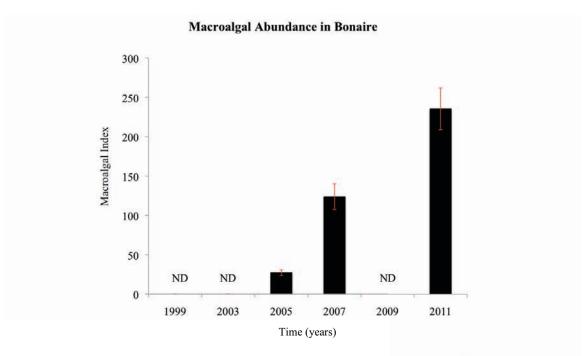


Figure 5: Trends in overall average macroalgal index (a proxy for macroalgal biomass) on Bonaire's reefs. A comparison of data from 2005 (data from Brown and Arnold 2005), 2007 (Barrett 2007) and 2011. Error bars denote \pm 1 standard error.

Discussion

In Bonaire, juvenile coral abundance remains reduced compared to previous monitoring years. Trend analysis indicates that juvenile population densities recorded in 2009 and 2011 are significantly lower than in 2003 and 2005 (Fig. 4). One explanation, which is supported by data from this report, is that the reefs of Bonaire are becoming increasingly hostile to settling corals. Herbivore populations are declining throughout Bonaire, while macroalgal abundance is increasing significantly (this report). Similar increases in algal abundance have been documented throughout the Caribbean and are most likely the result of declining herbivore populations (Hughes 1994, Williams and Polunin 2001 and Hughes *et al.* 2007). The clear negative relationship between macroalgal abundance and juvenile coral abundance (Fig. 3) suggests that macroalgae may be regulating the recruitment potential of Bonaire's reefs (Birkland 1977 and Brown and Arnold 2005). If macroalgal biomass continues to increase, coral recruitment may become vanishingly low (Hughes and Tanner 2000).

As of 2011, the abundance of juvenile corals did not differ significantly between the Fish Protected Areas and the control sites. However Bonaire's Fish Protected Areas were only recently established in 2008. Therefore it is likely too soon to see a management driven increase in recruitment potential at FPA sites. Furthermore, the abundance of territorial damselfishes has increased in recent years, which likely reduces the bite rates of scraping (scarid) and denuding herbivores further (acanthurids and yellow tail damselfishes) (Jaini 2009 and Arnold and Steneck 2010). The decrease in juvenile coral abundance coupled with the increase in macroalgal and damselfish abundance is cause for concern and therefore affirms the need to better understand the causes behind increasing algal biomass in Bonaire. Stricter regulations on the harvest of damselfish predators, in addition to FPAs, may be an appropriate management strategy for increasing coral recruitment and resilience on Bonaire's reefs.

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Appendix 2c.I

ABLAGRRA Bonaire monitoring sites		
Site	Type	Number of Transects
Playa Funchi	Control	2
Wayaka	Control	1
Playa Frans	NDA	2
Marine Reserve North	NDA	1
Karpata	Control	1
Oil Slick	Control	2
Barcadera	Control	2
Cliff	FPA	2
Reef Scientifico	FPA	1
Bari Reef	FPA	2
Front Porch	FPA	2
Something Special	FPA	2
Chachacha Reef	FPA	1
Calabas	FPA	1
Eighteenth Palm	FPA	1
Windsock	Control	1
Bachelor's Beach	Control	2
Angel City	Control	1
Salt City	Control	1
Tori's Reef	Control	2
Margate Bay	Control	2
Vista Blue	Control	2

Appendix 3.1 Average density, total length, and biomass of algal removing fish in Bonaire, Feb/March 2011

	Density (#/100m ²)		Total Le	ength (cm)	Biomass (Biomass (g/100m ²)		
Species observed	mean	<u>SD</u>	mean	SD	mean	SD		
Bachelor					4276.26	1138.34		
Acanthurus bahianus	1.25	0.37	17.78	0.44	116.41	9.68		
Acanthurus chirurgus	0.42	0.00	20.00	0.00	23.46	0.00		
Acanthurus coeruleus	1.53	1.26	18.09	1.04	222.46	55.18		
M. chrysurus	1.07	0.34	15.11	2.32	103.52	21.24		
Scarus iserti	2.50	4.06	11.33	7.72	132.58	177.28		
Scarus taeniopteris	2.62	1.44	21.23	3.79	507.57	314.38		
Scarus vetula	2.74	1.67	27.65	6.46	1047.72	1144.04		
Sparisoma aurofranatum	1.39	0.46	19.50	2.01	170.89	93.99		
Sparisoma rubripinne	1.67	0.00	21.00	4.24	80.08	81.44		
Sparisoma viride	2.50	1.01	27.54	5.91	1256.34	980.04		
Stegastes diencaeus	13.85	2.88	10.91	1.03	495.67	58.36		
Stegastes planifrons	7.19	5.73	8.19	1.47	119.56	44.18		
Barcadera					4485.29	1224.82		
Acanthurus bahianus	0.83	0.83	17.50	0.58	49.41	0.00		
Acanthurus coeruleus	1.25	1.27	17.50	0.55	112.20	0.00		
M. chrysurus	1.43	0.46	15.42	2.02	144.30	163.54		
Scarus iserti	1.50	0.96	23.11	1.96	205.63	69.28		
Scarus taeniopteris	1.67	1.44	19.71	6.04	294.17	330.06		
Scarus vetula	1.98	0.66	31.05	4.39	1144.42	1259.94		
Sparisoma aurofranatum	1.00	0.42	19.83	2.23	107.72	17.07		
Sparisoma viride	2.40	0.63	29.96	2.72	1416.80	689.68		
Stegastes diencaeus	20.31	3.00	11.54	0.87	846.68	52.85		
Stegastes planifrons	10.83	3.29	7.88	1.53	163.97	41.21		
Calabash					6643.81	1248.21		
Acanthurus bahianus	1.67	1.85	19.10	2.51	167.04	95.48		
Acanthurus chirurgus	0.42	0.59	25.00	0.00	37.29	0.00		
Acanthurus coeruleus	5.94	11.86	22.18	1.69	1834.36	118.10		
M. chrysurus	0.83	0.83	15.33	2.52	35.76	21.24		
Scarus iserti	0.56	0.48	15.50	3.54	14.29	0.00		
Scarus taeniopteris	7.60	8.94	21.32	3.03	1673.31	511.70		
Scarus vetula	1.67	1.11	31.29	7.03	924.61	752.66		
Sparisoma aurofranatum	0.83	0.00	21.67	1.03	134.49	0.00		
Sparisoma viride	2.50	2.50	31.33	1.91	1248.92	416.01		
Stegastes diencaeus	11.25	4.96	11.57	1.22	478.64	66.06		
Stegastes planifrons	4.27	2.09	9.12	1.45	95.10	36.28		

Appendix 3.1 cont. Average density, total length, and biomass of algal removing fish in Bonaire, Feb/March 2011

	Density (#/100m ²)		Total Le	ength (cm)	Biomass (g/100m ²)		
Species observed	<u>mean</u>	<u>SD</u>	mean	<u>SD</u>	<u>mean</u>	<u>SD</u>	
					2007.21	10-11-01	
Eighteenth Palm	0.02	0.50	15.40	0.00	3905.21	1261.21	
Acanthurus bahianus	0.83	0.59	17.40	0.89	60.94	10.55	
Acanthurus coeruleus	1.94	1.92	16.71	1.25	118.64	19.49	
M. chrysurus	0.56	0.48	15.00	0.00	21.05	0.00	
Scarus iserti	0.56	0.59	21.50	2.12	36.46	0.00	
Scarus taeniopteris	5.63	4.82	15.98	5.71	730.54	369.77	
Scarus vetula	1.67	0.75	30.50	4.24	908.21	519.13	
Sparisoma aurofranatum	0.83	0.48	22.00	1.41	93.76	47.36	
Sparisoma chrysopterum	0.42		35.00	0.00	73.63	0.00	
Sparisoma viride	1.98	0.93	29.68	4.56	1178.19	943.32	
Stegastes diencaeus	14.06	1.83	11.36	0.80	559.34	45.85	
Stegastes planifrons	7.92	5.25	7.95	1.70	124.44	39.61	
					2510.20	1101 10	
Forest			.=		3710.29	1101.42	
Acanthurus coeruleus	1.67	0.96	17.50	1.07	150.11	42.25	
M. chrysurus	0.63	0.42	16.00	3.46	42.22	0.00	
Scarus iserti	0.42	0.59	10.00	0.00	1.73	0.00	
Scarus taeniopteris	5.52	2.58	17.40	5.27	829.08	529.75	
Scarus vetula	0.97	0.70	29.43	3.82	352.59	206.52	
Sparisoma aurofranatum	1.81	1.83	19.62	2.81	230.53	118.18	
Sparisoma rubripinne	0.42	0.59	28.00	0.00	44.26	0.00	
Sparisoma viride	3.93	1.80	27.12	5.74	1653.93	916.84	
Stegastes diencaeus	3.69	1.73	11.35	0.88	128.49	44.63	
Stegastes planifrons	15.83	3.91	8.22	1.86	277.36	47.87	
F (P 1					1006460	1671.70	
Front Porch	1.20	0.70	20.20	2.20	10864.60	1671.79	
Acanthurus bahianus	1.39	0.70	20.20	2.30	195.54	28.19	
Acanthurus chirurgus	0.83	0.83	21.67	2.89	84.21	78.23	
Acanthurus coeruleus	1.17	0.46	19.86	1.46	175.20	64.76	
M. chrysurus	0.42	0.59	10.00	0.00	3.02	0.00	
Scarus iserti	0.56	0.48	26.00	8.49	74.90	0.00	
Scarus taeniopteris	2.08	1.04	21.45	6.33	510.80	516.46	
Scarus vetula	1.07	0.86	33.89	3.44	691.31	217.19	
Sparisoma aurofranatum	1.33	0.42	22.13	5.79	218.59	79.77	
Sparisoma rubripinne	0.56	0.48	26.00	8.49	82.41	0.00	
Sparisoma viride	16.88	2.93	28.23	3.55	8569.92	1025.10	
Stegastes diencaeus	6.67	3.95	10.66	1.66	231.43	73.07	
Stegastes planifrons	1.56	1.27	8.13	2.07	27.28	19.21	

Appendix 3.1 cont. Average density, total length, and biomass of algal removing fish in Bonaire,

Species observed	Density (#/	(100m ²) SD	Total Le	ength (cm) SD	Biomass ($\frac{g/100m^2}{SD}$
Karpata					3542.53	1188.33
Acanthurus coeruleus	1.11	0.95	17.38	3.16	153.01	51.97
M. chrysurus	1.19	1.02	17.20	4.89	205.23	54.25
Scarus taeniopteris	2.81	1.66	17.85	4.96	439.18	358.54
Scarus vetula	1.77	0.68	27.71	5.86	768.33	1069.94
Sparisoma aurofranatum	0.83	0.00	18.50	4.65	64.17	0.00
Sparisoma viride	2.29	1.12	28.32	6.47	1266.76	1392.91
Stegastes diencaeus	5.63	2.53	11.67	0.91	241.92	56.02
Stegastes planifrons	22.71	6.25	8.32	1.69	403.91	53.05
z regularez princigi en						
Oil Slick					5328.18	1300.27
Acanthurus bahianus	3.61	5.55	14.46	2.82	100.96	34.60
Acanthurus coeruleus	3.67	5.06	18.68	1.04	478.42	27.64
M. chrysurus	1.67	0.75	15.50	2.14	172.28	230.51
Scarus coelestinus	0.42	0.59	45.00	0.00	184.05	0.00
Scarus iserti	0.63	0.48	22.67	5.03	69.93	0.00
Scarus taeniopteris	2.92	2.35	17.29	6.51	462.58	451.48
Scarus vetula	1.55	0.97	31.31	4.15	795.72	638.65
Sparisoma aurofranatum	2.71	1.05	19.85	2.54	235.93	206.91
Sparisoma rubripinne	0.42	0.59	33.00	0.00	73.22	0.00
Sparisoma viride	3.33	1.65	28.53	4.91	1797.57	1172.41
Stegastes diencaeus	21.04	7.15	11.50	1.25	881.17	66.73
Stegastes planifrons	4.64	2.62	8.62	1.29	76.36	28.08
Reef Scientifico					3645.84	1147.09
Acanthurus bahianus	0.83	0.83	17.75	2.06	52.92	0.00
Acanthurus chirurgus	1.94	1.77	20.86	1.57	180.14	62.70
Acanthurus coeruleus	2.19	0.94	18.29	1.62	437.85	158.79
M. chrysurus	0.83	0.00	13.60	2.88	43.62	0.00
Scarus taeniopteris	2.71	1.15	19.27	5.98	521.25	712.84
Scarus vetula	1.31	0.68	31.18	2.99	650.30	415.56
Sparisoma aurofranatum	0.83	0.00	16.00	8.49	25.94	0.00
Sparisoma viride	1.88	0.68	29.17	3.88	1048.80	562.78
Stegastes diencaeus	14.79	3.84	11.26	1.02	578.17	57.54
Stegastes planifrons	7.62	4.40	8.08	1.46	106.85	33.11
Reserve					2523.49	549.35
Acanthurus coeruleus	0.83	0.00	18.50	1.00	113.32	0.00
M. chrysurus	1.11	0.48	14.00	2.71	49.73	0.00
Scarus taeniopteris	6.53	2.55	15.09	6.11	769.36	433.55
Scarus vetula	1.11	0.48	25.50	6.66	193.60	81.90
Sparisoma aurofranatum	1.04	0.80	22.40	1.34	164.08	47.36
Sparisoma viride	2.92	1.15	17.76	8.85	626.25	993.64
Stegastes diencaeus	2.22	2.55	12.13	0.99	53.33	16.36
Stegastes planifrons	27.08	3.90	8.76	1.72	553.83	42.91
Sugasus planinons	27.00	3.70	0.70	1./2	222.03	74.71

Appendix 4.I Observed herbivore species listed from highest to lowest bite rate:

Species	Bite rate (# bites/m²/5min)
Princess parrotfish (Scarus taeniopterus)	59.6
Queen parrotfish (Scarus vetula)	44.4
Longfin damselfish (Stegastes diencaeus)	31.7
Stripped parrotfish (Scarus isteri)	26.5
Stoplight parrotfish (Sparisoma viridae)	24.5
Blue tang (Acanthurus coeruleus)	19.2
Ocean surgeonfish (Acanthurus bahianus)	16.0
Three spot damselfish (Stegastes planifrons)	10.8
Yellowtail damselfish (Microspathodon chrysurus)	9.3
Redband parrotfish (Sparisoma aurofrenatum)	7.7
Redtail parrotfish (Sparisoma chrysopterum)	1.1
Bicolor damselfish (Stegastes partitus)	0.7

Appendix 4.II

Site	Quadrat	Depth	TAC	Genus	Species	Stage	Size	Bites
Bachelor's Beach	1	35	80	Stegastes	planifrons	TP	S	0.00
Bachelor's Beach	1	35	80	Scarus	isteri	JP	S	17.50
Bachelor's Beach	2	36	90	Stegastes	planifrons	TP	L	1.11
Bachelor's Beach	3	32	100	Stegastes	diencaeus	TP	L	0.00
Bachelor's Beach	4	33	90	Stegastes	planifrons	TP	S	12.22
Bachelor's Beach	5	30	95	Sparisoma	viridae	TP	M	3.16
Bachelor's Beach	5	30	95	Stegastes	diencaeus	TP	L	8.42
Bachelor's Beach	6	31	95	Scarus	vetula	TP	M	3.16
Bachelor's Beach	6	31	95	Scarus	taeniopterus	TP	L	29.47
Bachelor's Beach	6	31	95	Sparisoma	viridae	JP	M	2.11
Bachelor's Beach	6	31	95	Microspathodon	chrysurus	TP	M	2.11
Bachelor's Beach	7	25	80	Scarus	isteri	JP	S	21.25
Bachelor's Beach	7	25	80	Scarus	isteri	JP	S	20.00
Bachelor's Beach	7	25	80	Stegastes	planifrons	TP	S	0.00
Bachelor's Beach	7	25	80	Microspathodon	chrysurus	TP	L	1.25
Bachelor's Beach	7	25	80	Stegastes	partitus	TP	S	0.00
Bachelor's Beach	8	21	80	Stegastes	diencaeus	TP	S	2.50
Bachelor's Beach	8	21	80	Stegastes	planifrons	TP	L	0.00
Bachelor's Beach	9	24	95	Stegastes	diencaeus	TP	L	5.26
Bachelor's Beach	9	24	95	Microspathodon	chrysurus	TP	L	5.26
Bachelor's Beach	9	24	95	Stegastes	diencaeus	TP	L	10.53
Bachelor's Beach	10	23	90	Scarus	taeniopterus	TP	L	8.89
Bachelor's Beach	10	23	90	Microspathodon	chrysurus	TP	L	6.67
Bachelor's Beach	10	23	90	Stegastes	diencaeus	TP	L	0.00
Bachelor's Beach	11	25	80	Sparisoma	viridae	IP	L	2.50
Bachelor's Beach	11	25	80	Stegastes	diencaeus	JP	S	0.00
Bachelor's Beach	11	25	80	Scarus	taeniopterus	IP	S	18.75
Bachelor's Beach	11	25	80	Scarus	taeniopterus	IP	S	48.75
Bachelor's Beach	11	25	80	Acanthurus	coeruleus	TP	L	7.50
Bachelor's Beach	11	25	80	Microspathodon	chrysurus	TP	L	10.00

Bachelor's Beach	12	30	90	Stegastes	partitus	TP	S	0.00
Bachelor's Beach	12	30	90	Sparisoma	viridae	TP	L	0.00
Bachelor's Beach	12	30	90	Scarus	taeniopterus	IP	S	4.44
Bachelor's Beach	12	30	90	Acanthurus	bahianus	TP	S	15.56
Barcadera	1	18	95	Scarus	vetula	IP	L	0.00
Barcadera	1	18	95	Stegastes	diencaeus	TP	L	0.00
Barcadera	2	17	100	Stegastes	diencaeus	TP	L	0.00
Barcadera	2	17	100	Microspathodon	chrysurus	TP	L	2.00
Barcadera	2	17	100	Scarus	vetula	ΙP	L	4.00
Barcadera	3	24	100	Stegastes	diencaeus	TP	L	7.00
Barcadera	4	20	95	Microspathodon	chrysurus	TP	L	2.11
Barcadera	4	20	95	Stegastes	diencaeus	TP	L	5.26
Barcadera	5	24	80	Scarus	vetula	TP	XL	7.50
Barcadera	5	24	80	Stegastes	planifrons	TP	S	0.00
Barcadera	5	24	80	Stegastes	diencaeus	TP	L	0.00
Barcadera	6	19	90	Acanthurus	coeruleus	TP	L	6.67
Barcadera	6	19	90	Stegastes	planifrons	TP	S	1.11
Barcadera	7	15	80	Stegastes	planifrons	TP	S	0.00
Barcadera	7	15	80	Scarus	isteri	ΙP	S	40.00
Barcadera	7	15	80	Scarus	taeniopterus	ΙP	S	3.75
Barcadera	8	17	85	Stegastes	diencaeus	TP	L	7.06
Calabas	1	25	80	Stegastes	partitus	TP	S	0.00
Calabas	1	25	80	Stegastes	partitus	TP	S	0.00
Calabas	1	25	80	Stegastes	partitus	TP	S	3.75
Calabas	1	25	80	Stegastes	diencaeus	TP	L	1.25
Calabas	1	25	80	Stegastes	diencaeus	TP	L	2.50
Calabas	1	25	80	Scarus	isteri	TP	L	12.50
Calabas	1	25	80	Scarus	taeniopterus	TP	XL	0.00
Calabas	2	25	100	Stegastes	diencaeus	TP	L	6.00
Calabas	3	20	90	Stegastes	diencaeus	TP	L	2.22
Calabas	3	20	90	Stegastes	partitus	TP	S	0.00
Calabas	3	20	90	Scarus	vetula	TP	XL	14.44
Calabas	4	20	100	Scarus	isteri	JP	М	20.00
Calabas	4	20	100	Scarus	isteri	JP	S	22.00
Calabas	4	20	100	Scarus	isteri	JP	S	22.00
Calabas	5	20	95	Stegastes	diencaeus	TP	L	0.00
Calabas	6	20	95	Stegastes	diencaeus	TP	М	0.00
Calabas	7	26	95	Stegastes	diencaeus	IP	S	0.00
Calabas	7	26	95	Scarus	taeniopterus	TP	S	6.32
Calabas	8	23	95	Scarus	taeniopterus	JP	S	16.84
Calabas	8	23	95	Scarus	taeniopterus	JP	S	28.42
Calabas	8	23	95	Scarus	taeniopterus	IP	S	5.26
Calabas	8	23	95	Sparisoma	aurofrenatum	JP	S	7.37
Calabas	9	17	85	Stegastes	diencaeus	TP	S	0.00
Calabas	9	17	85	Stegastes	diencaeus	TP	L	0.00
Calabas	9	17	85	Scarus	taeniopterus	JP	S	31.76
Calabas	9	17	85	Stegastes	diencaeus	JP	S	0.00
Calabas	9	17	85	Stegastes	partitus	TP	S	0.00
Calabas	9	17	85	Sparisoma	viridae	IP	L	25.88
Calabas	10	21	90	Stegastes	diencaeus	TP	L	0.00
Calabas	10	21	90	Sparisoma	aurofrenatum	IP	S	15.56
Calabas	11	18	85	Stegastes	diencaeus	IP	S	7.06
Calabas	11	18	85	Sparisoma	chrysopterum	TP	M	11.76
Calabas	11	18	85	Scarus	taeniopterus	JP	S	7.06

Calabas	11	18	85	Stegastes	planifrons	TP	S	3.53
Eighteenth Palm	1	26	95	Stegastes	planifrons	TP	L	18.95
Eighteenth Palm	1	26	95	Stegastes	diencaeus	JP	S	6.32
Eighteenth Palm	1	26	95	Stegastes	diencaeus	TP	L	2.11
Eighteenth Palm	2	27	80	Stegastes	diencaeus	TP	S	15.00
Eighteenth Palm	3	26	90	Stegastes	partitus	TP	S	0.00
Eighteenth Palm	3	26	90	Scarus	isteri	JP	S	7.78
Eighteenth Palm	3	26	90	Sparisoma	viridae	TP	XL	5.56
Eighteenth Palm	3	26	90	Acanthurus	bahianus	TP	S	25.56
Eighteenth Palm	3	26	90	Scarus	vetula	IP	M	3.33
Eighteenth Palm	3	26	90	Scarus	taeniopterus	JP	S	11.11
Eighteenth Palm	3	26	90	Sparisoma	aurofrenatum	IP	S	3.33
Eighteenth Palm	4	25	100	Stegastes	diencaeus	TP	L	13.00
Eighteenth Palm	5	26	90	Scarus	vetula	IP	L	93.33
Eighteenth Palm	5	26	90	Stegastes	diencaeus	TP	S	1.11
Eighteenth Palm	5	26	90	Stegastes	diencaeus	TP	L	6.67
Eighteenth Palm	6	29	95	Stegastes	diencaeus	TP	L	11.58
Eighteenth Palm	7	24	85	Stegastes	diencaeus	TP	L	0.00
Eighteenth Palm	7	24	85	Sparisoma	viridae	TP	XL	17.65
Eighteenth Palm	7	24	85	Microspathodon	chrysurus	TP	L	10.59
Eighteenth Palm	7	24	85	Scarus	vetula	TP	XL	27.06
Eighteenth Palm	8	23	90	Stegastes	diencaeus	TP	L	2.22
Forest (Klein Bonaire)	1	16	90	Scarus	taeniopterus	IP	S	38.89
Forest (Klein Bonaire)	1	16	90	Stegastes	diencaeus	TP	L	12.22
Forest (Klein Bonaire)	1	16	90	Microspathodon	chrysurus	TP	- L	4.44
Forest (Klein Bonaire)	1	16	90	Stegastes	diencaeus	TP	- L	0.00
Forest (Klein Bonaire)	1	16	90	Stegastes	partitus	TP	S	0.00
Forest (Klein Bonaire)	1	16	90	Stegastes	partitus	TP	S	0.00
Forest (Klein Bonaire)	2	20	85	Stegastes	planifrons	TP	S	0.00
Forest (Klein Bonaire)	2	20	85	Scarus	vetula	TP	L	1.18
Forest (Klein Bonaire)	3	24	90	Scarus	taeniopterus	TP	M	11.11
Forest (Klein Bonaire)	3	24	90	Stegastes	diencaeus	TP	L	0.00
Forest (Klein Bonaire)	4	19	90	Stegastes	planifrons	TP	- L	2.22
Forest (Klein Bonaire)	4	19	90	Stegastes	partitus	TP	S	0.00
Forest (Klein Bonaire)	4	19	90	Sparisoma	viridae	IP	L	14.44
Forest (Klein Bonaire)	4	19	90	Microspathodon	chrysurus	TP	L	2.22
Forest (Klein Bonaire)	5	18	100	Stegastes	planifrons	TP	L	8.00
Forest (Klein Bonaire)	5	18	100	Sparisoma	viridae	IP	L	8.00
Forest (Klein Bonaire)	6	15	80	Microspathodon	chrysurus	TP	L	0.00
Forest (Klein Bonaire)	6	15	80	Stegastes	planifrons	TP	S	0.00
Forest (Klein Bonaire)	6	15	80	Stegastes	partitus	TP	S	0.00
Forest (Klein Bonaire)	7	23	95	Acanthurus	bahianus	TP	S	24.21
Forest (Klein Bonaire)	7	23	95	Sparisoma	aurofrenatum	IP	S	17.89
Forest (Klein Bonaire)	7	23	95	Stegastes	partitus	IP	S	0.00
Forest (Klein Bonaire)	7	23	95	Scarus	taeniopterus	IP	S	16.84
Forest (Klein Bonaire)	8	21	90	Acanthurus	coeruleus	TP	S	20.00
Forest (Klein Bonaire)	8	21	90	Stegastes	diencaeus	TP	L	3.33
Forest (Klein Bonaire)	8	21	90	Scarus	vetula	IP	М	34.44
Forest (Klein Bonaire)	8	21	90	Scarus	taeniopterus	IP	S	10.00
Forest (Klein Bonaire)	9	21	90	Sparisoma	viridae	IP	М	2.22
Forest (Klein Bonaire)	9	21	90	Stegastes	diencaeus	TP	L	0.00
Forest (Klein Bonaire)	9	21	90	Stegastes	planifrons	TP	S	0.00
Forest (Klein Bonaire)	9	21	90	Stegastes	diencaeus	IP	S	0.00
Forest (Klein Bonaire)	9	21	90	Acanthurus	coeruleus	TP	L	54.44
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Forest (Klein Bonaire)	9	21	90	Scarus	taeniopterus	IP	S	43.33
Forest (Klein Bonaire)	9	21	90	Microspathodon	chrysurus	TP	L	3.33
Front Porch	1	29	80	Sparisoma	viridae	TP	XL	3.75
Front Porch	1	29	80	Acanthurus	bahianus	TP	S	0.00
Front Porch	2	32	90	Stegastes	partitus	TP	S	0.00
Front Porch	2	32	90	Sparisoma	aurofrenatum	IP	M	2.22
Front Porch	2	32	90	Microspathodon	chrysurus	TP	L	1.11
Front Porch	3	28	100	Stegastes	partitus	TP	S	0.00
Front Porch	3	28	100	Acanthurus	coeruleus	TP	L	18.00
Front Porch	3	28	100	Acanthurus	coeruleus	TP	L	16.00
Front Porch	4	28	80	Scarus	vetula	TP	L	10.00
Front Porch	4	28	80	Stegastes	partitus	TP	S	0.00
Front Porch	4	28	80	Stegastes	partitus	TP	S	0.00
Front Porch	4	28	80	Stegastes	partitus	TP	S	0.00
Front Porch	5	27	100	Stegastes	partitus	TP	S	0.00
Front Porch	5	27	100	Stegastes	diencaeus	TP	S	10.00
Front Porch	5	27	100	Stegastes	partitus	TP	S	0.00
Front Porch	6	19	90	Stegustes	partitus	••	3	0.00
Front Porch	7	25	90	Scarus	vetula	JP	М	6.67
Front Porch	7	25	90	Stegastes	partitus	TP	S	0.00
Front Porch	7	25	90	Sparisoma	viridae	IP	L	13.33
Front Porch	, 7	25	90	Sparisoma	viridae	IP	L	11.11
Front Porch	, 7	25	90	Sparisoma	viridae	IP	L	35.56
Karpata	1	18	85	Sparisoma	viridae	IP	М	1.18
Karpata	1	18	85	Stegastes	diencaeus	TP	L L	0.00
Karpata	1	18	85	Stegastes	planifrons	TP	S	0.00
Karpata	1	18	85	Stegastes	partitus	TP	S	0.00
Karpata	1	18	85	Sparisoma	viridae	JP	S	5.88
Karpata	2	20	95	Stegastes	diencaeus	TP	L	4.21
·	2	20	95	Stegastes	partitus	TP	S	0.00
Karpata	3	17	95	Stegastes	diencaeus	TP	L	0.00
Karpata Karpata	4	15	90	Sparisoma	viridae	IP	L	3.33
Karpata	4	15	90	Sparisoma	viridae	IP	М	1.11
•	4	15	90	Stegastes	diencaeus	TP	L	0.00
Karpata	4	15	90	Stegastes	diencaeus	TP	L	4.44
Karpata Karpata	5	13	85	Stegastes	diencaeus	TP	L	2.35
Karpata	5	13	85	Scarus	vetula	TP	XL	10.59
Karpata	6	14	80	Stegastes	diencaeus	TP	L	6.25
Karpata	6	14	80	Microspathodon	chrysurus	TP	L	0.23
Karpata	6	14	80	Scarus	vetula	IP	М	7.50
Karpata	7	16	80	Stegastes	diencaeus	TP	L	0.00
Karpata	8	20	95	-	partitus	TP	S	0.00
Karpata	8	20	95	Stegastes Stegastes	partitus	TP	S	0.00
Karpata	8	20	95	Stegastes	planifrons	TP	S	1.05
Karpata	8	20	95	Scarus	taeniopterus	TP	M	3.16
Karpata	9	20 17	95 85	Scarus	taeniopterus	JP	S	4.71
Karpata		17	85		partitus	TP	S	
•	9 a	17	85	Stegastes	•	TP	s L	0.00 4.71
Karpata No Dive Reserve	9 1	18	85 95	Stegastes	diencaeus	TP	L	
No Dive Reserve	1	18	95 95	Stegastes	diencaeus	TP	L	0.00
No Dive Reserve	2	22		Microspathodon	chrysurus	TP	S	3.16 13.75
No Dive Reserve	2	22	80 80	Stegastes	planifrons	TP	S S	
No Dive Reserve			80	Stegastes	partitus			0.00
No Dive Reserve	2	22	80	Stegastes	partitus	TP TD	S	0.00
No Dive Reserve	2	22	80	Stegastes	partitus	TP	S	0.00

N D' D			00	6 .				7.50
No Dive Reserve	2	22	80	Sparisoma	viridae	IP TD	S	7.50
No Dive Reserve	3	19	80	Stegastes	planifrons	TP	S	5.00
No Dive Reserve	3	19	80	Stegastes	planifrons	TP	S	12.50
No Dive Reserve	4	20	80	Stegastes	planifrons	TP	S	8.75
No Dive Reserve	4	20	80	Stegastes	diencaeus 	TP	L	11.25
No Dive Reserve	5	19	75	Stegastes	partitus	TP	S	0.00
No Dive Reserve	6	21	95	Stegastes	partitus	TP	S	0.00
No Dive Reserve	6	21	95	Stegastes	diencaeus	TP	S	8.42
No Dive Reserve	6	21	95	Microspathodon	chrysurus	TP	L	3.16
No Dive Reserve	7	17	90	Stegastes	planifrons	TP	L	8.89
No Dive Reserve	7	17	90	Scarus	vetula	IP	M	27.78
No Dive Reserve	7	17	90	Microspathodon	chrysurus	TP	L	3.33
No Dive Reserve	7	17	90	Stegastes	diencaeus	TP	L	3.33
No Dive Reserve	8	17	90	Scarus	taeniopterus	TP	M	36.67
No Dive Reserve	8	17	90	Stegastes	planifrons	TP	L	2.22
No Dive Reserve	8	17	90	Microspathodon	chrysurus	TP	L	0.00
No Dive Reserve	9	18	90	Stegastes	planifrons	TP	L	1.11
No Dive Reserve	9	18	90	Stegastes	planifrons	TP	S	0.00
No Dive Reserve	9	18	90	Acanthurus	coeruleus	TP	S	4.44
No Dive Reserve	9	18	90	Acanthurus	coeruleus	TP	L	7.78
No Dive Reserve	10	17	95	Stegastes	planifrons	TP	L	1.05
No Dive Reserve	10	17	95	Stegastes	planifrons	JP	S	0.00
No Dive Reserve	10	17	95	Sparisoma	viridae	IP	S	3.16
No Dive Reserve	10	17	95	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	1	31	100	Stegastes	diencaeus	TP	S	0.00
Oil Slick Leap	1	31	100	Scarus	vetula	TP	L	0.00
Oil Slick Leap	2	25	100	Scarus	vetula	JP	L	2.00
Oil Slick Leap	2	25	100	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	2	25	100	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	2	25	100	Acanthurus	bahianus	TP	S	2.00
Oil Slick Leap	2	25	100	Acanthurus	bahianus	TP	S	0.00
Oil Slick Leap	2	25	100	Stegastes	diencaeus	TP	L	0.00
Oil Slick Leap	2	25	100	Sparisoma	aurofrenatum	IP	M	17.00
Oil Slick Leap	3	23	90	Stegastes	diencaeus	TP	S	3.33
Oil Slick Leap	4	18	85	Scarus	taeniopterus	ΙP	M	3.53
Oil Slick Leap	5	26	100	Stegastes	diencaeus	TP	S	8.00
Oil Slick Leap	5	26	100	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	6	21	95	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	6	21	95	Stegastes	diencaeus	TP	S	0.00
Oil Slick Leap	6	21	95	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	6	21	95	Scarus	vetula	ΙP	М	2.11
Oil Slick Leap	7	18	100	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	7	18	100	Stegastes	partitus	TP	S	0.00
Oil Slick Leap	7	18	100	Scarus	vetula	IP	L	2.00
Oil Slick Leap	8	24	100	Stegastes	diencaeus	TP	S	4.00
Oil Slick Leap	8	24	100	Microspathodon	chrysurus	TP	L	3.00
Oil Slick Leap	8	24	100	Microspathodon	chrysurus	TP	L	0.00
Oil Slick Leap	8	24	100	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	8	24	100	Chromis	mulitlineata	TP	S	1.00
Oil Slick Leap	8	24	100	Chromis	mulitlineata	TP	S	2.00
Oil Slick Leap	8	24	100	Chromis	mulitlineata	TP	S	3.00
Oil Slick Leap	9	20	95	Stegastes	diencaeus	TP	L	12.63
Oil Slick Leap	9	20	95	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	9	20	95	Microspathodon	chrysurus	TP	L	2.11
on suck reah	3	20	93	iviici ospatilouoil	ciii youluo	T.F.	L	2.11

Oil Slick Leap	10	22	90	Stegastes	partitus	TP	S	1.11
Oil Slick Leap	10	22	90	Sparisoma	viridae	JP	M	2.22
Oil Slick Leap	10	22	90	Stegastes	diencaeus	TP	S	2.22
Oil Slick Leap	10	22	90	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	10	22	90	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	10	22	100	Microspathodon	chrysurus	TP	L	11.00
Oil Slick Leap	10	22	100	Stegastes	diencaeus	TP	L	7.00
Oil Slick Leap	11	25	80	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	11	25 25	80	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	11	25 25	80	Chromis	mulitlineata	TP	S	0.00
Oil Slick Leap	11	25 25	80	Stegastes	planifrons	TP	L	3.75
Oil Slick Leap	11	25 25	80	Acanthurus	coeruleus	TP	L	0.00
•	11	25 25	80	Acanthurus	coeruleus	TP	S	0.00
Oil Slick Leap								
Oil Slick Leap	12	33	100	Stegastes	diencaeus	TP	L	2.00
Reef Scientifico	1	35	80	Stegastes	partitus	TP	S	0.00
Reef Scientifico	1	35	80	Stegastes	partitus	TP	S	0.00
Reef Scientifico	1	35	80	Stegastes	diencaeus	TP	L	1.25
Reef Scientifico	2	32	80	Stegastes	diencaeus	TP	L	8.75
Reef Scientifico	2	32	80	Sparisoma	aurofrenatum	TP	М	2.50
Reef Scientifico	3	37	100	Acanthurus	bahianus	TP	S	6.00
Reef Scientifico	4	28	80	Scarus	taeniopterus	IP	S	91.25
Reef Scientifico	4	28	80	Acanthurus	coeruleus	TP	S	41.25
Reef Scientifico	4	28	80	Stegastes	diencaeus	TP	L	6.25
Reef Scientifico	4	28	80	Stegastes	partitus	TP	S	0.00
Reef Scientifico	4	28	80	Scarus	taeniopterus	TP	M	13.75
Reef Scientifico	4	28	80	Sparisoma	aurofrenatum	ΙP	M	2.50
Reef Scientifico	5	31	85	Scarus	isteri	IP	S	8.24
Reef Scientifico	5	31	85	Sparisoma	aurofrenatum	JP	S	4.71
Reef Scientifico	5	31	85	Stegastes	partitus	TP	S	0.00
Reef Scientifico	5	31	85	Stegastes	partitus	TP	S	0.00
Reef Scientifico	5	31	85	Stegastes	partitus	TP	S	0.00
Reef Scientifico	5	31	85	Scarus	taeniopterus	JP	S	7.06
Reef Scientifico	5	31	85	Scarus	taeniopterus	JP	S	4.71
Reef Scientifico	5	31	85	Acanthurus	coeruleus	TP	L	8.24
Reef Scientifico	6	26	90	Stegastes	diencaeus	TP	L	0.00
Reef Scientifico	6	26	90	Scarus	isteri	IP	S	5.56
Reef Scientifico	6	26	90	Scarus	isteri	IP	S	8.89
Reef Scientifico	6	26	90	Scarus	isteri	IP	M	5.56
Reef Scientifico	6	26	90	Acanthurus	coeruleus	TP	L	13.33
Reef Scientifico	6	26	90	Scarus	taeniopterus	TP	M	21.11
Reef Scientifico	6	26	90	Sparisoma	aurofrenatum	IP	S	3.33
Reef Scientifico	6	26	90	Acanthurus	coeruleus	TP	S	11.11
Reef Scientifico	7	17	90	Sparisoma	viridae	TP	L	24.44
Reef Scientifico	7	17	90	Acanthurus	bahianus	TP	S	27.78
Reef Scientifico	7	17	90	Scarus	taeniopterus	ΙP	M	13.33
Reef Scientifico	7	17	90	Stegastes	diencaeus	ΙP	S	0.00
Reef Scientifico	7	17	90	Stegastes	partitus	TP	S	0.00
Reef Scientifico	7	17	90	Stegastes	partitus	TP	S	0.00
Reef Scientifico	7	17	90	Stegastes	partitus	TP	S	0.00
Reef Scientifico	, 7	17	90	Stegastes	partitus	TP	S	0.00
Reef Scientifico	, 7	17	90	Stegastes	partitus	TP	S	0.00
Reef Scientifico	7	17	90	Stegastes	partitus	TP	S	0.00
Reef Scientifico	8	21	90	Stegastes	diencaeus	TP	L	0.00
Reef Scientifico	8	21	90	Stegastes	partitus	TP	S	0.00
Meet Joiethilleu	O	21	90	Jicgusies	partitus	117	3	0.00

Reef Scientifico	8	21	90	Scarus	vetula	TP	XL	7.78
Reef Scientifico	8	21	90	Stegastes	diencaeus	IP	S	0.00
Reef Scientifico	9	23	80	Stegastes	diencaeus	TP	L	10.00
Windsock	1	25	80	Scarus	vetula	TP	M	15.00
Windsock	1	25	80	Stegastes	diencaeus	TP	S	6.25
Windsock	1	25	80	Sparisoma	viridae	TP	L	1.25
Windsock	1	25	80	Stegastes	partitus	TP	S	0.00
Windsock	2	23	100	Microspathodon	chrysurus	TP	L	2.00
Windsock	2	23	100	Scarus	vetula	IP	M	14.00
Windsock	3	26	90	Stegastes	partitus	TP	S	0.00
Windsock	3	26	90	Chromis	mulitlineata	TP	L	0.00
Windsock	3	26	90	Chromis	mulitlineata	TP	L	0.00
Windsock	3	26	90	Stegastes	diencaeus	TP	L	15.56
Windsock	3	26	90	Stegastes	diencaeus	TP	L	4.44
Windsock	3	26	90	Scarus	vetula	TP	L	2.22
Windsock	3	26	90	Scarus	vetula	JP	M	16.67
Windsock	4	22	90	Scarus	taeniopterus	TP	M	20.00
Windsock	4	22	90	Stegastes	diencaeus	TP	L	0.00
Windsock	4	22	90	Microspathodon	chrysurus	TP	L	7.78
Windsock	5	30	90	Stegastes	diencaeus	TP	L	10.00
Windsock	5	30	90	Microspathodon	chrysurus	TP	L	2.22
Windsock	5	30	90	Stegastes	partitus	TP	S	0.00
Windsock	6	20	95	Stegastes	diencaeus	TP	L	0.00
Windsock	7	19	80	Stegastes	diencaeus	TP	L	0.00
Windsock	7	19	80	Scarus	taeniopterus	TP	M	28.75
Windsock	7	19	80	Microspathodon	chrysurus	TP	L	6.25
Windsock	7	19	80	Scarus	vetula	IP	M	10.00
Windsock	8	24	90	Sparisoma	viridae	IP	S	13.33
Windsock	8	24	90	Scarus	vetula	IP	S	44.44
Windsock	8	24	90	Scarus	isteri	JP	S	33.33
Windsock	8	24	90	Scarus	isteri	JP	M	22.22
Windsock	8	24	90	Stegastes	partitus	TP	S	0.00
Windsock	9	27	90	Stegastes	diencaeus	TP	L	3.33
Windsock	9	27	90	Stegastes	partitus	TP	S	2.22
Windsock	9	27	90	Scarus	vetula	IP	M	32.22
Winsock	10	18	90	Stegastes	diencaeus	TP	S	0.00

Appendix 6a: Average biomass and density of predatory reef fish, Bonaire 2011.

			Density (# per 1	00 m2)	Fork Length (cm)	
No Dive Reserve - 10 m (Sample size = 7)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomus maculatus	8.1	8.1	0.0	0.0	4.3	4.3
Bodianus rufus	169.6	77.7	1.3	0.4	13.7	3.6
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	433.5	325.2	0.6	0.3	15.3	8.6
Epinephelus cruentatus	423.6	46.3	4.0	0.3	19.1	0.6
Epinephelus fulvus	0.8	0.8	0.1	0.1	2.3	2.3
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	0.0	0.0	0.0	0.0	0.0	0.0
Haemulon carbonarium	188.4	124.9	0.4	0.3	8.7	5.6
Haemulon chrysargyreum	0.0	0.0	0.0	0.0	0.0	0.0
Haemulon flavolineatum	118.7	43.9	1.4	0.5	11.4	3.0
Haemulon sciurus	295.1	190.5	0.3	0.2	11.4	7.4
Hypoplectrus sp	17.0	7.2	1.1	0.5	5.8	2.1
Lutjanus apodus	2422.1	699.7	2.7	0.7	32.0	6.2
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	129.0	65.8	2.0	1.4	10.0	3.6
Mycteroperca tigris	9.8	9.8	0.1	0.1	2.6	2.6
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	4042.9	3473.2	2.0	1.4	17.7	8.5
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	1771.4	995.8	2.0	1.1	24.0	8.5
Synodus intermedius	0.0	0.0	0.0	0.0	0.0	0.0
Serranus tigrinus	0.8	0.5	0.3	0.2	1.7	1.1
Pterois volitans	0.1	0.1	0.1	0.1	4.0	4.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	8.1	8.1	0.1	0.1	4.3	4.3
Carangidae	433.5	325.2	0.6	0.3	15.3	8.6
Haemulidae	602.3	359.3	2.1	1.0	31.6	16.0
Labridae	169.6	77.7	1.3	0.4	13.7	3.6
Lutjanidae	4322.5	1761.2	6.7	3.2	66.0	18.3
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	452.0	64.6	5.7	1.2	31.5	8.6
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	10030.9	6069.5	18.7	7.9	184.0	71.9

	Biomass (g per 10	0 m2)	Density (# per 10	00 m2)	Fork Ler (cm)	igth
Karpata - 10 m (Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	230.2	230.2	0.1	0.1	5.5	5.2
Aulostomus maculatus	0.0	0.0	0.0	0.0	0.0	0.0
Bodianus rufus	272.8	105.6	1.1	0.4	11.9	44.5
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	681.8	274.4	0.8	0.3	19.1	8.2
Epinephelus cruentatus	460.0	99.6	3.6	0.9	16.0	92.2
Epinephelus fulvus	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	29.0	19.9	0.3	0.2	11.3	7.1
Haemulon carbonarium	54.5	54.5	0.1	0.1	3.8	3.5
Haemulon chrysargyreum	1033.3	692.6	9.0	6.1	7.0	2.9
Haemulon flavolineatum	180.6	66.2	1.9	0.6	12.7	19.6
Haemulon sciurus	0.0	0.0	0.0	0.0	0.0	0.0
Hypoplectrus sp	10.9	4.2	0.5	0.2	4.5	2.1
Lutjanus apodus	890.2	457.1	0.9	0.3	19.3	215.4
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	72.1	37.2	0.4	0.2	8.8	4.2
Mycteroperca tigris	26.3	26.3	0.1	0.1	3.3	3.1
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	309.8	309.8	0.1	0.1	6.3	5.9
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	1525.2	525.4	1.4	0.5	29.4	161.1
Synodus intermedius	40.5	40.5	0.1	0.1	4.3	4.0
Serranus tigrinus	2.3	1.2	0.5	0.3	2.7	1.3
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	0.0	0.0	0.0	0.0	0.0	0.0
Carangidae	681.8	274.4	0.8	0.3	19.1	8.2
Haemulidae	1498.5	1043.5	11.1	7.0	29.0	31.2
Labridae	272.8	105.6	1.1	0.4	11.9	44.5
Lutjanidae	2487.5	1019.7	2.6	0.9	57.4	380.6
Muraenidae	29.0	19.9	0.3	0.2	11.3	7.1
Serranidae	499.5	131.2	4.8	1.4	26.4	98.7
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	40.5	40.5	0.1	0.1	4.3	4.0
All Predators	5819.4	2944.6	20.9	10.5	165.5	580.2

	Biomass (g per 10	0 m2)	Density (# per 10	00 m2)	Fork Len	gth
Bachelor's Beach - 10 m		0.5				
(Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	4494.6	4145.3	6.8	6.2	15.3	5.9
Aulostomus maculatus	94.7	45.6	0.6	0.3	15.8	7.7
Bodianus rufus	63.6	24.9	0.6	0.3	9.8	19.2
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	270.9	187.5	0.3	0.2	11.3	7.1
Epinephelus cruentatus	489.9	233.6	4.0	0.9	14.2	3.0
Epinephelus fulvus	2.2	2.2	0.1	0.1	3.0	2.8
Epinephelus adscensionis	394.9	394.9	0.1	0.1	7.5	7.1
Gymnothorax sp.	29.0	29.0	0.1	0.1	7.5	7.1
Haemulon carbonarium	191.3	109.9	1.1	0.7	8.5	4.0
Haemulon chrysargyreum	1107.8	594.2	13.9	7.0	8.3	114.6
Haemulon flavolineatum	297.2	163.1	7.5	4.5	8.8	8.8
Haemulon sciurus	180.6	118.4	0.3	0.2	8.9	5.5
Hypoplectrus sp	6.9	2.6	0.5	0.2	5.0	1.9
Lutjanus apodus	604.4	279.3	1.5	0.5	20.2	109.9
Lutjanus cyanopterus	2080.3	2080.3	0.1	0.1	12.5	11.8
Lutjanus jocu	880.5	880.5	0.1	0.1	10.0	9.4
Lutjanus mahogoni	83.1	29.6	1.3	0.5	9.9	10.1
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	900.1	420.6	1.0	0.5	14.6	7.9
Synodus intermedius	0.0	0.0	0.0	0.0	0.0	0.0
Serranus tigrinus	2.3	1.7	0.3	0.2	2.1	1.4
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	94.7	45.6	0.6	0.3	15.8	7.7
Carangidae	270.9	187.5	0.3	0.2	11.3	7.1
Haemulidae	6271.6	5130.9	29.5	18.5	49.6	138.9
Labridae	63.6	24.9	0.6	0.3	9.8	19.2
Lutjanidae	4548.3	3690.3	4.0	1.7	67.2	149.1
Muraenidae	29.0	29.0	0.1	0.1	7.5	7.1
Serranidae	896.2	635.0	5.0	1.5	31.8	16.1
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	12174.3	9743.2	40.1	22.5	192.9	345.1

	Biomass (g per 10	0 m2)	Density (# per 1	00 m2)	Fork Len (cm)	gth
Oil Slick - 10 m (Sample size = 11)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomus maculatus	36.7	19.0	0.4	0.2	10.0	5.1
Bodianus rufus	183.6	100.9	0.4	0.2	10.5	4.8
Bothus lunatus	95.7	95.7	0.1	0.1	3.6	3.5
Caranx rubber	515.7	193.4	0.7	0.3	18.0	6.3
Epinephelus cruentatus	235.7	79.3	2.9	0.7	14.5	2.1
Epinephelus fulvus	4.7	4.7	0.2	0.2	2.5	2.4
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	13.9	9.7	0.4	0.2	7.0	3.7
Haemulon carbonarium	51.4	40.2	0.2	0.1	4.5	3.0
Haemulon chrysargyreum	687.4	424.0	6.9	4.6	12.0	19.0
Haemulon flavolineatum	175.7	53.7	3.3	1.6	11.0	9.6
Haemulon sciurus	174.4	117.4	0.2	0.1	7.1	4.6
Hypoplectrus sp	26.2	5.8	1.2	0.3	9.5	1.4
Lutjanus apodus	456.2	272.8	0.8	0.4	11.4	11.1
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	143.8	49.9	1.7	0.8	13.5	3.0
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	826.6	826.6	0.2	0.2	8.2	790.7
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	97.6	97.6	0.1	0.1	3.6	3.5
Ocyurus chrysurus	640.6	289.6	1.8	0.7	14.6	4.4
Synodus intermedius	109.1	60.2	0.4	0.2	8.9	4.5
Serranus tigrinus	3.0	1.6	0.4	0.2	2.9	1.5
Pterois volitans	0.1	0.1	0.1	0.1	1.2	1.1
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	36.7	19.0	0.4	0.2	10.0	5.1
Carangidae	515.7	193.4	0.7	0.3	18.0	6.3
Haemulidae	1088.8	635.4	10.5	6.5	34.7	36.1
Labridae	183.6	100.9	0.4	0.2	10.5	4.8
Lutjanidae	1240.6	612.2	4.4	1.8	39.5	18.5
Muraenidae	13.9	9.7	0.4	0.2	7.0	3.7
Serranidae	269.6	91.4	4.6	1.3	29.3	7.4
Sphyraenidae	826.6	826.6	0.2	0.2	8.2	790.7
Synodontidae	109.1	60.2	0.4	0.2	8.9	4.5
All Predators	4477.9	2742.2	22.2	11.1	174.6	885.1

	Biomass (g per 10	0 m2)	Density (# per 1	00 m2)	Fork Len	gth
Barcadera - 10 m (Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	62.8	62.8	0.1	0.1	3.8	58.9
Aulostomus maculatus	202.2	166.8	0.1	0.1	16.9	158.6
Bodianus rufus	170.1	111.8	0.6	0.3	5.5	4.5
Bothus lunatus			0.8	0.3	4.0	3.8
Caranx rubber	64.6 0.0	64.6 0.0	0.1	0.0	0.0	0.0
Epinephelus cruentatus	190.3	50.1	2.4	0.6	14.3	47.7
Epinephelus fulvus	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	47.5	32.1	0.3	0.2	13.8	8.6
Haemulon carbonarium	211.5	150.9	0.4	0.3	4.3	5.1
Haemulon chrysargyreum	323.5	118.1	2.6	1.2	12.3	114.2
Haemulon flavolineatum	260.1	95.2	3.5	1.5	14.1	107.2
Haemulon sciurus	221.1	119.4	0.4	0.2	12.3	61.1
Hypoplectrus sp	17.8	4.7	1.0	0.3	8.1	2.9
Lutjanus apodus	359.5	82.9	0.8	0.2	19.6	45.1
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	88.2	28.1	0.6	0.2	13.0	17.6
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	265.5	134.8	0.4	0.2	9.6	6.9
Synodus intermedius	0.0	0.0	0.0	0.0	0.0	0.0
Serranus tigrinus	3.4	2.6	0.4	0.3	1.3	1.3
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	202.2	166.8	0.8	0.5	16.9	158.6
Carangidae	0.0	0.0	0.0	0.0	0.0	0.0
Haemulidae	1079.0	546.4	7.0	3.2	46.7	346.5
Labridae	170.1	111.8	0.6	0.3	5.5	4.5
Lutjanidae	713.1	245.7	1.8	0.5	42.3	69.6
Muraenidae	47.5	32.1	0.3	0.2	13.8	8.6
Serranidae	211.5	57.4	3.8	1.2	23.6	51.9
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	2488.0	1224.8	14.3	6.0	152.7	643.5

	Biomass (g per 10	0 m2)	Density (# per 1	00 m2)	Fork Len (cm)	gth
Reef Scientifico - 10 m						
(Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	62.8	62.8	0.1	0.1	3.8	58.9
Aulostomus maculatus	202.2	166.8	0.8	0.5	16.9	158.6
Bodianus rufus	170.1	111.8	0.6	0.3	5.5	4.5
Bothus lunatus	64.6	64.6	0.1	0.1	4.0	3.8
Caranx rubber	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus cruentatus	190.3	50.1	2.4	0.6	14.3	47.7
Epinephelus fulvus	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	47.5	32.1	0.3	0.2	13.8	8.6
Haemulon carbonarium	211.5	150.9	0.4	0.3	4.3	5.1
Haemulon chrysargyreum	323.5	118.1	2.6	1.2	12.3	114.2
Haemulon flavolineatum	260.1	95.2	3.5	1.5	14.1	107.2
Haemulon sciurus	221.1	119.4	0.4	0.2	12.3	61.1
Hypoplectrus sp	17.8	4.7	1.0	0.3	8.1	2.9
Lutjanus apodus	359.5	82.9	0.8	0.2	19.6	45.1
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	88.2	28.1	0.6	0.2	13.0	17.6
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	265.5	134.8	0.4	0.2	9.6	6.9
Synodus intermedius	0.0	0.0	0.0	0.0	0.0	0.0
Serranus tigrinus	3.4	2.6	0.4	0.3	1.3	1.3
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	303.1	153.3	1.1	0.5	24.3	14.4
Carangidae	964.7	350.9	0.8	0.3	25.3	270.1
Haemulidae	619.0	256.1	2.3	0.8	30.6	158.1
Labridae	119.3	98.2	0.8	0.5	5.8	4.6
Lutjanidae	7376.6	3553.3	9.8	3.2	96.6	210.5
Muraenidae	68.6	37.2	0.4	0.2	20.0	9.6
Serranidae	1101.0	170.8	7.3	1.0	31.2	113.2
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	10552.3	4619.9	22.3	6.5	233.7	780.6

	Biomass (g per 10	0 m2)	Density (# per 10	00 m2)	Fork Len	gth
Front Porch - 10 m (Sample size = 11)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomus maculatus	108.1	41.3	0.8	0.3	18.1	6.4
Bodianus rufus	126.6	81.2	0.5	0.2	6.7	3.5
Bothus lunatus	38.2	38.2	0.1	0.1	2.7	2.6
Caranx rubber	693.3	323.4	0.9	0.3	19.5	94.8
Epinephelus cruentatus	414.8	61.5	5.5	0.9	17.8	67.8
Epinephelus fulvus	4.5	4.5	0.1	0.1	3.1	3.0
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	115.6	41.1	0.5	0.2	28.2	9.7
Haemulon carbonarium	0.0	0.0	0.0	0.0	0.0	0.0
Haemulon chrysargyreum	771.4	592.0	8.6	6.3	2.4	183.5
Haemulon flavolineatum	189.0	51.8	2.8	0.9	15.4	19.7
Haemulon sciurus	690.8	206.2	0.5	0.2	23.3	88.1
Hypoplectrus sp	6.0	2.7	0.4	0.2	3.8	1.6
Lutjanus apodus	1393.2	452.3	1.5	0.3	29.1	21.0
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	377.3	153.3	4.4	2.0	10.4	21.2
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	0.0	0.0	0.0	0.0	0.0	0.0
Synodus intermedius	181.9	95.7	0.4	0.2	10.8	69.0
Serranus tigrinus	2.4	0.8	0.7	0.2	3.9	1.0
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	108.1	41.3	0.8	0.3	18.1	6.4
Carangidae	693.3	323.4	0.9	0.3	19.5	94.8
Haemulidae	1651.2	850.0	12.0	7.3	41.0	291.2
Labridae	126.6	81.2	0.5	0.2	6.7	3.5
Lutjanidae	1770.6	605.6	5.9	2.3	39.5	42.2
Muraenidae	115.6	41.1	0.5	0.2	28.2	9.7
Serranidae	427.7	69.5	6.6	1.3	28.6	73.3
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	181.9	95.7	0.4	0.2	10.8	69.0
All Predators	5113.1	2146.1	27.6	12.4	195.1	592.6

	Biomass (g per 10	0 m2)	Density (# per 10	00 m2)	Fork Ler (cm)	igth
Forest - 10 m		0.5		0.5		0.5
(Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomus maculatus	37.5	30.3	0.3	0.2	10.0	28.3
Bodianus rufus	279.2	195.7	0.5	0.3	11.8	5.6
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus cruentatus	951.5	432.5	3.8	0.8	19.9	14.0
Epinephelus fulvus	6.7	6.7	0.1	0.1	4.4	4.1
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	42.7	42.7	0.1	0.1	0.1	8.2
Haemulon carbonarium	98.8	65.1	0.3	0.2	7.3	50.7
Haemulon chrysargyreum	1049.5	988.5	9.1	8.7	8.1	938.0
Haemulon flavolineatum	32.9	22.5	0.4	0.3	4.1	19.3
Haemulon sciurus	0.0	0.0	0.0	0.0	0.0	0.0
Hypoplectrus sp	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus apodus	2388.4	1299.3	1.5	0.7	28.9	174.1
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	31.5	21.6	0.3	0.2	5.0	10.8
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	156.6	156.6	0.1	0.1	7.5	7.1
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	221.9	115.7	0.4	0.2	9.9	88.5
Synodus intermedius	0.0	0.0	0.0	0.0	0.0	0.0
Serranus tigrinus	1.1	0.7	0.3	0.2	1.8	1.1
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	37.5	30.3	0.3	0.2	10.0	28.3
Carangidae	0.0	0.0	0.0	0.0	0.0	0.0
Haemulidae	1181.2	1076.2	9.8	9.1	19.5	1007.9
Labridae	279.2	195.7	0.5	0.3	11.8	5.6
Lutjanidae	2641.8	1436.6	2.1	1.1	43.8	273.4
Muraenidae	42.7	42.7	0.1	0.1	0.1	8.2
Serranidae	959.3	439.9	4.1	1.1	26.0	19.2
Sphyraenidae	156.6	156.6	0.1	0.1	7.5	7.1
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	5298.3	3378.0	17.0	12.0	118.6	1349.8

	Biomass (g per 10	0 m2)	Density (# per 10	00 m2)	Fork Len (cm)	gth
Calabas - 10 m	Moon	CF	Maan	C.E.	Maan	CE
(Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomus maculatus	77.0	60.7	0.4	0.3	11.3	7.1
Bodianus rufus	39.4	39.4	0.3	0.2	3.8	3.3
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	644.8	408.3	0.8	0.3	12.1	7.0
Epinephelus cruentatus	196.9	59.8	2.1	0.5	13.8	3.0
Epinephelus fulvus	1.0	1.0	0.1	0.1	2.3	2.2
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	90.2	47.7	0.4	0.2	13.9	26.8
Haemulon carbonarium	8.3	8.3	0.1	0.1	2.0	1.9
Haemulon chrysargyreum	871.2	702.3	7.8	6.2	6.8	7.9
Haemulon flavolineatum	565.3	419.7	7.5	5.7	13.7	5.2
Haemulon sciurus	211.4	134.0	0.4	0.2	11.5	5.7
Hypoplectrus sp	23.9	7.8	1.0	0.3	7.3	6.9
Lutjanus apodus	1652.1	592.5	5.5	2.4	19.7	64.1
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	1586.5	1042.1	14.6	8.6	24.2	13.7
Mycteroperca tigris	36.4	24.1	0.3	0.2	3.1	3.6
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	870.8	503.9	1.6	0.8	11.8	6.0
Synodus intermedius	8.2	8.2	0.1	0.1	2.5	7.8
Serranus tigrinus	2.1	1.4	0.3	0.2	2.1	1.3
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	77.0	60.7	0.4	0.3	11.3	7.1
Carangidae	644.8	408.3	0.8	0.3	12.1	7.0
Haemulidae	1656.1	1264.2	15.8	12.1	34.0	20.7
Labridae	39.4	39.4	0.3	0.2	3.8	3.3
Lutjanidae	4109.5	2138.5	21.8	11.8	55.8	83.8
Muraenidae	90.2	47.7	0.4	0.2	13.9	26.8
Serranidae	260.3	94.1	3.8	1.2	28.6	17.0
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	8.2	8.2	0.1	0.1	2.5	7.8
All Predators	6885.4	4061.2	43.1	26.2	161.8	173.4

	Biomass (g per 10	0 m2)	Density (# per 1	00 m2)	Fork Len (cm)	gth
Eighteenth Palm - 10 m (Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	15.9	15.9	0.1	0.1	2.5	2.4
Aulostomus maculatus	39.7	29.9	0.4	0.2	12.5	6.3
Bodianus rufus	96.7	47.6	0.6	0.3	7.5	36.2
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	176.5	77.6	0.6	0.3	9.6	39.4
Epinephelus cruentatus	206.6	61.9	2.4	0.3	15.1	22.6
Epinephelus fulvus	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	0.0	0.0	0.0	0.0	0.0	0.0
Haemulon carbonarium	429.7	429.7	2.5	2.5	2.8	2.6
Haemulon chrysargyreum	0.0	0.0	0.0	0.0	0.0	0.0
Haemulon flavolineatum	192.5	30.4	2.3	0.3	14.4	17.7
Haemulon sciurus	54.5	54.5	0.1	0.1	3.8	51.0
Hypoplectrus sp	18.1	6.9	1.0	0.3	5.4	2.0
Lutjanus apodus	1172.6	575.0	2.9	0.8	19.8	80.0
Lutjanus cyanopterus	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	1083.4	752.9	13.4	8.7	7.8	4.0
Mycteroperca tigris	32.9	32.9	0.1	0.1	3.5	3.3
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	0.0	0.0	0.0	0.0	0.0	0.0
Ocyurus chrysurus	281.1	184.9	0.4	0.2	13.5	11.0
Synodus intermedius	148.7	53.6	0.9	0.3	17.0	17.7
Serranus tigrinus	1.2	0.9	0.3	0.2	0.9	1.1
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	39.7	29.9	0.4	0.2	12.5	6.3
Carangidae	176.5	77.6	0.6	0.3	9.6	39.4
Haemulidae	692.6	530.4	5.0	3.1	23.4	73.7
Labridae	96.7	47.6	0.6	0.3	7.5	36.2
Lutjanidae	2537.1	1512.9	16.6	9.7	41.1	95.0
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	258.8	102.6	3.8	0.9	24.9	29.0
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	148.7	53.6	0.9	0.3	17.0	17.7
All Predators	3950.1	2354.6	27.9	14.7	136.0	297.3

	Biomass (g per 10	0 m2)	Density (# per 10	00 m2)	Fork Len	gth
Windsock - 10 m (Sample size = 8)	Mean	SE	Mean	SE	Mean	SE
Anisotremus surinamensis	21.9	21.9	0.1	0.1	2.8	2.6
Aulostomus maculatus	89.1	36.4	0.8	0.3	20.3	8.0
Bodianus rufus	117.1	117.1	0.1	0.1	5.0	4.7
Bothus lunatus	0.0	0.0	0.0	0.0	0.0	0.0
Caranx rubber	746.9	375.4	0.9	0.4	16.1	25.8
Epinephelus cruentatus	392.7	191.4	3.4	0.5	16.1	13.7
Epinephelus fulvus	0.0	0.0	0.0	0.0	0.0	0.0
Epinephelus adscensionis	0.0	0.0	0.0	0.0	0.0	0.0
Gymnothorax sp.	18.4	18.4	0.1	0.1	6.3	5.9
Haemulon carbonarium	119.8	119.8	0.6	0.6	2.8	2.6
Haemulon chrysargyreum	1313.9	1216.5	13.8	12.4	3.3	2.0
Haemulon flavolineatum	144.7	22.3	1.9	0.4	13.9	6.5
Haemulon sciurus	492.3	180.9	0.8	0.3	21.4	6.6
Hypoplectrus sp	13.1	3.3	0.8	0.2	6.9	2.6
Lutjanus apodus	1118.7	452.4	1.9	0.3	24.8	462.3
Lutjanus cyanopterus	698.4	698.4	0.1	0.1	8.8	8.2
Lutjanus jocu	0.0	0.0	0.0	0.0	0.0	0.0
Lutjanus mahogoni	119.2	75.9	1.5	0.8	6.3	3.0
Mycteroperca tigris	0.0	0.0	0.0	0.0	0.0	0.0
Sphyraena barracuda	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosus sectatrix	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaena plumieri	29.7	29.7	0.1	0.1	3.0	2.8
Ocyurus chrysurus	349.8	229.0	0.3	0.2	12.5	163.6
Synodus intermedius	24.3	17.0	0.3	0.2	5.6	3.5
Serranus tigrinus	0.9	0.9	0.1	0.1	1.0	0.9
Pterois volitans	0.0	0.0	0.0	0.0	0.0	0.0
Scomberomorous regalis	264.7	264.7	0.1	0.1	8.8	8.2
Aulostomidae	89.1	36.4	0.8	0.3	20.3	8.0
Carangidae	746.9	375.4	0.9	0.4	16.1	25.8
Haemulidae	2092.7	1561.5	17.1	13.7	44.1	20.4
Labridae	117.1	117.1	0.1	0.1	5.0	4.7
Lutjanidae	2286.1	1455.8	3.8	1.4	52.3	637.1
Muraenidae	18.4	18.4	0.1	0.1	6.3	5.9
Serranidae	406.7	195.5	4.3	0.8	23.9	17.2
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	24.3	17.0	0.3	0.2	5.6	3.5
All Predators	6075.8	4071.6	27.5	17.2	185.2	733.8