

Status and Trends of Bonaire's Reefs in 2013: *Causes for Optimism*

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Executive Summary:

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Overview and conclusions

During November 2010, 10% of Bonaire’s reef corals bleached and died due to unusually warm sea temperatures. This event, along with an 8 to 10 year decline in herbivorous parrotfishes resulted in a sharp increase in reef-damaging seaweed (also called “macroalgae”) in 2011. The danger of seaweeds to coral reefs is well known. The role of grazing parrotfish is also well established, and Bonaire had been one of the most-grazed and least seaweed overgrown coral reef systems in the Caribbean (e.g., Kramer 2003). However, over the past decade the warning signs had been increasing and they had been announced in previous reports to STINAPA with subtitles such as “*Need for Action*” and “*Cause for Grave Concerns*” (Steneck et al 2009, 2011, respectively). STINAPA and Bonaire’s Marine National Park acted by establishing Fish Protection Areas (2008), and by banning the harvest of parrotfish and phasing out fish traps (2010). Possibly as a direct result of these measures, this report has a starkly different subtitle “*Causes for Optimism*”. Here we document evidence of some reversals of the troubling signs reported previously.

This, the sixth “Bonaire Report” prepared for STINAPA, covers the past 14 years of monitoring of specific and strategic reef sites (Table 1; All reports are available on the STINAPA website; <http://www.bmp.org/publications.html>). We focus on the specific components of coral reefs determined to best aid managers (Steneck and McClanahan 2005). Our monitoring philosophy is to follow *trends* in key metrics such as the abundance of coral and important algal groups including harmful macroalgae (seaweed) and favorable pink encrusting algae called “crustose coralline algae” (Chapter 1). Herbivory from parrotfishes, their bite rates and the abundance of sea urchins (Chapters 2 – 5) have also been shown to be important to the health of coral reefs. We include a chapter on damselfish (Chapter 6) because they can reduce the positive effects of grazing fishes, but they themselves may be limited by carnivorous reef fishes (Chapter 7).

Table 1. Reef monitoring sites listed north (top) to south (bottom). Six long-term monitoring sites were established in 2003. Four additional sites were added in 2009 following the establishment of the Fish Protection Areas (FPAs). Sites designated as “FPA” are within the protected area and controls are outside the FPAs. The “No-Dive Reserve” site monitors post-bleaching impacts (from Auscavitch and DeBey 2013; Chapter 7).

Site Name	Site Designation	Survey Years					
		2003	2005	2007	2009	2011	2013
No-Dive Reserve	Control					✓	✓
Karpata	Control	✓	✓	✓	✓	✓	✓
Oil Slick	Control				✓	✓	✓
Barcadera	Control	✓	✓	✓	✓	✓	✓
Reef Scientifico	FPA	✓	✓	✓	✓	✓	✓
Front Porch	FPA				✓	✓	✓
Forest	Control	✓	✓	✓	✓	✓	✓
Calabas	FPA				✓	✓	✓
Eighteenth Palm	FPA	✓	✓	✓	✓	✓	✓
Windsock	Control	✓	✓	✓	✓	✓	✓
Bachelor’s Beach	Control				✓	✓	✓

Trends in corals and seaweed

Coral cover had been remarkably stable until the 2010 coral bleaching event (Fig. 1A). However, following the sharp decline in coral abundance in 2011, coral cover has increased slightly at the long-term monitoring sites. Seaweed (or “macroalgae”) had been increasing slightly since 1999 until the bleaching event when it spiked to record high abundance (Fig. 1B). However, following that spike, macroalgae declined significantly by the 2013 monitoring and beneficial crustose coralline algae increased slightly (Figs. 1B, C) (see Steneck 2013; Chapter 1).

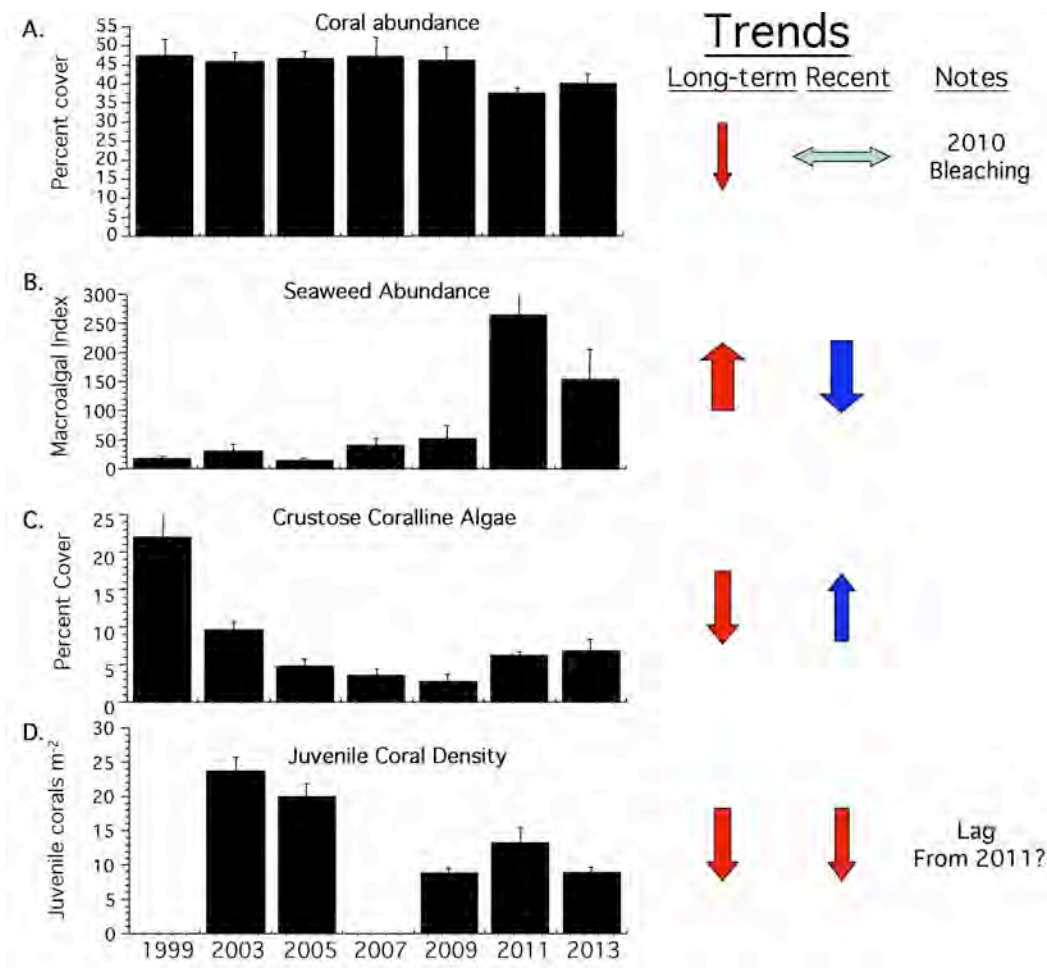


Fig. 1. Trends in coral, seaweed, crustose coralline algae and juvenile coral densities (A-D). Long-term trends and recent trends since 2011 shown as arrows with increases pointing up and width suggesting demographic importance. Despite algae declining, we observed a decline in juvenile corals, likely representing a lag in recruitment in 2011 due to the 2010 bleaching event. Vertical lines show variance as standard error.

Juvenile coral densities declined relative both over the long term (since 2003) and recently (since 2011; Fig. 1D; Manning and Protopopescu 2013 Chapter 8), however, corals less than 40 mm in diameter can be 1 – 4 years old so if the 2011 algal bloom significantly reduced the recruitment of corals in 2011, the demographic effect would not be evident until this survey. Likewise, the

upturn from 2009 to 2011 likely did not reflect the high algal abundance recorded in 2011.

Trends in herbivores and carnivores

Parrotfish population densities and biomass increased after 2011 (Fig. 2 A-B; Stamieszkin and Arnold 2013; Chapter 2). There had been escalating fishing on parrotfishes in recent years which may have contributed to the decline from 1999 to 2007 (Nenadocic 2007) however, this leveled off and the upturn could be the result of the new laws banning the harvest of parrotfish and the phasing out of fish traps.

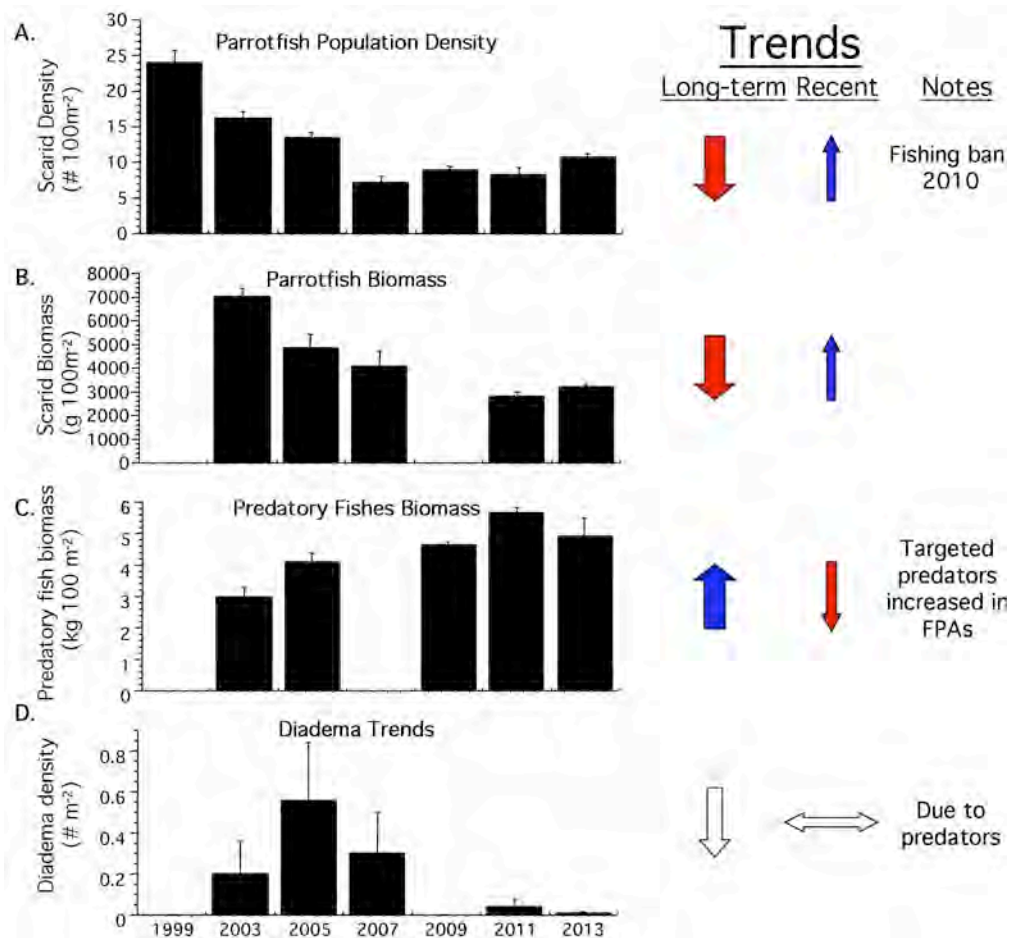


Fig. 2. Trends in parrotfish population density, parrotfish biomass, predatory fishes biomass and *Diadema* abundance. Variance as in Fig. 1.

Predatory fishes continue to trend upward across all sites (Fig 2C; Auscavitch and Debey 2013; Chapter 7). The recent slight decline in the biomass of predatory fishes may result from fishing pressure in all but the FPA sites. Note that four of the six monitored sites are fished (i.e., “control” sites; Table 1).

After parrotfishes, the most important herbivore on Caribbean coral reefs is the sea urchin, *Diadema antillarum* (Hughes 1994, Edmunds and Carpenter 2003). This urchin is rare on Bonaire’s reefs in both deep and shallow water (Kersula 2013, Chase and Wurtzell 2013; Chapters 4, 5). Although this species underwent a massive decline in 1983 due to disease, it has returned apparently disease free to functional densities at several overfished locations such as Jamaica. The fact that *Diadema* and most sea urchins cannot withstand heavy predation may explain its rarity in Bonaire. Specifically, *Diadema* abundance in Bonaire at both 10 m deep and shallower zones peaked in 2005 and 2007, respectively (Fig. 2D) but have declined ever since. Most of Bonaire’s predatory fishes feed on invertebrates (Auscavitch and DeBey 2013), including sea urchins. Thus, the steady rise in predators (Fig. 2C) could be causing the declining abundance of *Diadema antillarum* (e.g., 2D).

Damselfishes continue to increase at monitored sites (Fig. 3; Oppenheim 2013; Chapter 6). It is possible this is the result of relaxed predation pressure from specific fish-eating predators of damselfishes. Damselfishes are most susceptible to relatively small, ambush fish-eating “mesopredators” such as graysbys, coneys and hinds (Almany 2007, Mumby et al 2011; Auscavitch and DeBey 2013; Chapter 7).

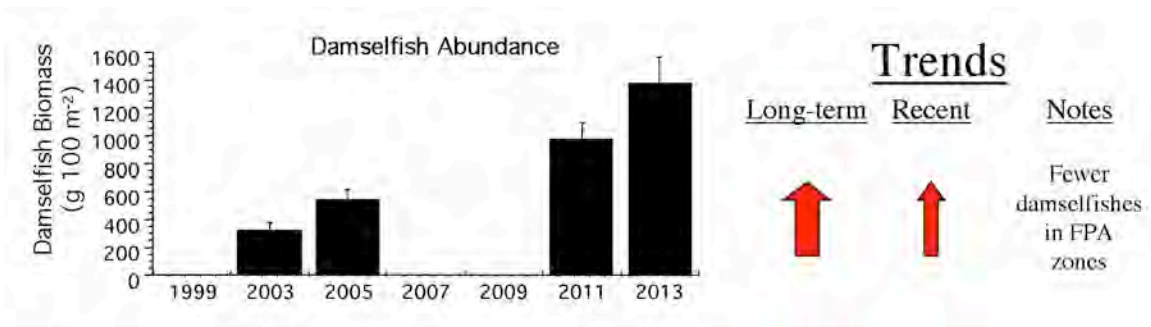


Fig. 3. Trends parrotfish population density of territorial damselfishes.

Mesopredator serranids (graysbys, coneys and hinds) are the three reef-dwelling predators most fished on the reefs of Bonaire (Nenadovic, M. 2007). This is because the primary method of fishing on coral reefs in Bonaire is hook and line rather than spear-fishing or trap-fishing. These three fishes show the greatest FPA and control difference on Bonaire’s reefs (Fig. 4; Auscavitch and DeBey 2013; Chapter 7).

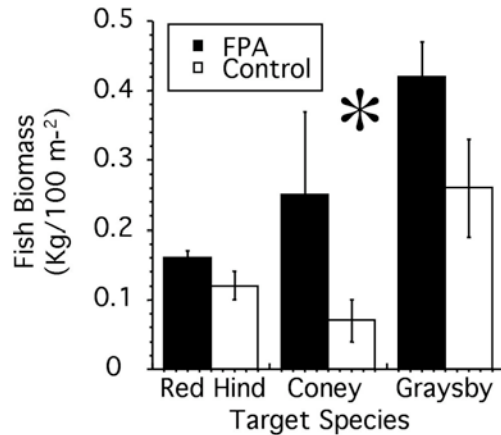


Fig. 4. Population densities in 2013 of the three targeted mesocarnivores on Bonaire’s fished (“control”) and unfished (“FPA”) reefs. Astrisk indicates significant difference at $P < 0.05$ T-test.

The population density and biomass of damselfish are inversely correlated with the biomass of the three targeted mesopredators (Fig. 5). Note that the highest biomass of targeted serranids (ie species in Fig. 4) was found in FPAs while the lowest serranid biomass was at control sites (Fig. 5).

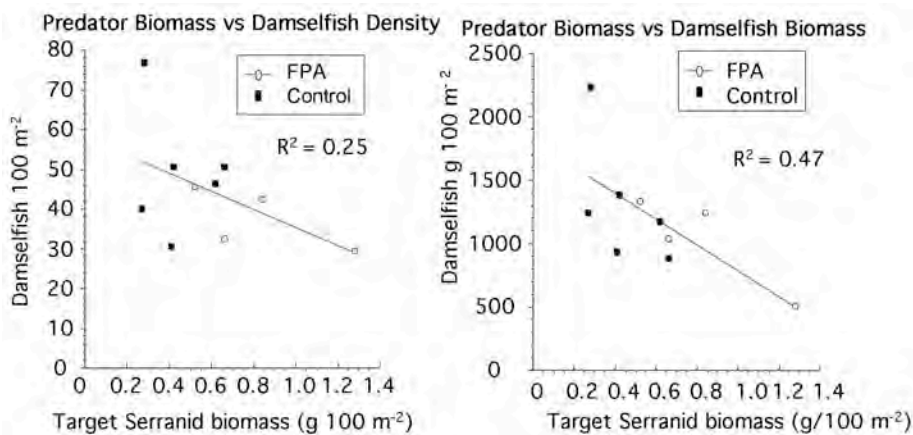


Fig. 5. Damselfish population density (left) and biomass (right) as a function of the biomass of sea bass predators that are both targeted and known to be important predators on damselfishes (i.e., Fig. 4; see text).

Managing for Function in Coral Reef Food Webs

Overfishing, especially as it relates to herbivores, is considered one of the key factors controlling the health of coral reef ecosystems (Bellwood et al 2004). Over the past few decades, we have come to understand the ecological role of grazing parrotfish (especially large parrotfish) in limiting the abundance of harmful seaweed (eg Mumby 2006). Parrotfishes also crop the fine fuzz called “turf algae” to a low canopy which, along with beneficial coralline algae, facilitate

the establishment of baby corals on reefs (Fig. 6; Arnold et al 2010).

Only in recent years have we come to understand the role top predators and “mesocarnivores” on Caribbean coral reefs. Large, fish-eating carnivores, such as groupers, feed on and control the abundance of mesocarnivores such as hinds, coney and graysby which in turn feed on and reduce the effectiveness of grazing parrotfishes (Mumby et al 2011; Fig 6). While most Caribbean coral reefs were thought to have been dominated by large predatory finfish and large herbivores prior to human impacts (Wing and Wing 2001, Mumby et al 2006), fishing relatively quickly reduces both the abundance and body size of those fishes (Fig. 6). Belize has lost both its large carnivorous and herbivorous fishes resulting in increases in formerly prey species of mesocarnivores (i.e., hinds, coney and graysby) and macroalgae (Fig. 6; Mumby et al 2011).

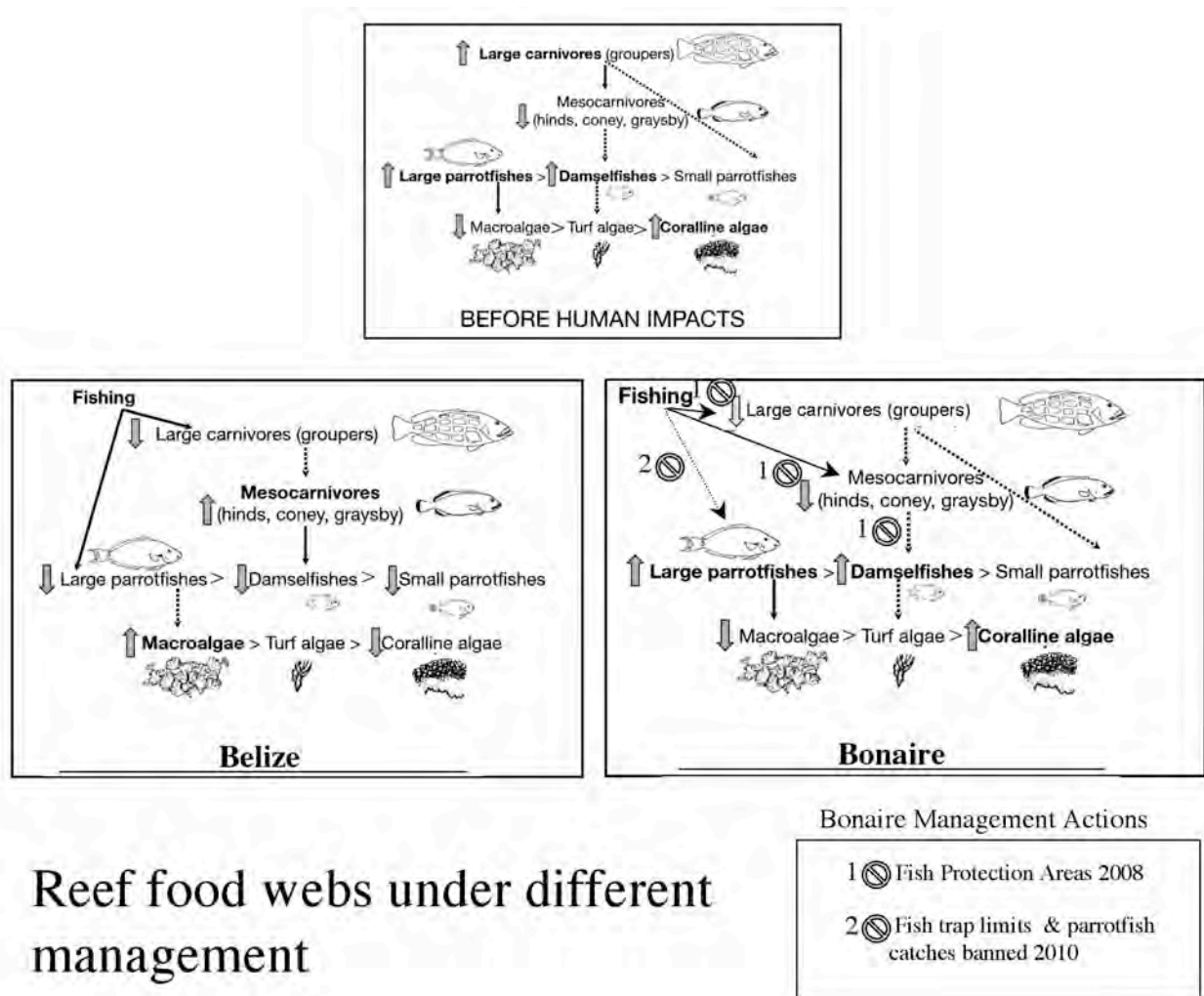


Fig. 6. Synthesis of fishing impacts on reef foodweb structure and function. **Boldface** species dominate foodweb structure. Gray arrows: abundance trends. Black arrows: strong ecological interactors. Dotted arrows: weak or nonexistent ecological interactors. Within a trophic level competitive interactions illustrate competitive dominant groups on left with subordinate species on the right (After Mumby et al 2011).

In Bonaire, where fish eating carnivores were fished but not algae eating parrotfish, the foodweb structure differs significantly from that in Belize (Fig. 6). Specifically, when Bonaire’s reefs

were assessed in 1999 they had among the lowest algal biomass and greatest herbivore biomass found in the Caribbean (Kramer 2003; Fig. 1B and C). While this was still evident in our assessment in 2003, it was clear as assessments continued that herbivore abundance was declining and that macroalgae and damselfishes were gradually increasing over nearly a decade through the period of our 2007 and 2009 assessments (Figs. 1-3).

In the context of these trends termed “troubling” (Steneck et al 2009), the 2010 coral bleaching event occurred resulting in the largest increase in harmful algae ever recorded in Bonaire (Fig. 1B). Because shifts to macroalgae can create “alternative stable states” that lock reefs into a coral-free state for a long time (Mumby 2009), the sudden shift in Bonaire was described in a report to the Bonaire National Marine Park as a “cause for grave concern”.

In considering the trends and changes in food webs, Figs 1 – 6 relate to the health of Bonaire’s reefs and ultimately to its management. We applied the trend scheme advanced by Steneck and McClanahan 2005 to the recent trends seen since the crisis observed in 2011 (Fig. 7).

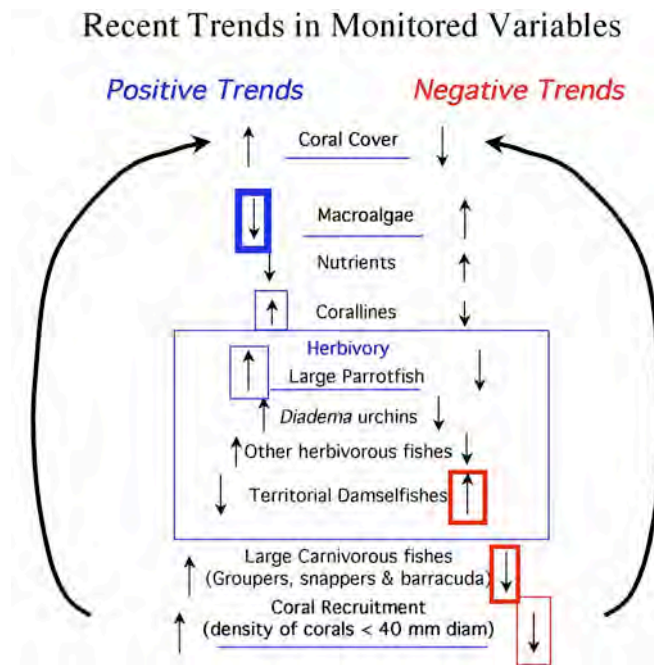


Fig. 7. Monitoring scheme suggested by Steneck and McClanahan 2005. The key factors are underlined. All aspects related to herbivory are within the large blue box. The positive trends are on the left side in blue and the negative trends are on the right side in red. Note that recent trends from Fig 1 and 2 include more positive trends than has been reported in the past two reports (2009 and 2011).

Considering the recent trends, we see significant causes for optimism for Bonaire’s coral reefs. For the first time since monitoring began, we see the addition of at least three positive trends (Fig 7). Chief among these is the strong decline in macroalgae and the weak increase in coralline algae, both of which could be the result of increases in herbivory (Rasher and Stamieszkin 2013, Chapter 3). Overall, Bonaire’s coral reefs today are doing better than they were in 2011. Given how rarely positive trends have ever been detected in Caribbean coral reefs (Connell 1997, Mumby 2009), these trends are promising and a real cause for optimism.

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Chapter 1: Patterns and trends in abundance of corals and seaweeds at monitored sites in Fish Protection Areas and control sites

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Abstract

Surveys of abundance of stony coral, seaweed (called “macroalgae”) and crustose coralline algae were conducted at 11 sites (total of 44 transects 10m each). Overall coral cover remains relatively high (36.2 % \pm 1.9 SE) and macroalgae relatively low (14.7% \pm 1.2 SE). The 2010 bleaching event caused coral cover to decline and macroalgae to increase. Since the 2011 survey coral cover and CCA have increased slightly and macroalgae have declined significantly. The dominant corals remain several species of *Montastraea*, followed by *Agaricia* and *Porites*. Those three genera comprise 80% of the coral space occupiers in Bonaire.

Introduction

Without stony corals there would be no coral reefs. Bonaire has been unique throughout the Caribbean because it has maintained live coral cover close to that found throughout the Caribbean in the 1970s (Gardner et al 2003). In many cases the loss of stony coral was replaced with seaweed (called “macroalgae”) that is harmful to both adult (Lirman 2001) baby coral (i.e., recently settled coral spat).

When the first standardized Caribbean-wide survey was conducted (Atlantic and Gulf Reef Rapid Assessment or “AGRRA”) Bonaire was found to have relatively high coral cover and low abundance of seaweed (macroalgae) (Kramer 2003). Since then, in a series surveys conducted on Bonaire’s reefs every other year since 2003, macroalgae increased slight but spiked to a record high in 2011 (Steneck et al 2011). Coral cover had been relatively stable until the 2010 bleaching event when 10% of the coral died.

This report is the next in this series of standardized surveys most conducted on permanent transects to assess patterns in the distribution and abundance of stony coral, macroalgae and crustose coralline algae in both space (along Bonaire’s coral reefs) and in time (since 1999).

Methods

The distribution and abundance of major reef-occupying groups such as stony coral, macroalgae and encrusting coralline algae (abbreviated CCA) were quantified along replicate 10 m line transects (methods of Benayahu and Loya 1977; Kramer 2003) at 10 m depth at each of our 11 study sites (listed in Fig. 2). Algae were subdivided into functionally important groups (see Steneck and Dethier 1994) such as crustose coralline, articulated coralline, foliaceous macroalgae (or simply “macroalgae”) and non-coralline crusts. All are listed in the appendix but only data for the more abundant groups of corals, macroalgae and crustose coralline algae.

At each of the 11 sites surveyed, four 10m long transects were quantified. All categories of information quantified among the 44 transects are in Appendix 1.

Data are presented for the Fish Protection Areas (FPAs) that were established in 2008 in which fishing is not allowed relative to control sites where fishing is allowed. Of the sites monitored since 2003, two are FPA sites (Eighteenth Palm, Reef Scientifico) and 4 (Windsock, Barcadera, Forest and Karpata) are control sites. Whereas only long-term monitoring sites were used in discussing trends (i.e., see Executive Summary), all 11 study sites were analyzed in this chapter.

Temporal trends among long-term monitoring sites were determined from repeated measures from fixed transects. Transect locations were marked with ceramic plates installed in 2003.

Results

Today, most Caribbean “coral reefs” are dominated by seaweed (or macroalgae) but Bonaire is an exception (Fig. 1). Despite the Caribbean-wide loss of elkhorn and staghorn corals (corals of the genus *Acropora*), Bonaire has generally maintained a high coral cover at our survey depth of 10 m.

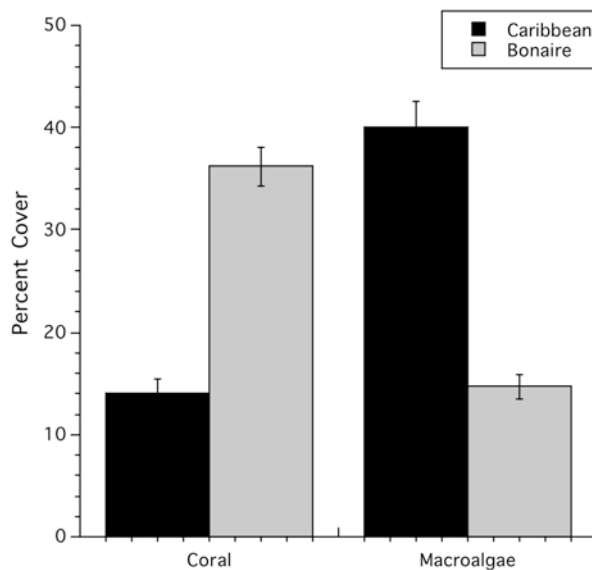


Fig. 1. Abundance of live coral and macroalgae for the entire Caribbean (Hughes et al 2010) and Bonaire (all reefs 2013, this report).

Although mean coral cover remained relatively high, some sites such as Forest on Klein Bonaire and Reef Scientifico were higher than average while Front Porch and Barcadera had lower than average coral cover (Fig. 2).

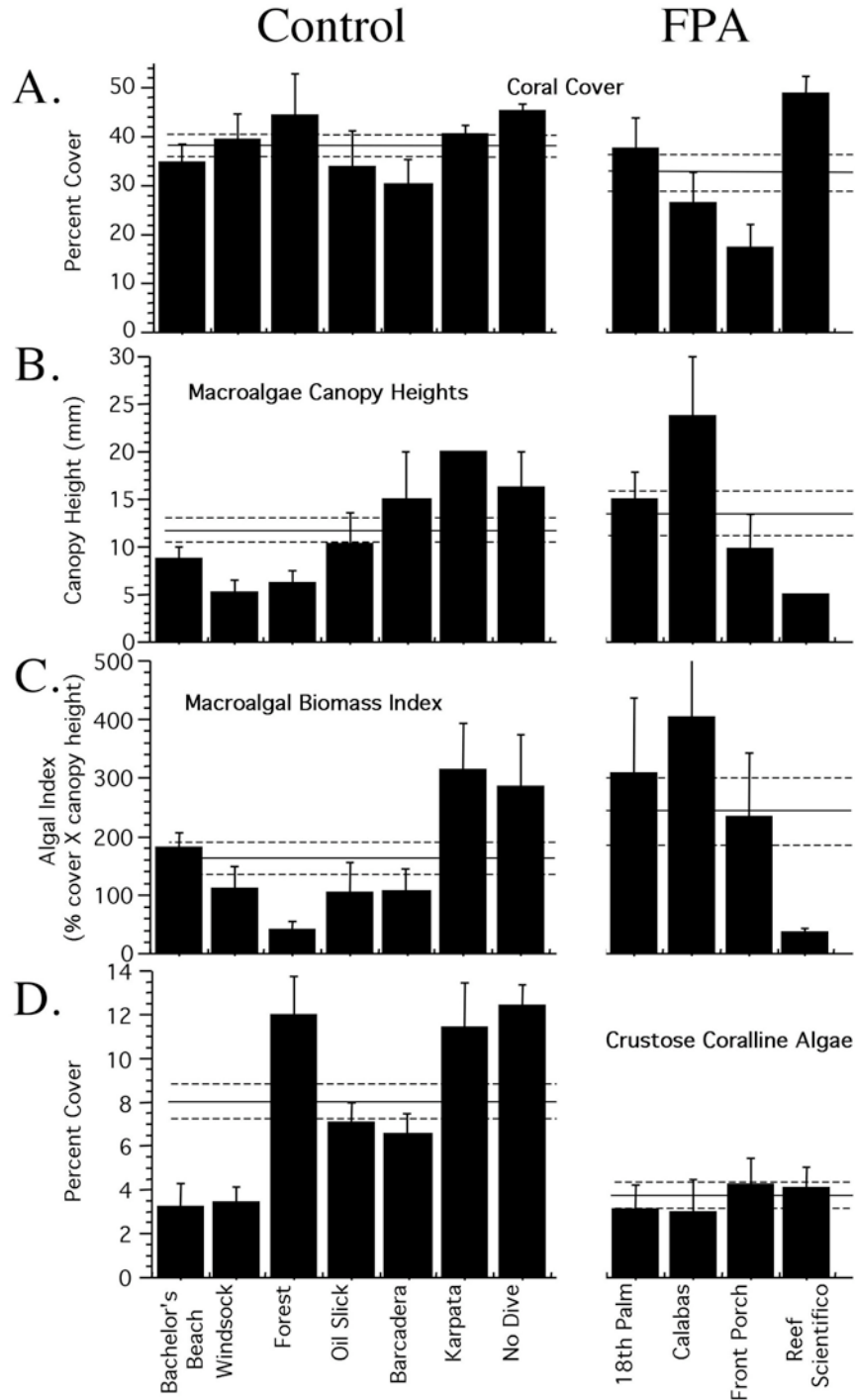


Fig. 2. Abundance of coral (A), macroalgal canopy heights (B), macroalgal biomass index (C) and crustose coralline algae (D) at control and FPA sites. Variance SE.

Coral cover was slightly higher among control sites relative to the FPA sites (Fig. 2A). Macroalgae showed the reverse pattern with slightly taller canopy heights (Fig. 2B) and algal abundance (Fig. 2C; represented as a macroalgal index or volume of algae).

Algal biomass (eg g m⁻²) is the best metric for representing algal abundance. Percent cover is least desirable since it may simply reflect coral mortality creating more space (thus increasing algal percent cover), without necessarily indicating a real increase in abundance. Collecting and laboratory facilities necessary to quantify algal biomass were lacking in Bonaire. The height of algal canopies is independent of percent cover and thus is a good metric to report (eg Fig. 2C). Interestingly, the algal index proxy for algal biomass corresponds more closely to variations in canopy heights (R² = 0.72) than in macroalgal percent cover (R² = 0.41).

Crustose coralline algae was much more abundant at control than FPA sites (Fig. 2D). Curiously, control sites having higher than average coral cover also had higher than average CCA abundance. However, that pattern did not hold among FPA site.

Coral species of *Montastrea annularis*, *M. faveolata*, *Agaricia agaricites* and *M. cavernosa* dominate Bonaire's coral reefs (Fig. 3).

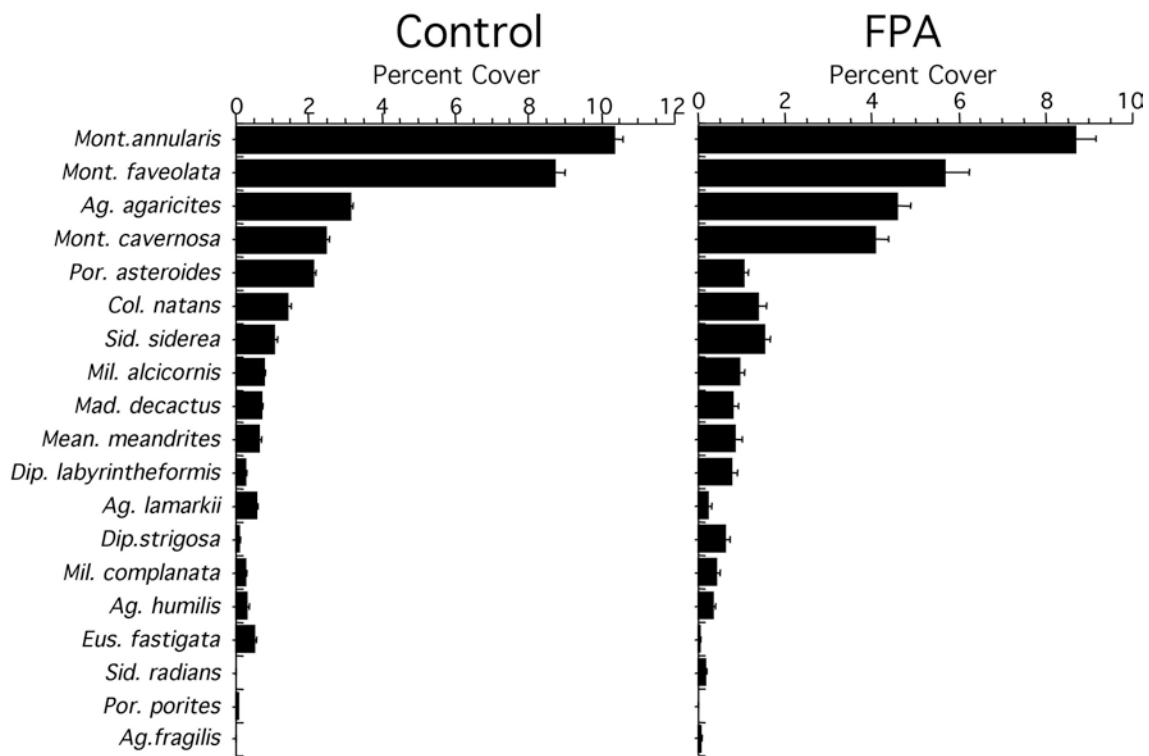


Fig. 3. Average percent cover of coral species from the seven control and four FPA sites listed in Fig. 2.

The dominant genus in Bonaire was *Montastraea* totaling nearly 20% cover. Second most abundant genus was *Agaricia* (14 % followed by *Porities* (nearly 5%). Those three genera accounted for nearly 80% of the coral cover (i.e., 79.8% of all coral cover).

Temporal trends since 1999 reveal several important changes. Coral cover has remained well above 40% cover from 1999 through 2009. Then coral bleaching in November of 2010 resulted in a 10% loss of coral cover which has since recovered slightly (Fig. 4A).

Macroalgae had been increasing slowly through 2009 suddenly increased in abundance following the 2010 bleaching event. The abundance of macroalgae has since declined (Fig. 4B).

Crustose coralline algae was over 20% cover in 1999 but declined for a decade to its low abundance in 2009 (Fig. 4C). It has been increasing slightly ever since.

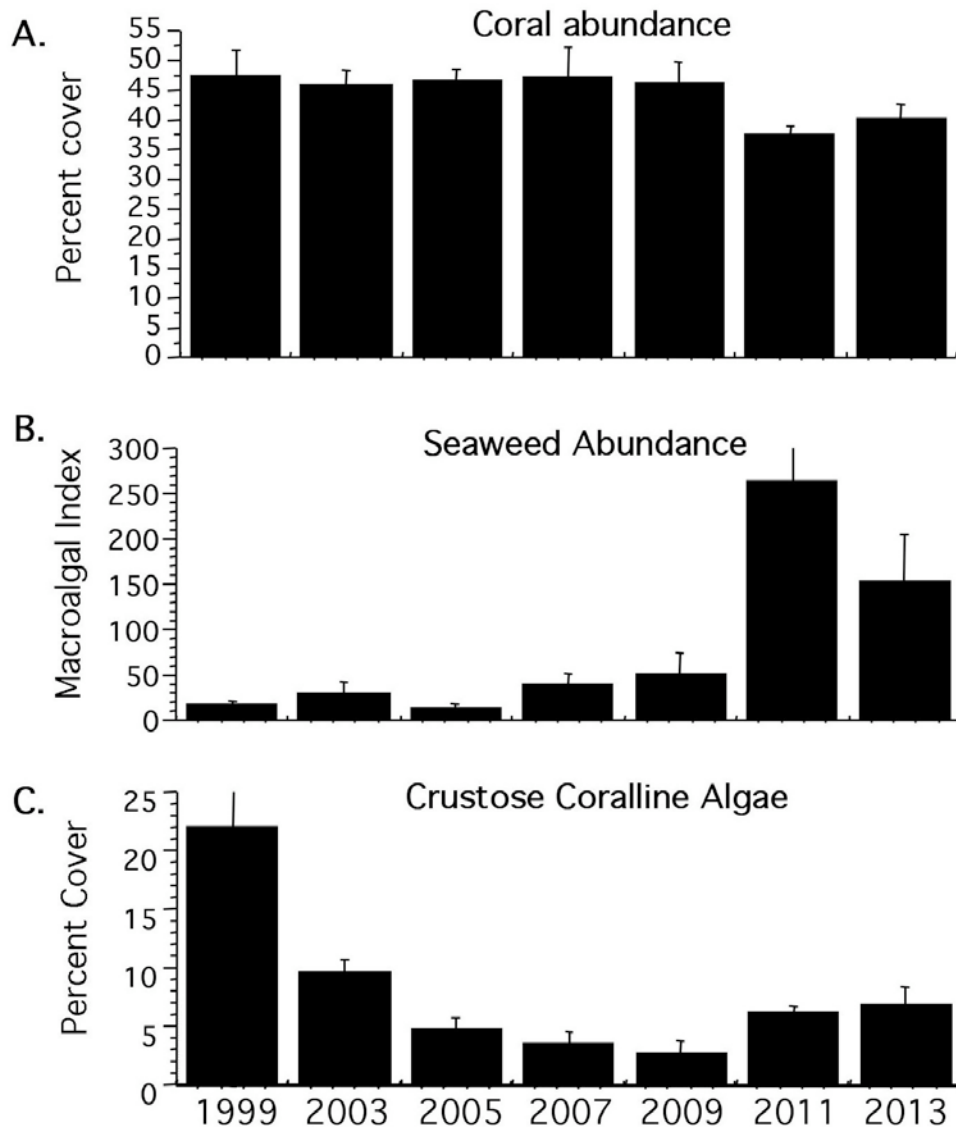


Fig. 4. Temporal trends in coral, seaweed and crustose coralline algal abundance. These data apply to the monitoring sites that have fixed permanent transects.

Discussion:

Coral cover not only remained relatively high (Fig. 1) relative to the rest of the Caribbean, it has shown signs of recovery following the bleaching event of 2010. This, along with the increase in CCA and the decline in macroalgae since the 2011 assessment (Fig. 4), suggests that Bonaire’s reefs are relatively resilient.

This is unusual for the Caribbean where reefs have most often been characterized as being incapable of recovery from disturbances (Connell 1997). The relatively low abundance of algae (Fig. 1) may contribute to the relative health of this reef system. Macroalgae can abrade and out-compete adult corals (Lirman 2001) and reduce coral recruitment (Kuffner et al 2006, Mumby et al 2007).

It is important to note that the change in slope among two of the three groups monitored is modest and awaits confirmation in 2015.

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Chapter 2: Trends in Bonaire's herbivorous fish: change over time, management effects and spatial patterns

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Abstract

Herbivorous fishes, most notably scarids (parrotfishes), help maintain coral reef health by denuding reef substrates of algae. Bonaire's parrotfish biomass has declined since monitoring began in 2003. However, we found that parrotfish density is, on average, increasing. Management banning fishing at Fish Protection Area sites had no effect on herbivorous fish density or biomass. Similarities in parrotfish populations at reserve and fished sites, and the increase in parrotfish density in recent years, is likely attributable to the 2010 system-wide ban on parrotfish harvest. We found a latitudinal trend in herbivorous fish density, with highest densities in the south, regardless of management measures in place. This may be due to abundant nursery habitat in the south, or a gradient in herbivore habitat quality. Protection of nursery habitat is important to the health of Bonaire's reef fish populations. Continued enforcement of the ban on parrotfish harvest should increase reef resilience against a phase shift from coral to algal dominance.

Introduction

Herbivorous fish, particularly scarids (parrotfish), are essential to coral reef ecosystem health (Steneck 1988; Hughes et al. 2007; Elmhirst et al. 2009). They help maintain coral, rather than algal dominance on reefs by removing and consuming algal biomass from hard substrates (Williams & Polunin 2001; Hughes et al. 2007). This grazing maintains algae-free substrate, allowing existing corals to grow (Lewis 1986; Tanner 1995), recruitment of new corals (McCook et al. 2001; Birrell et al. 2005; Arnold et al. 2010), and reduction in algal-induced chemical interference with coral health (Rasher & Hay 2010). Excess terrestrial runoff and anthropogenic nutrients are suggested causes of increased algal growth on coral reefs (Lapointe 1997; Littler et al. 2006); however, herbivory appears to be a dominant mechanism inhibiting algal propagation (Burkepile & Hay 2006; Rasher et al. 2012). Thus, maintaining robust herbivorous fish populations is critical to maintaining coral cover on reefs.

Over the last four decades, most of the Caribbean's coral reefs have undergone a dramatic phase shift from a coral-dominated to algal-dominated state (Done 1992; Hughes et al. 2010; Roff & Mumby 2012). Numerous studies implicate several biological changes as major contributors to the phase shift, including: the mass die-off of the reef building corals *Acropora palmata* and *A. cervicornis* due to white band disease by the end of the 1980's (Bythell & Sheppard 1993), the mass die-off of the grazing sea urchin *Diadema antillarum* in 1983-1984 (Lessios 1998), and chronic over-fishing (Hughes 1994). The fringing reef system that surrounds the island of Bonaire, Netherland Antilles, however, has remained resistant to a large-scale phase shift, despite the loss of both Acroporids and *D. antillarum*.

A history of strong marine conservation laws and relatively light fishing pressure on herbivorous fishes likely contributes to the resilience exhibited by Bonaire’s coral reefs, compared with other reefs in the Caribbean. The Bonaire government banned spearfishing for a five-year period in 1971, banning the practice permanently later that decade. Also, trap fishing, a method that indiscriminately catches parrotfish (Hawkins and Roberts 2004), has not been traditionally practiced in Bonaire. Today, Bonaire’s strong conservation ethic continues, encouraged by large revenue from tourism focused on SCUBA diving and snorkeling. In January 2008, STINAPA established the first two no-take “Fish Protected Areas” (STINAPA, 2010), and banned the harvest of parrotfish in 2010. Trap use is now tightly regulated by STINAPA, with the intent to phase it out. Despite these actions, Bonaire’s parrotfish populations declined between 2003 and 2011 (Arnold, 2011, p. 55).

We address the following questions in this study: 1) are Bonaire’s parrotfish populations recovering; 2) what are the effects of different management schemes on herbivorous fish density, biomass and individual size; 3) are there spatial trends in herbivorous fish independent of management?

Methods

Field data collection

We conducted visual surveys of herbivorous fish during March of 2013, at 11 dive sites along the western shore of Bonaire, Netherland Antilles (Table 1a). Five of these sites have been monitored every other year since 2003 (Table 1b). Four of the sites were Fish Protected Areas (FPAs) where no fishing, but SCUBA diving is allowed; six were control sites where fishing and SCUBA diving are allowed; and one was a no dive site, where SCUBA diving is not allowed by the public, but fishing is allowed (Table 1a). We surveyed the FPA site Front Porch twice: at 10:00 on 03 March 2013, and at 15:00 on 05 March 2013. These duplicate surveys were completed to test for time-of-day effects on survey results.

Table 1a Control and Fish Protected Areas surveyed in 2013 (1a; left), and areas monitored since 2003 (1b; right)

Control	Fish Protected Area	No Area	Dive
Bachelor's Beach	18th Palm	No	dive
Windsock	Calabas	reserve	
Forest (Klein Bonaire)	Front Porch*		
Barcadera	Reef		
Oil Slick	Scientifico		
Karpata			

Bonaire Dive sites surveyed 2003-2013		
Control	Fish Protected Area	Protected
Forest (Klein Bonaire)	18 th Palm	
Barcadera	Reef Scientifico	
Karpata		
Windsock		

* Surveyed twice; at 10:00 and 15:00 on different days

We completed eight to ten 30 x 4 m (120 m²) underwater visual belt transects at each dive site at 10 m depth. A 30 m reel was released while swimming and the observer swam at a rate that allowed eight transects per hour. This is a commonly used method for surveying reef fish (Samoilys & Carlos 2000). We recorded the number and total length (to nearest centimeter) of all scarids (parrotfishes), acanthurids (surgeonfish, doctorfish, tangs) and *Microspathodon chrysurus* (yellowtail damselfish). We estimated length by eye, and calibrated our estimates throughout the surveys with 20 cm rulers, maximizing consistency among these data. We also recorded the life history stage (juvenile, initial, terminal) of all parrotfish.

Data analysis

We calculated the biomass of each observed fish using species-specific allometric conversions of length (Bohnsack & Harper 1998). All density and biomass data were normalized to 100 m².

The scarid biomass trend between 2003 and 2013 was analyzed excluding data from the “No Dive Reserve” site. This site was managed differently from all other survey sites and has not been surveyed consistently in past years. Therefore, it was not included.

We compared average density and biomass of scarids, acanthurids, and total herbivores (including scarids, acanthurids and *M. chrysurus*) at each survey site to evaluate the effects of different management schemes. We also compared effects of each management scheme on juvenile, initial and terminal phase scarid density and length. We included all three phases in the analysis of density because fishing management could have indirect effects on juveniles, and direct effects on initial and terminals. We excluded juveniles from the analysis of management effects on length because fishing activities should not affect juvenile fish size. When FPA and control sites were compared, the “No Dive Reserve” site was treated separately to show differences between the three management schemes. We used 2-sided t-tests in Matlab®, with 95% confidence, to determine whether differences in fish populations among management schemes were significant.

We analyzed the average herbivorous fish density and biomass at each site for latitudinal trends (from south to north), regardless of management scheme. We conducted a linear regression and calculated p-values using the “regstats” function in Matlab®. In order to examine significance of differences between surveys conducted at Front Porch in morning and afternoon, we conducted a 2-sided t-test in Matlab®, with 95% confidence.

Results

Trends in Bonaire’s scarids (parrotfishes)

Averaged over all sites, parrotfish density increased at a higher rate from 2011 to 2013 compared with 2007 to 2011 (Fig. 1a). Average parrotfish biomass continued to decline slightly from 2011, but the rate of decrease leveled off since the precipitous decline from 2003 to 2007 (Fig. 1b).

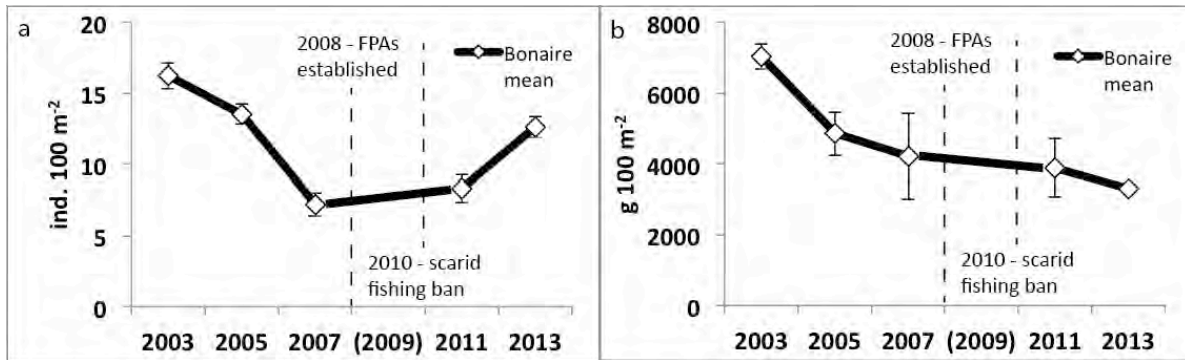


Figure 1. a) Average scarid density at all sites from 2003-2013; b) Average scarid biomass at all sites from 2003-2013; critical management dates shown in both; error bars in both indicate ± 1 standard error; 2009 excluded due to incomparable data.

The effects of different management schemes on herbivorous fish

Parrotfish density varied slightly among control, FPA and no dive sites, with control and FPA average densities nearly equal (Fig. 2a). The highest parrotfish density was found at the FPA site Calabas (13.7 ± 1.5 individuals 100 m^{-2}), and the lowest at FPA site Front Porch on 03 March, at 10:00 (7.9 ± 1.0 individuals 100 m^{-2}). Parrotfish biomass did not vary greatly among sites, especially control sites (Fig. 2b). Highest parrotfish biomass was estimated at FPA site Front Porch on 05 March, at 15:00 ($4070 \pm 397 \text{ g } 100 \text{ m}^{-2}$), while the lowest biomass was estimated at the No Dive Reserve ($1776 \pm 197 \text{ g } 100 \text{ m}^{-2}$). We found fairly consistent acanthurid density and biomass across all sites and management schemes, with the exception of the extreme maximum and minimum. Acanthurid density (Fig. 3a) and biomass (Fig. 3b) were highest at the control site Bachelor's Beach (7.2 ± 4.0 individuals 100 m^{-2} and $1479 \pm 994 \text{ g } 100 \text{ m}^{-2}$, respectively). An *Acanthurus coeruleus*-dominated school encountered on Transect 3 resulted in these anomalously high values. The high standard errors associated with these data resulted from the patchy distribution of acanthurids due to their schooling behavior. We found the lowest acanthurid density and biomass at FPA site Front Porch, surveyed on 03 March at 10:00 (0.3 ± 0.2 individuals 100 m^{-2} and $64 \pm 32 \text{ g } 100 \text{ m}^{-2}$, respectively). Total herbivorous fish density (Fig. 4a) and biomass (Fig. 4b) were somewhat variable among sites. Herbivorous fish density and biomass were highest at control site Bachelor's Beach (17.8 ± 3.9 individuals 100 m^{-2} and $4605 \pm 982 \text{ g } 100 \text{ m}^{-2}$, respectively). We found the lowest density at FPA site Front Porch, surveyed on 03 March at 10:00 (8.2 ± 1.0 individuals 100 m^{-2}), and lowest biomass at the No Dive Reserve site ($2032 \pm 217 \text{ g } 100 \text{ m}^{-2}$). Scarids made up the majority of herbivorous fish at all sites, both by density and biomass. *M. chrysurus* was present primarily at control sites (max: 0.8 ± 0.1 individuals m^{-2} ; min: 0.3 ± 0.1 individuals m^{-2}), and present at very low densities at FPA sites and No Dive Reserve (max: 0.2 ± 0.1 individuals m^{-2} ; min: 0.0 ± 0.0 individuals m^{-2}). The majority of herbivorous fish surveyed were scarids. On average, they represented 85% ($\pm 3\%$) by density, and 91% by biomass ($\pm 2\%$). Acanthurids were 12% ($\pm 3\%$) of herbivore, and 9% ($\pm 2\%$) of biomass. *M. chrysurus* represented 2% of herbivore density ($\pm 1\%$) and 1% of biomass ($\pm 0.2\%$).

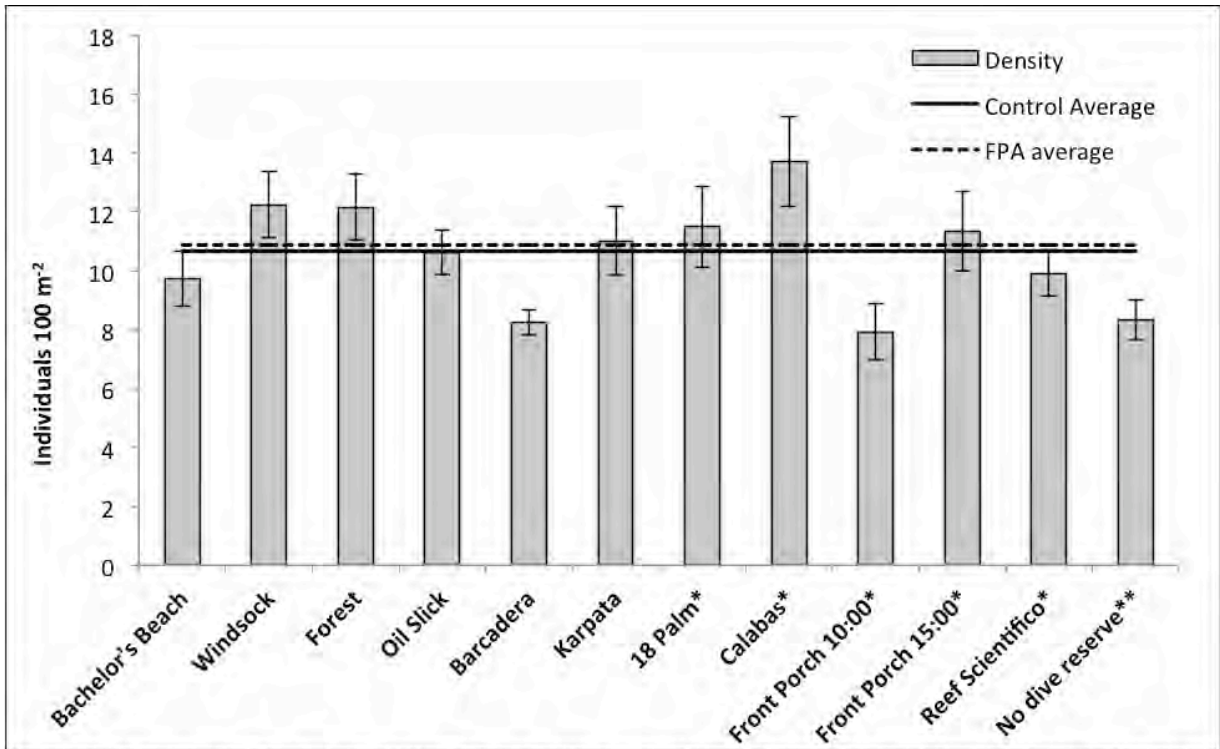


Figure 2a. Average scarid count per 100 m² for each site surveyed; error bars indicate ± 1 standard error; * indicates a Fishing Protected Area; ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

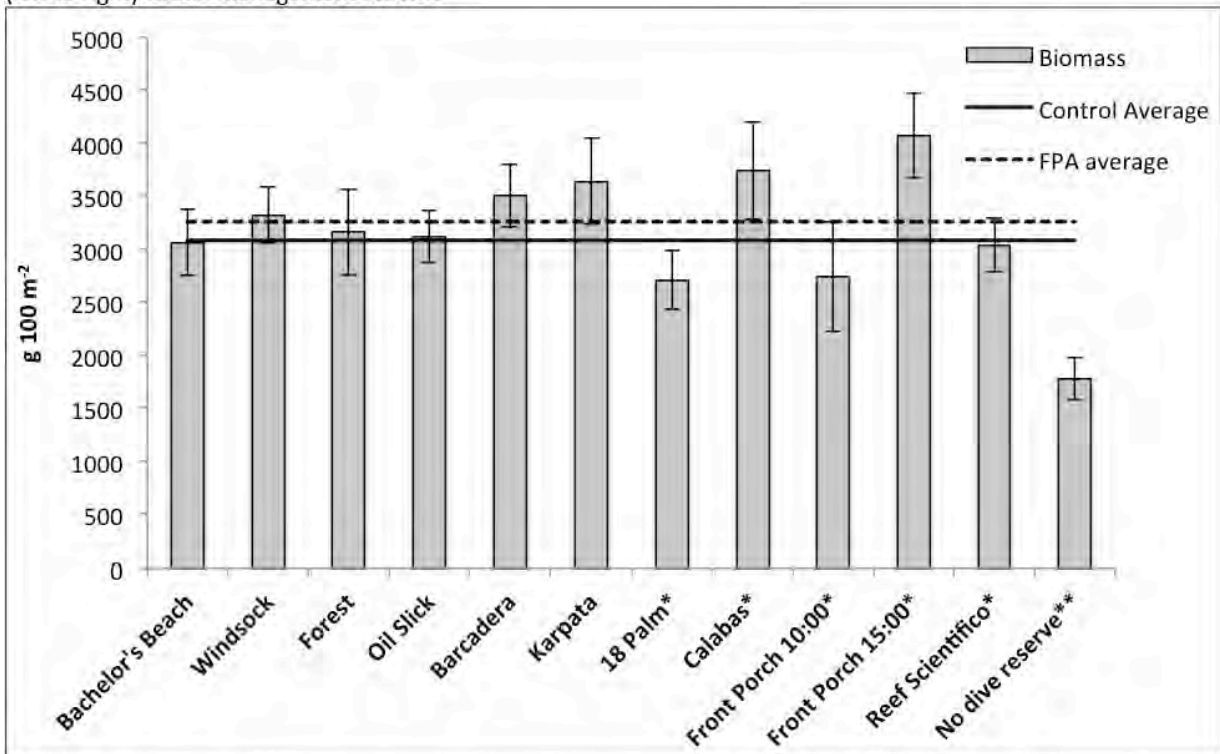


Figure 2b. Average scarid biomass per 100 m² for each site surveyed; error bars indicate ± 1 standard error; * indicates a Fishing Protected Area; ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

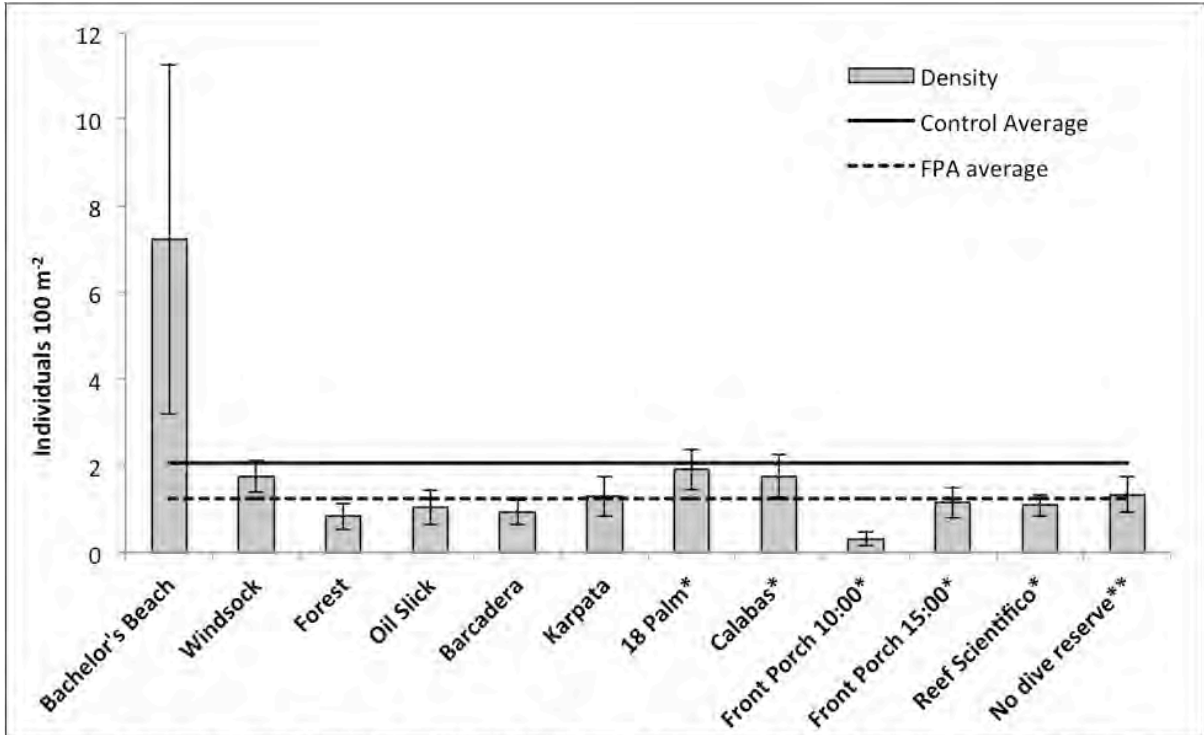


Figure 3a. Average acanthurid count per 100 m² for each site surveyed; error bars indicate ± 1 standard error; * indicates a Fishing Protected Area; ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

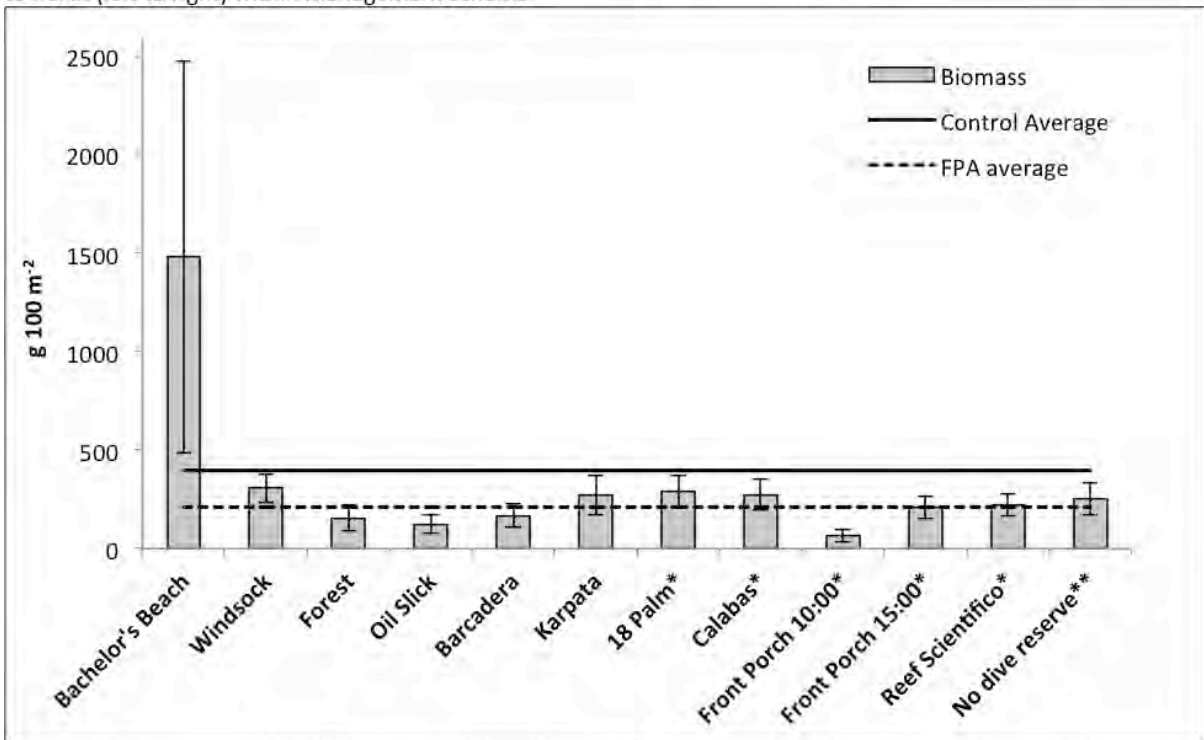


Figure 3b. Average acanthurid biomass per 100 m² for each site surveyed; error bars indicate ± 1 standard error; * indicates a Fishing Protected Area; ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

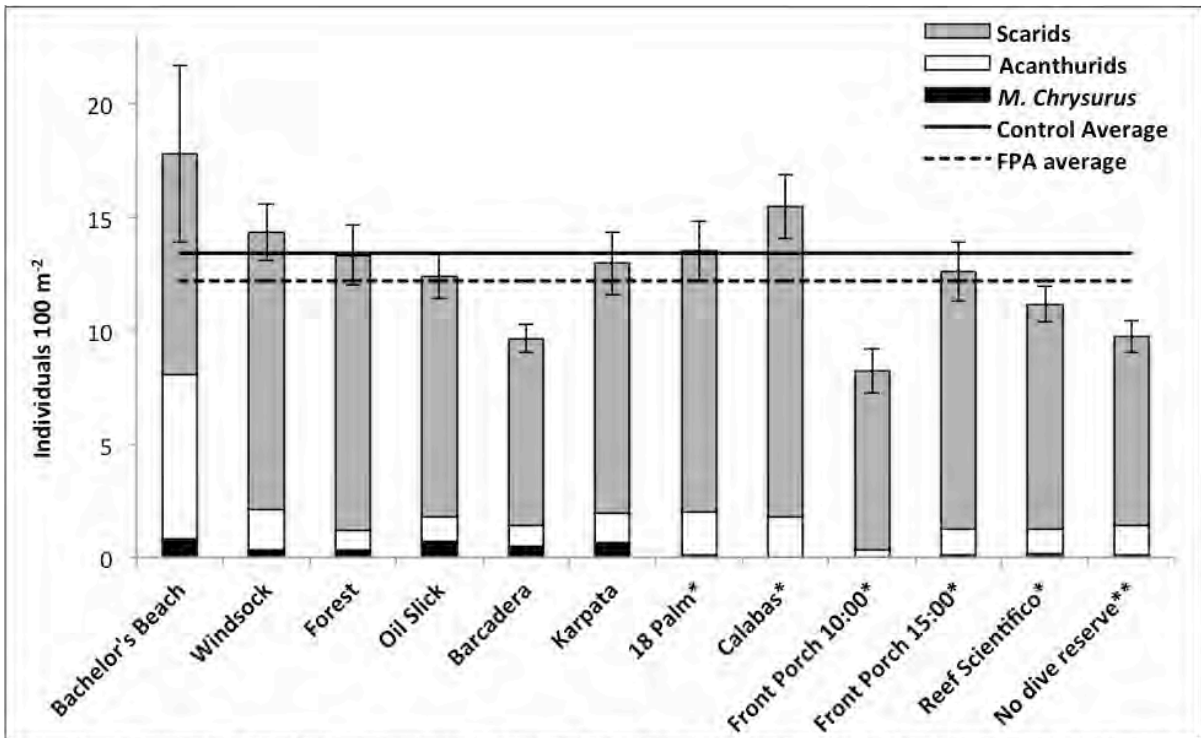


Figure 4a. Average total herbivore count per 100 m², including scarids (grey), acanthurids (white) and *M. chrysurus* (black); error bars indicate ± 1 standard error; * indicates a Fishing Protected Area; ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

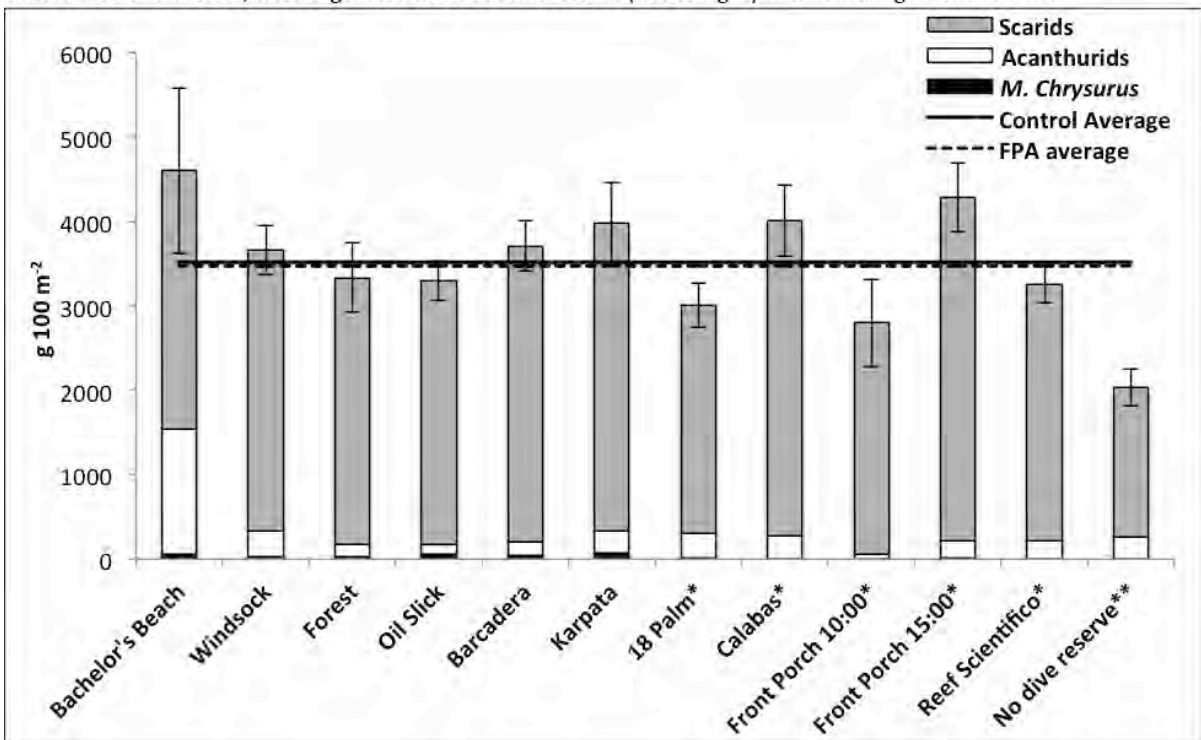


Figure 4b. Average herbivore biomass per 100 m², including scarids (grey), acanthurids (white) and *M. chrysurus* (black); error bars indicate ± 1 standard error; * indicates a Fishing Protected Area; ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

FPA had no significant effects on the density or biomass of any herbivorous fish group when compared with control sites (Table 2). Scarid and total herbivorous fish biomass was significantly lower at the no dive site, where diving is prohibited but fishing is allowed, than at either FPA or control sites. *M. chrysurus* density and biomass at control sites were significantly higher than FPA and the no dive sites. There was no difference in *M. chrysurus* at FPA sites compared with the no dive site.

Table 1. The significance of effects that the three management schemes have on fish density and biomass; p-values from a two-sided t-test comparing density (individuals 100 m⁻²) with management schemes, and biomass (g 100 m⁻²) with management schemes

DENSITY				
	Scarids	Acanthurids	<i>M. chrysurus</i>	Total Herbivores
Control to FPA	0.783	0.271	> 0.000*	0.271
Control to No Dive	0.265	0.623	0.010*	0.059
FPA to No Dive	0.054	0.898	0.914	0.069
BIOMASS				
	Scarids	Acanthurids	<i>M. chrysurus</i>	Total Herbivores
Control to FPA	0.764	0.2955	> 0.000*	0.275
Control to No Dive	> 0.000*	0.6861	0.010*	0.001*
FPA to No Dive	0.001*	0.6278	0.995	0.001*

* indicates significant difference between management schemes with 95% confidence

Average juvenile scarid density was significantly higher at FPA sites compared with control sites (Fig. 5, Table 3). In contrast, the densities of initial and terminal phase scarids did not differ between FPA and control sites (Fig. 5, Table 3). Terminal phase scarid density was significantly lower at the no dive site compared with both control and FPA sites (Fig. 5, Table 3), and the length of initial and terminal phase scarids did not differ between FPA and control sites (Table 4). However, initial phase scarid length was significantly lower at the no dive site compared with control and FPA sites (Fig. 6, Table 4).

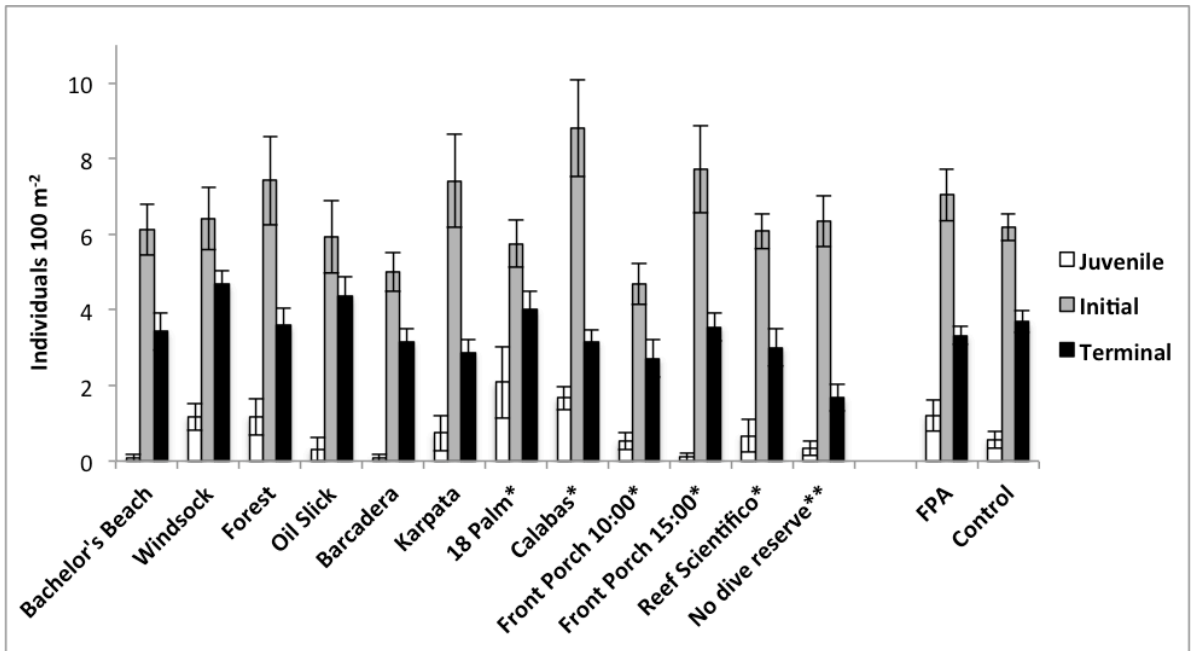


Figure 5. Scarid density separated by life history stage: juvenile (white), initial (grey) and terminal (black); error bars indicate ± 1 standard error; * indicates Fishing Protected Area (FPA); ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme.

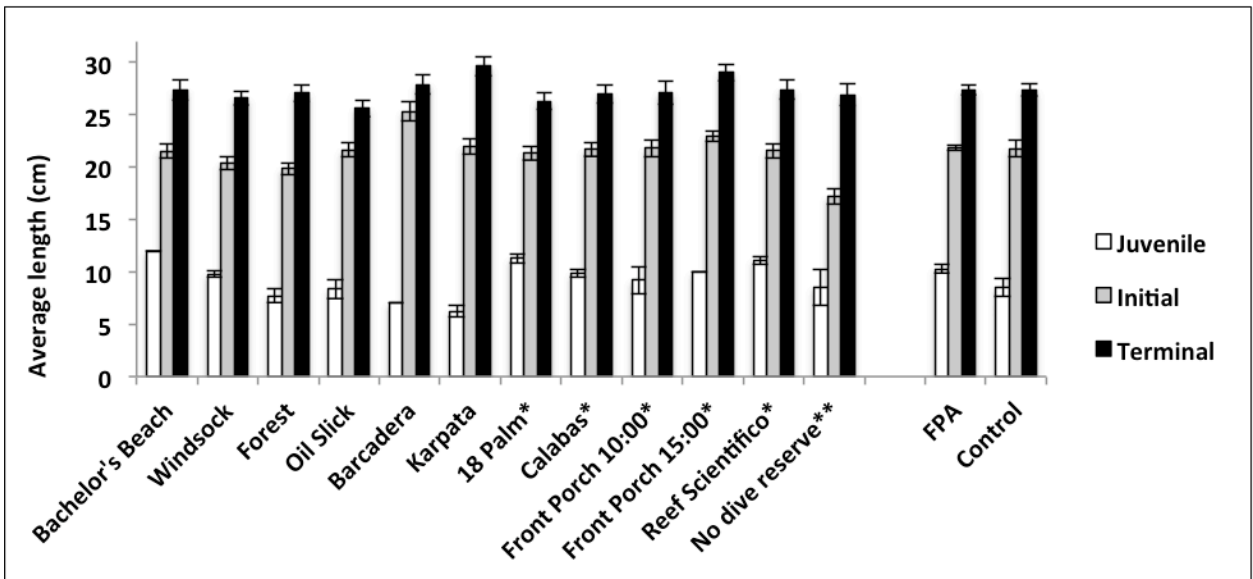


Figure 6. Scarid lengths separated by life history stage: juvenile (white), initial (grey) and terminal (black); error bars indicate ± 1 standard error; * indicates Fishing Protected Area (FPA); ** indicates a no dive site; all others are control sites; sites organized from south to north (left to right) within management scheme

Table 2. p-values produced from a two-sided t-test comparing densities (individuals per 100 m²) of juvenile, initial and terminal phase scarids between management schemes

Density			
	Juvenile	Initial	Terminal
Control to FPA	*0.012	0.883	0.065
Control to No Dive	0.430	0.937	> 0.000*
FPA to No Dive	0.088	0.864	*0.002

Table 4. p-values produced from a two-sided t-test comparing lengths (cm) of initial phase scarids between management schemes, and lengths (cm) of terminal phase scarids between management schemes

Length		
	Initial	Terminal
Control to FPA	0.407	0.775
Control to No Dive	> 0.000*	0.811
FPA to No Dive	0.000*	0.720

* indicates significant difference between management schemes with 95% confidence

In summary, parrotfish and total herbivore biomass (Table 2; Figs. 2b and 4b, respectively), as well as terminal phase parrotfish density (Table 3; Fig. 5), and initial phase parrotfish length (Table 4; Fig. 6), were all significantly lower at the no dive site than the control and FPA sites. *M. chrysurus* was the only species observed whose density (Fig. 4a) and biomass (Fig. 4b) was significantly different between FPA and control sites (Table 2).

Spatial trends in herbivorous fish populations

Herbivore population density declined latitudinally from south to north, with 95% confidence ($p=0.0125$; Fig. 7a) and regardless of management scheme. The latitudinal trend in herbivore biomass was not significant at the 95% confidence level, but was at a 90% confidence level ($p=0.913$; Fig. 7b). The trends for individual fish families were not significant.

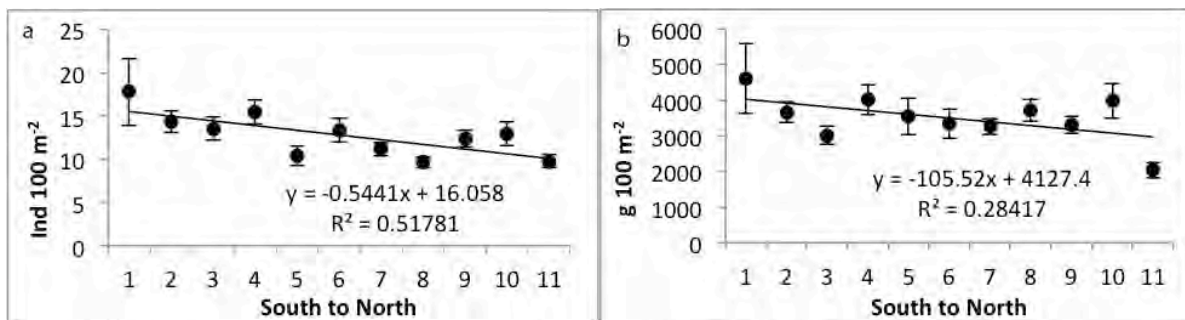


Figure 7. Herbivorous fish density (a) and biomass (b) at all sites from south to north, with trendline Sites: 1) Bachelor's Beach 2) Windssock 3) 18th Palm 4) Calabas 5) Front Porch (avg. of two times) 6) Forest 7) Reef Scientifico 8) Barcadera 9) Oil Slick 10) Karpata 11) No dive reserve; error bars indicate ± 1 standard error

The effect of parrotfish survey time on survey results

Time of day affected acanthurid and total herbivore density and biomass significantly with 95% confidence. When we compared scarid, acanthurid, and total herbivore density (Fig. 8a) and biomass (Fig. 8b) between two Front Porch surveys (03 Mar at 10:00 and 05 Mar at 15:00), we found that time of day had no significant effect on scarid parameters at the 95% confidence level, but did have significant effects at the 90% confidence level ($p = 0.057$).

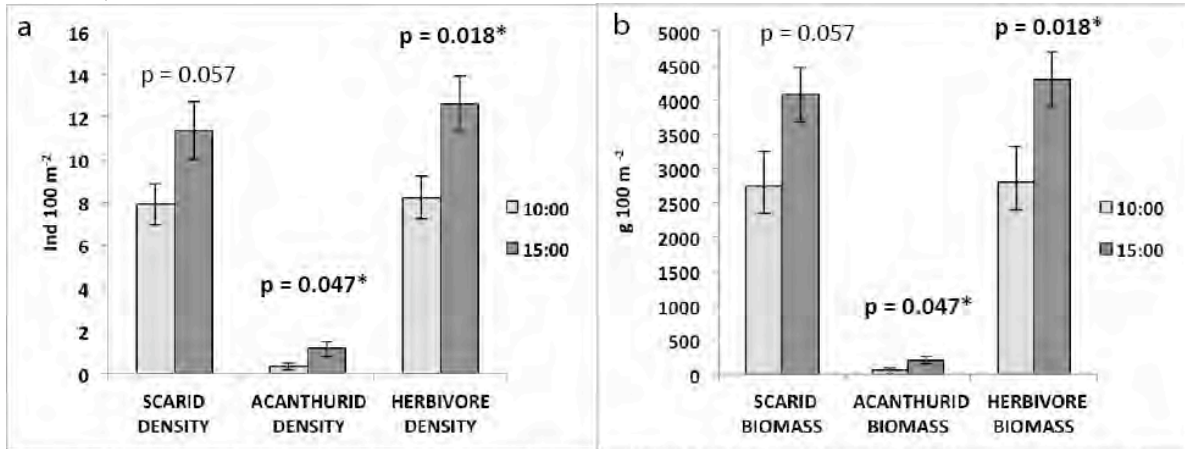


Figure 8. Herbivorous fish density (a) and biomass (b) at 10:00 and 15:00 on 03Mar and 05Mar, respectively, at Front Porch; error bars represent ± 1 standard error; p-values are the same for density and biomass because the latter was derived from the former; * indicates a statistically significant difference in count (a) and biomass (b) between the two surveys at a 95% confidence level

Discussion and Conclusion

The trajectory of Bonaire's scarids (parrotfishes) is of utmost importance due to their ecological significance in maintaining coral dominance (Steneck 1988; Hughes et al. 2007; Elmhirst et al. 2009). The slow increase in parrotfish densities from 2007 to 2009, following a steep decline, has continued in a positive trend and at a higher rate into 2013. The trend in parrotfish biomass, however, has continued to decrease but at a lower rate than before. The positive trajectory of scarid density is likely a result of the 2010 ban on parrotfish harvest. The discrepancy between density and biomass trends may be due to new recruitment of smaller individuals that will grow into larger adults. It may also be due to recruitment of smaller species. Differential effects of marine reserves on fish biomass and density have been documented (Anticamara et al. 2010). Future monitoring will be important in determining the driver of these incongruent scarid density and biomass patterns, and will show whether biomass increases over time, following density. The scarid and acanthurid communities at the No Dive Reserve site were consistently different from those at control and FPA sites. SCUBA diving is prohibited and fishing is allowed at the no dive site. The no dive site is the farthest north, as well as the most isolated from Bonaire's population center, making enforcement of the fish trap and other rules more reliant on park rangers alone, rather than combined civilian and ranger enforcement. Further, SCUBA diving and fishing are less than compatible coastal zone uses; SCUBA divers in Bonaire are known to destroy fish traps (pers. comm. R. de Leon). Therefore, the no dive site may be a preferred fishing location, and subject to

higher fishing pressure than the other sites surveyed, resulting in a relatively depleted herbivore community.

The damselfish *M. chrysurus* was the only fish group surveyed that was significantly affected by the FPA management scheme. Damselfish predators such as graysbys were protected from harvest in FPAs, but allowed at control sites, may explain the difference. Commercially and recreationally fished families, serranids (groupers), lutjanids (snappers) and sphyraenids (barracuda) (Nenadovic, 2007, p. 74), all contain species known to eat damselfish (Randall, 1967). Therefore, protection of predators from fishing in FPAs may explain lower *M. chrysurus* densities at those sites. The No Dive Reserve site did not follow this pattern; one would expect high damselfish densities, as fishing is not only allowed there, but it may be a preferred fishing site by fishermen. However, very low *M. chrysurus* densities were observed at the No Dive Reserve site. Given that this site is the farthest north, alternate processes may be acting along a south to north spatial gradient, in addition to the effects of varied fishing pressure.

We observed a trend of decreasing herbivore density from the southern- to northern-most survey sites, regardless of management scheme (Fig. 6). This pattern is driven by a combination of both scarid and acanthurid density, as the trend was not significant when the two families were considered alone. Lac Bay is a large saltwater bay at the southeastern edge of Bonaire (Fig. 8); it contains shallow seagrass beds, and is lined by Mangrove forests that are protected by law.

Seagrass beds and mangroves are known as important nursery habitats for reef fish

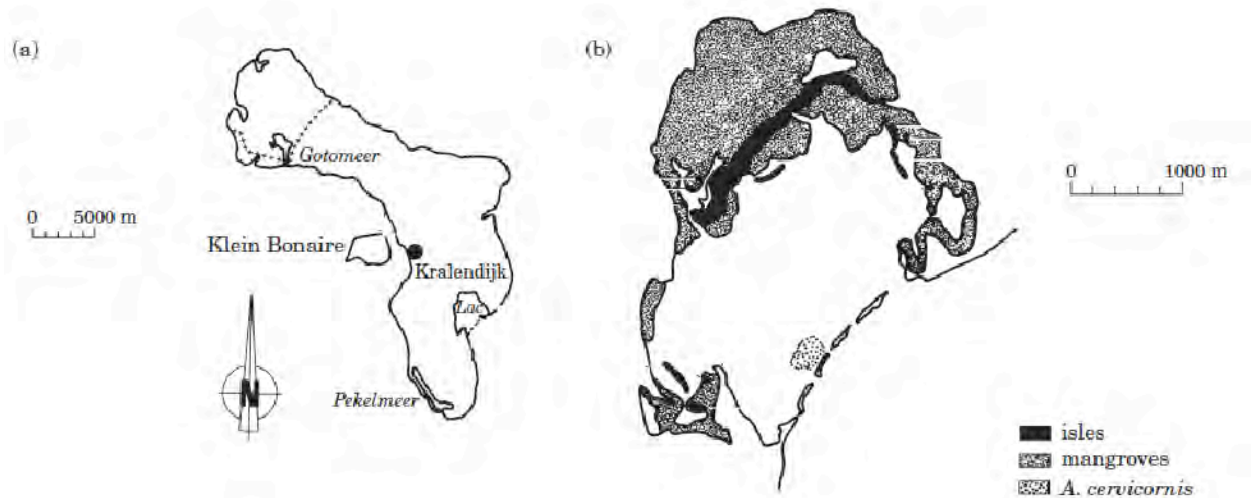


Figure 8. a) Bonaire, Netherland Antilles with Lac Bay labeled "Lac" and b) Enlarged view of Lac Bay and its nursery habitat; modified from Nagelkerken et al. 2000

(Nagelkerken et al. 2000; Mumby et al. 2004). Ontogenetic migrations occur from mangroves to reef habitat, making connectivity and the nursery habitat itself important (Mumby 2004). While ocean currents would have to provide the connectivity between Lac Bay's nursery habitat and Bonaire's western reefs, it is possible that the decrease in herbivorous fish from south to north could be related to nursery habitat proximity. Only some herbivorous fish are known to recruit from mangroves to reefs, most notably the

large parrotfish (6.5 to 122 cm length) *Scarus guacamaia* (rainbow parrotfish). Large parrotfish are disproportionately more important to maintaining algae-free substrate, compared with smaller fish (Lokrantz et al. 2008; Mumby et al. 2006). Therefore, at least for this parrotfish species, proximity to mangroves is important. It is possible that the nursery habitat also has indirect positive effects, such as a more intact food web, on the reefs nearby, resulting the spatial pattern that we observed. Other habitat quality factors may also influence the distribution of herbivorous fish, such as coral cover and habitat complexity. Further work is required to tease apart and test the possible drivers of this spatial pattern, as well as to monitor its durability over time.

We surveyed the FPA site “Front Porch” twice to determine whether time of survey (morning versus afternoon) had an effect on the numbers of parrotfish counted. High numbers of parrotfish observed at this site in 2011 were the impetus for this analysis. This was not a primary objective of our study, and would have to be repeated multiple times on multiple days, at several locations, for conclusive results. We suggest, from our brief analysis, that morning versus afternoon does not have a significant effect on the number and biomass of parrotfish counted (Fig. 7), which is consistent with past research (Lewis 1986). We did find significant effects on the numbers and biomass of acanthurids and total herbivores, however, with higher densities and biomass observed in the afternoon rather than the morning. *Acanthurus coeruleus* (blue tang), one of the most common acanthurid species that we surveyed, schools more at midday (11:00-14:00) than in the morning (06:00-7:45) (Morgan and Kramer 2005), and typically feeds actively in more exposed habitats when in a school (Reinthal and Lewis 1986). This active feeding and schooling behavior could make fish more mobile and more visible, potentially resulting in higher density estimates. Our findings are not in accordance with these, or other studies showing that the time of day effects are centered around sunrise and sunset (Lewis 1986), not morning versus afternoon. Time of day can affect fish survey results (Willis et al. 2006), and this question could therefore be explored further on Bonaire’s reefs.

In conclusion, Bonaire’s reefs would benefit from the continued phasing out of fish traps, strict enforcement of the ban on parrotfish harvest, and continued monitoring of parrotfish populations. Current management aimed to preserve nursery habitats is important, as is keeping connectivity in mind while crafting future management strategies (Mumby 2006). The continued and accelerated increase in Bonaire’s average parrotfish density lends optimism to the overall status of Bonaire’s coral reefs. Continued long-term monitoring will reveal whether biomass follows the same pattern, indicating recruitment of new individuals, or whether smaller species are simply recruiting more than larger species.

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Chapter 3: Rates of herbivory on Bonaire’s reefs: spatial variance, FPA effects, and long-term trends

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Abstract

In this study we quantified rates of herbivory by all parrotfish, surgeonfish, and damselfish at 11 leeward reef sites in Bonaire, Netherlands Antilles, as part of a long-term monitoring initiative. We conducted surveys at sites that have been monitored between 4 and 10 years, four of which were designated as no-take reserves (“FPAs”) in 2008. Scraping and excavating parrotfish (family: Scaridae), which exert the strongest effects on algal community structure, were responsible for the majority of herbivory. Scarid bite rates were generally high, with a Bonaire-wide average of 9.6 ± 3.4 bites $m^{-2} 5 \text{ min}^{-1}$, but varied markedly among sites. However, rates of scarid herbivory were similar among FPAs and were on average $>2x$ higher at FPA sites than at control sites. This pattern was likely driven by princess parrotfish and more broadly juvenile parrotfish, which exhibited grazing rates that were similar among FPAs and were on average 7x higher at FPA sites than at control sites. Factors controlling rates of scarid herbivory appear complex. Relationships across sites between scarid bite rates and scarid population density or biomass were weak and not significant. At the m^2 scale, scarid bite rates were not linearly related to benthic cover or damselfish grazing. However, scarid bite rates were invariably low within plots with high damselfish bite rates or modest amounts of macroalgae (“seaweed”). These small-scale patterns suggest that predator reductions of damselfish in FPAs could have elevated scarid grazing rates in FPAs, or alternatively that the greater abundance of unpalatable macroalgae in topographic low areas in FPAs caused elevated scarid grazing rates on topographic high-points in FPAs. Long-term trends in herbivory and reef community structure suggest that scarid populations responded to the 2010 coral bleaching event and subsequent macroalgal bloom with elevated grazing rates that limited and even reversed the spread of macroalgae. This reversal holds true for both FPA and control sites. Bonaire-wide rates of herbivory have declined slightly since 2011, potentially due to complex feedbacks between coral cover, macroalgal abundance, and herbivory. Notwithstanding it appears that herbivores have prevented a phase shift on Bonaire’s reefs. These findings suggest that high rates of parrotfish grazing may have played a critical role in maintaining the structure and function of Bonaire’s coral reefs amidst numerous perturbations in recent decades.

Introduction

Herbivory plays a fundamental role in shaping the structure and function of coral reef ecosystems. On coral reefs herbivores graze non-coral substrates up to 150,000 times $m^{-2} \text{ day}^{-1}$, consuming nearly 100% of daily algal production (Carpenter 1986). These high

grazing rates maintain the algal community in an early successional state dominated by diminutive algal turfs and encrusting coralline algae, and prevent the establishment of large fleshy macroalgae (i.e., “seaweed”) that dramatically reduce coral survival and reproduction (Lewis 1986, Steneck 1988, Hughes et al. 2007, Birrell et al. 2008). Therefore intense grazing by herbivores maintains the dominance of corals, the foundation species of tropical reefs.

High rates of herbivory are also essential to the recovery of corals following disturbances such as hurricanes and climate-induced coral bleaching events (Folke et al. 2004, Hughes et al. 2010). As coral cover declines in response to acute disturbance, the area of bare reef substrate rapidly increases. Herbivore populations may respond with intensified feeding and/or an increase in numbers to graze these new bare substrates, and in doing so, promote conditions needed for re-establishment of corals (Adam et al. 2011, Gilmour et al. 2013). However if herbivore populations have been reduced due to overfishing or disease, or if coral loss is too great, ambient grazing rates may be insufficient to keep pace with algal productivity, resulting in a community “phase shift” to macroalgae (Mumby et al. 2007a). Such phase shifts create ecological feedbacks that entrain the system in an algal dominated state, preventing coral recovery (Mumby and Steneck 2008). Over the past 30 years many Caribbean reefs have experienced phase shifts to macroalgae as a result of coral mortality and reductions in herbivory.

Historically both scraping and excavating parrotfishes (family: Scaridae) and the urchin *Diadema antillarum* exerted strong control over algal community structure on Caribbean reefs (Carpenter 1986, Steneck 1988), although their relative effect likely varied with fishing pressure. On remote or lightly fished reefs, herbivory was intense and scarids likely had a far greater impact on algae than did *Diadema* (Hay 1984), presumably because urchins were limited by predation on these reefs. However by the 1970’s, overfishing resulted in both diminished herbivorous fish populations and proliferation of *Diadema* at many locales, and thus a shift to *Diadema* as the primary grazer on many reefs. In 1983 the Caribbean-wide mass mortality of *Diadema* caused dramatic reductions in herbivory and increases in macroalgae at such sites (Hughes et al. 1987). This die-off, combined with reduced grazing pressure from overexploited fish populations, resulted in phase shifts to macroalgae throughout the Caribbean (Hughes 1994, Gardner et al. 2003, Hughes et al. 2010).

Diadema remain rare today throughout much of the Caribbean and as a result herbivorous fishes, principally scarids, drive the process of herbivory on Caribbean reefs. This is evidenced by a strong, negative region-wide relationship between herbivorous fish biomass and macroalgal abundance (Williams and Polunin 2001) and by experimental studies (Lewis 1986, Mumby et al. 2006, 2007b, Burkepile and Hay 2008). Yet coral cover remains low and scarid populations continue to be overexploited in many parts of the Caribbean, and so on many reefs herbivores are able to maintain only 40-60% of substrates in a cropped state (Williams and Polunin 2001). As a result grazing fish have rarely been able to reverse trends of macroalgal dominance on degraded reefs (e.g., Paddock et al. 2006, Huntington et al. 2011) except where marine reserves have been

effective in promoting the recovery of large parrotfish (Mumby et al. 2006, Mumby and Harborne 2010).

In contrast to much of the Caribbean, Bonaire's reefs have displayed remarkable resilience in the face of disturbance. Bonaire's reefs resisted a phase shift to macroalgae following the Caribbean-wide loss of *Diadema* and both major reef-building *Acropora* corals, and are showing signs of recovery from a recent coral bleaching event (Chapter 1). These reefs remain coral dominated and have very low macroalgal abundance by Caribbean standards (Chapter 1). Tracking the status of Bonaire's herbivorous fish populations, along with changes in rates and spatial distribution of herbivory, is therefore needed to understand key drivers and trends of reef resilience in this system.

Methods

Study sites and survey design

In March 2013 we quantified the rate at which herbivorous fishes grazed the reef substratum at 11 leeward reef sites in Bonaire, Netherlands Antilles, as part of a long-term monitoring initiative. Ecological surveys have been conducted at the sites Windsock, 18th Palm, Forest (Klein Bonaire), Reef Scientifico, and Baracadera every other year since 2003. In 2008 Bonaire established no fishing zones ["fish protection areas" (FPAs)] at 18th Palm, Calabas, Front Porch, and Reef Scientifico. Thus in 2009 Bachelor's Beach, Calabas, Front Porch, and Oil Slick were added as monitoring sites to track the effects of FPAs relative to control sites.

In the present study we conducted surveys at four FPA sites (south to north: 18th Palm, Calabas, Front Porch, Reef Scientifico), six control sites (south to north: Bachelor's Beach, Windsock, Forest, Oil Slick, Barcadera, Karpata), and within a no-dive reserve ("No Dive") north of Karpata. To employ a survey design consistent with previous years, at each site we visually estimated grazing rates within haphazardly selected 1 m² areas of the reef that were: (i) located at 8-10 m depth, (ii) represented topographic high-points on the reef, and (iii) possessed $\leq 50\%$ coral cover. We conducted 5-8 replicate surveys at each site.

Prior to each survey, within the 1 m² area we visually estimated coral/sponge/sand and macroalgal % cover (Dethier et al. 1993), quantified macroalgal canopy heights (mm) using a ruler, and assessed the presence/absence of territorial damselfish. Each survey consisted of a 5-minute observation period. Within that period we quantified the species, size (total length to nearest cm), and life phase (juvenile, initial, terminal) of each herbivorous fish that entered the 1 m² area to feed, as well as the number of bites it took from the substrate. Observations were restricted to herbivorous fishes in the families Scaridae, Acanthuridae, and Pomacentridae. We conducted surveys between 0900 and 1600 hrs.

Statistical analysis

We calculated rates of herbivory (average \pm SE; bites m⁻² 5 min⁻¹) of each herbivore functional group (scraper/excavator, denuder, non-denuder) at each site (Steneck 1988).

Scraping and excavating parrotfishes (family: Scaridae) consume a wide variety of algal types including algal turfs and structurally / chemically defended seaweeds and exert the greatest control over algal community structure. Denuding surgeonfishes (family: Acanthuridae) and the yellowtail damselfish *Microspathodon chrysurus* consume a limited set of algae and only have significant impacts on algal abundance when grazing in large groups. Non-denuding territorial damselfish (family: Pomacentridae) do not significantly reduce algal biomass and sometimes promote algal growth by defending their territories against the grazing of parrotfish and surgeonfish (Steneck 1988, Hixon 1997, Ceccarelli et al. 2001). Hence bite rates of only scrapers/excavators and denuders were combined for our calculation of total rates of herbivory (in Fig. 1A).

Scarids were the dominant grazer in our study (see Results). Thus we also calculated average (\pm SE) scarid bite rates at each site as a function of species, life phase, and size class. Scarids were grouped into the following size classes for analysis: small (<13 cm), medium, (13-20 cm), large (21-30 cm), extra large (>30 cm). Furthermore we calculated a Bonaire-wide average rate of scarid herbivory for 2013. To allow for rigorous comparison with previous years, we calculated this Bonaire-wide rate of herbivory using only data collected from the six sites that have been monitored since 2003.

After calculating site-specific rates of herbivory for each functional group and scarid demographic group, we assessed how these rates differed as a function of site protection status. The “No Dive” reserve was excluded from all control vs. FPA comparisons due to its unique protection. In all cases bite rate data, when examined with regards to FPA effects, were not normally distributed and thus violated assumptions for parametric t tests. As a result we compared bite rates between FPA and control sites with the non-parametric Mann-Whitney U test (Quinn and Keogh 2000) using the program “R” (v. 2.13.2).

We explored relationships between site-averaged scarid bite rates and scarid densities or biomasses (Chapter 2) with Spearman rank correlation tests using GraphPad Prism (v.6.0a). At the 1 m² quadrat scale, correlations between scarid bite rates and (i) coral/sponge/sand % cover, (ii) macroalgal index (a biomass proxy; macroalgal % cover x canopy height (mm)), or (iii) territorial damselfish bite rates were explored with Spearman rank correlation tests. Scarid vs. damselfish bite rate comparisons were made for all quadrats surveyed (n=76). However because we failed to score benthic cover within some quadrats, correlations between scarid bite rates and benthic cover/biomass could only be made using a subset of data (n= 61-64).

Results

Rates of herbivory in 2013: spatial variance and FPA effects

Rates of herbivory were generally high but varied markedly among sites (Fig. 1A). Herbivore bite rates were, however, similar among FPA sites (Fig. 1A) and were on average >2x higher at FPA sites than at control sites, although this difference was only nearly significant ($p=0.051$). Scraping and excavating parrotfishes (scarids) were responsible for the vast majority of grazing at all sites, with denuders (acanthurids and *M.*

chrysurus) contributing little to overall rates of herbivory (Fig. 1A-C). Thus by extension scarid bite rates also varied greatly among sites (Fig. 1B) and were on average >2x higher at FPA than at control sites but this difference was not significant ($p=0.067$). Denuder and non-denuder (territorial Pomacentrid) bite rates were low and did not differ between FPA and control sites ($p=0.345$ and $p=0.227$, respectively; Fig 1C-D).

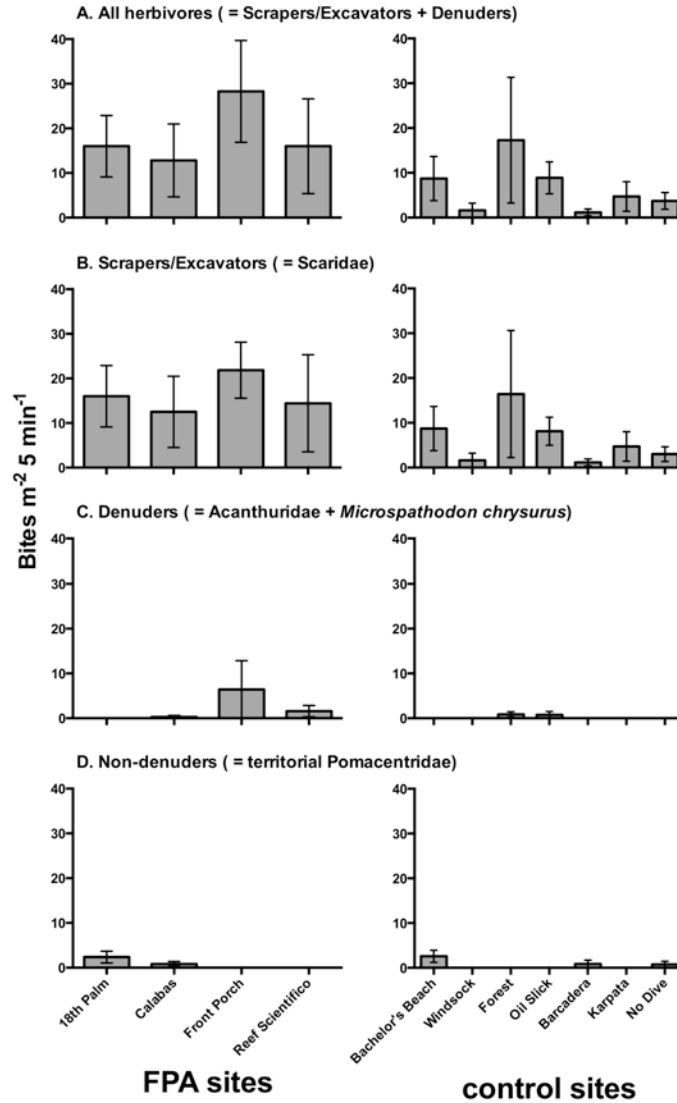


Figure 1. Grazing rates (average \pm SE; bites m^{-2} 5 min^{-1}) of (A) all herbivores, (B) scrapers/excavators (Scaridae), (C) denuders (Acanthuridae + *Microspathodon chrysurus*), and (D) non-denuders (territorial Pomacentridae) at 11 sites in Bonaire. Graphs are split between sites managed as no-take fish protection areas (“FPA sites”) and control sites open to fishing (“control sites”). Within each, sites are arranged south to north. $n = 5-8$ replicate surveys site $^{-1}$.

Princess parrotfish (*Scarus taeniopterus*), queen parrotfish (*Scarus vetula*), and stoplight parrotfish (*Sparisoma viride*) were responsible for the high rates of scarid grazing observed at each site (Fig. 2A). Striped parrotfish (*Scarus iserti*) and redband parrotfish (*Sparisoma aurofrenatum*), although common, were not observed grazing on topographic high-points on reefs (Fig. 2A). Grazing rates of the princess, queen, and stoplight

parrotfish were spatially variable (Fig. 2A). However princess parrotfish bite rates were consistently high at all four FPA sites (Fig. 2A) and were on average 7x higher at FPA than at control sites ($p<0.01$). Bite rates of other parrotfish species did not differ significantly between site types. Scarid bite rates, when examined by phase or size class, were also highly variable among sites (Fig. 2B-C). However bite rates of juvenile scarids were similar in FPAs and were on average 7x higher at FPA than at control sites ($p<0.01$) (Fig. 2B-C). Interestingly, terminal phase scarid bite rates were on average 5x higher at FPA than at control sites, but this difference was not significant ($p=0.067$). Scarid bite rates did not differ between site types when examined by size class.

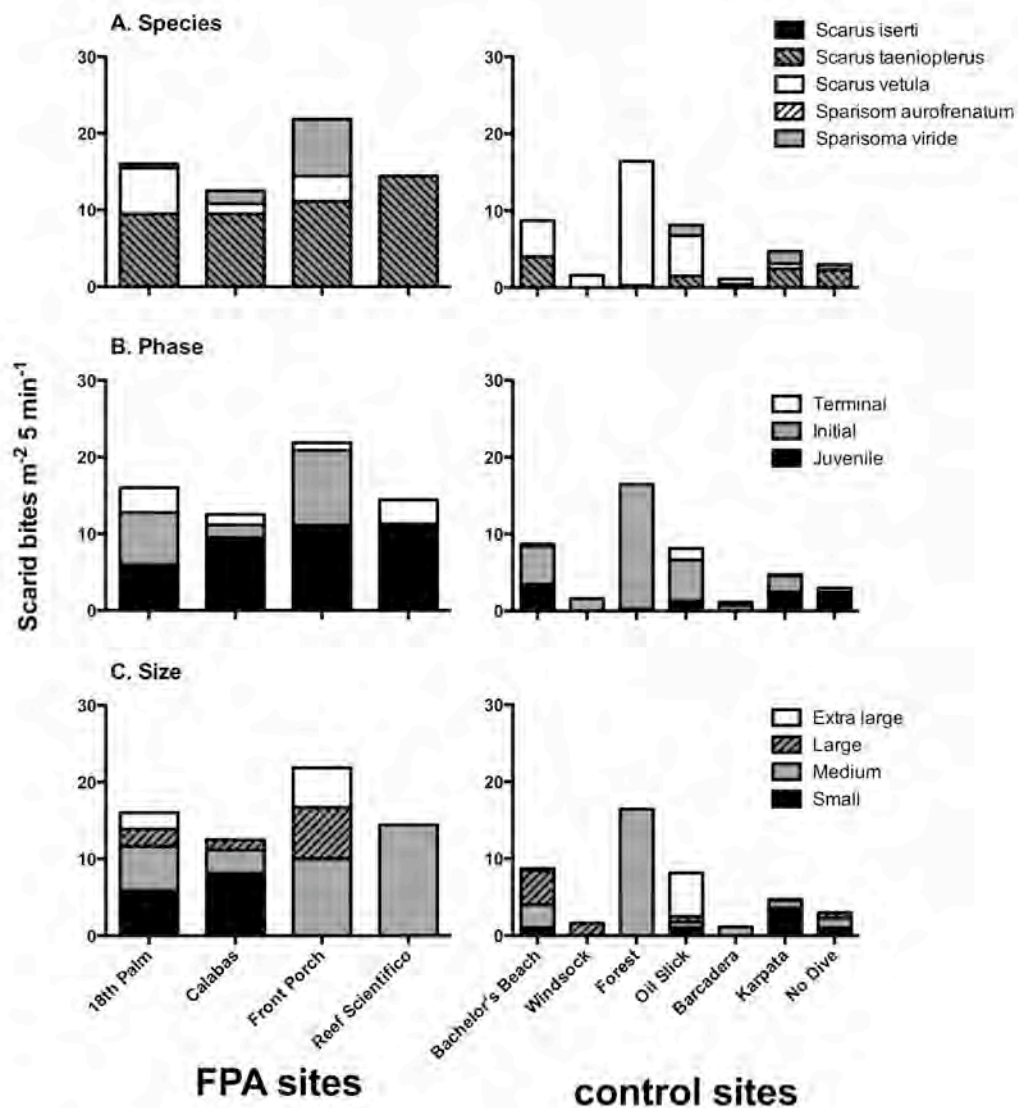


Figure 2. Grazing rates (average; bites $m^{-2} 5 \text{ min}^{-1}$) of parrotfishes at 11 sites in Bonaire, categorized by (A) species, (B) life history phase, and (C) size class. Average values are stacked within each bar. Species, phase, and size class are listed in the key of each respective panel. Size classes are small (<13 cm), medium, (13-20 cm), large (21-30 cm), extra large (>30 cm), based on total length (cm). Error bars were excluded to allow for clearer interpretation. See Figure 1 for site descriptions and graph layout.

Relationships between scarid herbivory and benthic / fish community structure in 2013

Scarid bite rates were not significantly correlated with either scarid density or biomass across sites (Fig. 3A-B). However the positive relationship between scarid bite rates and scarid density ($r = 0.42$) across sites is suggestive of density-dependence (Fig. 3A). Similarly, scarid bite rates were not significantly correlated with coral/sponge/sand abundance, macroalgal index (biomass proxy), or territorial damselfish feeding rate at the 1 m^2 scale (Fig. 4). However it is notable that when macroalgae and territorial damselfish bites were absent from our 1 m^2 survey plots scarid bite rates were highly variable, but when macroalgal biomass and territorial damselfish bite rates were modestly high, scarid bite rates were invariably low (Fig. 4B-C).

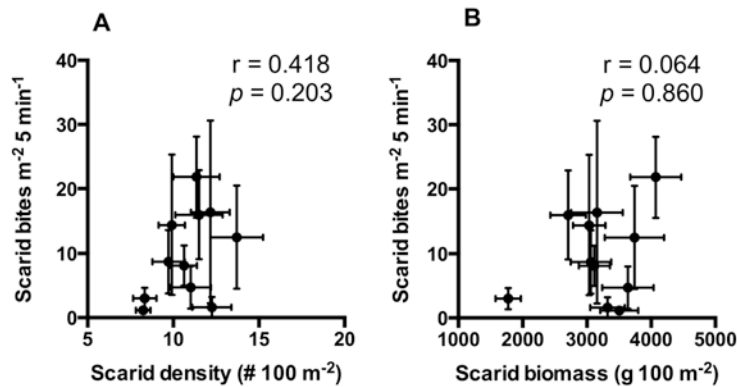


Figure 3. Relationship between scarid bite rates (bites $\text{m}^{-2} \text{ 5 min}^{-1}$) and (A) scarid density (# 100 m^{-2}) or (B) scarid biomass (g 100 m^{-2}) across 11 study sites in Bonaire. Each point represents the average (\pm SE) value from a site. Relationships were assessed using Spearman rank correlation coefficients.

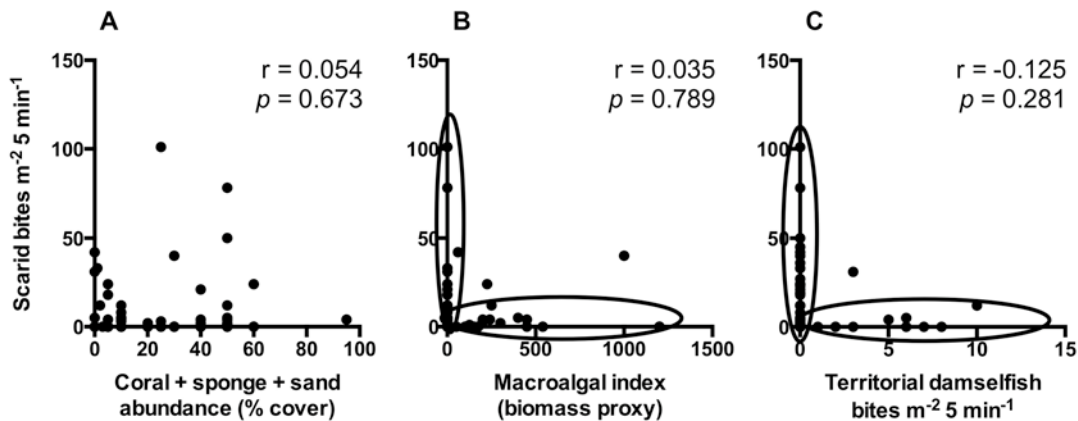


Figure 4. Relationship between scarid bite rates (bites $\text{m}^{-2} \text{ 5 min}^{-1}$) and (A) coral/sponge/sand abundance (% cover) or (B) macroalgal index (biomass proxy) or (C) territorial damselfish bite rates (bites $\text{m}^{-2} \text{ 5 min}^{-1}$) within 1 m^2 areas surveyed at 11 study sites in Bonaire. Relationships were assessed using Spearman rank correlation coefficients. $n = 61\text{-}76$ quadrats.

Long-term trends in scarid herbivory and community dynamics

The 2013 Bonaire-wide average scarid bite rate was $9.6 (\pm 3.4)$ bites $\text{m}^{-2} \text{ 5 min}^{-1}$. This Bonaire-wide average is appreciably lower than that of 2011, but is similar to or greater

than rates observed in 2005, 2007, and 2009 (Fig. 5A). A decline in scarid bite rates from 2003-2007 coincided with a decline in scarid abundance during that period; in contrast elevated bite rates in recent years (2011-2013) correspond with a recent upward trend in scarid densities (Fig. 5B). The uniquely high bite rates observed in 2011 occurred directly following a significant decline in coral cover (and thus an increase in non-coral substrate) due to the bleaching event in November 2010 (Fig. 5C). Bite rates have recently relaxed as coral cover has stabilized (Fig. 5C). Moreover the increase in scarid bite rates from 2009-2011 and subsequent decline in rates from 2011-2013 tracked closely the rise and fall, respectively, of macroalgal biomass (Fig. 5D).

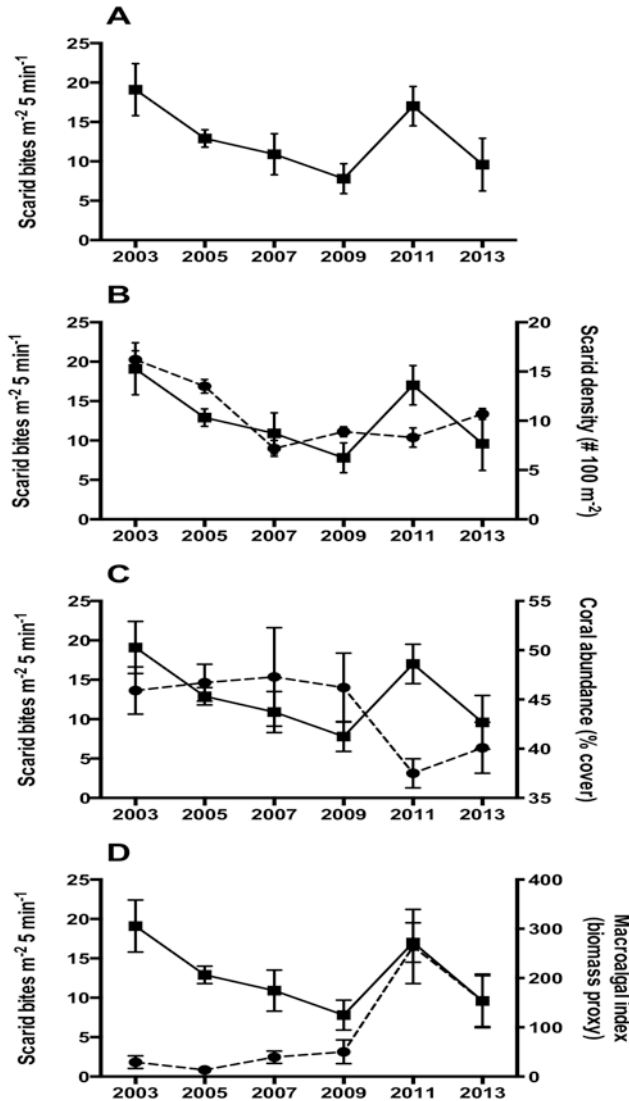


Figure 5. Bonaire-wide trends in scarid herbivory (bites $m^{-2} 5 min^{-1}$) from 2003-2013, plotted (A) alone, (B) with trends in scarid density ($\# 100 m^{-2}$), (C) with trends in coral abundance (% cover), and (D) with trends in macroalgal index (a biomass proxy) over that same period. Values for each year represent averages (\pm SE) generated using data only from six sites monitored since 2003. Herbivory data are plotted with black squares connected by black lines (on left Y axis), while other data are plotted with black circles connected by dotted black lines (on right Y axis).

Discussion

We observed spatially variable, but relatively high, rates of herbivory at 11 reef sites in Bonaire in 2013 (Fig. 1). Herbivory was largely attributable to scarids (Fig. 1A-D). Previous studies have demonstrated that scarids deeply scrape or excavate non-coral substrates, and in doing so, prevent macroalgal blooms and promote encrusting coralline and turf algal communities that are hospitable to coral recruitment and growth (Lewis 1986, Mumby et al. 2007a,b, Arnold et al. 2010, Burkepile and Hay 2010). Thus high rates of scarid herbivory are likely responsible for the relatively low macroalgal abundance on reefs in Bonaire, and may explain why Bonaire's reefs have resisted a large-scale phase shift to macroalgae even after the Caribbean-wide loss of important grazing and reef-building taxa.

Rates of scarid herbivory were on average >2x higher at FPA sites than at control sites. At greater resolution, princess parrotfish and juvenile parrotfish bite rates were on average 7x higher at FPA sites than at control sites ($p < 0.01$ for both comparisons). Effects of FPAs on parrotfish demography are unlikely to explain higher bite rates in FPAs, as the density and biomass of parrotfish did not differ between FPA and control sites (Chapter 2). However some predators of damselfish were more abundant in FPAs and in turn damselfish were less abundant in FPAs (Chapters 6, 7). Territorial damselfish are known to reduce grazing rates of parrotfish within their territories (Hixon 1997), and scarid bite rates were invariably low in our 1 m² plots when damselfish bite rates were high (Fig. 4C). Therefore protection afforded by FPAs may be promoting predator population increases, reductions in damselfish, and higher scarid grazing rates within FPAs. Recent studies have found similar complex and cascading effects of fishing vs. reef protection on the process of herbivory (Mumby et al. 2006, 2007b, 2012).

The abundance of corals and macroalgae are also known to affect rates of herbivory on coral reefs, and may partially explain the higher scarid grazing rates at FPA sites. Reductions in coral cover increase the area of bare substrate requiring grazing, and thus diffuse a given rate of herbivory over a wider area. In contrast increases in macroalgae (seaweed) may concentrate herbivory onto algal turf substrates if fishes avoid macroalgae due to their anti-herbivore defenses or density-related effects (McClanahan et al. 2000, Williams et al. 2001, Hoey and Bellwood 2011). FPA sites had lower coral cover and greater macroalgal biomass than did control sites (Chapter 1) despite not differing in scarid densities or biomasses (Chapter 2). Differences in coral cover were modest. However differences in macroalgal biomass between FPA and control sites were more substantial. Chemically defended *Dictyota* spp. macroalgae were the dominant macroalga in Bonaire, and were located almost exclusively in topographically low areas at all sites (Rasher and Steneck, unpubl. data). Thus if most scarids avoid this alga, then greater *Dictyota* biomass in the low lying areas of the FPAs could have concentrated grazing on topographic-highs points and caused the higher grazing rates at FPA sites. Macroalgal avoidance effects appear important, as we observed that 1 m² plots even with modest macroalgal biomass consistently had low scarid bite rates (Fig. 4B).

While the patterns and drivers of higher grazing rates at FPA sites are of interest, further experimental studies are needed to elucidate the mechanism(s) generating such differences. Moreover, it should be noted that current rates of herbivory at control sites appear sufficient to limit macroalgae, as indicated by the relatively low algal biomass found throughout Bonaire and the ongoing system-wide decline in macroalgae (Chapter 1). The system-wide effectiveness of grazing on Bonaire's reefs, regardless of reef protection status, could be due to the complete ban of parrotfish harvest in 2010.

Long-term trends in scarid population dynamics, benthic community dynamics, and herbivory (Fig. 5) suggest that these factors are linked in complex ways, and that Bonaire's reefs are exhibiting high resilience relative to the greater Caribbean. Prior to the 2010 coral bleaching event rates of scarid herbivory were in decline, likely due to a decline in scarid abundance during that period (Fig. 5A-B). However in the year following a significant coral bleaching event (2011) bite rates more than doubled (Fig. 5A). The 2010 bleaching event caused a significant decline in coral cover and subsequent increase in highly preferred turf algae on new bare substrates, as well as a spike in the abundance of *Dictyota* spp. macroalgae in topographic low areas of the reef (Fig. 5C-D). This increase of both micro and macroalgae, coupled with an increase in scarid densities in 2011 (Fig. 5B), are together likely responsible for the high grazing rates observed in 2011. Such exceptional rates of herbivory, triggered by functional or numerical responses among herbivores to reductions in coral, appear to be a key component of reef resilience (Adam et al. 2011, Gilmour et al. 2013). Large seaweeds (namely *Dictyota*) are now on a trajectory of decline, presumably due to these elevated rates of grazing (Fig. 5A&D), and coral cover has shown a light increase since 2010 (Fig. 5C); both of these trends are positive indications of resilience.

Interestingly, scarid grazing rates have slightly declined in concert with the recent decline in *Dictyota* biomass (Fig. 5D). A possible explanation for this decline is that *Dictyota* were initially being avoided by scarids during their bloom in topographic low areas in 2011 (thus increasing grazing rates on topographic high-points), but then *Dictyota* was subsequently targeted as food when preferred algal turf prey became limited. If so, reductions in *Dictyota* from 2011-2013 would have opened preferred grazing substrates on topographic low-points of the reef and thus diffused scarid herbivory over a wider area by 2013, resulting in decreased grazing rates on topographic high-points. Experimental studies are required to rigorously demonstrate such a phenomenon (e.g., McClanahan et al. 2000), but the patterns support this notion.

Our study suggests that herbivory is a dynamic, variable process shaped by complex interactions between herbivores and the reef community. Our long-term monitoring indicates that herbivores responded to the 2010 coral bleaching event and subsequent spike in macroalgae with increased grazing, thereby limiting and reversing the spread of macroalgae. These results highlight the potential for herbivores to prevent phase shifts to macroalgae, and the importance of herbivores to coral reef resilience (Hughes et al. 2010). It is worth considering whether the resilience of Bonaire's reefs, unparalleled in the Caribbean, may be attributable to Bonaire's progressive management plan that protects herbivorous fishes at large spatial scales.

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Chapter 4: Status and trends in sea urchins *Diadema* and *Echinometra* show still too few to play a role as herbivores role on Bonaire reefs

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Abstract

Sea urchins can be important drivers of macroalgal abundance in benthic marine ecosystems. In the Caribbean, the long-spined urchin *Diadema antillarum* is particularly important in controlling macroalgae, and to a far lesser extent so may the reef urchin *Echinometra viridis*. However both species were well below functional densities in Bonaire. In surveys conducted at eleven sites on Bonaire's leeward coral reefs in 2013, densities ranged from 0 to 0.04/m² and from 0.01 to 0.18/m² for *D. antillarum* and *E. viridis*, respectively. Over the past decade, *D. antillarum* peaked in abundance in 2005 but has stabilized at a lower density since 2011. In contrast, populations of *E. viridis* appear to be gradually increasing. Virtually all urchins found in this survey occupied small protective shelters. The presence of small juvenile *Diadema* in each survey but no adults, suggests something such as predators is killing them. Measures of predation pressure on urchins and comparisons of Fish Protected Area (FPA) sites with control treatments both reveal no significant effect of predator presence or FPAs on urchin densities. FPAs were established to protect fish-eating predators so it is not surprising that they show no impact on sea urchins. Populations of both species of urchin remain at very low densities on Bonaire.

Introduction

In 1983 and 1984, populations of the long-spined urchin *Diadema antillarum* collapsed (Lessios 1984). The ensuing absence of *D. antillarum* underlined its importance as a functional herbivore in Caribbean reef communities, where, if other herbivores were not sufficiently present, a phase shift towards macroalgae-dominated systems often occurred (Hughes 1994). This happened in conjunction with the Caribbean die-off of the structure-building *Acropora* coral species from the spread of white-band disease (Aronson & Precht 2001). Except for some isolated instances (Aronson et al. 2004), the reef urchin *Echinometra viridis* does not appear to be able to control macroalgae in *D. antillarum*'s stead and in fact may be associated with increased macroalgae (McClanahan 1999). With overfishing of both predatory and herbivorous fish continuing across much of the Caribbean and no other urchin able to control macroalgae, it is vital to monitor the status of *D. antillarum* for possible signs and associated causes of recovery.

Around a decade ago, researchers documented a small recovery for *D. antillarum* populations throughout the Caribbean (Carpenter & Edmunds 2006), especially in Jamaica (Bechtel et al. 2006). The upward trend has not persisted, however, and what spike there was consisted of densities at an order of magnitude below those found before the 1983 die-off (Hughes et al. 2010). However, many studies have found that even a

recovery in localized *D. antillarum* densities above about one per meter square is sufficient to limit macroalgae and promote coral recruitment at the scale of the patches where *D. antillarum* has returned (Tuya et al. 2004; Carpenter & Edmunds 2006; Myhre & Acevedo-Gutierrez 2007; Furman & Heck 2009; Roff & Mumby 2012).

Several factors may inhibit the return of *D. antillarum* to densities where it can effectively limit macroalgae. The prime causes may include low larval supply (Williams et al. 2011), possibly associated with density-dependent reproductive failures (Levitan 1991), and predation that limits densities of both *D. antillarum* and *E. viridis* (McClanahan 1999; Tuya et al. 2004; Brown-Saracino et al. 2007; Williams et al. 2011).

In this study I examine the status of urchins in reef communities on the island of Bonaire, Dutch Caribbean. The reefs of Bonaire are remarkable for their persistent health relative to the general decline in corals across the Caribbean (Kramer 2003, Gardner et al. 2003). The reefs of Bonaire were not spared the thorough die-off of *D. antillarum* in the early 80s, and chronic low densities have continued through the last decade (Cleaver 2011). As part of the report, I look at the current status of urchin abundances and size distributions across sites as part of an ongoing survey of Bonaire's reefs. I examine whether trends in *D. antillarum* abundance are positive or negative and the factors that could drive these trends in either direction. As Bonaire has recently instituted a system of Fish Protection Areas (FPAs), I pay particular attention to any possible effects from FPAs and urchin predator abundance on urchin densities. The fishing pressure on Bonaire's reefs comes primarily from hook and line fishers targeting fish-eating predators. Thus the expectation that these FPA reserves would have a negative effect on invertebrate eating predators is low.

Methods

We surveyed abundances of the sea urchins *D. antillarum*, *E. viridis*, *Echinometra lucunter*, *Tripneustes ventricosus*, and *Eucidaris tribuloides* along 2 by 10 meter belt transects at eleven dive sites in early March, 2013 as part of a long-term study on the health of Bonaire reefs. These sites included, from south to north, Bachelor, Windsock, 18th Palm, Calabas, Forest (on Klein Bonaire), Front Porch, Scientifico, Barcadera, Oil Slick, Karpata, and the No Dive Reserve north of Karpata. Between four and six transects were surveyed at each site, depending on time constraints. Each belt transect was placed along the reef at a depth of approximately 10 meters in areas dominated by hard substrates, with the surveyor combing the area 1 meter to either side of the belt, for a total of 20m² per transect. We documented the species and test diameter of every urchin counted. We did not record test diameters at Oil Slick reef due to technical difficulties.

I made several comparisons to investigate trends in urchin abundance and size distributions. I concentrated on *D. antillarum* and *E. viridis*, as the other species of sea urchins were either rare or nonexistent at most sites, and even where they do occur at very high densities appear to have little or no effect on algae (e.g. Furman & Heck 2009). I computed average density by site by taking the average of the transects for each site. For urchin sizes, I took the average of the test diameters for each transect by species, then

took the average of site transects to compute the site mean. I compared densities at FPA sites (18th Palm, Calabas, Front Porch, Scientifico) against densities at the remaining control sites. To test for a difference between the FPA and control sites in urchin densities, I performed a one-way ANOVA to test for a difference in mean densities of *D. antillarum*, as well as *E. viridis*. I performed a square-root transformation on *D. antillarum* densities to keep with the assumptions of normality and constant variance for the ANOVA, while densities for *E. viridis* met these assumptions without transformation (Shapiro-Wilk test $p > 0.05$; summary of variance function in R statistical package (r-project.org) $p > 0.05$).

For the purposes of this study, urchin predators were defined as those predators having *D. antillarum* or *Echinometra* species present in their stomachs in a comprehensive diet study from a time when *D. antillarum* was more abundant (Randall 1965). Auscavitch and DeBey (2013; this report, chapter 7) describes survey methods used for predator biomass and density. I tested for predation effects on urchin density using linear regressions. An Urchin Predation Index (UPI) by site served as the independent variable and urchin (*D. antillarum* and *E. viridis* separately) density by site the dependent variable. I transformed the dependent variable by adding 0.001 to counts in order to keep with the assumption of normality. The UPI was determined by multiplying the transect biomass for each predator species by the average proportion of urchins by volume in stomachs of that predator from Randall (1965). I took the sum of these products for all predators for each transect. The average of transect sums then served as an urchin predation index for each site. This UPI was developed to provide a better estimate of actual predation pressure on urchins by combining the relative presence of a predator with an estimate of its tendency to actually consume the urchins of interest.

Previous Bonaire reports available via STINAPA (Steneck et al. 2003, 2005, 2007, 2009, 2011) provided historical population densities for plotting trends in *D. antillarum* and *E. viridis* abundance. For each year the average of the site means was taken. The years 2003, 2005, and 2007 only included six sites, with nine sites in 2009, and ten in 2011 and 2013. For surveys from 2003-2009, a single researcher was tasked with quantifying trends in a host of taxa aside from urchins. For 2011 and 2013, urchins had a researcher specially assigned to their quantification. Counts for years previous to 2011 may be skewed towards lower densities as a result. Densities of urchins at the No Dive Reserve site were not included in analysis of population trends for 2013, as it was the first year that site was surveyed.

Results

Sea urchins were rare at all surveyed reefs on Bonaire. Nevertheless, we found a few individuals of *D. antillarum*, *E. viridis*, *E. tribuloides*, and *T. ventricosus* present at some of the sites surveyed in 2013, but only single individuals of both of the latter species.

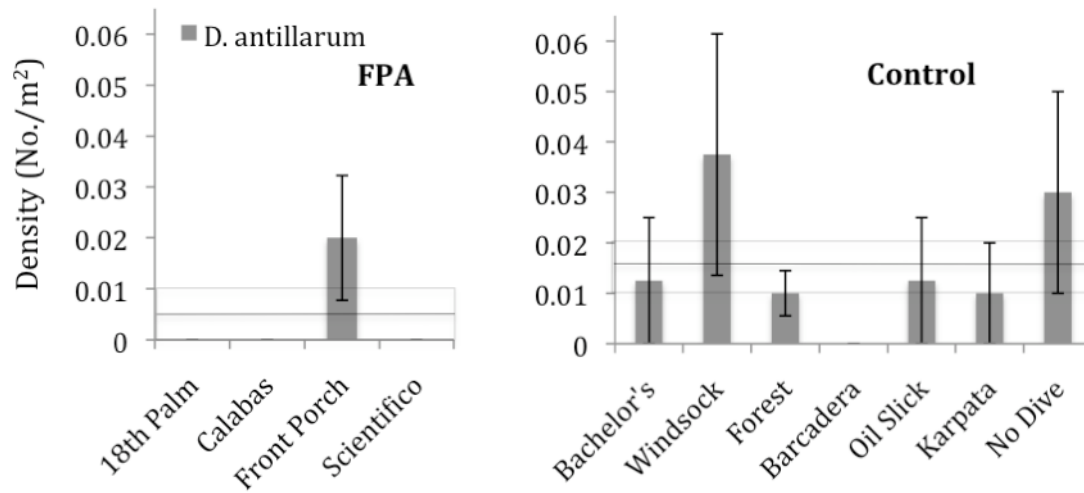


Figure 1. Average densities of *D. antillarum* at Fishing Protected Area (left) and control sites (right). Column bars represent \pm SE for site density. Lines represent average densities \pm SE for each treatment.

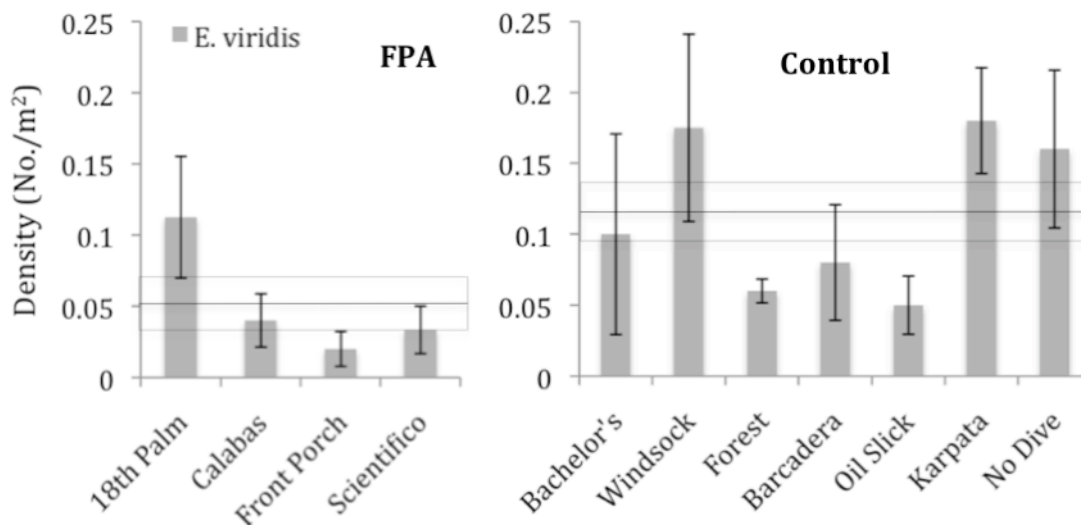


Figure 2. Average densities of *E. viridis* at Fishing Protected Area (left) and control sites (right). Column bars represent \pm SE for site density. Lines represent average densities \pm SE for each treatment.

The average density of *D. antillarum* in 2013 for all sites was $0.012(\pm \text{SE } 0.004)/\text{m}^2$. *Diadema antillarum* was only present at one of the four FPA sites (Fig. 1). At the control sites, *Diadema* was present at six of the seven sites surveyed (Fig. 1). As *Diadema* was rare at FPA sites, densities were accordingly low, with an FPA average of $0.005(\pm 0.005)/\text{m}^2$, compared to average densities at control sites of $0.016(\pm 0.005)/\text{m}^2$. *Echinometra viridis* was present at all sites surveyed in 2013 (Fig. 2). The average density of *E. viridis* in 2013 for all sites was $0.09(\pm 0.02)/\text{m}^2$. *Echinometra viridis* was present at all sites, but had a lower average density at FPA sites, with $0.05(\pm 0.02)/\text{m}^2$ compared to $0.115(\pm 0.02)/\text{m}^2$ at control sites. The results of a one-way ANOVA found no significant difference between FPA and control sites for either *D. antillarum* ($p=0.18$) or *E. viridis* ($p=0.08$) densities.

Test diameter means did not vary widely among or within sites (Fig. 3). The average test diameter of *D. antillarum* at the sites where it was quantified in 2013 was 23.5(±2.85)cm. For *E. viridis*, the average test diameter was 23.7(±0.83)cm.

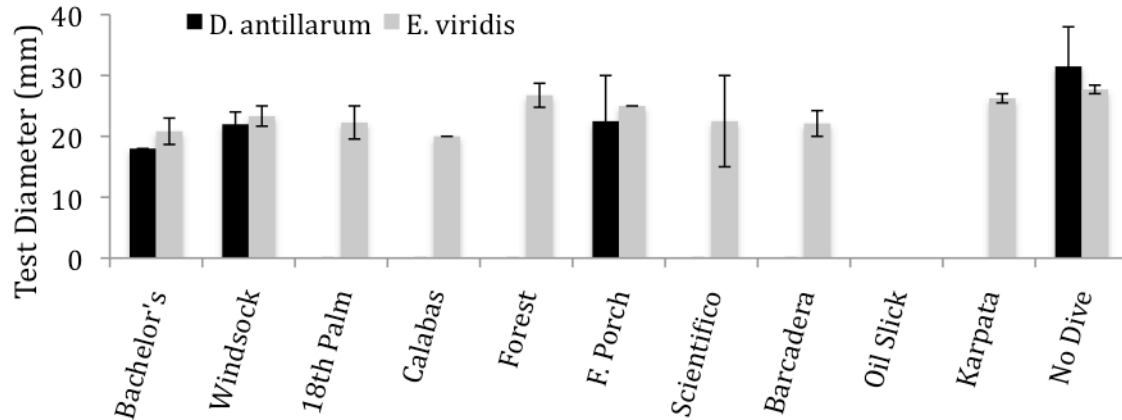


Figure 3. Test diameter averages ± SE of urchins at sites surveyed in 2013.

A look at historical trends of *D. antillarum* at monitored sites showed low densities continuing through the current survey (Fig. 4). Densities peaked at 0.027 (±0.02) individuals/m² in 2005, and have persisted since at lower levels around today's density of 0.012(±0.004) individuals/m².

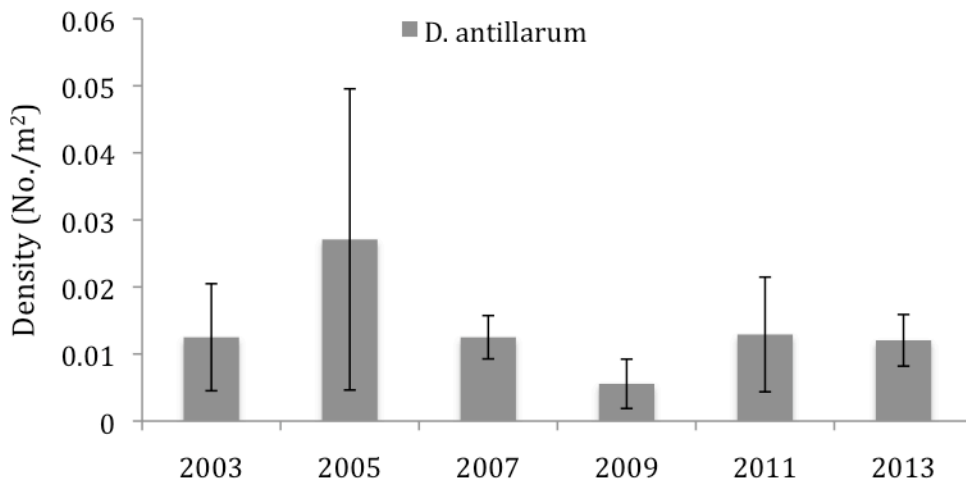


Figure 4. Densities of *D. antillarum* individuals at monitored sites over time.

Contrary to the trajectory of *D. antillarum* densities, *E. viridis* densities show a consistent upward trend in the last four years (Fig. 5). From when *E. viridis* was first observed in 2005 the densities have grown to 0.09(±0.02) individuals/m².

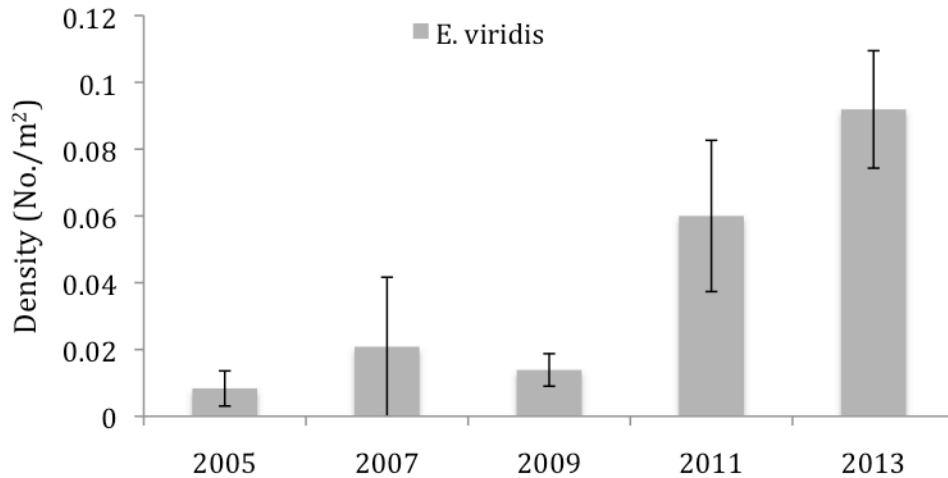


Figure 5. Densities of *E. viridis* individuals at monitored sites over time.

I built linear models for the relationships between *D. antillarum* and *E. viridis* densities and an Urchin Predation Index (UPI; see methods). The regression was neither significant for *D. antillarum* densities and the UPI ($p=0.93$), nor for *E. viridis* densities and the UPI ($p=0.98$).

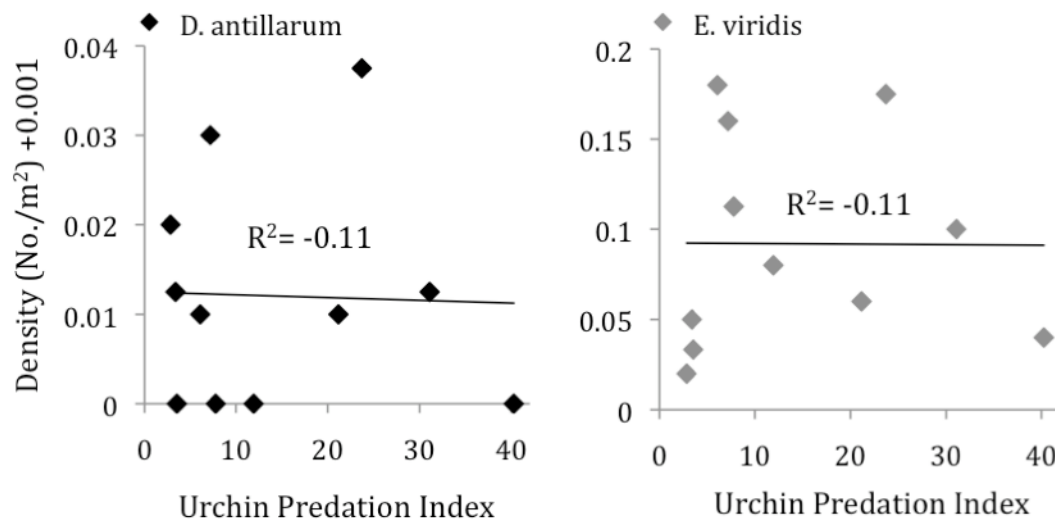


Figure 6. Scatterplots and linear regressions of *D. antillarum* and *E. viridis* densities as a function of an Urchin Predation Index based on known urchin predator biomass and their historical echinoid stomach volume (see methods for more details on computing index). Each point in scatterplots represents a 2013 site.

Discussion

At no sites on Bonaire are populations of *D. antillarum* (Figs. 1 & 4) anywhere near functional densities (Muthiga & McClanahan 2007). Populations of *E. viridis* continue to increase (Fig. 5), however they remain at densities substantially below those where *E.*

viridis has been reported to control algae (Aronson & Precht 2004). This species consumes drift algae and may be positively correlated with macroalgal abundance (McClanahan 1999). Thus, it is difficult to claim a significant role for *E. viridis* in controlling macroalgae. Currently, herbivorous fish appear to be sufficient on Bonaire reefs to control macroalgae.

Although before the 1983 *Diadema* mass mortality throughout the Caribbean, parrotfish and tangs were competitively excluded (eg Hay and Taylor 1985), at lower functional densities *Diadema* could provide additional resilience in this reef system.

The biggest unanswered question is why are *D. antillarum* populations not recovering? Should they recover, what is the threshold density above which they depress the abundance of macroalgae?

Evidence from elsewhere points to a negative relationship between predator biomass and urchin densities, especially in marine reserves where predator biomasses are higher (Tuya et al. 2004, Hereu et al. 2005; Brown-Saracino et al. 2007). On Bonaire, the local marine reserve or FPA system has been in effect for only a few years and as expected, the impacts have been restricted to fish eating serranids (Auscavitch and DeBey 2013; Chapter 7). Accordingly, there are no additional effect of FPAs on densities of either *D. antillarum* or *E. viridis*, though densities are somewhat lower in FPA treatments, and *Diadema* is absent at 75% of the FPA sites (Figs. 1 & 2). The urchin predation index for sites on Bonaire, calculated using urchin predator biomass as well as historical echinoid stomach volume for each species to weight their relative effects, produced an insignificant linear model when used in a regression with urchin densities (Fig. 6). The insignificant effect of FPA treatments and the uselessness of the urchin predation index in explaining urchin densities do not mean that predation pressure is not a key factor in keeping urchin numbers low. At such low urchin densities, relatively little predation pressure is required to keep densities low, and the entire range for the urchin predation indices found on Bonaire reefs may be sufficient to keep urchin densities low.

The small size of *D. antillarum* at Bonaire in 2013 (Fig. 3) is especially interesting because the small size has been observed on these sites since regular monitoring began a decade ago (Steneck personal observation). Chronic small size can result from intraspecific competition when *Diadema* persists at high population densities (Carpenter 1981). However, low sizes are attained at population densities exceeding 10/m² and very large urchins of nearly 100 mm diameter exist at densities of 2/m² (Carpenter 1981). Also urchins observed in Bonaire 2013 often had banded spines indicating they were newly settled juvenile urchins rather than the old trophically limited small urchins reported by Carpenter. Adult *Diadema* can reach larger sizes, with test diameters >90mm possible (Hughes 1994). Diameters of *E. viridis* at Bonaire reefs are similar to reports from elsewhere in the Caribbean (McPherson 1969; Cameron 1986). Similarity in the test diameters of *E. viridis* and *D. antillarum* at Bonaire sites points to a role for the size of refuge habitats at Bonaire. As *Diadema* grow, lack of sufficient larger crevices and other habitat (that may have been available before the die-off of *Acropora* sp.) may create a population bottleneck as the test diameter of individuals exceeds that of available

shelters. Beyond this size, larger *Diadema* individuals may be exposed to predation, and consequently are absent on Bonaire reefs (Fig. 3).

The availability of complex habitat, in particular crevices of the correct size to house an urchin and protect it from predation, has been shown to limit populations of *D. antillarum* and *E. viridis* elsewhere in the Caribbean (Lee 2006). In areas of sufficient preferred habitat for *D. antillarum* (such as the nooks of *Montastrea* heads) macroalgae is controlled better, which can result in a reinforcing feedback loop where areas with more complex habitat are better grazed, leading to higher recruitment success of juvenile corals that in turn add to habitat complexity (Lee 2006). *Diadema* larvae may have higher recruitment success in these areas of high rugosity, especially where aggregations of sympatric echinoids are already present (Bechtel et al. 2006).

Larval availability, subsequent settlement or survival to recruitment may be limiting *D. antillarum* populations on Bonaire and across the Caribbean (Williams et al. 2011). Low densities of *Diadema* continue to be the norm on most Caribbean reefs (Hughes et al. 2010). Density-dependent fertilization success for *D. antillarum* spawning has been shown (Leviton 1991), entailing possible Allee effects and low production of larvae and hence low larval availability at most sites across the Caribbean. Larval availability may decrease at sites further from larval sources due to settlement and larval mortality. As a result, recovery, if it happens, may occur in a pattern similar to that of the die-off of the early 1980s (Miller et al. 2003). However, there is no progressive increase in urchin density downstream so there is no support for connectivity with upstream reproductive populations as suggested for St. Croix (Miller et al 2003).

Diadema antillarum individuals measured on Bonaire in 2013 included mostly juveniles (*pers. observation*, Fig. 3). This pattern has been recorded on Bonaire for at least the last decade (Fig. 4), indicating recruitment, though, perhaps low, is not entirely absent for the species on Bonaire. Given the current and ongoing (R.S. Steneck, *pers. observation*) small test diameters of *Diadema* (Fig. 3), this means recruitment may be ongoing but survival to sizes larger than those protected by the reef's predator refugia, is not occurring.

The density at which effective recovery can be claimed for *D. antillarum* seems to be up for debate in the Caribbean. For the purposes of this discussion, recovery is defined as a density at which *Diadema* can control macroalgae. Recovery to densities as low as >0.6 individuals/m² has been reported to drive reef dynamics towards higher coral and lower macroalgae cover (Myhre & Acevedo-Gutierrez 2007). A return to *Diadema* densities of about 1/m² is enough to reverse hysteresis in systems that have flipped to algae-dominated states (Roff & Mumby 2012). A density of 2/m² may be ideal, as *D. antillarum* at this density exerts a strong control on macroalgae but not to the extent where it would exclude other herbivores (Muthiga & McClanahan 2007).

In conclusion, the combination of predation pressure and a lack of predator-free refugia for larger urchins contributes to the continued low densities of *Diadema*. If the ubiquitous and chronic small sizes of *Diadema* observed at Bonaire sites (Fig. 3) results from

predation pressure (Fig. 6) that crops them when they out grow smaller crevices, then crevice sizes for sheltering *Diadema* may be highly important. Current densities on Bonaire are steady well below a hypothesized ideal of 2/m² (Roff & Mumby 2012), or even the lowest level at which *Diadema* may control macroalgae (Myhre & Acevedo-Gutierrez 2007). *Diadema* recovery will likely be slow, if it in fact occurs at all, while predators persist on Bonaire.

Some studies have argued that *Diadema* abundance indicates locally high fishing pressure on their predators (Hay 1984, Levitan 1992) and thus, *Diadema* absence may be a proxy for good fisheries management. However, with continued and improved management of reef corals, larger spaces in the reef could develop and with them conditions for later post-settlement survival of *Diadema* could improve.

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Chapter 5: Patterns of distribution, abundance and temporal trends of the sea urchins *Diadema antillarum* and *Echinometra lucunter* in the shallow reef zones of Bonaire

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Abstract

Monitoring sea urchins in shallow water zones of Bonaire's leeward reefs began March 2005. In 2013 we surveyed urchin population densities at depths ranging between 0 and 5 m depth at ten sites, nine of which had been monitored in past years. Of the four species recorded, *Diadema antillarum*, *Echinometra lucunter*, *Tripneustes ventricosus*, and *Eucidaris tribuloides*, only the first two were commonly found. *Echinometra lucunter*, was abundant enough to effectively sample using a 1m² quadrat in the surf zone. Its average density of 8.8 ± 6.9 urchins m⁻² was the greatest of any urchin found in this or in all past surveys. The ecologically important *D. antillarum* was found at seven of the nine surveyed sites, with an average density of 0.00064 ± 0.0003 urchins m⁻², the lowest density found of all surveyed years. Since 2005, *D. antillarum* had increased slightly in 2007 but has since declined. *E. lucunter*, however, has increased steadily in recent years. Although none of the urchin species have a direct effect on Bonaire's coral reefs, both the decrease in *Diadema* and the increase in *E. lucunter* may indicate a general decline in reef health resulting from an increase in macroalgae.

Introduction

Many Caribbean reefs have transitioned from a coral-dominated to an algal-dominated ecosystem over the past few decades (Hughes 1994). In 1983 and 1984 *D. antillarum* experienced more than a 97% mortality rate; its disappearance revealed its importance as a reef herbivore (Mumby et al 2006). Before the mortality event, macroalgae was rare on reefs (Steneck 1998). Additionally, many studies have demonstrated the importance of this herbivore through removal or exclusion studies from small areas or with cages. All such experiments resulted in increases in macroalgal growth (Sammarco 1974; Carpenter 1981, 1986). Where *D. antillarum* was abundant prior to the die-off, it was capable of consuming 100% of daily algal production (Carpenter 1986). *Diadema* are recovering slowly in some places (Miller et al 2009) and they have reached relatively high population densities in a few places such as Jamaica (R.Steneck, *personal communication*)

Impacts of this mass mortality varied widely depending on the levels of herbivorous grazing fish. Locations with high fishing pressure, such as St. Croix and Jamaica, did not have enough grazing fish to keep up with the increase in algal growth; these reefs succumbed to the macroalgae shift (Steneck 1994) and have showed little or no signs of recovery since (Connell 1997). Bak et al. (1984) found a significant increase in both the length and density of filamentous algae only 1 week after the urchins began to die-off in Curaçao. Bonaire is one of the few places in the Caribbean that has managed to resist the algal phase shift after the *Diadema* die-off (Smith and Malek 2005). This is likely due to relatively high levels of herbivorous fish including parrotfish, surgeonfish, and

damsel fish (Scaridae, Acanthuridae, and Pomacentridae) that provide sufficient herbivore trophic function to keep reefs relatively free of macroalgae without the grazing urchins.

Echinometra lucunter also feeds on algae and in places may be present at higher densities than *Diadema*; however *E. lucunter* feed mostly at night on drift algae (Hendler et al 1995) and is not as effective for reducing macroalgae and increasing coral cover (Furman and Heck 2009). *E. lucunter* is a rock boring urchin, and burrows created by these urchins may contribute significantly to the breakdown of coral substrate and bioerosion of beach rock. A minimum estimate for the amount of beach rock eroded by *E. lucunter* is 14 cm³ per year (McLean 1967).

Study Species

Diadema antillarum is commonly referred to as the long-spined urchin. This species is very recognizable because of its long black spines protruding from a black test (the spherical shell on which the spines attach). Juvenile spines are white or banded white and black. Including the spines, these urchins can grow up to 500 mm in diameter (Hendler et al 1995). *Diadema* prefer complex reef habitat or artificial structure (Lee 2006), typically remaining in crevices during the day, emerging at night to graze (Hendler et al. 1995). Before the 1983/84 die-off, in their preferred habitats, they could be found at densities of more than 20 individuals per square meter in Barbados (Scoffin et al 1980). A study performed in nearby Curacao found densities as high as 12 urchins/m² prior to the die-off (Bak et al. 1984). They feed on algal turf which helps prevent coral-dominated areas from becoming algal-dominated. Interestingly, Williams and Carpenter (1988) found that algal turfs grazed by *D. antillarum* were 2 to 10 times more productive due to supplemental nitrogen from the urchin's excretion.

Echinometra lucunter is a rock boring urchin and inhabits limestone reef rock in shallow intertidal zones. These urchins have short, dark spines and a test that can range in color from dark brown to reddish. *E. lucunter* is found throughout the Caribbean and Central America, as well as north to the mid-Atlantic coast of North America and south to Brazil (Hendler et al 1995). Individuals can grow to be 15cm in test diameter, but most are up to 8cm in diameter.

Predators include fish such as triggerfish, grunts, jacks, and wrasses. However, *E. lucunter* are relatively safe from predation by fish in their intertidal habitat. This shallow water habitat, however, makes *E. lucunter* more susceptible to being eaten by shorebirds such as the ruddy turnstone (Schneider 1985).

Methods

Shallow Water Snorkel Surveys

Ten sites on the leeward reefs of Bonaire, Netherlands Antilles, nine of which were previously selected for monitoring, were surveyed for sea urchin abundance: 18th Palm, Calabas, Front Porch, Reef Scientifico, Bachelor's Beach, Windsock, Forest, Oil Slick Leap, Barcadera, and Karpata. Shallow water snorkel surveys were performed at all 9

sites. Snorkelers performed area searches out to 5m deep. Snorkelers measured 50m sections along the shore and also the distance out to 5m depth to calculate total area searched. This method was selected because of the anticipated low density of urchins. Snorkelers thoroughly searched the entire area, diving down to look under coral heads and in crevices. When urchins were found, the species, size, and water depth were recorded. Shallow water patch reefs have been surveyed for urchins every other year since 2005, with the exception of 2011. Therefore, this was the first survey of this kind to occur since 2009.

Surf Zone Quadrat Surveys

E. lucunter populations were surveyed in the intertidal zones of sites with accessible shorelines. Sites with either cliff or boulder shorelines were not surveyed for *E. lucunter* using the 1 m² quadrat method; these included Reef Scientifico, Bachelor's Beach, Forest, Oil Slick Leap, and Barcadera. At sites with accessible shoreline, the intertidal zone was surveyed on foot and a 1 m² quadrat was randomly placed along the shore adjacent to the shallow water urchin surveys. The number of quadrats per site varied from five to eleven. The number of urchins in each quadrat was recorded, as well as the test size of each urchin in centimeters.

Results

Diadema antillarum

Of the ten sites surveyed with shallow water snorkeling, 17 individual *Diadema antillarum* were found. The site-by-site population density ranged from 0 to 0.0026 urchins m⁻², with the highest density found at Front Porch (Fig. 1). The mean number of urchins found at all sites was 0.000639 ± 0.000311. A Kruskal-Wallis test was performed to determine any difference between the nine sites; no statistically significant difference was found ($\chi^2=9$, DF=9, p=0.437). There was no significant difference in urchin densities found in 2009 vs. 2013 (Fig. 2), but there were some notable differences. In 2009, the highest population densities were found at Reef Scientifico (0.24 urchins m⁻²). In contrast, this year, no urchins were found at that site. The mean density of *Diadema* found in the Fish Protected Areas was higher than the Control Sites (0.001217 urchins m⁻² vs. 0.000254 urchins m⁻²) (Fig. 1). This is not a statistically significant difference ($\chi^2 =0.755$, DF=1, p=0.388).

The size-frequency distribution (Fig. 3) of *Diadema* by test size diameter shows a range from 2 to 6cm, with a mean of 3.88cm. Data from past reports differed the 2009 report indicated a mean test size of 4.5cm (Prendiville 2009); in 2005 the majority of individuals were larger than 8cm (Smith and Malek 2005).

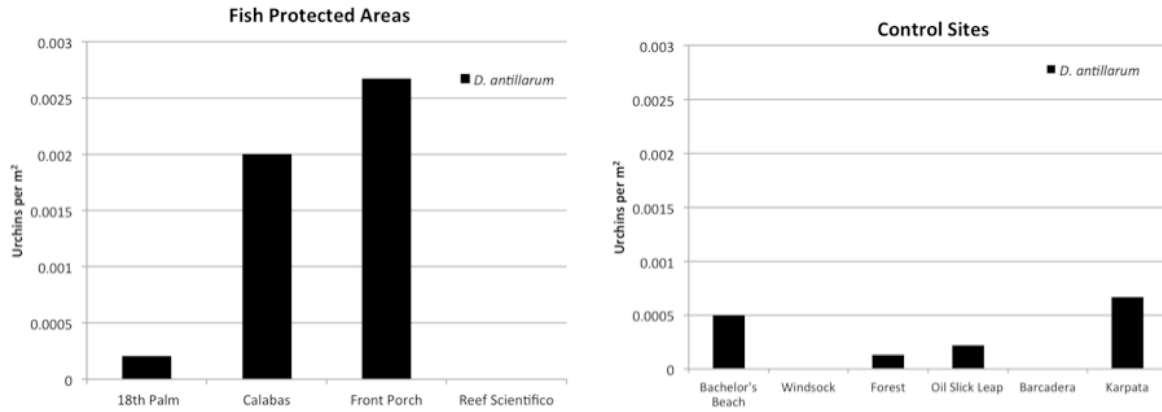


Figure 1. Abundance of *D. antillarum* per m² at both fish protection area sites (left) and control sites (right). Zero *Diadema* were found at Reef Scientifico, Windsock, and Barcadera.

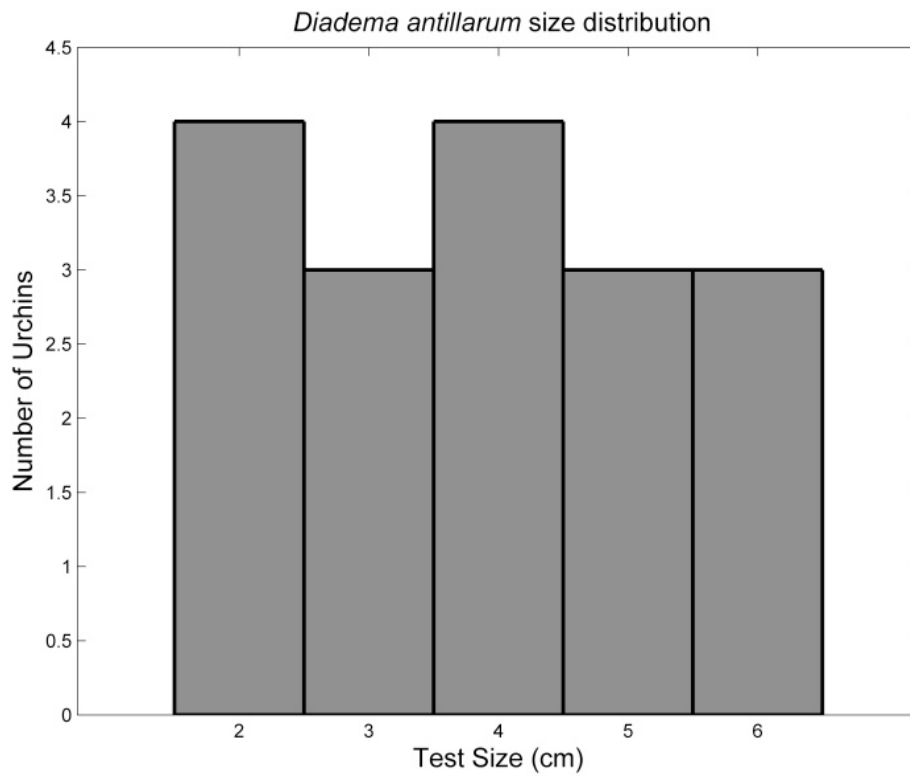


Figure 2: Size distribution of *Diadema antillarum* test size (cm). Data is summed from all nine sites. N=17.

D. antillarum per m² per year

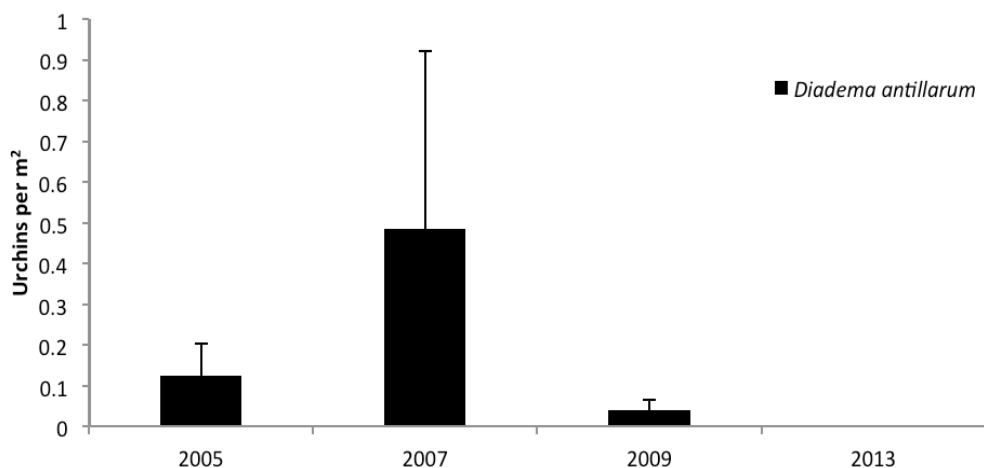


Figure 3: Population density of *Diadema antillarum* across four years; values are averages of all sites. Error bars show standard error. Note that shallow urchin surveys were not conducted during the 2011 Bonaire coral reef surveys.

Echinometra lucunter

Populations of *E. lucunter* largely were restricted to sites where rocky intertidal habitat (e.g. beachrock) was available. Several sites had either cliff or boulder shoreline impossible to survey and thus are designated “ND” (no data in Fig. 4). Of the remaining five sites that have more gradual intertidal zones, population density ranged from 0.2 urchins m⁻² at Front Porch to 36.2 urchins m⁻² at Calabas. Population density is displayed on a logarithmic scale to allow for visualizing of abundance spanning several orders of magnitude (Fig. 4). Mean abundance for FPA sites was 12.8 (± 11.7) *E. lucunter* m⁻², and mean abundance for control sites was 2.8 (± 2.3) *E. lucunter* m⁻².

Size distribution of *E. lucunter* test diameter was dominated by individuals with a 2 cm diameter test, and normally distributed around 2 cm (Fig. 5).

Populations of *E. lucunter* have generally been low over the past eight years, with the lowest abundance in 2007, but this has recently changed. We recorded the highest echinoid population densities in 2013 (Fig. 6). In 2005, mean population abundance over all sites surveyed that year (18th Palm, Reef Scientifico, Windsock, Forest, Barcadera, Karpata) was 0.18 (± 0.18) urchins m⁻². In 2007, five sites were surveyed for shallow urchins (18th Palm, Reef Scientifico, Windsock, Barcadera, Karpata) and the average abundance was 0.017 (± 0.011) urchins m⁻². Nine sites were surveyed in 2009 (18th Palm, Calabas, Front Porch, Reef Scientifico, Bachelor’s Beach, Windsock, Forest, Oil Slick Leap, and Barcadera) and the average abundance was 0.28 (± 0.08) urchins m⁻². Average population abundance across all sites in 2013 (8.8 \pm 6.9) is just over a ten-fold increase since 2009; however large standard error in 2013 due to high variation between sites results in an insignificant difference between abundance in 2009 and 2013 (P-value = 0.36).

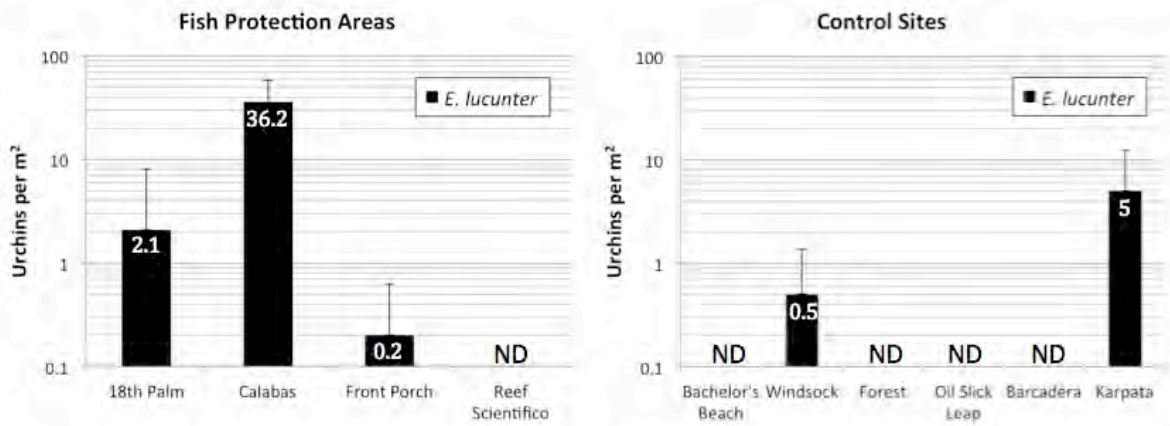


Figure 4: Abundance of *E. lucunter* m⁻² at both fish protection area sites (left) and control sites (right). Error bars show standard deviation. “ND” represents sites where 1-m² quadrat surveys were not conducted. Ordinate values are on a log scale, and values of abundance are shown in white near the top of each column.

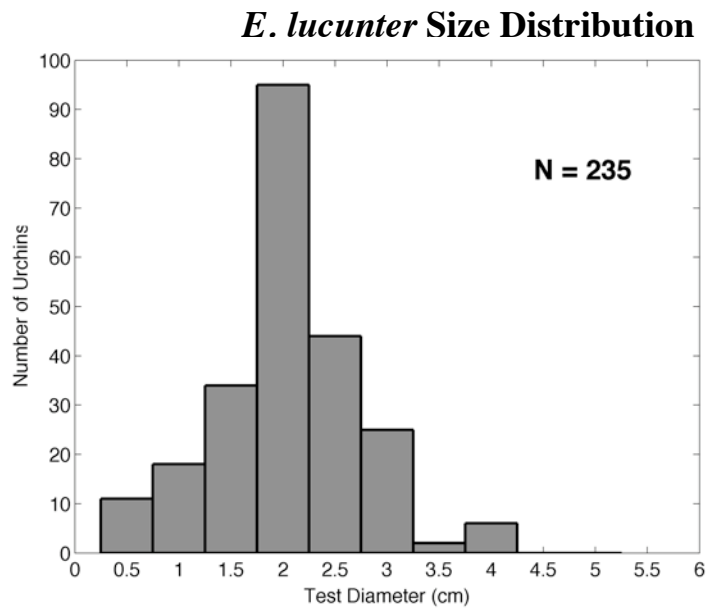


Figure 5: Distribution of *E. lucunter* test diameter (cm) from 1 m² quadrat data at all sites surveyed.

E. lucunter Intertidal Abundance

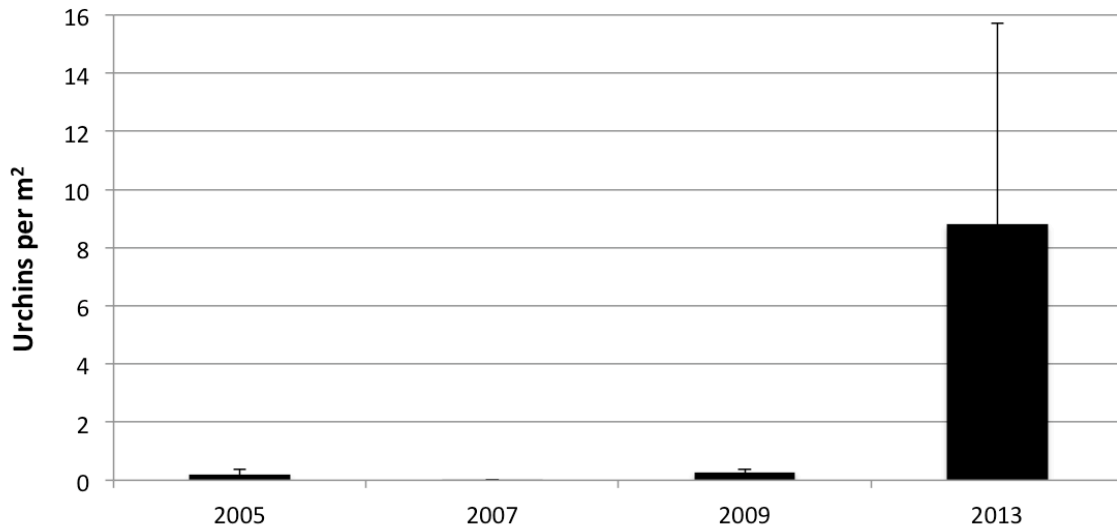


Figure 6: Population abundance of *E. lucunter* across several years; values are averages of all sites. Error bars show standard error. Note that shallow and intertidal urchin surveys were not conducted during the 2011 Bonaire coral reef surveys.

No *Echinometra viridis* were found at any sites. Two *Tripneustes ventricosus* specimens were found in the snorkel surveys, one at Reef Scientifico and one at Oil Slick Leap. In the surf zone quadrat surveys, 23 *T. ventricosus* individuals were found.

Discussion

Diadema antillarum

Diadema populations have remained low and patchy in Bonaire since the mass mortality event in 1984. The recovery has been slow throughout the Caribbean (Miller et al 2009) but population densities of *Diadema* found by this survey this year are the lowest on record. There are a few reasons that the populations may be rebounding slowly including high predation and low larval supply.

The most likely reason behind the low urchin population densities is high predation rates. Studies from the Indian Ocean show that fish can account for 90% of urchin predation and that predation can occur at levels high enough to regulate predation (McClanahan and Muthiga 1989). The major predators of *Diadema antillarum* are triggerfish, grunts, jacks, and wrasses (Hendler et al 1995). Predatory fish have shown an increasing trend since 2003 in subtidal areas (DeBey 2011), though shallow reef zones have not been surveyed for predators. Additional evidence for this hypothesis is that urchin sizes from 2013 were average smaller than those found in past reports. Most likely, this size distribution is indicative of a healthy predator population consuming the urchins before they can reach larger sizes.

Low larval supply has been proposed as a factor limiting recovery of *D. antillarum* in both Panama and the Florida Keys (Miller et al 2009, Lessios 2005). Williams et al (2011) studied the spatial variation of larval *Diadema antillarum* settlement in Puerto Rico. They found that the optimal depth for larval settlement was 9 meters, with the lowest settlement in shallower waters. If this is the case in Bonaire, it would explain low *Diadema* in shallow-water reef habitats; the dead *Acropora cervicornus* stands between the reef slope and the shallow patch reefs would serve as a barrier to the urchins. Migrating between the two areas would require traversing a large area without any hiding spots, leaving them vulnerable to easy predation. It is also possible that newly settled sea urchins are being consumed by grazing herbivores before they can reach a growth refuge (found to be ~10mm for another urchin species) (Scheibling and Robins 2008). However, *Diadema* herbivory may facilitate recruitment by reducing macroalgae and increasing coralline algae (R. Steneck, *Pers. Comm*). Low larval supply is also likely as local population densities are so low and recovery of populations has been slow in most other Caribbean locations (Miller et al 2009).

Despite the *Diadema* populations, Bonaire has not experienced the major increase in macroalgal abundance found in other Caribbean islands such as Jamaica (Hughes 1994, Steneck 1994). Because fishing pressure is relatively low in Bonaire, other herbivores such as parrotfish (Scaridae), yellow-tail damselfish (Pomacentridae) and tangs (Acanthuridae) are at levels high enough to keep the turf algae down. These herbivorous fishes may provide a degree of functional redundancy to the system that was lacking in Jamaica at the time of the die-off. A system with multiple herbivores would likely be more resilient to macroalgal dominance after disturbances such as hurricanes, overfishing, and changing nutrient levels. Functional redundancy is a sign of a healthy reef, however, in Bonaire the story might be slightly different because of the substantial herbivorous fish populations and effective management practices.

Echinometra lucunter

The increase in *E. lucunter* intertidal abundance over previous years is largely influenced by the very high density of urchins at Calabas. Calabas was only surveyed previously in 2009, when *E. lucunter* density was approximately 0.56 urchins m⁻². The values found this year are noticeably higher (36.2 urchins m⁻²), and it is possible that the urchin population at Calabas has been increasing due to lower mortality rate in the more sheltered surf zone of the Calabas site (Lewis and Storey 1984). One possible reason this may be occurring now and not in previous years is an increased abundance in macroalgae and thus drift algae, which *E. lucunter* feeds on.

Although the mean abundance of *E. lucunter* determined from quadrat surveys showed an order of magnitude increase in abundance at FPA sites compared to control sites, we do not expect a no-take reserve effect on quadrat data since the intertidal area is a microhabitat that is difficult for fish to access. Thus, observed patterns when comparing FPA and control sites for quadrat surveys may instead be due to the varying presence of beachrock in the intertidal area of different sites, which is the preferred habitat of *E. lucunter*.

The size distribution of *E. lucunter* observed in the quadrat surveys of this study was noticeably smaller than the full-grown test diameter for the species. This may indicate that the majority of *E. lucunter* observed during this study are from a more recent year-class, perhaps indicating recent population increase at several areas where high density was recorded. In comparison, *E. lucunter* from a 2008 study in Bermuda found a majority of urchins had a test diameter of 5-7cm (Ebert et al 2008). Although Bermuda is farther north and has a higher abundance of algae, it may be the case that increased macroalgae and thus drift algae in Bonaire has allowed for a recent increase in *E. lucunter* populations.

Most urchins are omnivores, which increases their available food supply and makes it possible for different species to occupy the same habitat (McPherson 1969). Despite this, no *Echinometra viridis* were observed in the 2013 intertidal quadrat surveys, whereas *E. viridis* were found at several sites in 2009 (Prendiville 2009). However, *E. lucunter* and *T. ventricosus* were found cohabiting some of the same tide pools at 18th Palm.

An interesting pattern in the populations of *Diadema* and *E. lucunter* in the shallow reef zones over the past eight years is a decrease in *Diadema* (Fig. 3) and an increase in *E. lucunter* (Fig. 6). In addition, there is an increasing trend in deeper *E. viridis* that parallels the increase in *E. lucunter* (Fig. 5 in Kersula 2013 Chapter 4, this report). These patterns may indicate that fewer *Diadema* are related to an increase in macroalgae, which then leads to an increase in drift algae as pieces of macroalgae dislodge and enter the water column. *Echinometra* species are ecosystem passengers in the sense that they do not control algal abundance, but instead are positively correlated with the presence of fleshy algae (McClanahan 1999). Therefore, the inverse relationship between the decreasing trends in *Diadema* and the increasing trends in *Echinometra* populations may be indicative of a general decline in reef health on the leeward coast of Bonaire.

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Chapter 6: Patterns of Distribution and Abundance in Territorial Damselfish Populations in Bonaire

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Abstract

Population densities of territorial damselfish were quantified at seven monitored sites open to fishing and four sites closed to fishing. The surveys quantified damselfish species distribution, abundance, size, and developmental stage damselfish abundance increased over the past decade, and corresponds with spatial differences in species distribution. Damselfish biomass was weakly inversely correlated with the fish protected area (FPA) program. but the factors directly mediating this relationship remain unknown. Bottom-up and top-down demographic controls may be of equal importance to the regulation of territorial damselfish populations in Bonaire.

Introduction

Herbivory can limit algal biomass facilitating coral recruitment on reefs (Steneck 1988, Arnold et al 2010). However, territorial damselfishes (*Stegastes spp.*) functionally reduce grazing due to their aggression against herbivores resulting in increases of algal biomass within their territories (Hixon 1997). Even a modest increase of filamentous turf algae from 2 mm outside territories to 4 mm within damselfish territories can result in a 75% reduction in coral settlement (Arnold et al 2010). Importantly, the abundances of the two predominant territorial damselfishes in Bonaire, the threespot (*Stegastes planifrons*) and longfin (*Stegastes diencaeus*) damselfishes, have increased since 1990 (Bruggeman *et al.* 1995, Arnold 2011), it is not known why or at what rate.

Several factors are thought to drive the abundance of territorial damselfishes. They include predation (Hixon and Beets 1993), habitat suitability (Precht *et al.* 2010), inter- and intraspecific competition (Hixon and Jones 2005), food availability (Booth and Hixon 1999), and climate (Cheal *et al.* 2007). While some believe that increased predator abundance depresses both the abundance and behavior of damselfishes (Hixon and Beets 1993, Belmaker *et al.* 2008), others argue the availability of coral habitat rather than predators drives their abundance (Precht et al 2010).

Most research has focused on top-down predatory dynamics regulating territorial damselfish density in recent years (Hixon and Beets 1993, McClanahan 2005, Ceccarelli *et al.* 2006). In the Great Barrier Reef the increased predator abundance within no-take reserves (the “Green Zones”) increased predation on damselfish and the reduced territories in the reef resulted in increased coral recruitment and abundance (Almany 2004). Although the ecological argument for this relationship and evidence of its strength in Bonaire remains lacking and alternative factors governing territorial damselfish abundance have not been explored. The implementation of Bonaire’s fish protected areas

(FPAs) in 2010, creates an experiment to test impact of fishing on predators and ultimately determine if changes in predator abundance affects damselfish abundance.

To examine these alternatives, I conducted surveys of territorial damselfish abundance in Bonaire using methods commensurable with studies conducted on fixed transects along monitored reefs since 2003. My goal is to determine if territorial damselfish abundance has increased over the past decade and see if damselfish density, biomass, and species distribution, correspond to geography, predator biomass (resulting from FPAs) and average coral cover.

Methods

SCUBA diver-based visual census surveys of territorial damselfish abundance were conducted at 11 sites on the leeward shore of Bonaire and Klein Bonaire from 3-7 March 2013. Four of the sites were located within FPAs. Eight 2x10 meter belt transects were placed at approximately 10 meters depth along the fore reef. The species ID, developmental stage, and estimated fork length of all *S. planifrons* and *S. diencaeus* within each transect area were recorded.

The biomass of damselfishes and predators was estimated using the allometric length-weight relationships described in Bohnsack and Harper (1988) and Marks and Klomp (2003). Length-weight parameters for *S. planifrons* were assumed accurate for *S. diencaeus* because of their taxonomic similarity and the lack of an empirically derived relationship for *S. diencaeus*. The list of damselfish predators detected in the survey that are known to consume damselfishes include derived from Randall (1965) and include serranids (tiger grouper, graysby, and rock hind), lutjanids (schoolmaster, yellowtail snapper, and mahogany snapper), carangids (bar jack) and scorpaenids (spotted scorpionfish). Predator survey data from Auscavitch and DeBey (Chapter 7). Average coral cover data were provided by R. Steneck. Damselfish abundance data from previous surveys were derived from previous editions of this report and a similar survey conducted in the 1989 (Bruggeman *et al* 1995).

All statistical analyses were performed using the JMP 10 statistical software package. ANOVAs were performed when appropriate; nonparametric tests were performed when the residual variance of the data was not normally distributed. Densities and biomass estimates were standardized to quantity per 100 m².

Results

Spatial Patterns:

Average damselfish density was 44.9 individuals per 100 m². Densities differed significantly between sites (Student's t-test, $\alpha = 0.05$; Fig. 1). Barcadera had the highest density of all the sites, 52% greater than Forest, the next-highest site. Bachelor, Calabas, Front Porch, Scientifico and Oil Slick were grouped together at the lowest density level.

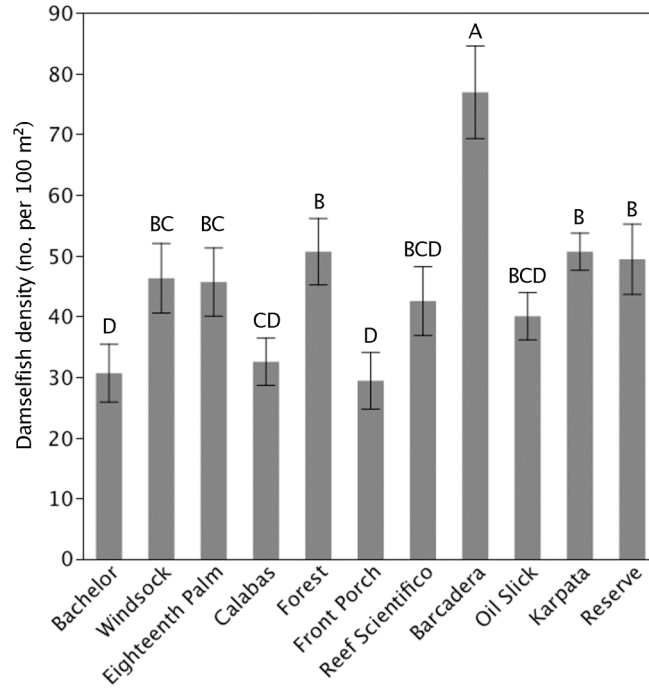


Figure 1. Territorial damselfish density, by site arranged by latitude. Bars indicate \pm one standard error from the mean. Letters indicate significance level; levels not connected by the same letter are significantly different. Note that FPA sites include Eighteenth Palm, Calabas, Front Porch and Reef Scientifico.

Average damselfish biomass was 1221 grams per 100 m². Biomass differed significantly between sites (Student's t-test, $\alpha = 0.05$; Fig. 2). Barcadera had the highest biomass of all the sites. Front Porch and Forest were grouped together at the lowest level of biomass.

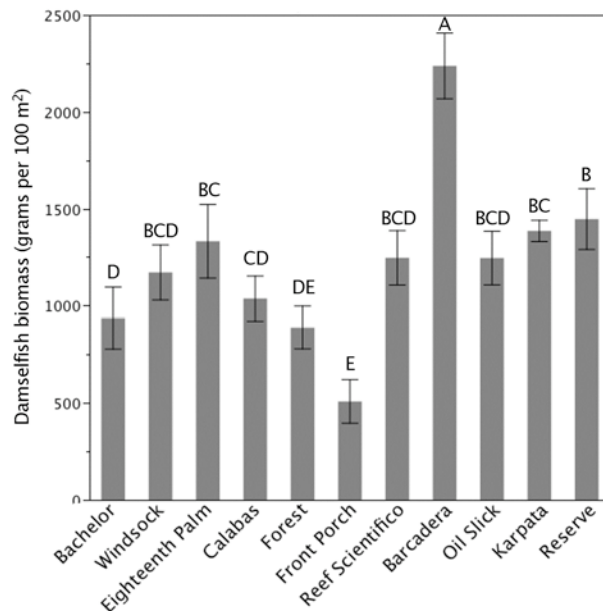


Figure 2. Territorial damselfish biomass, by site arranged by latitude. Bars indicate \pm one standard error from the mean. Letters indicate significance level; levels not connected by the same letter are significantly different.

Damselfish were significantly smaller at Forest and Front Porch than all other sites (Student's t-test, $\alpha = 0.05$; Fig. 3). Similarly, the proportion of fish in the adult phase was significantly lower at Forest and Front Porch (Student's t-test, $\alpha = 0.05$; Fig. 4).

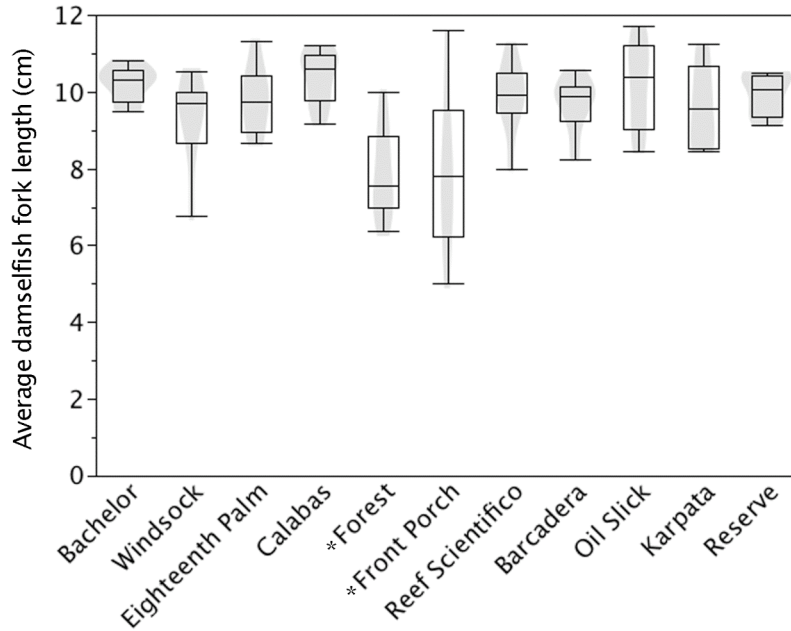


Figure 3. Average territorial damselfish length, by site arranged by latitude. Box plots are the standard five-point summary format. Contour plots represent the number of replicates occurring along a spectrum of size. Sites with statistically significantly lower average lengths than the rest indicated by asterisks.

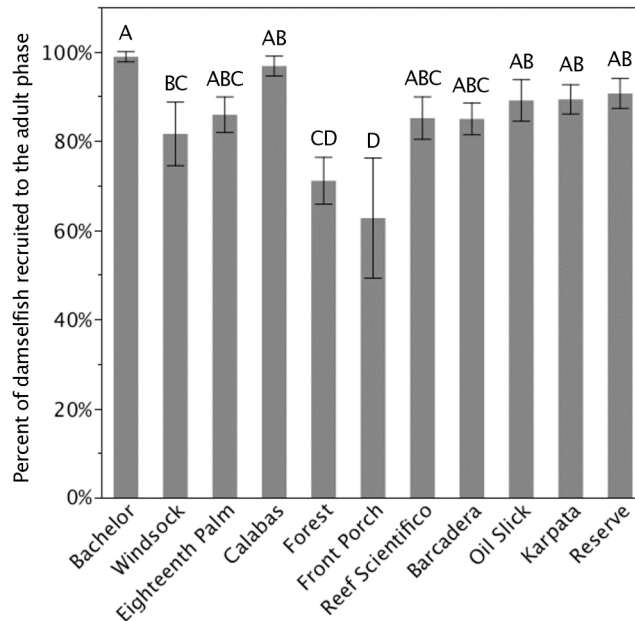


Figure 4. Percent of territorial damselfish recruited to the adult phase, by site arranged by latitude. Bars indicate \pm one standard error from the mean. Letters indicate significance level; levels not connected by the same letter are significantly different.

The species distribution of damselfishes displayed geographic patterns that may relate to wave exposure (Fig. 5). *S. planifrons* was predominant in the more exposed sites to the north and west, whereas *S. diencaeus* was predominant in the more sheltered sites to the south and east. The statistical relationship between the abundance of the two species was weak (Linear regression: $R^2 = 0.265$), indicating that some factor other than interspecific competition is mediating geographic distribution.

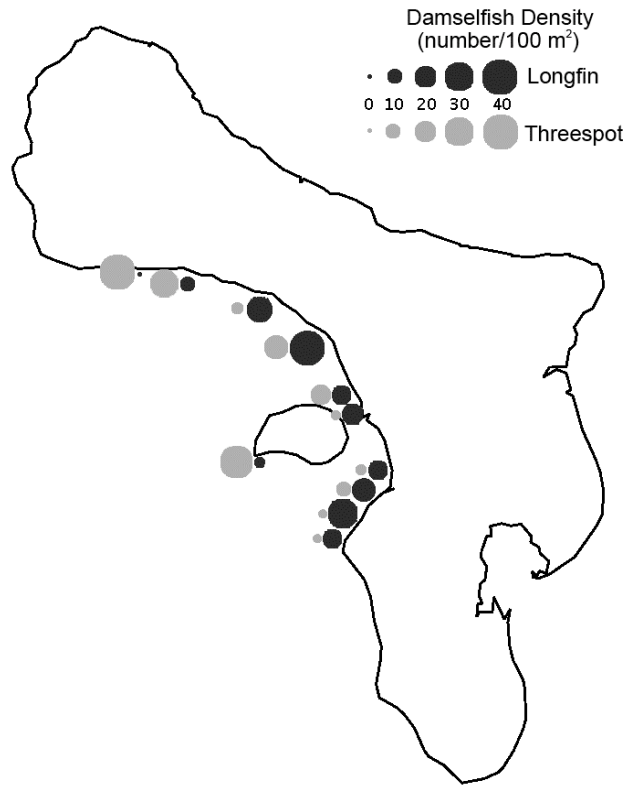


Figure 5. Geographic distribution of *Stegastes planifrons* (gray) and *Stegastes diencaeus* (black) densities, indicated by marker size, at each surveyed site in Bonaire.

Temporal Patterns:

Damselfish abundance in Bonaire has doubled over the past two decades (Fig. 6). Surveys from 1990 to 2013 were assessed for methodological consistency. Surveys in 2005 and 2011 were not commensurable with methods used earlier and this year. Thus they may have misrepresented damselfish biomass and were not considered in this analysis.

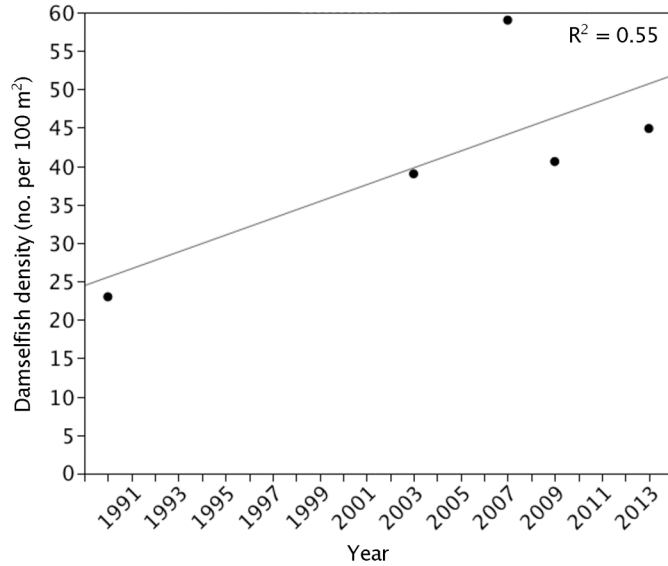


Figure 6. Territorial damselfish densities over time. 1990 data are from Bruggeman *et al.* (1995).

Patterns of Abundance Relative to Predator Abundance:

Estimated damselfish biomass was significantly lower at the sites inside FPAs than those outside (ANOVA: $F = 6.261$, $DF = 1$, $p = 0.0142$; Fig. 7). This effect, however, is due in large part to the anomalously high biomass estimates from the survey at Barcadera, which had a mean biomass estimate 55% greater than the next-highest site (Reserve) and 79% greater than the site immediately adjacent to it (Oil Slick). When Barcadera is omitted from the analysis, the null hypothesis that damselfish biomass is the same inside and outside of FPAs cannot be rejected.

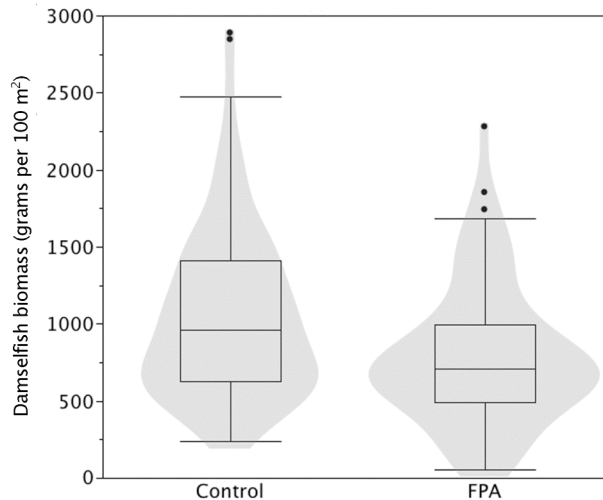


Figure 7. Estimated damselfish biomass by FPA treatment, grouped by transect. Box plots are the standard five-point summary format. Contour plots represent the number of replicates occurring along a spectrum of biomass.

Estimated biomass of territorial damselfish predators was quantified and compared to several damselfish demographic variables. There was no correlation between mean damselfish biomass and mean damselfish predator biomass (Linear regression: $R^2 = 0.03$ Fig. 8). Mean predator biomass did not correlate with FPAs (ANOVA: $F = 1.466$, $DF = 1$, $p = 0.228$; Fig. 9). No correlation was detected between mean predator biomass and the relative abundance of damselfish juveniles at each site (ANOVA: $F = 0.237$, $DF = 1$, $p = 0.638$).

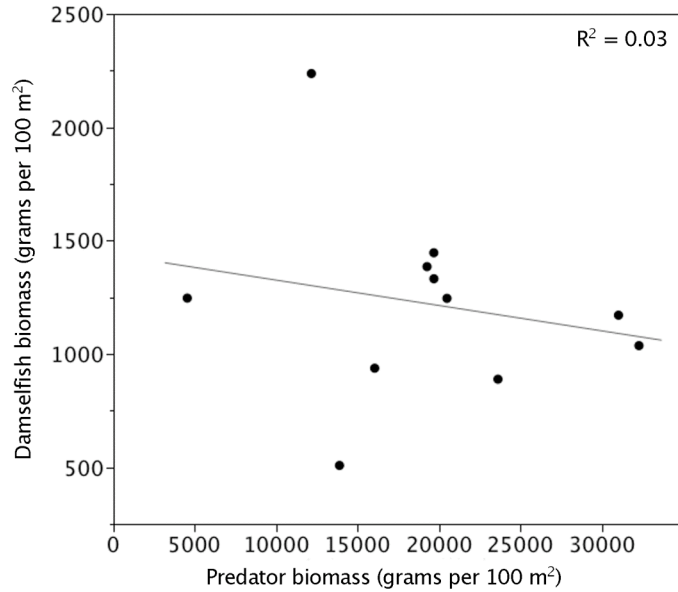


Figure 8. Estimated damselfish biomass by estimated predator biomass.

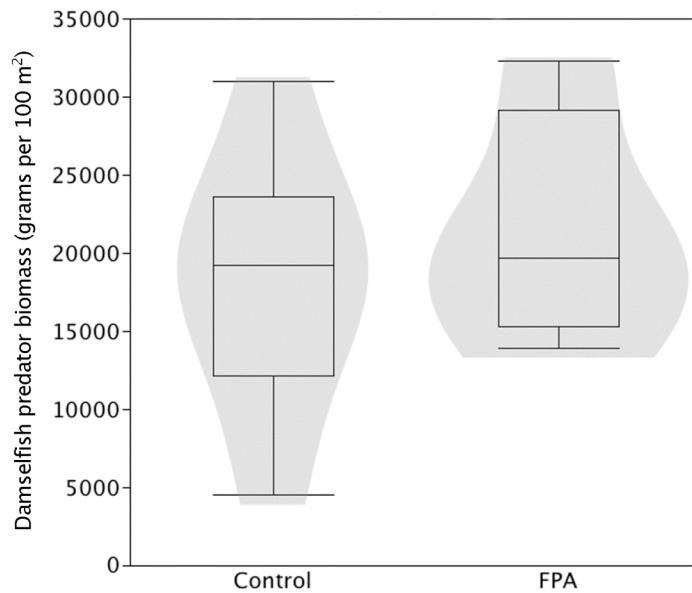


Figure 9. Estimated damselfish predator biomass by FPA treatment. Box plots are the standard five-point summary format. Contour plots represent the number of replicates occurring along a spectrum of biomass.

Serranids, the primary piscivorous reef predator family in Bonaire, were analyzed separately from the other predators detected in the survey. There was no correlation between mean damselfish biomass and mean serranid biomass (Linear regression: $R^2 = 0.18$). Mean estimated serranid biomass did not correlate with FPAs (ANOVA: $F = 0.328$, $DF = 1$, $p = 0.581$; Fig. 10).

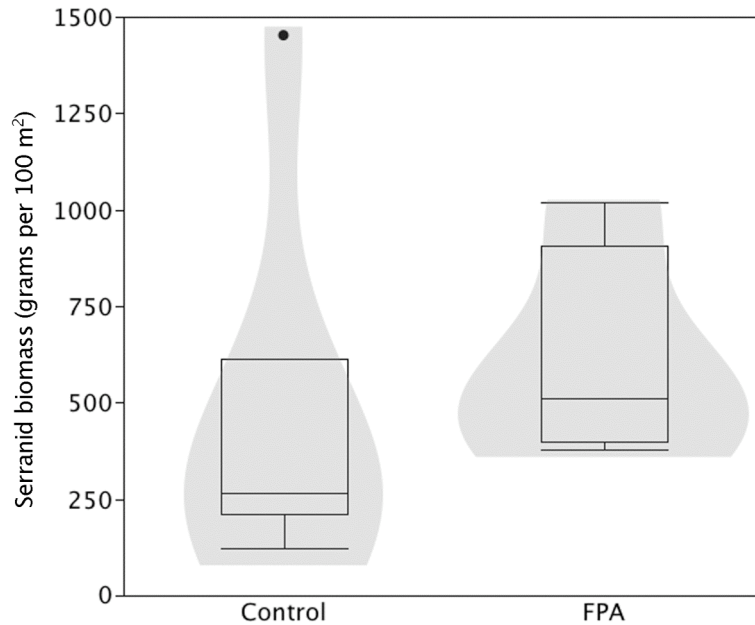


Figure 10. Estimated serranid biomass by FPA treatment. Box plots are the standard five-point summary format. Contour plots represent the number of replicates occurring along a spectrum of biomass.

Although some averages are suggestive that damselfish biomass was lower (Figs 7,8) and predator biomass was higher (Figs 9 and 10), those averages may be misleading since their interactions do not occur at the scale of the island of Bonaire but at the scale of individual reef sites. Not all listed predators will likely show abundance trends; especially if they are not targeted by fishers. Accordingly, the FPA reserves will likely only have an impact on fished species and not on all serranids. Based on interviews with fishermen, the most heavily fished species are relatively small reef-dwelling serranid such as graysbys, coneys and red hind (Nenodovic 2007). Those targeted serranids all were more abundant in FPA sites than control sites (Auscavitch and DeBey 2013; Chapter 7).

Damselfish population density and biomass both decline significantly as a function of the biomass of targeted serranids (Fig. 11). Three of the four FPA sites had lower than average population densities and biomass among sites with higher than average targeted serranid biomass.

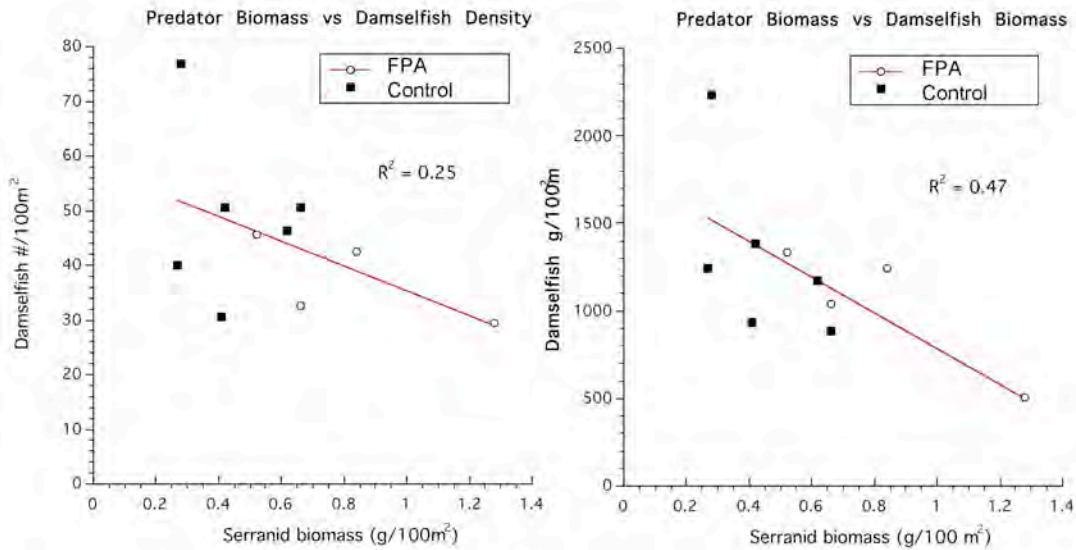


Figure 11. The population density (left) and biomass (right) of territorial damselfishes. Target serranid biomass was lowest in the fished (control) areas relative to the FPA sites.

The mean percent coral cover of each of the surveyed sites was compared to several damselfish demographic variables. There was no significant correlation between percent coral cover and damselfish biomass (ANOVA: $F = 0.696$, $DF = 1$, $P = 0.426$; Fig. 12). There was a weakly statistically significant correlation between percent coral cover and relative species abundance, whereby the ratio of abundance of *S. diencaeus* to *S. planifrons* increased in proportion to coral cover (ANOVA: $F = 5.175$, $DF = 1$, $p = 0.049$). This could relate to how species use specific aspects of their habitat.

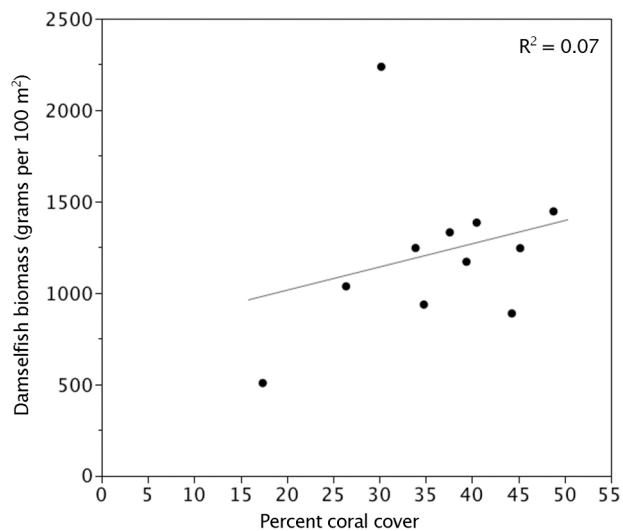


Figure 12. Estimated territorial damselfish biomass by average coral cover.

Discussion

Territorial damselfish populations have increased over the past two decades (Fig. 6) and it is unclear whether these populations have stabilized in recent years. There is also evidence dating back to the 1990s that predatory fishes have declined over the same period (e.g., Hawkins et al 1999 with some groups showing the lowest biomass in a decade this year (Auscavitch and DeBey 2013; Chapter 7). These sorts of patterns have largely been attributed to top-down predatory interactions (Hixon and Beets 1993), but in recent years there has been more consideration of bottom-up habitat resource limitations. For example, Hixon and Jones (2005) proposed that predation is a key driver, but its demographic effects scale inversely with habitat complexity. More recently, Precht *et al.* (2010) attributed demographic control of territorial damselfishes to coral-generated habitat complexity.

The most parsimonious explanation for the results represented in my study is that intersite increase in targeted predators of graysbys, coneys and red hind corresponds well with the decline in damselfish density and biomass (Fig. 11). The relationship of damselfish density and coral-generated habitat complexity can only be considered with respect to coral cover. However, over the past decade when damselfish densities were increasing, coral cover was either constant (ie 1999 – 2009) or declining (2011 and 2013) (Steneck 2013; Chapter 1). Coral cover described only 7% of the variance among sites with coral cover (Fig. 12). So the pattern described by Precht et al (2010) does not seem to fit the patterns in space or time in Bonaire.

The strength of these drivers is context-specific and may scale in proportion to complex variables. From the conservation and management perspectives, it is important to assess the nature and strength of forces affecting the negative drivers of the ecosystem. For the managers of Bonaire's coral reefs, a thorough and up-to-date assessment of the nature of the drivers of territorial damselfish abundance is crucial in order to both steer conservation efforts and assess the success of policies already in place.

Although interannual variability exists at many sites the overall trend between 1990 and 2013 results in a positive slope. Although perhaps anomalously high in the 2013 survey, Barcadera had significantly greater abundance than all but two other sites in 2011 (Arnold 2011). Territorial damselfish abundance at Front Porch was significantly lower than at other sites in 2013. Trends in estimated biomass of damselfish predators did not parallel those seen in damselfish biomass. It is unclear whether the factors that regulate damselfish abundance scale similarly between trophic levels and across sites in Bonaire; further detailed investigation of these drivers should be conducted.

The relationship between density and biomass at the sites was relatively consistent. However, at Forest, the abundance of surveyed damselfish was grouped among the higher levels, whereas the estimated biomass was grouped among the lowest. In general, the average size of territorial damselfish observed in the surveys decreased significantly from 2011 to 2013. It is unclear whether this is due to increased local recruitment, increase in suitable habitat availability, a decline in predation on juveniles, or other factors. Forest

may serve as a recruitment hotspot for juvenile damselfish, or recruitment on Klein Bonaire may be elevated relative to Bonaire. A strong recruitment pulse in 2013 may result in increases in territorial damselfish recruits in future years. Further spatial replication with the inclusion of additional sites with high juvenile abundance may be necessary to address this question.

Species distribution displayed interesting geographic trends that imply interspecific interactions not detected in this study. The northwestern shift of *S. planifrons* abundance and the southeastern shift of *S. diencaeus* were discrete and statistically significant, but were significantly correlated with each other. This suggests that interspecific competition, whether for space or some other resource, is not a factor regulating the relative abundance of these two fishes. Although not quantified here, it was qualitatively noted that in areas of greater interspecific overlap *S. planifrons* occupied territories at topographic highs on the reef whereas *S. diencaeus* occupied territories at topographic lows. This may be an example of niche compression due to competition without noticeable demographic effects (MacArthur 1958). Further study of this interspecific interaction is certainly required.

A weakly statistically significant correlation was detected whereby damselfish abundance is reduced within FPAs. The correlation between damselfish biomass and FPAs was statistically significant for the 2011 survey results (Arnold 2011), suggesting that this may be a robust relationship over time. Additional analyses in subsequent surveys may help elucidate the causal factors.

While damselfish biomass was lower in FPAs, the patterns with respect to predators is complicated. Considering all known damselfish predators, biomass was not significantly higher in FPAs. Similarly, there was no significant relationship between all serranid biomass and FPAs and damselfish biomass. The only significant relationship exists among the serranids that are specifically targeted on Bonaire's coral reefs (Nenadovic 2007). Fishers are known to snorkel and dangle baited hooks over the graysbys, coneys and red hinds they prefer to catch. These species, and only these species show both a clear FPA effect and a clear relationship with damselfishes.

It does not appear that damselfish predator biomass had any differential effect on the relative abundance of juveniles, the stage at which damselfishes are most likely to be preyed upon. This reinforces the idea that other process relevant to Bonaire's FPAs, such as habitat complexity, competition with other herbivores, or proximity to the major population center on the island, may be responsible for some of the variance observed in damselfish biomass observed among study sites.

While top-down control of territorial damselfish biomass has been described extensively within this series of field reports, bottom-up regulation has not been fully considered. This study, while not specifically designed to assess bottom-up effects, was nonetheless able to detect interactions between damselfish populations and bottom-up processes that may regulate them. Damselfish biomass a weak correlation with percent coral cover across all of the sites surveyed. In combination with the weak correlation with predator

biomass, it may be that forces other than predation exert significant demographic control over territorial damselfish populations in Bonaire. If recruitment and habitat-limitation could constrain damselfish populations such simplified predator prey feedback effects on Bonaire's coral reefs may need further detailed study.

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Chapter 7: Patterns of predatory fish biomass and density within and around Fish Protection Areas of the Bonaire Marine Park

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Abstract

Predatory fishes are important functional members for structuring overall coral reef fish communities. We examined changes in Bonaire's predatory fish communities over the past decade with specific comparison of distribution of fishery-targeted predators in fished (control) and in fish protection areas (FPA). We surveyed 11 long-term reef monitoring sites on Bonaire and Klein Bonaire, 4 FPA and 7 control sites, by conducting belt transects along the 10m isobath, quantifying the abundance and sizes of reef predatory fishes. The most abundant predatory fish families by biomass were the largely invertebrate-feeding grunts (Family: *Haemulidae*) and snappers (*Lutjanidae*). Overall, predator biomass and density were not significantly different between FPA and control sites despite significantly higher grouper (*Serranidae*) biomass in FPA sites versus control sites. Serranids are an important piscivorous predator of reef fishes and most susceptible to Bonaire's baited hook and line fishing fleet. Among three highly prized serranids (coney, graysby, and red hind), biomass averaged consistently higher but only coney had significantly higher biomass in the FPAs. Tracking specific functional groups of predators, like grouper, is important for realizing the effects of FPAs for those that would benefit most. Nevertheless, monitoring and phasing-out of indiscriminate removal strategies, like fish traps, continues to be an important strategy for providing relief to Bonaire's predator metapopulation as a whole.

Introduction

Predatory fishes (e.g. groupers, snappers, and grunts) are important megafaunal community members that drive patterns of biodiversity in coral reef ecosystems (McClanahan, 2005). As a functional group, piscivores specifically can directly influence the abundance and distribution of prey species (Hixon & Carr, 1997). Due to the interrelatedness of prey availability, predator density, and habitat preferences, understanding distribution patterns of carnivorous fishes can provide insight to reef functionality and resilience of fish communities to potential disturbance or fishing intensity (Dulvy et al, 2004).

Marine protected areas or fish reserves are important components of reef ecosystem management, designed with the intent of relieving stress on target predator populations induced by fishing. Throughout the world, fishing activities often preferentially remove large ecologically important predators (Jackson et al, 2001). Furthermore, life history traits of predators in general (i.e. late-stage maturity, slow growth, territoriality, aggregation spawning) make them susceptible to overfishing, functional extinction, or extirpation (Coleman et al, 2000). Maintaining a high predator biomass, including a large

adult spawning biomass, is important to realizing full advantage of reserve effects. Further still, high grouper biomass, in conjunction with well-designed marine reserves, are suggested to act as natural controls of invasive Indo-Pacific Lionfish (*Pterois volitans*) by directly increasing natural predation potential and initiating space-competition (Mumby et al, 2011).

We examined how Bonaire’s predatory fish populations have changed since the beginning of monitoring in 2003 and also since implementation of fish protection areas in 2008. Predatory fish surveys using SCUBA have been useful in tracking changes in fish communities over time. In following with previous assessments in this series, we continued to monitor differences in predator populations using a Before-After-Control-Impact (BACI) assessment scheme. In this case, the BACI-type study attempts to determine significant differences in targeted predator populations (Nenadovic, 2007) between impacted (i.e. FPA) and control (i.e. fished) areas. Since the implementation of fish protection areas in 2008, there has been some evidence of increased predator biomass within FPA sites compared to control sites (De Bey, 2011). If working as intended, target predator densities and biomass should be higher within FPA boundaries. Over time, this effect may be visible in adjacent areas as a result of potential spillover effects (McClanahan & Mangi, 2000).

Methods

Survey Area

Predatory fishes were quantified at 11 fringing reef locations along the leeward margin of Bonaire and Klein Bonaire (Table 1).

Table 1: Present and past predator site survey history (modified from De Bey, 2011)^{1,2}.

Site Name	Site Designation	Survey Years						# transects in 2013
		2003	2005	2007	2009	2011	2013	
No-Dive Reserve	Control					✓	✓	12
Karpata	Control	✓	✓	✓	✓	✓	✓	12
Oil Slick	Control				✓	✓	✓	14
Barcadera	Control	✓	✓	✓	✓	✓	✓	12
Reef Scientifico	FPA	✓	✓	✓	✓	✓	✓	13
Front Porch	FPA				✓	✓	✓	9
Forest	Control	✓	✓	✓	✓	✓	✓	12
Calabas	FPA				✓	✓	✓	10
Eighteenth Palm	FPA	✓	✓	✓	✓	✓	✓	12
Windsock	Control	✓	✓	✓	✓	✓	✓	12
Bachelor's Beach	Control				✓	✓	✓	13

Notes: ¹All site names correspond to dive locations as designated by STINAPA-Bonaire and are ordered by latitude (North-South) ²No-Dive Reserve is not included in the long-term abundance trends (2003-2013) due to only recent incorporation into the survey scheme.

Survey Methods

Along-reef belt transects were conducted on SCUBA at the 10m (33 feet) isobath at 10 locations along the leeward (western) side of Bonaire and 1 location on the southwest corner of Klein Bonaire. Transects dimensions were standardized to 30m in length by 4m in width (Total area = 120m²). Replicate transects at each site were laid end to end to maximize coverage and reduce the chance of characterizing immediately adjacent sites. Dive bottom times ranged from 55 to 67 minutes each. Predatory fish species within the

bounds of the transect area were identified, enumerated, and sized by fork length to the nearest centimeter.

Data Analysis & Treatment

Fish biomass was calculated using length-weight conversion factors from Bohnsack & Harper (1988) and Marks & Klomp (2003). Length-weight conversion factors for lionfish were obtained from Barbour et al (2011).

Results

In all, 37 species of predatory fishes were counted among all sites surveyed. A complete list of individual species biomass, density, and length has been provided in Appendix 7. Eel species (Families: Muraenidae & Ophichthidae) and juvenile unidentifiable hamlets (Serranidae) were grouped by genera to facilitate analysis. Grunts (Haemulidae), snappers (Lutjanidae), and grouper (Serranidae) were the most commonly recorded families observed at all reef sites (Appendix 7).

Trends

Predator biomass and density were not significantly different between control and FPA sites (Figures 1, 2). However, while overall predator biomass and density was lower than 2011, the differences are not statistically significant. Sites with the highest predator biomass were Windsock (6.5 kg/100m²), Calabas (7.1 kg/100m²), Forest (5.8 kg/100m²), and Reef Scientifico (4.2 kg/100m²) (Figure 3). The lowest predator biomass was observed at Oil Slick (1.6 kg/100m²). Sites with the highest predator biomass also had the highest predator density (Fig 4). Among predators overall, we observed no significant effect on biomass or density as a result of fish protection areas.

Groupers & Sea Basses (Serranidae)

Ten species of serranids including graysby (*Cephalopholis cruentatus*), coney (*Cephalopholis fulva*), rock hind (*Epinephelus adscensionis*), red hind (*Epinephelus guttatus*), creolefish (*Paranthias furcifer*), harlequin bass (*Serranus tigrinus*), tiger grouper (*Mycteroperca tigris*), and 3 species of hamlet (*Hypoplectrus spp.*) dominated the predator fauna.

Serranid biomass has declined slightly since 2011, while density has remained constant (Fig. 5). The highest serranid biomass and density was observed at Front Porch (1.0 kg/100m² and 8.1 fish/100m²) (Fig 8). Oil slick had the lowest observed biomass and density, 0.1 kg/100m² and 2.1 fish/100m², respectively. Serranids also displayed a strong FPA-effect with significantly higher biomass and density in FPA sites compared to control sites ($p=0.04$, $t=2.33$, $df=9$).

Snappers (Lutjanidae)

We observed five species of lutjanids including mahogany snapper (*Lutjanus mahogoni*), schoolmaster (*Lutjanus apodus*), yellowtail snapper (*Ocyurus chrysurus*), cubera (*Lutjanus cyanopterus*), and lane snapper (*Lutjanus synagris*).

Snapper biomass and density have remained fairly constant since the start of monitoring in 2003 despite a decrease in biomass since 2011 (Fig. 6). Snapper biomass and density were highest at Calabas (3.7 kg/100m², 5.7 fish/100m²) and lowest at Oil Slick (0.2 kg/100m², 0.4 fish/100m²) (Fig. 9). There was no observed FPA-effect for this family between control and protected sites by biomass or density.

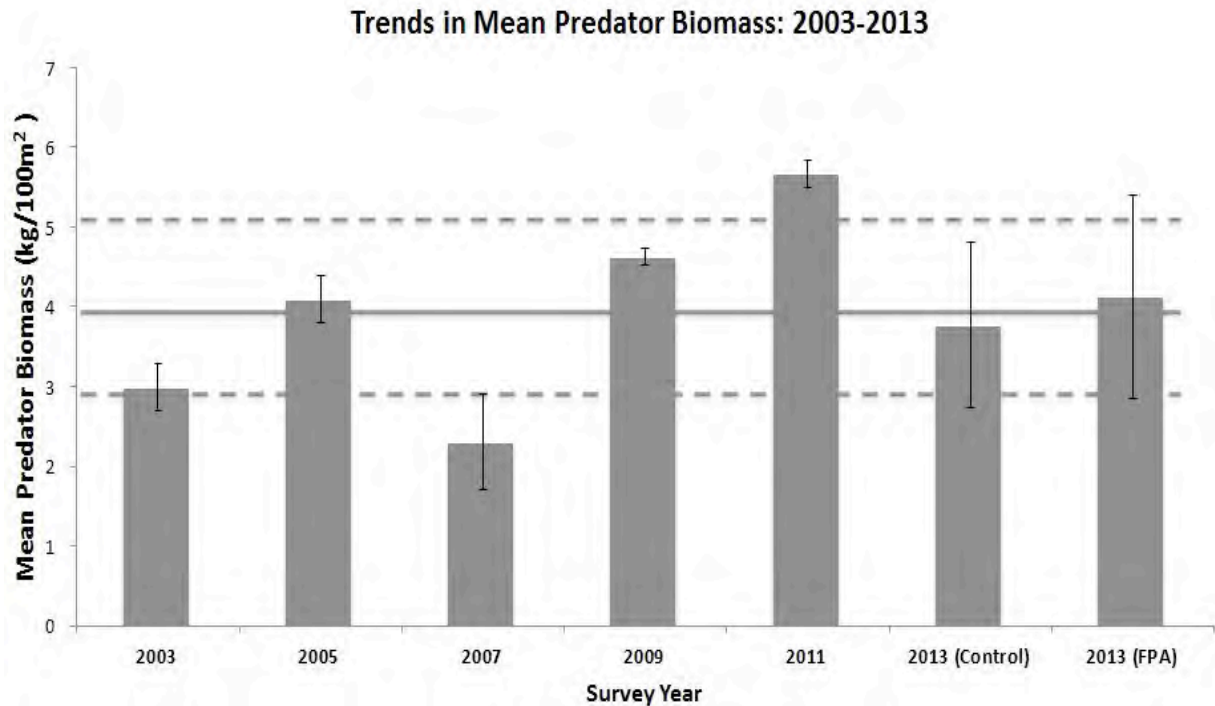


Figure 1: Mean predator biomass trends between 2003 and 2013. The solid horizontal line represents the mean biomass for all sites surveyed in 2013 (+/- SE, dashed lines).

Trends in Mean Predator Density: 2003-2013

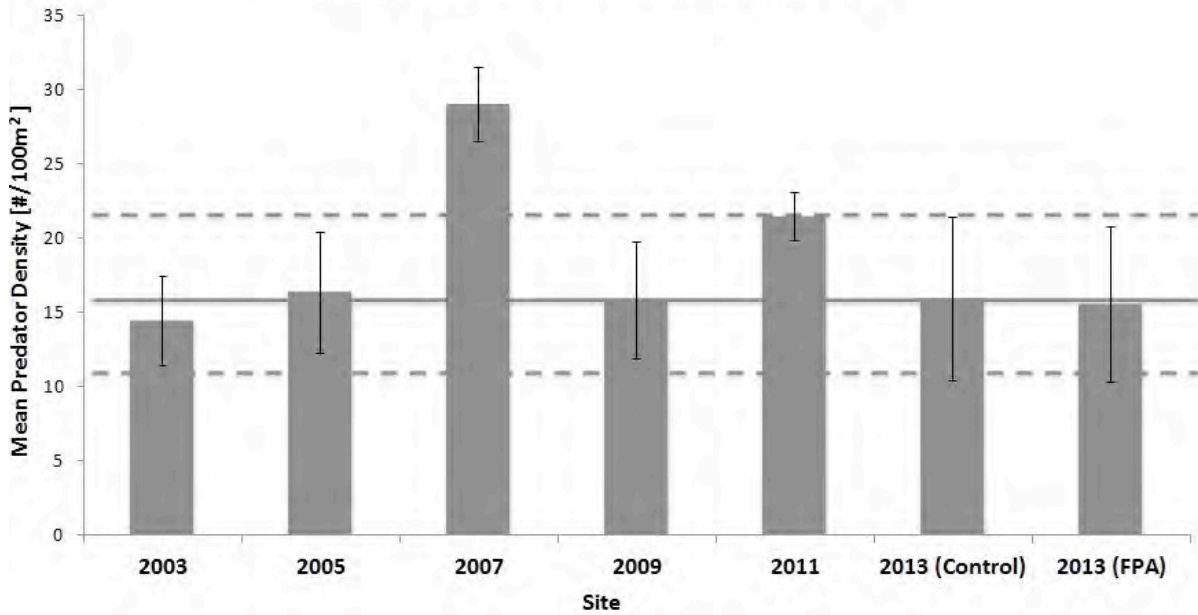


Figure 2: Mean predator density trends between 2003 and 2013 (+/- SE). The solid horizontal line represents the mean density for all sites surveyed in 2013 (+/- SE, dashed lines).

Mean Predator Biomass by Location

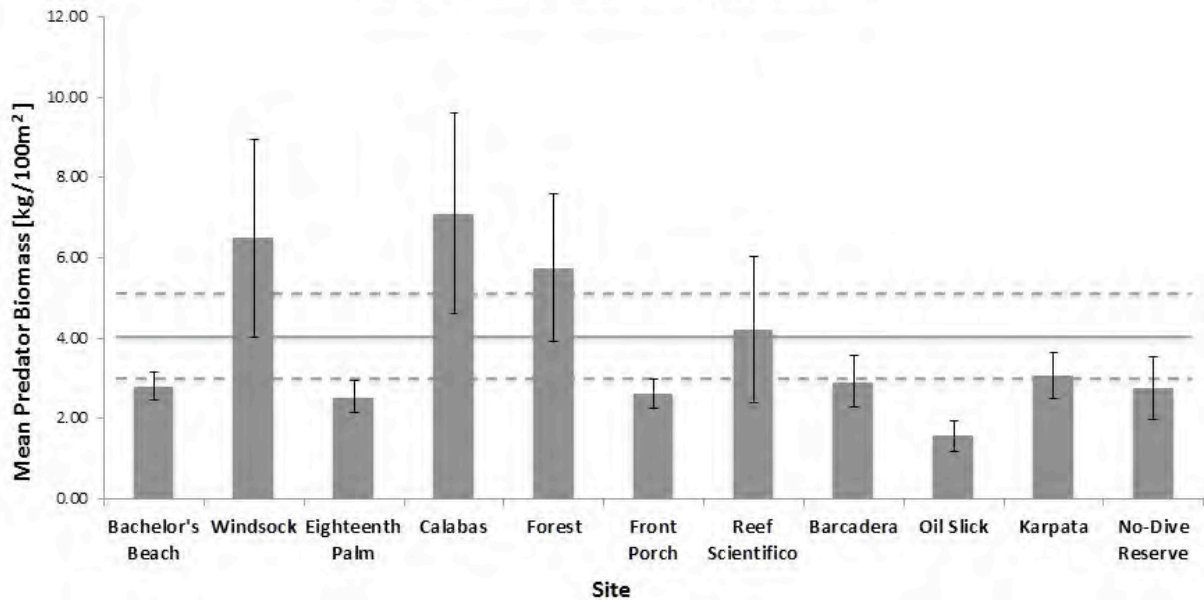


Figure 3: Mean predator biomass arranged by site. Locations are arranged latitudinally from south (left) to north (right). The solid horizontal line represents the mean biomass for all sites (+/- SE, dashed lines).

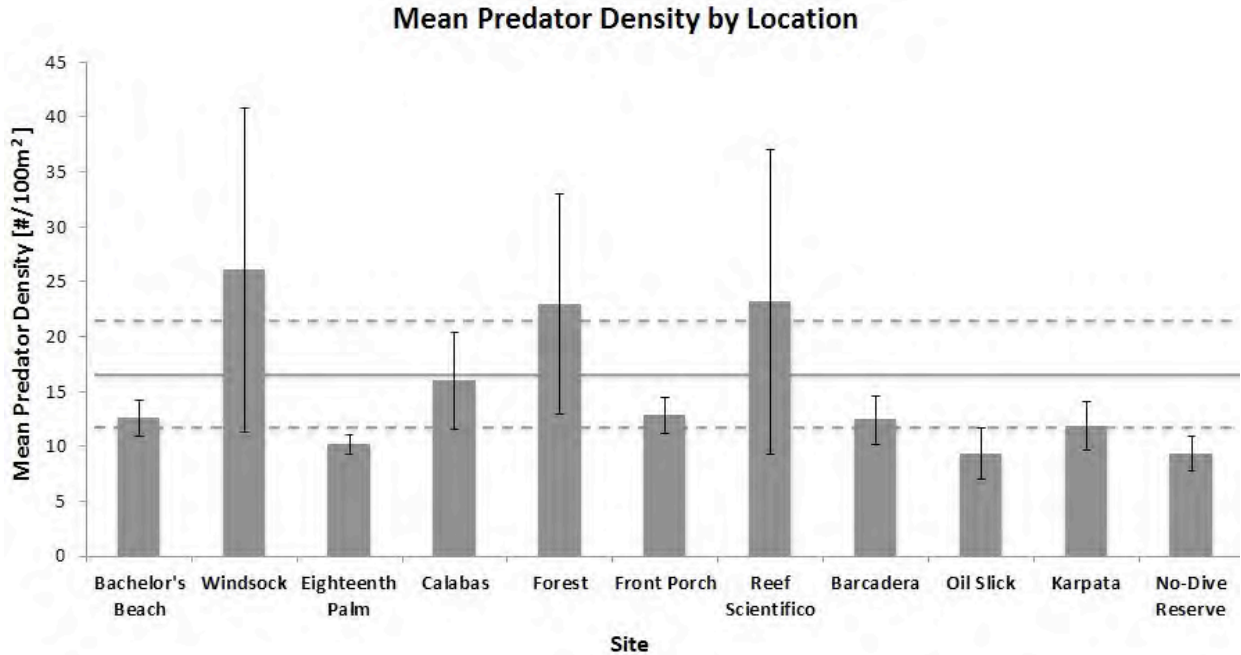


Figure 4: Mean predator density arranged by site. Locations are arranged latitudinally from south (left) to north (right). The solid horizontal line represents the mean density for all sites (+/- SE, dashed lines).

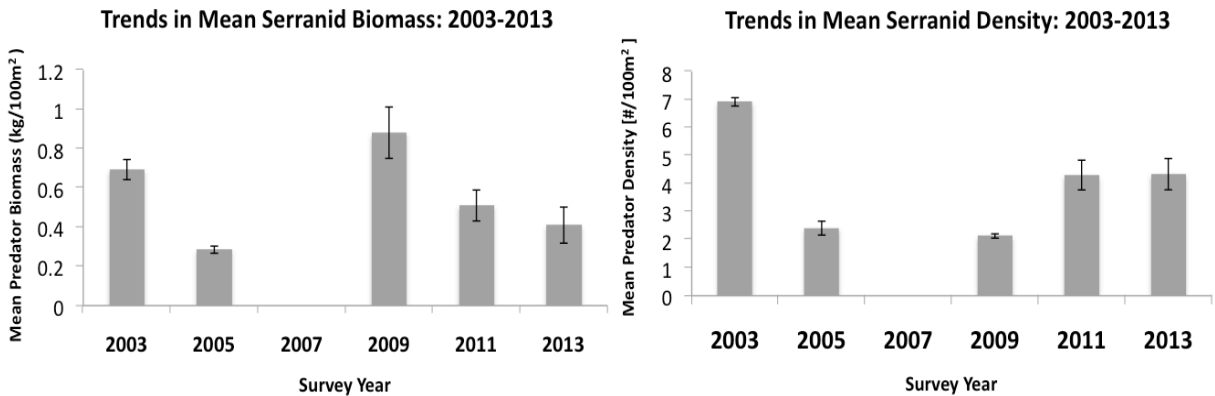


Figure 5: Trends in mean serranid biomass (left) and density (right) among all locations surveyed, 2003-2013. Blank year slots represent no available data.

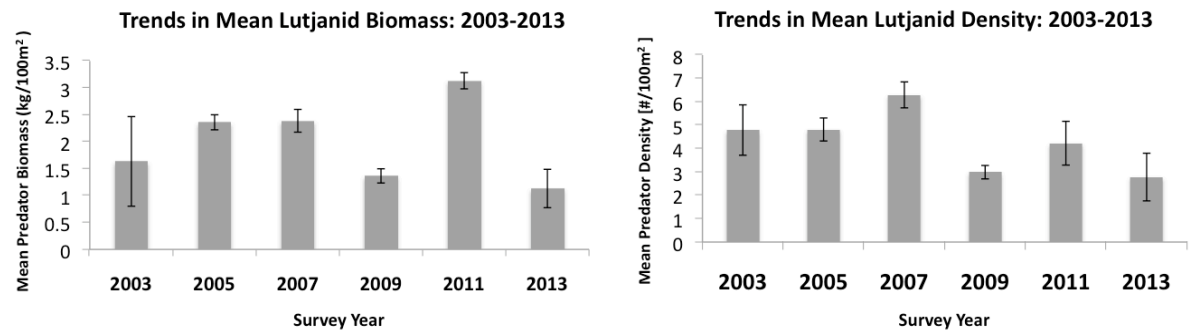


Figure 6: Trends in mean lutjanid biomass (left) and density (right) among all locations surveyed, 2003-2013.

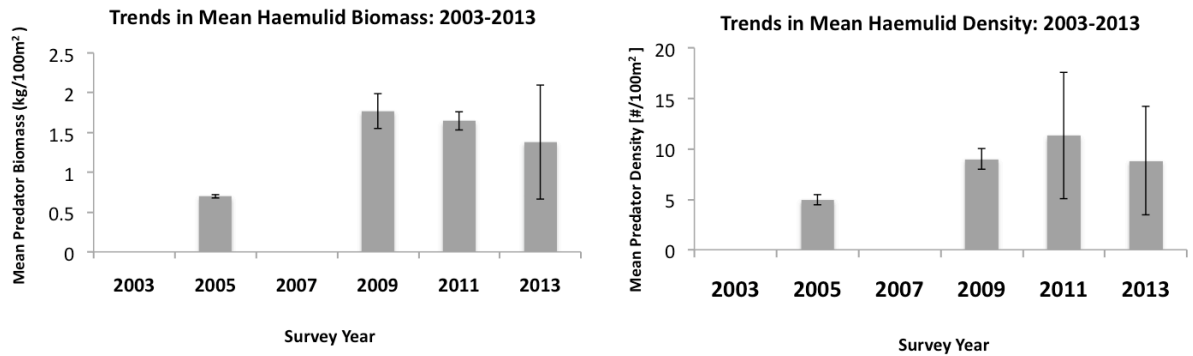


Figure 7: Trends in mean haemulid biomass (left) and density (right) among all locations surveyed, 2003-2013. Blank year slots represent no available data.

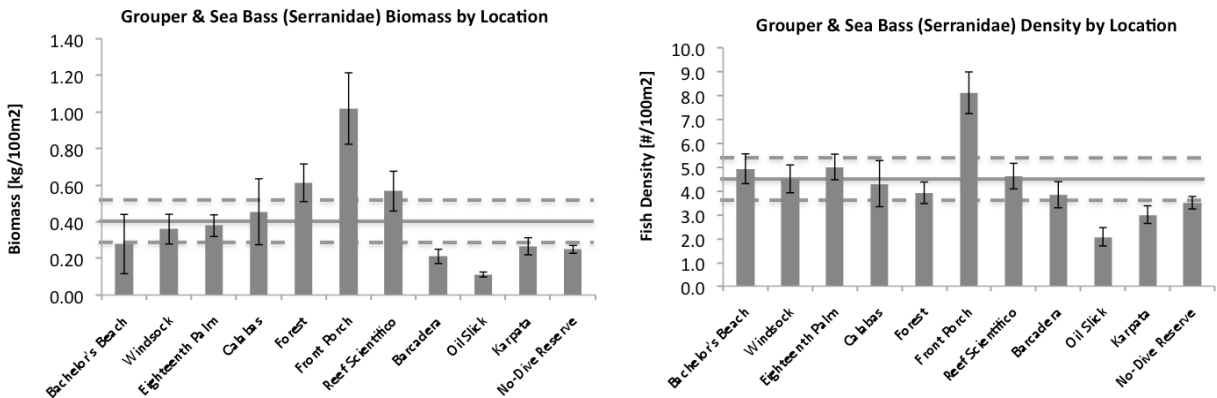


Figure 8: Mean grouper and sea bass biomass (left) and density (right) by survey site. The solid horizontal lines represents the mean biomass or density, respectively, for all transects at all sites (+/- SE, dashed lines).

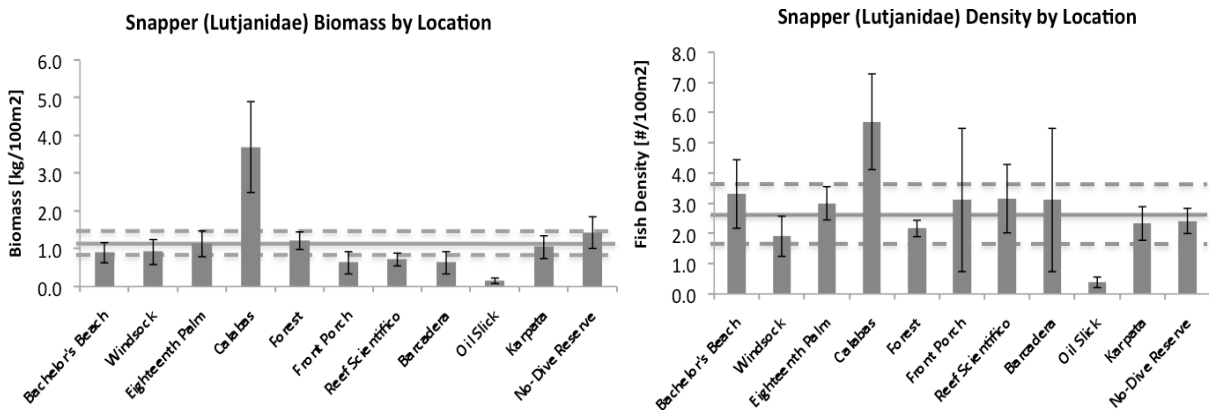


Figure 9: Mean snapper biomass (left) and density (right) by survey site. The solid horizontal lines represents the mean biomass or density, respectively, for all transects at all sites (+/- SE, dashed lines).

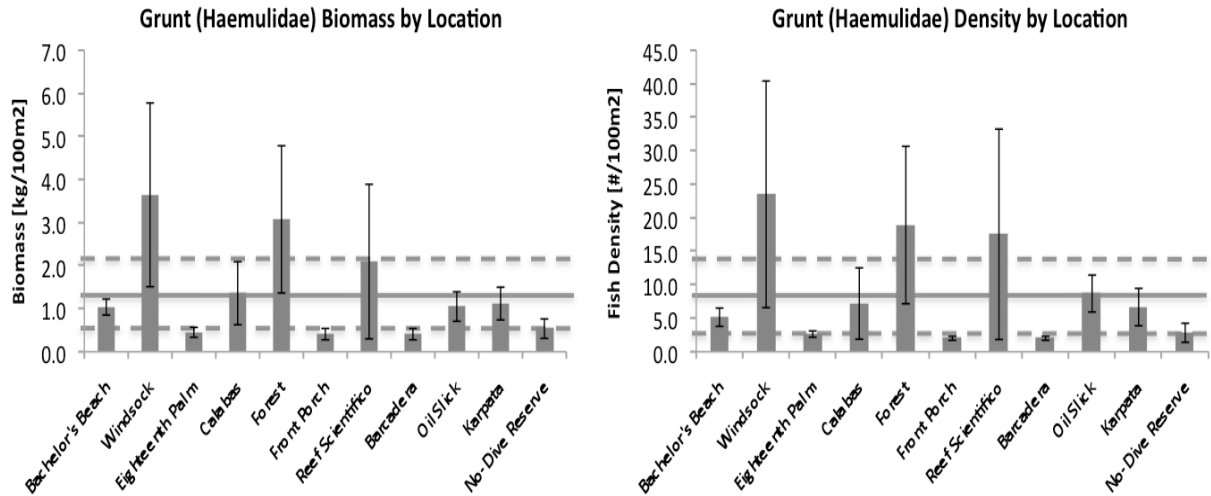


Figure 10: Mean grunt biomass (left) and density (right) by survey site. The solid horizontal lines represents the mean biomass or density, respectively, for all transects at all sites (+/- SE, dashed lines).

Grunts (*Haemulidae*)

We recorded eight species of grunts including smallmouth grunt (*Haemulon chrysargyreum*), French grunt (*Haemulon flavolineatum*), black margate (*Anisotremus surinamensis*), white margate (*Haemulon album*), caesar grunt (*Haemulon carbonarium*), Spanish grunt (*Haemulon macrostomum*), white grunt (*Haemulon plumierii*), and bluestriped grunt (*Haemulon sciurus*).

Grunt biomass and density have remained unchanged since 2011 (Fig. 7). Grunt biomass and density were highest at Windsock with 3.6 kg/100m² and 23.5 fish/100m², respectively (Fig.10). The lowest biomass was observed at both Front Porch and Barcadera (0.4 kg/100m²) and the lowest density at Front Porch (0.2 fish/100m²). No FPA-effect was observed for this family between control and protected sites by biomass or density.

Targeted Predatory Fishes

Target species were identified predominantly as reef-associated piscivorous fishes that could be caught using hook and line and landed throughout the year (Nenadovic, 2007). Fishery target species included great barracuda (*Sphyraena barracuda*), yellowtail snapper (*Ocyurus chrysurus*), coney (*Cephalopholis fulva*), graysby (*Cephalopholis cruentatus*), red hind (*Epinephelus guttatus*), and rock hind (*Epinephelus adscensionis*).

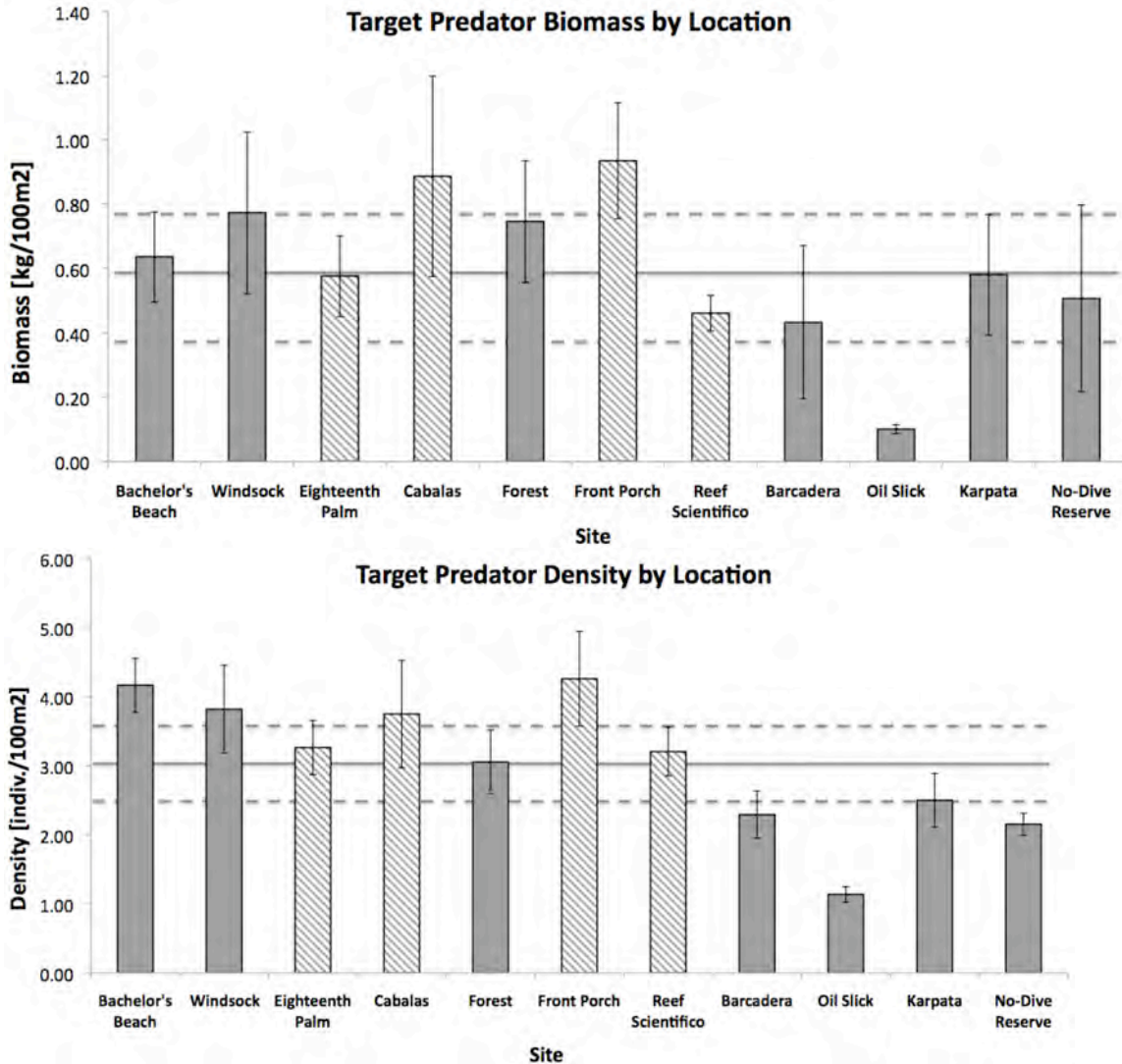


Figure 11: Biomass (top) and density (bottom) patterns of fishery-targeted reef fish predators. Solid bars show control sites and patterned bars represent FPA sites. The solid horizontal lines represents the mean biomass or density, respectively, for all transects at all sites (+/- SE, dashed lines).

Collectively, target fish species showed no significant pattern between FPA and non-FPA sites as a whole (Fig. 11). The highest recorded biomass and densities for this group were observed at Front Porch (0.94 kg/100m², 4.3 indiv./100m²) and Cabalás (0.89 kg/100m², 3.8 indiv./100m²) while the lowest was recorded at Oil Slick (0.1 kg/100m², 1.1 indiv./100m²). Mesopredatory fishes (i.e. coney, graysby, red hind) were the most commonly recorded (>90%) target fish among all transects. Despite non-significant patterns of target fish biomass, the percentage of target species recorded as a function of biomass was higher in FPAs (27.7% +/- 6.7%) than in control sites (14.0% +/- 2.9%). Among the most targeted serranids (coney, red hind and graysby), these three averaged higher biomass in FPA than control sites. Collectively the differences were not significant except for coney (Fig. 12).

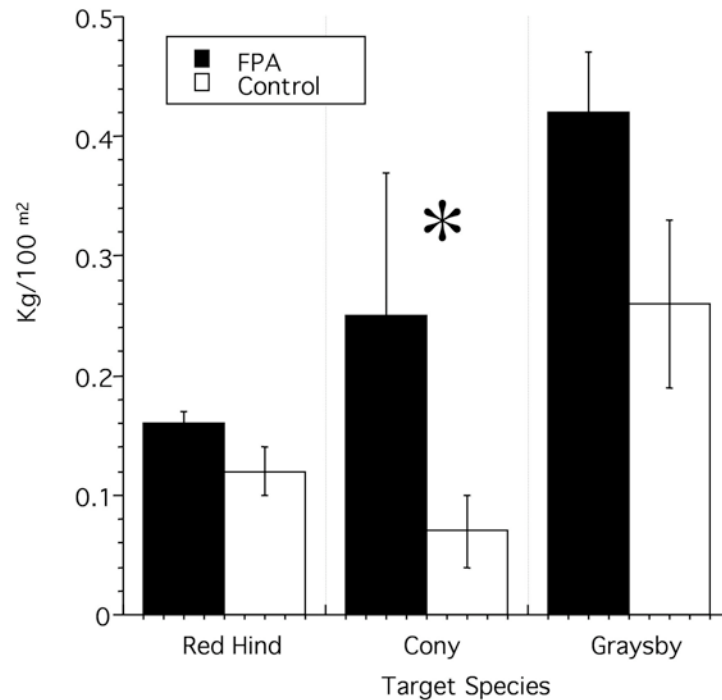


Figure 12: Average biomass of most targeted serranid species in fish protection areas (FPA) and control sites (e.g. Fig. 11). Variance is presented as +/- one standard error. Star (*) indicates significant difference ($p = 0.02$, $F = 11.78$, $df = 3$).

Lionfish

Lionfish were observed at 7 of the 11 sites surveyed. The site with the highest lionfish biomass was Forest (0.17 kg/100m²). Lionfish biomass at the 6 other sites (Eighteenth Palm, Front Porch, Barcadera, Oil Slick, No-Dive Reserve) was substantially lower (<0.01 kg/100m²), usually amounting to only 1 or 2 small (<15cm TL) individuals (Pers. Obs.). Given the active efforts in lionfish removal by local residents and STINAPA officials on Bonaire, this was seen as a positive sign for the long-term mitigation of the lionfish populations.

Discussion

Overall, there has been no net change in predatory fish populations on Bonaire's leeward reefs since 2011 (Figs. 1, 2). However, mostly non-significant trends in overall predator biomass and density between years, as well as between FPA and control sites, are not entirely unexpected. Emerging patterns of functionally important predators, like groupers, are encouraging and suggest robust benefits associated with fish protection areas.

Fish protection areas may not necessarily show across-the-board increases in biomass and density for predators as a lumped group; however specific families and groups of fishes (e.g. targeted fish, serranids) do show some signs of intended FPA functionality. Grouper distribution patterns show significantly higher biomass and density within FPA sites (Fig. 8). This is an important finding considering that this pattern had not previously been

observed in 2011 surveys (De Bey, 2011). Unlike groupers and sea basses, other predatory fish families did not show a clear FPA effect (Fig. 9, 10). This finding is not unexpected given that snappers and grunts are largely macro-invertivores and thus less likely to be landed using baited hook and line methods, compared to grouper.

Grouper biomass and density were largely driven by piscivorous mesopredators including graysby, hinds, and coney, which composed over 90% of the observed targeted fish species (Fig. 11, 12). Reef-associated serranid fishes (e.g. small-bodied grouper) are likely to experience the strongest FPA effect on biomass and density. Since these predators are one of the most commonly targeted, they would likely receive the greatest benefit from protected zones. These species are known consumers of territorial damselfishes (Randall, 1967). Because damselfish gardens are known to reduce coral recruitment (Arnold et al 2010), their predators will likely be functionally important drivers of reef resilience (Mumby et al, 2012). Thus it will be important to continue to monitor predator populations together with patterns of known prey fishes, including baitfish and damselfish.

Maintaining robust predatory fish populations can promote resilience in coral reef fish communities (Bellwood et al, 2004). More specifically, it is more important to evaluate patterns of fishery-targeted species to understand the efficacy of fish protection areas. Higher fish biomass and density within FPAs may yield higher reproductive potential as more fish mature to full reproductive capacity. Maintaining fishing strategies that allow for predators to grow and become reproductively mature, such as closed or preferred seasons and size limits, as well as phasing out fish traps may also help increase target-species biomass.

Future work should focus on quantifying patterns of specific target species that are important to the fishing community (Nenadovic, 2007). Increased mesopredator abundance within FPAs should be seen as a positive trend for both the fishing community and long-term reef resilience. Mesopredators may act as a bio-control for damselfish, while providing a forage base for valuable large-bodied groupers (Mumby et al, 2012). Still, fish reserve effects may take 3-5 years or longer before manifestation, depending on initial conditions (Steneck et al, 2011). Continued monitoring will be necessary to observe the lasting effects of abundant mesopredator populations.

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Chapter 8: Abundance and species composition of juvenile corals on the reefs of Bonaire: a comparison between fish protection and control areas

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Abstract

Globally the health of coral reefs is declining due to a combination of local disturbances and climate change. This decline is marked by a decrease in coral cover and an increase in macroalgal abundances, which leads to reduced availability of nursery habitat for settling juvenile corals. In this study, we quantified the abundance of coral juveniles at 11 sites on the reefs of Bonaire, both in fish protection areas (FPAs) and in control areas where fishing is still allowed. We also analyzed the species composition of these juveniles and found that the majority were “weedy” species, which are slow growing and contribute relatively little to the three-dimensional structure that is so important to reefs. We did not identify any significant differences in the abundance of juvenile corals between FPA and control sites during this study. Lastly, we found that the density of coral juveniles has been relatively stable since 2009, but these numbers are still considerably lower than the numbers seen when monitoring of these sites first began.

Introduction

Many of the most severe coral declines are reported from the Caribbean (Hughes 1994, Knowlton 2001, and Pandolfi *et al.* 2003), where coral cover reductions have been accompanied by increases in macroalgal abundance and reduced rates of herbivory (Hughes *et al.* 2007, Lirman 2001, and Hughes 1994). Shifts to macroalgal dominated states are reported from Jamaica and many other areas in the Caribbean (Hughes 1994). However, Bonaire has avoided this shift and exhibits relatively high coral cover and low macroalgal biomass (Kramer 2003). In 2008, Fish Protection Areas (FPAs) were established in Bonaire, in an effort to mitigate the local stressor of overfishing and maintain resilient reefs. Despite this effort, in 2011 a 10% drop in coral cover and an increase in macroalgal abundance were reported for Bonaire’s reefs (Steneck 2011). This was due to the bleaching event that occurred in the fall of 2010 (Jekielek 2011, Phillips 2011, and Steneck 2011).

Maintaining adequate herbivorous fish stocks is critical in preventing macroalgal shifts (Williams and Polunin 2001, Hughes *et al.* 2007). There is a short time frame after the opening of available substrate on reefs, during which rates of coral recruitment are the highest (Arnold and Steneck 2011). Early successional species such as coralline algae and polychaete tube worms facilitate recruitment of juvenile corals (Arnold and Steneck 2011). Crustose coralline algae (CCA) seem particularly important as facilitators of juvenile coral recruitment, often inducing settlement (Harrington *et al.* 2004, Heyward and Negri 1999, and Raimondi and Morse 2000). However, in the absence of adequate rates of herbivory, after about a year these successional species begin to be replaced by macroalgae, turf algae, and other inhibitors of recruitment which reduce available

substrate and chemically inhibit settlement (Arnold and Steneck 2011, Arnold *et al.* 2010, Birrell *et al.* 2008, Hughes *et al.* 2007, and Kuffner *et al.* 2006). Macroalgae not only prevent larval settlement, but they can also overgrow, shade, and smother established juveniles and adult corals (Lirman 2001).

Our study aimed to achieve four main goals. First, we wanted to quantify the abundance and species composition of juvenile corals at both control (fishing permitted, N=7) and FPA (fishing prohibited, N=4) sites in Bonaire during the spring of 2013. Second, we sought to determine if the FPAs were having any effect on the abundance of coral juveniles. Third, we wanted to isolate any evident trends over time in the number of juvenile corals. Four, we were also interested in identifying relationships (if any) between the abundance of coral juveniles and the abundance of macroalgae and CCA.

Materials and Methods

We conducted surveys via SCUBA at 11 sites on the western side of the island of Bonaire (Netherlands Antilles, Southern Caribbean) in both Fish Protected Areas (FPA – no fishing permitted, n=4) and control areas (fishing permitted, n=7). The sites listed from south to north were: Bachelor's Beach, Windsock, Eighteenth Palm (FPA), Calabas (FPA), Forest (off Klein Bonaire), Front Porch (FPA), Reef Scientifico (FPA), Barcadera, Oil Slick, Karpata, and the No Dive Reserve. We conducted quadrat sampling to quantify the distribution, abundance, and size of juvenile corals and algae along a 10 m transect tape placed parallel to the shore at 10 m depth. Five locations per transect were sampled at the 0, 2.5, 5, 7.5, and 10 m marks by placing a 1/16 m² quadrat (25 cm X 25 cm) on hard available substrate. We rejected any area that exhibited more than 25% sediment and live invertebrate (adult coral, gorgonians, sponges, etc) cover and proceeded to place our quadrat at the nearest suitable location.

In each quadrat, we measured all juvenile corals (coral colonies equal or less than 40 mm; Bak & Engel 1979) and identified them to the lowest possible taxon (species or genus). Algae were subdivided into functional groups such as crustose coralline algae (CCA), turf algae, fleshy macroalgae (designated “macroalgae”), non-coralline crusts, and articulated algae. We visually estimated percent cover and measured canopy height where appropriate. Subsequently, algal indices (proxy for biomass) were calculated by multiplying percent cover and canopy heights (Steneck and Dethier 1994).

Statistical analyses were performed on the data in order to determine if there were differences in juvenile coral densities, macroalgal biomass, and crustose coralline percent cover between sites (FPA versus control areas). Non-parametric one-way ANOVA tests on ranks (non-normal data) were performed on all of the above variables to detect differences among sites. Mann-Whitney rank sum tests were performed to determine differences among pooled sites (all FPA sites versus all control sites). In order to investigate the relationship between juvenile coral density and macroalgal index and the relationship between juvenile coral density and crustose coralline cover, we performed Spearman rank order analyses on ranks (non-normal data). The No Dive Reserve site was

not included in any statistical analyses (different from all other sites; fishing is allowed but not diving).

The methods employed in this survey were also detailed in Chapter 8 of the 2005 Bonaire report (Steneck and Arnold 2005).

Results

In this study, the overall mean density of juvenile coral across all of the 10 sites was 8.82 individuals per m² (± 0.90 SE). Front Porch and 18th Palm (both FPA sites) exhibited the highest density of juvenile corals, each with 12.8 individuals per m² (± 3.69 and ± 2.7 SE, respectively), while Karpata (control site) exhibited the lowest density with 5.12 individuals per m² (± 2.39 SE; Figure 1). Out of all the juvenile coral taxa identified, *Agaricia* spp., *Porites astreoides*, and *Montastraea annularis* were the most abundant with 3.27 individuals/m² (± 0.48 SE), 1.6 individuals/m² (± 0.38 SE), and 1.58 individuals/m² (± 0.47 SE), respectively (Figure 2). Non-parametric ANOVA on ranks revealed that there was no significant difference between these 10 sites ($p = 0.12$). We also determined that there was no significant difference in the mean density of juvenile corals between FPAs (sites pooled) and controls (sites pooled; $p = 0.15$). Temporal trends indicate that juvenile coral abundance has decreased by more than 50% when compared to 2003 and 2005, but this decline seems to have stabilized between 2009 and 2013 (Figure 3).

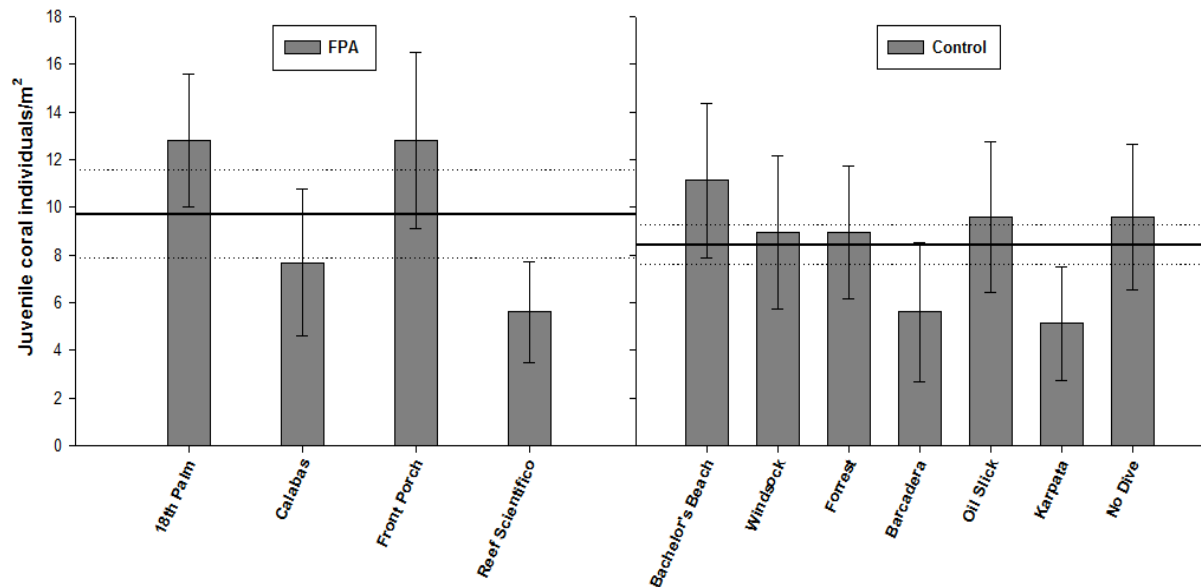


Figure 1 – Densities of juvenile corals in FPA sites (n = 95) versus control sites (n = 138). Error bars denote ± 1 standard error.

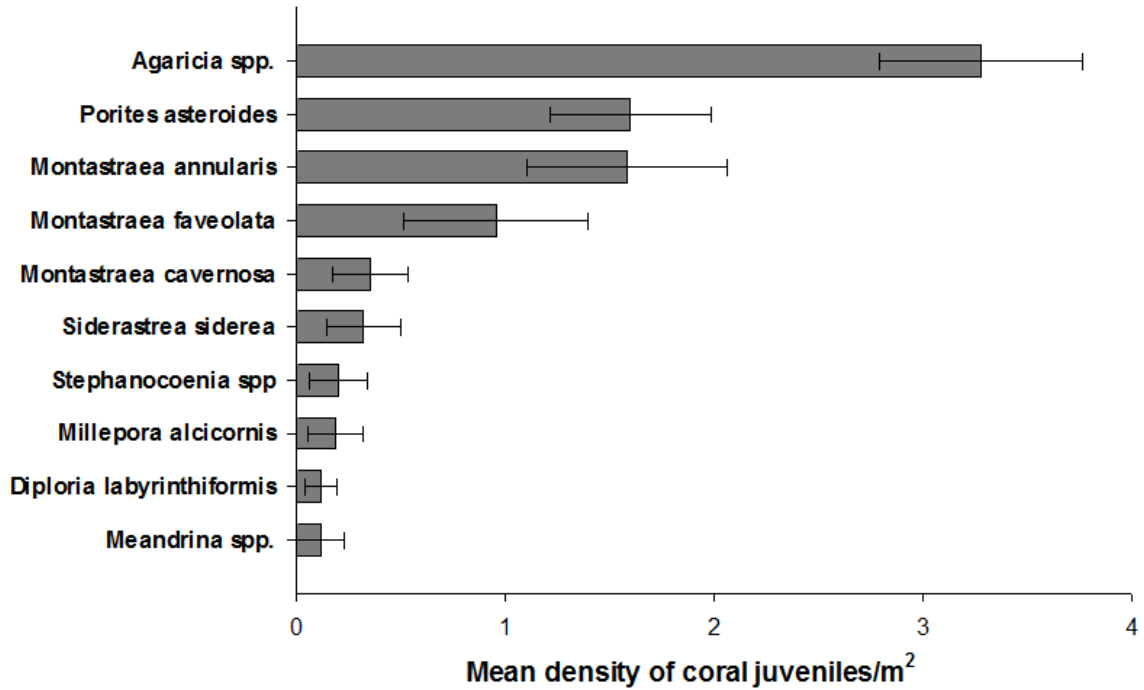


Figure 2 - Mean densities of juvenile corals (per m²) by taxa (n = 233). Error bars denote ± 1 standard error.

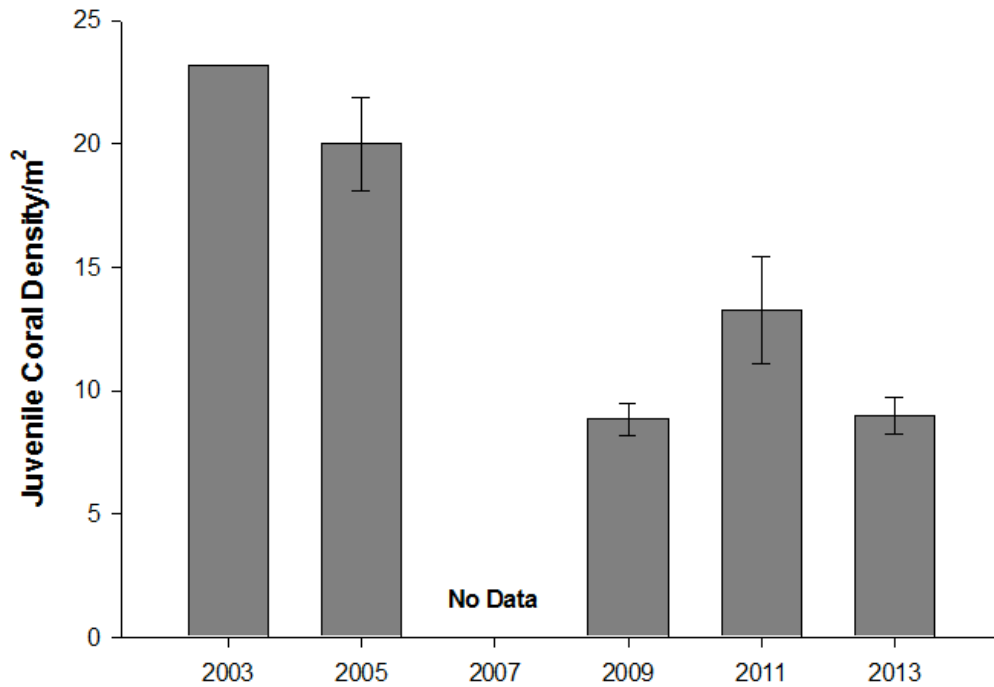


Figure 3 - Mean densities of juvenile corals by year. Error bars denote ± 1 standard error.

Spearman correlation analyses on the density of juvenile corals versus macroalgal index and density of juvenile corals versus macroalgal percent cover determined that there was no correlation between the parameters ($p = 0.85$ and $p = 0.74$, respectively).

The overall macroalgal index across all the sites was 82.22 (± 14.95 SE) and there was no significant difference between the mean macroalgal indices in the FPA sites (pooled) and control sites (pooled; $p = 0.28$, Figure 4). The overall crustose coralline algal (CCA) percent cover was 3.21 % (± 0.43 SE) and there was no significant difference in CCA percent cover between the FPA sites (pooled) and control sites (pooled; $p = 0.19$, Figure 5). A Spearman correlation analysis revealed a significant positive correlation between juvenile coral density and CCA percent cover ($p = 0.0011$, Figure 6).

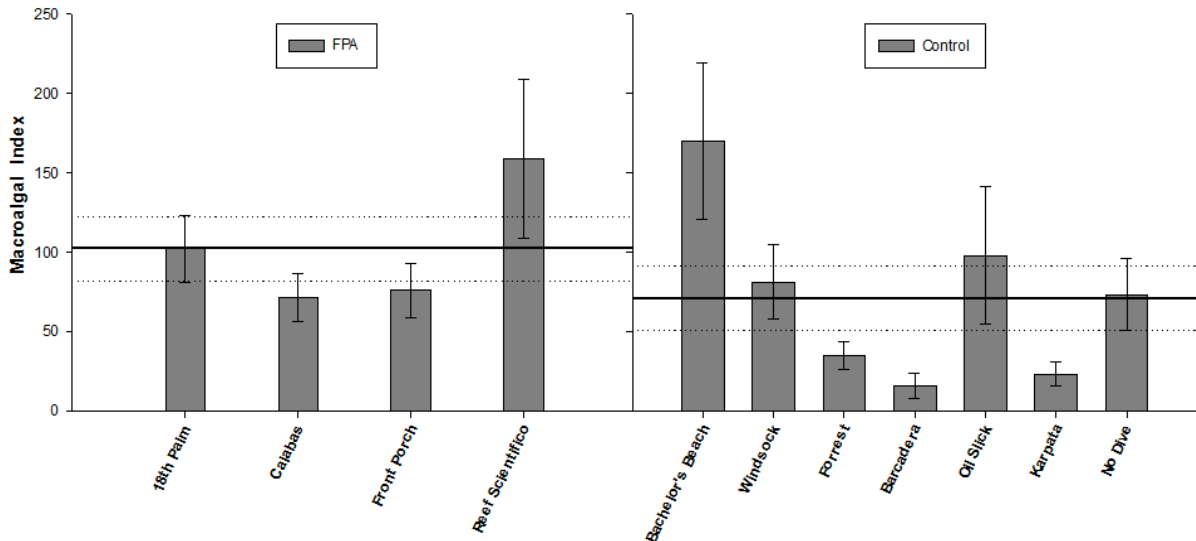


Figure 4 – Macroalgal indices in FPA sites (n = 95) versus control sites (n = 138). Error bars denote ± 1 standard error.

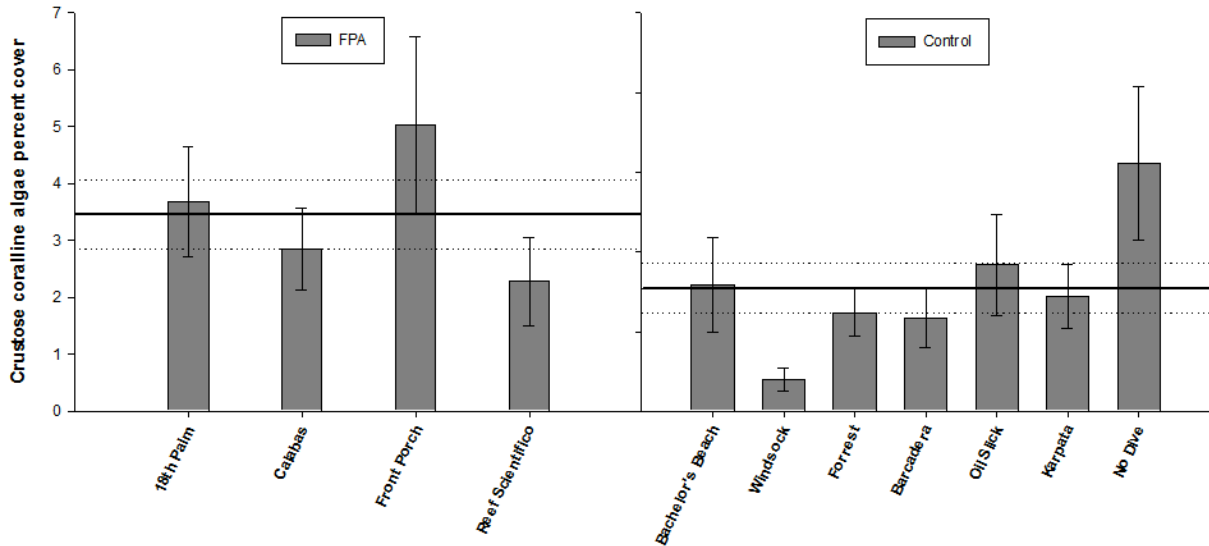


Figure 5 – Crustose coralline algal percent cover in FPA sites (n = 95) versus control sites (n = 138). Error bars denote ± 1 standard error.

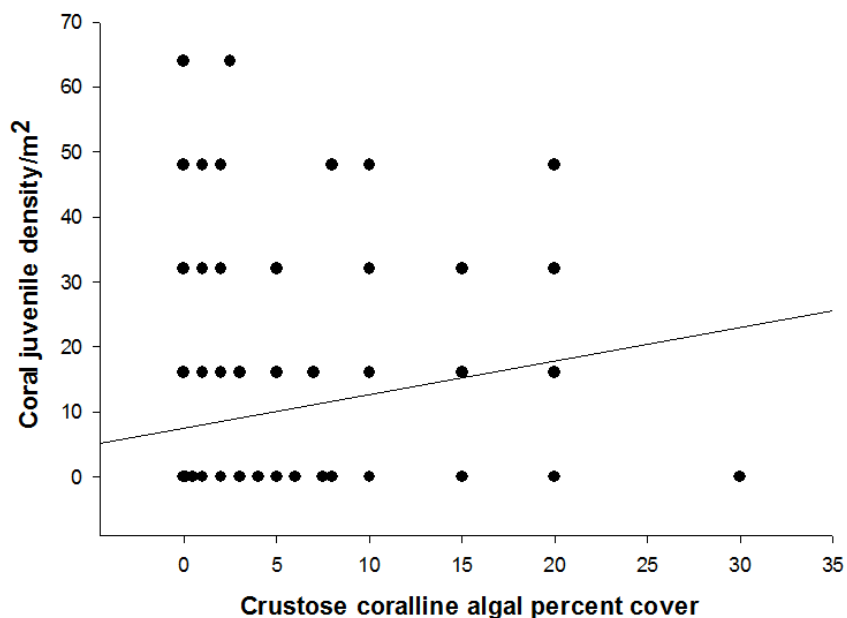


Figure 6 – Crustose coralline algal percent cover and juvenile coral density. Untransformed quadrat data (n = 233).

Discussion

The reefs of Bonaire continue to exhibit low juvenile coral abundances compared to levels observed in 2003 and 2005. One plausible explanation for this could be a lower recruitment potential of the benthos mediated by macroalgae, possibly as a result of decreasing numbers of scraping herbivores (parrotfish; Arnold and Steneck 2011, Arnold *et al.* 2010, and Birkeland 1977). The density of juvenile corals in Bonaire has followed a trend similar to that of the parrotfish, which have shown a marked decline in numbers since 2003, but whose populations seem to have stabilized since 2007 (see Stamieszkin and Arnold chapter in this report). While this stabilization coincides with the introduction of FPAs in 2008, it difficult to envision a possible correlation between these protected areas and herbivore biomass as fishing pressure in Bonaire is primarily hook and line fishing for carnivores. Herbivore fish communities as well as macroalgal abundances should be unaffected by the implementation of FPAs. Moreover, the lack of significant differences in juvenile coral abundance between FPAs and controls suggests that recruits fare equally well under both management schemes.

The lower numbers of juvenile corals seen this year in Bonaire versus two years ago are most likely the result of drastically higher macroalgal biomass documented in 2011 (Steneck 2011). Macroalgae are severely detrimental to the process of coral settlement and recruitment, as well as the health of already established juvenile and adult corals (Arnold and Steneck 2011, Arnold *et al.* 2010, Birrell *et al.* 2008, Hughes *et al.* 2007, Kuffner *et al.* 2006, and Lirman 2001). A slight decrease in macroalgal biomass has been observed this year compared to 2011, although biomass remains higher than in any year prior to 2011 (see Steneck chapter in this report). Consequently, available nursery habitat for juvenile corals is likely more limited than it has been in previous years, and this

instance may result in further decreases in juvenile coral densities if macroalgal biomass does not decrease over the coming years.

Macroalgal abundance did not correspond with juvenile coral population densities in our study. This outcome is not consistent with the majority of the literature dealing with this topic, which discuss an inverse relationship between algal abundance and the abundance of juvenile corals (Arnold *et al.* 2010, Birkeland 1977, Kuffner *et al.* 2006, and Ritson-Williams *et al.* 2009). On the other hand, percent cover of CCA did correlate positively with the density of juvenile corals (Figure 6) confirming results found in the literature. Certain species of crustose coralline algae enhance the recruitment of many coral species (Arnold *et al.* 2010, Harrington *et al.* 2004, Heyward and Negri 1999, and Raimondi and Morse 2000). In fact, Arnold and Steneck (2011) found that the abundance of juvenile corals directly corresponded to the abundance of CCA. Macroalgal biomass and percent cover of CCA revealed no significant differences between the control and FPA sites (Figure 4 and 5, respectively), which suggests that the two management schemes have no discernible impact on these variables.

Agaricia spp. and *Porites astreoides* were the most abundant juvenile corals on the reefs of Bonaire (Figure 2) and have been the most abundant juvenile corals on these reefs since monitoring began in 2003 (Bégin and Stephenson 2003). The high abundance of these two species may indicate a shift from large framework building corals to a more diminutive assemblage of corals that has been seen on many Caribbean reefs since the demise of the acroporids (Green *et al.* 2008, Steneck *et al.* 2009, Pandolfi and Jackson 2006). This shift may decrease the amount of cryptic nursery habitat available for settling corals and other key driver species (i.e. herbivorous fish; Arnold and Steneck 2011, Lee 2006).

In summary, our results indicate that juvenile coral densities on the reefs of Bonaire remain relatively depressed relative to previous years, but seem to have leveled off. We did not expect, nor did we detect any significant effects of FPA sites on algal abundance or the recruitment of corals in this study. Species composition analysis of recruits across all sites revealed a high abundance of “weedy” corals (*Agaricia* spp. and *Porites astreoides*), which could act to reduce the habitat complexity of these reefs. Continued monitoring of these sites is strongly encouraged as well as management approaches focused on maintaining and/or increasing coral recruitment, including but not limited to the maintenance of herbivorous fish populations. These management approaches will become more and more important to the resilience of reefs on Bonaire in light of increasing threats to coral recruitment from climate change (Doropoulos *et al.* 2012).

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Appendix 1: Coral and algae distributin and abundance. “CH” denotes canopy heights measured in mm.

All Sites

AVE macroalgae	Ave Macroalgae %	Ave Macroalgae-CH	Ave T-CH	Ave Coral cover %	Corallines %	
403.39	16.85	23.75	2.25	26.37	3.01	Calabas
232.99	21.28	9.75	2.00	17.37	4.24	Front Porch
104.25	9.05	10.25	2.50	33.87	7.10	Oil Slick
111.32	19.91	5.25	2.50	39.35	3.43	Windsock
181.55	21.01	8.75	2.25	34.80	3.24	Bachelor's Beach
308.12	21.08	15.00	3.50	37.56	3.11	18th Palm
35.88	7.18	5.00	1.75	48.82	4.09	Reef Scientifico
41.29	6.19	6.25	1.25	44.33	12.00	Forest
107.18	7.06	15.00	2.75	30.25	6.55	Barcadera
315.15	15.76	20.00	2.00	40.47	11.40	Karpata
184.11	14.54	11.90	2.28	35.32	5.82	AVERAGE
108.32	0.54	6.25	0.25	12.78	2.95	Calabas
109.23	6.05	3.66	0.00	9.39	2.35	Front Porch
51.77	1.46	3.33	0.50	14.79	1.81	Oil Slick
37.97	2.73	1.25	0.29	10.59	1.45	Windsock
25.37	1.34	1.25	0.25	7.19	2.12	Bachelor's Beach
128.10	6.11	2.89	0.65	12.58	2.22	18th Palm
7.25	1.45	0.00	0.25	7.22	1.92	Reef Scientifico
14.13	0.88	1.25	0.25	17.05	3.53	Forest
38.04	0.68	5.00	0.48	10.22	1.82	Barcadera
78.29	3.91	0.00	0.00	3.61	4.13	Karpata
39.86	2.04	2.02	0.19	2.87	1.08	

Monitored sites only

AVE macroalgae	Ave Macroalgae %	Ave Macroalgae-CH	Ave T-CH	Ave Coral cover %	Corallines %	
111.32	19.91	5.25	2.50	39.35	3.43	Windsock
308.12	21.08	15.00	3.50	37.56	3.11	18th Palm
35.88	7.18	5.00	1.75	48.82	4.09	Reef Scientifico
41.29	6.19	6.25	1.25	44.33	12.00	Forest
107.18	7.06	15.00	2.75	30.25	6.55	Barcadera
315.15	15.76	20.00	2.00	40.47	11.40	Karpata
153.16	12.86	11.08	2.29	40.13	6.76	AVERAGE
37.97	2.73	1.25	0.29	10.59	1.45	Windsock
128.10	6.11	2.89	0.65	12.58	2.22	18th Palm
7.25	1.45	0.00	0.25	7.22	1.92	Reef Scientifico
14.13	0.88	1.25	0.25	17.05	3.53	Forest
38.04	0.68	5.00	0.48	10.22	1.82	Barcadera
78.29	3.91	0.00	0.00	3.61	4.13	Karpata
51.76	2.81	2.61	0.33	2.57	1.64	STANDARD ERROR

Appendix 2: Herbivorous fishes: Population density, body size and biomass

	Density (Ind per 100 m ²)		Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
18th Palm						
<i>Acanthurus bahianus</i>	0.92	0.62	16.36	1.57	90.99	59.73
<i>Acanthurus chirurgus</i>	0.17	0.00	18.50	2.12	32.16	68.97
<i>Acanthurus coeruleus</i>	0.83	1.01	18.20	1.93	165.65	213.47
<i>M. chrysurus</i>	0.08	n/a	16.00	n/a	10.27	32.49
<i>Scarus iserti</i>	0.92	1.81	14.36	6.42	72.86	112.66
<i>Scarus taeniopterus</i>	5.58	3.40	16.10	5.20	713.36	342.48
<i>Scarus vetula</i>	1.67	1.00	28.85	4.57	779.99	442.81
<i>Sparisoma aurofrantum</i>	1.33	0.77	21.19	3.66	285.09	191.45
<i>Sparisoma chrysopteron</i>	0.08	n/a	30.00	n/a	41.20	130.27
<i>Sparisoma viride</i>	1.92	1.50	26.09	5.15	815.17	764.75
Bachelor's Beach						
<i>Acanthurus bahianus</i>	1.39	1.32	16.60	2.56	149.51	179.12
<i>Acanthurus chirurgus</i>	0.37	1.18	21.25	1.50	95.00	228.63
<i>Acanthurus coeruleus</i>	5.46	13.12	19.29	1.70	1233.99	2836.43
<i>M. chrysurus</i>	0.83	0.29	13.44	2.13	64.66	46.63
<i>Scarus iserti</i>	0.56	0.48	23.17	0.98	120.86	158.58
<i>Scarus taeniopterus</i>	3.89	1.25	17.86	4.17	590.61	274.11
<i>Scarus vetula</i>	2.59	0.88	29.46	4.06	1272.01	463.21
<i>Sparisoma aurofrantum</i>	0.74	0.75	20.00	2.83	132.61	139.76
<i>Sparisoma viride</i>	1.94	0.76	27.67	4.12	946.17	572.89
Barcadera						
<i>Acanthurus bahianus</i>	0.09	n/a	20.00	n/a	16.30	48.89
<i>Acanthurus chirurgus</i>	0.19	0.00	16.50	0.71	28.00	55.70
<i>Acanthurus coeruleus</i>	0.65	0.80	17.71	1.98	121.28	187.95
<i>M. chrysurus</i>	0.46	0.42	13.80	2.39	39.17	55.31
<i>Scarus iserti</i>	0.28	0.59	19.67	6.66	44.63	88.56
<i>Scarus taeniopterus</i>	2.59	1.53	18.86	5.03	457.83	246.19
<i>Scarus vetula</i>	1.94	1.02	31.67	2.90	1155.75	674.71
<i>Sparisoma aurofrantum</i>	0.19	0.00	22.00	0.00	41.37	82.08
<i>Sparisoma chrysopteron</i>	0.09	n/a	23.00	n/a	24.72	74.15
<i>Sparisoma viride</i>	3.15	0.81	29.50	2.61	1779.19	504.59

	Density (Ind per 100 m ²)		Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Calabas						
<i>Acanthurus bahianus</i>	0.56	0.37	17.50	1.87	67.56	69.74
<i>Acanthurus chirurgus</i>	0.28	0.00	16.33	1.15	41.23	62.48
<i>Acanthurus coeruleus</i>	0.93	1.36	17.30	1.64	163.62	212.48
<i>Scarus iserti</i>	0.46	0.42	20.00	3.74	69.35	97.09
<i>Scarus taeniopterus</i>	6.94	2.89	16.73	5.27	964.15	335.36
<i>Scarus vetula</i>	2.41	1.07	30.88	4.19	1360.92	684.14
<i>Sparisoma aurofrantum</i>	1.20	0.62	20.54	1.90	226.84	123.59
<i>Sparisoma chrysopteron</i>	0.09	n/a	30.00	n/a	45.77	137.32
<i>Sparisoma viride</i>	2.59	1.64	25.82	5.72	1090.46	757.99
Forest						
<i>Acanthurus coeruleus</i>	0.83	0.94	17.60	2.41	155.02	213.54
<i>M. chrysurus</i>	0.33	0.00	13.25	1.50	23.69	32.82
<i>Scarus taeniopterus</i>	6.17	2.89	16.92	5.44	882.08	458.52
<i>Scarus vetula</i>	1.92	0.70	27.04	6.32	790.14	554.87
<i>Sparisoma aurofrantum</i>	1.58	1.17	19.26	3.72	265.81	231.84
<i>Sparisoma viride</i>	2.50	1.44	26.60	7.54	1219.35	829.74
Front Porch 10:00						
<i>Acanthurus bahianus</i>	0.10	n/a	20.00	n/a	18.33	51.86
<i>Acanthurus coeruleus</i>	0.21	0.00	19.00	1.41	45.18	84.43
<i>Scarus iserti</i>	0.10	n/a	28.00	n/a	40.24	113.80
<i>Scarus taeniopterus</i>	3.65	1.83	18.03	4.88	580.96	251.12
<i>Scarus vetula</i>	0.83	0.46	31.75	3.45	502.79	468.20
<i>Sparisoma aurofrantum</i>	1.04	0.68	20.60	4.22	211.98	163.63
<i>Sparisoma chrysopteron</i>	0.10	n/a	32.00	n/a	59.81	169.17
<i>Sparisoma rubripinne</i>	0.10	n/a	30.00	n/a	54.67	154.64
<i>Sparisoma viride</i>	2.08	0.77	27.55	5.24	1029.03	444.21
Front Porch 15:00						
<i>Acanthurus bahianus</i>	0.21	0.00	16.00	1.41	19.09	36.15
<i>Acanthurus chirurgus</i>	0.21	0.00	17.50	3.54	36.37	71.02
<i>Acanthurus coeruleus</i>	0.73	0.34	18.57	1.40	150.61	111.87
<i>M. chrysurus</i>	0.10	n/a	15.00	n/a	10.53	29.77
<i>Scarus iserti</i>	0.21	n/a	21.50	2.12	36.46	103.11
<i>Scarus taeniopterus</i>	3.13	1.98	19.80	4.24	598.64	301.09
<i>Scarus vetula</i>	0.94	0.91	31.67	3.28	559.63	591.86
<i>Sparisoma aurofrantum</i>	0.42	0.48	21.00	1.41	82.60	134.42
<i>Sparisoma chrysopteron</i>	0.21	0.00	22.50	0.71	52.89	98.11
<i>Sparisoma rubripine</i>	0.21	n/a	32.00	0.00	133.26	376.91
<i>Sparisoma viride</i>	6.25	2.14	26.37	4.11	2663.30	967.17

	Density (Ind per 100 m2)		Length (cm)		Biomass (g per 100 m2)	
	mean	SD	mean	SD	mean	SD
Karpata						
<i>Acanthurus bahianus</i>	0.09	n/a	20.00	n/a	16.30	48.89
<i>Acanthurus coeruleus</i>	1.20	1.26	18.77	0.83	253.55	311.71
<i>M. chrysurus</i>	0.65	0.46	15.14	2.12	71.14	80.09
<i>Scarus taeniopterus</i>	3.80	3.09	15.39	5.60	449.53	421.45
<i>Scarus vetula</i>	2.96	1.19	29.41	5.30	1489.29	768.61
<i>Sparisoma</i>						
<i>aurofrantum</i>	1.20	0.43	21.23	3.09	255.02	159.60
<i>Sparisoma rubripine</i>	0.09	n/a	34.00	n/a	71.31	213.94
<i>Sparisoma viride</i>	2.96	1.57	26.28	7.07	1373.26	678.03
No dive reserve						
<i>Acanthurus coeruleus</i>	1.33	0.86	17.88	0.96	251.79	259.98
<i>M. chrysurus</i>	0.08	n/a	12.00	n/a	4.23	13.38
<i>Scarus taeniopterus</i>	4.92	2.02	15.75	4.79	585.19	284.53
<i>Scarus vetula</i>	0.33	0.48	31.00	2.94	184.75	369.23
<i>Sparisoma</i>						
<i>aurofrantum</i>	1.00	0.79	20.92	2.84	202.05	176.33
<i>Sparisoma viride</i>	2.08	0.98	22.92	9.74	804.13	307.95
Oil Slick						
<i>Acanthurus bahianus</i>	0.63	0.83	15.83	2.14	57.33	96.14
<i>Acanthurus coeruleus</i>	0.42	0.00	16.50	1.73	66.17	73.60
<i>M. chrysurus</i>	0.73	0.34	13.57	2.07	57.69	44.14
<i>Scarus iserti</i>	0.42	0.48	19.50	3.32	56.83	93.08
<i>Scarus taeniopterus</i>	3.44	1.44	18.91	4.98	609.79	300.21
<i>Scarus vetula</i>	2.08	0.89	28.15	4.34	898.21	392.82
<i>Sparisoma</i>						
<i>aurofrantum</i>	1.35	0.62	19.69	3.79	242.56	137.83
<i>Sparisoma chrysopterum</i>	0.10	n/a	28.00	n/a	43.88	124.11
<i>Sparisoma viride</i>	3.23	1.57	25.35	4.98	1264.40	742.82
Scientifico						
<i>Acanthurus bahianus</i>	0.08	n/a	20.00	n/a	14.67	46.38
<i>Acanthurus coeruleus</i>	1.00	0.45	18.50	1.57	205.24	147.17
<i>M. chrysurus</i>	0.17	0.00	16.50	0.71	22.66	48.03
<i>Scarus iserti</i>	0.25	0.59	15.33	8.39	26.01	71.59
<i>Scarus taeniopterus</i>	4.92	2.34	18.41	4.28	802.45	329.45
<i>Scarus vetula</i>	1.58	0.88	30.42	4.49	863.26	595.43
<i>Sparisoma</i>						
<i>aurofrantum</i>	0.67	0.75	21.13	2.17	136.19	161.37
<i>Sparisoma viride</i>	2.50	0.79	26.93	6.42	1208.60	472.66

	Density (Ind per 100 m2)		Length (cm)		Biomass (g per 100 m2)	
	mean	SD	mean	SD	mean	SD
Windsock						
<i>Acanthurus bahianus</i>	0.92	0.43	17.73	1.95	116.28	75.56
<i>Acanthurus chirurgus</i>	0.25	0.59	20.67	1.15	60.41	138.30
<i>Acanthurus coeruleus</i>	0.58	0.34	19.14	1.57	129.22	126.28
<i>M. chrysurus</i>	0.33	0.00	14.25	2.22	30.45	44.57
<i>Scarus iserti</i>	0.33	0.00	17.50	8.66	48.31	94.71
<i>Scarus taeniopterus</i>	6.00	2.51	18.63	4.85	1026.14	369.41
<i>Scarus vetula</i>	2.50	1.04	27.30	7.03	1083.11	319.26
<i>Sparisoma</i>						
<i>aurofrantum</i>	0.75	0.70	20.33	3.32	142.66	138.13
<i>Sparisoma</i>						
<i>chrysopteron</i>	0.17	n/a	22.00	0.00	40.13	126.91
<i>Sparisoma viride</i>	2.50	1.80	24.53	7.08	981.16	803.58

Appendix 3: Herbivore Bite Rates

Bite Rates: Functional Groups

Site	<i>All herbivores</i>				<i>Scrapers/Excavators</i>				<i>Denuders</i>				<i>Non-Denuders</i>			
	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE
18th palm	16.0	19.5	8.0	6.9	16.0	19.5	8.0	6.9	0.0	0.0	8.0	0.0	2.4	3.7	8.0	1.3
Bachelor's Beach	8.7	13.1	7.0	4.9	8.7	13.1	7.0	4.9	0.0	0.0	7.0	0.0	2.6	3.6	7.0	1.3
Barcadera	1.1	2.0	7.0	0.8	1.1	2.0	7.0	0.8	0.0	0.0	7.0	0.0	0.9	2.3	7.0	0.9
Calabas	12.8	20.0	6.0	8.2	12.5	19.6	6.0	8.0	0.3	0.8	6.0	0.3	0.8	1.3	6.0	0.5
Forest	17.3	37.1	7.0	14.0	16.4	37.5	7.0	14.2	0.9	1.6	7.0	0.6	0.0	0.0	7.0	0.0
Front Porch	28.3	30.2	7.0	11.4	21.9	16.6	7.0	6.3	6.4	17.0	7.0	6.4	0.0	0.0	7.0	0.0
Karpata	4.7	8.7	7.0	3.3	4.7	8.7	7.0	3.3	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0
No Dive	3.0	4.4	7.0	1.6	3.0	4.4	7.0	1.6	0.0	0.0	7.0	0.0	0.7	1.9	7.0	0.7
Oil Slick	8.9	10.1	8.0	3.6	8.1	8.9	8.0	3.1	0.8	2.1	8.0	0.8	0.0	0.0	8.0	0.0
Reef Scientifico	16.0	28.1	7.0	10.6	14.4	28.8	7.0	10.9	1.6	3.4	7.0	1.3	0.0	0.0	7.0	0.0
Wind Sock	1.6	3.6	5.0	1.6	1.6	3.6	5.0	1.6	0.0	0.0	5.0	0.0	0.0	0.0	5.0	0.0
control	7.4	17.1	41.0	2.7	7.1	17.1	41.0	2.7	0.3	1.1	41.0	0.2	0.6	1.9	41.0	0.3
FPA	18.4	24.2	28.0	4.6	16.3	20.7	28.0	3.9	2.1	8.6	28.0	1.6	0.9	2.2	28.0	0.4

Bite Rates: Scarid Species

Site	<i>S. aurofrenatum</i>				<i>S. iserti</i>				<i>S. taeniopterus</i>				<i>S. vetula</i>				<i>S. viride</i>			
	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE
18th palm	0.0	0.0	8.0	0.0	0.0	0.0	8.0	0.0	9.5	15.3	8.0	5.4	6.0	5.5	8.0	1.9	0.5	1.4	8.0	0.5
Bachelor's Beach	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	4.0	8.9	7.0	3.4	4.7	11.6	7.0	4.4	0.0	0.0	7.0	0.0
Barcadera	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	0.4	1.1	7.0	0.4	0.7	1.9	7.0	0.7	0.0	0.0	7.0	0.0
Calabas	0.0	0.0	6.0	0.0	0.0	0.0	6.0	0.0	9.5	14.9	6.0	6.1	1.3	3.3	6.0	1.3	1.7	4.1	6.0	1.7
Forest	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	0.3	0.8	7.0	0.3	16.1	37.7	7.0	14.2	0.0	0.0	7.0	0.0
Front Porch	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	11.1	13.6	7.0	5.1	3.3	7.8	7.0	3.0	7.4	16.8	7.0	6.3
Karpata	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	2.4	6.4	7.0	2.4	0.7	1.5	7.0	0.6	1.6	2.1	7.0	0.8
No Dive	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	2.3	4.5	7.0	1.7	0.0	0.0	7.0	0.0	0.7	1.5	7.0	0.6
Oil Slick	0.0	0.0	8.0	0.0	0.0	0.0	8.0	0.0	1.5	3.5	8.0	1.2	5.3	8.0	8.0	2.8	1.4	2.1	8.0	0.7
Reef Scientifico	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0	14.4	28.8	7.0	10.9	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0
Wind Sock	0.0	0.0	5.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	5.0	0.0	1.6	3.6	5.0	1.6	0.0	0.0	5.0	0.0
control	0.0	0.0	41.0	0.0	0.0	0.0	41.0	0.0	1.5	4.8	41.0	0.7	5.0	16.6	41.0	2.6	0.5	1.4	41.0	0.2
FPA	0.0	0.0	28.0	0.0	0.0	0.0	28.0	0.0	11.1	18.2	28.0	3.4	2.8	5.4	28.0	1.0	2.4	8.7	28.0	1.6

Bite Rates: Scarid Phase

Site	<i>Juvenile</i>				<i>Initial</i>				<i>Terminal</i>			
	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE
18th palm	6.0	12.8	8.0	4.5	6.8	14.2	8.0	5.0	3.3	4.9	8.0	1.7
Bachelor's Beach	3.4	9.1	7.0	3.4	5.0	11.6	7.0	4.4	0.3	0.8	7.0	0.3
Barcadera	0.0	0.0	7.0	0.0	0.7	1.9	7.0	0.7	0.4	1.1	7.0	0.4
Calabas	9.5	14.9	6.0	6.1	1.7	4.1	6.0	1.7	1.3	3.3	6.0	1.3
Forest	0.3	0.8	7.0	0.3	16.1	37.7	7.0	14.2	0.0	0.0	7.0	0.0
Front Porch	11.1	13.6	7.0	5.1	9.7	17.4	7.0	6.6	1.0	2.6	7.0	1.0
Karpata	2.4	6.4	7.0	2.4	2.1	2.9	7.0	1.1	0.1	0.4	7.0	0.1
No Dive	2.3	4.5	7.0	1.7	0.1	0.4	7.0	0.1	0.6	1.5	7.0	0.6
Oil Slick	1.3	3.5	8.0	1.3	5.4	7.8	8.0	2.8	1.5	4.2	8.0	1.5
Reef Scientifico	11.3	29.4	7.0	11.1	0.0	0.0	7.0	0.0	3.1	6.7	7.0	2.5
Wind Sock	0.0	0.0	5.0	0.0	1.6	3.6	5.0	1.6	0.0	0.0	5.0	0.0
control	1.3	4.7	41.0	0.7	5.3	16.6	41.0	2.6	0.4	1.9	41.0	0.3
FPA	9.4	18.0	28.0	3.4	4.7	11.7	28.0	2.2	2.3	4.6	28.0	0.9

Bite Rates: Scarid Size Class

Site	<i>Small</i>				<i>Medium</i>				<i>Large</i>				<i>Extra Large</i>			
	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE	mean	Stdev	N	SE
18th palm	5.9	14.0	8.0	5.0	5.8	11.7	8.0	4.1	2.3	6.4	8.0	2.3	2.1	4.4	8.0	1.5
Bachelor's Beach	1.0	2.6	7.0	1.0	3.0	6.4	7.0	2.4	4.4	11.7	7.0	4.4	0.3	0.8	7.0	0.3
Barcadera	0.0	0.0	7.0	0.0	1.1	2.0	7.0	0.8	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0
Calabas	8.2	12.7	6.0	5.2	3.0	7.3	6.0	3.0	1.3	3.3	6.0	1.3	0.0	0.0	6.0	0.0
Forest	0.0	0.0	7.0	0.0	16.4	37.5	7.0	14.2	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0
Front Porch	0.0	0.0	7.0	0.0	10.0	14.0	7.0	5.3	6.7	11.6	7.0	4.4	5.1	10.2	7.0	3.9
Karpata	3.6	7.5	7.0	2.8	1.0	1.7	7.0	0.7	0.0	0.0	7.0	0.0	0.1	0.4	7.0	0.1
No Dive	1.0	1.7	7.0	0.7	1.3	3.4	7.0	1.3	0.7	1.5	7.0	0.6	0.0	0.0	7.0	0.0
Oil Slick	1.0	2.8	8.0	1.0	0.8	1.5	8.0	0.5	0.8	1.5	8.0	0.5	5.6	7.8	8.0	2.8
Reef Scientifico	0.0	0.0	7.0	0.0	14.4	28.8	7.0	10.9	0.0	0.0	7.0	0.0	0.0	0.0	7.0	0.0
Wind Sock	0.0	0.0	5.0	0.0	0.0	0.0	5.0	0.0	1.6	3.6	5.0	1.6	0.0	0.0	5.0	0.0
control	1.0	3.5	41.0	0.6	3.8	15.9	41.0	2.5	1.1	5.0	41.0	0.8	1.2	4.0	41.0	0.6
FPA	3.4	9.7	28.0	1.8	8.4	17.1	28.0	3.2	2.6	7.0	28.0	1.3	1.9	5.7	28.0	1.1

Appendix 4

Distribution and abundance of *Diadema antillarum* and *Echinometra viridis* at 10 m depths (SE=standard error)

Treatment	Reef	<i>D. antillarum</i>	<i>E. viridis</i>	SE <i>D. antillarum</i>	SE <i>E. viridis</i>	Monitored Diad
FPA (m)	18th Palm	0	0.113	0	0.043	0.00
FPA (m)	Scientifico	0	0.033	0	0.017	0.00
Control (m)	Windsock	0.038	0.175	0.024	0.066	0.04
Control (m)	Forest	0.01	0.06	0.004	0.008	0.01
Control (m)	Barcadera	0	0.08	0	0.041	0.00
Control (m)	Karpata	0.01	0.18	0.01	0.037	0.01
FPA	Calabas	0	0.04	0	0.019	0.01
FPA	Front Porch	0.02	0.02	0.012	0.012	
Control	Bachelor's	0.013	0.1	0.013	0.071	
Control	Oil Slick	0.013	0.05	0.013	0.02	
Control	No Dive	0.03	0.16	0.02	0.056	

Note: Monitored sites designated (m)

Test diameters (mm) of *D. antillarum* and *E. viridis* (SE=standard error)

Site	<i>D. antillarum</i>	<i>E. viridis</i>	SE <i>D. antillarum</i>	SE <i>E. viridis</i>
Bachelor's	18	20.83	0	2.17
Windsock	22	23.33	2	1.67
18th Palm	0	22.28	0	2.72
Calabas	0	20	0	0
Forest	0	26.75	0	1.97
F. Porch	22.5	25	7.5	0
Scientifico	0	22.5	0	7.5
Barcadera	0	22.11	0	2.11
Oil Slick	No data	No data	No data	No data
Karpata	0	26.25		0.75
No Dive	31.5	27.71	6.5	0.7

Urchin Predation Index (UPI) based on predator biomass and historical stomach volumes; urchin counts (see text)

Site	UPI(biomass)	D.	
		<i>antillarum</i>	<i>E. viridis</i>
Bachelor's	31.09	0.013	0.1
Windsock	23.71	0.038	0.175
18th Palm	7.8	0	0.113
Calabas	40.26	0	0.04
Forest	21.16	0.01	0.06
Front			
Porch	2.85	0.02	0.02
Scientifico	3.55	0	0.033
Barcadera	11.93	0	0.08
Oil Slick	3.41	0.013	0.05
Karpata	6.09	0.01	0.18
No Dive			
Reserve	7.2	0.03	0.16

Appendix 5: Population density and abundance of shallow water sea urchins 0 – 5m

AREA SURVEYS:(# of urchins/m ²)	<i>Diadema</i>	<i>Tripneustes</i>	<i>E. lucunter</i>
18th Palm	0.000	0.000	0.000
Calabas	0.002	0.000	0.000
Front Porch	0.003	0.000	0.000
Reef Scientifico	0.000	0.000	0.000
Bachelor's Beach	0.001	0.000	0.000
Windsock	0.000	0.000	0.000
Forest	0.000	0.000	0.000
Oil Slick Leap	0.000	0.000	0.000
Barcadera	0.000	0.000	0.000
Karpata	0.001	0.000	0.010

QUADRATS: (# of urchins/m ²)	<i>Lucunter</i>	<i>Tripneustes</i>	<i>Diadema</i>	E.lucunter SD
18th Palm	2.09	2.09	0.18	5.96
Calabas	36.20	0.00	0.20	21.42
Front Porch	0.20	0.00	0.00	0.42
Reef Scientifico				
Bachelor's Beach				
Windsock	0.50	0.00	0.00	0.85
Forest				
Oil Slick Leap				
Barcadera				
Karpata	5.00	0.00	0.00	7.35

FPA quadrat SE	11.70
FPA quadrat mean	12.83
Control quadrat SE	2.25
Control quadrat mean	2.75

E. lucunter through the

years (#/m ²)	2005	2007	2009	2013
18th Palm (Plaza)	0.00	0.03	0.33	2.09
Calabas			0.57	36.20
Front Porch			0.09	0.20
Reef Scientifico	0.00	0.00	0.00	
Bachelor's Beach			0.00	
Windsock	0.00	0.06	0.26	0.50
Forest	1.09		0.67	
Oil Slick Leap			0.49	
Barcadera	0.00	0.00	0.13	
Karpata	0.00	0.00		5.00
MEAN	0.18	0.02	0.28	8.80
SE	0.18	0.01	0.08	6.90
p value	0.19	0.09	0.20	0.36
	2013 vs	2009 vs	2013 vs	2013 vs
	2005	2007	2007	2009

Appendix 6

Population density and biomass of territorial damselfishes. (M) denotes the sites that have been monitored since 2003 (see Executive Summary).

Site	Density		Biomass	
	per m ²	100 se	per m ²	100 se
Barcadera (M)	76.88	7.61	2236.91	169.60
Eighteenth Palm (M)	45.63	5.63	1331.54	190.07
Forest (M)	50.63	5.46	888.43	109.24
Karpata (M)	50.63	3.05	1384.98	54.81
Reef Scientifico (M)	42.50	5.67	1246.10	140.37
Windsock	46.25	5.73	1170.79	141.65
Bachelor	30.63	4.77	936.90	159.02
Calabas Front	32.50	3.90	1036.49	115.68
Porch	29.38	4.67	507.90	112.37
Oil Slick	40.00	3.90	1245.10	138.49
Reserve	49.38	5.78	1446.21	157.00

Appendix 7: Distribution, abundance and body sizes of carnivorous fishes.

Bachelor's Beach	N=13	Biomass (kg/100m ²)		Density (indiv./100m ²)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	1.31	0.02	0.3	0.1	39.8	0.1
<i>Aulostomus maculatus</i>	Trumpetfish	0.05	0.01	0.3	0.2	35.3	1.5
<i>Bodianus rufus</i>	Spanish Hogfish	0.45	0.04	0.4	0.2	25.0	3.0
<i>Calamus bajonado</i>	Jolthead Porgy	1.77	0.00	0.1	0.1	46.0	-
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	0.61	0.11	0.4	0.2	30.7	1.3
<i>Cephalopholis cruentatus</i>	Graysby	0.14	0.03	1.4	0.4	16.5	0.8
<i>Cephalopholis fulva</i>	Coney	0.18	0.04	0.8	0.4	17.8	1.2
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.09	0.02	0.6	0.3	17.3	0.9
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.12	0.00	0.1	0.1	43.0	-
<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.12	0.00	0.1	0.1	20.0	-
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	0.64	0.22	2.1	1.4	16.3	0.3
<i>Haemulon flavolineatum</i>	French Grunt	0.21	0.02	1.7	0.4	17.1	0.8
<i>Haemulon macrostomum</i>	Spanish Grunt	0.39	0.00	0.1	0.1	26.0	-
<i>Haemulon plumieri</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.44	0.06	0.1	0.1	32.0	1.6
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.05	0.00	0.1	0.1	15.0	-
<i>Hypoplectrus sp.</i>	Hamlet	0.04	0.00	0.4	0.2	12.3	0.2
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	0.79	0.17	0.5	0.2	31.8	2.6
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.49	0.17	1.5	1.1	21.0	0.9
<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.58	0.15	0.8	0.3	25.6	2.5
<i>Paranthias furcifer</i>	Creolefish	0.20	0.04	0.1	0.1	24.0	2.0
<i>Pterois volitans</i>	Red Lionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.02	0.00	0.8	0.3	9.0	0.4
<i>Sphyaeneia barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>	Sand Diver	0.39	0.00	0.1	0.2	27.0	2.7

Barcadera	N=12	Biomass (kg/100m ²)		Density (indiv./100m ²)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	0.37	0.14	0.3	0.2	23.8	1.9
<i>Aulostomus maculatus</i>	Trumpetfish	0.06	0.00	0.1	0.1	40.0	-
<i>Bodianus rufus</i>	Spanish Hogfish	0.27	0.07	0.2	0.1	23.3	3.4
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	0.67	0.10	0.4	0.2	31.5	0.7
<i>Cephalopholis cruentatus</i>	Graysby	0.15	0.03	1.8	0.3	16.8	1.2
<i>Cephalopholis fulva</i>	Coney	0.09	0.02	0.1	0.1	18.5	1.4
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.04	0.01	0.2	0.1	16.7	0.7
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.46	0.09	0.6	0.3	27.4	1.8
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	1.04	0.45	4.3	2.9	17.0	0.6
<i>Haemulon flavolineatum</i>	French Grunt	0.16	0.04	1.3	0.4	17.3	0.5
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumieri</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.46	0.04	0.3	0.1	32.8	0.9
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.09	0.00	0.1	0.2	14.0	0.8
<i>Hypoplectrus sp.</i>	Hamlet	0.02	0.00	0.1	0.1	12.0	0.0
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.63	0.00	0.1	0.1	32.0	-
<i>Lutjanus apodus</i>	Schoolmaster	0.69	0.16	0.7	0.2	29.8	2.6
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.29	0.08	0.6	0.1	25.1	2.6
<i>Lutjanus synagris</i>	Lane Snapper	0.08	0.00	0.1	0.1	18.0	-
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.19	0.00	0.1	0.1	24.0	-
<i>Paranthias furcifer</i>	Creolefish	0.00	0.00	0.0	0.0	-	0.0
<i>Pterois volitans</i>	Red Lionfish	0.01	0.00	0.1	0.1	10.0	-
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.04	0.01	0.8	0.4	10.5	1.1
<i>Sphyraena barracuda</i>	Great Barracuda	2.85	0.00	0.1	0.1	70.0	-
<i>Synodus intermedius</i>	Sand Diver	0.22	0.00	0.1	0.1	30.0	-

Calabas	N=10	Biomass (kg/100m2)		Density (indiv./100m2)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	3.20	0.93	0.2	0.1	49.0	4.9
<i>Aulostomus maculatus</i>	Trumpetfish	0.07	0.01	0.3	0.2	43.0	1.8
<i>Bodianus rufus</i>	Spanish Hogfish	0.44	0.05	0.3	0.3	23.5	2.1
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.01	0.00	0.1	0.1	80.0	-
<i>Caranx ruber</i>	Bar Jack	1.70	0.58	0.7	0.4	35.8	3.4
<i>Cephalopholis cruentatus</i>	Graysby	0.43	0.18	2.4	0.7	19.6	1.9
<i>Cephalopholis fulva</i>	Coney	0.11	0.00	0.2	0.2	16.0	0.0
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.12	0.00	0.3	0.3	16.3	0.2
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	0.85	0.00	0.3	0.4	20.0	0.0
<i>Haemulon flavolineatum</i>	French Grunt	0.59	0.37	5.3	4.9	16.3	0.3
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumierii</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.82	0.00	0.2	0.1	40.0	0.0
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>	Hamlet	0.03	0.00	0.2	0.1	13.0	0.4
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Kyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	1.66	0.37	2.3	0.8	30.4	3.0
<i>Lutjanus cyanopterus</i>	Cubera Snapper	5.22	1.05	0.3	0.2	59.5	4.6
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.48	0.09	1.3	1.0	18.8	1.5
<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Mycteroperca tigris</i>	Tiger Grouper	0.16	0.02	0.2	0.1	22.0	0.9
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	1.11	0.37	0.8	0.5	30.7	3.9
<i>Paranthias furcifer</i>	Creolefish	0.00	0.00	0.0	0.0	-	0.0
<i>Pterois volitans</i>	Red Lionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.02	0.00	0.4	0.3	9.2	0.7
<i>Sphyraena barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>	Sand Diver	1.55	0.00	0.3	0.3	38.7	2.6

Eighteenth Palm	N=12	Biomass (kg/100m ²)		Density (indiv./100m ²)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Aulostomus maculatus</i>	Trumpetfish	0.10	0.01	0.2	0.1	48.0	2.1
<i>Bodianus rufus</i>	Spanish Hogfish	0.25	0.00	0.1	0.1	26.0	-
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	2.42	0.00	0.1	0.1	51.0	-
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	0.57	0.06	0.4	0.2	32.0	1.0
<i>Cephalopholis cruentatus</i>	Graysby	0.30	0.06	2.1	0.5	19.2	1.4
<i>Cephalopholis fulva</i>	Coney	0.04	0.01	0.3	0.1	14.0	0.7
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.18	0.02	0.6	0.3	20.9	1.2
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax sp.</i>	Eel sp.	0.29	0.03	0.2	0.1	56.7	1.7
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.35	0.04	0.1	0.1	28.5	1.0
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon flavolineatum</i>	French Grunt	0.20	0.03	1.6	0.3	17.6	0.6
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumierii</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.50	0.06	0.3	0.1	33.5	1.4
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.06	0.00	0.1	0.1	16.0	-
<i>Hypoplectrus sp.</i>	Hamlet	0.03	0.00	0.3	0.1	12.4	0.6
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	1.05	0.27	1.9	0.6	27.0	2.5
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.09	0.01	0.3	0.1	17.8	0.6
<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.55	0.15	0.3	0.1	32.6	3.5
<i>Paranthias furcifer</i>	Creolefish	0.00	0.00	0.0	0.0	-	0.0
<i>Pterois volitans</i>	Red Lionfish	0.01	0.00	0.1	0.1	10.0	-
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.02	0.00	0.8	0.2	10.2	0.5
<i>Sphyraena barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>	Sand Diver	0.13	0.01	0.4	0.2	23.2	0.6

Forest	N=12	Mean Biomass (kg/100m ²)		Density (indiv./100m ²)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
Scientific Name	Common Name						
<i>Anisotremus surinamensis</i>	Black Margate	2.09	0.47	0.1	0.1	44.0	3.3
<i>Aulostomus maculatus</i>	Trumpetfish	0.04	0.01	0.4	0.2	32.5	2.8
<i>Bodianus rufus</i>	Spanish Hogfish	0.23	0.07	0.6	0.3	18.9	2.6
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.1	0.1	49.0	-
<i>Caranx ruber</i>	Bar Jack	0.39	0.06	0.5	0.1	29.6	1.5
<i>Cephalopholis cruentatus</i>	Graysby	0.55	0.11	2.6	0.5	21.9	1.9
<i>Cephalopholis fulva</i>	Coney	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.11	0.01	0.3	0.1	22.4	0.9
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.56	0.00	0.1	0.1	70.0	-
<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon album</i>	White Margate	2.60	0.00	0.1	0.1	54.0	-
<i>Haemulon carbonarium</i>	Caesar Grunt	0.28	0.04	0.2	0.1	26.3	1.2
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	4.05	1.89	14.9	11.6	16.1	0.1
<i>Haemulon flavolineatum</i>	French Grunt	0.18	0.05	0.4	0.2	19.8	1.0
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumieri</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>	Hamlet	0.04	0.00	0.1	0.1	14.0	-
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	1.21	0.24	1.3	0.3	34.2	2.8
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.22	0.04	0.3	0.2	21.2	2.1
<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Paranthias furcifer</i>	Creolefish	0.14	0.00	0.1	0.2	17.5	0.2
<i>Pterois volitans</i>	Red Lionfish	0.27	0.07	0.6	0.2	24.4	2.3
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.00	0.00	0.1	0.1	6.0	-
<i>Sphyræna barracuda</i>	Great Barracuda	1.77	0.00	0.1	0.1	60.0	-
<i>Synodus intermedius</i>	Sand Diver	0.22	0.00	0.1	0.1	30.0	-

Front Porch	N=9	Mean Biomass (kg/100m2)		Density (indiv./100m2)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Aulostomus maculatus</i>	Trumpetfish	0.06	0.01	0.6	0.2	38.3	0.8
<i>Bodianus rufus</i>	Spanish Hogfish	0.59	0.10	0.4	0.2	26.8	4.8
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	0.54	0.10	0.4	0.2	32.8	2.0
<i>Cephalopholis cruentatus</i>	Graysby	0.67	0.17	3.3	0.9	22.2	1.8
<i>Cephalopholis fulva</i>	Coney	0.56	0.10	0.7	0.4	27.0	2.0
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.16	0.00	0.2	0.2	20.0	1.9
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax sp.</i>	Eel sp.	0.38	0.09	0.2	0.1	60.0	4.7
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	0.13	0.00	0.1	0.1	16.0	-
<i>Haemulon flavolineatum</i>	French Grunt	0.33	0.12	1.5	0.3	20.5	1.7
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumieri</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.60	0.00	0.1	0.1	36.0	-
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>	Hamlet	0.01	0.00	0.1	0.1	10.0	-
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	0.89	0.14	1.0	0.8	24.8	3.2
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.70	0.32	1.6	1.6	19.9	0.5
<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Paranthias furcifer</i>	Creolefish	0.21	0.04	0.7	0.5	18.0	0.9
<i>Pterois volitans</i>	Red Lionfish	0.01	0.00	0.1	0.1	9.0	-
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.01	0.00	0.1	0.1	29.0	-
<i>Serranus tigrinus</i>	Harlequin Bass	0.02	0.00	1.7	0.4	7.8	0.4
<i>Sphyraena barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>	Sand Diver	0.05	0.00	0.1	0.1	18.0	-

Karpata	N=12	Mean Biomass (kg/100m2)		Density (indiv./100m2)		Fork length (cm)			
		Scientific Name	Common Name	Mean	SE	Mean	SE	Mean	SE
		<i>Anisotremus surinamensis</i>	Black Margate	0.00	0.00	0.0	0.0	-	0.0
		<i>Aulostomus maculatus</i>	Trumpetfish	0.09	0.03	0.6	0.2	39.5	3.9
		<i>Bodianus rufus</i>	Spanish Hogfish	0.30	0.12	0.9	0.3	17.1	3.3
		<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
		<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
		<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
		<i>Caranx ruber</i>	Bar Jack	0.83	0.29	0.3	0.1	34.8	3.6
		<i>Cephalopholis cruentatus</i>	Graysby	0.26	0.05	1.9	0.5	19.5	0.8
		<i>Cephalopholis fulva</i>	Coney	0.00	0.00	0.0	0.0	-	0.0
		<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
		<i>Epinephelus guttatus</i>	Red Hind	0.16	0.00	0.1	0.1	26.0	-
		<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
		<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
		<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
		<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
		<i>Haemulon carbonarium</i>	Caesar Grunt	0.38	0.01	0.3	0.2	26.8	1.2
		<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	1.51	0.45	3.5	2.6	16.9	0.4
		<i>Haemulon flavolineatum</i>	French Grunt	0.17	0.03	1.3	0.2	18.1	0.8
		<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
		<i>Haemulon plumierii</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
		<i>Haemulon sciurus</i>	Bluestriped Grunt	0.56	0.11	0.3	0.1	33.8	2.4
		<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.01	0.01	0.2	0.1	25.0	1.5
		<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.09	0.00	0.1	0.1	18.0	-
		<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
		<i>Hypoplectrus sp.</i>	Hamlet	0.02	0.00	0.1	0.1	12.0	0.0
		<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
		<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
		<i>Lutjanus apodus</i>	Schoolmaster	1.05	0.29	1.0	0.3	32.2	2.4
		<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
		<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.27	0.05	0.6	0.3	21.1	0.9
		<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
		<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
		<i>Ocyurus chrysurus</i>	Yellowtail Snapper	1.13	0.21	0.3	0.2	41.5	0.9
		<i>Paranthias furcifer</i>	Creolefish	0.00	0.00	0.0	0.0	-	0.0
		<i>Pterois volitans</i>	Red Lionfish	0.00	0.00	0.0	0.0	-	0.0
		<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
		<i>Serranus tigrinus</i>	Harlequin Bass	0.02	0.01	0.3	0.1	9.5	1.4
		<i>Sphyraena barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
		<i>Synodus intermedius</i>	Sand Diver	0.32	0.00	0.1	0.1	34.0	-

No-Dive Reserve	N=12	Mean Biomass (kg/100m ²)		Density (indiv./100m ²)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	0.93	0.00	0.1	0.1	36.0	-
<i>Aulostomus maculatus</i>	Trumpetfish	0.05	0.02	0.3	0.2	34.2	3.0
<i>Bodianus rufus</i>	Spanish Hogfish	0.16	0.08	0.9	0.4	12.5	2.7
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	0.97	0.00	0.1	0.2	32.0	1.6
<i>Cephalopholis cruentatus</i>	Graysby	0.20	0.03	1.9	0.2	18.3	1.1
<i>Cephalopholis fulva</i>	Coney	0.08	0.00	0.1	0.1	18.0	0.0
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.04	0.00	0.1	0.1	16.0	-
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.62	0.09	0.2	0.2	30.0	1.2
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	1.37	0.00	1.0	1.2	14.0	0.0
<i>Haemulon flavolineatum</i>	French Grunt	0.17	0.04	1.0	0.3	17.2	1.0
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumierii</i>	White Grunt	1.00	0.00	0.1	0.1	38.0	-
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.50	0.00	0.1	0.1	34.0	-
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>	Hamlet	0.03	0.00	0.4	0.2	11.7	0.2
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.10	0.01	0.2	0.2	16.3	0.2
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	1.37	0.38	1.4	0.3	34.0	3.2
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.34	0.06	0.6	0.3	24.1	1.7
<i>Lutjanus synagris</i>	Lane Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Paranthias furcifer</i>	Creolefish	0.00	0.00	0.0	0.0	-	0.0
<i>Pterois volitans</i>	Red Lionfish	0.06	0.01	0.5	0.2	13.9	0.7
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.03	0.01	0.2	0.1	11.3	1.7
<i>Sphyraeana barracuda</i>	Great Barracuda	3.53	0.00	0.1	0.1	75.0	-
<i>Synodus intermedius</i>	Sand Diver	0.30	0.00	0.1	0.1	33.0	-

Oil Slick	N=14	Biomass (kg/100m2)		Density (indiv./100m2)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>	Black Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Aulostomus maculatus</i>	Trumpetfish	0.05	0.01	0.2	0.2	34.8	1.3
<i>Bodianus rufus</i>	Spanish Hogfish	0.68	0.10	0.2	0.2	24.7	5.2
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	1.16	0.25	0.1	0.1	41.0	3.0
<i>Cephalopholis cruentatus</i>	Graysby	0.10	0.02	0.7	0.2	17.3	0.7
<i>Cephalopholis fulva</i>	Coney	0.08	0.00	0.1	0.1	18.0	0.0
<i>Epinephelus adscensionis</i>	Rock Hind	0.00	0.00	0.0	0.0	-	0.0
<i>Epinephelus guttatus</i>	Red Hind	0.09	0.01	0.1	0.1	21.0	1.1
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>	Spotted Moray	0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax sp.</i>	Eel sp.	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon album</i>	White Margate	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>	Caesar Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	1.34	0.36	3.3	2.1	16.7	0.5
<i>Haemulon flavolineatum</i>	French Grunt	0.27	0.07	3.2	1.3	15.5	0.5
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumieri</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.64	0.09	0.3	0.1	35.8	1.8
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>	Hamlet	0.05	0.01	0.2	0.2	13.5	0.3
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	0.48	0.08	0.2	0.1	30.7	1.9
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus synagris</i>	Lane Snapper	0.56	0.00	0.1	0.1	27.5	0.6
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Paranthias furcifer</i>	Creolefish	0.00	0.00	0.0	0.0	-	0.0
<i>Pterois volitans</i>	Red Lionfish	0.01	0.00	0.1	0.1	9.0	-
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.02	0.00	0.6	0.3	9.2	0.5
<i>Sphyræna barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>	Sand Diver	0.00	0.00	0.0	0.0	-	0.0

Reef Scientifico	N=13	(kg/100m2)		(indiv./100m2)		Fork length (cm)			
		Scientific Name	Common Name	Mean	SE	Mean	SE	Mean	SE
<i>Anisotremus surinamensis</i>		Black Margate		0.00	0.00	0.0	0.0	-	0.0
<i>Aulostomus maculatus</i>		Trumpetfish		0.12	0.02	0.4	0.3	38.1	1.0
<i>Bodianus rufus</i>		Spanish Hogfish		0.36	0.11	0.6	0.3	16.6	3.6
<i>Calamus bajonado</i>		Jolthead Porgy		0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>		Ocean Triggerfish		0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>		Horse-eye Jack		0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>		Bar Jack		0.77	0.12	0.5	0.2	34.6	2.1
<i>Cephalopholis cruentatus</i>		Graysby		0.39	0.07	1.7	0.5	21.0	1.5
<i>Cephalopholis fulva</i>		Coney		0.28	0.00	0.3	0.2	22.0	0.6
<i>Epinephelus adscensionis</i>		Rock Hind		1.32	0.00	0.1	0.1	24.0	-
<i>Epinephelus guttatus</i>		Red Hind		0.17	0.03	1.2	0.4	19.6	1.2
<i>Gymnothorax miliaris</i>		Goldentail Moray		0.00	0.00	0.0	0.0	-	0.0
<i>Gymnothorax moringa</i>		Spotted Moray		0.85	0.11	0.2	0.1	78.3	3.5
<i>Gymnothorax sp.</i>		Eel sp.		0.27	0.03	0.1	0.1	55.0	2.0
<i>Haemulon album</i>		White Margate		0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon carbonarium</i>		Caesar Grunt		0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon chrysargyreum</i>		Smallmouth Grunt		22.88	0.00	12.9	15.5	15.0	0.0
<i>Haemulon flavolineatum</i>		French Grunt		0.19	0.03	1.5	0.3	17.8	0.9
<i>Haemulon macrostomum</i>		Spanish Grunt		0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumierii</i>		White Grunt		0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>		Bluestriped Grunt		0.47	0.03	0.3	0.1	33.0	0.7
<i>Heteropriacanthus cruentatus</i>		Glasseye Snapper		0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>		Yellowtail Hamlet		0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>		Barred Hamlet		0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>		Hamlet		0.03	0.00	0.2	0.1	12.7	0.3
<i>Hypoplectrus unicolor</i>		Butter Hamlet		0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>		Bermuda Chub		0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>		Schoolmaster		0.61	0.15	1.2	0.3	27.8	1.8
<i>Lutjanus cyanopterus</i>		Cubera Snapper		0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>		Mahogany Snapper		0.27	0.05	1.3	0.9	18.0	1.3
<i>Lutjanus synagris</i>		Lane Snapper		0.15	0.01	0.1	0.1	22.0	0.8
<i>Mycteroperca tigris</i>		Tiger Grouper		0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>		Yellowtail Snapper		0.15	0.00	0.1	0.1	22.0	-
<i>Paranthias furcifer</i>		Creolefish		0.00	0.00	0.0	0.0	-	0.0
<i>Pterois volitans</i>		Red Lionfish		0.00	0.00	0.0	0.0	-	0.0
<i>Scorpaena plumieri</i>		Spotted Scorpionfish		0.01	0.00	0.1	0.1	32.0	-
<i>Serranus tigrinus</i>		Harlequin Bass		0.02	0.01	0.4	0.2	9.6	1.0
<i>Sphyraena barracuda</i>		Great Barracuda		0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>		Sand Diver		0.30	0.00	0.1	0.1	33.0	-

Windsock	N=12	Biomass (kg/100m ²)		Density (indiv./100m ²)		Fork length (cm)	
		Mean	SE	Mean	SE	Mean	SE
Scientific Name	Common Name						
<i>Anisotremus surinamensis</i>	Black Margate	2.09	0.31	0.1	0.1	45.0	2.0
<i>Aulostomus maculatus</i>	Trumpetfish	0.03	0.00	0.1	0.1	32.0	0.8
<i>Bodianus rufus</i>	Spanish Hogfish	0.07	0.04	0.5	0.2	10.7	2.3
<i>Calamus bajonado</i>	Jolthead Porgy	0.00	0.00	0.0	0.0	-	0.0
<i>Canthidermis sufflamen</i>	Ocean Triggerfish	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx latus</i>	Horse-eye Jack	0.00	0.00	0.0	0.0	-	0.0
<i>Caranx ruber</i>	Bar Jack	0.77	0.07	0.5	0.2	34.6	2.1
<i>Cephalopholis cruentatus</i>	Graysby	0.37	0.06	2.8	0.5	18.8	1.4
<i>Cephalopholis fulva</i>	Coney	0.05	0.01	0.1	0.1	15.0	1.2
<i>Epinephelus adscensionis</i>	Rock Hind	12.34	0.00	0.1	0.1	48.0	-
<i>Epinephelus guttatus</i>	Red Hind	0.20	0.07	0.6	0.3	20.8	1.7
<i>Gymnothorax miliaris</i>	Goldentail Moray	0.60	0.00	0.1	0.1	72.0	-
<i>Gymnothorax moringa</i>	Spotted Moray	0.85	0.00	0.1	0.1	80.0	-
<i>Gymnothorax sp.</i>	Eel sp.	0.34	0.00	0.1	0.1	60.0	-
<i>Haemulon album</i>	White Margate	1.82	0.00	0.1	0.1	48.0	-
<i>Haemulon carbonarium</i>	Caesar Grunt	0.44	0.00	0.1	0.1	31.0	-
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	8.12	3.57	17.6	16.9	15.8	0.2
<i>Haemulon flavolineatum</i>	French Grunt	0.20	0.03	1.5	0.3	17.7	0.9
<i>Haemulon macrostomum</i>	Spanish Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon plumierii</i>	White Grunt	0.00	0.00	0.0	0.0	-	0.0
<i>Haemulon sciurus</i>	Bluestriped Grunt	0.64	0.11	0.3	0.1	35.0	2.9
<i>Heteropriacanthus cruentatus</i>	Glasseye Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus chlorurus</i>	Yellowtail Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus puella</i>	Barred Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Hypoplectrus sp.</i>	Hamlet	0.02	0.00	0.1	0.1	12.0	-
<i>Hypoplectrus unicolor</i>	Butter Hamlet	0.00	0.00	0.0	0.0	-	0.0
<i>Khyphosus sectatrix</i>	Bermuda Chub	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus apodus</i>	Schoolmaster	0.82	0.12	0.6	0.2	33.0	2.4
<i>Lutjanus cyanopterus</i>	Cubera Snapper	0.00	0.00	0.0	0.0	-	0.0
<i>Lutjanus mahogoni</i>	Mahogany Snapper	0.18	0.04	0.5	0.3	18.7	0.4
<i>Lutjanus synagris</i>	Lane Snapper	0.08	0.00	0.1	0.1	18.0	-
<i>Mycteroperca tigris</i>	Tiger Grouper	0.00	0.00	0.0	0.0	-	0.0
<i>Ocyurus chrysurus</i>	Yellowtail Snapper	1.43	0.36	0.3	0.2	40.2	2.8
<i>Paranthias furcifer</i>	Creolefish	0.06	0.00	0.1	0.1	17.0	-
<i>Pterois volitans</i>	Red Lionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Scorpaena plumieri</i>	Spotted Scorpionfish	0.00	0.00	0.0	0.0	-	0.0
<i>Serranus tigrinus</i>	Harlequin Bass	0.01	0.00	0.1	0.1	10.0	-
<i>Sphyraeana barracuda</i>	Great Barracuda	0.00	0.00	0.0	0.0	-	0.0
<i>Synodus intermedius</i>	Sand Diver	0.53	0.00	0.1	0.1	40.0	-

Appendix 8A. Mean density of coral juveniles/m² per species in Bonaire, March 2013

Coral Species	Mean	Standard Error
<i>Agaricia</i> spp	3.27	0.48
<i>Porites asteroides</i>	1.6	0.38
<i>Montastraea annularis</i>	1.58	0.47
<i>Montastraea faveolata</i>	0.95	0.44
<i>Montastraea cavernosa</i>	0.35	0.18
<i>Siderastrea siderea</i>	0.32	0.17
<i>Stephanocoenia</i> spp.	0.19	0.13
<i>Millepora alcicornis</i>	0.18	0.13
<i>Diploria labyrinthiformis</i>	0.11	0.07
<i>Meandrina</i> spp.	0.11	0.11

Appendix 8B. Numbers of Juvenile Coral/m² Across Sites in Bonaire, March 2013

Type of Site	Site Name	Mean	Standard Error
Controls	Bachelors Beach	11.13	3.24
	Windsock	8.96	3.21
	Forest	8.96	2.78
	Oil Slick	9.6	3.15
	Barcadera	5.6	2.90
	Karpata	5.12	2.39
FPA	18th Palm	12.8	2.77
	Calabas	7.68	3.08
	Front Porch	12.8	3.69
	Reef Scientifico	5.6	2.10
	Total	8.82	0.90

Appendix 8C. Crustose Coralline Algae % Cover Across Sites in Bonaire, March 2013

Type of Site	Site Name	Mean	Standard Error
Controls	Oil Slick	3.67	1.27
	Windsock	0.79	0.28
	Bachelors Beach	3.17	1.18
	Forest	2.48	0.60
	Barcadera	2.35	0.76
	Karpata	2.88	0.80
FPA	18th Palm	3.68	0.96
	Calabas	2.84	0.72
	Front Porch	5.02	1.55
	Reef Scientifico	2.27	0.77
	Total	3.21	0.43

Appendix 8D. Macroalgae Biomass Index/m² Across Sites in Bonaire, March 2013

Type of Site	Site Name	Mean	Standard Error
Controls	Oil Slick	97.77	43.22
	Windsock	81.16	23.22
	Bachelors Beach	170.0	49.10
	Forest	35.2	8.92
	Barcadera	15.5	7.97
	Karpata	23.28	7.38
FPA	18th Palm	102.36	21.18
	Calabas	71.48	15.50
	Front Porch	75.94	17.13
	Reef Scientifico	158.75	49.95
	Total	83.14	14.95