

# Status and Trends of Bonaire's Coral Reefs in 2015:

*Slow but steady signs of resilience*

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# **Executive Summary:**

## **Status and Trends of Bonaire's Reefs in 2015:**

### **Slow but steady signs of resilience**

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#### **Overview and approach**

Bonaire's coral reefs remain among the healthiest in the Caribbean. Although the island's reefs have suffered bleaching disturbances similar to those plaguing reefs throughout the Caribbean, they uniquely show signs of recovery. Here we highlight key findings from our March 2015 biennial coral reef monitoring expedition. We put the findings in the context of both the trends recorded since 2003 when we began our regular monitoring and the most recent research related to the factors controlling the structure and functioning of healthy coral reef ecosystems.

There are many ideas about how best to monitor coral reef ecosystems. We considered these when STINAPA asked us to develop a monitoring protocol for Bonaire in 2005 (see Steneck and McClanahan 2005). We determined it is best to keep monitoring simple and focused on the key indicators and drivers of coral health.

Although coral reefs are complex ecosystems, relatively few “drivers” control much of their structure and how they function. “*Drivers*” are key processes that control functionally important aspects of coral reefs. Several processes can interact with one another (Fig. 1). For example seaweed (also called “*macroalgae*”) are known to poison corals (Rasher and Hay 2010) and reduce or halt the settlement and survival of reef corals (Arnold et al 2010 and Steneck et al 2014). It has also been shown that herbivorous fishes are capable of reducing or eliminating macroalgae from coral reefs (Lewis 1986, Williams and Polunin 2001). Thus herbivores such as parrotfish facilitate the recruitment of reef corals, reduce toxic seaweed and create complex habitats into which juvenile reef fish recruit (Caselle and Warner 1996). These drivers and their interactions have been viewed as integral to a complex system of feedbacks that maintain healthy coral reefs (Fig. 1: Mumby and Steneck 2008).



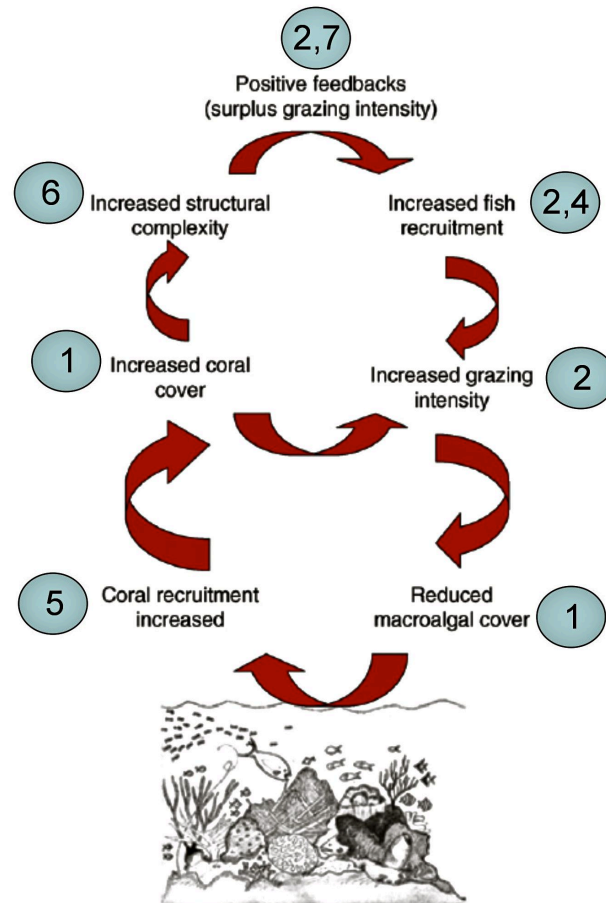


Fig. 1. Conceptual model illustrating the reinforcing feedback processes driving a reef toward a healthy state dominated by corals with high structural complexity (from Mumby and Steneck 2008). The numbers in circles represent the chapters containing information for each relevant node in this model.

Monitoring Bonaire's coral reefs focused on key drivers identified in Fig. 1. Since all components interact, it is difficult or impossible to define a specific amount as being particularly healthy or unhealthy for any given coral reef. Therefore, our monitoring protocol measures components such as the abundance of live coral and determines its trends (i.e., change through time) because there is a consensus on what constitutes a reef trending towards better condition. For example, increasing live coral cover or decreasing macroalgal abundance are both trending towards good condition (Fig. 2). This allows us to create a very simple means of reporting condition with trends in key drivers clearly identified (this was the model developed a priori in Steneck and McClanahan 2005).

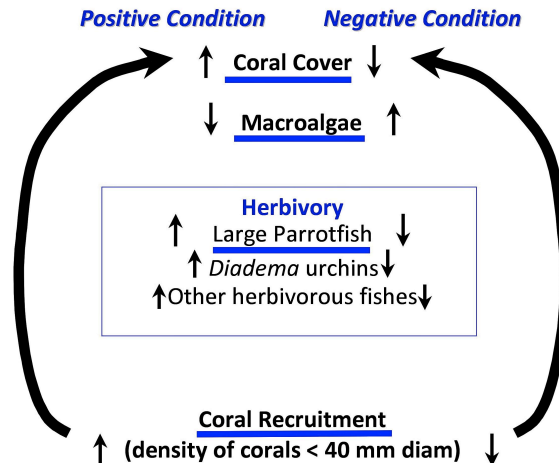


Fig. 2. Key drivers of reef health and the focus for monitoring Bonaire's reefs (from Steneck and McClanahan 2005).

## Results

### *Key Findings and Trends:*

Coral reefs are defined by the abundance of live coral. Bonaire's reefs remain among the healthiest in the Caribbean in that corals occupy more space than any other group (especially seaweed: Fig. 3; Steneck Chapter 1). Most formerly coral-dominated reefs are now seaweed-reefs throughout the Caribbean, especially in specific regions (e.g., eastern Caribbean) and at specific locations (e.g., Dominican Republic) (Fig. 3). Nevertheless, a static measure of coral or algal cover for Bonaire is not as telling as are the trends.

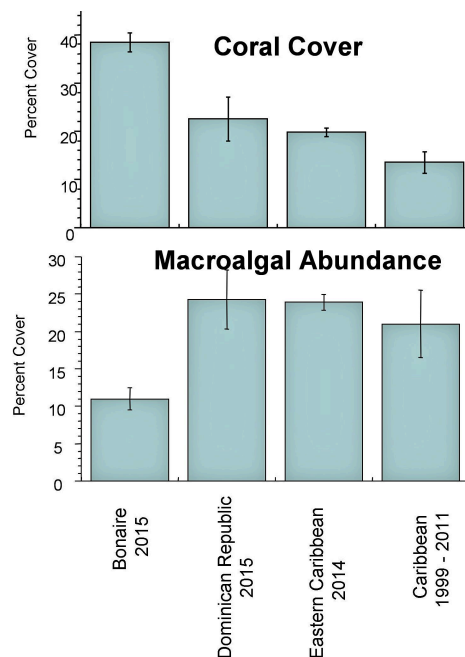


Fig. 3. Comparisons of the abundance of live coral and macroalgae for Bonaire, Dominican Republic, the eastern Caribbean (Steneck et al in prep) and the Caribbean (Jackson et al 2014).

At all the monitored sites, coral cover was nearly 50% and algal cover was extremely low from 1999 until the coral bleaching event of 2010, when about 10% of the coral died and macroalgal abundance markedly increased (Fig. 4 A, B; Steneck Chapter 1). For these two indicators of coral reef health, the impact of the bleaching event is easy to see. However, how the ecosystem responded after the event is extremely important. Coral cover increased very slightly in 2015 and we observed some of the heavily impacted coral species such as *Colpophyllia natans* recovering from the bleaching event.

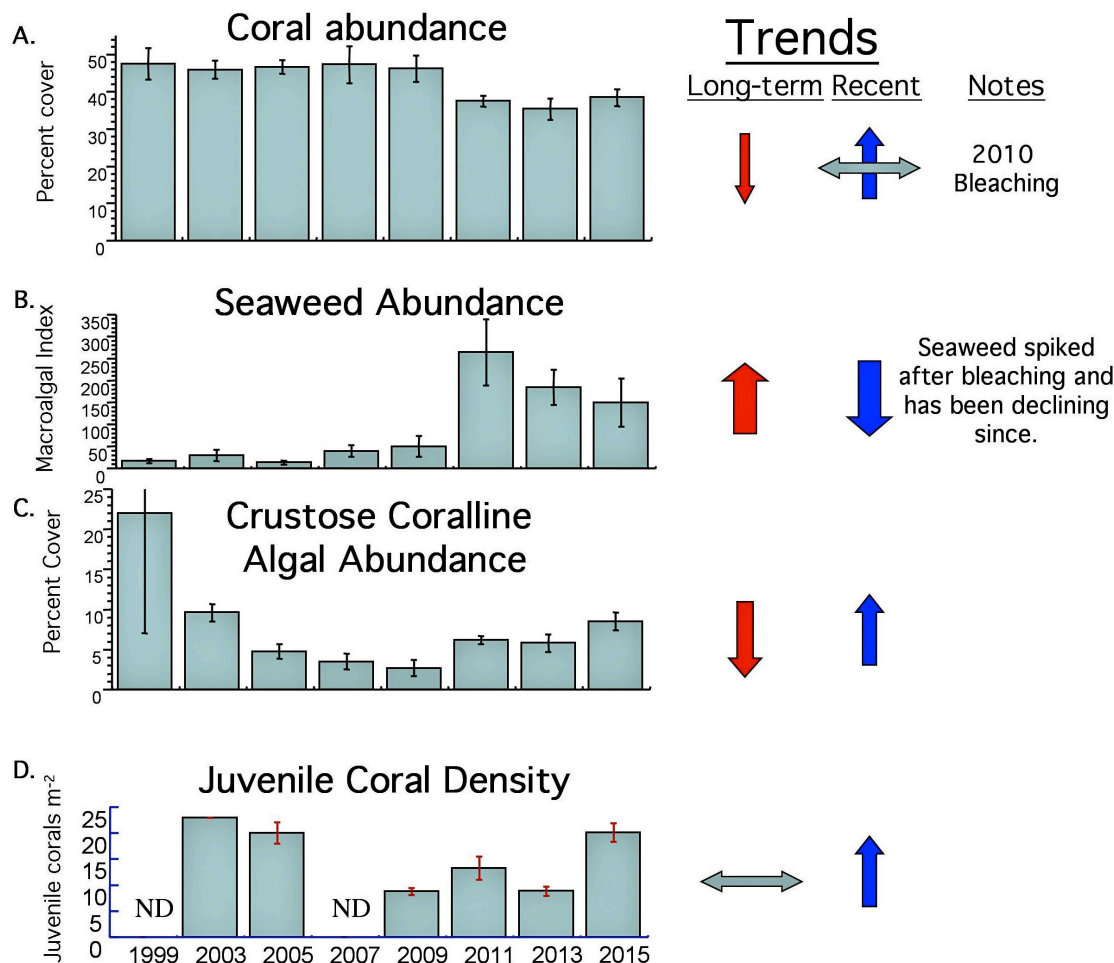


Fig. 4. Trends in coral, seaweed, crustose coralline algae and juvenile coral densities (A-D). Long-term trends and recent trends since 2011 (post-2010 bleaching). Arrows point upward for increases, downward for decreases with negative trends in red and positive trends in blue. Horizontal arrows reflect stasis. Vertical lines on bars show variance as standard error.

The trend in harmful seaweed abundance is positive because it is low and declining. The impact of seaweed scales with its volume. A cover of low-canopy seaweed has much less impact on reef corals than does one with a high canopy. This is represented by an “algal index” (e.g., Steneck et al., 2014), which is the volume of macroalgae. The macroalgae index recorded in 2011 was less than 300 whereas the Caribbean average ranges between 700 and 900.

Nevertheless, seaweed abundance has been steadily declining since the 2010 bleaching event to the 2015 monitoring (Fig. 4B).

The decline in harmful seaweed was accompanied with an increase in crustose coralline algae (Fig. 4C). These trends suggest that herbivory was sufficient to improve conditions for juvenile corals (called “*surplus herbivory*” Mumby and Steneck 2008). Accordingly, juvenile coral abundance has been increasing over the past four monitoring periods (Fig. 4D; Feehan Chapter 5). These patterns suggested herbivory from parrotfishes especially was sufficient to control seaweed abundance. Interestingly, parrotfish biomass has remained relatively static over the past three monitoring periods (Fig. 5A; Arnold Chapter 2), suggesting that herbivore abundance could be adequate to maintain sufficient grazing to reduce the post-bleaching algal increase.

Unlike the stasis seen among parrotfish (Fig. 5A), predators have been declining (Fig. 5B; Camacho Chapter 4) since 2011. This could be because the primary allowable mode of fishing is via hook and line, which selects for carnivorous fish and against herbivores. Since predatory fish abundance is the main controller in sea urchin populations, the decline observed in predatory fish might explain the increase in sea urchins abundance such as the long-spined sea urchin *Diadema antillarum*, which has steadily increased in abundance since 2009 (Fig. 5C; Boyle Chapter 3).

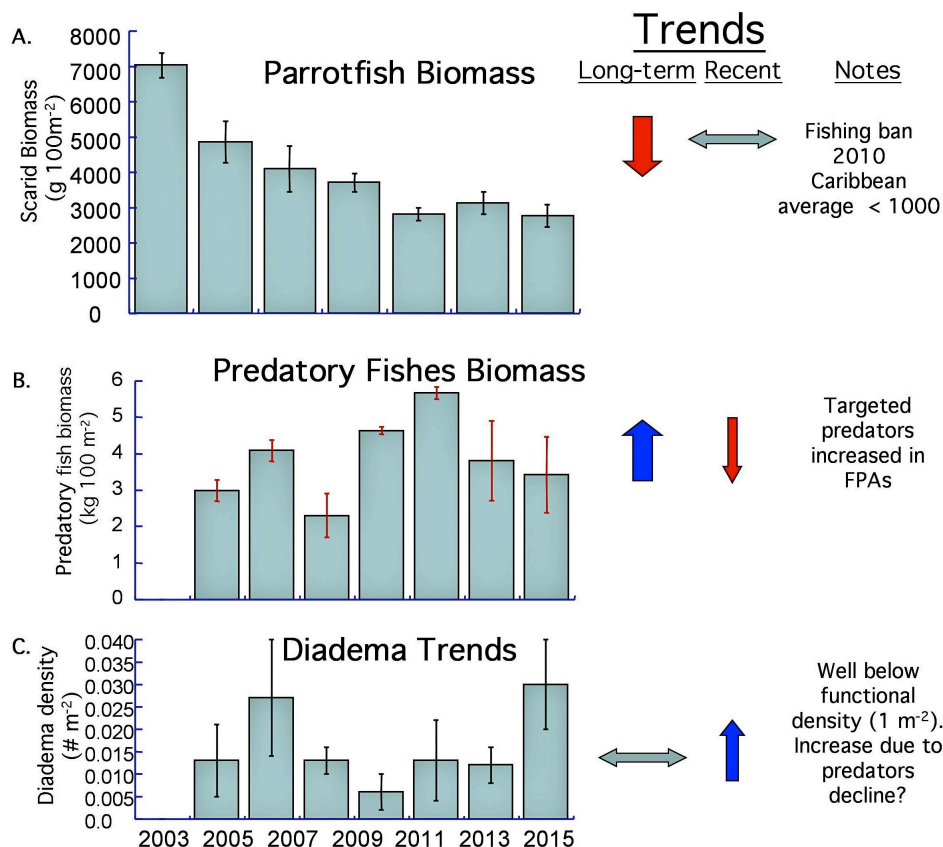


Fig. 5. Trends in the abundance of parrotfish, predatory fishes and the sea urchin *Diadema*. All notations as in Fig. 4.

Except for parrotfish that have been relatively static since 2011, trends over the past five years for the strongest drivers of reef health (i.e., Fig. 2) have been positive (Fig. 6). However, the

stasis in parrotfish could be because they live close to their carrying capacity. For example, the 2011 – 2015 average biomass for parrotfish on Bonaire’s reefs was 29 g m<sup>-2</sup>. This was twice the maximum reported in a large-scale study of herbivores on Caribbean reefs (Williams and Polunin 2001). Analyses of bite rates suggest algal food may be limiting for parrotfish (Chandler and Rasher; Chapter 7). When algal food is scarce, parrotfish may fight with each other (i.e., intraspecific competition). Reefs with the highest parrotfish population density generally had the lowest per-area bite rates (Chandler and Rasher; Chapter 7) possibly due to their fighting. Under these conditions, “*surplus herbivory*” (*sensu* Mumby and Steneck 2008) provides a critical buffer to algal pulses, as has occurred in Bonaire in 2010. That year algal food resources increased thereby relaxing intraspecific competition resulting in greater bite rates (less fighting over food) and declining algal abundance. This is exactly what was observed (see Fig. 5 in Chapter 7).

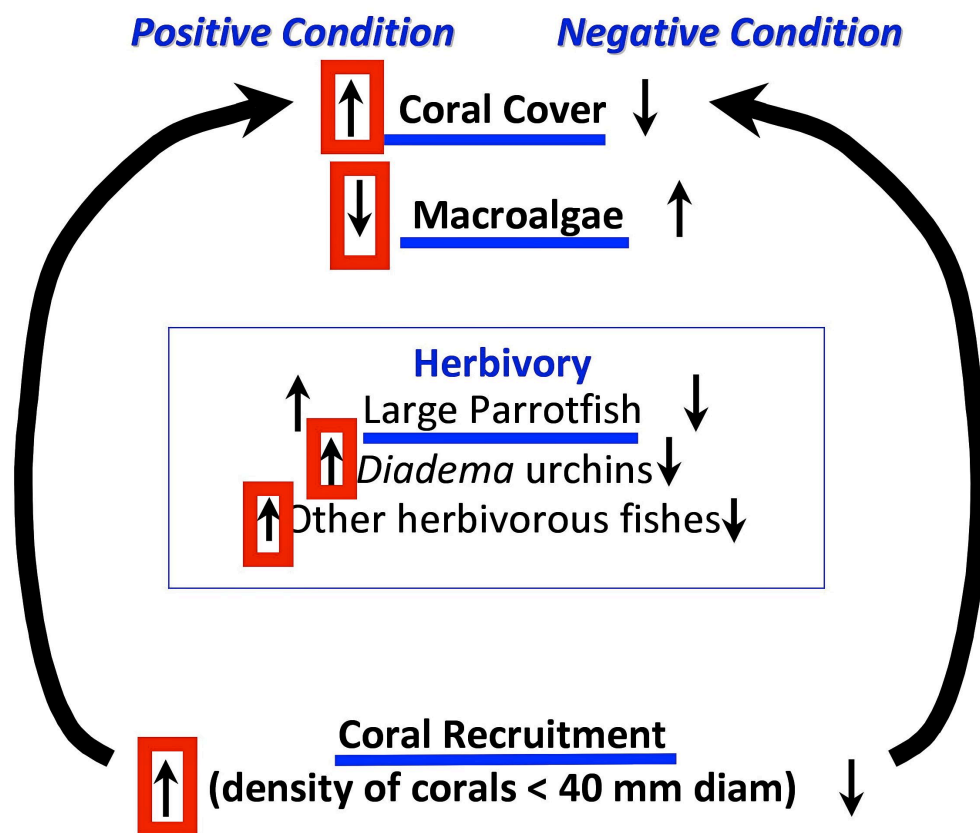


Fig. 6. Reef conditions based on recent trends (from Fig. 5). Red rectangles represent the direction of the trends from the 2015 survey.

Parrotfish abundance on Bonaire’s monitored reefs scaled with rugosity (Fig. 7: Wilson Chapter 6). Rugosity, measured as the number of meters of reef under each linear meter (also called a “spatial index”), correlated significantly with parrotfish population density. Generally, the reefs with highest coral cover also had the highest rugosity (Wilson Chapter 6) and this may have increased nursery habitats for settling parrotfish (e.g. as described in Mumby and Steneck 2008; Fig. 1).



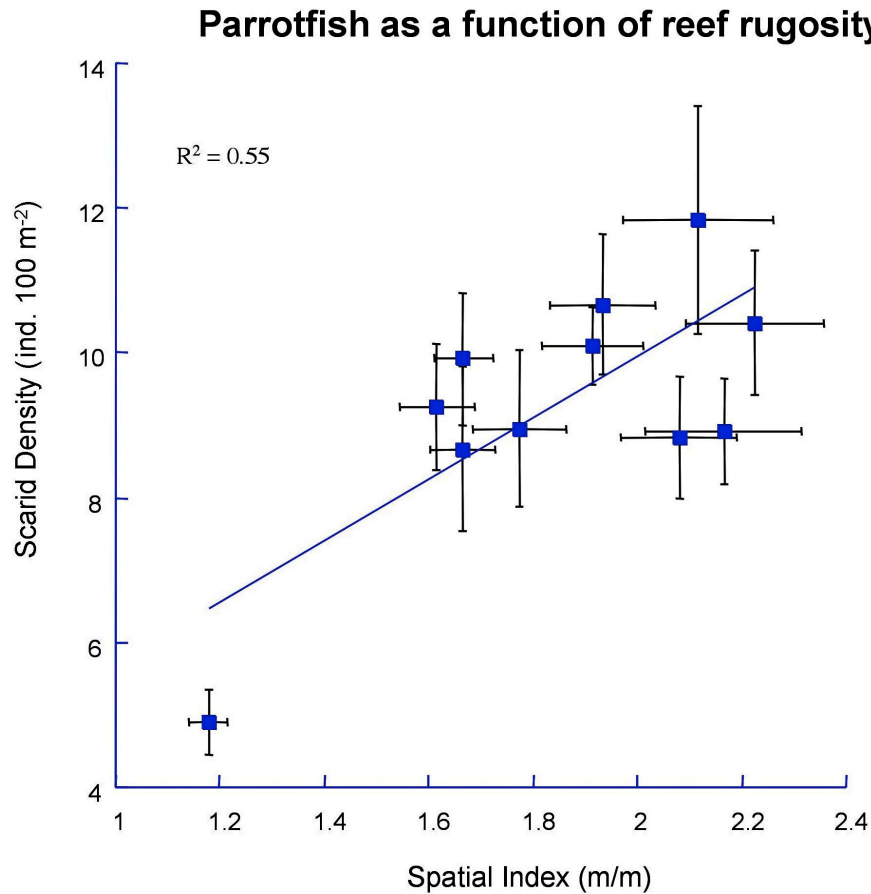


Fig. 7. Parrotfish abundance (i.e., scarid density) as a function of rugosity (i.e., spatial index). The most structurally complex reefs had the highest parrotfish abundance.

Overall, Bonaire’s monitored coral reefs have relatively abundant fish that contribute to healthy reinforcing ecological feedbacks (Fig. 1) thus maintaining resilient reefs (Fig. 6). Recently a review of reef fish abundance for the ocean systems of the Pacific, Indian and Caribbean determined that reef fish biomass was “functional” around 1000 kg ha<sup>-1</sup> (Fig. 8; MacNeil et al 2015) and that it could take as long as 30 years for a reef depleted of fish to recover to functional abundances. However, Bonaire’s reef fish biomass is similar to the biomass of fully protected reefs within no-take reserves (Fig. 8).

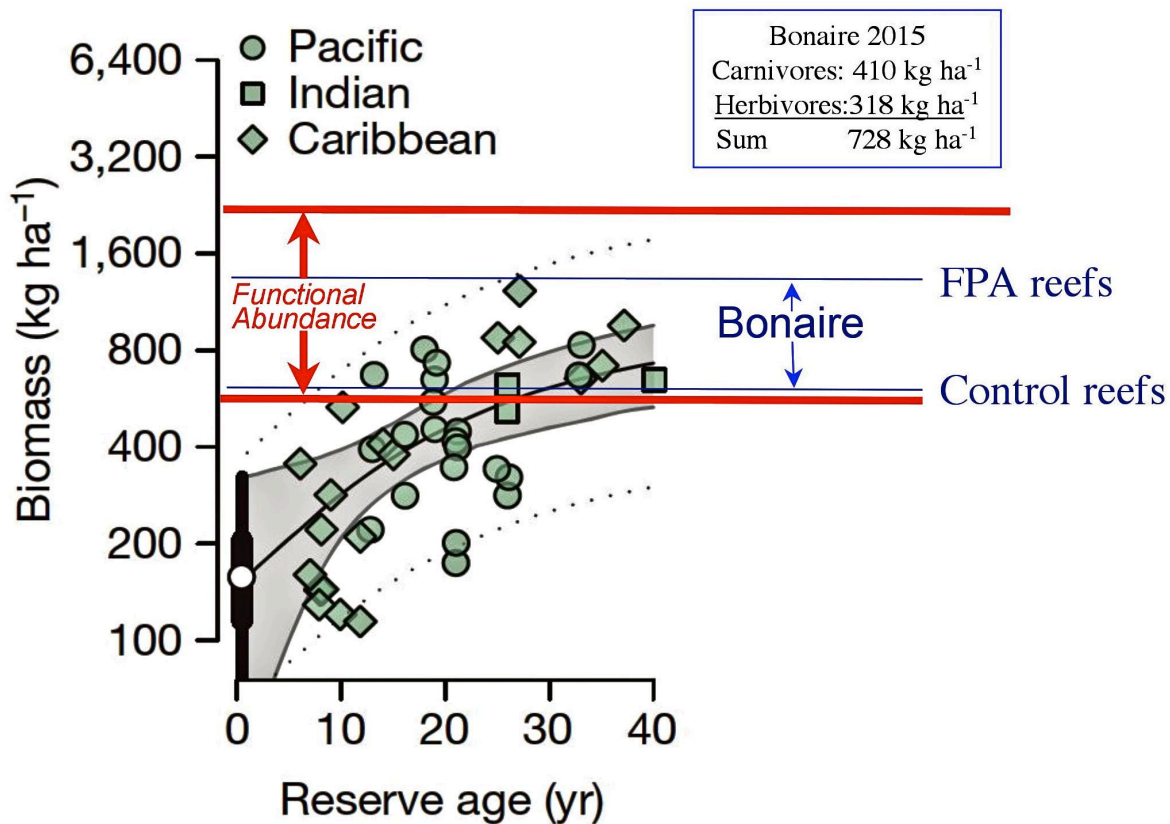


Fig. 8. The time required for depleted fish stocks to reach functional abundances (red lines) in the absence of fishing (from MacNeil et al 2015). Fish abundance in Bonaire (FPA and control reefs) in March of 2015 (blue lines).

Given this, what effect do Fish Protection Areas (FPAs) create? We would not expect to see changes in parrotfish or other herbivorous fish because they usually do not take a baited hook (which is the primary mode of fishing in Bonaire). While the FPAs typically have greater predator biomass than the fished control reefs, in general this difference existed upon establishment of the FPAs in 2007 with enforcement beginning in 2008 (Camacho Chapter 4). Among the carnivorous fishes, all of the large predators (groupers, snappers and barracuda) were rare or absent at the monitored reefs (Camacho; Chapter 4). However, mesopredators such as graysby's and conies that are most-targeted (Nenadovic 2007) did show a relative increase (i.e. comparing fished and FPA reefs) since the establishment of FPAs (Fig. 9).

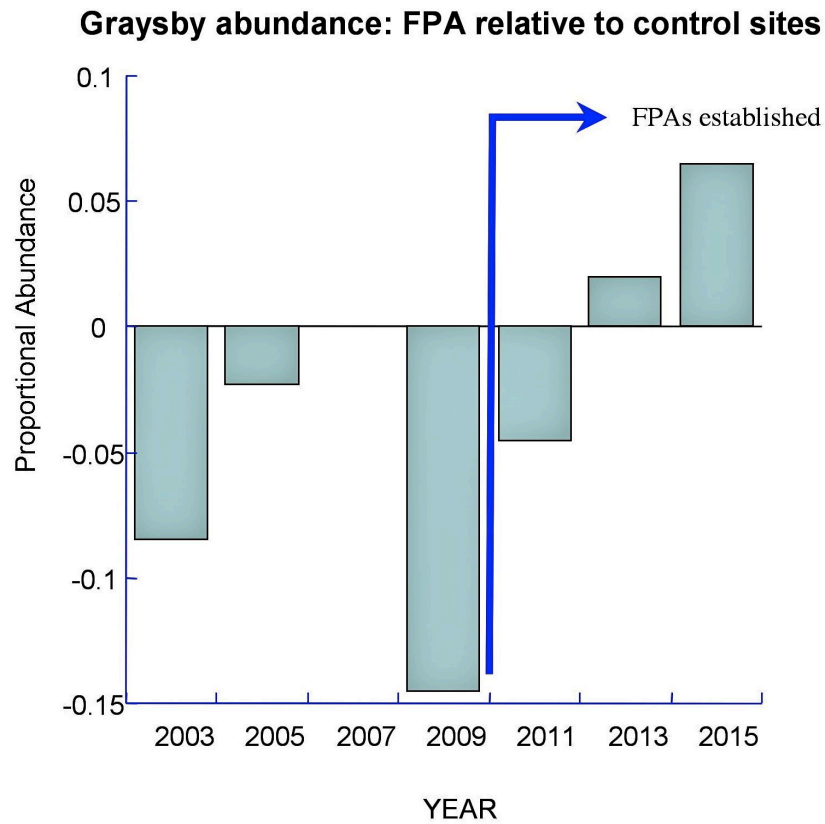


Fig. 9. The proportional abundance of graysbys (a heavily fished species) relative to fished reefs. If abundances were equal, they would fall on the 0-line. If fished (control) reefs had higher graysby densities, it plots negative, whereas if FPAs had more graybys, it plots in the positive direction. Note the shift in graysbys since the establishment of FPA reefs.

The value of studying corals, seaweed, herbivorous fishes and carnivorous fishes using standardized methods such as AGRRA, is that regional comparisons can be made. This way, we can determine what the baseline is and how important aspects of reef health are changing relative to that baseline. This year's report included parasites that are clearly visible on juvenile fishes (see DeGraff ; Chapter 8). While parasites were visible and clearly differed among reef sites in Bonaire, we do not know if the values described in Chapter 8 are relatively high, low or which way they are trending.

#### *Lingering Concerns and Management Implications:*

Despite Bonaire's relatively healthy coral reefs and its virtually unique capacity to recover from disturbance, troubling trends persist. Key among these are the predator decline, illegal fishing and coastal development. We expand on each below.

Predator populations continue to decline in Bonaire. This is especially noticeable among the large bodied groupers that are virtually absent in Bonaire (see Chapter 4). It is well known that reef fish have a limited capacity to be harvested sustainably (Birkeland 1997) because they grow

slowly and they are relatively old when they reach reproductive maturity (Birkeland 1997). So even with the current fishing restrictions, fishing may still be taking a toll.

Recent studies in Bonaire determined that predator decline can contribute to an increase in territorial damselfishes that prevent other herbivorous fishes such as parrotfish from keeping macroalgae in check (Vermeij et al 2015). Damselfish abundances in Bonaire are especially high (Chapter 9) so this could be the result of the island's fishing-induced loss of predators.

During the week we conducted our monitoring, we observed people fishing in the FPA (see Chapter 2 for a description of the illegal fishing). At least some of the fishing in FPAs is due to the absence of signs informing everyone that fishing is not allowed in the specific FPA areas.

Finally, the recent increase in coastal development is evident in town. While this development may appear innocuous, the increased number of visitors and residents may have unintended consequences for the coral reef. For example, there are large piles of white sand at Front Porch. This may improve the site for visitors on land, but the sediment often finds its way into the ocean where it can be lethal to reef corals (Nugues and Roberts 2003, Weber et al 2012). One of Bonaire's attributes that makes the island so attractive to divers is the close proximity of its fringing reefs. These are exactly the type of reefs most affected by sediment runoff which can happen during a significant rain storm.

Evidence from Bonaire and the wider Caribbean clearly indicates that investing to preserve healthy coral reefs is much more cost-effective than having to resort to very expensive and rarely successful reef restoration projects.

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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, 10 m each). Overall coral cover remains relatively high ( $38.4\% \pm 1.9$  SE) and macroalgae relatively low ( $10.9\% \pm 1.5$  SE). The 2010 bleaching event caused a steep 10% decline in coral cover resulting in a steep increase in macroalgae. Since the 2011 survey, coral cover and crustose coralline algae have increased slightly and macroalgae have declined significantly. The dominant corals remain two species of *Orbicella* (mountainous star coral), *Madracis*, *Montastraea* and *Agaricia*. Those four genera comprise 74% of the coral space occupiers in Bonaire. The Fish Protection Areas (FPAs) continue to have lower coral and crustose coralline algal abundance and higher algal and turf canopy heights. There has not been a consistent change in benthic communities within the FPAs since they were established. Given the relatively low fishing pressure on Bonaire’s reefs, a strong FPA effect is not expected.

### **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). The general pattern in this region is that stony corals have been replaced by seaweed (called “macroalgae”) on many reefs, which is harmful to both juvenile and adult corals (Jackson et al 2014, Webster et al 2015). However, some people have questioned the value of meta-analyses such as that performed by Gardner et al. (2003) and others have questioned the prevalence of the shift from coral to macroalgae (Bruno et al 2009). One problem was the general lack of commensurable survey methods.

In 1999-2000 the first standardized, high-resolution Caribbean-wide, assessment of coral reefs was developed and performed as the Atlantic and Gulf Reef Rapid Assessment or “AGRRA” protocol. Those assessments of 20 reef areas determined that Bonaire had among the highest coral cover and lowest seaweed abundance in the Caribbean (summarized in Kramer 2003). Building from this baseline in 2003, a team from the University of Maine began long-term monitoring of Bonaire’s coral reefs. The surveys were conducted at fixed depths (10 m) on specific reefs selected by STINAPA. I have monitored the reef corals and algae during the first two weeks of March every other year since 2003. During this period we recorded consistently high abundance of coral and low abundance of macroalgae through the 2009 monitoring period (Steneck et al 2009). In 2010 Bonaire suffered a bleaching event during which 10% of the coral died and macroalgae increased significantly (Steneck et al 2011 and 2013).

Coral reefs of the Caribbean are notorious for their apparent inability to recover from serious disturbances (Connell 1997). Some have argued this problem results from feedbacks in which herbivore loss contributes to increased seaweed which further kills adult corals and inhibits recruitment of juvenile corals (Mumby and Steneck 2008, Rasher and Hay 2010, Steneck et al 2014)

This report is the next in the series of standardized surveys all conducted by R. Steneck on permanent transects to quantify patterns in the distribution, abundance and species composition of stony coral, macroalgae and crustose coralline algae in both space (along Bonaire's coral reefs) and in time (since 1999). With this study, we can assess the trajectory of the reef corals and algae to determine if there is evidence of recovery from the 2010 bleaching event.

## **Methods**

The distribution and abundance of major reef-occupying groups such as stony coral, macroalgae and crustose coralline algae (abbreviated “CCA”) were quantified along replicate 10 m line transects (methods of Benayahu and Loya 1977; commensurate with the AGRRA protocol, Kramer 2003) at 10 m depth at each of our 11 study sites (listed in Fig. 2). Algae were subdivided into ecological “functional groups” (see Steneck and Dethier 1994) such as crustose coralline, articulated coralline, foliaceous macroalgae (or simply “macroalgae”) and non-coralline crusts. This chapter consists of data for the most abundant and diagnostic groups of corals, macroalgae and crustose coralline algae.

At each of the 11 sites surveyed, four 10m long transects had all organisms living under the transect quantified. All categories of information among the 44 transects are in Appendix 1. Specifically, I measured the length of each substrate component (ie functional groups listed above, sponges, gorgonians and each species of coral) to the nearest centimeter.

I compare results from Fish Protection Areas (FPAs) (established in 2008 in which fishing is not allowed) with “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.

Because reefs differed at the start of the study, conditions are best considered for trends in key groups such as reef corals, CCA and macroalgae. Transect locations were established and marked with ceramic plates installed in 2003. Temporal trends were determined from repeated measures from those fixed transects. Sites lacking ceramic plates had transects placed in approximately identical locations at 10 m at each site.

## **Results**

Today, most Caribbean “coral reefs” have a higher abundance of seaweed (or macroalgae) than of reef corals but Bonaire is an exception (Fig. 1). Despite the Caribbean-wide loss of elkhorn and staghorn corals (ie. the genus *Acropora*), Bonaire has maintained significantly higher coral

cover (38%) and lower abundance of macroalgae (11%) than other recent studies conducted at 10 m depth.

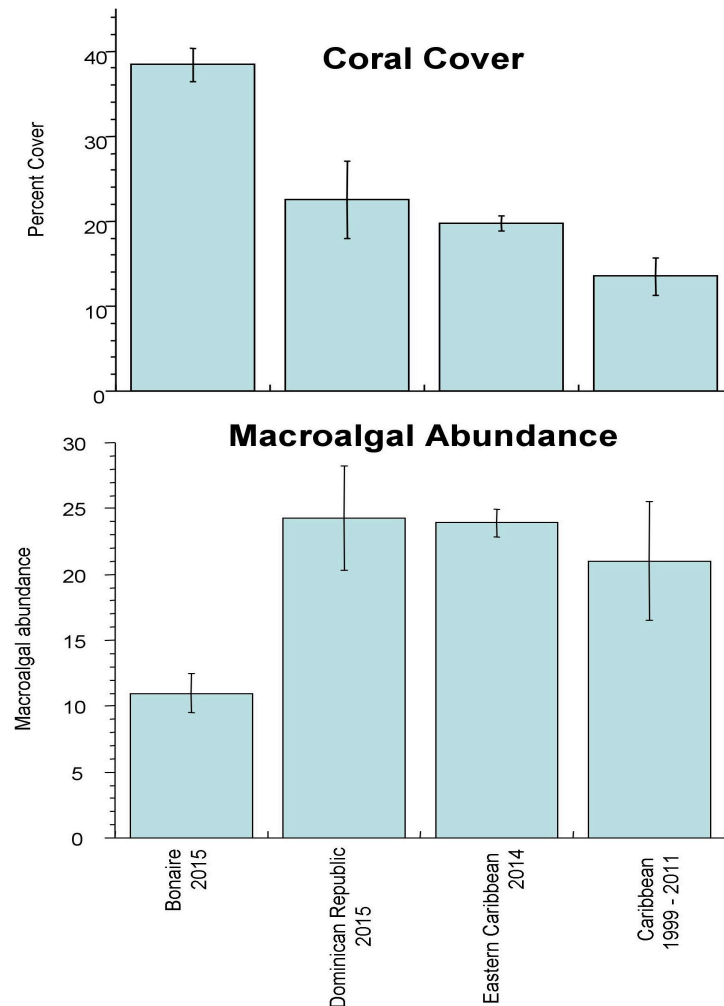


Fig. 1. Abundance of live coral and macroalgae for Bonaire (this study), the Dominican Republic (March 2015; Steneck and Torres 2015), the entire eastern Caribbean from Anguilla to Grenada (2014; Steneck and Mumby in prep) and the entire Caribbean 1999 – 2011 (Jackson et al 2014).

Although mean coral cover remained relatively high, some sites such as Forest on Klein Bonaire and Reef Scientifico were higher than average while 18<sup>th</sup> Palm and Oilslick Leap had lower than average coral cover (Fig. 2).

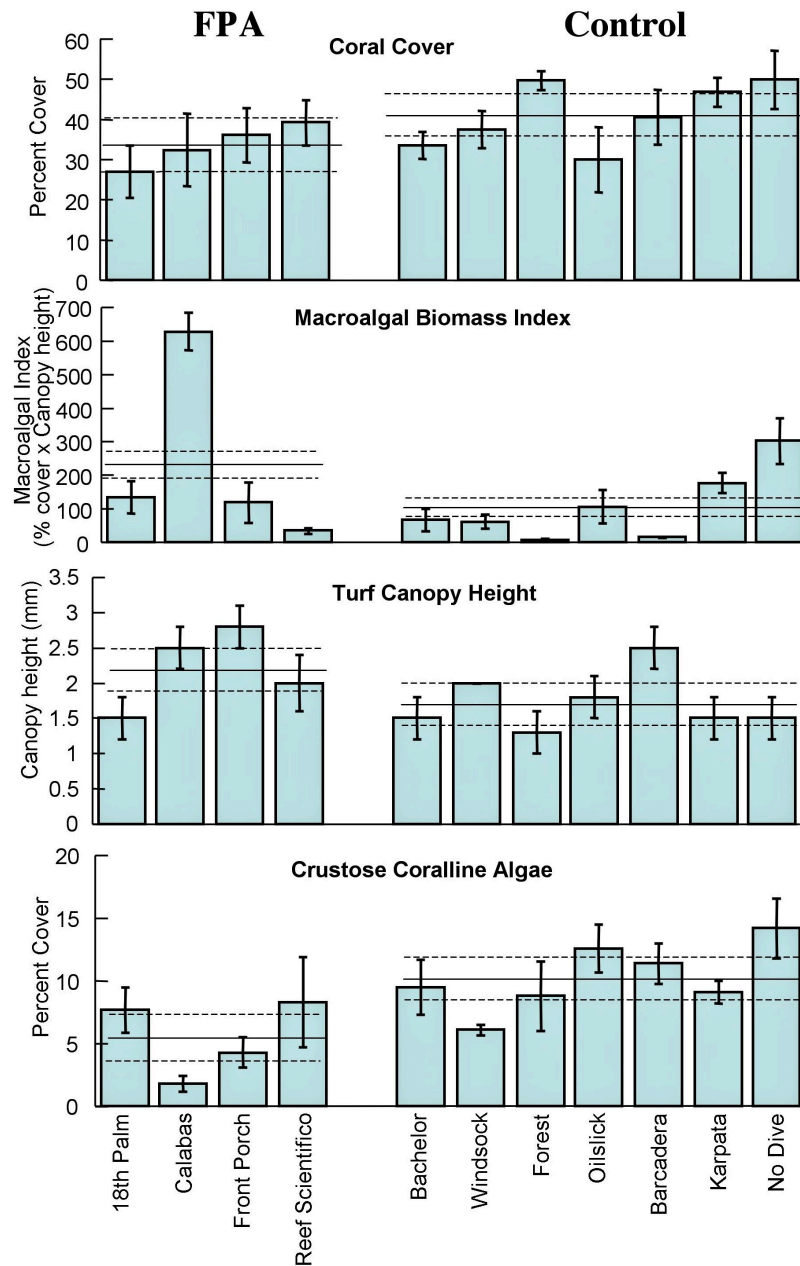


Fig. 2. Abundance of coral (top), macroalgal biomass index, turf canopy heights and abundance of crustose coralline algae (bottom) at FPA and control sites. Variance is expressed as standard error with vertical lines on bars representing individual sites. Horizontal lines represent the mean (solid) and variance (SE dotted lines) when pooling all FPA and control sites.

Overall, coral cover and crustose coralline algae were slightly more abundant at control sites compared to FPA sites (Fig. 2). Algae showed the reverse pattern with greater macroalgal abundance and turf canopy heights at FPA sites. These patterns were evident in the first assessment after the establishment of FPA sites (Steneck et al 2011) and so they are not the result of the no-take (FPA) reserves.

Algal biomass (eg. g m<sup>-2</sup>) is the best metric for representing algal abundance. Percent cover is less desirable because it may simply reflect coral mortality creating more space (thus increasing algal percent cover), without necessarily indicating any other change in the ecosystem. An increasingly widely used surrogate for algal biomass is the volume of algae. That is the percent cover multiplied by the canopy height of the algae (often called the macroalgal index). Several recent studies used an algal index or algal volume to illustrate abundance (e.g., Mumby et al 2013, Webster et al 2015).

The height of algal canopies is independent of percent cover and thus is a good way to monitor the effective rates of herbivory. This is necessary because the accumulation of algae is both a function of rates of algal growth and rates of algal removal by herbivores. This metric can be usefully applied to diminutive filamentous turf algae which grows remarkably rapidly. Thus, the average canopy height of algal turfs at any location integrates the rates of algal growth (increasing the canopy height) and the rates of herbivore cropping (reducing canopy heights). Turf canopy heights were slightly greater at FPA sites relative to control sites (Fig. 2).

The composition of coral species varied somewhat between FPA and control reefs (Fig. 3). For both treatments, the most abundant corals were *Orbicella annularis* and *O. faveolata* (formerly called *Montastraea annularis*, *M. faveolata*). However, FPA reefs maintained abundant populations of *Montastraea cavernosa* and *Agaricia agaricites* corals whereas control reefs had significantly more *Madracis auretenra* and to a lesser extent *Colpophyllia natans* (Fig. 3).

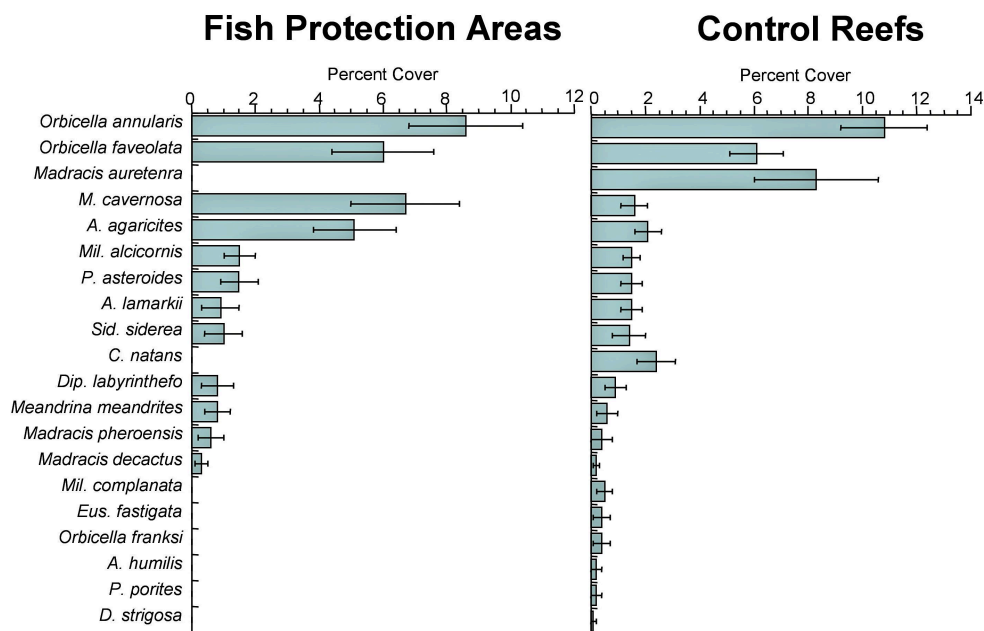


Fig. 3. Average percent cover of coral species from the seven control and four FPA sites listed in Fig. 2. Variance expressed as one standard error.

The dominant genera in Bonaire were *Orbicella*, *Madracis*, *Montastraea* and *Agaricia*. Those genera comprised 74% of the coral cover in Bonaire.



Temporal trends since 1999 reveal several important changes. Coral cover had 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. 4). Coral cover was lowest in 2013 but showed a slight increase since then. I observed *Colpophyllia* colonies that had suffered most severely in the 2010 bleaching event, recovering slowly.

Macroalgae had been increasing slowly through 2009. They suddenly increased in abundance following the 2010 bleaching event (Fig. 4). However, algal abundance has continued to decline since its peak in 2011.

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

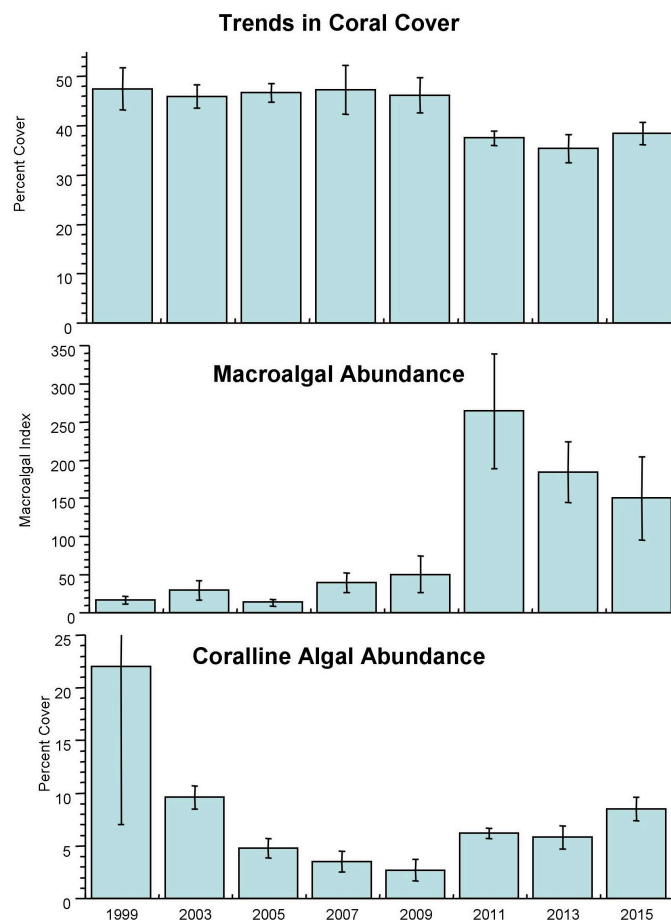


Fig. 4. Temporal trends in coral, seaweed and crustose coralline algal abundance. These data apply to the monitoring sites that have fixed permanent transects.

## Discussion

Coral cover has not only remained 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). Key to the recovery may be in maintaining low algal biomass. This is particularly difficult in the Caribbean because algal colonization rates and growth are greater in the Caribbean than in other reef systems (Roff and Mumby 2012). This was recently shown in an experiment in which large parrotfish were restricted from grazing in small areas that phase-shifted to macroalgae and reduced coral recruitment (Steneck et al 2014). Other studies have demonstrated toxic effects of macroalgae on reef-building corals (Rasher and Hay 2010). Therefore the steady decline in macroalgal abundance (Fig. 4) and the modest increases in CCA and coral are generally positive trends.

## Positive interactions

The Bonaire averages determined by pooling our study reefs (e.g., Figs 1 and 4) could be misleading because key interactions do not occur on an island-wide scale. Reef-scale interactions (ie at the scale of our study sites) would be a more appropriate scale over which important reef interactions occur.

Other chapters explore the distribution, abundance and grazing rates of herbivorous fishes. However, the degree to which they meet or exceed the rates of algal production is important to consider. The specific interactions I explore below are between filamentous turf canopy heights and CCA abundance. Then I explore CCA abundance and live coral cover (Fig. 5).

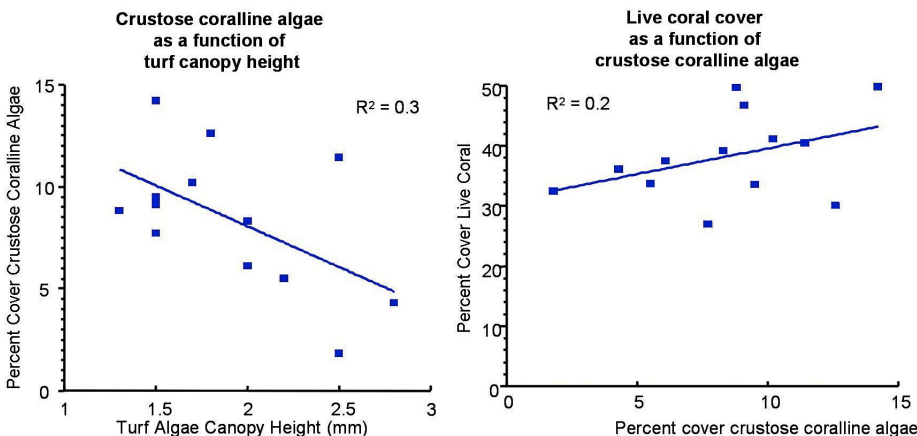


Fig. 5. The relationship between turf algae canopy height and crustose coralline algae abundance (left) and between CCA abundance and live coral cover (right).

As turf canopies increase, CCA abundance declines and as CCA declines so does live coral (Fig. 5). These patterns correspond to previous studies that demonstrated that an increase in

filamentous turf canopy height from 2 to 4 mm can result in a 75% reduction in coral recruitment (Arnold et al 2010). Turf algae, when it develops a tall (often sediment trapping) canopy, can negatively affect the abundance of crustose coralline algae (Steneck 1997). Since coralline algae can facilitate coral settlement, metamorphosis and survival (Harrington et al 2004), turf canopy height could be a good indicator of reef health.

The bigger picture requires integrating other key drivers of reef health into this analysis (eg Mumby and Steneck 2008; Steneck et al this volume). However, rapid assessments such as these not only illustrate patterns, when applied over time they can provide valuable insight into trends in reef health.

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## Chapter 2: Status and trends of Bonaire's herbivorous fishes

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### Abstract

The overall population trend of Bonaire's herbivorous fishes is one of decline from 2003 to 2011, followed by relative stasis from 2011 to 2015. There has been no significant increase in parrotfish abundance since the ban on parrotfish harvest (instated in 2010). This is not entirely surprising, given that parrotfish were not highly targeted prior to protection. Moreover, parrotfish abundances in Bonaire are among the highest reported for the Caribbean, indicating they may be nearing carrying capacity and thus room for improvement may be limited. At FPA sites Calabas and Front Porch, grazing fish actually decreased. These are two of the three sites with the greatest improvements in predator biomass. Thus it is possible that declines among grazers at these sites are due to increases in predators. Also of note, during our five days of surveys, we saw three instances of fishing taking place within the FPAs. Shoreside development in front of FPA sites has also ramped up since 2013, with the most obvious impacts to the reef occurring at Front Porch. Local management measures to improve compliance with the FPAs and strengthen regulations on land use practices and coastal development can further mitigate stress on Bonaire's reefs.

### Introduction:

In the Caribbean, instances of shifts from coral to macroalgae abound. Phase shifts, originally defined as transitions from coral dominance to coral depletion and/or algal dominance (Done 1992), have come to be synonymous with macroalgal phase shifts because of the predominance of foliose algae replacing live coral (Hughes 1994). In a classic example, Hughes (1994) documented the shift from a coral- to algal-dominated system along 250 km of coastline in Jamaica. Between 1977 and 1993, macroalgal cover increased from 4 to 92 %, as corals declined from 52 to 3 %. In the US Virgin Islands, Hurricane Hugo caused major damage to the reefs, and the dead coral was rapidly overgrown by macroalgae in St. John (Rogers and Miller 2006) and St. Croix (Steneck 1994). Similar large-scale changes have been reported from other locations in the Caribbean, ranging from Florida (Porter and Meier 1992), to Belize (McClanahan and Muthiga 1998), and Panama (Schulman and Robertson 1996).

Importantly, not *all* Caribbean reefs to suffer coral declines have succumb to phase shifts to macroalgal dominance. Despite the vast literature addressing such phase shifts, little attention has been paid to areas that deviate from this trend (Edmunds and Bruno 1996). Bonaire has not been exempt from disturbances leading to coral mortality, yet the reefs remain relatively macroalgae-free. The *Acropora* spp. die-off in the 1980s and a cold-water bleaching event in the early 1990s caused a decline in coral cover in Bonaire (Kobluck and Lysenko 1994). Hurricane Lenny in 1999 caused extensive damage to branching and platy corals at affected sites, including those with a N-S, NW-SE, and NNW-SSE coastal orientation, normally the leeward side of the island (Bries et al. 2004; Bak et al. 2005). In 2004, Hurricane Ivan created > 12 m waves along



the eastern coastline (Scheffers and Scheffers 2006), with the corals on the more developed western reef experiencing damage from sedimentation (Arnold, personal observation). Even following the loss of the grazing urchin *Diadema antillarum* in 1983 (Bak et al. 1984), which led to slight increases in algal cover in Curacao (de Ruyster van Stevenick and Bak 1986), no shift occurred in Bonaire. Most recently, in November 2010, 10% of Bonaire's corals bleached and died due to unusually warm temperatures. This decline in coral cover resulted in a sharp, but only temporary increase in macroalgae. Since 2011, macroalgal abundance has continued to drop and is once again low by Caribbean standards (Steneck, Chapter 1).

The most important drivers of algal community structure on reefs are large denuding and scraping herbivores, including herbivorous fishes and urchins (Steneck 1988). The reefs of Bonaire are a unique laboratory in the Caribbean because of their intact parrotfish populations, relatively high coral cover, and low algal biomass compared to the rest of the Caribbean (Kramer 2003). With the advent of the SCUBA industry, Bonaire began instating marine conservation laws. These included establishing fishing size limits and a prohibition on harvesting egg-bearing lobsters in 1961, establishing areas off limits to seine nets and enacting mesh-size regulations in 1963, and a ban on spear fishing in the 1970's. Bonaire's modest level of reef fishing consists primarily of hook and line (Nenadovic, Chapter 8, Bonaire Report 2007) compared to spear, trap, and hook and line fishing in other areas of the Caribbean. Continuing with that tradition, two no-take "Fish Protected Areas" (FPAs) were established in January 2008. Based on recent consensus that managing for herbivory is a feasible action to safeguard reef resiliency (Roberts 1995; Rakitin and Kramer 1996; Mumby 2006; Steneck et al. 2009; Mumby and Steneck 2011), legislation to regulate the use of fish traps (which incidentally trap parrotfish; Hawkins and Roberts 2004) and ban the harvest of parrotfish was passed in 2010.

This study quantifies the abundance of herbivorous fishes in Bonaire, both inside and outside of FPAs, including at six sites monitored since 2003.

## Methods

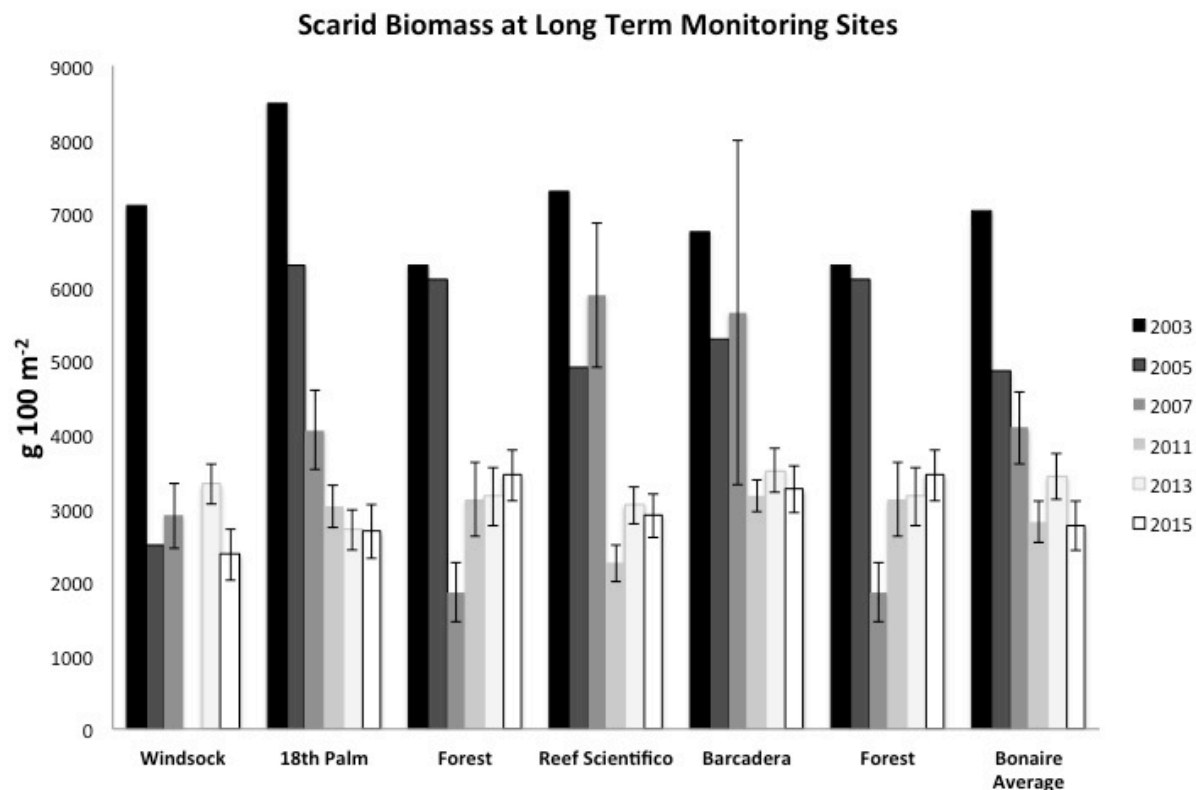
Visual surveys of herbivorous fishes were conducted at 11 sites in Bonaire in March 2015. Control sites (from south to north) included Bachelor's Beach, Windsock, Barcadera, Oil Slick Leap, Karpata, the no-dive Reserve, as well as Forest on Klein Bonaire. FPA sites included Eighteenth Palm, Calabas, Front Porch, and Reef Scientifico. The 6 sites monitored since 2003 include Windsock, Eighteenth Palm, Reef Scientifico, Barcadera, Karpata, and Forest (herbivorous fish data from Windsock was not obtained in 2011).

Abundances of scarids (parrotfishes), acanthurids (surgeonfish, doctorfish and tangs), and yellow tail damselfish were quantified inside replicate 30 x 4 m (120 m<sup>2</sup>) transects deployed at 10 m depth (n = 8 to 10 per site). Each fish encountered within a transect was identified to species and its life phase (juvenile, initial, or terminal) determined. Its size was also visually estimated (total length to the nearest cm). The 30 m tape was released while swimming; I swam at a rate that allowed me to complete 8 transects per hour.

Length was converted to biomass using the allometric coefficients of Bohnsack and Harper (1998), some of which have been modified by Mumby. See Appendix 2 for species composition and size details and for biomass coefficients and equations used for each species.

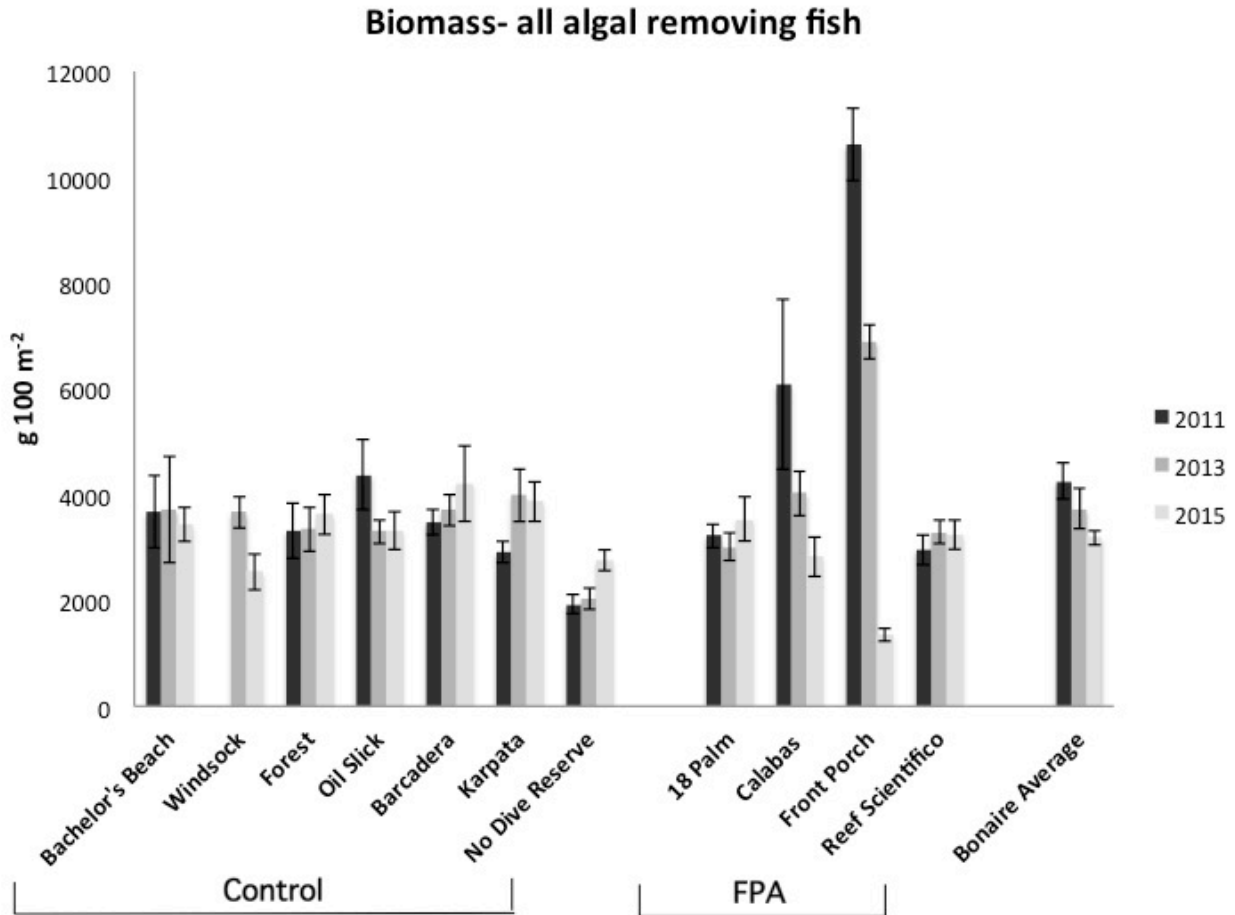
## Results

Scarids (parrotfish) are the dominant grazers on Bonaire's reefs, like most Caribbean reefs (Steneck 1988). At the six long-term monitoring sites, scarid biomass has declined since 2003. However, at these sites, scarid biomass has leveled off since 2011, with the exception of a continued decline at Windssock (Figure 1). Herbivorous fish data from 2009 was not included in any analysis because the 2009 observer did not include juvenile parrotfishes in the survey. Also, no data was collected from Windssock in 2011.



**Figure 1.** Scarid biomass at six sites from 2003-2015. Error bars are  $\pm$  SE.

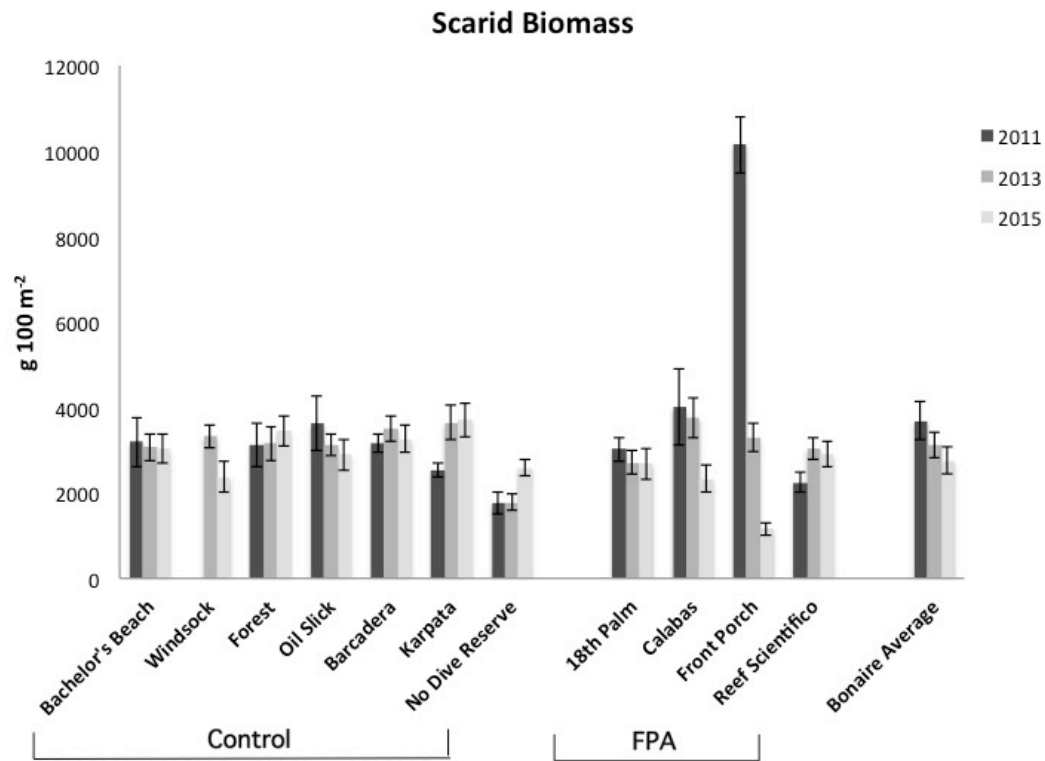
More detailed multi-year, intrasite comparisons are available from 2011-2015 because I was the observer for these three sampling years. Average biomass of all algal removing herbivorous fishes over all sites continued to decline in 2015, though not substantially (Figure 2). The only two sites to see a dramatic drop were Front Porch and Calabas. The No Dive Reserve saw an increase since 2013.



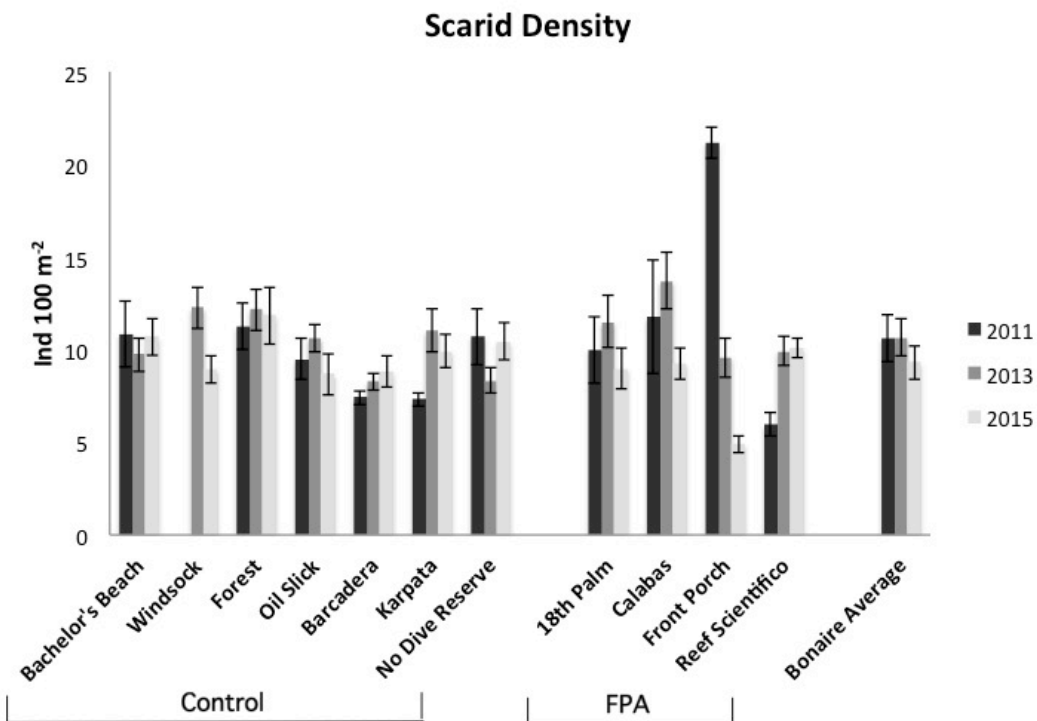
**Figure 2.** Biomass of all herbivorous fishes (scarids, acanthurids, and yellowtail damsels) at each site. Error bars are  $\pm$  SE.

The high scarid biomass and density in FPA sites in 2011 (Figure 3) was largely due to the high number of terminal phase stoplight parrotfish observed at Front Porch. Both the biomass and density of scarids at Front Porch declined by over half between 2011 and 2013, and then declined by another 50% between 2013 and 2015. Biomass (Figure 3a) and density (Figure 3b) of scarids at Calabas also decreased dramatically from 2013 to 2015. Windsock was the only control site that decreased significantly in biomass and density of scarids, whereas the No Dive Reserve was the only site to see increases.

a.



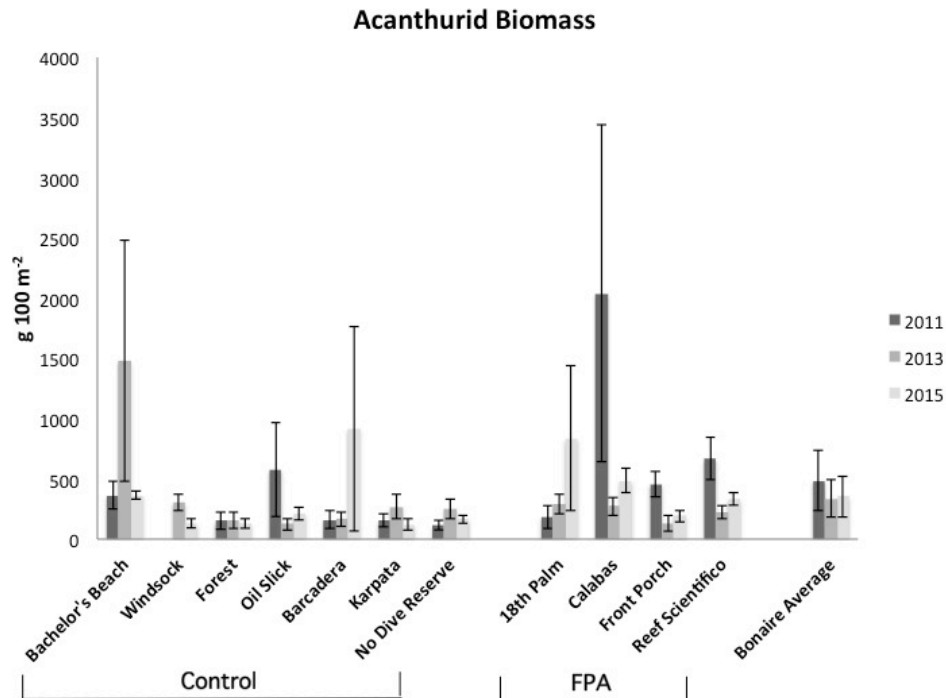
b.



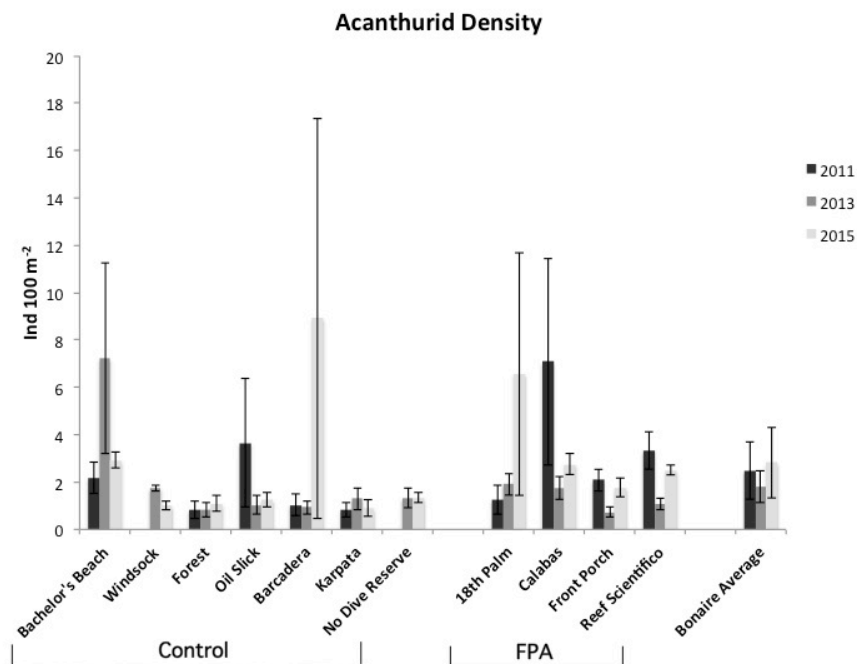
**Figure 3.** Biomass (a) and density (b) of scarids. Error bars are  $\pm$  SE.

The overall Bonaire biomass and density of acanthurids did not change significantly from 2011 or 2013 (Figure 4). Windssock had declines in acanthurid biomass and density, and all of the FPA sites have seen slight increases since 2013.

**a.**



**b.**



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

## Discussion

The overall population trend of Bonaire's herbivorous fishes is one of decline from 2003 to 2011, followed by relative stasis from 2011 to 2015. There has been no significant increase in parrotfish abundance since the ban on parrotfish harvest (instated in 2010). With the complete ban on the harvest of parrotfishes in 2010, by 2015 we could expect to see increases in parrotfish populations at sites where they were previously targeted, such as Oil Slick. For example, after between 1 and 9 years of protection in the Philippines, biomass of targeted fish increased by a factor of 3.1, and clear differences in fish biomass between reserve and non-reserve sites were noted after approximately 6 years (Alcala et al. 2005). Similarly, in St. Lucia, after 5 years of protection, no-take reserves encompassing 35 % of the local fishing grounds resulted in 46-90% increases in catch (Roberts et al. 2001).

There are several plausible reasons why we are not seeing substantial increases in grazing fish since protection. First, it is possible that Bonaire's herbivorous fish populations are close to carrying capacity. For example, parrotfish biomass in Bonaire is more than twice that of the Exuma Cays Land and Sea Park in the Bahamas, which is the oldest protected area in the Caribbean, with fishing banned since 1986 (Mumby et al. 2006). Additionally, Bonaire's overall reef fish biomass (FPA and control sites), observed in this study as  $\sim 6,680 \text{ g}/100\text{m}^2$  ( $3180 \text{ g}/100\text{m}^2$  for herbivores and  $\sim 3500 \text{ g}/100\text{m}^2$  for predators – see Fig. 8 in Executive Summary) is actually in line with Caribbean reserves that have been closed for nearly 35 years, according to a recent study on the recovery potential of the world's coral reefs (MacNeil et al. 2015). The same study shows that, worldwide, reef fish biomass in the absence of fishing averages approximately  $1,000 \text{ kg}/\text{ha}$  ( $10,000\text{g}/100\text{m}^2$ ). Thus, while Bonaire has not yet reached this average, improvements in predator biomass in FPAs observed in this study are moving Bonaire in that direction (see Camacho, Chapter 4).

Furthermore, parrotfish traditionally have not been highly sought after on Bonaire. However, with the changing demographic of Bonaire's population including some cultures that do target parrotfish, it is possible fishing pressure on parrotfish may have increased prior to the ban (Nenadovic, Chapter 8, Bonaire report 2007). Compliance with the harvest ban is largely unknown. In Belize, a country where in some areas parrotfish made up 28% of the catch (Wildlife Conservation Society 2010), a ban on the harvest of herbivorous fish (scarids and acanthurids) was instated in 2009 in response to extremely high cover of macroalgae. Several years later, 5-7% of fillets in fish markets across Belize were actually parrotfish, despite being labeled as grouper or, more commonly, snapper (Cox et al. 2013). Thus, while illegal harvesting and mislabeling was clearly occurring, the ban was effective in decreasing parrotfish harvest. No such evaluation of compliance has been conducted on Bonaire and it is unlikely there is significant fishing for at any of our 11 monitored reefs. Nevertheless, during our five days of surveys, we saw three instances of fishing taking place within the FPAs (twice at Calabas with one man fishing from shore and a family fishing from a moored sailboat, and once north of Reef Scientifico near the northern border of the FPA with three men fishing out of a boat specifically for fishing). All were hook and line fishing for carnivorous fish.

Other possibilities for the relative stasis in herbivorous fish is that the predator increases in FPAs could be having an impact on grazer populations, specifically at Calabas and Front Porch. An

increase of predation combined with areas of low spatial heterogeneity could equate to higher predation and fewer crevices for small grazers to take refuge. Sites with higher structurally complexity had higher parrotfish abundance.

Finally, while not explicitly addressed in our studies, land-use changes, primarily in front of FPA sites, particularly Front Porch may be negatively impacting the reef. At Front Porch, large swaths of vegetation were removed since the last study in 2013. This vegetation likely anchored the soil, preventing excess run-off of sediment and nutrients to the adjacent reef. Also, sand piles dumped on the shore were blowing onto the reef with the easterly winds. While it is difficult to separate reef-site processes from effects of poor land-use in the area, it is notable that the sites adjacent to these land-use changes are the sites that are doing the poorest in terms of the reef conditions monitored in this report.

Certainly global stressors, such as warming and ocean acidification, are contributing stressors to Bonaire's reefs. However, local measures can be taken to mitigate stress, including improving land-use practices such as restricting coastal development and reducing nutrient input.

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## Chapter 3: The status and trends of sea urchins *Diadema antillarum* and *Echinometra viridis* on the leeward coral reefs of Bonaire

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### Abstract

When abundant, the sea urchin *Diadema antillarum* plays a major role in controlling seaweed abundance on coral reefs. *Diadema antillarum* and *Echinometra viridis* were the most common urchins among the reefs; however both species had low population densities. In surveys conducted in 2015, at 11 sites along Bonaire's leeward reefs, population densities for *D. antillarum* ranged from 0 to 0.08/m<sup>2</sup> and densities of *E. viridis* ranged from 0.1 to 0.55/m<sup>2</sup>. Thus, urchin abundances are well below what are considered ecologically relevant. Since 2009 *D. antillarum* abundance has slowly increased from about 0.05/m<sup>2</sup> in 2009 to 0.3/m<sup>2</sup> in 2015, while *E. viridis* abundance has been increasing since 2005 from about 0.02/m<sup>2</sup> in 2005 to 0.22/m<sup>2</sup> in 2015. All *D. antillarum* and *E. viridis* found in surveys were small ( $\leq 3\text{cm}$  and  $\leq 4\text{cm}$  respectively) and most were restricted to tight crevices of the coral *Orbicella annularis*. Together, these findings suggest that predation may currently limit urchin size and distribution in this system. Our comparisons of Fish Protection Areas (FPAs) vs. control areas indicate that population densities of *Diadema* and *Echinometra* are presently higher in FPAs.

### Introduction

*Diadema antillarum* was a dominant herbivore on many Caribbean coral reefs until its mass mortality in 1983 and 1984 (Lessios, 1984). Upon decline, it became obvious how important this herbivore was to overfished Caribbean reefs. In areas around the Caribbean where there were no other herbivores to maintain low seaweed abundance, reefs quickly underwent a phase shift to macroalgal (seaweed) dominance (Hughes 1994).

In recent decades, *D. antillarum* populations have increased in select locations such as St. Croix (Miller 2003), Barbados (Hunte and Younglao 1988) and Jamaica (Idjadi 2010). However, most of these increases were modest ( $< 1/\text{m}^2$ ) and have not persisted; consequently, they did not limit seaweed and promote coral recruitment and settlement (Tuya et al. 2004, but see Carpenter and Edmunds 2006).

Predation and limited recruitment are factors that may be inhibiting the return of *D. antillarum* to functional densities, i.e., those sufficient to control macroalgae cover (Levitan 1991, Williams et al. 2011). Protection of predatory fishes within FPAs may therefore produce different urchin population trajectories inside vs. outside of FPAs.

Another common Caribbean sea urchin is *Echinometra viridis*. Unlike the active grazing of *Diadema*, *E. viridis* feeds primarily on drift seaweed (Steneck 2013). Since seaweed abundance

increased following the 2010 bleaching event, it is of interest to know whether this species of sea urchin has also increased recently.

In this study I quantified the distribution, abundance and body size of all species of sea urchins on Bonaire's monitored coral reefs.

## Methods

As part of an ongoing long-term monitoring program, urchin abundances were surveyed at 11 sites along the leeward side of Bonaire in March 2015. The sites surveyed were, from south to north, Bachelors Beach, Windsock, Eighteenth Palm, Calabas, Forest (Klein Bonaire), Front Porch, Reef Scientifico, Barcadera, Oil Slick, Karpata and the No Dive Reserve north of Karpata. At each site, 10 m transect tapes were deployed at the 10 m depth horizon, laid parallel to the reef and across the plates demarking each permanent transect ( $n = 4$  per site). While swimming along each tape, I scored the species identity and size (test diameter, nearest mm) of each urchin I encountered within 1 m of either side of the tape (i.e., a 2 x 10 m band transect). I also scored the habitat that each urchin occupied.

The majority of urchins found were *D. antillarum* and *E. viridis* but a few *Eucidarus tribuloides* and *Lytechinus williamsi* were also found. Given the relative dominance of *D. antillarum* and *E. viridis* in our surveys, I focused solely on these two species when examining results to find trends in the data. I computed average density for each species at each site, and average density among all sites. Average test sizes were also computed for each species at each site and among all sites. Further, densities were compared after pooling data among FPA sites (Eighteenth Palm, Calabas, Front Porch, and Reef Scientifico) and control sites.

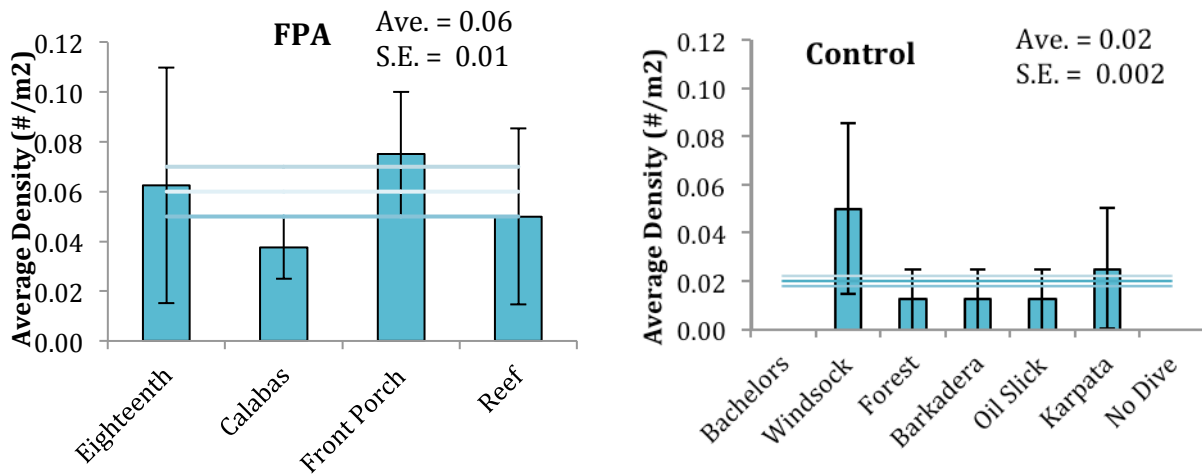
The mean population density for all sites was compared to previously reported densities. Only nine sites were studied in 2009, and ten sites were studied in 2011 and 2013. Previous Bonaire reports are available through STINAPA. They are produced every two years since 2003.

## Results

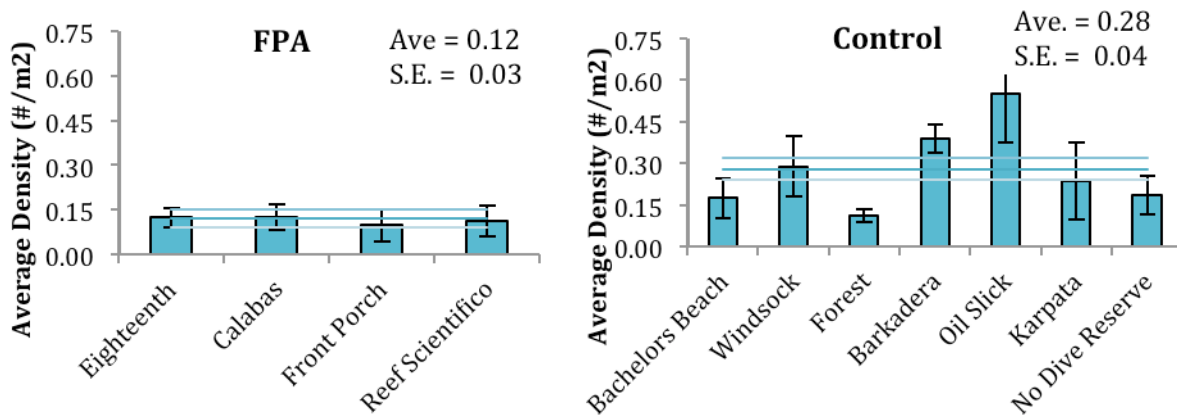
Sea urchins were found at all 11 sites surveyed in 2015. Species found during our surveys were *D. antillarum*, *E. viridis*, *E. tribuloides* and *L. williamsi*.

The average density of *D. antillarum* in 2015 for all sites was  $0.03 (\pm \text{SE } 0.01)/\text{m}^2$ . *Diadema antillarum* were found at all sites except Bachelors Beach and the No Dive Reserve. Highest densities were found to be at Windsock, and Front Porch (FPA), with Front Porch having the highest densities overall (Fig. 1).

The average density of *E. viridis* in 2015 for all sites was  $0.22 (\pm \text{SE } 0.03)/\text{m}^2$ . *Echinometra viridis* were found at all eleven sites. Their highest densities were at Oil Slick and Barcadera, with Oil Slick having the highest densities overall (Fig. 2).

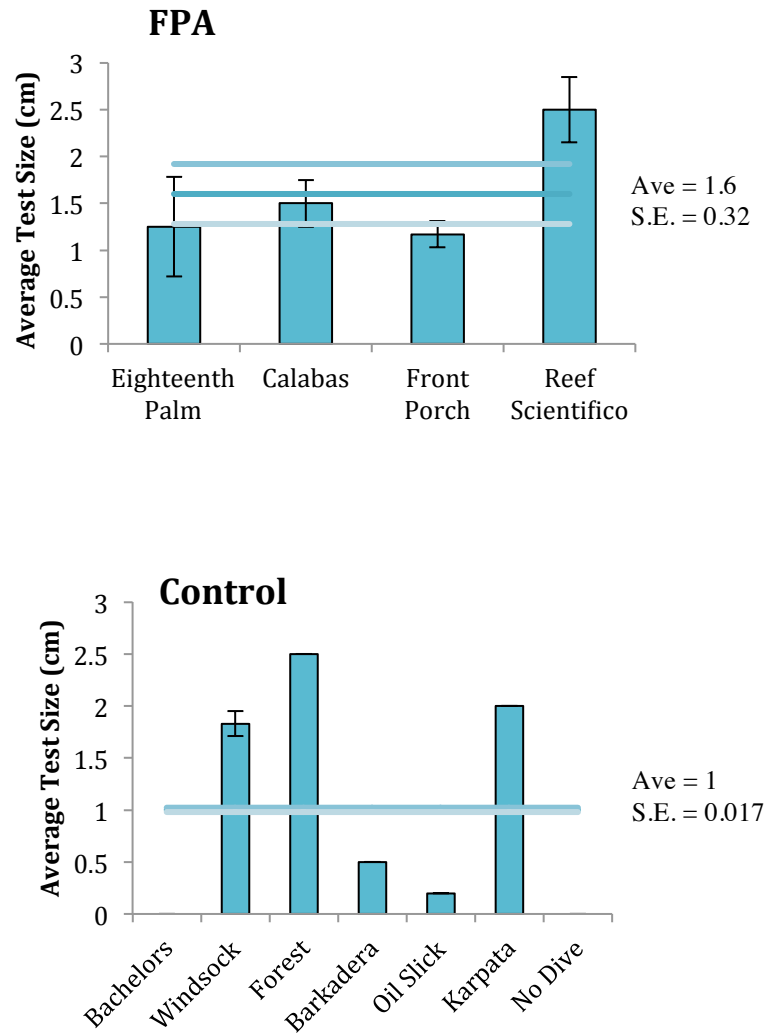


**Figure 1.** Average densities of *D. antillarum* at Fish Protection Areas (FPAs, left) and control sites (right). Vertical line on each bar represents standard error (S.E.). Horizontal lines represent average  $\pm$  S.E. for each site type.

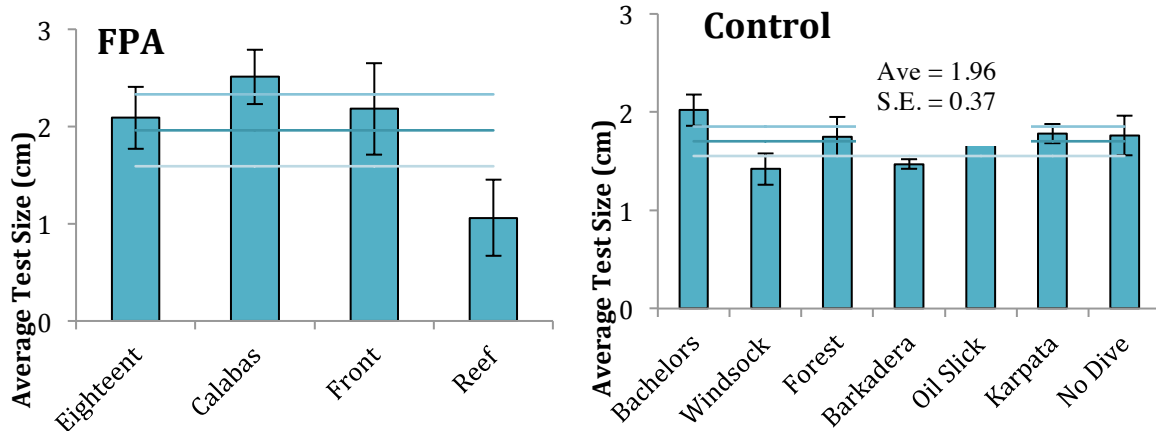


**Figure 2.** Average densities of *E. viridis* at Fish Protection Areas (FPAs, left) and control sites (right). Vertical line on each bar represents standard error (S.E.). Horizontal lines represent average  $\pm$  S.E. for each site type.

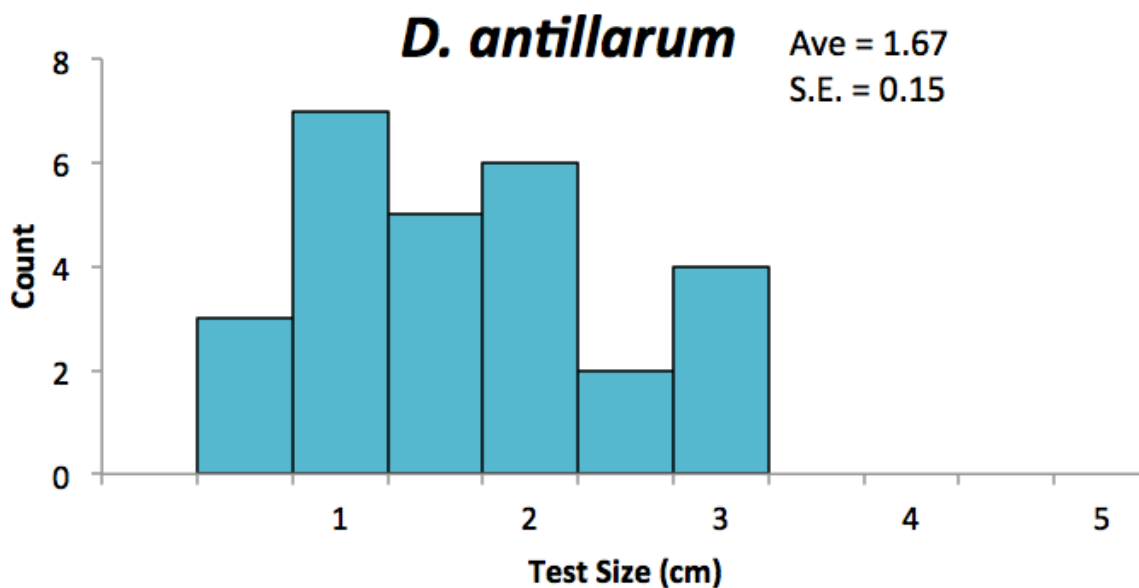
The average test size of *D. antillarum* varied among control sites (Fig. 3). The Bonaire-wide average test size of *D. antillarum* was 1.67 cm ( $\pm$  SE 0.15) (Fig. 5). The average test diameter for *E. viridis* was less variable among all sites (Fig. 4). The Bonaire-wide average test diameter of *E. viridis* was 1.79 cm ( $\pm$  SE 0.06) (Fig. 6).



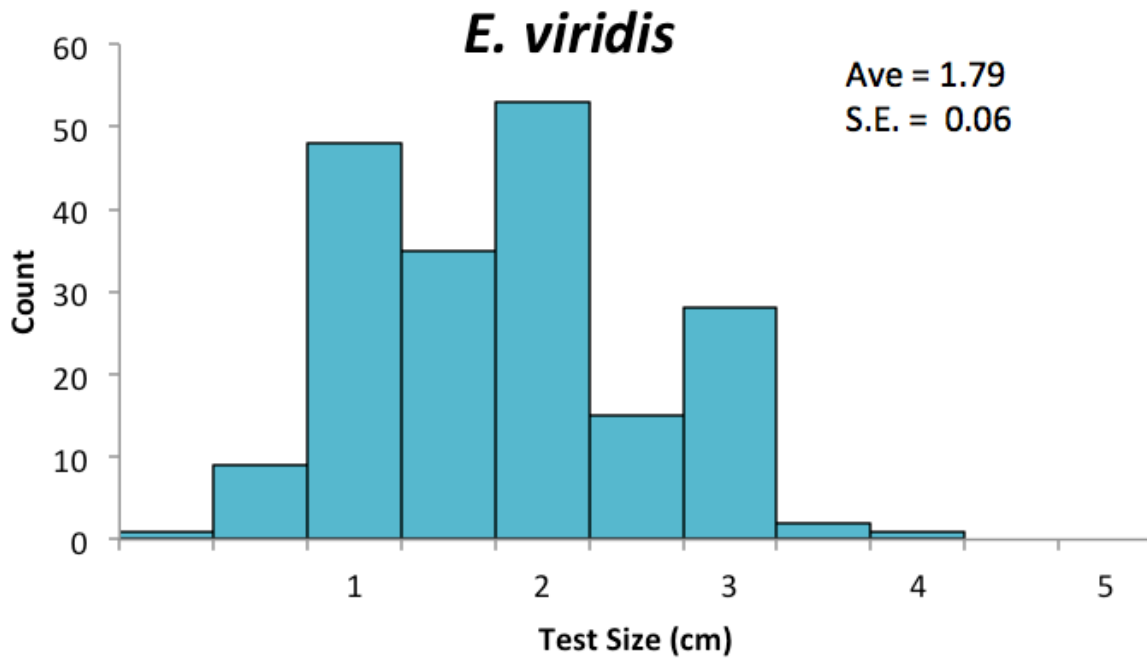
**Figure 3.** Average test size of *D. antillarum* at each site. Vertical line on each bar represents standard error (S.E.). Horizontal lines represent average  $\pm$  S.E. for each site type.



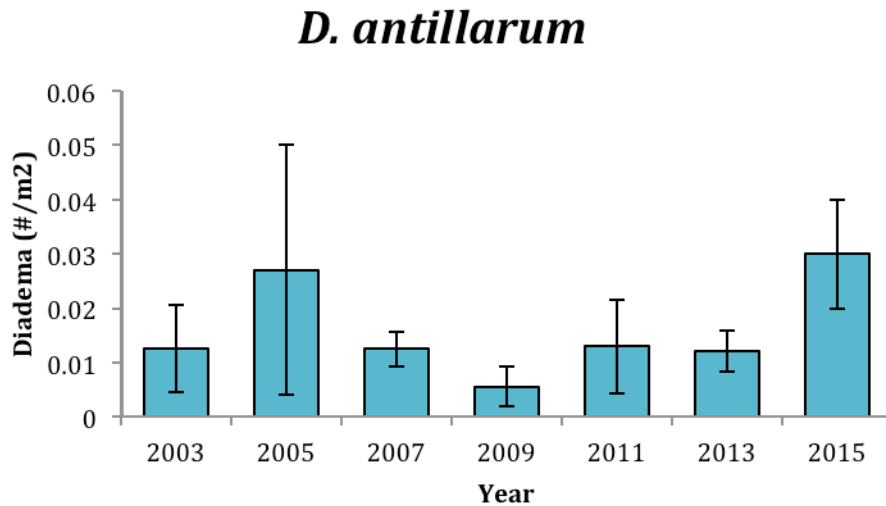
**Figure 4.** Average test size of *E. viridis* at each site. Vertical line on each bar represents standard error (S.E.). Horizontal lines represent average  $\pm$  S.E. for each site type.



**Figure 5.** Size frequency distribution of test size for *Diadema antillarum*.  $n = 27$ .

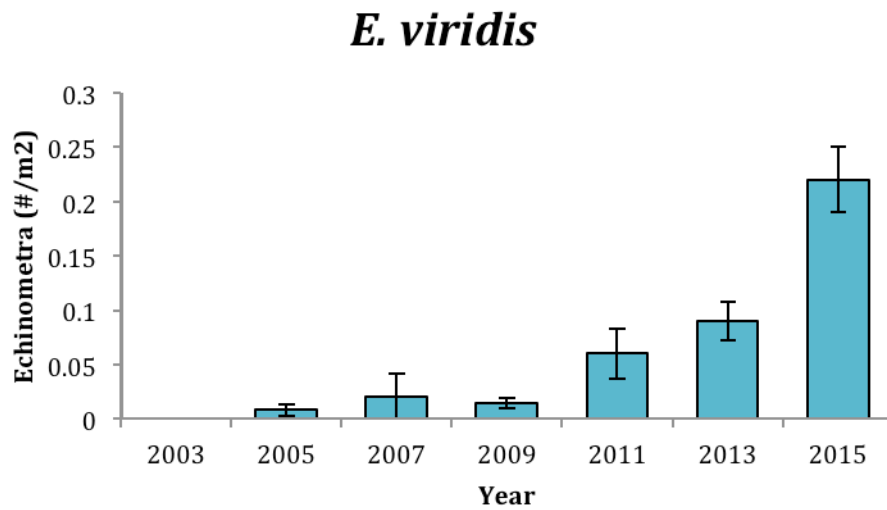


**Figure 6.** Size frequency distribution of test size for *Echinometra viridis*. n = 192. *Diadema antillarum* densities have been fluctuating since 2003 with a peak in 2005 and 2015. We have seen an increase from 0.0056/m<sup>2</sup> ( $\pm$  SE 0.0037) in 2009 to 0.03/m<sup>2</sup> ( $\pm$  SE 0.01) in 2015 (Fig. 7).



**Figure 7.** Densities of *D. antillarum* at monitored sites over time. Vertical lines represent S.E.

*Echinometra viridis* densities have recently increased from 0.0083/m<sup>2</sup> ( $\pm$  SE 0.0053) in 2005 to 0.22/m<sup>2</sup> ( $\pm$  SE 0.03) in 2015 (Fig. 8).



**Figure 8.** Densities of *E. viridis* at monitored sites over time. Vertical lines represent S.E. I observed a Spanish hogfish preying upon an *E. viridis* in ~5 m of water (Fig. 9). This observation provides evidence that predation may be restricting urchins to habitats that are inaccessible to predators, such as cracks and crevices created by coral.



**Figure 9.** Spanish Hogfish preying upon *E. viridis* in Bonaire (March 5, 2015). Photo by Kaitlyn Boyle.

## Discussion

Sea urchin densities have increased in Bonaire since 2003 (Figs. 5, 6). However *Diadema* remain rare and as such, they likely do not play a functional role in this reef system. *Diadema antillarum*

has increased since 2009, with densities more than doubling in the last two years (Fig. 7). *Echinometra viridis* also has an increasing trend since 2003 (Fig. 8). Prior to the 1983/84 mass mortality of *Diadema*, population densities throughout the Caribbean easily reached up to 25/m<sup>2</sup>. Average density after the die off has remained less than 0.3/m<sup>2</sup> (Hughes et al. 2010).

Though *D. antillarum* densities have increased in Bonaire in the last 6 years, they are not close to the 1/m<sup>2</sup> that is needed to effectively control seaweed abundance (Mumby et al. 2006). This means that even though there is a presence of *D. antillarum* on Bonaire's reefs, they are only playing a minor role in the process of herbivory on Bonaire's reefs. The low algal abundances observed throughout the system are attributable to the high grazing rates of herbivorous fishes, principally parrotfish and surgeonfish.

The small test size of urchins found in 2015 (Figs. 3, 4), which has been seen in all past years, suggests that post-settlement mortality is preventing large adults from becoming prevalent within the population. Small size can occur when there is intraspecific competition at high densities of 10/m<sup>2</sup> (Carpenter 1981), however urchin densities in Bonaire are nowhere close to such levels. Mature adult *D. antillarum* can reach large sizes, with test diameters over 9 cm (Hughes 1994), while *E. viridis* are generally smaller (Cameron (1986)). Average test diameter for both species was almost the same (1.7 cm; Figs 5,6), suggesting that predation may be creating a bottleneck whereby only small urchins that fit within sheltered habitat persist in each population. As urchins pass this size threshold they exceed the size of their refuge and must leave to seek larger shelters, but are not yet large enough to avoid predation. Predation during this exploratory period may explain why larger urchins are scarce (Fig. 9).

The two species of urchins are very different. *Echinometra viridis* has a smaller body size, a smaller foraging range, as well as smaller spines, making them easier prey items. It feeds primarily on drift algae. Being small and having relatively small spines restricts *E. viridis* to feeding within the crevices of the corals. In contrast, *D. antillarum* is larger and faster and can forage out in the open. McLanahan (1999) found that *E. viridis* populations were positively correlated with algal abundance, rather than inversely as is the case with *D. antillarum*. This is shown in our observations of an increase in seaweed since 2010 and an increase in *E. viridis* since 2005 (Fig. 8).

The availability of a physically complex habitat has been shown to limit the distribution of *D. antillarum* and *E. viridis* in the Caribbean (Lee 2006). Urchin recruitment to complex habitat creates a reinforcing feedback loop. High urchin densities, usually in the crevices of *Orbicella annularis*, result in high rates of macroalgal removal, a benefit to the coral. Reduction of macroalgae increases the potential area for coral recruitment, which can create more habitat complexity (Lee 2006). It is unclear why *Diadema* densities are still lower than what is required to be functional in the reef system. However, given that physically complex habitat abounds in Bonaire, post-settlement predation is a likely explanation.



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## **Chapter 4: Status and trends in Predatory Fish with special emphasis on Fish Protected Areas**

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### **Abstract:**

Carnivorous fishes have declined on reefs throughout the Caribbean. Bonaire took management steps to locally counter the decline by establishing Fish Protected Areas (FPAs as no-take reserves). Using belt transects, I surveyed 11 sites (four FPAs and seven Control sites) on Bonaire and Klein Bonaire at a depth of 10m. I quantified the size of fish (to the nearest cm) and determined biomass and density for each site. Overall there has been no net change in total biomass or population density since 1999. Groupers, snappers and grunts showed increases in biomass within the FPAs, but no significant changes in density were recorded. There was very little effect of FPA on the most targeted species, which may be an indicator of poaching within the protected zones. However, the use of FPAs continues to be an effective management strategy, and provides an example for other Caribbean islands.

### **Introduction**

Overfishing is prevalent throughout the Caribbean region (Jackson et al. 2001). Spatial marine reserves, such as Fish Protected Areas (FPAs), are one form of reef management that has aided the recovery of fish stocks on overfished, degraded reefs as well as that of adjacent areas (Roberts et al. 2005). In theory, FPAs function by removing the top-down pressure of fishing on reef ecosystems, allowing recovery of the abundance and biomass of the targeted fish species. In the Caribbean, fishing pressure is often directed initially to predatory fish (e.g. groupers, snappers, grunts), although studies have shown that fishing pressure can also extend to herbivorous fish species through the process of fishing down the food web (Mumby et al. 2012). Predatory species are particularly susceptible to the effects of overfishing as a result of their life history traits (aggregation spawning, slow growth rates, late-stage maturity) and provide an excellent indicator of the effect of FPAs on the reef ecosystem.

Predatory species, an important aspect of the megafaunal community in the reef ecosystem, drive patterns of biodiversity (McClanahan, 2005) by directly influencing the abundance and distribution of prey species (Almany 2004). The maintenance of a high predator biomass, inclusive of a high adult spawning biomass, may be essential for reserves to achieve the spill over effects that would enhance the health of surrounding reefs in conjunction with providing a greater return for fishers utilizing adjacent reefs (McClanahan and Mangi 2000, Abesamis and Russ 2005). In addition, the recovery of grouper populations, a possible product of functioning FPAs, may provide a natural deterrent to the invasion of lionfish (*Pterois sp.*) through increased predation pressure and competition for space (Mumby et al. 2011)

Bonaire is unique to the Caribbean in that it is one of the few islands to have such extensive marine management. Spearfishing was banned in 1971, fish traps were rarely used historically and a law enacted in 2010 was designed to phase out the use of fish traps. As a result, only hook and line remains as a major fishing method and this focuses fishing pressure mostly on predatory fish. I quantified predatory fish abundance and biomass on 11 monitored reef sites in Bonaire to assess changes in these metrics since the establishment of the FPAs in 2008. Since 2003, fish surveys have been used in Bonaire to assess changes in the fish communities over time. Here I report specifically on the predatory fish population to assess changes that the establishment of the FPAs are having on the predator community on Bonaire's reefs. I compared FPA sites with control sites to determine the impact on the targeted predator populations as a result of the removal of top-down fishing pressure.

## **Methods**

### *Survey Areas*

Predatory fishes were quantified at 11 fringing reef locations along the leeward margin of Bonaire and Klein Bonaire. Six sites have been regularly surveyed since 2003. The sites names were: No-Dive Reserve, Karpata, Oil Slick, Barcadera, Reef Scientifico\*, Front Porch\*, Forest, Calabas\*, Eighteenth Palm\*, Windsock and Bachelor's Beach. The asterisk (\*) denotes the sites that are fish protection areas (FPAs).

### *Survey Methods*

Belt transect surveys were conducted at 10m depth along 10 sites on the leeward side of the main island of Bonaire, and one site at the southwest corner of Klein Bonaire in March 2015. All monitoring since 2003 has been conducted in the first two weeks of March every other year. This method is commensurable with the Atlantic Gulf Reef Rapid Assessment (AGRRA) survey method. Five transects, 30m long by 4m wide, were used and separated by a minimum distance of 5m. Each transect consisted of two swims in which the abundance and size of all fish species were recorded. The first swim recorded the most mobile fish species and the return swim recorded the less mobile species. Observations of the fork lengths of each fish were estimated to the nearest cm and recorded on a PVC wrist slate covered with translucent Mylar paper. The researcher used PVC pipes cut to various lengths (2cm, 5cm, 10cm, 20cm) to calibrate his eyes on average every two days during the observation period. Dive times ranged between 66 and 85 minutes and 5 transects were recorded per site.

### *Data Analysis and Treatment*

Fish biomass was calculated using length-weight conversion factors from Marks and Klomp (2003), with missing conversion factors obtained from the website FishBase. All analyses were performed using R statistical software. For a full list of species observed and conversion factors used, see appendix.

## Results

A total of 49 species of predatory fish were recorded during surveys conducted in March 2015 (see species list in appendix). Fish were grouped by family due to their functional similarities. The most commonly targeted fish families [groupers (Serranidae), grunts (Haemulidae) and snappers (Lutjanidae)] were analyzed to determine the differences between FPAs and control sites.

### *Trends*

Despite a positive trend, there was no significant increase in predatory fish biomass between pre-FPA years (2003-2007) and post-FPA (2009-2015) from 3.13 kg/100m<sup>2</sup> to 4.38 kg/100m<sup>2</sup> [Welch's t test:  $p=0.1462$ ] (Figure 1). Figure 2 shows the long-term trend in predatory fish biomass from when monitoring started in 2003 to 2015. No significant change in biomass was observed between the two most recent monitoring periods (2013 and 2015).

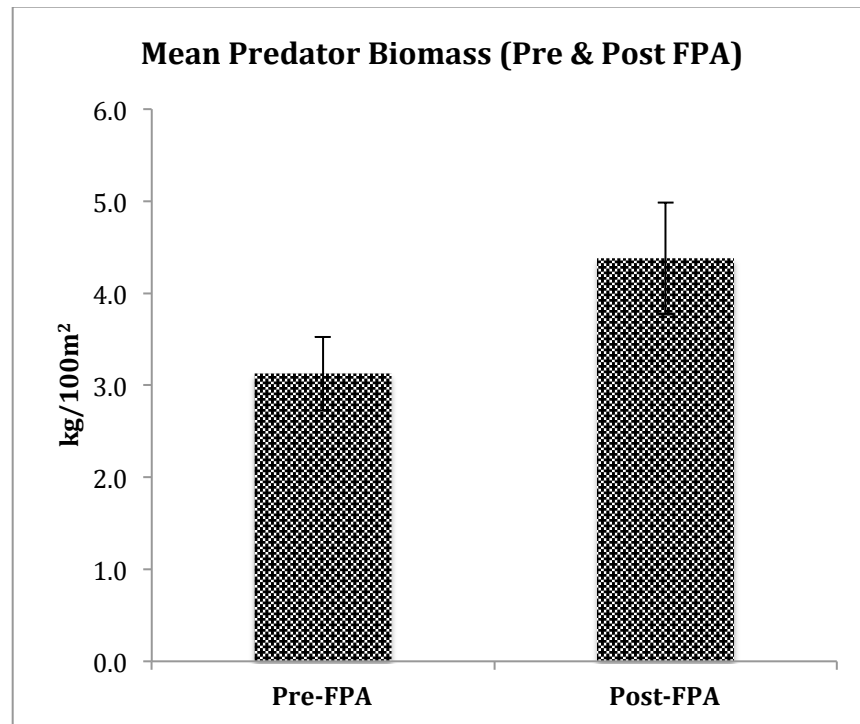


Figure 1. Biomass of predatory fishes before and after establishing FPAs. Error bars are +/- s.e. (Welch's t test:  $p=0.1462$ )

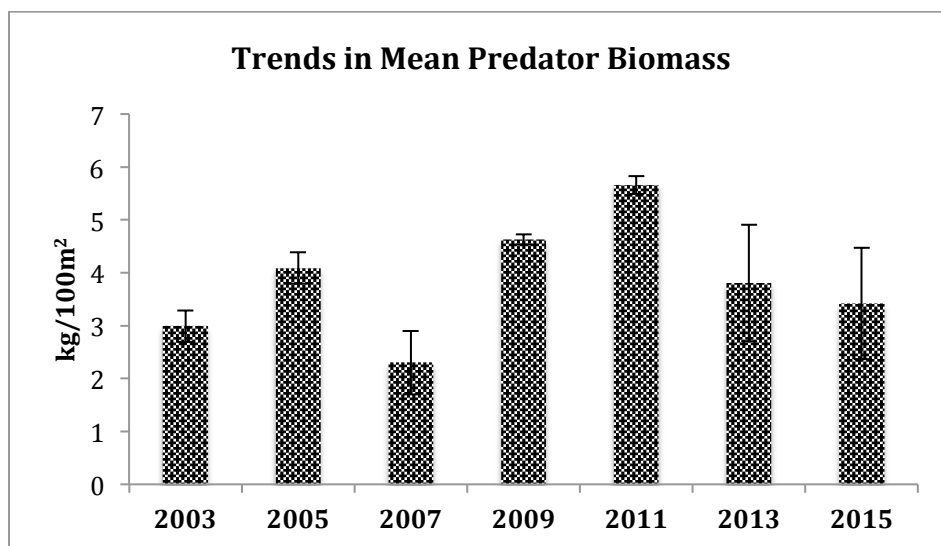


Figure 2. Showing long-term trend of predatory fish biomass since monitoring begun in 2003. Error bars as in Fig. 1.

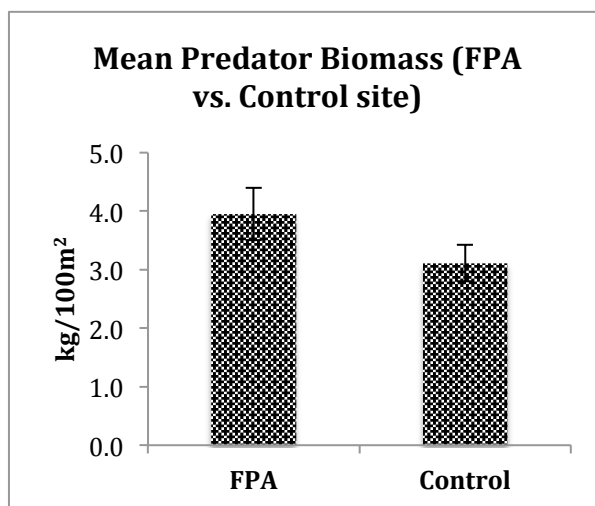


Figure 3a. Mean predatory fish biomass for FPA and control sites. Error bars as in Fig. 1. (Welch's t test:  $p=0.17$ ).

The observed mean predator biomass was greater in FPAs than the control sites (Welch's t test:  $p=0.1759$ ) (Figure 3). Highest predator biomass was observed at Reef Scientifico (FPA) ( $5.06 \text{ kg}/100\text{m}^2$ ) while the lowest biomass was observed at Oil Slick (control site) ( $1.25 \text{ kg}/100\text{m}^2$ ) (Figure 4). Predator density was greater at the FPAs than the control sites [Welch's t test:  $p=0.09843$ ](Figure 5). Highest predator density was observed at Reef Scientifico and Front Porch (FPAs) ( $46.33/100\text{m}^2$ ) while the lowest predator density was observed at Karpata (control site) ( $22.5/100\text{m}^2$ ) (Figure 6). However, these differences were not statistically significant..

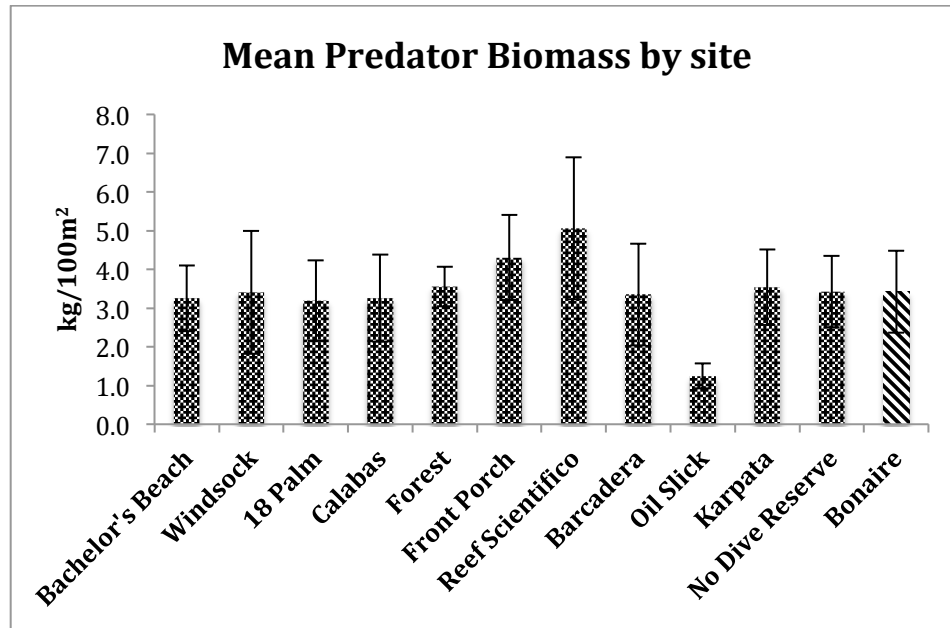


Figure 4. Mean predator biomass by site. Error bars as in Fig. 1.

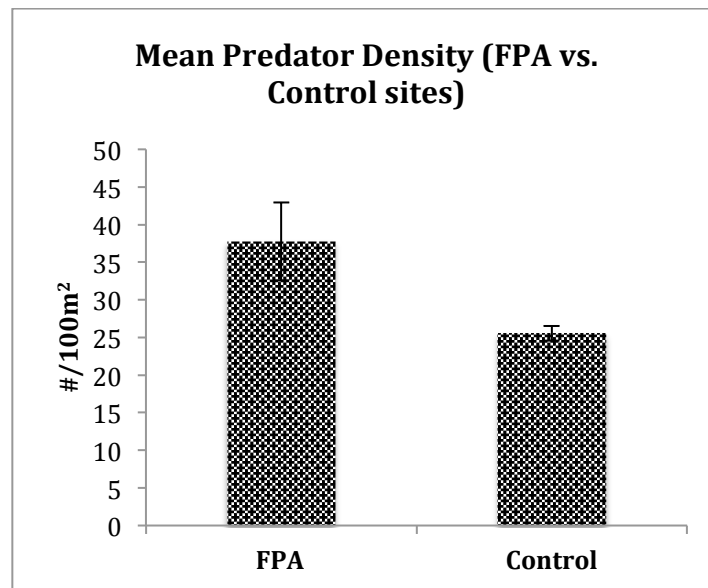


Figure 5. Mean predatory fish density for FPA and control sites in 2015. Error bars are  $\pm$  s.e. (Welch's t test:  $p=0.09843$ )

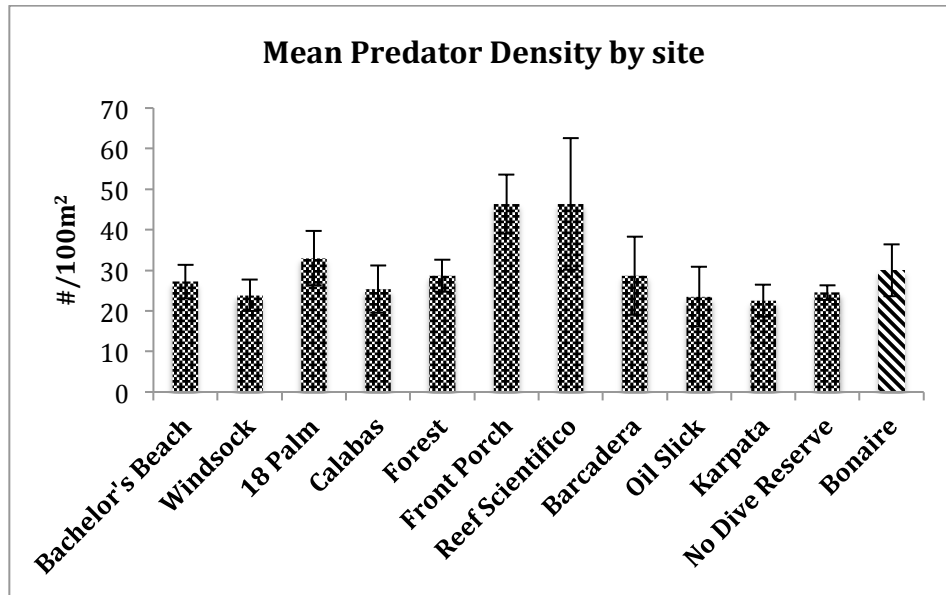


Figure 6. Mean predator density by site. Error bars are +/- s.e.

#### *Serranids (Grouper)*

Six species of fish in the grouper family were recorded in the surveys conducted in March 2015. They were coney (*Cephalopholis fulva*), creole fish (*Paranthias furcifer*), graysby (*Cephalopholis cruentata*), hamlet (*Hypoplectrus spp.*), soapfish (*Rypticus saponaceus*), and tiger grouper (*Mycteroperca tigris*). Groupers including graysby, hinds and coney are highly prized and often most targeted by fishers in Bonaire.

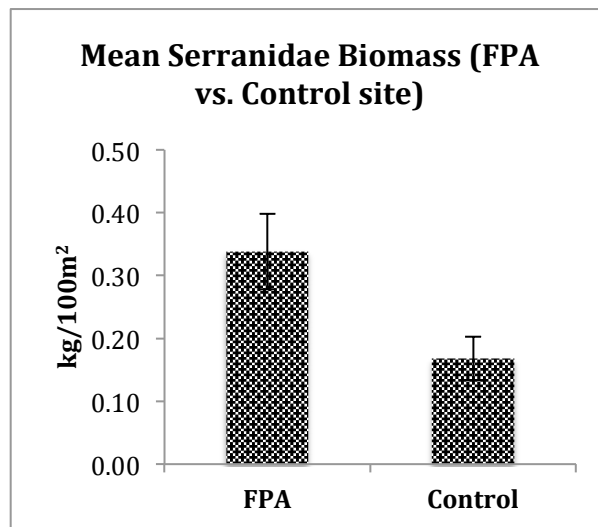


Figure 7. Mean grouper biomass for FPA and control sites. Error bars as in Fig. 1. (Welch's t test:  $p=0.058$ ).



There was a marginally-significant effect of the FPAs on serranid biomass [Welch's t test:  $p=0.05767$ ] (Figure 7). The greatest Serranidae biomass was observed at Calabas (FPA) ( $0.42 \text{ kg}/100\text{m}^2$ ) while the lowest was observed at Oil Slick ( $0.044 \text{ kg}/100\text{m}^2$ ) (Figure 8). Although there was a difference in observed in serranid density between the FPAs and the control sites, this difference was not significant [Welch's t test:  $p=0.1112$ ] (Figure 9). The greatest density was observed at Front Porch ( $6.5 /100\text{m}^2$ ) with the lowest being observed at Oil Slick ( $1.83 /100\text{m}^2$ ) (Figure 10).

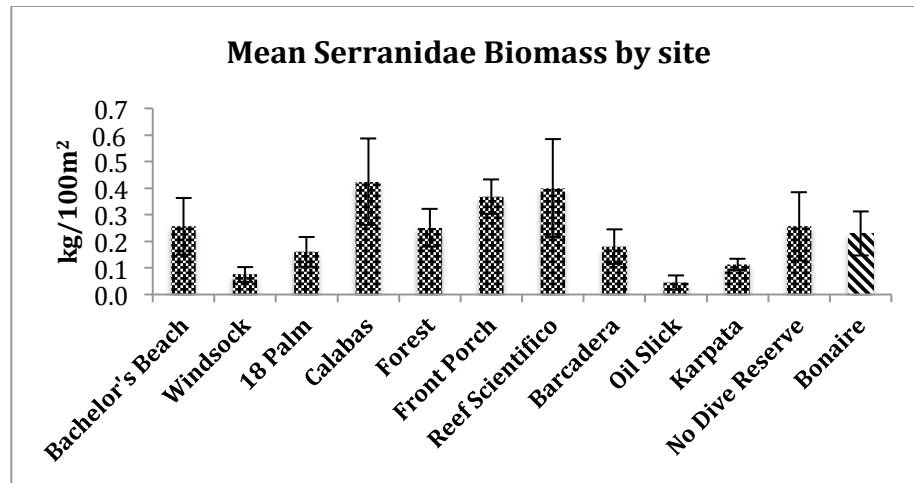


Figure 8. Mean grouper biomass by site. Error bars as in Fig. 1.

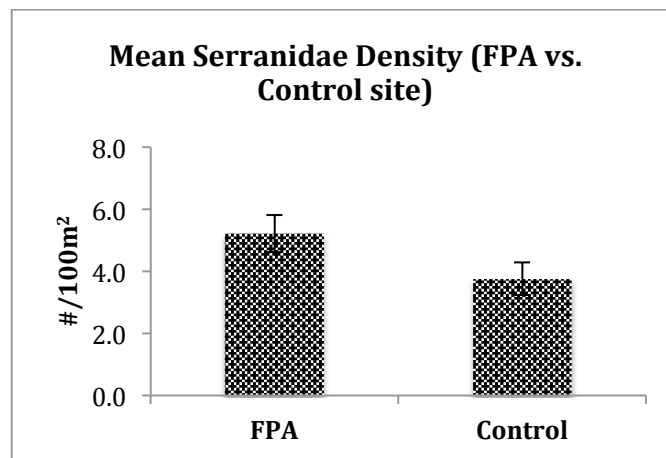


Figure 9. Mean grouper density for FPA and Control sites. Error bars are  $\pm$  s.e. (Welch's t test:  $p=0.1112$ ).

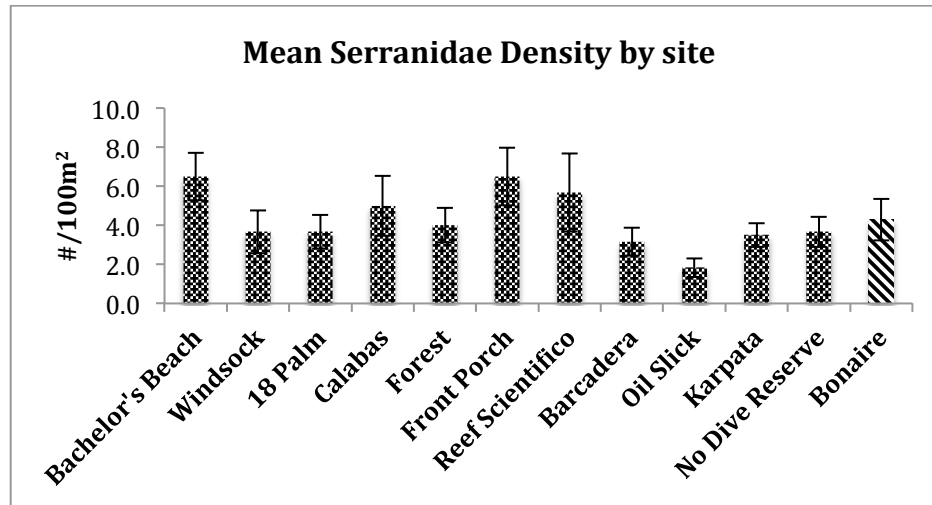


Figure 10. Mean grouper density by site. Error bars are +/- s.e.

#### *Haemulidae* family (Grunts)

Seven species of fish in the grunt family were observed over the survey period in March 2015. These included: black margate (*Anisotremus surinamensis*), blue stripped grunt (*Haemulon sciurus*), Caesar grunt (*Haemulon carbonarium*), French grunt (*Haemulon flavolineatum*), sailors choice (*Haemulon parra*), smallmouth grunt (*Haemulon chrysargyreum*) and white grunt (*Haemulon plumieri*).

FPA's had a non-significant effect on the biomass of haemulids [Welch's t test:  $p=0.5976$ ] (Figure 11) with the highest biomass seen at Reef Scientifico (1.02 kg/100m<sup>2</sup>) and the lowest at Windsock (0.07 kg/100m<sup>2</sup>) (Figs. 11 and 12). There was no effect of FPA's on the density of haemulids [Welch's t test:  $p=0.5518$ ], with the highest density observed at Barcadiera (11.67 /100m<sup>2</sup>) and the lowest at No Dive Reserve (0.83 /100m<sup>2</sup>) (Figs. 13 and 14).

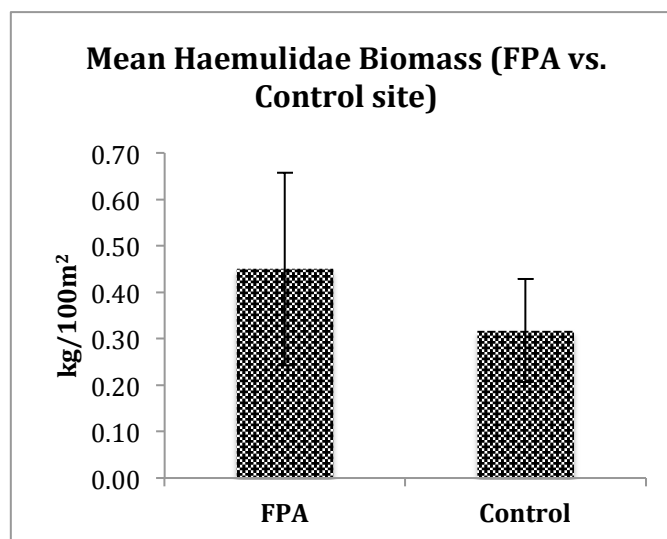


Figure 11. Mean grunt biomass for FPA and control sites. Error bars are  $\pm$  s.e. (Welch's t test:  $p = 0.59$ ).

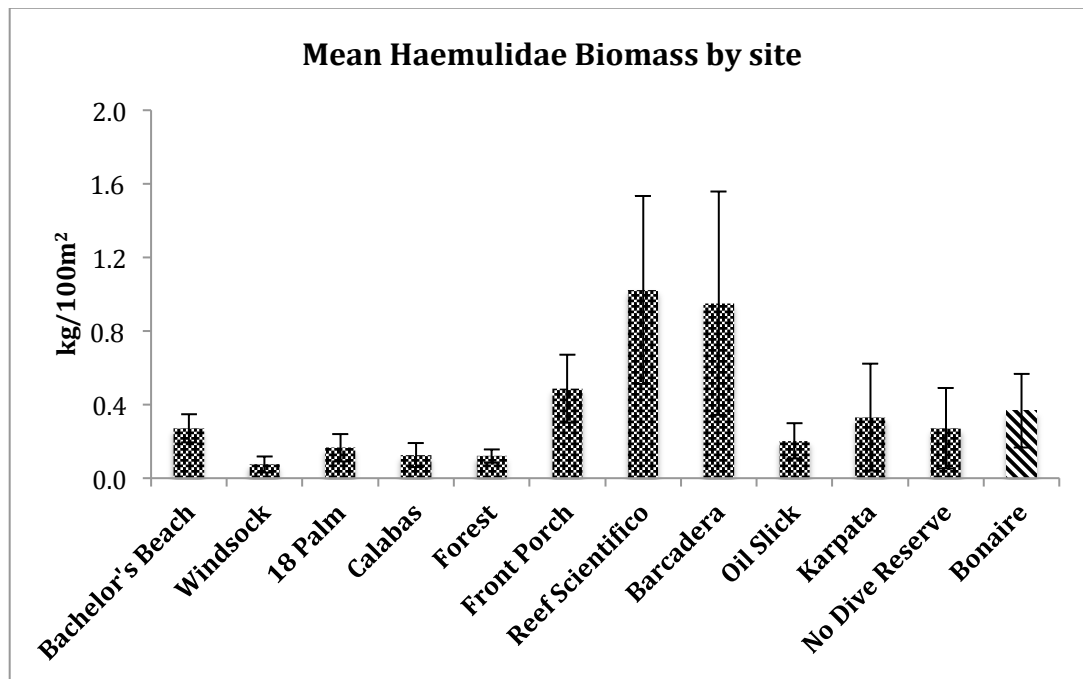


Figure 12: Mean grunt biomass by site. Error bars are  $\pm$  s.e.

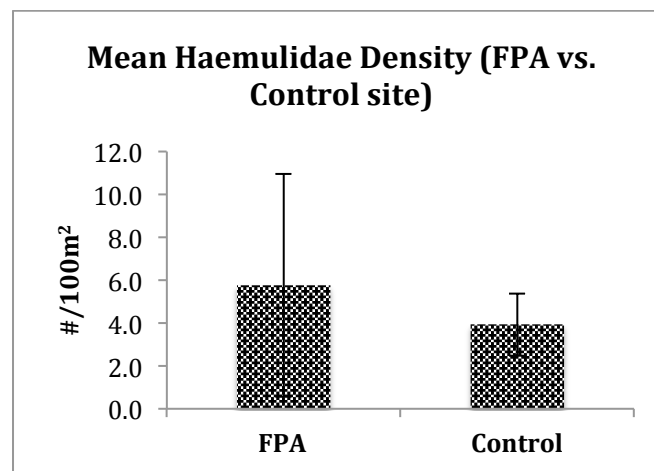


Figure 13: Mean grunt density for FPA and control sites. Error bars are  $\pm$  s.e. (Welch's t test:  $p=0.5518$ ).

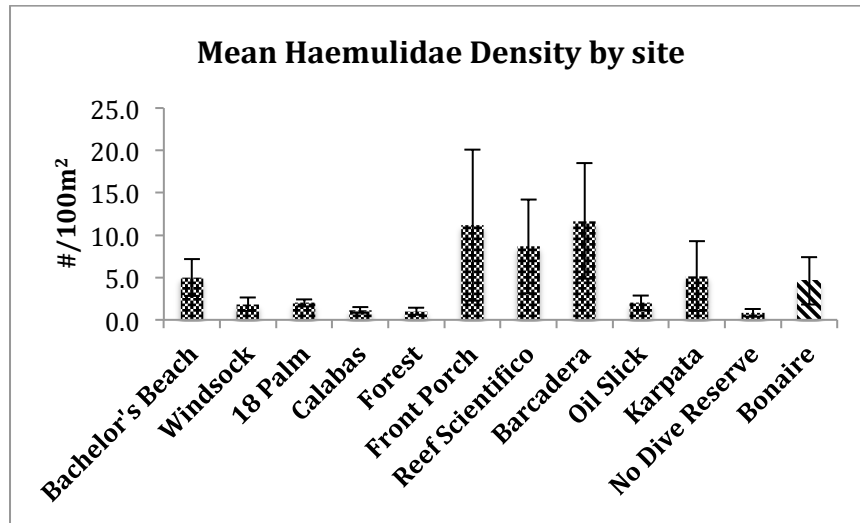


Figure 14: Mean grunt density by site. Error bars are +/- s.e.

#### *Lutjanidae* family (Snapper)

Four species of fish in the snapper family were observed. They were: lane snapper (*Lutjanus synagris*), mahogany snapper (*Lutjanus mahogoni*), schoolmaster (*Lutjanus apodus*), and yellowtail snapper (*Ocyurus chrysurus*).

FPA's had no significant effect on the biomass of Lutjanids [Welch's t test:  $p=0.6605$ ] (Figure 15). The highest biomass was observed at Forest ( $1.86 \text{ kg}/100\text{m}^2$ ) (control site) while the lowest biomass was observed at Barcadera ( $0.13 \text{ kg}/100\text{m}^2$ ) (control site) (Figures 16). There was a significant effect of FPA's on the density of Lutjanids [Welch's t test:  $p=0.0119$ ] (Figure 17), with the highest density observed at Reef Scientifico ( $7.5/100\text{m}^2$ ) and the lowest at Barcadera ( $0.83/100\text{m}^2$ ) (Figure 18).

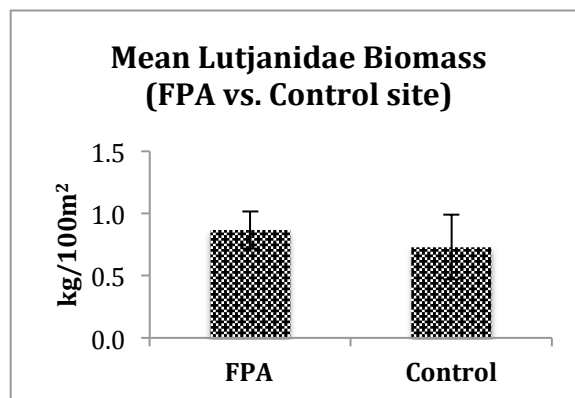


Figure 15. Mean grunt biomass for FPA and control sites. Error bars are +/- s.e. (Welch's t test:  $p=0.66$ ).

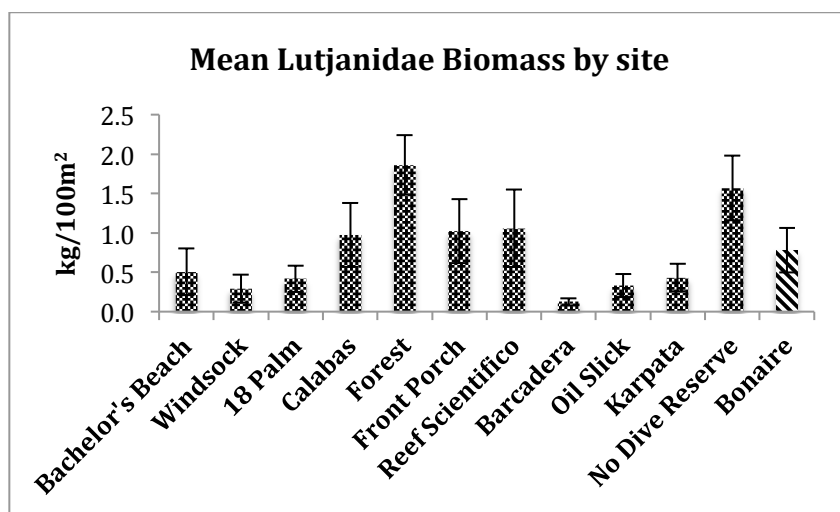


Figure 16: Mean snapper biomass by site. Error bars are +/- s.e.

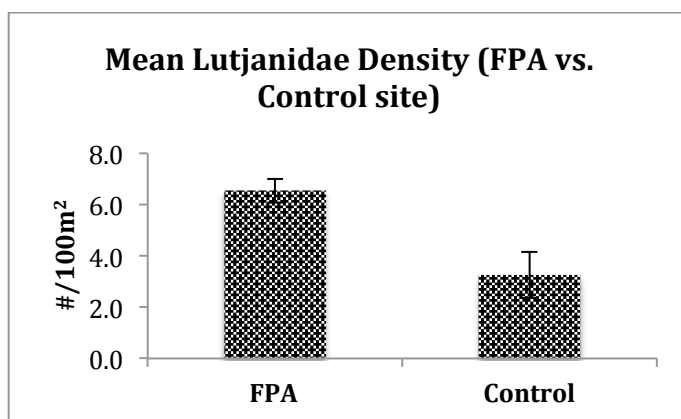


Figure 17: Mean snapper density for FPA and control sites. Error bars are +/- s.e. (Welch's t test:  $p=0.0119$ ).

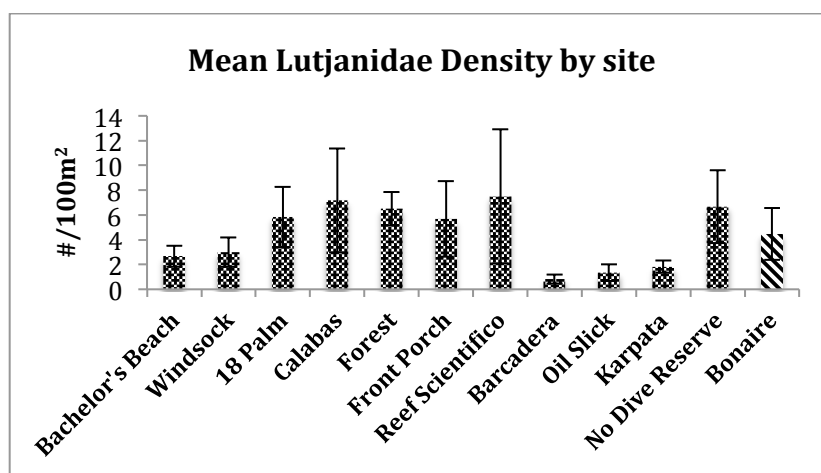


Figure 18: Mean snapper density by site. Error bars are +/- s.e.

### *Targeted Species*

The most commonly targeted species by fishermen in Bonaire are graysby, coney, red hind, and yellowtail snapper. The effect of FPA on the biomass of targeted species was positive but non-significant [Welch's t test:  $p=0.5809$ ] (Figure 19). The highest biomass of targeted species was seen at Forest (Control site) ( $1.06 \text{ kg}/100\text{m}^2$ ) and the lowest at Karpata ( $0.11 \text{ kg}/100\text{m}^2$ ) (Figure 20). The effect of FPA on targeted species density was not significant [Welch's t test:  $p=0.8631$ ] (Figure 21), with Forest (control site) having the highest density ( $6.83 /100\text{m}^2$ ) and Oil Slick having the lowest density ( $1.67/100\text{m}^2$ ) (Figure 22).

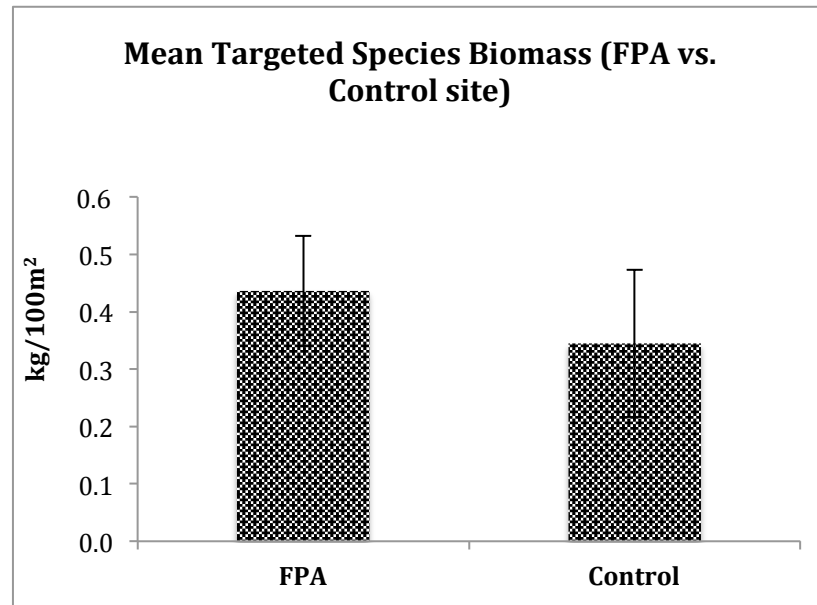


Figure 19. Mean biomass of targeted species for FPA and control sites. Error bars are  $\pm$  s.e. (Welch's t test:  $p=0.58$ ).

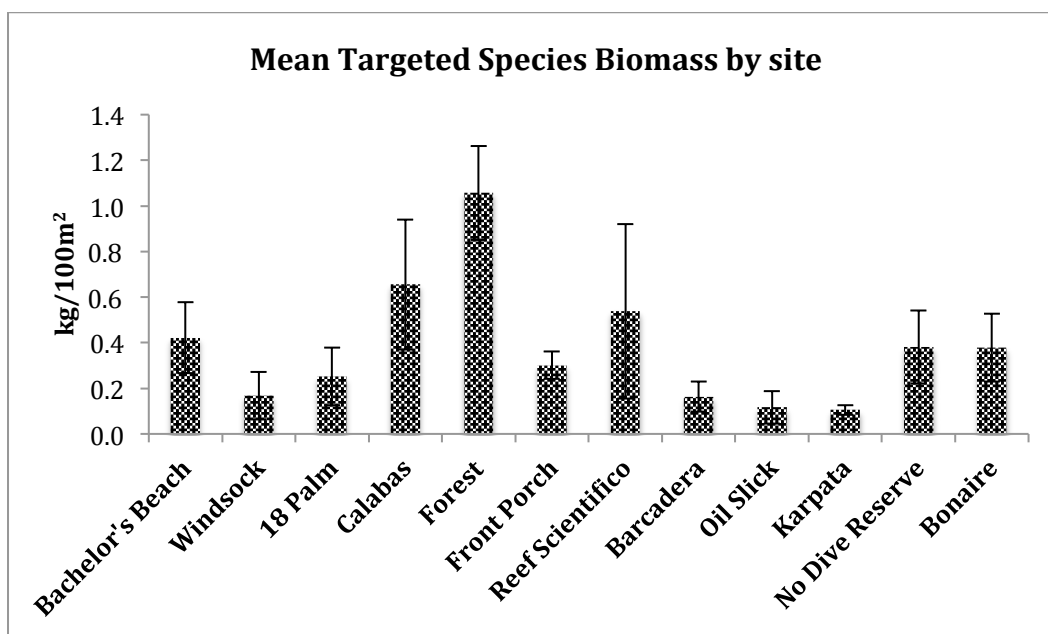


Figure 20. Mean targeted species biomass by site. Error bars are +/- s.e.

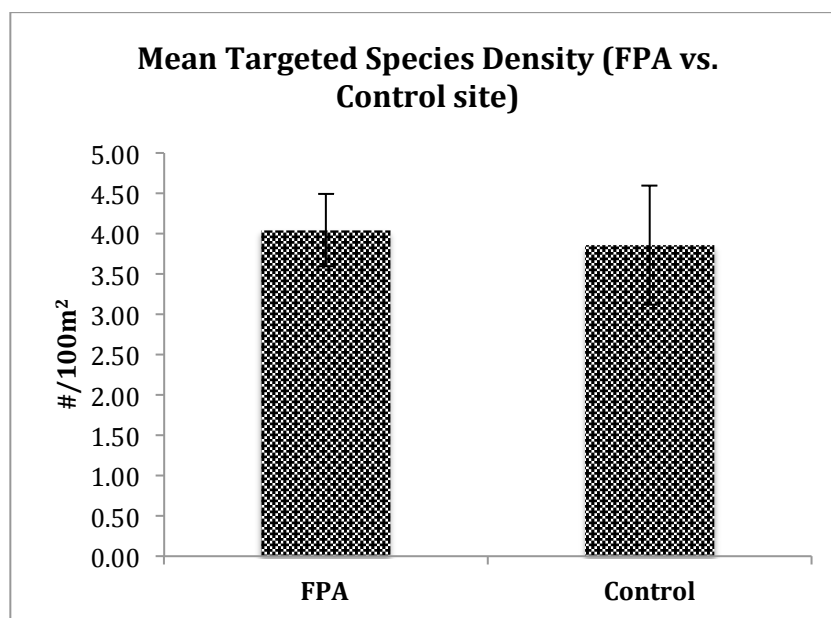


Figure 21: Mean targeted species density for FPA and control sites. Error bars are +/- s.e. (Welch's t test:  $p=0.8631$ ).

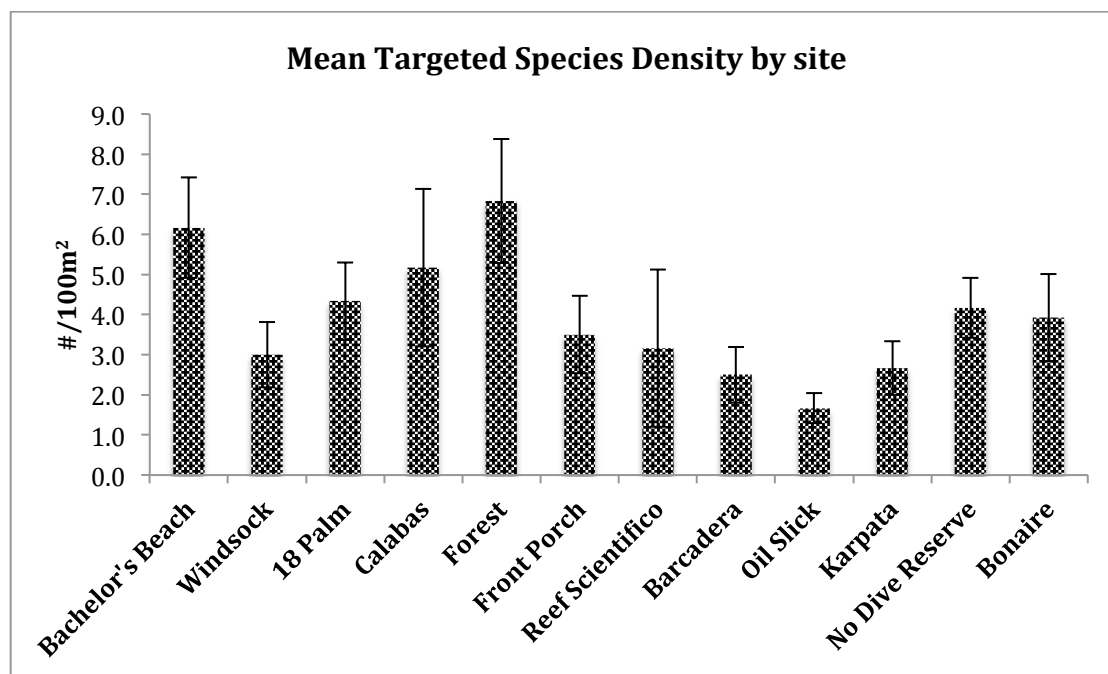


Figure 22. Mean targeted species density by site. Error bars are +/- s.e.

## Discussion

The average biomass for pre vs. post Fish Protected Area (FPA) establishment shows a clear positive, but non-significant, effect (Figure 1) of FPA on overall predatory fish species biomass. This demonstrates that FPAs are likely having a positive effect on predatory fish biomass, but effects may require more time to clearly manifest. The data trends observed in Figure 2 shows no change in the average biomass or density of predatory species on Bonaire from 2013 to 2015. The lack of change between these two most recent sampling years may be due to increased fishing pressure in the control sites due to the unavailability of the FPAs to fishermen as a target zone, thus reducing the average biomass and density in the control areas in comparison to the FPA zones. A comparison of the FPA vs. control zones shows higher overall predatory biomass (Figure 3), as well as higher biomass within the major predatory fish families (Serranidae, Haemulidae and Lutjanidae) in the FPAs (Figure 7, 11 and 15). None of these increases were statistically significant at the 95% confidence level. FPA zones were seen to have a positive effect on all groups (Figure 5, 9, 13, 17), with a significant increase observed in the snapper family (Figure 17,  $p=0.0119$ ). While for groupers, this follows the increase observed in 2013 (Auscavitch and DeBey 2013), the increase in Lutjanidae and Haemulidae was previously unobserved. Fish reserve effects may take upwards of 5 years to take effect, depending on initial conditions (Steneck et al. 2011), so this delayed increase is not surprising, considering these FPAs were established in 2008 and it may have taken some time for full enforcement to take effect. This increase in predatory biomass may also result in greater reproductive biomass, especially when considering that many predatory species achieve sexual maturity late in life. A larger predatory biomass in the FPA could result in greater numbers of juveniles available to recruit to surrounding reef areas, making the reef community more resilient (Bellwood et al. 2004), as well as result in increase catches in zones adjacent to FPAs due to spill-over effects



(McClanahan and Mangi 2000). However, one would need to conduct a catch-per-unit effort experiment to be confident of this effect.

The species most commonly targeted in Bonaire include coney, graysby, red hind, and yellowtail snapper. Although positive, the effect of the FPA on the biomass (Figure 19) and the density (Figure 21) was not statistically significant. Although those species are said to be most-targeted, all serranids are susceptible to hook and line fishing and as a family the FPA effect was marginally significant. Nevertheless, simply focusing on graysbys which are the most targeted species in Bonaire and comparing sites before and after they became FPAs shows a clear trend of increasing abundance since the no-fishing ban was established (see Fig. 9 in the Executive Summary). Today, most large groupers are absent from most of Bonaire's reefs. No red hind were observed in the belt transects in 2015.

Overall, Bonaire does not experience the intense fishing pressure that is common throughout most Caribbean islands. Since hook and line, fishing pressure is selective and not effective for some fish species. The lack of significant effects on the targeted species could result from access. For example, Klein Bonaire, a control site that it is far from shore has high predator biomass whereas Karpata also a control site but close to shore and has low predator biomass. Poaching could reduce the FPA effect. During the week we conducted our surveys, we observed poaching in the FPAs from yachts and tourists in fishing boats. The absence of red hind in all transects is a worrying observation, as it may be an indicator of the loss of reproductive populations throughout the region.

The positive effect of Fish Protected Areas on predatory fish biomass, particularly those of commonly targeted species such as graysby, reinforces the usefulness of these FPAs as a management tool for facilitating the recovery of fish biomass in reef ecosystems. The benefit of the FPAs to stakeholders can be measured by monitoring spill over effects (Roberts et al. 2001, Abesamis and Russ 2005) in reefs adjacent to the protected zones. However, there are no signs for yachts that FPAs are present and no-fishing is allowed so there is room for improvement in public education and enforcement.

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## **Chapter 5: Patterns of juvenile coral abundance on Bonaire's reefs: trends in time and management areas**

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### **Abstract**

The purpose of this study was to assess juvenile coral abundance on 11 of Bonaire's reefs, both control sites (n=7) and Fish Protected Areas (n=4). Juvenile coral abundance has significantly increased from the last three surveys conducted in 2009, 2011 and 2013 (ANOVA: p-value = 0.001, 0.035, 0.001 respectively). No differences in juvenile coral densities were found between control and FPA sites. Seaweed has steadily decreased over the last five years (2011-2015). The Fish Protected Areas had more seaweed compared to the control sites, but seaweed abundances are generally very low by Caribbean standards. No negative relationships were found between juvenile coral populations, turf algae, crustose coralline algae (CCA) or spatial heterogeneity. Surprisingly, the opposite trends were seen between juvenile coral abundance and macroalgae and juvenile coral abundance and CCA than what most published studies have found. Ultimately, this study provides hope for Bonaire's reefs and demonstrates the success of their marine management program.

### **Introduction**

In recent decades coral cover and habitat complexity has decreased throughout the Caribbean, resulting in a phase shifts from coral-dominated states to algal-dominated states (Hughes 1994, Kramer 2003). This change resulted from white band disease, the mass mortality of the herbivorous sea urchin *Diadema antillarum*, reduction of herbivorous fishes, and hurricanes that reduce reef complexity (Edmunds and Carpenter 2001, Alvarez-Filip *et al.* 2009, Burkepile and Hay 2010). In contrast to the rest of the Caribbean, Bonaire's reefs have maintained high coral cover and low seaweed (macroalgae) abundance. However, herbivore biomass in Bonaire has decreased in recent years causing concern that these coral-dominated reefs may shift to an algal-dominated state (Bowdoin and Wilson 2005).

Macroalgae abundance reduces the recruitment potential of the benthos for corals (Tanner 1995, Edmunds and Carpenter 2001, Kuffner *et al.* 2006). Macroalgae can smother, shade or even poison corals making areas with high algal biomass hostile to juvenile corals (Box and Mumby 2007, Rasher *et al.* 2011). Herbivore abundance (such as parrotfish and surgeonfish populations) is an important driver maintaining a coral-dominated state (Lirman 2001, Hughes *et al.* 2007, Mumby and Steneck 2008). However, because parrotfish biomass declined steadily from 2003 through 2007 on Bonaire's reefs, along with an increase in macroalgae (eg see the Bonaire Report for 2007), and because there was a widespread concern about declines in reef fish, four Fish Protection Areas (FPA) (Eighteenth Palm, Calabas, Front Porch and Reef Scientifico) were established in Bonaire in January 2008.

The objective of my study was to determine juvenile coral abundance and macroalgal biomass at 11 sites on Bonaire's reefs. Juvenile coral abundances and macroalgal indices were compared between control and FPA sites to illustrate patterns related to fishing and long-term trends. This study may inform managers on the capacity of Bonaire's reefs to maintain or increase its live coral cover into the future.

## Materials and Methods

We surveyed 11 sites via SCUBA on the leeward side of Bonaire (Netherlands Antilles, Southern Caribbean) from March 8<sup>th</sup> - March 12<sup>th</sup>, 2015. The 11 reef sites were composed of both controls (n=7) and Fish Protected Areas (FPA, no fishing permitted, n=4). The sites 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. At each dive site, I placed a 25 cm x 25 cm quadrat every 2.5 meters (starting at 0 m) along a 10 meter transect at 10 meters depth. Quadrats were randomly placed on "available substrate" avoiding live coral, gorgonians and sponges. Substrate with greater than 25% invertebrate cover (adult coral, gorgonians and sponges) was ignored and the quadrat was placed on the closest available substrate with < 25% invertebrate cover. Within each quadrat I quantified percent cover of coral, macroalgae, turf algae and crustose coralline algae as well as macro and turf algae canopy heights. In addition I identified the species and recorded the size of all juvenile corals (those  $\leq 40$  mm in diameter) with each quadrat (Bak and Engel 1979). Algal indices (proxy for algal biomass) were calculated by multiplying percent cover of macroalgae by their respective canopy heights (Steneck and Dethier 1994).

Data were analyzed to determine mean juvenile coral densities and macroalgal indices for all 11 sample sites. These parameters were compared between control and FPA sites. Average percent cover of crustose coralline algae was also determined for each site. Statistical significance was determined using a non-parametric one-way ANOVA with an alpha ( $\alpha$ ) of 0.05.

## Results

Overall mean juvenile coral abundance for all 11 sites in Bonaire was 20.1 ( $\pm 1.8$  SE) individuals per m<sup>2</sup> (Fig. 1). The 2015 overall mean juvenile coral density is significantly greater than values reported in the last three Bonaire reports 2009, 2011, and 2013 (p-value = 0.001, 0.035, 0.001 respectively).

*Agaricia* species (*A. agaricites* and *A. lameric*), *Porites astreoides*, and *Orbicella annularis* (formally *Montastraea annularis*) were the three most abundant juvenile corals identified (Fig. 2). These three taxa were also the most abundant in 2013 however their abundances have significantly increased in the past two years (*Agaricia* spp.  $p = 0.0001$ , *P. astreoides*  $p = 0.0001$ , and *O. annularis*  $p = 0.0002$ ). Of the 11 sites, Eighteenth Palm (FPA) 28 No./m<sup>2</sup> ( $\pm 3.6$  SE) and the No Dive Reserve 28 No./m<sup>2</sup> ( $\pm 3.2$  SE) had the greatest juvenile coral densities (Fig. 3). Bachelor's Beach and Oil slick ranked equally for the lowest juvenile coral densities among the 11 sites, 12 No./m<sup>2</sup> ( $\pm 2.5$  SE) and 12 No./m<sup>2</sup> ( $\pm 2.8$  SE) respectively. Average juvenile coral

density was slightly higher at FPA sites compared to control sites however the two means are not statically significant ( $p = 0.5092$ ).

Macroalgal indices have slowly decreased since 2011 (Fig. 4). Macroalgal indices were greatest at Calabas (FPA)  $353.65 (\pm 1.75 \text{ SE})$  and the No Dive Reserve  $289.1 (\pm 14.22)$  (Fig. 5). The Fish Protected Areas had a significantly greater mean macroalgal index compared to the control sites ( $p = 0.0001$ ). Total average macroalgal index for all 11 sites was  $115.37 (\pm 35 \text{ SE})$ . No significant relationship was found between juvenile coral densities and crustose coralline algae percent cover, macroalgae indices nor spatial heterogeneity indices.

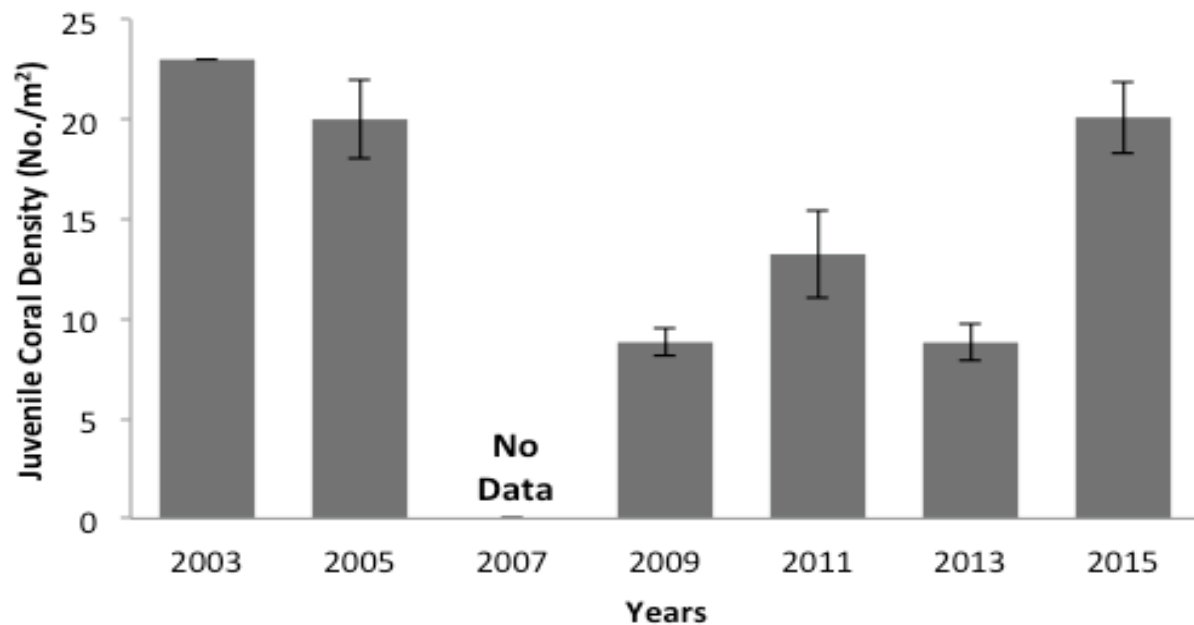
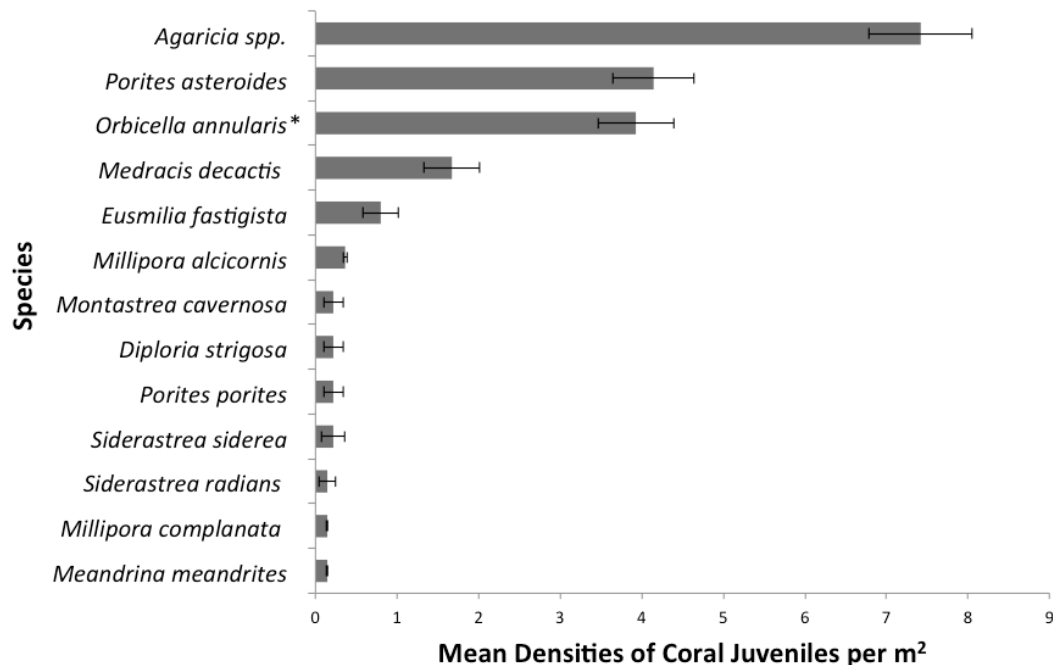
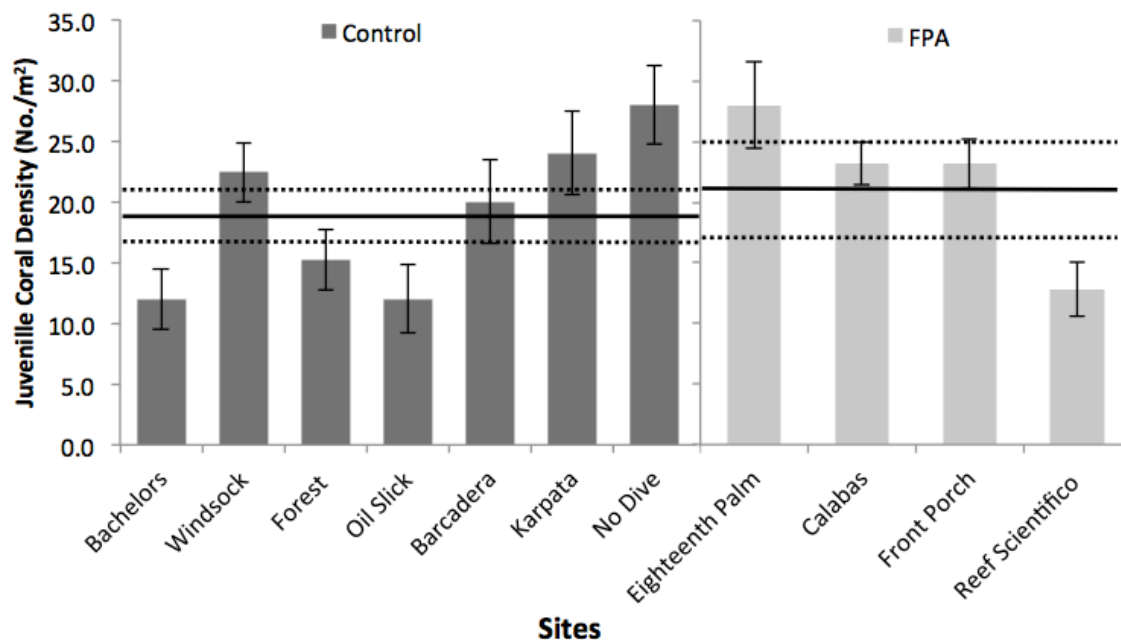


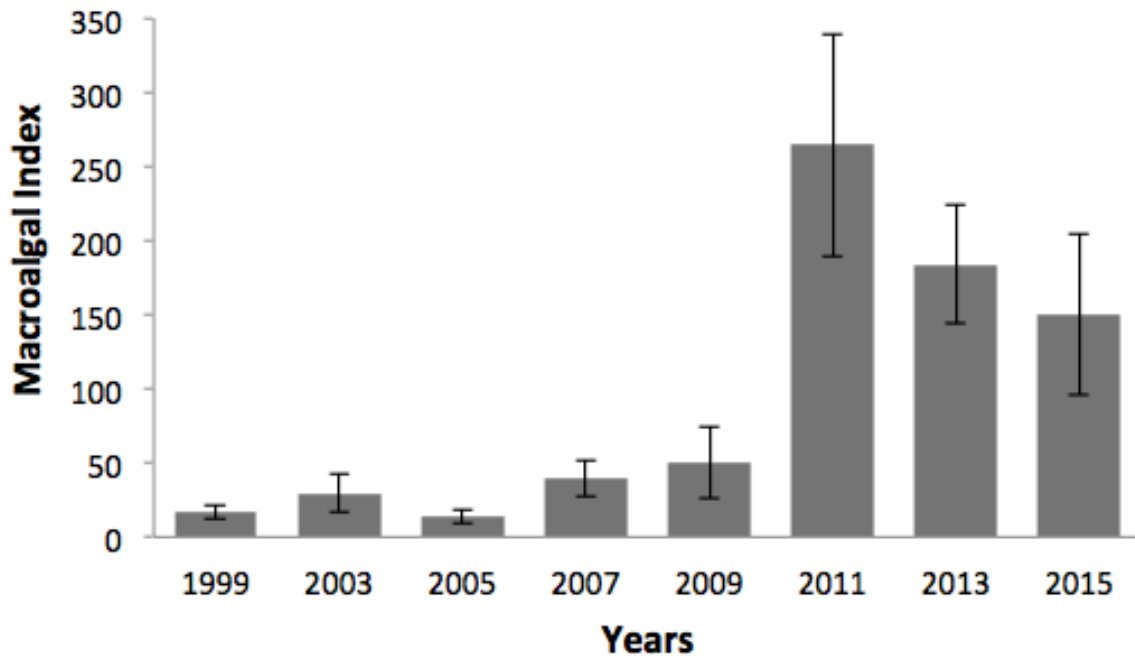
Figure 1. Mean juvenile coral density per sample year. Error bars indicate  $\pm$  one standard error. No data available for the year 2007.



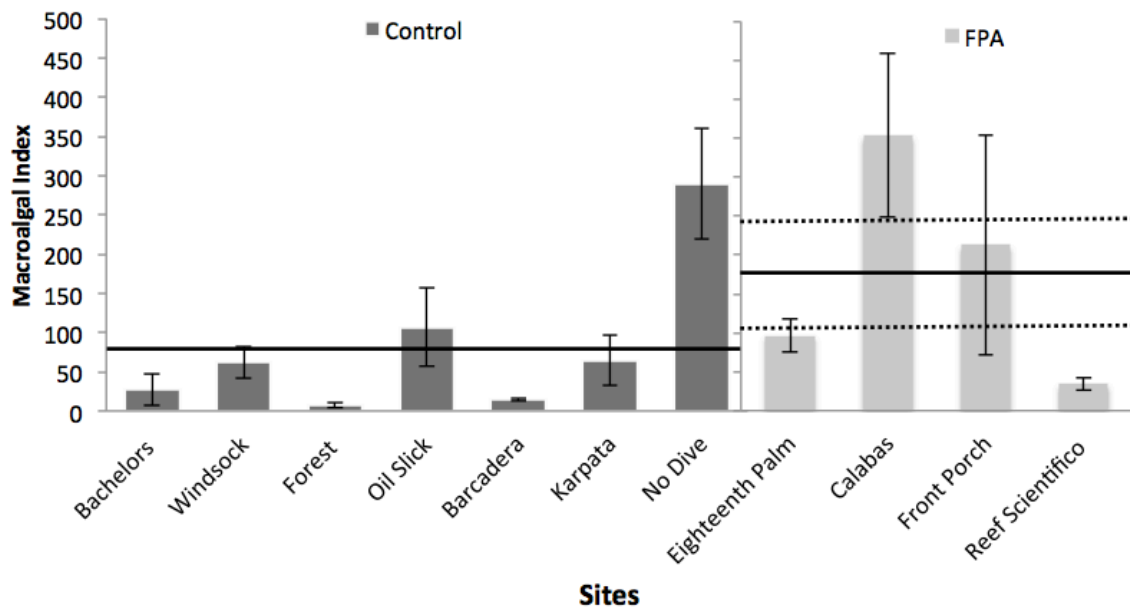
**Figure 2:** Mean juvenile coral densities (No./m<sup>2</sup>) by species on Bonaire's reefs at 10 m depth during the month of March, 2015 (n=220). Error bars denote  $\pm$  one standard error. \**Orbicella annularis* juvenile coral were likely remnants of larger individuals that suffered partial mortality.



**Figure 3:** Juvenile coral densities (No./m<sup>2</sup>) per sample site. Dark grey bars indicate control sites (n=140) and light grey bars represent fish protected area (n=80). Solid horizontal line represents total average juvenile coral density per control and FPA sites; dotted lines are their respective  $\pm$  standard error. Error bars denote  $\pm$  one standard error.



**Figure 4:** Mean macroalgal indices per survey year on Bonaire's leeward facing reefs. Error bars denote  $\pm$  one standard error.



**Figure 5:** Macroalgal index per sample site. Dark grey bars indicate control sites (n=140) and light grey bars represent fish protected area (n=80). Solid horizontal line represents total average macroalgal index per control and FPA sites, dotted lines are their respective  $\pm$  standard error. Error bars denote  $\pm$  one standard error.

## Discussion

This study reveals a recent increase in juvenile coral abundances on Bonaire's leeward reefs in comparison to the three previous monitoring years (2009, 2011, and 2013). The 2015 juvenile coral abundances are more similar of those reported in 2003 and 2005. This study indicates the reefs of Bonaire have become a more suitable nursery habitat for settling juvenile corals over the past two years. This upward trend in juvenile coral densities is likely in response to decreasing abundances of seaweed. A bleaching event caused an increase in macroalgae on Bonaire's reef in 2010. In 2011 Bonaire's reef had relatively high algal abundance and only moderate juvenile coral densities. The presence of macroalgae is believed to be a major factor in regulating the recruitment potential of the benthos on Caribbean coral reefs (Arnold *et al.* 2010). Macroalgae out competes settling corals through shading and abrasion and subsequently reduces the available nursery habitat for juvenile corals (Box and Mumby 2007). Macroalgae biomass is inversely related to coral recruitment (Steneck *et al.* 2014). Over the last 5 years, since the bleaching event in 2010 and initial spike in seaweed abundance, it is probable we have witnessed an improvement in the recruitment potential of the benthos (Fig. 1 and Fig. 4). It is important to note seaweed abundance in Bonaire, during all survey years, is still low by Caribbean standards and thus the effect of macroalgae on juvenile corals would likely be modest (Kramer 2013).

Interestingly, there was no significant difference between control and FPA sites in terms of juvenile coral abundance. This suggests that both management approaches have equal effects on coral recruitment. Macroalgal index did indeed show differences between the control and FPA sites; FPA's had significantly greater algal biomass. This has been a consistent trend since 2009 (Steneck and Arnold 2009, Steneck 2011, Steneck 2013). This is an unlikely trend due to the nature and purpose of fish protected areas. By establishing an FPA fishing pressure on carnivores was reduced but the hook and line fishery may have had little effect on herbivorous parrotfish prior to establishment. The high macroalgae biomass in FPA's could be attributed to increasing abundances of damselfishes, who's presence increases algal biomass and or productivity and reduces parrotfish (scarids) bite rates (Brawley and Adey 1977, Arnold *et al.* 2010).

The three most abundance juvenile corals *Agaricia* spp. *Porites astreoides*, and *Orbicella annularis* have platy or mound forming physiologies. As such they lack the structural complexity common in Caribbean reefs prior to the disease induced mass mortality of *Acropora* species (Alvarez-Filip *et al.* 2009). *Oribella annularis* is a large mounding coral and thus provide higher habitat complexity as an adult. High habitat complexity is an important aspect for recruiting reef fishes and thus important to herbivory (McCormick 1994, Beukers and Jones 1998). The *O. annularis* juveniles identified in this study are likely not new recruits but adults who have suffered biomass lost because this species recruits only rarely. So although these juveniles will grow into large mounding coral, *O. annularis* likely still rarely recruits to the benthos. In conclusion, juvenile coral abundance has increased on Bonaire's reefs while macroalgae biomass has slowly declined. This provides hope that Bonaire's reef management is working and should continue.



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## Chapter 6: Architectural Complexity of Bonaire's Coral Reefs

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### Abstract:

The architectural complexity of coral reefs plays a critical role in reef ecosystems. As reefs become degraded they begin to lose their complexity and are no longer able to provide these integral services. For the first time in the Bonaire Reports' ongoing assessments, I measured reef structural complexity at our 11 long-term monitoring sites. I found that Bonaire's reefs are more architecturally complex than a region-wide estimate of the Caribbean in 2008. Within my surveyed sites, I found that architectural complexity was positively correlated with scarid (parrotfish) population densities, which are likely both benefitting from and contributing to architectural complexity. Protection of scarids and other herbivores should continue to be prioritized to maintain their role in facilitating architectural complexity. Future Bonaire Reports should continue to assess reef architectural complexity to identify longitudinal trends.

### Introduction:

The architectural complexity of coral reefs underpins the rich ecosystems that are associated with them. The structure produced by reef building corals plays a critical role in providing predator refuges, increasing recruitment habitat, and reducing competition by increasing the surface area of reefs. Reefs with higher rugosity have been shown to have increased post-recruitment survivorship of juvenile fish (Connell and Jones 2006), increased abundances of both juvenile and adult fish (Beukers and Jones 1998; Jones et al. 2004; Almany 2004), increased fish species diversity (Jones et al. 2004; Gratwicke and Speight 2005), and increased densities of the foundation herbivore *Diadema antillarum* (Lee 2006).

An ever-increasing list of factors threaten corals and the structures they provide, ranging from disease to ocean warming and acidification to algal competition exacerbated by herbivore overfishing and nutrification (Hughes et al. 2010). As corals become stressed and die, biological and physical erosion processes will begin to exceed accretion from coral growth, resulting in net reef erosion (Perry et al. 2013). These degraded structures become more susceptible to larger physical disturbances like hurricanes. Structures that were once highly complex begin to flatten, losing the integral services they once provided to the ecosystem. Reef building corals are replaced by more stress-tolerant species, which tend to be less structurally complex (Alvarez-Filip and Dulvy 2011).

This flattening dynamic is particularly apparent in many of today's Caribbean reefs. In an analysis of reef architectural complexity in the Caribbean between 1969 and 2008, Alvarez-Filip et al. (2009) found a declining trend in reef rugosity throughout the region. What does this mean for Bonaire's reefs? As reef architectural complexity has been shown to have critical implications for the larger reef ecosystem, it is essential to assess complexity as part of complete reef monitoring. This study quantified architectural complexity on Bonaire's reefs to address three central objectives. First, it is valuable to compare Bonaire's reef complexity to other areas

of the Caribbean to provide a more complete picture of reef ecosystem state. Second, quantifying complexity at each of the 11 monitoring sites will allow us to test for correlations with other components surveyed in this larger study such as fish and benthic communities. Third, as architectural complexity has not been assessed in previous Bonaire studies, these data serve as a valuable baseline in assessing reef growth or flattening trends in the future.

## Methods:

I quantified reef architectural complexity using a spatial index, sometimes referred to as a rugosity index (Wilson et al. 2007; Alvarez et al. 2009). The spatial index is measured by laying a taut transect line over the top of a reef structure and then using a second line to measure the actual contours that fall underneath the transect line (Fig. 1). The ratio between the length of the line when molded against reef contours and the taut line comprises the spatial index. A perfectly flat structure would have a spatial index of 1.0, while higher values would indicate increasing structural complexity.

I measured the spatial index on four or eight 10m transects on each of the 11 long-term study sites in Bonaire. Within the total contour measurements I also quantified contour types by distinguishing tops (flat or gently sloping surfaces at topographical reef highs), sides (heavily slanted or vertical surfaces), and bottoms (flat or gently sloping surfaces below topographical reef highs). Additionally, I measured benthic substrate on topographical highs by quantifying live coral and sponges, macroalgae, turf algae, and crustose coralline algae underneath the transect tape.

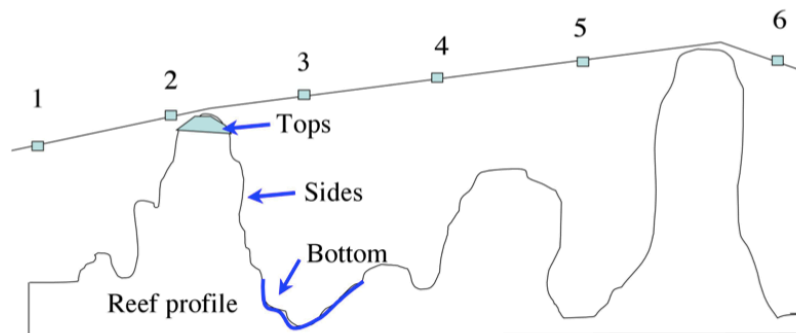


Fig. 1 Spatial Index measurement protocol (Robert Steneck, personal communication, March 8, 2015).

I calculated average spatial indexes for all 11 sites. Within each site I quantified the frequency of side contour heights. I tested for pairwise correlations between the average spatial index of each site with average scarid biomass and density (Arnold 2015: this report) and macroalgal, coral, and coralline percent cover and turf algae canopy height (Steneck 2015: this report). I also ranked each site based on their relative values for each of these variables and compared rankings across variables to identify trends.

## Results:

The average spatial index across all eleven sites surveyed in Bonaire was 1.85, which is substantially greater than the 2008 regional Caribbean average reported by Alvarez-Filip et al. (2009) (Fig. 2). A spatial index of 1 is a flat surface.

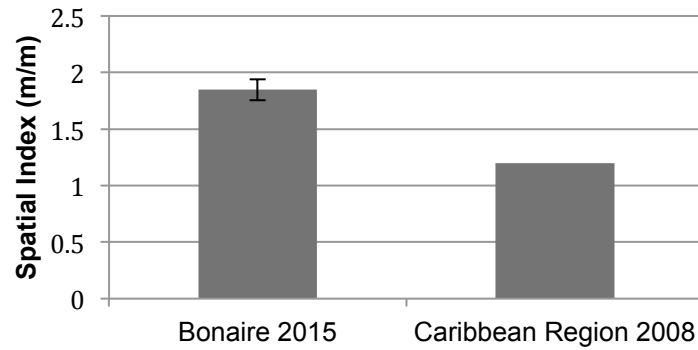
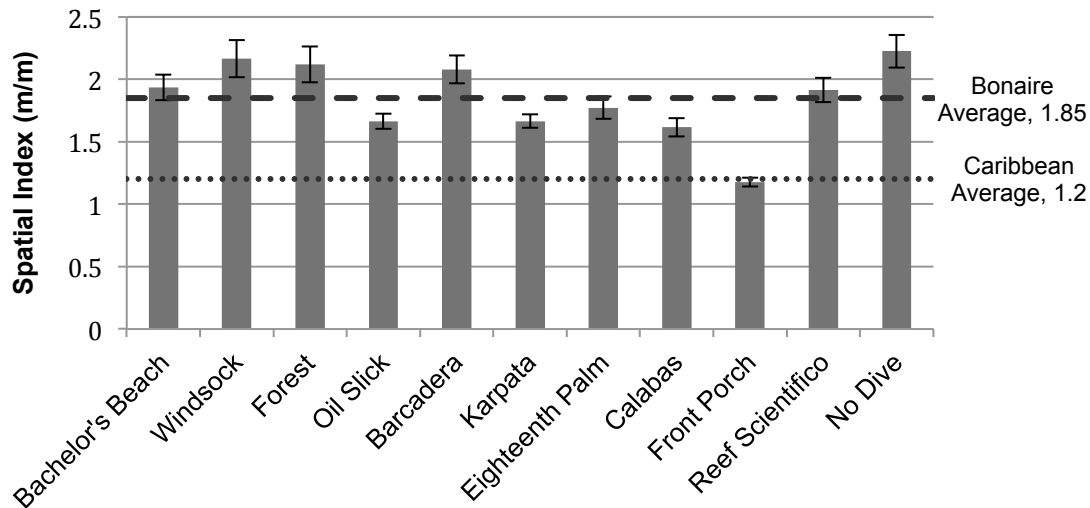


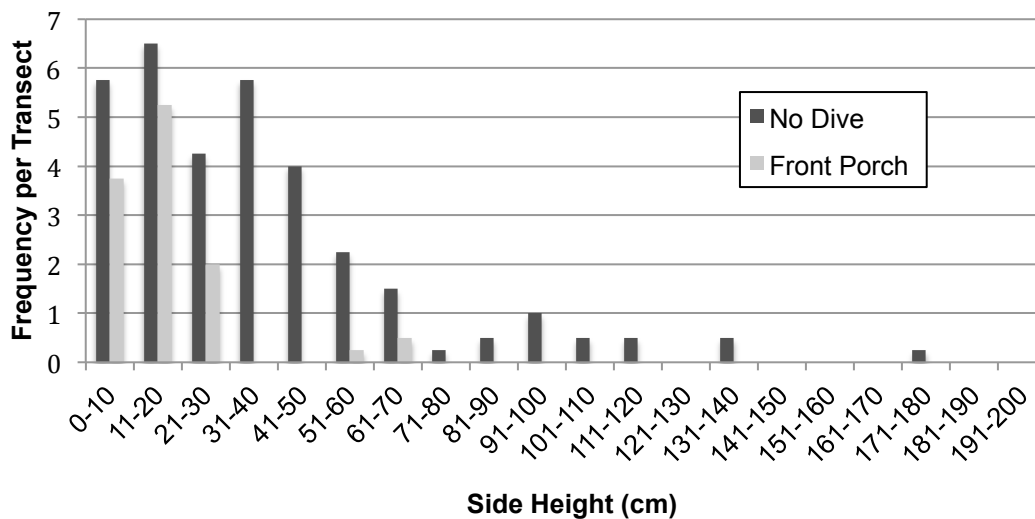
Fig. 2 Average spatial index of all Bonaire sites surveyed in 2015 compared to the 2008 regional Caribbean average reported by Alvarez-Filip (2009). Error bars indicate standard error. No standard error data was available for the 2008 regional average.

The average spatial index of all sampled sites was significantly greater than the 2008 Caribbean average of 1.2, with the exception of Front Porch, which had an average of 1.18 (Fig. 3). No Dive, Windsock, Forest, and Barcadera were among the most architecturally complex sites with spatial indices greater than 2.



**Fig. 3** Average spatial index measured at each site relative to the overall 2015 Bonaire average and 2008 Caribbean average. Error bars indicate standard error.

Examining the heights of side contours at each site reveals more about architectural structure. No Dive, the site with the highest spatial index, had more and longer side contours than Front Porch, the least architecturally complex site (Fig. 4). It is these vertical and semi-vertical faces that add contour length within a given segment.

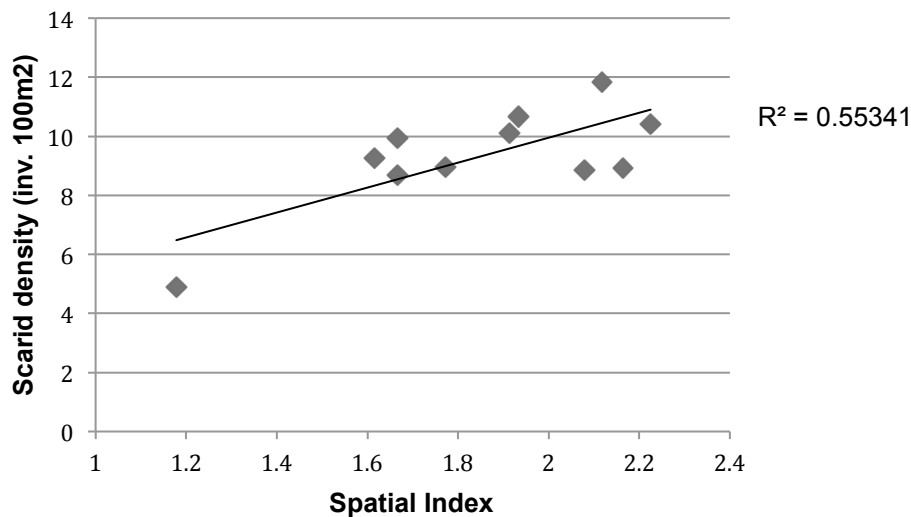


**Fig. 4** Frequency of contour side heights for sites with the highest (No Dive) and lowest (Front Porch) spatial indexes

As presented in the introduction, reef architectural complexity can both influence and be influenced by a number of other factors in coral reef ecosystems. I examined the relationships between architectural complexity and scarid populations (biomass and density), benthic cover (macroalgae, coral, and coralline algae), and turf algae canopy heights. First I used a ranking index to identify trends (Table 1). Higher spatial indices tended to be associated with higher scarid densities, coral cover, and coralline cover and lower macroalgal cover and turf canopy heights. Of these relationships, spatial index and scarid density had the only statistically significant correlation ( $p=0.009$ ) (Fig. 5).

| Site                          | Site Rankings (1-11) |                |                |               |         |               |                   |
|-------------------------------|----------------------|----------------|----------------|---------------|---------|---------------|-------------------|
|                               | Spatial Index        | Scarid Biomass | Scarid Density | Macro % Cover | Turf CH | Coral % Cover | Coralline % Cover |
| No Dive Windsock Forest       | 1                    | 8              | 3              | 2             | 7       | 1             | 1                 |
|                               | 2                    | 9              | 8              | 7             | 4       | 6             | 9                 |
|                               | 3                    | 2              | 1              | 11            | 11      | 2             | 6                 |
| Oil Slick Calabas Front Porch | 9                    | 6              | 10             | 6             | 6       | 10            | 2                 |
|                               | 10                   | 10             | 6              | 1             | 2       | 9             | 11                |
|                               | 11                   | 11             | 11             | 4             | 1       | 7             | 10                |

**Table 1** Rankings of the three most and least architecturally complex sites by scarid density, macroalgal percent cover, turf canopy height, coral percent cover, and coralline algae percent cover relative to the 11 sites surveyed, with 1 being the highest ranking and 11 being the lowest. Cell color reflects a grayscale from 1 to 11. In general, more complex sites tended to have higher scarid densities, higher coral and coralline cover, and lower macroalgal cover and turf canopy heights.



**Fig. 5** Correlations between spatial index and scarid density by site (n=11).

## Discussion:

The high architectural complexity of Bonaire's reefs relative to the rest of the Caribbean is a positive indicator of reef ecosystem health. Alvarez-Filip et al. (2009) report a decline in reef complexity from a spatial index of 2.5 to 1.5 between 1969 and 1985 and a further decline to about 1.2 between 1998 and 2008. They attribute the initial decline to the loss of acroporid corals from white band disease and the second decline to a major regional bleaching event in 1998. While a lack of historical data precludes making direct over-time comparisons of Bonaire's reef architectural complexity, it can be inferred that Bonaire's reefs retained more of their structural complexity through these disturbances and perhaps had more rapid recoveries of reef building corals.

Reef architectural complexity plays an important role in feedback loops within coral reef ecosystems (Lee 2006; Nyström et al. 2012). As reef structures degrade, they are unable to provide the same habitat and recruitment services discussed above, often leading to reduced species diversities and abundances of fish and urchins. Any loss in herbivores will in turn further reef degradation by releasing suppression of algal populations. As flattening reefs become dominated by algae, they become inhospitable to recruiting corals as well as fish. This creates a reinforcing feedback loop, which can lock the system in this degraded state. Conversely, reefs with high architectural complexity provide greater surface area and habitat for fish and benthic organisms. Increased herbivore populations will facilitate coral growth and recruitment and thus further increase reef structural complexity. Bonaire has retained relatively high reef complexity while the majority of the Caribbean has experienced significant declines.

Within Bonaire's reef network, I found that reefs with the highest spatial indexes had the highest scarid densities and vice versa. It is impossible to say to what extent architectural complexity is a driver of scarid densities or a consequence, but efforts to protect scarid populations should

continue to be prioritized as they are a key component in these reinforcing feedback loops. This study provided a preliminary investigation of relationships between architectural complexity and other factors such as herbivory pressures and benthic communities, but more in-depth analyses of these relationships would also be valuable as the unit of analysis here is the site average, making the sample size relatively small (n=11). Architectural complexity should continue to be measured in future years so that trends can be identified and addressed.

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## Chapter 7: Fish herbivory on Bonaire's Reefs: spatial variability, FPA effects, and long-term trends

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### Abstract

In this study, we quantified herbivorous fish bite rates at 11 sites along Bonaire's leeward shore in the context of benthic composition, four within fish protection areas (FPAs) and seven at control sites. Parrotfish, tangs and damselfish (Scaridae, Acanthuridae and Pomacentridae, respectively) grazing rates were expressed by functional groups and, due to the disproportionately important impact of parrotfish on benthic structure and function, we further considered parrotfish bite rates by species identity, life phase and size. Relationships between parrotfish grazing rates and benthic and fish community structure were explored for 2015 survey sites as well as in the context of Bonaire-wide averages since 2003. Parrotfish are the dominant grazers on Bonaire reefs. Since the 2010 bleaching event, parrotfish grazing rates have closely tracked macroalgal abundance and varied inversely with coral abundance. The continued decline in parrotfish grazing rates and macroalgal abundance from 2011 to 2015 suggests that, in the context of stable scarid biomass and density and increasing coral cover, parrotfish grazing may be limited by the abundance of macroalgae on Bonaire's reefs and/or that grazing intensity may be diluted across increased grazeable substrate. These scenarios are not mutually exclusive and both reinforce the significance of herbivorous fish, particularly parrotfish, in the resilience of the Bonaire reefs in response to disturbance.

### Introduction

Coral reefs are ecologically and economically valuable resources that provide important services to tropical countries. Local human populations depend on coral reefs for food and protection from storms. However, increased human exploitation of reefs, particularly in the Caribbean, has contributed to a general decline of coral reef health. This decline has resulted from a number of interacting stressors, many of which in turn compromise the recovery potential of Caribbean reefs (Jackson et al. 2014). The extent of degradation is not uniform across the region, and Bonaire's reefs have persisted as examples of comparative resilience in the Caribbean.

The Caribbean-wide decline in coral reef health over the last four decades has resulted from disturbances such as storm and bleaching events, as well as increased fishing pressure and the mass die-off of the herbivorous urchin *Diadema antillarum* in 1983 (Jackson et al. 2014). Herbivores greatly enhance the resilience of reef systems by facilitating coral recovery following disturbance (Adam et al. 2011, Gilmour et al. 2013). By consuming algae, herbivores maintain low algal cover and canopy height and inhibit the establishment of fleshy macroalgae, thereby promoting coral recruitment post-disturbance (Mumby and Steneck 2008). Declines in herbivore

abundance, as well as the loss of structurally complex *Acropora* corals due to disease (Bythell and Sheppard 1993), have therefore likely contributed to the decline of Caribbean reefs and their lack of recovery (Hughes et al. 2010). With increased exploitation of herbivores, many degraded Caribbean reefs have undergone a marked phase shift to an algal-dominated state (Mumby et al. 2007).

In contrast to the phase shifts seen throughout much of the Caribbean, Bonaire's reefs have remained coral dominated and have, thus far, resisted such a shift. By way of progressive fisheries management policies (such as the banning of spear fishing in 1971 and the harvest of parrotfish in 2010), Bonaire's herbivorous fish populations are thriving compared to the rest of the Caribbean (Kramer 2003). This unusually high abundance of herbivores likely underpins the observed resilience of Bonaire's reefs (Mumby and Steneck 2008, Hughes et al. 2010). Monitoring trends in herbivore community structure and function should therefore increase our understanding of how these reefs have resisted a phase shift to macroalgae.

Here, we assessed rates of herbivory at 11 sites on the leeward shore of Bonaire, many of which have been continuously monitored since 2003. We compared grazing rates among sites and as a function of herbivore functional group, parrotfish demography, and whether sites were fished (Control sites) or protected from fishing since 2008 (FPA sites). Furthermore, we evaluated how the Bonaire-wide average herbivory rate has changed through time.

## Methods

### *Study sites and survey design*

Bite rates of herbivorous fish were quantified between March 8<sup>th</sup> and 13<sup>th</sup> at 11 sites located on the leeward shore of Bonaire, Dutch Caribbean. These sites are part of an ongoing monitoring initiative. Monitoring at six sites began in 2003 (south to north: Windsock, 18<sup>th</sup> Palm, Forest on Klein Bonaire, Reef Scientifico, Barcadera and Karpata). After the Bonaire government and STINAPA established Fish Protected Areas (FPAs) in 2008, four additional sites were added to the monitoring program in 2009 (south to north: Bachelor's Beach, Calabas, Front Porch and Oil Slick) to assess the potential ecological and fisheries benefits of fish protection. Finally, a monitoring site at the No Dive Reserve was added in 2011 to monitor recovery from the bleaching event that occurred in 2010. With four monitoring sites located within FPAs (south to north: 18<sup>th</sup> Palm, Calabas, Front Porch and Reef Scientifico) and seven at non-FPA sites serving as controls (south to north: Bachelor's Beach, Windsock, Forest on Klein Bonaire, Oil Slick, Barcadera, Karpata and the No Dive Reserve), comparisons can be made between the sites with fishing restrictions in place and those without.

At each site, bite rates of parrotfishes, tangs, and damselfishes (Scaridae, Acanthuridae, Pomacentridae, respectively) were evaluated in replicate 1 m<sup>2</sup> areas that: (1) occurred on a topographic high point of the reef (average relief of 1 m, min 0.45 m, max 2.50 m), (2) were comprised of  $\leq 30\%$  live coral cover and (3) occurred at 8 m water depth (min 5 m, max 11 m). Prior to counting bite rates, benthic cover (% cover of stony coral, sponges and gorgonians, crustose coralline algae, turf algae and macroalgae, as well as turf and macroalgal canopy heights) within each 1 m<sup>2</sup> area was recorded. The depth and relief of each observation station, as well as whether territorial damselfish were present, were also recorded.

Surveys were conducted between 0800 and 1600 hr. Bites were observed and recorded at a distance of approximately 5 m from the topographic high. Rates were recorded over a 5-minute period. During this time, we recorded the species, life phase and size (to the nearest cm) of each herbivore that entered the 1m<sup>2</sup> area, as well as the number of bites it took from the substrate. 5-8 surveys were conducted per site, with 17 at Calabas (as a result of multiple dives at this site).

### *Analysis*

Average bite rates for each site were determined for each herbivore functional group (scraper/excavator, denuder, and non-denuder). Because parrotfish are known to have a disproportionately important impact on benthic structure and function, we also analyzed parrotfish bite rates at each site as function of their species identity, life phase and size. Bite rates in each of the above categories were also pooled across sites that were either fished (Control sites) or protected from fishing (FPA sites) and their averages were compared.

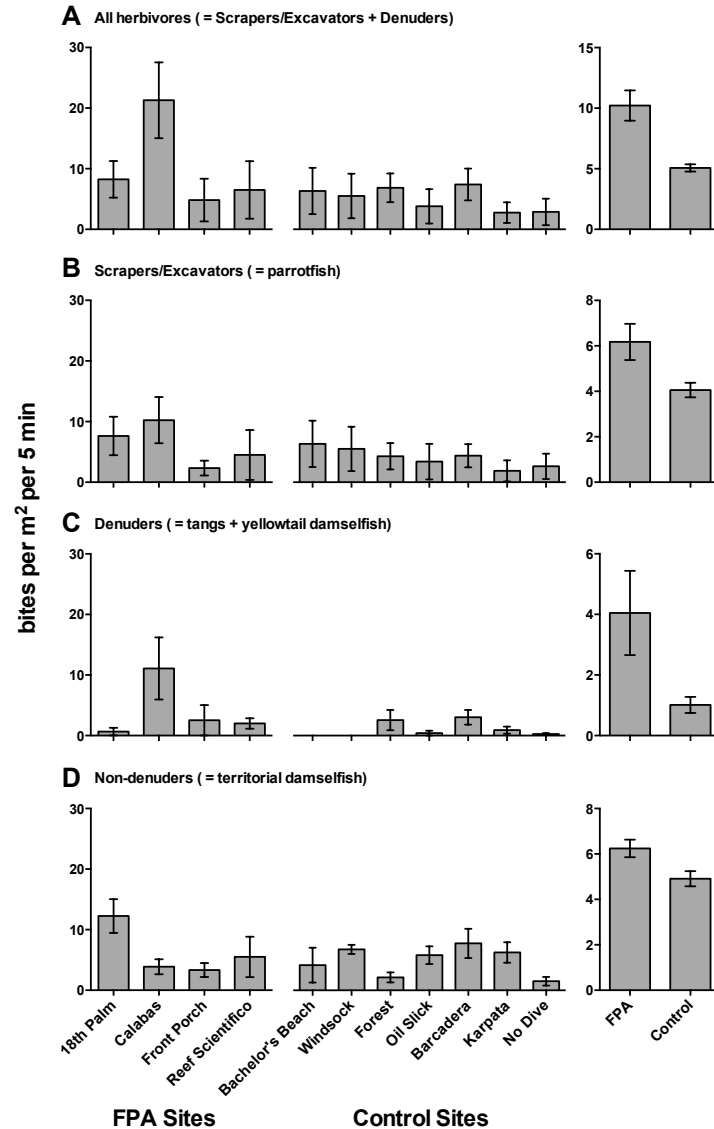
We plotted the relationship between scarid bite rate and scarid abundance (density and biomass) across sites, to look for broad scale relationships between these parameters. Additionally scarid bite rates were also considered in the context macroalgal index (the product of macroalgal cover and canopy height) and coral and sponge cover for each quadrat monitored to examine potential links between benthic composition and foraging behavior.

Finally, the Bonaire-wide average scarid bite rate was determined using only data from the six sites monitored since 2003. We explored the relationship between this long-term trend and trends in scarid abundance, coral abundance and macroalgal abundance since 2003.

## **Results**

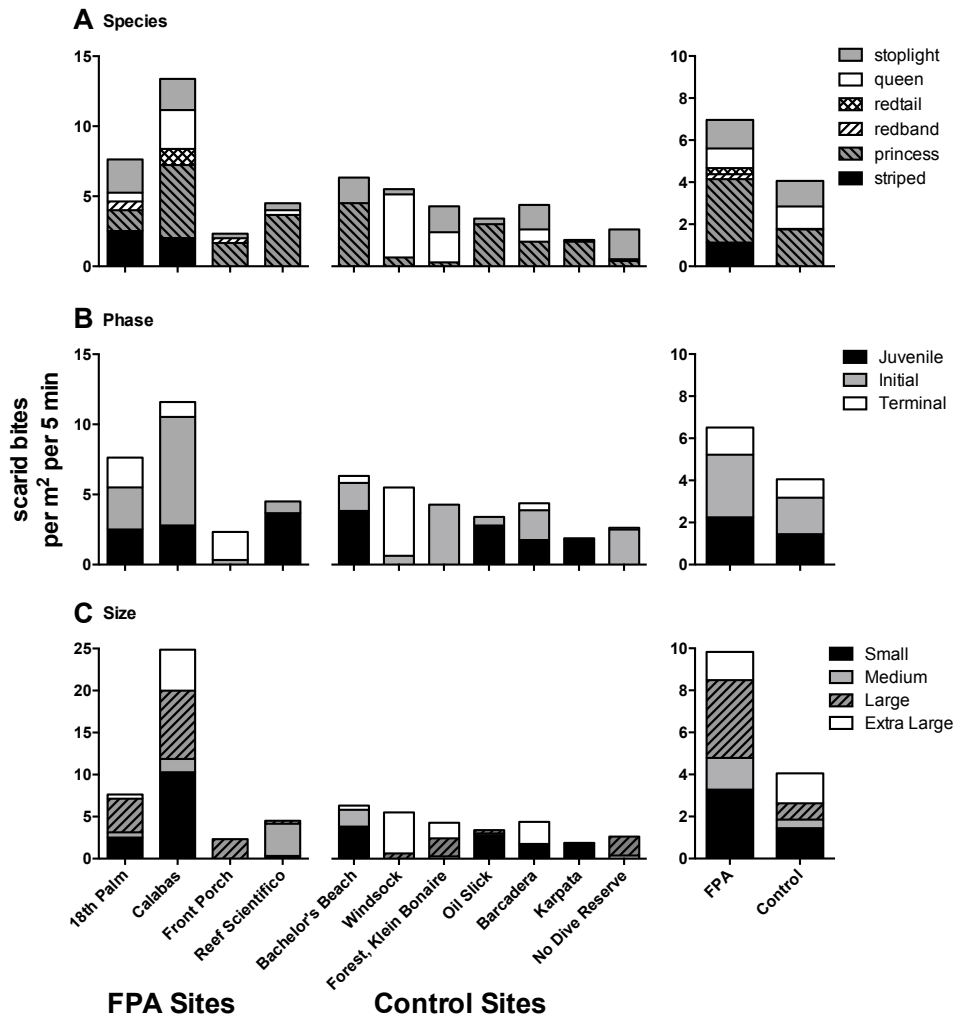
### *Herbivory Rates: FPA effects and spatial variability*

Overall, rates of herbivory were greater at FPA sites than at control sites (Fig. 1). Bite rates for all herbivores (scrapers/excavators and denuders) were two times greater at FPA than control sites. Scrapers/excavators (parrotfish) grazed most frequently and their average bite rates were roughly 30% greater at FPA than control sites. Denuders (tang and yellowtail damselfish) grazed the least frequently among functional groups, yet their average bite rates differed the most and were four times greater at FPA sites. Average bite rates of non-denuders (territorial damselfish) differed least between FPAs and controls, with an average of nearly 25% greater at FPA than control sites.



**Figure 1:** Bite rates (average  $\pm$  SE: bites per  $m^2$  per 5 min) of A) all herbivores, B) scrapers/excavators (parrotfish), C) denuders (tangs + yellowtail damselfish) and D) non-denuders (territorial damselfish) at 11 sites in Bonaire. Bars are clustered by sites designated as no-take fish protection areas (FPA sites) and those open to fishing (control sites). Within each designation, sites are arranged south to north;  $n = 5-8$  replicate surveys per site, except Calabas where  $n = 17$ .

The dominant grazers were parrotfish (Fig. 1); therefore, we further examined scarid grazing rates as a function species identity, life phase and size (Fig. 2). Princess, stoplight and queen parrotfish exhibited the highest bite rates at control sites whereas princess, stoplight and striped parrotfish bite rates were highest at FPA sites. Grazing rates of initial phase parrotfish were only slightly higher than those of juvenile and both were higher than those of terminal phase fish at FPAs and control sites. Small, medium and large parrotfish grazing rates were higher at FPA sites, while extra large parrotfish ( $>30$  cm) rates were similar among site types.



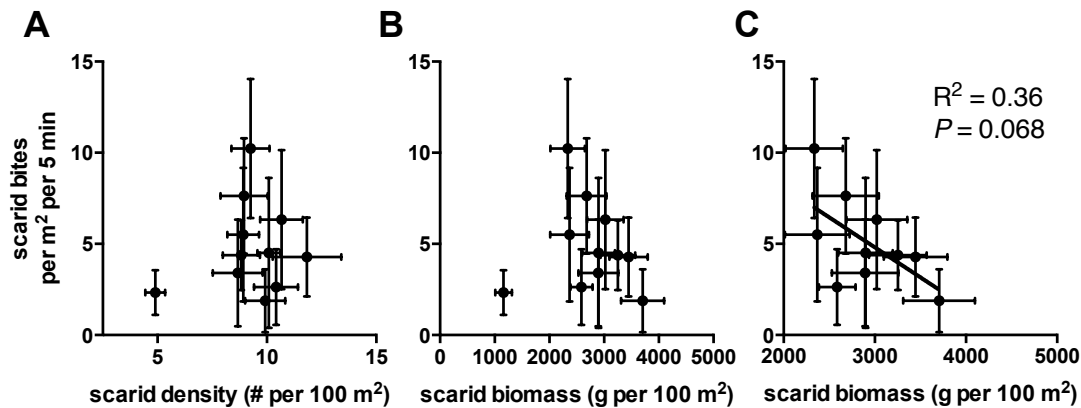
**Figure 2:** Parrotfish bite rates (average bites per m<sup>2</sup> per 5 min) by A) species, B) life phase and C) size class. Size classes are small (<13 cm), medium (13-20 cm), large (21-30 cm) and extra large (>30 cm). Average bite rates are stacked within each bar, with a legend in each table. Error bars are omitted to allow for clearer interpretation. See Figure 1 for site descriptions and graph format.

#### *Scarid herbivory in relation to fish community structure and benthic composition*

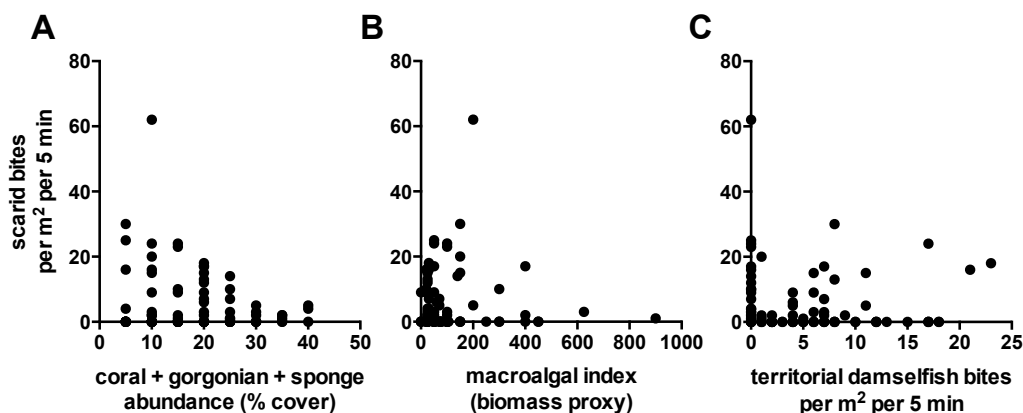
There was no significant relationship between parrotfish bite rate and parrotfish density or biomass (Fig. 3 A and B). However when Front Porch was discounted from the analysis due to its uniquely low herbivore abundance, a marginally significant, negative relationship between grazing rate and biomass emerged (Fig. 3C).

Scarid bite rates declined with increasing stony coral, gorgonian and sponge cover and increased with increasing macroalgal abundance (Fig. 4). While average scarid bite rates appeared to decline with increasing average territorial damselfish bites (Fig. 4C), this trend was somewhat less pronounced. In all three panels, the outlier datum (scarid grazing rate = 62 bites m<sup>-2</sup> per 5

min) represents a plot at Calabas (an FPA site) that was intensely grazed by juvenile and initial phase princess and striped parrotfish.



**Figure 3:** Relationship between scarid bite rate (average: bites per m<sup>2</sup> per 5 min) and A) scarid density (# per 100 m<sup>2</sup>), B) scarid biomass (g per 100 m<sup>2</sup>) and C) scarid biomass (g per 100m<sup>2</sup>) excluding data from Front Porch. Points represent the average ( $\pm$  SE) from 11 study sites in Bonaire.

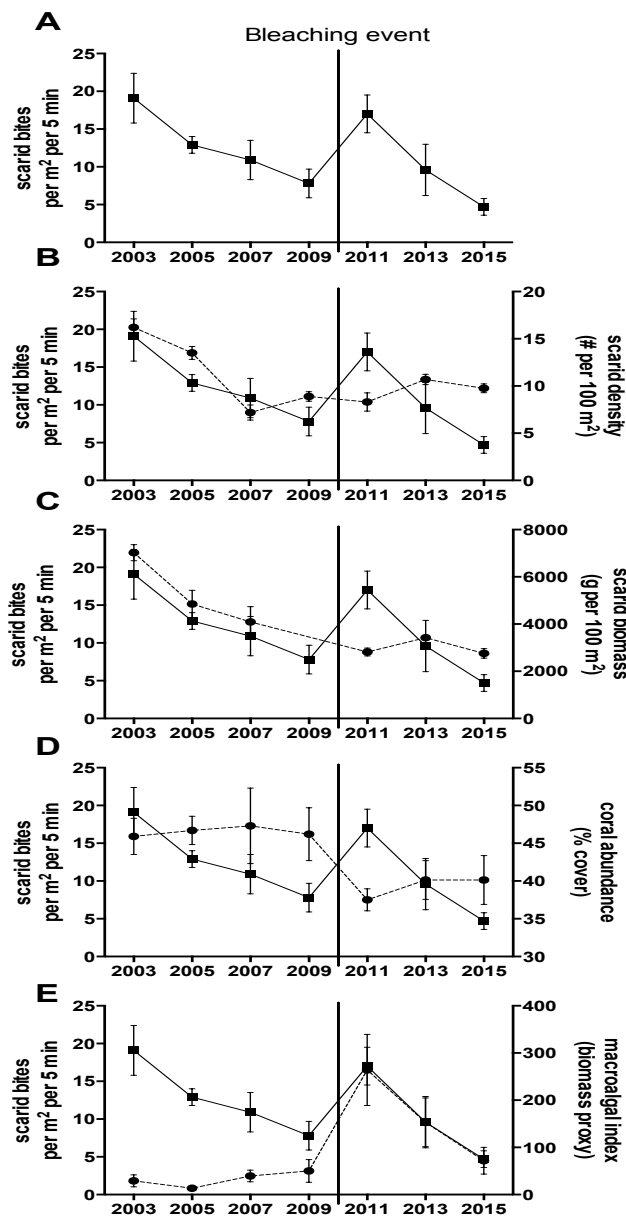


**Figure 4:** Relationship between scarid bite rate (average: bites per m<sup>2</sup> per 5 min) and A) coral, gorgonian sponge abundance (% cover), B) macroalgal index (biomass proxy) and C) territorial damselfish bite rates (average  $\pm$  SE: bites m<sup>-2</sup> 5 min<sup>-1</sup>) within 1 m<sup>2</sup> areas surveyed at 11 study sites in Bonaire. n = 87.

#### *Long-term herbivory trends and community dynamics*

The 2015 Bonaire-wide herbivory rate was 4.71 ( $\pm 1.1$ ) bites per m<sup>2</sup> per 5 minutes (Fig. 5A). It is the lowest herbivory rate recorded since 2003 and represents a continuation of the negative trend in herbivory since 2003, with the exception of a markedly high rate in 2011. The decline in herbivory from 2003-2007 corresponded with a modest decline in scarid density and biomass over that period, whereas the recent decline (2011-2015) in herbivory is characterized by a relatively constant scarid density and biomass (Fig. 5B and 5C). This lack of a clear relationship between herbivory and scarid population dynamics suggests that other factors have been at play. The dramatic increase in herbivory from 2009-2011 coincided with a notable decrease in coral abundance owing to the 2010 bleaching event (Fig. 5C), as well as a marked increase in macroalgal biomass (Fig. 5D). By 2013, grazing rates returned to pre-disturbance levels, macroalgal biomass declined markedly and coral abundance appeared to be stabilizing. From 2013-2015, herbivory rates continued to decline in concert with a decline in macroalgal biomass,

and coral abundance slightly increased. The timing of such changes to herbivory rates is suggestive of an herbivore functional response to the 2010 disturbance.



**Figure 5:** Bonaire-wide scarid herbivory trends from 2003-2015 represented A) alone, B) with scarid density (# per 100 m<sup>2</sup>), C) with scarid biomass (g per 100 m<sup>2</sup>), with D) coral abundance (% cover) and E) with macroalgal index (biomass proxy). Averages ( $\pm$  SE) were calculated using data from only the six sites that have been monitored since 2003. Bite rates are plotted as squares with solid lines (scale on left Y axis) whereas other data are plotted as circles with dotted lines (scale on right Y axis). A solid vertical line represents the 2010 bleaching event.

## Discussion

The relatively high abundance of herbivorous fish on Bonaire's reefs has greatly contributed to their resilience to disturbance by reducing macroalgal cover through grazing and facilitating coral recruitment (Arnold et al. 2010). The negative trend in scarid bite rates recorded from

2011-2015 closely tracks availability of macroalgae on reefs during that period and illustrates a functional response of parrotfish to the 2010 bleaching event. Parrotfish continue to be the primary grazers on Bonaire reefs (Fig. 1), reinforcing their functional significance as effective scrapers/excavators (*Scarus* spp.) or browsers (*Sparisoma* spp.) that remove macroalgae from the substrate. Parrotfish are widely recognized for their ability to crop and maintain low macroalgal cover and thereby facilitate coral recruitment (Adam et al. 2011, Arnold et al. 2010).

Grazing rates for all functional groups were consistently greater within FPAs than at control sites (Fig. 1), which corresponded with, on average, greater algal abundance at FPA than control sites (Steneck, this volume). Scarids were responsible for the majority of the grazing (by species, largely princess and stoplight; by life phase, largely juvenile and initial) and grazed at greater rates within FPAs than at controls. This was not a function of greater scarid biomass or density at these sites as these parameters were lower at FPA sites than at control sites (Arnold, this volume). Furthermore, the relationships between grazing rate and scarid biomass and density were not significant, underpinning that scarid grazing rates are not a direct result of fish biomass or density. Thus, higher grazing rates within FPAs are likely a result of the greater availability of food resources that require cropping.

Grazing rates of territorial damselfish were comparable to those of parrotfish. The presence of non-denuding territorial damselfish is known to discourage parrotfish grazing (Hixon 1997). This trend is evident in this study (Fig. 4C), as scarid grazing rates are, for the most part, low when damselfish grazing rates are high. However, roughly a quarter of the survey sites displayed simultaneous grazing of parrotfish and damselfish. Closer examination of the sites for which greatest scarid and territorial damselfish grazing rates were measured revealed that, in most instances, the grazing scarids were large or extra large in size. Perhaps large terminal phase parrotfish can overwhelm damselfish aggression and gain access to damselfish-farmed turfs. During observation periods, two or three scarids would graze, with varying intensity, in the presence of a longfin damselfish. These observations may help explain the simultaneous grazing observed at some sites, and further reinforce the concept that large parrotfish are disproportionately important grazers, capable of removing larger volumes of macroalgae from the substrate (Lokrantz et al. 2008, Steneck et al. 2014).

Herbivory rates, while inherently dependent on population density and biomass on some level, are directly related to benthic composition and the amount of open substrate present. This is particularly evident in the Bonaire-wide long-term scarid herbivory trend (Fig. 5), in which bite rates correspond positively with macroalgal abundance (a grazeable substrate) and negatively to coral abundance (which is inversely related to the abundance of algal turfs, a preferred food). This finding is unusual in that bite rates typically do not correspond with algal abundance (Steneck et al. 2014). This trend is also evident at some individual sites. For example, the highest scarid grazing rates measured in this study were at Calabas  $10.2 \pm 3.8$  bites per  $m^2$  per 5 min), which was the site with the highest macroalgal abundance measured ( $628.1 \pm 56.7$  macroalgal index) (Steneck, this volume).

In general, scarid herbivory rates track macroalgal and coral abundance in space and time, particularly in response to the November 2010 bleaching event. Following this disturbance, coral mortality promoted both algal growth and herbivore grazing. Since 2013, bite rates and



macroalgal cover have decreased in concert while coral cover has increased, indicative of a functional response among herbivores and of a resilient Caribbean reef ecosystem.

While the exact mechanism driving the functional response is not known, several possible explanations exist. One such explanation is that the very high abundance of herbivores in the reef system has led to food limitation, and thus the sudden increase in food resources (turfs and macroalgae) in 2011 led to a decrease in interspecific competition for food and a rapid increase in bite rates post-disturbance. In this scenario, herbivores sufficiently controlled macroalgal growth and prevented its proliferation. Once macroalgal cover was suppressed by herbivores and coral cover began to recover in 2011-2013 (reducing grazeable substrate), food resources again became limited. Despite relatively constant scarid biomass and density from 2011-2015 (Arnold, this volume), intense competition for food resources would have resumed and bite rates would have declined from 2012-2015. A marginally significant inverse relationship between scarid bite rates and biomass today (Fig. 3C) is suggestive of intraspecific competition between parrotfish restricting bite rates. When present in higher densities, such as is the case on Bonaire's reefs, intraspecific competition increases, particularly as food is a defended resource (Mumby and Wabnitz, 2002).

A second explanation for declining bite rates relates to changes in the availability of grazeable substrate on Bonaire's reefs. Coral abundance has increased slightly since the 2010 bleaching event but may have stabilized at a new, lower level. This has resulted in an overall increase of grazeable substrate on Bonaire reefs. If scarids effectively graze and maintain low macroalgal canopy heights, and macroalgal abundance decreases, the decline in grazing rates could be a result of dilution of grazing intensity over a greater grazeable area. Relatively constant scarid biomass and density since the 2010 bleaching event may have allowed grazing rates to reach a maximum given the population size, yet grazeable substrate has increased. Thus, as bite rates are distributed over a larger area, grazing intensity has been effectively diluted (Mumby et al. 2007). The two proposed explanations need not be mutually exclusive, and could together account for the spike and subsequent decline of bite rates since the 2010 bleaching event.

This study quantified herbivory rates exclusively on topographic highs. There is generally little macroalgae at our study sites, but that which is present is confined primarily to topographic low points. Thus, it is likely that grazing rates on topographic lows differ from those observed at topographic highs, and the two likely interact. Therefore, reef complexity and topography may have an important effect on herbivory.

Relatively abundant herbivore populations, low macroalgal abundance and high coral abundance characterize Bonaire's reefs. They remain resilient in the wake of the 2010 bleaching event, effectively resisting a phase shift to macroalgae. The functional response of the herbivorous fish populations to the 2010 disturbance may have played a large role in this display of resilience. Herbivores have apparently continued to drive down macroalgal abundance on the reefs from 2013-2015, despite an apparent decline in bite rates.

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## **Chapter 8: ‘Quick scan’ to assess the prevalence of dermal parasites among coral reef fishes of Bonaire.**

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### **Abstract**

In the past decades infections and diseases have had significant impacts on coral reef ecosystems in the Caribbean. A recent study on Curaçao documented infection rates of dermal parasites (trematodes, turbellarians and protozoans) on coral reef fishes, which were almost 10 times higher than on reef fish in Mexico and Belize. We used a "quick scan" protocol to determine the current prevalence of dermal parasites among the coral reef fish of Bonaire. Surveys were conducted at 17 different sites around the island resulting in the visual inspection of 16040 coral reef fish for the presence of dermal parasites. Not only was the number of infected coral reef fish species on Bonaire considerably higher than on Curaçao, Belize and Mexico but also the proportion of infected individuals for nearly all species was markedly higher on Bonaire than on Curaçao. The increased parasite rates could be correlated with water quality. However, the proper identification of the different parasites and the cause and effect of the extreme high prevalence of dermal parasites remains to be determined in future studies.

### **Introduction**

In the past, diseases and infections have had dramatic impacts on Caribbean coral reef ecosystems (e.g. white band disease in corals (Pantos and Bythell 2006); mass mortality of the sea urchin *Diadema* (Lessions 2005)). Regular monitoring of reef organisms for signs of disease and infections may be important as an “early warning system” to possibly prevent devastating outbreaks.

In September 2013 an unusual number of reef fish species (e.g. Scaridae (Fig. 1), Acanthuridae and Pomacanthidae) infected with dermal parasites were observed during a dive at Salt Pier (M. de Graaf, pers. obs.). In September 2014 one princess parrotfish infected with dermal parasites was dissected and internal and external samples were sent to the Central Veterinary Institute (CVO) in Lelystad (Netherlands) for further histopathological examination. According to CVO the parrotfish suffered from a microspore parasitic infection of the skin, muscles and digestive tract. The cysts caused fibrotic abscesses and necrosis on the fins.

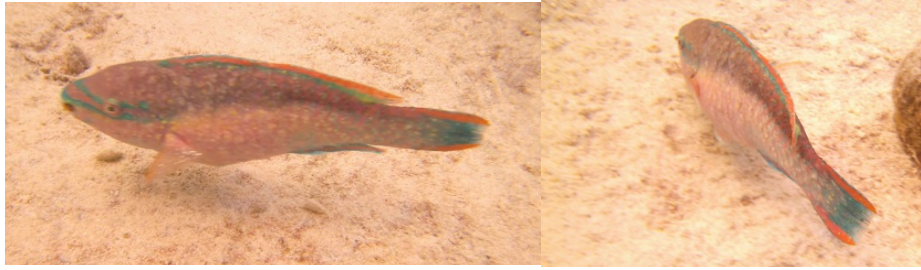


Figure 1. A princess parrotfish (*Scarus taeniopterus*) heavily infected with dermal parasites (Salt Pier, Bonaire, September 2013; photo's M. de Graaf).

Similar dermal parasites were observed in a recent survey of coral reef fishes on Curaçao and the observed external blemishes were associated with infections by trematodes (digenean metacercaria), turbellarians and protozoans (*Cryptocaryon*) (Bernal et al. 2015). Bernal et al. (2015) reported that infection rates of coral reef fish on Curacao were almost ten times higher compared to infection rates of coral reef fish surveyed in Mexico and Belize. To date, only anecdotal observations exist of parasite infections on coral reef fish on Bonaire but no quantitative assessment of the prevalence of dermal parasites is available.

The objective of the study was to:

- 1) conduct a “quick scan” to determine the current prevalence of dermal parasites among the coral reef fish of Bonaire, and
- 2) advise the Dutch Ministry of Economic Affairs on possible consequences and future actions depending on the outcome of the “quick scan”.

## Methods

On Bonaire visual surveys were conducted at 17 different sites (Fig. 2) between 7 and 16 March 2015. The selection of sites was largely based on the water quality study of Slijkerman et al. (2014), resulting in a selection of sites known to vary in water quality (e.g. City-Salt locations versus northern locations). Some sites were added to the ‘quick scan’ as a reference based on assumed good water quality (e.g. east coast with minimal human influence) or as additional sites potential eutrophic sites based on the presence of deep-water cyanobacterial mats (Salt Pier and Windsock; Becking & Meesters 2014). In general, the reef system on the west coast begins at the waterline and gently slopes down to 10 m depth from where the reef steeply drops to 30-40m (Bak, 1977). The study sites were located on the shallow plateau (back reef) between 1-5 m depth and at the top of the drop off between 10-15 m depth. Two divers swam (3-5m distance between the divers) for 30 minutes parallel to the coast at each of the two reef zones. During each survey both observers recorded the presence or absence of dermal parasites on 41 selected common reef fish species belonging to 16 families (see Table 1). For highly abundant species like brown chromis the presence of dermal parasites was recorded for a maximum of 50-75 individuals recorded in each reef zone. On the east coast the back reef at Lac Kai was surveyed by snorkel while the drop off reef zone was surveyed by SCUBA. Result of the ‘quick scan’ will be simply presented as infection rates per species, reef zone and/or geographical location.





species, dermal parasites were also observed incidentally on the sand tile fish (*Malacanthus plumieri*), palometa (*Trachinotus goodei*), sharpnose pufferfish (*Canthigaster rostrata*) and spotfin butterflyfish (*Chaetodon ocellatus*). Not only was the number of infected coral reef fish species on Bonaire considerably higher than on Curaçao, Belize and Mexico but also the proportion of infected individuals for nearly all species was markedly higher on Bonaire than on Curaçao (Fig. 1. Table 1).

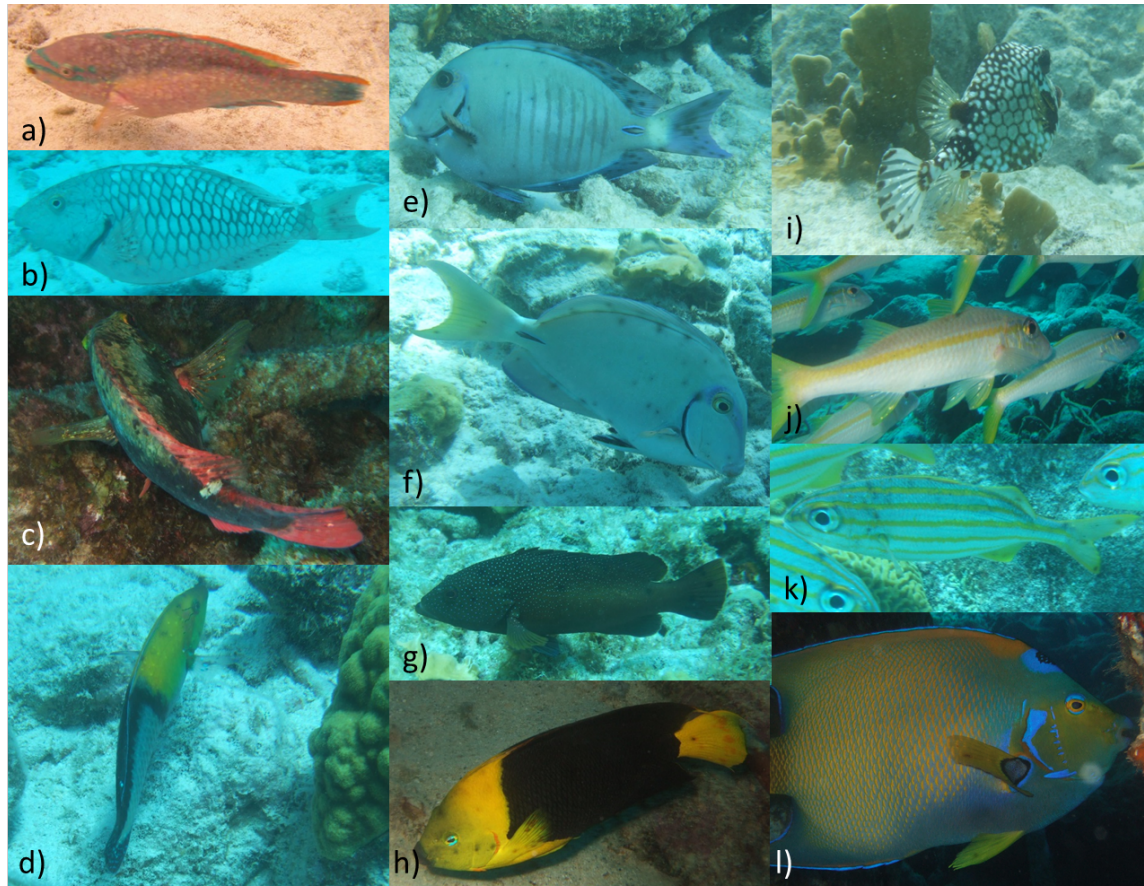


Figure 3. Examples of coral reef fish species infected with dermal parasites on Bonaire: a) *Scarus taeniopterus* (princess parrotfish), b) *Sparisoma viride* (stoplight parrotfish), c) *Sparisoma aurofrenatum* (redband parrotfish), d) *Halichoeres garnoti* (yellowhead wrasse), e) *Acanthurus chirurgus* (doctorfish), f) *Acanthurus tractus* (ocean surgeonfish), g) *Cephalopholis fulva* (coney), h) *Holacanthus tricolor* (rock beauty), i) *Lactophrys triqueter* (smooth trunkfish), j) *Mulloidichthys martinicus* (yellow goatfish), k) *Haemulon chrysargyreum* (smallmouth grunt) and l) *Holacanthus ciliaris* (queen angelfish). Photo's by Martin de Graaf.

#### *Spatial variation in infection rates*

Based on this 'quick scan' study, infection rates of dermal parasites seem to be different in the two reef zones (Fig. 2, left). The percentage of infected individuals of four abundant reef fish species and 'all fish pooled' appeared to be higher on the shallow back reef compared to the drop-off zone. A similar result was reported by Grutter (1998) for the blackedge thicklip wrasse, where infection rates were much higher on the shallow reef flat compared to the deeper reef slopes due to a higher abundance of parasitic (monogenean) eggs on reef flats.

Table 1 Observed dermal parasites infection rates among 13 species of coral reef fish on Bonaire and Curaçao (Bernal et al. 2015). More details in Appendix 8.

| Species   | Bonaire      |                 |                 | Curacao      |                 |                 |
|---|--------------|-----------------|-----------------|--------------|-----------------|-----------------|
|   | Total<br>(#) | Infected<br>(#) | Infected<br>(%) | Total<br>(#) | Infected<br>(#) | Infected<br>(%) |
| <i>Acanthurus coeruleus</i> (blue tang)             | 955          | 94              | <b>10</b>       | 241          | 17              | <b>7</b>        |
| <i>Acanthurus chirurgus</i> (doctorfish)            | 185          | 59              | <b>32</b>       | 52           | 6               | <b>12</b>       |
| <i>Acanthurus tractus</i> (ocean surgeonfish)       | 1266         | 720             | <b>57</b>       | 147          | 29              | <b>20</b>       |
| <i>Caranx ruber</i> (bar jack)                      | 231          | 40              | <b>17</b>       | 17           | 3               | <b>18</b>       |
| <i>Haemulon chrysargyreum</i> (smallmouth grunt)    | 1041         | 148             | <b>14</b>       | 151          | 2               | <b>1</b>        |
| <i>Halichoeres garnoti</i> (yellowhead wrasse male) | 110          | 7               | <b>6</b>        | 266          | 2               | <b>1</b>        |
| <i>Lutjanus apodus</i> (schoolmaster)               | 353          | 5               | <b>1</b>        | 36           | 1               | <b>3</b>        |
| <i>Cantherhines pullus</i> (orangespotted filefish) | 24           | 13              | <b>54</b>       | 11           | 2               | <b>18</b>       |
| <i>Mulloidichthys martinicus</i> (yellow goatfish)  | 1388         | 262             | <b>19</b>       | 27           | 6               | <b>2</b>        |
| <i>Lactophrys triqueter</i> (smooth trunkfish)      | 165          | 83              | <b>50</b>       | 20           | 1               | <b>5</b>        |
| <i>Sparisoma viride</i> (stoplight parrotfish)      | 707          | 58              | <b>8</b>        | 221          | 1               | <b>0.5</b>      |
| <i>Scarus iseri</i> (striped parrotfish)            | 223          | 12              | <b>5</b>        | 224          | 2               | <b>1</b>        |
| <i>Sparisoma rubripinne</i> (yellowtail parrotfish) | 156          | 19              | <b>12</b>       | 13           | 1               | <b>8</b>        |

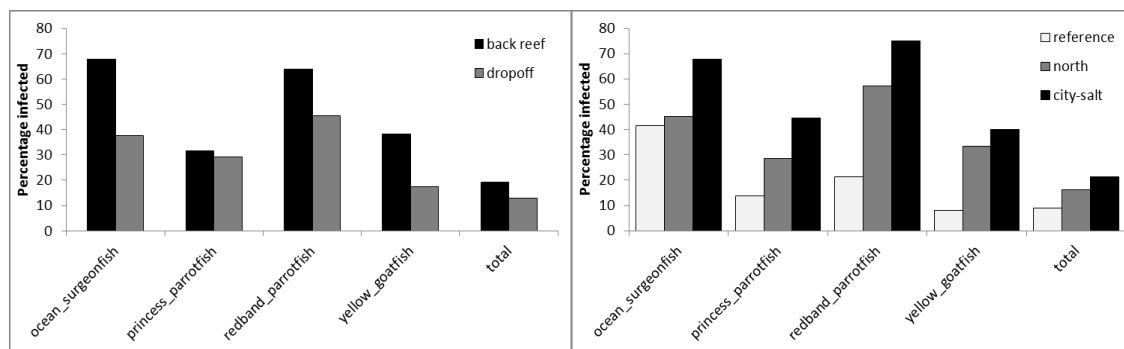


Figure 2. Trends in infection rates between reef zones (left) and among geographical areas (right).

In addition, infection rates of dermal parasites did not appear to be similar all over Bonaire (Fig. 2, right; Fig. 3). The highest infection rates of the four common reef fish species and “all fish pooled” seem to occur along the west coast between the Salt Pier (Cargill Salt Bonaire N.V.) and Kralendijk. The lowest infection rates were observed on reference study sites (Red slave in the south, the three sites on the east coast and the two sites on Klein Bonaire). The northern study sites (around BOPEC) showed intermediate infection rates.

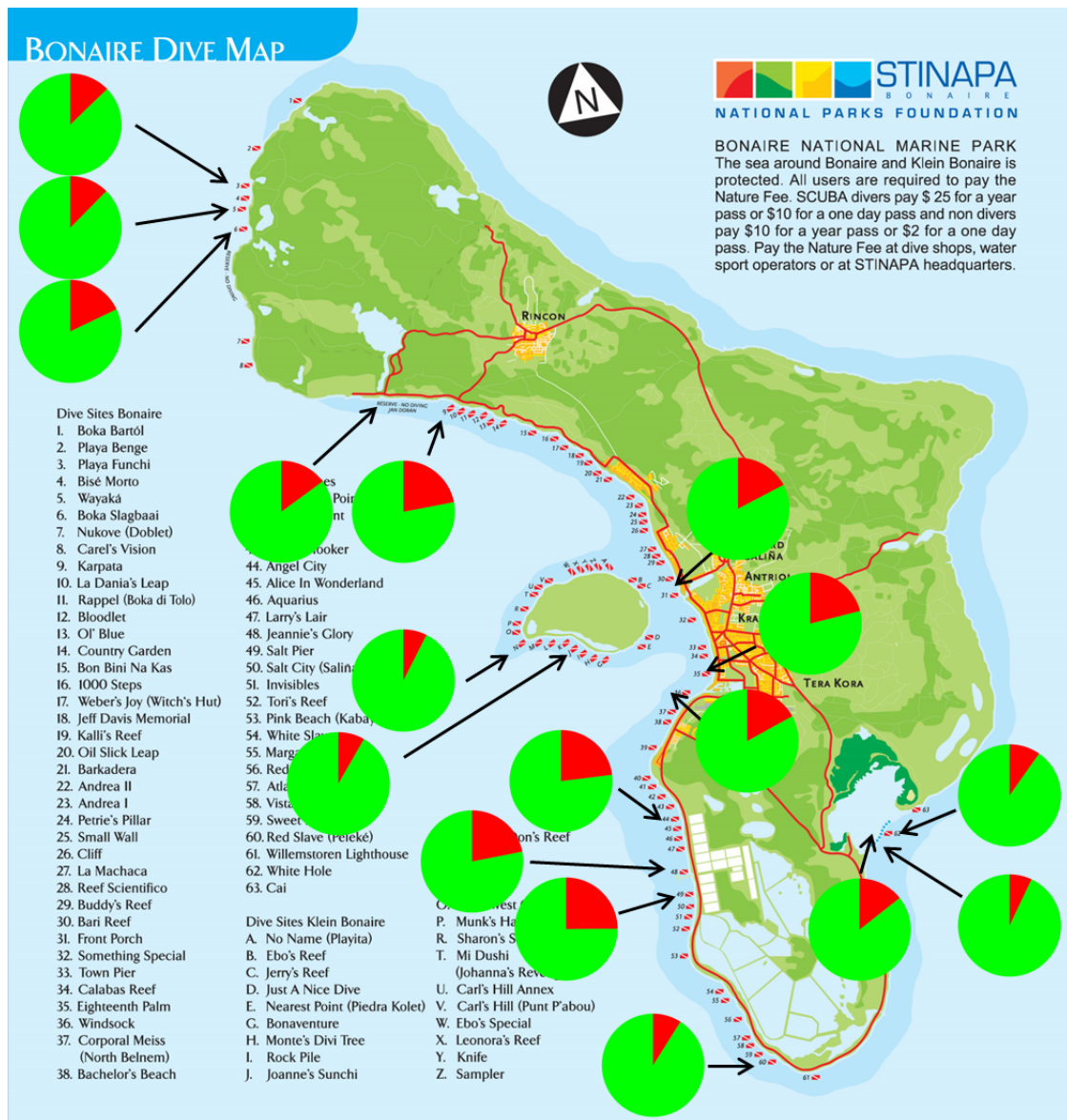


Figure 3. Spatial variation in dermal parasite infection rates among the 17 study sites.

### *Infection rates in an environmental context*

Increased parasite rates maybe correlated with water quality. The spatial differences in infection rates were roughly similar to the spatial differences in water quality reported by Slijkerman et al. (2014). Slijkerman et al. (2014) showed that threshold level for nitrogen were exceeded for urban and southern locations (i.e. ~City-Salt study sites), indicating eutrophic conditions, probably due to outflow of sewage water and to brine leaching into the sea from salt works.

A decline in environmental conditions (water quality) cause by wastewater or industrial pollutants can increase the prevalence of parasites in fish due to a diminished resistance to infections and decline in immunological defences (Sasal et al. 2007 and references therein).



In impoverished environments parasites with simple, single host life cycles (monoxenous) will proliferate. Monogenean parasites can be an indicator of water quality as these parasites are usually more abundant in eutrophic water (Valtonen et al. 1987) or other polluted areas (Skinner 1982). Lafferty (1997) reported a similar increase in digenean abundance with eutrophication. However, anthropogenic activities such as increased pollution or fishing pressure can also cause a decline in the abundance and prevalence of heteroxenous (multi-host complex life history) parasites due to a lack of intermediate hosts (Sasal 2007 and references therein; Lafferty 2008).

The identification of the dermal parasite(s), their associated life cycles and the possible causes and/or ecological consequences of the widespread and extremely high prevalence of dermal parasites was not part of the ‘quick scan’ study and remain unknown. Since 2003 regular fish surveys have been conducted at several sites along the west coast of Bonaire (Steneck et al. 2013). Future co-operation with the research team of Dr. B. Steneck (University of Maine, USA) during a potential follow-up project may enable us to analyse trends in density and abundance of several heavily infected herbivorous species (e.g. ocean surgeon fish, redband parrotfish and princess parrotfish) in the geographic zone zones.

#### *Recommendations for future research*

Based on the results of the ‘quick scan’, we advise to a stepped follow up on this study, focusing on the type of parasite(s) and possible factors influencing the infection rate. More specifically:

- collect infected coral reef fish to identify the dermal parasite species,
- determine the life cycle of the dermal parasite species, i.e. heteroxenous (complex, multi host life cycle) or monoxenous (simple single host life cycle),
- a detailed study in the spatial and temporal patterns in the occurrence of dermal parasites, and
- determine the cause and effect of the extreme high prevalence of dermal parasites, including co-factors steering the high infection rates.

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## **Chapter 9: Damselfish on the reefs of Bonaire**

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### **Abstract**

Territorial damselfishes are the most abundant fish recorded at 10 m depth on Bonaire's monitored reefs. Three-spot and longfin damselfishes are the functionally most important species because they maintain high algal biomass gardens. Population densities may result from the interplay of reef rugosity and predator abundance but more work must be done on that subject.

### **Introduction**

Territorial damselfish have been described as keystone species on coral reefs because of the great impact they have on other species of reef fishes (Hixon and Brostoff 1983). Specifically, their aggression keeps other herbivores from grazing the reef (Vermeij et al 2015). The build up of algae can result in reduced coral recruitment (Arnold et al 2010) and mortality of adult corals (Vermeij et al 2015).

Here we briefly describe the patterns of distribution, abundance and species composition of damselfish on 11 monitored coral reefs in Bonaire. The dominant damselfish are distributed among four species in three functional groups. The strongest territory-holding aggressive species at 10 m survey depths are longfin and 3-spot damselfishes. They actively chase all potential competitors from their territories and typically create patches that have elevated algal biomass in their territory. The yellow-tail damselfish are less territorial but they are large and feed repeatedly in the space they occupy. Usually benthic algal biomass is lower in their territory. The third functional group is the bicolor damselfish which is a planktivore. They maintain a home range but are not aggressively territorial.

### **Results and Discussion:**

As a group, damselfish are the most abundant fish on Bonaire's coral reefs. On some reefs the group exceeds an average of 1.4 fish per square meter (Fig. 1).

By far the bicolor damsel is most abundant (Fig. 1). However, its impact on other reef fish is modest. The longfin damsel is most often most abundant (Fig. 1) however on some reefs the threespot exceeds longfin.

Among the monitored site, the lowest damselfish density was recorded at Front Porch while Karpata, Reef Scientifico and 18<sup>th</sup> Palm had the highest densities. We could find no single correlate to account for the pattern observed this year. It may be significant that a very low density of juvenile damselfish were recorded this year (see Appendix 9) so it is possible that the density is heavily driven by patterns of recruitment which are highly variable from year to year and from site to site.

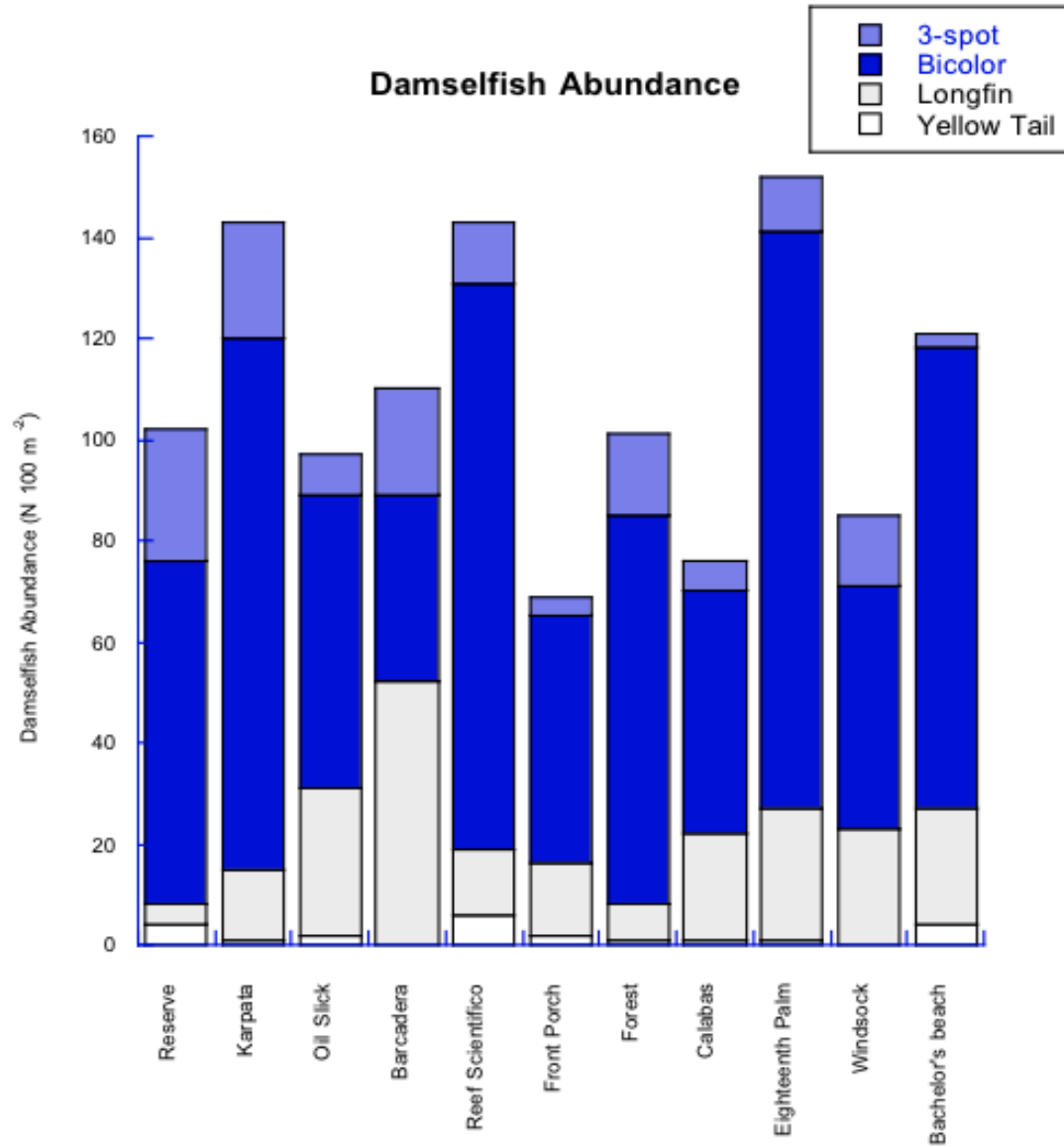


Fig. 1. Damselfish abundance (number per 100 m<sup>2</sup>), for all monitored reefs. The long-fin and 3-spot damselfish are the strongest interacting (most aggressive) of the four pomacentrids quantified.

In 2013 we found an inverse relationship between damselfish predators and damselfish but that pattern was not significant this year. Temporal trends reveal no consistent pattern for the highly aggressive three spot and longfin damselfishes (Fig. 2). Invariably the highest density of those damselfish species was recorded in 2011 however we suspect that pattern may be the result of computational differences (unresolved at present).

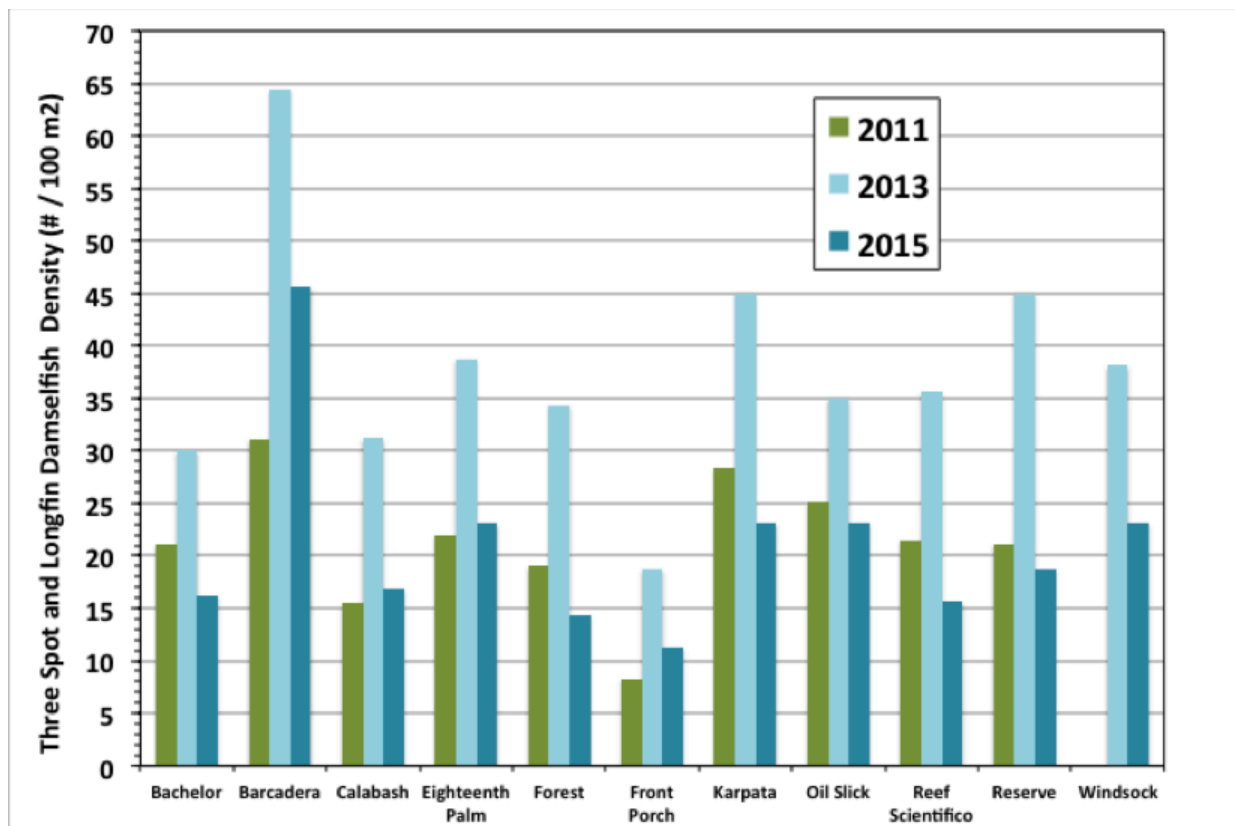


Fig. 2. Temporal trends of three-spot and longfin damselfishes from 2011 to 2015 at the 11 monitored reef sites.

Nevertheless, Front Porch consistently had the lowest density of highly aggressive damselfishes. The highest densities over the three years were distributed broadly from the highest to lowest density as follows: Barcadera, Karpata, Windsock and 18<sup>th</sup> Palm (Fig. 2).

It is possible that different factors drive the damselfish abundances. Front Porch has the lowest rugosity of any of the monitored coral reefs (see Wilson; Chapter 6) whereas Barcadera and Windsock have above average rugosity (Chapter 6). However, sites such as Forest on Klein Bonaire have moderately high rugosity and high predator abundances (Camacho; Chapter 4). The chronically low density of territorial damselfishes at Front Porch may well be due to the high predator density at that FPA site (Chapter 4).

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