- of Bonaire in 2007 With-Results from Monitoring 2003 - 2007

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# A Report on the Status of the Coral Reefs of Bonaire in 2007 with Results from Monitoring 2003 – 2007

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# **Executive Summary:** Status and Trends of Bonaire's Reefs & Need for Immediate Action

Bob Steneck, Pete Mumby, and Suzanne Arnold

### Introduction

Bonaire's reefs remain among the best in the Caribbean. However, our monitoring has revealed some potentially troubling trends that may require management action.

In 2005, we reported to the Bonaire Marine National Park on the status of Bonaire's coral reefs, and we suggested a strategy for monitoring <u>trends</u> among four key reef attributes we believe track the health and resilience of Bonaire's reefs (Steneck and McClanahan 2005). Here we report the results of monitoring studies conducted 2003, 2005 and now 2007 at each site. Where appropriate, we drew from Bonaire's first AGRRA assessment conducted in February 1999 (Kramer and Bischof 2003) to extend temporal trends over a period of eight years.



**Figure 1.** Monitoring strategy and key results for Bonaire's reefs. Key monitoring variables (boldface) are coral cover, macroalgae abundance, herbivory and coral recruitment. Arrows on the left in indicate the direction of positive trends toward healthy reefs whereas arrows to the right indicate negative trends. The boxes around the arrows indicate significant trends since 2003. Superscripted numbers refer to chapters where the study can be found (ND means no data).

## **Troubling trends**

We see three troubling trends of increased macroalgae, declining herbivory from parrotfish, and increases in damselfish populations (See boxes in Fig. 1). Of these, the first two are most serious (see Chapters 1, 2 and 3). Secondary trends of concern, increases in damselfish populations (Chapter 4) and declines in coralline algae (Chapter 1), could lead to reduced recruitment of reef corals (Chapter 7), but to date this is not evident (Chapter 7). Importantly, coral cover remains relatively high (Chapter 1). The monitored group of carnivorous fishes, the lutjanid snappers, are holding constant but we remain concerned about the past (Steneck and McClanahan 2003) and continued loss of other larger bodied reef carnivores such as groupers and barracuda.

The positive ecological role of parrotfish is well documented (e.g. Mumby *et al.* 2006) so their decline is troubling. It is unclear exactly why their population densities are declining. While parrotfish are not currently a widely sought group of reef fish (Chapter 8), fishing pressure on them is growing. It is possible they are vulnerable to even modest fishing pressure, particularly from fish traps. <u>Accordingly, we recommend that the capture and killing of parrotfish be stopped</u> because of their key ecological role on Bonaire's coral reefs. Further, other groups of grazing herbivores such as the long-spined sea urchin (*Diadema antillarum*) are increasing but too slowly to effectively replace the functional role of parrotfish (Chapter 1).

We suggest continued monitoring of key drivers of reef health (coral cover, algal abundance, herbivory and coral recruitment; Fig. 1). Some standard protocols such as the Atlantic and Gulf Rapid Reef Assessment (AGRRA) are entirely commensurable with the data presented in our reports in 2003, 2005 and 2007 (this report). A streamlined monitoring protocol is likely to be most useful to managers to alert them as a potential problem is growing and, perhaps more importantly, to show improvement when it occurs.

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# **Chapter 1: Trends in the abundance of corals, coralline algae and sea urchins 1999 – 2007 on Bonaire's monitored coral reefs**

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# Abstract

The abundance of live coral, coralline algae and sea urchins was monitored over the past eight years (1999 – 2007) at six reef sites in 10 m of water in Bonaire. The pooled results from all sites recorded remarkably little change in live coral cover remains constant averaging 47% from 1999 to 2007. In contrast, coralline algal abundance declined an order of magnitude from over 20% in 1999 to below 4% in 2007. The grazing sea urchin, *Diadema antillarum* increased during the monitored interval. None were recorded in 1999 but by 2007 they were recorded at five of the six monitored reefs and have reached an average abundance of about 0.3/ 200 m<sup>2</sup>. This is three orders of magnitude below the functional population density needed to graze the reefs (minimally between 1 and  $2/m^2$ ). The decline in coralline abundance and the increase in macroalgal abundance (Olsen and Steneck , *this report*) may be the result of the decline in parrotfish abundance (Alvarado, Mumby , and Steneck , *this report*). These trends are all cause for concern.

## Introduction

Here I report on only three aspects of Bonaire's coral reefs: 1) coral abundance, 2) coralline abundance and 3) Diadema abundance. The very important benthic component of macroalgae is found in the chapter by Olson and Steneck in this Report.

To extend our time trends, we drew from the Atlantic and Gulf Reef Rapid Assessment (AGGRA) data (Kramer 2003) because AGRRA methods are commensurable with those used for this monitoring project (see Steneck and McClanahan 2005).

# Methods

The distribution and abundances of major reef-occupying groups such as stony coral, gorgonians, sponges and algae were quantified using 10 m long line transects placed on reefs (methods of Benayahu and Loya 1977, Kramer 2004) at 10 m depth at each of our six monitoring sites (see Executive Summary). Algae were subdivided into functionally important groups (see Steneck and Dethier 1994) such as crustose coralline, articulated coralline, foliaceous macroalgae (hereafter: "macroalgae") and noncoralline crusts. The macroalgal results are reported elsewhere (Olsen and Steneck chapter, *this report*). Transect methods used were modified from the AGGRA protocol (Steneck *et al.* 2003). Specifically, we measured the number of cm occupied by each organism group and all coral species along each transect. We quantified five transects per reef site.

### Results

Coral cover has remained remarkably constant since 1999 (Figure 1). The average coral cover of nearly 50% is considerably higher than the Caribbean wide average of nearly 10% (Gardner *et al.* 2003).



**Figure 1.** Percent coral cover based on multiple 10 m transects at fixed locations for 2003, 2005, and 2007. The 1999 data were from Kramer and Bischoff 2003 AGRRA results for our monitored reefs.

In contrast to coral abundance, coralline algal cover has declined nearly an order of magnitude from 22% cover in 1999 to 3.5% cover in 2007 (Figure 2). This could have implications to settling corals (Arnold, *this report*).



Figure 2. Percent cover of coralline algae. Data collected as described in Figure 1.

The abundance *Diadema antillarum* has increased from 0 in 1999 to  $0.3 / 200 \text{ m}^2$  in 2007 (Figure 3). Although this increase is real and reflects similar increases seen throughout the Caribbean, this population density is well below that needed to provide a reef-wide positive grazing impact. For example, about 1 - 17 *Diadema* /m<sup>2</sup> were common throughout the Caribbean prior to the *Diadema* die off in the early 1980s. Those population densities would translate to  $200 - 3,400 / 200 \text{ m}^2$  (the spatial units reported in Figure 3).



Figure 3. Population densities of *Diadema antillarum* at monitored reefs.

### Discussion

While coral cover has remained constant, the decline of coralline algae is cause for concern. Coralline abundance will reflect their rate of growth as well as the rates of grazing that keeps their surfaces free of algae (Steneck 1997). It is likely this decline is the result of one or both of those rates.

*Diadema antillarum* abundance is well below functional population densities. There is evidence from other studies that their recovery is greatest where predator abundances are lacking. While predatory fish are not lacking in Bonaire, their densities have declined in recent decades (see Steneck and McClanahan 2003). Therefore the presence of this urchin should not be taken necessarily as an indication of healthy reefs.

A more detailed discussion of what these trends might mean can be found in the Executive Summary.

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# Chapter 2: Trends in macroalgae abundance in Bonaire, 2003-2007

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### Abstract

Most Caribbean coral reefs have become macroalgae dominated reefs since the 1980s. Bonaire's coral reefs have been the exception with high live-coral cover (averaging nearly 50%) and little to no macroalgae abundance (averaging 5% or less). A large, healthy population of herbivores maintaining intense grazing pressure is proposed as the reason for the continued health of Bonaire's coral reefs. Our survey of Bonaire's coral reefs in March 2007 found a significant increase in the abundance of macroalgae (ANOVA:  $F_{2,15} = 3.93$ , P = 0.04) compared to abundances observed in 2003 and 2005.

### Introduction

Coral reefs throughout the Caribbean have experienced dramatic declines in live-coral cover over the past three decades (Hughes 1994; Edmunds & Carpenter 2001; Williams & Polunin 2001; Gardner et al. 2003; Kramer 2003; Bak et al. 2005; Aronson & Precht 2006; Idjadi et al. 2006; Lee 2006; Nugues & Bak 2006). Reefs once dominated by live coral now are principally dominated by species of macroalgae (i.e., large, fleshy seaweed). This transition of a reef from a coral-dominated system to one dominated by macroalgae is commonly called a "phase shift" (Hughes 1994; McManus et al. 2000; Edmunds & Carpenter 2001; Williams & Polunin 2001; Miller et al. 2003; Idjadi et al. 2006; Lee 2006). Such phase shifts reduce the resilience of the reef to biotic (e.g., disease) and abiotic (e.g., hurricanes) disturbances (Hughes & Connell 1999; Lugo et al. 2000; Diaz-Pulido & McCook 2003; Aronson & Precht 2006; Mumby 2006; Hughes et al. 2007). Resilience is the ability of a system, such as a coral reef, to withstand and recover from a perturbation (Birkeland 1997; Hughes & Connell 1999; Lugo et al. 2000; Lee 2006). Resilient reefs recover from natural disturbances, such as bleaching or hurricanes (Hughes 1994; Lugo et al. 2000; Idjadi et al. 2000; Idjadi et al. 2000; Idjadi et al. 2000; Idjadi et al. 2000; Lee 2006). Resilient reefs recover from natural disturbances, such as bleaching or hurricanes (Hughes 1994; Lugo et al. 2000; Idjadi et al. 2005).

While most reefs throughout the Caribbean experienced a phase-shift from coraldominated systems, with little macroalgae, to macroalgae-dominated systems, with little coral, during the 1980s-1990s, coral reefs in Bonaire remained dominated by live coral and little to no macroalgae (Hughes 1994, Steneck and Dethier 1994, Kramer 2003). The Atlantic and Gulf Rapid Reef Assessment (AGRRA) conducted between 1997 and 2000 (Kramer 2003) reported an average live-coral abundance of 46.5% at deep (>5 m) sites around Bonaire compared to an average live-coral abundance of 26% for the Caribbean; average macroalgae abundance at deep (>5 m) sites in the Caribbean was 23% compared to an average abundance of ~5% in Bonaire. Similar values of average macroalgae abundance were reported, respectively, for shallow ( $\leq 5$  m) sites. Subsequent reports conducted in Bonaire (Steneck and McClanahan 2003, 2005) had similar results. Specifically, past studies show that Bonaire's reefs have a low abundance of macroalgae for 2003 and 2005 (i.e., 5% and 2% respectively) and a relatively high live-coral cover, averaging 46% in 2003 and 47% in 2005.

A low abundance of macroalgae is essential for coral reef health as macroalgae, once sufficiently large, can smother adult corals by blocking out sunlight and out-compete coral polyps for available open space (Lirman 2001; Williams & Polunin 2001; Szmant 2002; Diaz-Pulido & McCook 2003; Aronson & Precht 2006; Mumby 2006; Nugues & Bak 2006). Therefore, the percent cover of macroalgae serves as a good indicator of coral reef health (Kramer 2003). Since macroalgae are a good indicator of coral reef health, monitoring macroalgae abundance is an important component of any reef monitoring program (Steneck & McClanahan 2005). In this study we report on the abundance and canopy height of macroalgae and its algal index (a proxy for algal biomass) at six reef sites on the west side of Bonaire. We compare these results with those taken in 2003 and 2005 at the same locations in order to determine if there are trends in abundance of harmful macroalgae. We also compare these results with those found throughout the Caribbean (Kramer 2003).

### Methods

The distribution and abundance of macroalgae, turf algae, and other reef-occupying groups (i.e., sponges, coralline algae, stony corals and gorgonians) were quantified using 10 m long-line transects at 10 m depth at each of six study sites: Windsock, Plaza, Forest (Klein Bonaire), Reef Scientifico, Barcadera, and Karpata. The number of centimeters occupied by each organism along each transect was recorded. Here we report only on macroalgae. Macroalgal biomass is a critical indicator of coral reef health and was calculated by the algal index method of Kramer (2003) as the product of percent cover multiplied by algal canopy height measured in millimeters. Four transects were quantified at each reef.

Statistical analysis of the data was conducted using the Excel Data Analysis program in Microsoft Office XP. Simple ANOVA (Analysis of Variance) was used to compare years for differences in algal abundance (measured as percent cover), canopy height (measured in millimeters (mm)), and algal index (i.e., a proxy for biomass, which is calculated by multiplying the percent cover x canopy height). A t-Test: Paired Two Samples for Means, with year as a fixed factor, was done when a significant difference was found with any ANOVA.

The data used in this report to create the figures and to calculate the percent cover, canopy height, and algal index for macroalgae on the Bonaire study sites for 2003, 2005, and 2007 were provided by Robert S. Steneck.

### Results

#### Macroalgal abundance

Macroalgae abundance was low on the six reefs we studied in terms of percent cover (Figure 1) and canopy height (Figure 2). The lowest macroalgae abundance was at the reef sites Forest (Klein Bonaire) and Windsock, and the greatest macroalgae abundance was at the reef sites Karpata and Plaza (Figure 1). There was a significant increase in the average abundance (measured as mean percent cover  $\pm$  standard error) of macroalgae on Bonaire's reefs in 2007 (ANOVA:  $F_{2,15} = 3.93$ , P = 0.04) compared to the average abundance observed in 2003 and 2005 (Figure 1). Results of t-Test: Paired Two Sample for Means on years: year 2007 had significantly greater macroalgae cover than 2003 (P = 0.04) and 2005 (P = 0.01). Average abundance of macroalgae increased at all sites, not just one or two. The 2007 average percent cover was approximately twice the 2003 average and four times the value recorded in 2005.





### Macroalgal Canopy

Average canopy height of macroalgae (Figure 2) was approximately 5.0 mm ( $\pm$  0.76 SE) in 2007 and was not significantly different than years 2003 or 2005 (ANOVA  $F_{2, 15}$ ; P = 0.76).



**Figure 2**. Canopy height of macroalgae (mean  $\pm$  standard error) at Bonaire study sites by year. Grand Total bars show approximate pooled (rounded) average of macroalgae canopy height at all six study sites by year:  $2003 \approx 4.0 \text{ mm}$ ,  $2005 \approx 4.0 \text{ mm}$ , and  $2007 \approx 5.0 \text{ mm}$ . Data is from the same source as Figure 1.

# Algal Index- Macroalgae

The algal index (Figure 3), as a proxy for the biomass of algae on the coral reefs in Bonaire, did not increase significantly in 2007 compared to 2003 and 2005 (ANOVA  $F_{2,15}$ ; P = 0.10). It was calculated as the product of the percent cover (Figure 1) by the canopy height (Figure 2). The approximate average algal index for Bonaire in 2007 was 39.2. This is slightly more than three times higher than the average algal index of 12.9 calculated by Steneck and McClanahan (2005), and the algal index of 12.0 calculated by Kramer (2003) during the 1997 – 2000 AGRRA.



**Figure 3.** Algal index of macroalgae on Bonaire study sites by year. Grand Total bars show approximate pooled (rounded) average macroalgae algal index by year:  $2003 \approx 16.6$ ;  $2005 \approx 12.9$ ;  $2007 \approx 39.2$ . Data is from the same source as Figure 1.

### Discussion

Macroalgae abundance on Bonaire's coral reefs in 2007 was significantly greater than it had been in 2003 and 2005 (Figure 1). At the same time, parrotfish biomass on Bonaire's coral reefs has declined (Alvarado 2007; this report). This result is troubling because the abundance of macroalgae on Bonaire's coral reefs has increased above values observed during the 1997-2000 Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program conducted across a spectrum of western Atlantic coral reefs - with a reported mean abundance of approximately 5% (Kramer 2003) and by Steneck and McClanahan (2003 and 2005) that had reported mean abundance of 5% and 2% respectively. Increased abundances of macroalgae can be an indicator of reef degradation (Steneck 1988; McManus 2000; Aronson & Precht 2006; Idjadi et al. 2006). While the mean abundance (percent cover) of 8% for Bonaire's reefs is well below the 23% mean abundance recorded for other Caribbean reefs (Kramer 2003) and is far from being the dominant group on the reef, we may be witnessing the beginning of a phase shift in Bonaire that mirrors that already seen in the greater Caribbean (e.g., Jamaica) (Hughes 1994; Edmunds & Carpenter 2001; Williams & Polunin 2001; Gardner et al. 2003; Miller et al. 2003; Bak et al. 2005; Idjadi et al. 2006; Lee 2006; Nugues & Bak 2006; Aronson & Precht 2006; Hughes et al. 2007).

The massive "phase shift" of reefs in the Caribbean from coral-dominated to macroalgaedominated reefs resulted from coral disease and a mass mortality in sea urchins among reefs where large herbivorous fish had been extirpated (Hughes 1994; Roberts 1995; Hughes & Connell 1999; Mumby 2006). As herbivorous and carnivorous fish were depleted, stocks of *D. antillarum* increased, replacing herbivorous fish as the dominant grazers on the reefs (Hughes 1994; Roberts 1995; Gardner et al. 2003); this demonstrates the resilience of a coral reef ecosystem in that there is redundancy in the species that can fill the same functional groups (in this case herbivory) (Bellwood *et al.* 2003). When the mass mortality of *D. antillarum* occurred in 1983-1984 (Hughes 1994; Williams & Polunin 2001; Miller et al. 2003; Aronson & Precht 2006), however, there were no major grazers left on the reefs to keep the abundance of macroalgae in check. With the absence of herbivory, macroalgae out-competed juvenile corals for available open space and smothered adult corals under their large canopies (Hughes 1994; Lirman 2001; Williams & Polunin 2001; Szmant 2002; Diaz-Pulido & McCook 2003; Aronson & Precht 2006; Mumby 2006; Nugues & Bak 2006).

Until now Bonaire's coral reefs have evaded the macroalgal degradation observed on reefs throughout the rest of the Caribbean. High rates of herbivory and low anthropogenic impact (i.e., low fishing pressure) may explain why Bonaire's coral reefs have succeeded so far. However, our study suggests that these conditions may be changing and that managers should take note of the potential long-term impact of these changes.

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# **Chapter 3:** Trends in distribution and abundance of carnivorous and herbivorous reef fish populations on Bonaire

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### Abstract

Fish surveys conducted at monitored sites of Windsock, Plaza, Forest (on Klein Bonaire), Reef Scientifico, Barcadera and Karpata, compared similar surveys from 2003 and 2005. Overall biomass of parrotfish has steadily declined since 2003. However, larger parrotfish ranging between 21-30 cm have increased over the period. Parrotfish bite rates corresponded with their biomass. Snapper (Lutjanidae) biomass and population density, has not changed significantly since 2003. Most lutjanids were relatively large, between 21-30 cm. It will be critically important to monitor biomass and body size of ecologically important grazing parrotfish.

### Introduction

Fish are important herbivores and carnivores in coral reef ecosystems. Herbivorous fishes reduce macroalgae on reefs which improves coral recruitment and subsequent survival (Lirman 2001). Since the mass mortality of the sea urchin, *Diadema antillarum* (Hughes 1994), parrotfishes (Scaridae) are the dominant herbivore on most Caribbean reefs (Mumby *et al.* 2006). However, parrotfish are threatened by spear and trap fishing in many parts of the Caribbean today. Bonaire has historically had little such fishing and as a result it was reported to have relatively high levels of herbivores and a low abundance of macroalgae (Kramer 2003, Paddock *et al.* 2003, Simpson and Steneck 2003).

Our study monitored the distribution and abundance of herbivorous fishes (scarids and acanthurids) to determine if trends exist in this important group. We did this by comparing commensurable fish surveys conducted during March of 2003, 2005 and 2007 (Paddock *et al.* 2003 and Brown and Hansen 2005 and this study, respectively).

Similarly, trends of large carnivorous reef fish can indicate fishing pressure. Thus we quantified the abundance of several species of snappers (Lutjanidae). This family is a sensitive indicator of fishing pressure because they are highly valued by consumers. Lutjanids are susceptible to hook and line fishing which is the predominate fishing method used in Bonaire (Nenadovic, *this report*). Again, we will compare our results with those from the same month in 2003 and 2005 from past studies conducted at the same reef sites and using commensurable methods. We expect that trends in lutjanid carnivore abundance will reflect trends in fishing pressure on the monitored reefs over time.

## Methods

To quantify differences in herbivores and carnivores among different sites on Bonaire reefs, we conducted visual surveys at 10 meters depth. Sites were surveyed from south to north as follows: Windsock, Plaza, Forest on Klein Bonaire, Reef Scientifico, Barcadera, and Karpata.

Herbivorous fish abundance, size, grazing intensity (i.e. bite rates), life phase and species type were determined at each site along Bonaire reefs. Population densities of Scaridae (parrotfish) and Acanthuridae (surgeonfish) were estimated by visual censuses of individuals within 2 m on each side of a 30-m transect deployed five times at each study site.

Herbivores grazing intensity was measured at each study site during March of 2007. Meter square quadrats were haphazardly chosen at 10 meters depth on the reef and five minutes observation were made of the number of bites taken by all algal removing herbivores (scarids and acanthurids). Note that the size of the quadrat was located using a 1 m rule, and this was removed prior to taking observations in order not to bias fish associations with the substratum. The specie phase, size and number of bites was recorded. Appendix A provides a list of all the herbivorous species recorded in the surveys.

Three species of Lutjanidae (snappers) were used to indicate large predator abundance on the monitored reef carnivores (Appendix B). All fish sizes were recorded to the nearest centimeter and converted to biomass using length-weight conversions (Bohnsack and Harper 1988).

# Results

# Herbivore Biomass

We have previously reported on a slight decline in herbivore biomass from 2003-2005. The 2007 data points to a further decline at some sites. However, different sampling techniques are preventing us from making a definitive conclusion. We will compile data in March 2008 using the same methods as those used in 2007, and this will clarify whether the decline in parrotfish biomass from 2003 to 2005 is continuing.

The average biomass of herbivorous acanthurid and scarid species was  $4203 \text{ g}/100\text{m}^2$  and ranged between  $1916-5962\text{g}/100\text{m}^2$  in 2007 (Figure 1; see Appendix for all detailed results). Scarid biomass has steadily declined since 2003 (Figure 2). Acanthurid (tang) biomass comprised less than a twentieth of the biomass of scarids (Figure 3). They are also less effective, and thus, less important herbivores (Steneck 1988) and will not be treated further in this study.





Figure 1. Biomass of surgeonfish and parrotfish. Variance is represented as one  $\pm$  standard error.



**Trends in Scarid Biomass** 

Figure 2. Scarid biomass from 2003, 2005, and 2007 (from Paddock *et al.* 2003, Brown and Hansen 2005, and this study, respectively). Variance as in Figure 1.

#### Acanthurid Biomass, March 2007



Figure 3. Average biomass of acanthurids among sites. Variance as in Figure 1.

Scarid bite remained relatively relatively constant, though possibly declining slightly, since 2005 (Figure 4). Declines at Windsock may be significant and declines at Plaza were probably significant.



**Figure 4.** Bite rates of parrotfish at different sites on Bonaire's reef. Data combined from observations made Summer 2004, November 2004, March 2005 (Brown and Hansen 2005) and March 2007 (*this study*). Variance is represented as one (±) standard error.

### **Snapper Biomass**

Overall lutjanid snapper biomass has remained relatively constant since 2005 after a nonsignificant increased in 2005 (Brown and Hanson 2005). Among sites, Karpata had the lowest lutianid biomass (126 g/100 m<sup>2</sup>) while Forest had the highest biomass (5075 g/100  $m^2$ ). For most of the monitoring period, Forest, Plaza and Windsock had higher than average abundance while Karpata had lower than average abundance (Figure 5).



Figure 5. Biomass of the three monitored species of snapper compared among years and sites along the Bonaire reef.

Three common lutianid species, schoolmaster (Lutianus apodus), mahogany snapper (Lutjanus mohogani), and yellowtail snapper (Lutjanus chysurus) were monitored among sites and among years (Figures 6-8). Yellowtail snapper was most abundant at Forest on Klein Bonaire (700-750 g/100 m<sup>2</sup>) and lowest at Karpata (100-200 g/100 m<sup>2</sup>; Figure 6). Schoolmasters were the most abundant species of the three species of snappers. The highest average biomass of 2400-2500 g/100 m<sup>2</sup> was found at Plaza and the lowest was at Karpata (Figure 7). The second most abundant species, mahogany snapper, ranged between 1500-2000 g/100 m<sup>2</sup> at Plaza (highest) to zero at Karpata (lowest) (Figure 8).

Trends in Snapper (Lutjanidae) Biomass



### Trends in Yellowtail Snapper Biomass 2003-2007

**Figure 6.** Biomass of yellowtail snapper among sites and among years (data sources same as Figure 5).



Trends in Schoolmaster Snapper Biomass 2003-2007

**Figure 7.** Biomass of schoolmaster snapper among sites and among years (data sources same as Figure 5).

#### Trends in Mahogany Snapper Biomass 2003-2007



**Figure 8.** Average biomass of mahogany snapper among sites and among years (data sources same as Figure 5).

# **Snapper Population Densities**

Density of snappers varied among the six sites and among the three sampling periods (Figure 9). The highest population densities were at Plaza (11.2 fish/100 m<sup>2</sup>) and Barcadera (10.1 fish/100 m<sup>2</sup>) and the lowest density was at Karpata (1.42 fish/100 m<sup>2</sup>). Since 2003, there was no conspicuous trend. Brown and Hansen (2005) reported a significant increase in lutjanid densities between 2003 and 2005. However, from 2005 to 2007 there was virtually no change.



**Figure 9.** Density of the most important carnivorous reef fish family in Bonaire 2003, 2005 and 2007. Variance is represented as one  $\pm$  standard error.

### Discussion

Scarid parrotfish have steadily declined in abundance since 2003 (Figure 2). This may be serious problem for Bonaire. Although we did not see a concomitant decline in grazing rates (Figure 4), algal abundance has increased (Olsen and Steneck, *this report*). Since increases in algal biomass cause a decline in coral recruitment (Mumby *et al.* 2007, Arnold, *this report*), this trend could result in a decline in the health of Bonaire's coral reefs.

Carnivorous fishes are often targeted by the fishing community. However, we saw little change in snappers in Bonaire since 2003 (Figure 5). Future surveys should also record the abundance of barracuda and the family of groupers (serranids) because coneys, graysbys and red hind are targeted by fishermen of Bonaire (Nenadovic, *this report*).

Most of the total biomass of carnivorous reef fish on Bonaire reefs consists of middle sized snappers ranging between 21-30 cm. These snappers include schoolmasters, yellowtail and mahogany. These carnivorous fishes depend on other reef fish for food. If carnivorous fishes are over exploited by heavy fishing pressure, smaller prey such as the damselfish could increase (see Spencer, *this report*).

# Conclusion

Herbivory reduces algal biomass and controls community structure by reducing macroalgae and increasing coral growth (Williams and Polunin 2001, Lirman 2001). This can increase the recruitment potential of the benthos for corals (Arnold 2007). Thus, a depletion of grazers (especially parrotfish) could have a large negative impact on the dynamics of Bonaire's coral reef. Carnivores, such as barracuda, groupers as well as snappers should be monitored in the future to determine trends in these predators. Immediate action must be taken to stem the decrease in the biomass of herbivorous species in order to protect Bonaire's reef.

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# **Chapter 4: Population trends of territorial damselfish 2003-2007 on Bonaire**

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### Abstract

Population densities of territorial damselfish were quantified in March of 2007 at five reef sites on Bonaire's western shore that were monitored in 2003 and 2005. Damselfish are very abundant on Bonaire's reefs and they have increased significantly at four of the five sites surveyed since 2003. The overall increase in damselfish population could be the result of declines in predatory reef fish in Bonaire.

### Introduction

Territorial damselfish (Pomacentridae *Stegastes sp.*) are non-denuding herbivorous fish that negatively effect coral reefs, (Hixon and Brostoff 1983, Hinds and Ballantine 1987, Hixon 1997) by killing coral (Kaufman 1977), and reducing grazing pressure from other herbivores (Brawley and Adey 1977, Ceccarelli et al. 2001, Brown and Hansen 2005). Specifically, some damselfish species (*Stegastes sp.*) reduce herbivory by actively expelling other grazers, thereby increasing the abundance of algae on reefs (Brawley and Adey 1977, Hixon and Brostoff 1983, Paddack *et al.* 2003). This can also reduce coral recruitment because algae interferes with coral settlement (Arnold and Steneck 2005), thereby reducing the resilience of coral reefs to disturbance.

Damselfish populations may be controlled by predatory fish (Hixon and Beets 1989). However, large predatory fish have declined throughout the Caribbean due to fishing (Hughes 1994, Steneck and Sala 2005). Recent studies showed that recruitment of damselfish and damselfish population densities are inversely correlated with resident piscivores (Hixon and Beets 1993, Almany 2004, McClanahan 2005, Ceccarelli *et al.* 2006). If the loss in predatory fish species can increase territorial damselfish, then the recent trends indicating a decline in carnivorous fish populations in Bonaire (Steneck and McClanahan 2003) could be cause for concern. This report quantifies the density of territorial damselfish to determine if there have been increases since 2003 and 2005.

# Methods

Abundance of territorial damselfish *Stegastes sp.* (primarily longfin, threespot and bicolor) was determined using visual census techniques at five sites in Bonaire including: Windsock, Plaza, Forest (Klein Bonaire), Reef Scientifico, and Barkadera. Methods are similar to the 2003 and 2005 studies conducted at the same sites in Bonaire, though slight

adjustments were made in transect size. All data from 2003 is referenced from Paddack *et al.* (2003) and all data from 2005 is referenced from Brown and Hansen (2005). Transect surveys were conducted at 10m depth using SCUBA. Abundance of territorial damselfish were recorded along 10m by one meter transects ( $10 \text{ m}^2$ ). Two 25m transect tapes were used to define the transect area. The transect area was reduced from previous studies, where an  $80\text{m}^2$  transect was surveyed. The reduction in transect size allowed for an increase in repetitions for each site. Each transect was surveyed four times, to ensure accuracy. Transects were located at previously monitored sites, and specific sites were identified by referencing permanent markers on the reef. Since most fish surveys underrepresent resident fish populations, the convention is to report the highest number of fish counted per transect (Sale 1997). In accordance with this convention, the largest species numbers from each transect were used in the analysis. A maximum of eight and a minimum of one transect was conducted at each study location.

The planktivorous bicolor damselfish was not quantified in 2003 and 2005 and so this species was omitted from trend analysis of the benthic feeding species (longfin and threespot damselfish).

The data were transformed as necessary (log transformation) to meet assumptions required for analysis of variance (ANOVA). Two factor ANOVA's were used to test for differences among species, sites and years for the surveys conducted in March 2003, 2005 and 2007. Bonferroni adjusted comparisons with the factor level error rate set at 5% were used to identify which years differed and which sites differed.

### Results

### Population Densities of Territorial Damselfish

*Stegastes partitus* (bicolor damselfish) was consistently the most abundant species in each of the sites surveyed on Bonaire in 2007 (Figure 1). The abundance of *Stegastes planifrons* (threespot damselfish) and *Stegastes diencaeus* (longfin damselfish) is inversely correlated (Figure 2).



Stegastes species Density March 2007

Figure 1. Density of three dominant *Stegastes* species at 10m in Bonaire's five monitoring sites.

Significant differences in damselfish density were found among years ( $F_{5,37}$ =15.98, P=0.000) and sites ( $F_{5,37}$ =6.44, P=0.000). Sites indicating significant differences (Bonferroni adjusted comparisons), at a significance level of 5% include: Windsock and Forest, Plaza and Forest and Reef Scientifico and Forest. Years indicating significant differences (Bonferroni adjusted comparisons), at a significance level of 5% include: 2003 vs 2005 and 2005 vs 2007. The interaction between years and sites was not significant.

*Stegastes* population densities were highest at Forest on Klein Bonaire in 2005 (Brown and Hansen 2005) and in 2007, closely followed in 2007 by Barcadera (Figure 3). Overall, Bonaire's *Stegastes* population densities are high (to about 100m<sup>2</sup>) and are increasing (Figure 4). Five out of six sites have linearly increased since 2003 (Figure 3).



**Figure 2.** Density of herbivorous territorial damselfish (longfin and threespot) in 2003, 2005 and 2007 on Bonaire (data for 2003 and 2005 from Paddack *et al.* (2003) and Brown and Hansen (2005) respectively). Each bar represents the sum of the average densities of longfin and threespot damselfish according to year and site. Average densities for all of the sites surveyed indicate a drop in density since 2005, but 2007 numbers remain significantly above 2003 levels. Numbers above bars indicate the proportion of variance in abundance explained by time. The sign represents whether the slope is positive or negative.

### Linear Regression of Average Damselfish Density Over Time



**Figure 3.** Linear regression of average damselfish density. Reference 2003 and 2005 data sources as mentioned in Figure 2.

### Discussion

Damselfish abundance has significantly increased on Bonaire since 2003. Specifically, the highly territorial species of *Stegastes* (threespot and longfin damselfish) were most abundant at Forest in 2003, 2005 and 2007(Figure 2), with significant differences in *Stegastes* abundance between Forest and the other sites surveyed in 2007. Increases in *Stegastes* densities at Plaza in 2007 mimic those at Forest. These trends suggest an increase in damselfish densities overall, as damselfish density significantly increased in all but one monitored site between 2003 and 2007 on Bonaire (Figure 2). Since territorial damselfish are thought to have a negative footprint, it is possible that the increasing trends in damselfish density have negative implications for Bonaire's coral reefs unless immediate steps are taken to remedy this problem.

The bicolor damselfish were most abundant in each of the monitored sites (Figure 1), but this species was not included in the overall abundance at each site (Figure 2) as previous studies did not numerically account for their presence. Bicolor damselfish are planktivores, not benthic herbivores and they do not exhibit the same territoriality as the longfin and threespot damselfish. This explains their absence from data sets in 2003 and 2005, as those surveys focused solely on territorial species. Still, the significant abundance of bicolor damselfish (Figure 1) suggests that populations of this species should continue to be measured in future studies, as it may provide insight into what controls their abundance over time.

Damselfish are widely distributed throughout tropical reef systems in the Caribbean and beyond. In some locations they control almost half of the available benthos. It is possible that territorial damselfish may affect small-scale patchiness within a reef ecosystem (Hixon and Brostoff 1983) by killing coral or altering the grazing behavior of other herbivores (Paddock *et al.* 2003), thereby indirectly increasing algal cover and reducing coral settlement (Ceccarelli *et al.* 2001, Arnold and Steneck 2005). Declining predator abundance on Bonaire's reefs (Steneck and McClanahan 2003, 2005), may have caused or contributed to the increases in damselfish abundance since 2003 (Figure 2). Predators are thought to limit the abundance of damselfish in some Indopacific reefs (Almany 2004). While the role of predators in Caribbean reef systems is still not fully understood (Hixon and Beets 1993), it is possible that predators influence reef systems and in particular control damselfish populations within these systems (Hixon and Beets 1989, McClanahan 2005). If so, predator declines in Bonaire will likely result in increases in some fish species that are potentially harmful to coral reefs such as damselfishes.

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# Chapter 5: The abundance of sea urchins (*Diadema antillarum*, *Echinometra lucunter* and *Tripneustes ventricosus*) and macroalgae in shallow reef zones of Bonaire

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#### Abstract

Sea urchin and macroalgal abundance were determined at five sites on the leeward reefs of Bonaire, N.A. in March 2007. Population densities of *Diadema antillarum*, *Tripneustes ventricosus*, and *Echinometra lucunter* were quantified at each site using a  $1m^2$  quadrat. Percent macroalgal coverage was estimated for each quadrat. *Diadema* was found at four of the five study sites with population densities ranging from 0.03 (±0.03) urchins/ m<sup>2</sup> at Plaza to 1.79 (±0.39) urchins/ m<sup>2</sup> at Karpata. *Diadema* was by far the most important herbivore on coral reefs. At sites with relatively high densities of *Diadema*, no macroalgae were observed. Population densities have increased significantly at the Karpata site compared to a similar study conducted in 2005. *Tripneustes ventricosus* was observed at Scientifico and Karpata reefs, but at very low population levels. The only two *Echinometra lucunter* sea urchins were recorded at Windsock and Plaza.

#### Introduction

Caribbean coral reef ecosystems have undergone a phase shift over the past few decades from coral dominated to macroalgal dominated reefs. Contributory factors of the shift include a gradual reduction in grazing parrotfish, followed by the mass mortality of the herbivorous sea urchin, *Diadema antillarum* in 1983 (Hughes 1994). This mass mortality event functionally eliminated the key grazer, *Diadema*, throughout the entire Caribbean and West Atlantic (Lessios 1988), reducing its population by at least 97% (Miller *et al.* 2003). The combined loss of herbivorous fish and urchins lead to the macroalgal phase shift.

Bonaire escaped the phase shift to macroalgae that occurred throughout the Caribbean following the *Diadema* die-off (Smith and Malek 2005), due to the abundance of herbivorous fish, such as parrotfish and surgeonfish (Kramer 2003).

The health of a coral reef ecosystem is indirectly influenced by the process of herbivory from sea urchins and herbivorous fish, which can improve coral survival and increase coral recruitment. Recent high densities of *Diadema* in Jamaica resulted in low macroalgae cover and high juvenile coral abundances (Edmunds and Carpenter 2001).

Although *Diadema* is considered the primary grazer on many Caribbean coral reefs, other species, such as *Tripneustes ventricosus* and *Echinometra lucunter* are also present and may help maintain the overall health and structure of the reef. A redistribution of

*Tripneustes* from the back-reef to the fore-reef has greatly reduced the abundance of macroalgae in Jamaica after the *Diadema* mass mortality (Woodley 1999), and *Echinometra lucunter* is a major grazer of drift algae (Haley and Solandt 2001). It is important to consider factors such as predation when monitoring for sea urchin abundance. Predation, for instance, can limit urchin abundance and could contribute to a multispecies increase in sea urchin abundance. Thus, trends in urchin abundance are worthy of attention.

Our study seeks to determine the population density of sea urchins in shallow reefs less than five meters deep. The study sites and methods are identical to those used in 2005 in order to determine if trends exist in sea urchin densities over time (Smith and Malek 2005). Monitoring of urchin populations is useful to assess the health of Bonaire's coral reefs.

#### **Study Species**

There are three species of sea urchins, *Diadema antillarum, Echinometra lucunter*, and *Tripneustes ventricosus*, commonly found on Bonaire's reefs.

*Diadema antillarum* has long, fragile, sharp, black spines and is commonly known as the long-spined urchin. The spines of a fully grown individual are up to four times the diameter of the test. This highly active urchin reached densities of more than 20 individuals per square meter prior to 1983 (Scoffin *et al.* 1980). High population densities of *Diadema* likely increase protection from predators and spawning success. *Diadema* resides primarily on coral reefs in *Thalassia* sea grass beds, mangroves and sandy or rocky bottoms with low wave action. *Diadema* is predominantly a grazer, feeding on algal turf. This species is by far the most important grazing urchin in the Caribbean.

*Tripneustes ventricosus* is a large urchin with a brown test and short white spines. The species resides in grassy areas on sandy bottoms and among reefs, rocks, and rubble. *Tripneustes* can successfully persist in areas with modest wave energy. Young are commonly found in the intertidal while adults are generally limited to the subtidal zone (Hendler *et al.* 1995).

*Echinometra lucunter* is reddish in color with black to red, long, sharp spines that are thick at the base and become slender at the tip. *Echinometra* occupies various habitats ranging from regions of low wave action, together with branching corals, to high wave action regions located on limestone reef rock. *Echinometra* bore into the reef rock using their thick spines and robust teeth, thus they create their own shelter. Drift algae is thought to be their primary food, although they also feed on attached and boring algae (Hendler *et al.* 1995).

#### Methods

Five previously selected monitoring sites were surveyed on the leeward reefs of Bonaire, N.A. for sea urchin and macroalgal abundance: Windsock, Plaza, Reef Scientifico, Barcadera, and Karpata. The area of surveyed sites ranged from19m<sup>2</sup> to 31m<sup>2</sup>. At each site, up to six transects perpendicular to the shore were sampled every 10 meters for a total shoreline distance of no more than 60m. One meter squared quadrats were placed every four meters along each transect and no more than 28 meters offshore for a total of 114 quadrats. Urchins found in a quadrat were identified to species level and test diameter measured to the nearest centimeter. Percent macroalgae was estimated for each quadrat.

#### Results

*Diadema antillarum* was the most abundant of the three urchins surveyed. Karpata had the highest *Diadema* population density out of the five sites with a density of 1.79 ( $\pm 0.39$ ) urchins per m<sup>2</sup> (Figure 1). *Diadema* was present at all sites except Barcadera, although Windsock, Plaza and Scientifico had significantly lower population densities than Karpata. Barcadera was the only site where no individuals were observed outside of the study area. Of the five sites surveyed, the population density of *Tripneustes ventricosus* was the lowest recorded, with individuals only found at Reef Scientifico and Karpata (Figure 2). *Echinometra lucunter* was observed at Windsock and Plaza with very low population densities (Figure 2).



**Figure 1.** *Diadema antillarum* population density per square meter for all five sites. Standard error indicated by error bars.



**Figure 2.** *Echinometra lucunter* and *Tripneustes ventricosus* population densities per square meter for all five sites. Standard error indicated by error bars.

Macroalgal percent coverage at Barkadera was highest while Windsock, Plaza, and Karpata had no observed macroalgae (Figure 3).



**Figure 3.** Macroalgal percent cover per square meter for all five sites. Standard error indicated by error bars

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The test size of *Diadema* ranged from one to nine centimeters with the majority of individuals test being three to four centimeters (Figure 4). Results from the 2005 Bonaire Report differed from this survey in that the majority of individuals were above eight centimeters in diameter. Only two *Echinometra* urchins were observed in the five sites with diameters of two and three centimeters. Only two *Tripneustes* urchins were observed measuring nine and ten centimeters in diameter.



Figure 4. Size frequency of *Diadema antillarum*. Data was combined for all five sites.

*Diadema* population density increased significantly at Karpata reef since 2005 (Figure 5). *Diadema* was present at Windsock and Plaza in 2007 whereas in 2005 no urchins were recorded. Individuals were absent at Barkadera in both 2005 and 2007. The 2007 population density exceeded the 2005 densities at all sites excluding Scientifico.



**Figure 5.** Comparison of 2005 and 2007 *Diadema antillarum* population densities. Standard error indicated by error bars.

From 2005 to 2007, the *Echinometra* population density did not increase. In 2005, Forest was the only site where *Echinometra lucunter* was present. Rough wave action in 2007 prevented data collection at Forest. Low population densities of *Echinometra lucunter* were observed in 2007 at Windsock and Plaza.

*Tripneustes ventricosus* was absent from Windsock, Plaza, and Barkadera in both 2005 and 2007 (Figure 6). *Tripneustes* was observed at Scientifico and Karpata in 2007 with low population densities. In 2005, individuals were observed only at Scientifico, but in greater abundance than 2007.



**Figure 6.** Comparison of 2005 and 2007 *Tripneustes ventricosus* population densities. Standard error indicated by error bars.

#### Discussion

The population density of *Diadema* remains low and patchy in Bonaire (Figure 1). *Diadema* density was relatively high when macroalgal coverage was 0% (Figures 1 & 3). Macroalgal cover was highest when the three study species were absent. The low macroalgae cover coupled with low densities of *Diadema* indicates that other herbivorous species such as parrotfish, surgeonfish, and damselfish replaced *Diadema* as key grazers. Herbivorous fish populations are relatively abundant on Bonaire's reefs when compared to other Caribbean reefs. This may explain why Bonaire's reefs have remained healthy without macroalgal grazing *Diadema*.

Recent monitoring has revealed a steady decline in parrotfish abundance. This could be a problem if itcontinues and if it is not offset by Diadema population increases. Low rate of recovery of *Diadema* populations could be the result of poor fertilizations success since *Diadema* requires a minimum distance between individuals (Moses and Bonem 2001). It is also possible that newly settled sea urchins may fail to recruit due to consumption by predators.

Studies on sea urchins in the Indian Ocean (McClanahan et *al* 1989) and elsewhere (Sala et *al* 1996) suggest that fish predation can limit adult sea urchin population densities. Thus, if large urchin eating predators such as triggerfish and hogfish decline in abundance, urchin populations may expand. Interestingly, Karpata often has low densities of predatory fish (Brown and Hansen 2005) and is the location of highest *Diadema* densities (Figure 5).

Surveys observed from all five sites in Bonaire indicate that sea urchin populations remain extremely low and patchy. Despite the population decline, macroalgal coverage remains low when compared with Jamaica and St. Croix (Aronson and Precht 2000; Edmunds and Carpenter, 2001; Haley and Solandt 2001).

Echinoids are responsible for more than 90% of bioerosion in the Caribbean (Hendler 1995). If the abundance of *Echinometra* had been greater, not only would a slight increase in grazing occur, but a substantial amount of coral rock could be eroded, changing the reef morphology. Although bioerosion was not assessed in this study, previous studies have examined bioerosion rates throughout the Caribbean. For example, in the Virgin Islands *Echinometra* eroded 3.9kg/m<sup>2</sup> per year (Hendler 1995).

*Tripneustes* is relatively immune to the chemical defenses of macroalgae and as a result can reduce the accumulating algae (Moses and Bonem 2001). Thus, the younger macroalgae preferred by *Diadema* thrive due to the herbivory of *Tripneustes*. However, *Tripneustes*' population levels in Bonaire were well below functional densities, therefore inhibiting growth of younger macroalgae.

Macroalgal abundance remains low in Bonaire when compared with other reefs in the Caribbean (Simpson and Steneck 2003). The high grazing capacity of herbivorous fish may have prevented a macroalgal phase shift in Bonaire's reefs so far, but the future is

less certain. Karpata had lower population densities of predatory fishes in the past (Brown and Hansen 2005). If predatory fish populations such as snappers, groupers, graysbys, and conys continue to decline, an increase in sea urchin abundance could occur. Parrotfish population densities appear to be declining (Alvarado and Steneck, this report). Thus, even if *Diadema* populations recover, Bonaire could be as precarious as were most Caribbean reefs prior to the sea urchin die-off in the early 1980s. Alternatively, coral reefs maintaining high population densities of both sea urchins and parrotfish will be more resilient to unexpected disturbances from hurricanes and disease. Monitoring *Diadema* will help determine if this sea urchin will continue to increase in Bonaire.

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# **Chapter 6: Running the gauntlet to coral recruitment through a sequence of local multiscale processes**

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#### Abstract

Coral reefs around the globe are suffering from increasing rates of disturbances from bleaching, disease, and algal overgrowth and many show little to no sign of recovery. While we know much about what causes coral reefs and other ecosystems to collapse, we know relatively little about what contributes to their recovery. We sought to determine if critical sequential phases in settlement and post settlement processes control coral recruitment on the reefs of Bonaire (Netherlands Antilles) where coral abundance is high and algal abundance is low relative to other Caribbean coral reefs. To manipulate algal biomass surrounding potential coral nursery habitats, we placed standardized terra-cotta coral settlement plates inside and outside of damselfish territories and wire cages. We found local turf algal cover may impede larvae from accessing the benthos, and after 27 months, spat densities were 73% higher in well-grazed treatments. Spat settled preferentially on crustose coralline algae, biofilms, and calcareous polychaete worm tubes, suggesting demographic importance of facilitator substrates. Our study suggests there may be a dynamic balance between the positive effects of settlement facilitators and the negative effects of turf algal abundance and other settlement inhibitors that limit coral settlement and survival. Elevated abundance of turf algae within centimeters of possible settlement habitats decreased the recruitment potential of reefs by impeding larval access to settlement habitats and decreasing post-settlement survivorship. Thus, this dynamic interaction affects recruitment at several points during and immediately following larval settlement. This illustrates the "gauntlet" of sequential processes through which corals must pass to recruit to coral reefs. With the highest proportion of surviving coral spat successfully running the gauntlet under conditions of relatively low turf algal biomass, this study suggests that herbivory, or a lack thereof, explains a considerable portion of the variance associated with coral recruitment at a very local scale. Thus, careful management and monitoring of herbivores could improve the potential for coral reefs to recover from disturbances.

#### Introduction

Coral reefs worldwide have suffered from large scale and relatively sudden disturbances due to coral bleaching, disease, and other insults (e.g. Knowlton 2001, Hughes *et al.* 2003, Buddemeir *et al.* 2004). Unfortunately, we know much more about what causes coral reefs to collapse than we do about what contributes to their recovery (Vermeij 2006). In the Caribbean this was most evident in recent decades when many coral-dominated reefs phase-shifted to algal-dominated reefs (e.g. Hughes 1994, Gardner *et al.* 2003). Further, most Caribbean reefs have shown little or no recovery from disturbances (Connell 1997, Hughes *et al.* 2005), and while they decline, the debate regarding how to best manage for reef recovery persists.

Coral recruitment is central to the recovery of coral reefs. Logically, this involves three sequential steps: 1) availability of competent larvae ready to settle to the benthos, 2) the propensity to settle; often aided by chemical cues that induce settlement and metamorphosis, and 3) the availability of nursery habitats where post-settlement mortality is low.

It is widely thought that most larvae contributing to coral settlement originate relatively locally (Sammarco and Andrews 1989, Hughes et al. 2000, Shanks et al. 2003). This is because corals have relatively short larval durations (most settlement occurs between 2-14 days, Edinger and Risk 1995) compared to other reef organisms such as reef fish (months) or reef lobsters (up to a year). Within this local domain, settlement occurs only after certain conditions bring competent larvae to specific depths, light, and biogenic substrata (e.g. coralline algae) that induce metamorphosis and settlement (Raimondi and Morse 2000). Thus, for coral settlement, larval availability and propensity to settle involve both complex organismal and environmental factors. Larval behaviour is necessary for movement, metamorphosis, and settlement, and environmental conditions enable advection of larvae and algal chemical cues for settling. New recruitment to adult populations also requires post-settlement survival. This, too, is strongly influenced by the local biological environment. For example, post-settlement survival for Indo-Pacific corals was enhanced by particular species of coralline algae (Harrington et al. 2004). Conversely, areas of high algal biomass are known to be poor nursery habitats for settling corals (Birkeland 1977, Harriott 1983). Thus, it is possible that phase shifts to high algal biomass could reduce post-settlement survival and thereby suppress coral recruitment (Hughes and Tanner 2000).

In the Caribbean, coral settlement rates have declined sharply over the past few decades (Hughes and Tanner 2000, Vermeij 2005). While Hughes and Tanner (2000) argued that loss of live coral in Jamaica reduced the number of available larvae and caused recruitment failure, Vermeij (2005), comparing coral recruitment studies in Curacao, Netherlands Antilles, concluded that macroalgal growth had caused the reef to become hostile to settling corals and resulted in a five-fold decline in coral recruitment there between 1979 and 1998. Thus, there is no consensus on whether the decline in coral recruitment results from a supply-side limitation in larval availability, a change in the

receptivity of the reef itself due to fewer recruitment-facilitating microhabitats, higher post-settlement mortality, or both.

To address these questions and better manage for reef recovery, it is important to understand the causes of recruitment failure. We seek to determine what enables a coral larva to run the gauntlet of processes leading to coral recruitment. Specifically, are there bottlenecks involving the availability of larvae, a larva's propensity to settle, its postsettlement survivorship, or any combination of the three?

To examine the scale and rate at which recruitment operates and to develop a processlevel understanding of the three critical steps to recruitment, we conducted experiments measuring settlement and post-settlement survival in Bonaire, Netherlands Antilles. We chose Bonaire's coral reefs because the abundance of algae there is the lowest in the Caribbean (Kramer 2003), thus, the receptivity or "recruitment potential of the benthos" (*sensu* Steneck and Dethier 1994) should be high. By conducting common-garden experiments on reefs with abundant corals, supply side limitations should be relatively low, and low macroalgal abundance may allow us to focus on factors that operate at finer spatial scales.

Although macroalgal abundances are low, territorial damselfish create small patches of elevated biomass in their filamentous turf "gardens" (Brawley and Adey 1977) by reducing herbivory in their territories (Myrberg and Thresher 1974, Sammarco and Williams 1982, reviewed by Ceccarelli *et al.* 2001). We used the gardens from the two dominant territorial damselfish species on Bonaire, the three-spot (*Stegastes planifrons*) and the longfin damselfish (*Stegastes diencaeaus*), to determine if these localized differences in algal biomass affect the settlement and subsequent recruitment of corals.

In effect, our study design is set at spatial scales close enough to factor out regional supply side effects. Thus, we seek to ascertain the relative role of each of three distinct steps in coral recruitment: 1) local supply of available larvae, 2) propensity to settle, and 3) availability of nursery grounds, by using damselfish-induced algal turf gardens and wire cages to simulate locally elevated algal overgrowth. We also determine the microhabitat on or near which corals settle and, with micro-spatially explicit monitoring, establish the per capita survivorship and growth of newly settled corals under our experimental treatments.

#### **Materials and Methods**

#### Study Sites

The study was conducted on the lee reef of the island of Bonaire, Netherlands Antilles in the southern Caribbean (12° 15' N, 68° 28' W). Our six replicate sites, all greater than 1 km apart, were along the major fringing reef track on the western (lee) side of Bonaire. Site names, from north to south, are Karpata, Barcadera, Reef Scientifico, Forest (on Klein Bonaire), Eighteenth Palm, and Windsock. The sites were chosen to characterize

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coral settlement on the lee reefs of Bonaire. None of the sites were seriously damaged by Hurricane Lenny, which impacted several sites on Bonaire in November 1999.

#### Settlement Plates

At each site, four replicate, 10 x 2 m permanent belt transects were established parallel to the shore at 10 m depth. Within each belt, damselfish territories were determined through observations of both three-spot and longfin damselfish over three minute intervals. In March 2004, 40 10 x 10 x 1 cm terra-cotta coral settlement plates were deployed within the belts at each site (Figure 1, methods of Mundy 2000), half inside and half outside of damselfish territories. Holes of 0.79 cm diameter were drilled into dead substrate with a pneumatic drill, and stainless steel lag screws (6.35 cm in length) were threaded through the plate's 0.8 cm center hole and screwed into 3.81 cm nylon anchors inserted into the drill holes. The terra-cotta plates mimicked natural bare substrate opened up on a reef following a disturbance. Bare surfaces are rare on a coral reef; however, these can occur following a catastrophic disturbance, or an event damaging or killing an individual or colony (Sousa 1984). Using plates allowed not only for tracking rates of coral settlement but also for the opportunity to track succession of colonizing organisms. Plates also homogenized variance at the mm scale due to the simplified architecture provided by the smooth-fired terra-cotta and the standardized 1 cm spacer separating the plate from the reef. The damselfish acclimated almost immediately to this new sessile object within their territories (S. N. Arnold, *personal observation*), and the changes in territory location were negligible according to high-resolution maps created every three months within the first year (Brown 2006).



Figure 1. Sketch of  $10 \ge 10 \ge 10$  cm terra-cotta coral settlement plate. The subcryptic settlement microhabitat, where 83% of all spat settled, is the outside 1.5 cm perimeter of the plate underside hidden from grazers but in close proximity to the photic zone.

#### Quantifying Patterns in Algae and Juvenile Corals

Algal community structure and density of juvenile corals were quantified at each site. Approximately 237, 25 x 25 cm, quadrats were placed inside and outside of damselfish territories within the belt transects on hard substrate where algae or corals could recruit. Substrates with sediment or live invertebrates such as sponges, gorgonians, and adult coral were avoided.

In each quadrat, visual estimates of percent cover of turf algae, macroalgae, crustose coralline algae, non-coralline algal crusts (primarily peyssonnelids) articulated algae (primarily *Halimeda opuntia*, although rare on Bonaire), and any adult coral or gorgonians and sponges were recorded. Algal turfs, or the epithilic algal community (*sensu* Hatcher 1983), include a multispecific group of primarily filamentous algae with canopy heights of <10 mm (i.e. *Coelothrix irregularis, Galaxaura spp., Ceramium spp., Polysiphonia spp., Herposiphonia spp., Centroceras spp., Taenioma spp., and Ectocarpus spp.*) (Steneck 1988). Macroalgae on Bonaire is rare (Kramer 2003) and primarily included diminutive forms of both *Dictyota spp.* and *Lobophora variegata*. Crustose coralline algae refers to nongeniculate encrusting calcified red algae in the order *Corallinales*. Peyssonnelid algae are encrusting red algae that differ from crustose coralline algae by being variably calcified with aragonite or not calcified at all, and possessing tetrasporangial sori rather than conceptacles. The average canopy heights of foliose algae were recorded. We calculated an algal index as a proxy for algal biomass by multiplying per group (e.g. turf) canopy height with its percent cover (Kramer 2003).

Densities of juvenile corals having recruited to the reef were determined by recording all juveniles, identified to the lowest possible taxon, in each quadrat. Juvenile corals included those with a maximum diameter of 40 mm or less (Bak and Engel 1979, Edmunds and Carpenter 2001), omitting those with characteristics of asexual fragmentation and those species that are characteristically small as adults (for which there are relatively few). The 237 quadrats were scored, and numbers were extrapolated to come up with square meter densities.

#### Manipulated Settlement Microhabitats- Damselfish Territories/Cages

In June 2004, six plates at each site were affixed with galvanized wire mesh (6.35 mm) cages to mimic the inhibitory effects of macroalgal overgrowth on coral recruitment microhabitats. Bonaire has low abundances of macroalgae (Kramer 2003) compared to most Caribbean reefs that have phase-shifted to macroalgae as a result of the overfishing of grazers (Hughes 1994). Grazers, such as large denuding and scraping (*sensu* Steneck 1988) herbivorous fish including parrotfish (Scaridae) and surgeonfish (Acanthuridae), are effective at cropping algae on reefs and are still relatively intact in Bonaire (Bruggeman 1994, Choat *et al.* 2003). Thus, the study consisted of settlement plates in the following four treatments representing a gradient of algal community structure according to actual and simulated grazing pressure: uncaged plates outside of damselfish territories, caged plates outside of damselfish territories. These treatments test the hypothesis that anything reducing water flow (i.e. turf algae or macroalgae) reduces larval availability, thereby reducing settlement densities.

Fluorescene dye experiments were employed to determine hydrodynamic differences in the subcryptic microhabitat where corals settle for the four treatments simulating the

herbivory spectrum from fully grazed (treatments outside territories) to gardens of algal turfs (treatments inside territories) to full algal overgrowth (caged treatments). Less than one cubic mm of dye was ejected from a syringe through a 1 mm hole drilled through the center of the plates. The duration from the time of ejection to the time the dye exited the plate underside was recorded as the treatment's flushing time.

# Determining Substrate Selectivity and Availability and Quantifying Early Post-Settlement Survival

The plates were monitored six times during a 27-month deployment period (June 2004, August 2004, November 2004, March 2005, July 2005, and June 2006). Half of the plates from each site, including all caged plates, were analyzed under the microscope each of the six times for newly settled corals and their subsequent survival relative to the successional community states that may positively or negatively impact recruitment. The plates censused microscopically were transported in seawater, analyzed, and returned to the reef within six hours. The other half of the plates remained in the water until the July 2005 monitoring period in order to be able to detect any negative impacts of handling on the regularly sampled plates, none of which were observed. Newly settled corals, or spat, are coral larvae that have recently attached themselves to the substratum. The larvae then metamorphose, defined by Morse *et al.* (1988) as a developmental event following attachment consisting of the differentiation and calcification of the septal ridges. For the purposes of this paper, a newly settled coral larva is said to have undergone recruitment, or become a "recruit", if it had survived metamorphosis and thus had a recognisable skeleton, dead or alive, at the time of the retrieval of plates (Keough and Downes 1982).

We censused plate undersides for new and surviving spat. Studies have shown that spat are most frequently found on the undersides of surfaces (Carleton and Sammarco 1987, Maida *et al.* 1994). Specifically in Bonaire, Raimondi and Morse (2000) reported that, given the choice, larvae of *Agaricia humilis* settle on underside surfaces. Steneck *et al.* (2004) found 85% of spat on over 1300 settlement plates throughout the Caribbean had settled on the undersides of plates.

Each spat on the plate underside was identified to genus, measured, determined to be dead or alive based on the presence or absence of coral tissue and responsive polyps, and mapped for its location on the plate as well as its settlement substrate. The location of *Titanoderma prototypum*, an early successional coralline algae thought to be an inducer to coral settlement (Harrington *et al.* 2004), was also mapped on the plate underside. The specific locations of spat and *T. prototypum* were recorded for the purposes of tracking survivorship and dispersion patterns over time. All 240 plate tops and undersides were photographed underwater to monitor for succession of fouling species. Percent coverage of encrusting biota on plate undersides (crustose coralline algae, non-coralline algal crusts, articulated algae, macroalgae, turf algae, sponges, bryozoans, and polychaete worm tubes) was determined from these digital pictures. Thus, we recorded and analyzed time series data on recruitment, growth, and mortality in reference to the succession of fouling organisms.

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#### Statistical Analyses

All t-tests were conducted using the Microsoft Excel 2003 data analysis toolpack. All other analyses were conducted using R version 2.5.0. Turf algal biomass inside and outside of damselfish territories was compared with a two-tailed *t*-test (assuming unequal variances). The mean number of spat per plate outside and inside of territories was rank transformed and analyzed using a one-way ANOVA. The mean number of juvenile corals (those 40 mm or less) on natural substrate outside and inside of territories was compared with a two-tailed *t*-test (assuming equal variances). A model simplification with step-wise deletion was used to compare coral settlement in all four treatments. This enabled us to aggregate all non-significant factor levels in a step-wise a posteriori fashion. Thus, the outside territory/uncaged treatment was compared to the three other treatments pooled. Flushing rates in the four treatments were analyzed using a one-way ANOVA with non-transformed data, and pairwise comparisons were made with Tukey's Honest Significant Difference test. For the deviation in annual settlement rate data, we calculated confidence intervals for the slopes (deviation in settlement from 2004 to 2005 for each treatment) to see if they overlapped, and compared 2005 rates to 2004 rates in each treatment with *t*-tests. To determine if there was a treatment effect on the survivorship of the August 2004 cohort, an ANCOVA was performed. Additionally, for this data, requirements of residuals and normality were checked and we determined confidence intervals for the slopes of the survivorship curves.

#### Results

#### Small-Scale Abundance Patterns in Algae, Newly Settled, and Juvenile Corals

Macroalgae were rare or absent at all study sites, so all analyses focus on the abundance of algal turfs (*sensu* Steneck and Dethier 1994). Turf algal biomass was significantly greater and newly settled coral spat density was significantly lower inside damselfish territories than outside damselfish territories across all six sites (Figure 2. A. & B.). Of the 303 spat recorded on 240 plates, 230, or 76 %, of them were found on the 120 plates that were examined microscopically, negating any possibility of a negative handling effect. This high percentage included the 36 plates surrounded with wire mesh, on which 38 of the settlers were found. Of the total spat recorded, 83% settled along the outside 1.5 cm perimeter of the plate underside (see Figure 1). Turf algae grew on all upward facing non-coral substrata, but, although a major space occupant, it was not measurably more abundant in this subcryptic settlement microhabitat.

Spat were made up of the genera *Agaricia* (88.8%) and *Porites* (8.3%), with the remaining 2.9% unidentifiable. At this early stage, without the use of molecular techniques, spat are only visibly discernible with a dissecting microscope to the family or genus level (Hughes *et al.* 1999, Baird and Hughes 2000). Molecular markers could be applied in the future, but based on juvenile abundance in the area, the Agaricids most likely consisted of two species, *Agaricia humilis* and *Agaricia agaricites*, and the *Porites* spat were most certainly *Porites astreoides*. Recruitment on plates outside of damselfish territories (Figure

2. B.). This increased settlement outside of damselfish territories was consistent with population densities of juvenile coral ( $\leq 40$  mm) growing on natural reef substrata. Juvenile coral densities were also significantly greater outside of damselfish territories (Figure 3).



**Figure 2.** Turf algal biomass and mean number of spat per plate outside and inside of damselfish territories. A) Proxy for turf algal biomass ("algal index") average at six sites outside and inside damselfish territories (n=109 for outside territory, n=127 for inside territories including 74 three-spot territories and 53 longfin territories). Algal index inside of territories was significantly higher (*t*-test, P<0.01) than outside of territories. B) Mean number of spat per terra-cotta plate (underside surface only) outside vs. inside damselfish territories after 809 days. The means were significantly different (rank transformed one-way ANOVA, P=0.034). Note that damselfish and other fish were unable to access these spat located on the underside of the plate, elevated 1 cm from the reef substrate (see Figure 1). Error bars are ±1 standard error.



**Figure 3.** Mean population density of juvenile corals per  $m^2$  at six sites outside and inside damselfish territories (n= 109 for outside territory, n= 127 for inside territories including three-spot territories and 53 longfin territories). Mean number of juvenile corals per  $m^2$  was significantly higher (*t*-test, P<0.01) outside of territories than inside of territories. Error bars are ±1 standard error.

#### Settlement Microhabitat: Manipulations and Dispersal Rates

Cages surrounding the coral settlement plates were designed to increase algal biomass around the plates. These treatments were established inside and outside damselfish territories in June 2004. Algal biomass was higher on the cages by August 2004. By July 2005, rates of settlement were highest on uncaged plates outside of damselfish territories compared to all other treatments (Figure 4. A.).

The increase in algal biomass reduced the rates of water flow (Figure 4. B.) in the recruitment microhabitat on the underside of the settlement plate (illustrated in Figure 1). The dispersal rates of dye from the gap between the plate and the reef were significantly slower among caged plates inside and outside of damselfish territories than among uncaged plates outside of damselfish territories (Figure 4. B.). In fact, dye retention was greater in all tested states including uncaged plates inside damselfish territories relative to uncaged plates outside of damselfish territories (Figure 4. B.).



**Figure 4.** Coral settlement in the four treatments with corresponding flushing rates. A) Coral spat densities on caged and uncaged plates inside and outside of damselfish territories from August 2004 through July 2005. Different letters above bars mean significant differences in mean number of recruits. A model simplification by step-wise deletion was performed, aggregating the non-significant factor levels ("Inside Territory/Uncaged", "Outside Territory/Uncaged", and "Inside Territory/Caged"). P=0.05, thus the mean number of spat per plate in the "Outside Territory/Uncaged" treatment was significantly greater than the mean number of spat per plate in the other three treatments. B) Dispersal rates of fluorescene dye from the plate underside for simulated treatments. Different letters above bars mean significant differences in dye dispersal rates determined by Tukey's honest significance multiple comparison test. Error bars are ±1 standard error.

#### Settlement Substrate Selectivity and Larval Availability

When coral larvae had access to the plate undersides, a high percentage settled directly on crustose coralline algae (hereafter abbreviated as CCA), despite its low abundance. Over half of all spat in the outside 1.5 cm perimeter of the plate undersides were found specifically on the CCA *Titanoderma prototypum* (27.5%), and on other species of CCA combined (23.5%) (Figure 5). Spat appear not to be settling arbitrarily on substrates (Figure 5). If spat settled on substrates in proportion to their abundance, the percentage of settling spat would approximate the percentage of substrate available on the plate underside, with all data points falling along the line of equal selectivity in Figure 5. Clearly, *T. prototypum* and CCA had settlement densities much higher than their abundance (i.e. they facilitate coral settlement (Figure 5), and do so irrespectively of

coral species since spat settling on *T. prototypum* were 94.6 % *Agaricia* spp. and the overall makeup of spat on all substrates was 88.8 % *Agaricia* spp.). Conversely, turf algae and encrusting invertebrates had few settlers relative to their abundance, so they appear to inhibit coral settlement. The high incidence of settlement on polychaete worm tubes is in line with the finding that many marine invertebrate larvae prefer irregular settlement substrata, including annelids (Knight-Jones 1951, Carleton and Sammarco 1987). All other natural substrata fell along the line of equal selectivity. Once it develops a thin layer of biofilm, bare terra-cotta, though an unnatural substrate, appears to be a suitable substrate for settling corals.

On the outer 1.5 cm perimeter of plate undersides, substrate-specific population densities were greatest on polychaete worm tubes, followed by *Titanoderma prototypum*, other species of CCA, bare terra-cotta, *Peyssonnelia spp.*, and invertebrate crusts respectively (Figure 6). Some substrates, such as polychaete worm tubes, with high spat density are relatively unimportant for settling corals because they occupy such little surface area (Figure 5).



**Figure 5.** Substrate selectivity of settling corals shown by the percent cover of potential settlement substrates growing on the 1.5 cm perimeter of plate undersides (see Figure 1) with corresponding settlement and a drawn line of equal selectivity. Settlement selectivity data is based on the preferences of the 251 spat that settled in the subcryptic settlement microhabitat (Figure 1). The percent cover of fouling organisms on the plate underside was recorded at the time of first observation of the newly settled spat. Error bars are  $\pm 1$  standard error.





**Figure 6.** Spat densities of per cm<sup>2</sup> of substrate on the outside 1.5 cm perimeter of the undersides of uncaged settlement plates. Status of facilitators and inhibitors were determined in previous figure. Error bars are  $\pm 1$  standard error.

To determine the contribution of localized larval availability to coral settlement, we measured settlement densities on facilitator substrata (i.e. Figure 5) in our four experimental treatments over time. We assumed that if competent larvae came in contact with cues from these facilitator substrates, they would metamorphose and settle on them.

Settlement on plates inside of damselfish territories was reduced after the first plate monitoring in June 2004. At this time, a subset of plates was affixed with wire mesh cages. Turf algae gradually fouled the cages following their deployment in June 2004. Two months following installation, with minimal algal fouling of the cages, settlement rates remained lower among plates inside of damselfish territories, but had dropped off on caged plates outside of territories. By November 2004, the cages were fouled with turf algae, and settlement on the caged plates outside of territories had dropped to rates similar to those plates inside of damselfish territories. To test for reductions in settlement due to reduced larval availability from algal fouling, we compared the rates of settlement in each of the four treatments in the summer of 2004 before fouling occurred to settlement rates in the summer of 2005, following algal biomass increases on the cages. The deviation in rates of settlement between the treatments on standardized densities of coralline crustose algae (facilitator species) support the importance of larval availability (Figure 7. A.). By the summer of 2005, after the plates were adequately conditioned with biofilms and other successional species making conditions better for settlement, only uncaged settlement plates outside of damselfish territories had increased settlement rates on these facilitators (Figure 7. B.). Settlement on plates inside territories remained low or declined slightly, and settlement outside of territories (initially well-grazed) that were caged in June 2004 declined significantly.



**Figure 7.** Changes in rates of coral settlement on CCA resulting from elevated algal abundance surrounding but not on the settlement microhabitats (i.e. inside damselfish territories and inside algal fouled cages). A) The deviation from initial annual settlement (2004) for the treatment "Outside Territory/Uncaged" was significantly greater from all other treatments (no overlap of 95% CI). B) "Outside Territory/Uncaged" treatment's increase in settlement from 2004 (after 158 days) to 2005 (after 486 days) was significant (*t*-test, P=0.035). Conversely, when a cage was added to a well grazed area, settlement declined significantly (Outside Territory/Caged treatment P=0.048). Error bars are ±1 standard error.

Coral spat settled preferentially on early successional substrates. Abundance of "recruitment facilitators", specifically *Titanoderma prototypum* and other CCA declined over time (Figure 8. A.), whereas the plates became increasingly fouled with heterotrophic successional species inimical to settlement and survival, or "recruitment inhibitors" such as invertebrate crusts and turf algae (Figure 8. B.).



**Figure 8.** Succession of recruitment facilitator species (A. *Titanoderma prototypum* and other coralline algae) and recruitment inhibitors (B. turf algae and invertebrate crusts) over time on the outside 1.5 cm perimeter of plate undersides in all treatments.

#### Early Post Settlement Survivorship

Average cohort survivorship was 18% after 365 days, and despite slightly different trajectories, mortality converged to a value greater than 90% for those cohorts followed for nearly 2 years (Figure 9). A closer look at post-settlement survival of the August 2004 cohort (the cohort with observations closest to a 12 month time frame) revealed that only recruits in the well-grazed treatment (uncaged, outside of a damselfish territory) had significantly greater survivorship (Figure 10). This cohort consisted of 87.0% *Agaricia spp.*, 6.5% *Porites sp.*, and 6.5% unidentified spp.



**Figure 9.** Survivorship curves for each cohort (including all treatments) from each subsequent monitoring period. A 5th order polynomial trendline curve fits all cohorts in bold, highlighting an average survivorship of 18% after 365 days and overall mortality converging to greater than 90% by the end of the study.



**Figure 10.** Proportion of August 2004 cohort (n=27) surviving in the four treatments during the first year of life. Survivorship of the cohort in treatment "Outside Territory/Uncaged" was significantly greater (ANCOVA, P=0.004; no overlap of 95% CI) than the other three treatments.

Of the spat that settled on the plates from March 2004 through June 2006, very few survived to large size, but a high percentage of the survivors were found under fully grazed conditions. The mean yearly growth rate of the *Agaricia spp*. spat monitored over the course of the study period was  $3.46 \pm 0.47$  SE mm. In the uncaged plates outside of territories 51.2% of the spat observed survived past 3.5 mm in diameter. Pooling the other three treatments resulted in decreased survivorship, with only 32.3% of spat surviving beyond 3.5 mm (Figure 11). Considering only the surviving *Agaricia spp*. spat from the August 2004 cohort (n=25), those in the well-grazed treatment (uncaged plates outside of territories treatment, n= 13) had greater survivorship over time (Figure 12). Pooling the three other treatments (only n=12) resulted in only one spat surviving beyond 200 days and zero spat surviving until the final monitoring in June 2006.



**Figure 11.** Size frequency of all *Agaricia spp.* observed alive on June 2006 in grazed habitats on uncaged plates outside of damselfish territories (A.) and on plates in all

**Figure 12.** Size frequency of surviving *Agaricia spp*. cohort (spat settled between June 2004 and August 2004, n=25) over the duration of 23 months.



indicates percentage of spat in each size class. The age of surviving spat can not be other treatments, less grazed damselfish territories and algal fouled cages (B.). Y-axis

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#### Discussion

Our study suggests there may be a dynamic balance between the positive effects of facilitators and the negative effects of turf algal abundance and other inhibitors that limit coral settlement and survival. Elevated abundance of turf algae within centimetres of possible settlement habitats decreased the recruitment potential of reefs by impeding larval access to settlement habitats and decreasing post-settlement survivorship. Thus, this dynamic interaction affects recruitment at several points during and immediately following larval settlement. We view this "gauntlet" as a series of sequential processes necessary for successful coral recruitment, 1) the availability of competent larvae, 2) their propensity to settle, and 3) available nursery habitats (i.e. microhabitats where post-settlement mortality is low). We found that the highest proportion of surviving coral spat successfully ran the gauntlet under conditions of relatively low turf algal biomass (Figure 13).



**Figure 13.** Conceptual model of sequential processes leading to coral recruitment to the benthos (i.e. "the gauntlet"). Arrows to the right represent possible recruitment limitation due to demographically significant bottlenecks. Arrows down indicate a coral larva's successful progression through the sequential steps to recruitment.

What reduces larval availability to subcryptic settlement microhabitats will reduce coral settlement. We used the density of coral spat on settlement-facilitating substrates (i.e. crustose coralline algae; Figure 5) as a measure of larval availability (Figure 7). We reasoned that at this microhabitat scale (Figure 1), spat will readily settle on inducing substrata when present (Raimondi and Morse 2000, Harrington *et al.* 2004) so the resulting spat densities on these substrates reflect the abundance of competent larvae.

Over the first 158 days of the experiment, the settlement density on coralline substrates did not vary among treatments (Figure 7. B.). However, over the next year, only the well-grazed uncaged plates had elevated rates of settlement (Figure 7. A.). The other turf-covered cages and damselfish territories maintained the same or slightly lower rates of settlement (Figure 7. A. & B.). We interpret these results to indicate that there were more larvae available to settle in 2005 than 2004, but the turf-fouled plates and their lower rates of larval advection and flushing (Figure 4) prevented larvae from accessing settlement substrata on all but the fully grazed treatment. Thus, the cage effect of reduced larval availability to subcryptic habitats may mimic the effect of macroalgal dominated or damselfish garden-dominated coral reefs. However, when extrapolating the results of this study to the greater Caribbean, it is important to consider that no amount of turf algal fouling can simulate the inhibitory characteristics of a dense cover of macroalgae, such as *Halimeda opuntia*.

Coral larvae undergo a sequence of behavioral changes that put them at specific depths, seeking specific light intensities and often illuminated cryptic spaces just prior to contact with the benthos (Raimondi and Morse 2000). Once in close proximity to the benthos, coral larvae that detect biologically derived chemical signals metamorphose and settle (Morse *et al.* 1988). The abundance of encrusting coralline algae is often linked to the recruitment potential of the benthos (Edmunds and Carpenter 2001, Steneck *et al.* 2004). Lab studies illustrate that larval selection and survival can be enhanced by the Pacific equivalent to the Caribbean crustose coralline alga species, *Titanoderma prototypum* (Harrington *et al.* 2004).

We found that spat settle preferentially on *T. prototypum* (27.5%) and other coralline crusts (23.5%) despite their low abundance (Figure 5). Unlike studies in the Indo-Pacific, where *Titanoderma sp.* was by far the strongest facilitator of coral recruitment, we found other subcryptic coralline species performed as well as *T. prototypum*. These substrates do not appear to facilitate a particular species or group of corals. The overall spat composition was 88.8% *Agaricia spp.* and the makeup of spat settling on *T. prototypum* was 94.6 % *Agaricia spp.* Our overall spat composition was in line with juvenile coral species composition on natural substrates in Bonaire dating back over 30 years. A study done by Bak and Engel (1979) in 1975 found the species composition of naturally recruiting juvenile corals to be 80.6% Agaricia spp. and 7.60% *P. astreoides.* 

The well-established role of scraping herbivores such as parrotfishes and sea urchins on coral reefs and encrusting coralline algae (Steneck 1988, 1997; Steneck and Dethier 1994) may be necessary for facilitating coral settlement. Thus, both the low algal biomass and high abundance of crustose coralline algae in Bonaire may work together to increase coral settlement by improving larval availability and increasing the propensity for coral settlement. In contrast, algal overgrowth may impede larval access and create an environment hostile to these facilitator species (Steneck 1997), as was evident in the caging treatments.

While particular settlement substrates did not improve survivorship of spat, the availability of subcryptic habitats was important. This brings up some of the pros and

cons of using terra-cotta plates as an artificial settlement substrate. For experimental purposes, this desired subcryptic settlement habitat is difficult to standardize. While the plates have a simplified geometry that is internationally consistent, the smooth fired terracotta lacks the interstices and crevices found on natural reef substrate. Plate undersides are known to be important for settling larvae of some species (Carleton and Sammarco 1987, Maida, et al. 1994, Raimondi and Morse 2000, Steneck et al. 2004). Our study found, more specifically, that 83% of all spat settled in the outside 15 mm perimeter of the plate underside (Figure 1), demonstrating the importance of tracking succession in this subcryptic settlement microhabitat. This preference for settlement on the undersides of plates doesn't preclude settlement onto natural irregular spaces on upper surfaces of the reef that the plates didn't replicate; however, hospitable habitats on upper surfaces in the Caribbean may be declining. Vermeij (2006) compared his recruitment study in Curacao, Netherlands Antilles, from 1998-2004 to that of Van Moorsel's (1989) from 1979-1981 in the same location. Recruit density on the top-sides of settlement panels in the more recent study were 5.16 times less than the 1979-1981 study, whereas recruitment on the undersides was only 1.14 times less. Macroalgae had replaced CCA as the dominant top-side space occupier in the later study and spawning species were no longer recruiting. Another inherent methodological problem with measuring recruitment with settlement plates is that the plates can't easily be standardized for water flow. Much of the settlement variance within treatments could be due to the placement of the plate on the reef. In several cases, those plates on topographical highs had greater settlement rates than neighboring plates in the same treatment placed in depressions. We attributed this increase in settlement to enhanced advection of available larvae to the plate underside.

Succession changes the receptivity of subcryptic habitats to coral settlement. During the course of our experiment, the underside perimeter of plates became increasingly fouled with turf algae and heterotrophic successional species inimical to settlement and survival, like invertebrate crusts (Figure 8). Recruitment facilitators, T. prototypum and other CCA species increased in abundance rapidly within the first half a year, but by day 257, their abundances declined through the duration of the study. Since thinner crusts are more easily overgrown, crustose coralline algae, particularly T. prototypum, lose out to competition in the long run due to their thin thalli (Steneck et al. 1991). In an intensely competitive environment like the underside of a foliaceous coral (or settlement plate), the growth of one organism, comes at the expense of another (Jackson and Hughes 1985). Hence, it was not surprising that the abundance of recruitment inhibitors, turf algae and the even more detrimental invertebrate crusts, continued to increase. Invertebrate crusts accounted for approximately 50% of the substrate in the perimeter by the last monitoring period. Thus, it is possible that immediately following a disturbance that bares primary substrate, a "recruitment window" develops, during which time early successional species such as *Titanoderma prototypum* (see Adey and Vassar 1975, then *Tenarea prototypum*) become established before being outcompeted by the recruitment inhibitors. During this window, spat are more likely to successfully "run the gauntlet" of recruitment and recruit to the population due to the presence of more hospitable settlement substrates.

Post-settlement mortality generally converged over time to the same high mortality of approximately 90% after nearly two years (Figure 9). Although survivorship was not

improved on these early successional species, there did appear to be a treatment effect. Spat in the fully grazed treatment (uncaged plates outside damselfish territories) showed increased survivorship over the other three treatments (Figures 10 & 11). Also, considering all agaricids over the entire study period, that treatment had a greater proportion making it to larger size classes (Figure 11). However, as observed by Richmond (1997), survival was not merely a function of the attributes of the settlement substrate, but of the ability to resist overgrowth by algae and encrusting invertebrates. As recruits grow, their mortality rates are expected to decline and they are less likely to be overgrown by competitors (Hughes and Jackson 1985). Often, the slow growth rates of newly settled corals make this a losing battle.

As the decline of Caribbean reefs persists, so too does the dichotomy surrounding the current thinking of why they fail to recover. Is it a supply-side story, with corals failing to recruit as a result of the loss of adult populations and decreased larval pool, or is it more of a local story, due to decreased recruitment potential of the benthos (Hughes and Tanner 2000, Bellwood *et al.* 2004)? Whereas previous studies (e.g. Hughes and Tanner 2000) suggested that recruitment declines may result from the loss of reproductive potential due to adult mortality, we propose that the herbivory-induced receptivity of the reef may be most important to recruiting corals. In Jamaica, where live coral cover was remarkably low (e.g. Hughes 1994), as herbivorous sea urchins increased in abundance, so did the abundance of juvenile corals (Edmunds and Carpenter 2001) and ultimately adult corals (Idjadi *et al.* 2006).

This study suggests that herbivory, or the lack thereof, at a very local scale explains a considerable portion of the variance associated with coral recruitment. The management implications are obvious. First, the conservation of herbivorous fish, especially parrotfish, may be critical for reef recovery due to their positive effects on the recruitment potential of reefs. Second, if large predators control damselfish abundance (Hixon and Beets 1993), then predator abundance may indirectly control the availability of subcryptic coral nursery habitats on reefs. This scenario would suggest an importance of large damselfish populations beyond their ability to act as biological cages used to mimic reduced herbivory systems, and may lend support to not only preserving herbivores, but also carnivores in order to keep prey populations, such as damselfish, in check. Finally, given the demonstrable evidence of the importance of a small spatial scale to recruitment and increased evidence pointing towards the limited larval dispersal kernal of corals (Sammarco and Andrews 1988), might we rethink the magnitude of the larger scale supply-side component, rely less on potential spillover from healthier upstream reefs, and direct our focus more locally (Steneck 2006)? While massive die-offs on reefs can be caused by pulse events, successful coral recruitment is a highly variable, long-term process requiring optimal conditions for the completion of three sequential steps. Managing for the receptivity of a local reef through the conservation of local fish stocks can help corals successfully run the gauntlet of recruitment and aid in reef recovery and resilience (Hughes et al. 2007).

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# Chapter 7: Juvenile coral and associated macroalgal abundance observed in space and time on Bonaire Reefs

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### Abstract

Juvenile coral ( $\leq$  40mm diameter) densities and macroalgal abundance were quantified in Bonaire in 2007 at six monitored reefs and compared to past studies in 2005. Since 2005 both juvenile coral density and macroalgal abundance increased throughout the monitored reefs. Among sites there is an inverse relationship between algal abundance and juvenile coral density. Although algal abundance in Bonaire remains low, if abundances continue to increase, coral recruitment may decline thereby reducing the resilience of Bonaire's reefs.

### Introduction

In recent decades, many coral reefs shifted from coral to algal dominance (Hughes 1994, Hughes *et al.* 2007). The reefs of Bonaire are an exception in that they are still dominated by corals, and macroalgae are relatively rare (Kramer 2003). Studies have shown that the long term survival of reef systems rely greatly on successful coral recruitment (Kojis and Quinn 2001). However coral recruitment can be jeopardized by macroalgae. Increased macroalgae on coral reefs can kill corals by smothering them and blocking available sunlight (Lewis 1986, McClanahan *et al.* 1999, Kramer 2003). Significantly, it also reduces the amount of available substrate conducive to coral settlement (Birkeland 1997, Hughes 1994, Lirman 2001, Steneck *in prep.*).

The objective of this study was to quantify and monitor juvenile coral recruitment and demography relative to the macroalgal abundance in the habitat in which they live. For this, data were gathered in the spring of 2007 and compared to previous studies using the same methods during the same month in 2003 and 2005 (Slingsby and Steneck 2003, Brown and Arnold 2005). Specifically, I seek to determine if coral recruitment and algal biomass is increasing, decreasing or holding constant.

## **Methods and Materials**

The methods followed by this study were from Brown and Arnold (2005). The study was conducted at six monitoring sites in Bonaire; Forest, Plaza, Windsock, Barkadera, Reef Scientifico and Karpata, where a 25cm X 25cm quadrat was placed every two and a half meters along a ten meter transect located at the monitored locations marked by settlement plates at a depth of 10 meters. Four such transects were surveyed at each dive site. Quadrats were placed on substrate amiable to coral recruitment few adult corals (< 25%)
and little sand or holes. I recorded species and size of juvenile corals (those  $\leq 40$  mm in diameter (Rogers *et al.* 1984)) as well as the percent cover of macroalgae, turf algae, coralline algae, and live coral present within the quadrat. Canopy height measurements were recorded for macroalgae. A proxy for algal biomass, called algal index (Kramer 2003), was calculated by multiplying percent cover by canopy height (mm).

#### Results

Overall average juvenile coral abundance, for Bonaire, was 39.2 individuals per m<sup>2</sup> ( $\pm$  2.3 SE). This is greater than the density of juvenile corals per m<sup>2</sup> recorded in 2005 (20.0  $\pm$  SE of 1.9 individuals per m<sup>2</sup>) and 2003 (23.2 individuals per m<sup>2</sup>) (Figure 1). Note, however, that unlike the 2005 and 2007 data, the 2003 data is not from the same marked transects. Among sites, "Reef Scientifico" and "Forest" had the highest and lowest density of juvenile corals per m<sup>2</sup> respectively (Figure 2). Algal biomass approximated using an algal index found four times greater algal abundance in 2007 then was found in 2005 (Figure 3).

Agaricia agaricites and Porites astreoides were the most abundant juvenile corals in 2007 and in 2005 (Figure 4). A slight inverse relationship between macroalgal abundance and juvenile coral abundance ( $R^2=0.2$ ) was recorded in 2007 (Figure 5). In 2005, macroalgae were uniformly rare, preventing a similar regression analysis (Figure 5).



#### Juvenile Coral Abundance in Bonaire

**Figure 1.** Comparison of the overall average juvenile coral densities ( $\leq$  40 mm diameter) from the spring of 2003 (data from Slingsby and Steneck 2003), 2005 (data from Brown and Arnold 2005) and 2007.



Juvenile Coral Density by Site

**Figure 2.** Comparison of juvenile coral densities by site between the spring of 2005 (data from Brown and Arnold 2005) and the spring of 2007.



**Figure 3.** Overall average macroalgal indices (%cover of macroalgae\* macroalgae canopy height in mm) of all sites in the spring of 2007 compared with data from the spring of 2005 (data from Brown and Arnold 2005).



**Figure 4.** Coral abundance by species in 2007 compared with 2005 (data from Brown and Arnold 2005).



### Macroalgae and juvenile coral interactions

**Figure 5.** Comparison of the relationships among macroalgal abundance and juvenile coral abundance between the spring of 2005 (data from Brown and Arnold 2005) and the spring of 2007.

#### Discussion

No clear trend in juvenile coral densities are apparent since 2003. In contrast, macroalgae seem to be increasing significantly at several sites in Bonaire. The increase of macroalgae may be cause for concern. Similar increases have been observed throughout the Caribbean over the past two decades and are most likely due to a decrease in grazing herbivores on the reefs (Hughes 1994, Williams and Polunin 2004). Declines in herbivorous reef fishes (Williams and Polunin 2001) and the mass mortalities of the urchin *Diadema antillarum* (Hughes 1994) resulted from overfishing of herbivorous fish and the disease of urchins (Hughes and Tanner 2000). Given the strong negative relationship between macroalgal biomass and coral recruits (Birkland 1997, Brown and Arnold 2005) the preservation of herbivores may be critical to re-establishment of corals following disturbance.

This study suggests an increase in juvenile coral densities since 2005. This is a positive result for the status of Bonaire's reefs. However, if macroalgal abundance increases on a long-term basis, effort towards the restoration of herbivore population densities should be a priority of managers in Bonaire. Increases in juvenile coral density also increase coral diversity which could increase the stability of the reef, making it more resistant to and resilient from disturbances (Bellwood *et al.* 2004). Given the troubling results of this study further monitoring of coral and macroalgal abundance is advised.

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# **Chapter 8: The impact of traditional fishing practices on the abundance of major herbivorous fish species in Bonaire, Netherlands Antilles**

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#### Abstract

Fishermen surveys were conducted among inshore fishing communities during March of 2007 to better understand the level of fishing effort and the composition of the catch. Results suggest that the inshore fishermen rely mostly on pelagic fish and carnivorous reef fish such as barracuda, groupers, snappers, graysbies, and conies. Inshore fishermen who do not own a boat, fish from the shore and appear to be more opportunistic. They fish across all trophic levels of coral reef fish community. Compared to most Caribbean reefs where fish traps are heavily deployed and spear fishing is rampant, Bonaire's reefs have relatively low fishing pressure. Importantly, fishing pressure on, and landings of, parrotfish are relatively low. However, even though parrotfish are enjoying high level of protection from fishing, mainly due to the ban of spear fishing in Bonaire, recent demographic changes may be resulting in higher fishing pressure on this group. This could have an impact on the reef fish community structure if more stringent fishing regulations are not put in place.

#### Introduction

Overfishing is thought by some to be the largest threat to marine ecosystems by disrupting the structure and function of marine food webs (Jackson *et al.* 2001; Myers and Worm 2003; Myers and Worm 2005; Pauly *et al.* 2005; Worm *et al.* 2006). In tropical marine ecosystems, coral reef fishing can be the major cause for the reduced biodiversity (Roberts 1993; Roberts 1995; Pandolfi *et al.* 2005).

Throughout the Caribbean, fishing is recognized as an important part of cultural, economical, and social environment. Most Caribbean fisheries are small-scale and rural (Mahon and McConney 2004) relying on traditional fishing methods (Johannes 1997). Many artisanal fishing communities depend on fishing as a principal mean of financial support and food supply (Birkeland 1997; Mahon *et al.* 2003). Some 60,000 artisanal fishers target coral reefs in the Caribbean bringing approximately 180 species of reef fishes to market (Birkeland 1997). With increasing human populations, the number of people depending on fish protein has also increased. Growing number of artisanal fishermen and their greater mobility facilitated by technological improvements allowed for the increase in fishing intensity, negatively affecting the abundance of coastal fish stocks (Roberts 1995; Hawkins and Roberts 2004). Although predator species are initially targeted (Bellwood *et al.* 2004; Pauly 2005), their removal leads to targeting species at lower trophic levels, a process known as "fishing down marine food webs" (Pauly 1998).

Local fishing practices affect the composition of the catch. This allows fisheries managers to limit fishing on important and highly interactive fish species. For example, herbivory is a major ecosystem driver of coral reef ecosystems (Mumby 2006; Hughes *et al.* 2007). When herbivory declines coral reefs switch from live coral to seaweed dominated ecosystem (Bellwood *et al.* 2004; Bellwood *et al.* 2006; Hughes et al. 2007). Such "phase shifts" (*sensu* Hughes 1994) result in reduced resilience (Bellwood *et al.* 2004).

The key herbivores on Caribbean reefs are the fish families Scaridae (parrotfish) and Acanthuridae (surgeonfish), and an echinoid species *Diadema antillarum* (long-spined sea urchin). With the mass mortality of *Diadema* in the early 80's, most coral reefs that had already lost herbivorous fish due to overfishing experienced a rapid phase shift (e.g. Jamaica, Hughes 1994). A few places in the Caribbean that have maintained ecologically viable herbivorous fish communities may serve as an example for which processes maintain resilient reefs. Recent research indicates certain herbivorous functional groups can prevent harmful phase shifts. According to Mumby *et al.* (2006), with the *Diadema* die off, parrotfish have become the major grazer on Caribbean reefs. Therefore, it is important to determine the fishing pressure on parrotfish to determine if stocks are at risk. If they are, managers should know this and find ways for their protection allowing parrotfish to maintain their ecological function, thus providing a healthy coral reef ecosystem.

The coral reefs of Bonaire, Netherlands Antilles, are among the healthiest reef ecosystems in the Caribbean (Kramer 2004). In this study, I evaluated the impact of traditional fishing practices on the major herbivorous fish species on the coral reefs of Bonaire. I also discuss ways of improving protection of reefs from artisanal fishing.

#### **Materials and Methods**

In March 2007, 11 interviews, in the form of questionnaire (Appendix 1), were conducted among the inshore fishing community of Bonaire (Figure 1). *Inshore fisherman* was defined as any fishermen whose boat is powered by an outboard motor or by man power (rowing). In addition, fishermen who did not own a boat and fish either from the shore or borrow someone else's boat were also considered inshore fishermen. The distinction between full-time and part-time fisherman was established on the basis of days actively fishing. If a fisherman was fishing more than two days per week he was considered a full-time fisherman. Each questionnaire contained 23 questions: six questions were of the general character, asking information about the fisherman's background; eight related to fishing effort; and the last nine dealt with the fishing preferences (species). Four of the interviewed fishermen were from the small fishing village, located at the Northwestern tip of the island, Playa Frans, while the rest were form the Klarendijk region. Data from the questionnaires were transferred and stored into a Microsoft Access database from which the queries regarding fishing effort and fishing preferences were generated in order to search for any major trends.

#### Results

The number of inshore boats was the highest in the Klarendijk area (Figure 1). The other two fishing communities are Playa Frans and the Lac region (Figure 1). The total number of fishing boats was 130, with more inshore than offshore vessels (Table 1). There are two major fishing seasons in Bonaire according to the inshore fishermen (Figure 2). One season is for offshore and coastal pelagic fish species such as tuna, wahoo, and dolphinfish, while the other season is largely focused on deep-water fish, red snapper, and reef associate barracuda (Figure 2). Additionally, reef associated fish such as yellowtail snapper, coney, graysby, and red hind are not targeted in a specific season, but are recognized as important species for fishermen.



**Figure 1.** Location of the study sites on Bonaire and associated number of inshore and offshore vessels for every harbor on the island.

Vessel type	Number
Inshore	98
Offshore	32
TOTAL	130

Table 1. Total number of vessels in Bonaire at the time of the study.

Background questions revealed that eight fishermen stated tradition as the major reason for becoming a fisherman, six fish as a source of additional income while only one fisherman characterized fishing as a primary source of income. Six fishermen declared to be part-time while the other five considered fishing as a full-time job. Most of the fulltime fishermen acknowledged becoming full-time after retiring. Nine fishermen mentioned local knowledge as the major factor when deciding on where to go fishing; personal knowledge was mentioned by seven of the fishermen. The fishing expenses averaged ( $\pm$  SD) at US \$24.67  $\pm$  10.19 per trip (Table 2).



**Figure 2.** Major species fished in Bonaire and their corresponding habitat and approximate fishing seasons. Names for every species are given in English and Papiamento with the maximum recorded weight in kg. Species are arranged from the offshore pelagic at the top of the figure to reef associates at the bottom. Image size for every species is approximated to the maximum recorded length in cm (fish images courtesy of www.rodnreel.com and www.boat-ed.com).

Fishing effort in Bonaire is relatively low. Fishing consists of daily fishing trips that are in deep, near shore waters (Table 2). Even though most of the fisherman fish alone, it is not uncommon to go and fish with a friend or family. The most common type of fishing gear used is handline. Nine out of 11 fishermen fished using this method, while two reported fishing with a rod. Only one of the fishermen reported fishing with a net occasionally. Nine fishermen own a boat and of which eight have an engine (Table 2). Seven boats are over 10 years old and none of the boats has GPS or onboard freezer.

Question Topics	Average Responses +/- SD	units	sample size (n)
Distance from the coast while fishing	260.00 +/- 124.28	meters	10
Water depth at the fishing site	99.11 +/- 58.21	meters	9
Boat length	4.00 +/- 0.94	meters	9
Boat motor horse power	19.75 +/- 9.95	HP	8
Catch size	12.71 +/- 6.95	kilos	7
Expenses per trip	24.67 +/- 10.19	US \$	10
Length of fishing trip	6.85 +/- 1.25	hours	10
Fishing per week	3.45 +/- 2.15	days	10

**Table 2.** Measures of fishing effort per fishing trip presented as the average  $(\pm SD)$  with corresponding units and sample size.

Fish species preferred by fishermen are wahoo, grouper, snapper, dolphinfish, tuna, and barracuda. Of these, only the grouper, most snapper species, and barracuda are reefdwellering fishes. Coral reef fishing is limited by Bonaire's laws prohibiting anchoring on or near coral reefs. Only traditional fishermen using traditional stone anchors can anchor on reefs. This seriously limits the boat size that can fish on reefs. Coral reef fishing targets grouper, snapper and coney. The size of the catch averaged ( $\pm$  SD) at 12.71  $\pm$  6.95 kg, but the content of the catch was highly variable (Table 2). None of the fishermen who owned a boat or could borrow one to go fishing suggested that he was catching parrotfish. However, the only surveyed participant who fishes from the shore commented that he was catching parrotfish mostly for selling at the local market. There was no clear species preference associated with parrotfish fishing. When asked about any potential change in fish abundance within the last 10 years, eight fishermen responded that there are fewer fish now than in the past and that they are forced to go further offshore to catch fish. One participant commented that the number of grouper increased after the ban on spear fishing was introduced.

#### Discussion

The inshore fishermen depend primarily on the pelagic fish species. Certain reef fish species, even though still popular among fishermen such as groupers and snappers, were reported to be declining in numbers on Bonaire's reefs (Hoetjes *et al.* 2002; Steneck and McClanahan 2003; Hawkins and Roberts 2004). General decreases in abundance of the large carnivorous fish coupled with the increase in the fishing pressure lead to the shifts in fishing towards species of lower trophic levels (Hawkins and Roberts 2004). In Bonaire, because of the relatively abundant pelagic fish, this shift is not so apparent among inshore fishermen. In the case of pelagic fish, it is hard to adequately estimate the size and health of the stock because of the size of the area they inhabit and the complex migration patterns (Mahon and McConey 2004). Especially it becomes difficult to scale down in space and predict the patterns in local abundance (Mahon and McConey 2004). Inshore fishermen recognized that there was a noticeable decline in the abundance of these stocks in last 10 years. Mahon and McConey (2004) suggested the perception of

locally abundant pelagic fish is a function of changes in regional and local dynamics and may not be representative of the entire stock.

Parrotfish in Bonaire still remain abundant, but this biomass has dropped steadily since 2003 (Brown and Hansen 2005 and Alvarado 2007 this report). Hoetjes *et al.* (2004) also confirms that parrotfish are abundant in Bonaire and recognizes that fishermen do not normally target them. Similarly, I found that inshore fishermen who own a boat, or borrow one, do not fish for parrotfish. In contrast, Belize fishermen reported that parrotfish was the second most commonly landed species at Glover's Reef (Gibson and Hoare 2006). 20% of the ten most commonly fished species in Belize were parrotfish. The ongoing study found that grazing rates in Belize are lower than those in Bonaire (Mumby, *in prep.*). When compared to Bonaire, Belizean fishermen are fishing at lower trophic levels (Table 3).

Bona	ire	Belize			
Species	Trophic level	Species	Trophic level		
Barracuda	4.5	Barracuda	4.5		
Wahoo	4.4	Parrotfish	2.0		
Grouper	4.1	Blackfin snapper	3.8		
Yellowtail snapper	4.0	Hogfish	3.6		
Dolphinfish	4.4	Mutton snapper	3.9		
Tuna	4.3	Stoplight	2.0		
Coney	4.0	Yellowtail snapper	4.0		
Graysby	4.2	Black grouper	4.5		
Red hind	3.9	Nassau grouper	4.1		
Red snapper	4.0	Schoolmaster	4.2		
Average	4.2	Average	3.7		
SD	0.2	SD	0.9		

**Table 3.** List of the most commonly fished species in Bonaire and Belize and their corresponding trophic levels (apex predators have the highest number, >4; intermediate predators are 3; and herbivores are 2). Comparison is done in terms of the average ( $\pm$ SD) trophic level between the two countries. Data on trophic levels obtained from fishbase.org.

The exploitation of parrotfish is also evident in many other parts of the Caribbean (Mumby *et al.* 2006), including Curacao (Hoetjes *et al.* 2004), and the rest of the world (Bellwood *et al.* 2004). Historical perspective suggests drastic shifts in species catch composition (Birkeland 1997). During the 1950's, a large majority of the catch consisted of grouper, whereas parrotfish represented less than 1% of the total catch. The percentage of parrotfish increased greatly over time (Birkeland 1997). Apart from the decline in preferred carnivorous fish species, Bellwood *et al.* (2004) mentioned another factor as a contributor to the increasing fishing pressure on coral reefs- power of the free market. The free market can operate locally or globally. Locally, the simple demand for protein shifted demand and value to lower trophic levels, i.e. from carnivorous to herbivores. This transition happened decades ago in Jamaica (Hughes 1994) and may be happening now in Belize (Table 3). The other, more recent, driver is the globalization of reef fisheries (Bellwood *et al.* 2003, Berkes *et al.* 2006). Fish of low local value may be very valuable in a distant market and may be capable of receiving a very high price locally. Cultural diversification also introduces new fishing pressure on locally low-

value species. In Bonaire, some Asian immigrants seek and highly value parrotfish. Thus, with constantly increasing demand for fish protein, high retail prices have allowed for the exploitation of previously uneconomical fish markets and species, creating long-term ecological consequences: "The exploitation of reef fish, such as groupers and parrotfish, clearly illustrates a mismatch between the global demand for reef fishes and the fundamental role of functional groups in ecosystem resilience." (Bellwood *et al.* 2004).

In Bonaire, fish prices are not open to the free market forces but they are rather a product of command economy and government-regulated prices. With little exchange of fish product between neighboring countries (de Leon, *pers. comm.*), the relatively low population of Bonaire, and a command economy in place, fishermen have no incentive to fish more than they need to in order to support their families. Without financial incentives in place that could be created by the open economy and the free market, the race for fish and associated capitalization in vessels and gear appears to be absent. In the support of this argument my findings suggest that the inshore fleet consists of small and mostly old boats, which in most cases are powered by a small outboard motor. There appear to be no technological advancements present in the form of fish finders, GPS, or onboard freezers in the inshore fishery. There is also a high level of cooperation among local inshore fishermen in terms of sharing the information related to fishing and helping each other. In terms of local supply and demand, there is no information on how much local tourism industry affects fish catches. In the case of Curacao, Bruckner and Bruckner (2003) commented that Venezuela is the major fish supplier for local restaurants and markets.

Table 4. Current Status	of Fishing on Bonaire	
FISHING TRADITIONS	CURRENT FISHING REGULATIONS	PREDOMINANT CONCERNS
Fish traps rarely used	No spear fishing	Proliferation of trap fishery
Hook and line fishing	No anchoring on reef	Proliferation of parrotfish in catch
Fishing from shore or small boat		

Fishing practices are important (Johannes 1997). Different fishing methods select different species and different size ranges within species, which can have large impacts on the entire coral reef ecosystem (Roberts 1995; Hawkins and Roberts 2004). In Bonaire, there are strict fishing regulations (Table 4) that prohibit the use of any fishing method that is not considered traditional, which is defined by law (Bonaire Marine Environment Ordinance A.B. 1991 Nr. 8). Spear fishing has been also regulated in Bonaire since it was banned in 1971. The only traditional fishing gear that can be used effectively to catch parrotfish is fish trap (Mumby et al. 2006). There are approximately 20 active traps in Bonaire (de Leon, pers. comm.), but none of the fishermen I interviewed commented on actively fishing with them. Most of the interviewed fisherman use handline or pole, a practice that has little effect on parrotfish. The largest threat to parrotfish and other reef fish comes from fishermen who fish from the shore and whose number is not known at this time. They seem to be targeting parrotfish, which they would sell locally. In the case of Curacao, reef fish communities are reported to be overfished "as a result of heavy artisanal fishing pressure and the use of spearguns, fishtraps, and gill nets" (Bruckner and Bruckner 2003). Gibson and Hoare (2006)

reported that the most common gear type in Glover's Reef, Belize, was also handline, but spear gun fishing was the second most dominant practice which could explain such large catches of parrotfish.

Mumby *et al.* (2006) recognized that the herbivorous functional group is important to the stability of Caribbean reefs, where "even intermediate levels of [herbivorous] exploitation resulted in a steady decline of coral cover." Many authors recognize Marine Protected Areas, in the form of no-take areas, as a way of protecting herbivorous fish species from overfishing (Birkeland 1997; McClanahan *et al.* 2001; McClanahan and Mangi 2001; Hawkins and Roberts 2003; Mumby *et al.* 2006). However, a reduction in fishing pressure on this functional group is another mechanism which can lead to their increased protection. By regulating fishing practices and activities, protection can be extended beyond no-take areas. If we do not protect herbivorous fish outside the reserve, the question becomes whether the size of the protected areas will be large enough to provide sufficient levels of grazing outside of the reserve to prevent phase shift from occurring. In order to achieve the long-term goal of maintaining coral reef resilience, fishery managers must be prepared to provide broader protection to herbivorous fish than just an MPA.

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	Biomass (g/per 100		2		
	m <sup>2</sup> )	-	Density (# per	$(100 \text{ m}^2)$	
Windsock	Mean	SD	mean	SD	
Acanthurus bahianus	74.8	0	0.07	0.25	
Acanthurus chirurgus	357.9	0	0	0	
Acanthurus coeruleus	126.5	0	0.37	0.77	
Scarus iserti	100.3	98	0.15	0.50	
Scarus guacamaia	0	0	0	0	
Scarus taeniopteris	219.4	94.2	4.31	1.65	
Scarus vetula	341.7	194.6	0.83	0.74	
Sparisoma aurofrenatum	0	0	0.83	0.98	
Sparisoma chrysopterum	0	0	0	0	
Sparisoma viride	501.8	202.3	0.98	0.81	
Acanthuridae	141.8	122.9			
Scaridae	321.2	203.3			
Denuding (Acanthurids)	141.8	122.9			
Excavating (scarids)	321.2	203.3			
Algal removers (Acanthurids &					
Scarids	462.9	326.2			
Total	3111.2	1568			
				2	
			Density (# per	$r 100 \text{ m}^2$ )	
Plaza	Mean	SD	mean	SD	
Acanthurus bahianus	67.8	8.0	0.16	0.40	
Acanthurus chirurgus	0	0	0.25	0.35	
Acanthurus coeruleus	117.7	17.5	0.50	0.70	
Scarus iserti	308.5	22.9	0.75	0.73	
Scarus guacamaia	0	0	0	0	
Scarus taeniopteris	181.6	100.6	3.58	1.57	
Scarus vetula	386.4	177.9	1.16	1.31	
Sparisoma aurofrenatum	89.9	24.8	1.25	0.90	
Sparisoma chrysopterum	0	0	0	0	
Sparisoma viride	436.2	103.1	1.75	1.14	
Acanthuridae	97.2	29.5			
Scaridae	200.4	70.9			
Denuding (Acanthurids)	97.2	29.5			
Excavating (scarids)	200.4	70.9			
Algal removers (Acanthurids &					
Scarids)	297.5	100.5		ļ	
Total	2480.8	756.2	-		
			Density (# per	r 100 m <sup>2</sup> )	
Forest, Klein Bonaire	Mean	SD	mean	SD	
Acanthurus bahianus	60.9	0	0.15	0.38	
Acanthurus chirurgus	123.9	0	0.23	0.50	
Acanthurus coeruleus	126.5	0	0.30	0.56	
Scarus iserti	0	0	0	0	

## Appendix A. Average biomass and density of herbivorous fish, Bonaire 2007

Scarus guacamaia	0	0	0	0
Scarus taeniopteris	136.1	108.9	4.24	1.76
Scarus vetula	360.9	159.3	0.53	0.56
Sparisoma aurofrenatum	206.2	109.5	0.83	0.83
Sparisoma chrysopterum	0	0	0	0
Sparisoma viride	265.1	219.2	0.53	0.56
Acanthuridae	311.3	0		
Scaridae	968	597		
Denuding (Acanthurids)	311.3	0		
Excavating (scarids)	968.4	597		
Algal removers (Acanthurids &				
Scarids	1279.7	597		
Total	5118.8	2388		
			Density (# per	100 m <sup>2</sup> )
Reef Scientifico	Mean	SD	mean	SD
Acanthurus bahianus	82.7	11.2	0.58	0.26
Acanthurus chirurgus	0	0	0.08	0.88
Acanthurus coeruleus	126.5	0	0.33	0.58
Scarus iserti	184.9	0	0.25	0.56
Scarus guacamaia	0	0	0	0
Scarus taeniopteris	118.1	72.7	5.25	1.92
Scarus vetula	422.4	213.9	1.08	0.96
Sparisoma aurofrenatum	188.4	134.6	0.83	0.87
Sparisoma chrysopterum	0	0	0	0
Sparisoma viride	414.6	113.2	1.51	1.29
Acanthuridae	209.2	11.2		
Scaridae	1328.5	534.5		
Denuding (Acanthurids)	209.2	11.2		
Excavating (scarids)	1328	534.5		
Algal removers (Acanthurids &				
Scarids	1537.7	545.7		
Total	6150.7	2182.9		
			Density (# per	100 m <sup>2</sup> )
Barcadera	Mean	SD	mean	SD
Acanthurus bahianus	0	0	0	0
Acanthurus chirurgus	0	0	0.16	0.35
Acanthurus coeruleus	170.9	130.0	0.58	0.88
Scarus iserti	273.2	0	0	0
Scarus guacamaia	2502.4	441.7	0	0
Scarus taeniopteris	104.7	78.7	2.08	2.23
Scarus vetula	466	266.1	1.5	1.22
Sparisoma aurofrenatum	2119.1	1793.5	0.92	0.47
Sparisoma chrysopterum	354.7	0	0.16	0.35
Sparisoma viride	379.1	135.5	1.91	1.11
Acanthuridae	170.9	130		
Scaridae	6199	2715.6		
Denuding (Acanthurids)	170.9	130		

Excavating (scarids)	6199.4	2715.6		
Algal removers (Acanthurids &				
Scarids	6370.3	2845.6		
Total	25481	11382		
			Density (# pe	er 100 m <sup>2</sup> )
Karpata	Mean	SD	mean	SD
Acanthurus bahianus	61.6	20.6	0	0
Acanthurus chirurgus	53.4	0	0.16	0.35
Acanthurus coeruleus	138.9	43.6	0.42	0.58
Scarus iserti	290.6	24.6	0	0
Scarus guacamaia	0	0	0	0
Scarus taeniopteris	173.7	106.8	2.25	1.47
Scarus vetula	293.2	173.1	1.5	0.94
Sparisoma aurofrenatum	358.9	375.6	0.83	0.68
Sparisoma chrysopterum	0	0	0	0
Sparisoma viride	417.6	152.3	2.12	1.48
Acanthuridae	253.9	64.2		
Scaridae	1534.1	832.5		
Denuding (Acanthurids)	253.9	64.2		
Excavating (scarids)	1534.1	832.5		
Algal removers (Acanthurids & Scarids	1788.0	896 7		
Total	7152.1	3586.8		
	7152.1	5500.0	Density (# p	er 100 m <sup>2</sup> )
Bonaire Average	Mean	SD	mean	SD
Acanthuridae	1184.3	357.8		
Scaridae	10552	4953.9		
Denuding (Acanthurids)	1183.8	357.8		
Excavating (scarids)	10551	4953.3	1	
Algal removers (Acanthurids &			1	
Scarids	11775	5463.2		
Total	62118	168710		

	Biomass (kg/100 m <sup>2</sup> )		Density	(#/100 m <sup>2</sup> )
Windsock	Mean	SD	Mean	SD
Lutjanus apodus	0.8	8.8	22.0	14.6
Lutjanus mahogani	0.1	0.4	6.4	1.3
Ocyurus chrysurus	0.6	3.7	16.2	7.6
All predators	1.6	12.9	44.6	23.5
1 	Biomass (kg/100 m <sup>2</sup> )		Density	(#/100 m <sup>2</sup> )
Forest	Mean	SD	Mean	SD
Lutjanus apodus	0.48	46.8	15.7	4.77
Lutjanus mahogani	0.26	0.8	10.1	2.29
Ocyurus chrysurus	0.12	0	0	0
All predators	O.86	47.8	25.8	7.06
	Biomass (kg/100 m <sup>2</sup> )		Density	(#/100 m <sup>2</sup> )
Reef Scientifico	Mean	SD	Mean	SD
Lutjanus apodus	0.33	0.26	12.6	0.66
Lutjanus mahogani	0	0	0	0
Ocyurus	0	0	0	0
All predators	0.33	0.26	12.6	0.66
	Biomass (g/100 m <sup>2</sup> )		Density	(#/100 m <sup>2</sup> )
Barcadera	Mean	SD	Mean	SD
Lutjanus apodus	0.35	1.5	13.0	5.6
Lutjanus mahogani	0	0	0	0
Ocyurus chrysurus	0	0	0	0
All predators	0.35	1.5	13.0	5.6
	Biomass kg/100 m <sup>2</sup>		Density	(#/100 m <sup>2</sup> )
Karpata	Mean	SD	Mean	SD
Lutjanus apodus	0.4	1.39	14.1	3.1
Lutjanus mahogani	0	0	0	0
Ocyurus chrysurus	9.7	0	13	0
Total Predators	10.1	1.39	27.1	3.1
	Biomass (kg/100 m <sup>2</sup> )		Density	(#/100 m <sup>2</sup> )
Plaza	Mean	SD	Mean	SD
Lutjanus apodus	0.349	0.58	12.9	1.42
Lutjanus mahogani	0.235	0.65	9.8	1.88
Ocyurus chrysurus	0	0	28	0
All predators	0.58	1.23	50.7	3.3

Appendix B. Average biomass and density of predatory fish, Bonaire 2007

Date:										
Site										
Transect #	-									
Denth (m)	-									
Diadema (#/20m)										
Quad #	0 m	2.5 m	5 m	7.5 m	10 m	0 m	2.5 m	5 m	7.5 m	10 m
Stony Coral (adult)	_ •	210 111	5 111	710 111	10 111	_ 0 m	210 111	5 111	710 III	10
Gorgos/sponges										
Gorgos/sponges										
Coramnes										
TUFI										
1-CH (MM)										
Macro.										
M-CH (mm)										
NCC	-									
Art										
A-CH (mm)										
Sid. siderea										
Por. astreoides										
Agarica spp.										
Mont. ann.										
Stephanocena										
Mont. caver.										
Site										
Transect #										
Depth (m)	1									
Diadema (#/20m)										
Quad #	0 m	2.5 m	5 m	7.5 m	10 m	0 m	2.5 m	5 m	7.5 m	10 m
Stony Coral (adult)	-					-				
Gorgos/sponges										
Corollines										
Cordinates Turf										
T CH (mm)										
Maana										
Macro.										
NCC										
NCC										
Art										
A-CH (mm)										
Sid. siderea										
Por. astreoides										
Agarica spp.										
Mont. ann.										
Stephanocena										
Mont. caver.										
Site										
Transect #										
Depth (m)										
Diadema (#/20m)										
Quad #	_0 m	2.5 m	5 m	7.5 m	10 m	_0 m	2.5 m	5 m	7.5 m	10 m
Stony Coral (adult)	_									
Gorgos/sponges	1									
Corallines	t									
Turf	1									
T-CH (mm)	1									
Magro	ł									
M CH (myr)	<u> </u>									
NCC	<u> </u>									
NUL And										
Art	<u> </u>									
A-CH (mm)	<u> </u>									
Sıd. siderea	<u> </u>									
Por. astreoides	<u> </u>									
Agarica spp.	I									
Mont. ann.	Į									
Stephanocena	I									
Mont. caver.	<u> </u>									
	I									
	1									

## Appendix C: Juvenile Coral Demography Template

## Appendix D: Coral transects template

Date				
Site				
Depth (m)				
Transect #				
Diadema #/20m2				
Tripneustes				
Ech. viridis				
Ech. lucunter				
Stony Coral				
Gorgos (sponges				
Corallines				
Turf				
I- CH (MM)				
Macro.				
M-CH (MM)				
NCC				
Art				
A-CH (mm)				
M. annularis				
M. faveolata				
M. cavernosa				
M. franksi				
A. agracites				
A. humilis				
A. grahamae				
P. asteroides				
P. porites				
D. Jabyrinthefo				Ì
D. stokessii				
M aleinei-				
m. alcincornis	 	 		
m. complanata		 	 	 
S. siderea				 
S. radians				
C. natans	 	 		
E. fastigiana				
Helioceris				
Madracis				
M. meandrites				
Mycetophyllia				
T. coccinea				
Date				
Date Site				
Date Site Depth (m)				
Date Site Depth (m) Transect #				
Date Site Depth (m) Transect # Diadema #/20m2				
Date Site Depth (m) Transect # Diadema #/20m2 Trinneustes				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Fch. viridis				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. vicunter				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stopy Coral				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corrallione				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral Gorgos/sponges Corallines Turf				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral Gorgos/sponges Corallines Turf Turf				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral Gorgos/sponges Corallines Turf T- CH (mm) Macro				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral Gorgo/sponges Corallines Turf Turf TCH (mm) Macro.				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Gorgot/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) Necc				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Stony Coral Gorgot/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Ech. viridis Gorgos/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Stony Coral Gorgos/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm)				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral Gorgos/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm)				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Gorgeot/sponges Corallinges Corallinges Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) K. a. annularis M. faveolata				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Stony Coral Gorgos/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. anvularis M. faveolata M. faveolata				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corgalines Turf Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. cavernosa M. franksi				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Gorgot/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. areularis M. faveolata M. faveolata A. faracites				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. lucunter Stony Coral Gorgos/sponges Corallines Turf T- CH (mm) Macro. Art A-CH (mm) NCC Art A-CH (mm) M. faveolata M. faveolata M. favesite A. agracites A. humilis				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Gorgool;sponges Corallines Corallines Turf T-CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. cavernosa M. franksi A. agraicites A. humilis A. grahamae				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corrallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. faveolata M. faveolata M. faveolata M. favarles A. agracites A. grahamae P. asteroides				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corgal:sponges Corgalines Turf Turf T-CH (mm) Macro. M-CH (mm) MACC Art A-CH (mm) M. cavernosa M. franksi A. graihamae P. asteroides P. porites				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) NCC Art M. annularis M. faveolata M. cavernosa M. fraveolata A. agrahamae P. asteroides P. portes D. labyrinthefo				
Date Site Depth (m) Transect # Diadema #/20m2 TripneuStes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corgallines Turf C-CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. faveolata M. franksi A. agracites A. humilis A. agracites P. porites D. labyrinthofo D. stokessii				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corallines Corallines Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) M. caventos M. faveolata M. caventos A. humilis A. grahamae P. asteroides D. labyrinthefo D. stokessii M. alcincornis				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Ech. viridis Gorgov/sponges Corallines Turf T- CH (mm) Macro. M-CH (mm) NCC Art A-CH (mm) NCC Art A-CH (mm) K. faveolata M. cavernosa M. fravesia A. agracites A. agracites P. asteroides P. asteroides P. asteroides P. asteroides D. labyrinthefo D. stokessii M. acinocrnis M. complanate				
Date Site Depth (m) Transect # Diadema #/20m2 Tripneustes Ech. viridis Ech. viridis Ech. viridis Ech. viridis Corgalines Turf Turf Turf T-CH (mm) Macro. M-CH (mm) Macro. Art A-CH (mm) M. Caverosa M. franksi A. grahamae P. asteroides P. porites D. labyrinthefo S. stokessii M. aulcinomis M. acionomis A. sidenomis				
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