A Report on the Status of the Coral Reefs of Bonaire in 2005 with Advice on a Monitoring Program

Pew Fellows Program in Marine Conservation

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Executive Summary and Recommendations for Monitoring

Bob Steneck and Tim McClanahan

Introduction

•*The coral reef crisis and resilience*

This report characterizes the state of Bonaire's reefs as of March 2005. We pay particular attention to structural and functional attributes of reefs that have changed in so many other Caribbean reefs. We characterize coral reefs by their resident organisms and the forces regulating their distribution and abundance. Thus, corals, algae and fish define the "structure" of coral reefs but climate changes, diseases, hurricanes, overfishing, sedimentation and excess nutrients may affect how they "function". Recent unfavorable changes in the structural and functional attributes of reefs have caused "*the coral reef crisis*" (Bellwood et al. 2004). In Caribbean coral reefs the most alarming changes have been the declines in the abundance of corals, sea urchins and reef fishes and the accompanying increases in large harmful seaweeds (called "macroalgae"). The decline in coral and increase in macroalgae, called a "phase shift", represents a significant change in the structure of coral reef ecosystems that could lower its resilience.

Resilience, in the context of ecosystems, refers to a coral reef's ability to: 1) resist a phase shift to an unfavorable state such as shifting from coral to macroalgal dominance and 2) recover to their previous state once they are disturbed, as demonstrated on Palau's reefs following the 1998 bleaching event. In a recent Caribbean-wide rapid AGRRA assessment of 20 regions, only three reef ecosystems (Bonaire, Los Roques and the Flower Gardens) were listed in good condition (Kramer 2004). This leads to some fundamental questions. Why haven't *all* Caribbean reefs collapsed? Why have some reefs recovered from a disturbance while so many others have not?

The goals for our study are to report on the key structural and functional components that contribute to the resilience of Bonaire's reefs. For this, we measured the abundance of corals (to species), algae (to functional groups) and reef fish (to species and functional groups). In addition, processes such as carnivory and herbivory from fishes were estimated from fish surveys and bite rate measurements. Other processes that factor heavily into the resilience of coral reefs, such as coral settlement and recruitment, were studied directly and as a function of their interactions with macroalgae. Our monitoring was designed so they could be directly compared with the studies conducted on the same reefs in March of 2003.

In this report, we will present the state of Bonaire's reefs both in terms of their structural and functional attributes. We will also suggest possible links between the functional roles played by reef fish and the resilience of coral reefs. We then provide a simple conceptual model describing the relationship between fish protection areas and the health of Bonaire's reefs. This model provides some concepts around which managers can take

actions such as establishing FPAs and developing monitoring protocols designed to determine whether trends point to maintenance or loss of resilience.

The Biological Status of the Coral Reefs of Bonaire and the Management Implications

In March of 2005, a team of graduate students from the University of Maine revisited six study reefs on Bonaire to determine the status of those reefs and to detect if any change has occurred since March of 2003 when the last such survey was conducted. The study sites established in 2003 from north to south are: Karpata, Barcadera, Reef Scientifico, Forest on Klein Bonaire, Plaza and Windsock.

Bonaire's shallow (10 m) reefs remain in good condition. Coral cover averaged 47% in 2005 compared to 46% in 2003 (no change). Turf algae have increased and coralline algae have declined slightly over the past two years. Harmful seaweed "macroalgae" abundance remains low (2% in 2005 and 5% in 2003; see Steneck in this report) at the 10 m depth we studied. At depths below 20 m, macroalgae are now and have been (for at least the past 30 years) much more abundant (e.g. Van den Hoek et al. 1975)

The absence of macroalgae in Bonaire most likely relates to the abundance of seaweed-eating species or "herbivores". Caribbean-wide, harmful macroalgal seaweed abundance corresponds inversely with the abundance of grazing fish such as parrotfish and tangs (Fig. 1). No comparable plot exists for seaweed abundance and any other measured factor on reefs.
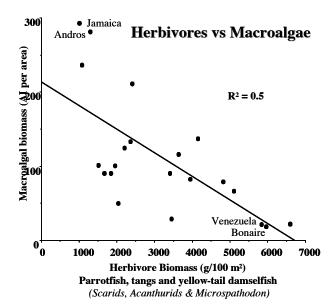
Fig. 1. The abundance of harmful seaweed "macroalgae"relative to the abundance of grazing fish. Note that Bonaire has abundant grazing fish and little macroalgae. Data from AGGRA (Lang 2003).

Herbivorous fishes such as parrotfish remain abundant although have decreased in biomass since 2003 (Brown and Hansen this report). Similarly, measured rates of fish grazing, especially from large parrotfishes are high at most sites in Bonaire. Fish are

probably most responsible for the absence of seaweed on most of Bonaire's shallow reefs. The abundance of large parrotfish is particularly important. The grazing sea urchin *Diadema antillarum* remains relatively rare (0.03 urchins/ m^2) and thus has little or no functional importance as an herbivore on Bonaire at this time.

Herbivory contributes to the resilience of coral reefs by keeping macroalgal abundance low which both reduces rates of mortality of adult corals (Lirman 2001) and increases rates of recruitment among juvenile corals (Steneck et al. 2004). For example in Bonaire, newly recruited juvenile corals were most abundant where algal biomass was low (Brown and Arnold this report). This pattern was evident when comparing the high coral recruitment rates in Bonaire with the low rates recorded a week earlier in Belize. At a much smaller scale, the same relationship was apparent in and around damselfish territories in Bonaire. Specifically, three-spot and longfin damselfishes reduce rates of grazing by parrotfish and other herbivores within their highly defended territories (Brown and Hansen this report). Within those territories, algae were more abundant and coral settlement and recruitment were significantly reduced (Arnold et al. this report).

Thus, the high rates of herbivory on Bonaire's reefs, especially from large parrotfish, may contribute to the success of reef corals by reducing the abundance of potentially lethal macroalgae that can kill adult corals (Fig. 2) and by increasing the reef's receptivity to settling corals.
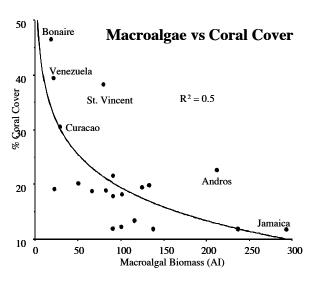
Fig. 2. The Caribbean-wide relationship between macroalgae and coral abundance (AGRRA data, Lang 2003). Bonaire has abundant coral and relatively little macroalgae. While little macroalgae does not insure high coral cover, note that no coral reef in the Caribbean with abundant seaweed has abundant coral.

Fishing pressure should be managed because there is growing evidence that large carnivorous and herbivorous fishes are important (either directly or indirectly) to the recruitment of corals and thus the resilience of coral reefs (Fig. 3). Specifically, large bodied fish are often the target of fishermen. In Bonaire, the predominance of hook and line fishing disproportionately affects large carnivores over large herbivores so it is not surprising that large parrotfish remain relatively abundant while large carnivores have declined in recent decades (see Bonaire report 2003). If small carnivores and small herbivores come to dominate reefs (Fig. 3 right side) then macroalgae may rise in

abundance reducing the receptivity of the reefs to settling corals thus reducing the resilience of this ecosystem. Fish Protection Areas are proposed as a means to maintain a healthy trophic cascade on reefs that will lead to increased coral recruitment (see McCollum et al. this report). Their effectiveness can be determined by monitoring.

Fish Protection Areas   Fished Areas
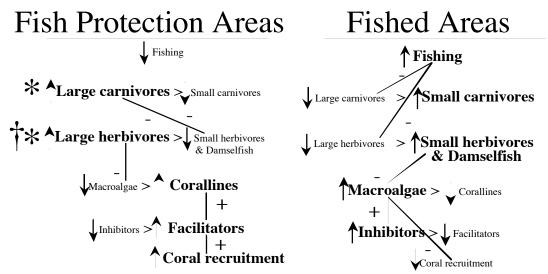
Fig. 3. The hypothetical relationships among fishing, trophic cascades, coral recruitment and thus the resilience in Caribbean coral reef food webs. Asterisks represents the expected results of FPA. The dagger represents current conditions in Bonaire since only hook and line fishing for carnivores is allowed (i.e., no spearing or trapping)). This "interaction web" results in cascade-driven increases in abundance (boldface). Trends in the abundance and importance are reflected by the arrow's direction (up for increasing). Strong interactions among trophic levels are identified by straight lines with associated signs indicating positive or negative interactions. "Cross linkages" within a trophic level indicate competitive or predatory dominance with ">" over subordinate groups.

Bonaire's Shifting Baselines and the Challenges of Monitoring

•*Changes over the past two decades*

Comparisons between the status of reefs over a few years tell us little about long-term changes. For example, today there is a distinct demarcation between where Bonaire's fringing reefs begin at 5 to 10 m depth and the shore. This region today is largely coral-free and dominated by rubble and sediment laden turf algae. However, this may not have always been the case. Prior to whiteband disease that killed nearly 90% of the elkhorn and staghorn corals in the Caribbean (i.e. *Acropora palmata* and *A. cervicornis*) (Aronson et al. 1998, Aronson and Precht 2001), most of the near shore zone was coral-dominated.

In 1981 Van Duyl (1985) mapped the near shore habitats and reefs of Bonaire and Curacao. She found acroporid corals often dominated the shallow near shore zone (Van Duyl 1985). However, she stated:

"During the survey period a coral disease broke out, the white band disease… Along Curacao and Bonaire A. palmata *was only slightly affected by the disease while* A. cervicornis *was almost extirpated in 2 years. More than 90% of all* A. cervicornis *died… Since March 1982, recovery from the disease was locally observed…. Whether the former distribution pattern will be recovered and how it will change remains to be seen. Mapping the* A. cervicornis *community in another 10/20 years and comparing them with the present maps will settle this question."* (Van Duyl 1985: 16)

We took up Van Duyl's challenge and revisited several of the mapped coastal areas 24 years after those surveys in order to reconstruct some of the long-term changes. We mapped some of the same areas using similar methods to those she applied in 1981 (Bowdoin and Wilson this report).

Coral cover in the near shore zone surrounding Bonaire has declined dramatically and is now dominated by dead coral rubble where once elkhorn and staghorn corals had formed near monocultures prior to white band disease. Five of our six study sites have changed dramatically over the past 20 years except for Karpata. The decline of the *Acropora* species may have allowed competitively inferior species such as lettuce, pencil, finger and fire corals (*Agaricia* spp, *Madracis* spp, *Porites porities* and *Millepora complanata*) to expand since all have increased in abundance since the Van Duyl study (1985).

Corals are not the only group to have changed dramatically since the 1980s. *Diadema antillarum*, the dominant grazing sea urchins was abundant in the near shore zone until it succumbed to the mass mortality of the mid 1980s. Today, more than 20 years later it remains below detectable levels at most of the sites we studied (Smith and Malek this report, Steneck this report). These changes, along with the significant declines in large predator finfish (see Bonaire Report 2003) indicate that several key players for the resilience of coral reefs (e.g. Fig. 3) have declined in abundance.

• Recommendations for monitoring

Obviously large changes in dominant corals and herbivores have occurred in Bonaire and yet, it remains one of the healthiest reefs in the Caribbean (Kramer 2003). Thus, we ask, what reef attributes should be monitored to track the health and resilience of Bonaire's Reefs?

A good monitoring program for coral reefs accomplishes what a good doctor accomplishes for people. A doctor may monitor blood pressure looking for trends that pose risks to human health. Monitoring is necessary for preventative or therapeutic actions to be taken. However, in many ways coral reef ecosystems are much more complicated than humans because they involve many different types of inputs and species.

Monitoring must be strategically limited in scope to be effective because there are too many reef attributes to measure. Any monitoring protocol that does not strictly limit the categories of information it documents will be burdened with an untenable amount of data to record, analyze and digest. Such information-overload may distract managers from detecting the most important and most timely management actions.

Managers and decision makers must take action based on imperfect information. Ideally, monitoring should establish baselines on the most critical features and then track trends to determine if they are moving towards or away from conditions dangerous to the coral reef ecosystem. Further, by establishing baselines of critical reef attributes, management actions can be monitored to see if conditions improve.

There are several monitoring protocols. They differ primarily by the categories of information they collect and by the degree of expertise needed. Next we briefly describe the chief monitoring protocols used in the Caribbean today, and then we suggest the subset of information we think will be most useful for Bonaire's reefs.

Atlantic and Gulf Rapid Reef Assessment (AGRRA). This is the highest resolution and most widely used assessment protocol. It measures percent cover, mortality (recent and old), and recruitment of coral. It also measures macroalgal biomass (via an algal index), sea urchin density, the abundance and size of key fish families. This is the scientifically most rigorous of the assessment protocols. Results are repeatable and it is an excellent way to monitor reefs. It requires a high degree of scientific expertise such as being able to identify coral and fish to the species level (estimate sizes of the latter) and identify algae to the functional group level. This protocol is inappropriate for modestly trained, short-term volunteers. A very important advantage to AGRRA is that all of the results from the 1999-2001 assessments were published in a large volume (Lang 2004) so results, including those from Bonaire, can be compared among regions (e.g. see Figs 1 and 2 that include Bonaire).

Caribbean Coastal Marine Productivity Program (CARICOMP). This is a regional scientific program designed to assess land-sea processes. It was established in 1992. The concept of studying mangroves, seagrass beds and coral reefs regionally is laudable, but the results have been mixed. Incomplete data and poor compliance from some regions makes the data of limited use.

Reef Check. This was designed to rapidly assess the coral reefs of the world with minimal training. It involves counting key indicator species but measures nothing. It is a very low-resolution method. It has excellent educational value but is less valuable for monitoring.

The Mesoamerican Barrier Reef System Manual for Synoptic Monitoring. This monitoring protocol draws heavily from AGRRA and CARICOMP methods to monitor coral reefs, seagrass communities and mangroves. It includes methods for monitoring water quality (e.g. pollution and eutrophication) and physical oceanography. Its methods are generally well explained but there are errors in some of the techniques. The basic

data on coral cover, algae, fish and *Diadema* are adequate (once the errors have been corrected) but it suffers from information overload. The manual alone is over 140 pages long. To do all of the monitoring described in the MBRS manual would require large teams of individuals and sophisticated analytical laboratories.

Recommendations for Monitoring Bonaire's Coral Reefs:

The monitoring priorities for Bonaire are (beginning with the highest priority): measurements of live coral cover, macroalgal abundance, herbivory (especially from large parrotfish) and coral recruitment (see boldfaced categories in Fig. 4). For these and all monitored variables, **temporal trends** are most important. If coral cover increases or holds constant and macroalgae declines or holds constant, the reef itself is in good health. If either trend changes, then other monitored information would be useful. Herbivory most often drives the abundance of macroalgae (e.g. Fig. 1) and it should be monitored for the abundance and body size of herbivorous fishes (including large parrotfish and other species) as well as for *Diadema* urchin densities (Fig. 4). Regular and consistent (by time of year and sites sampled) monitoring of parrotfish abundance is recommended to determine if the decline in the biomass of parrotfish seen between 2003 and 2005 may be an indication of fishing-related changes to the ecosystem or simply a result of differences between samplers or of natural population fluctuations between sampling years. Macroalgae has, on a few occasions, resulted from increased nutrient levels (nitrogen and phosphorous compounds). Despite the relatively few examples nutrient enrichment (eutrophication) resulting in increased seaweed abundance, periodic nitrate and phosphate samples should taken to establish baselines against future which nutrient measurements can be gauged. If macroalgal abundance remains low then there is little need to frequently monitor this variable.

Positive Trends   *Negative Trends*

Coral Cover [1]

Macroalgae [2]

Nutrients[3]

Herbivory

Large Parrotfish [4]

Diadema urchins[5]

Other herbivorous fishes[6]

Territorial Damselfishes[7]

Large Carnivorous fishes[8]
(Groupers, snappers & barracuda)

Coral Recruitment [9]
(density of corals < 40 mm diam)
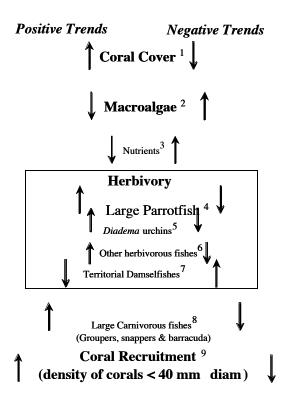
Fig. 4. Proposed monitoring priorities for Bonaire. In all cases, temporal trends are to be monitored at fixed monitoring sites and depths. Key features to monitor (e.g. coral cover, macroalgal abundance, herbivory and coral recruitment) are in the largest boldface fonts. Arrows on the left indicate the direction of positive trends toward healthy reefs, arrows to the right indicate negative trends. In most cases the variables are listed so the one immediately below it has the strongest interaction strength (down to large carnivorous fishes. In some cases, such as macroalgae, the primary control is likely from herbivory but nutrient increases cannot be ruled out and thus should be monitored periodically. Coral recruitment is the multifactor result of a trophic cascade (illustrated in Fig. 3) .

The resilience of coral reefs relates both to the ability of the reef to resist change and its ability to recover from that change. If coral cover remains high or increases (up arrow, Fig. 4) and macroalgae remains low or declines (down arrow, Fig. 4), then the reef is resilient and relatively healthy. High rates of herbivory and high rates of coral settlement should keep it in good condition. If a disturbance occurs such as a hurricane or a bleaching event, then the rate of coral recruitment will be one important factor contributing to the second part of the resilience definition or the reef's ability to recover from the disturbance.

If negative trends appear (arrows on right side of Fig. 4), other monitoring protocols should be used. For example, if coral cover declines, it would be interesting to know the cause of death. The AGRRA protocol has methods to measure the rates and sources of mortality (such as physical damage, sedimentation, disease or bleaching). If the managers of Bonaire's reefs have the personnel and funding to monitor rates and sources of mortality, they can be regularly monitored. Our reason for suggesting that rates and sources of mortality are of secondary importance is because there are few if any management actions that can be taken to reverse many of the agents of mortality (e.g. bleaching or hurricanes). However, if the reefs are resilient, they will recover from those events provided they are not too frequent.

We suggest that herbivory be regularly monitored (boldface in Fig. 4). This is because trends in the herbivorous fish population are very manageable. If the abundance of large parrotfish increases or hold constant in future FPAs then this could be a direct link to the reduction of macroalgae and indirectly contribute to increases in coral recruitment (e.g. Fig. 3) thus maintaining the resilience of the coral reef ecosystem.

In summary, we propose a simplified, prioritized and adaptive monitoring protocol for Bonaire. Methods for all monitoring priorities can be found in this report or in the AGRRA volume (Lang 2003). Herbivory is among the most important factors to monitor (see box in Fig. 4) because it is both important (Fig. 1) and manageable.

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Chapter 1: Patterns of abundance in corals, sea fans, seaweeds and sea urchins with recommendations for monitoring

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Abstract

Surveys of the abundance of live coral, sea fans (known as gorgonians), sponges, seaweed (known as macroalgae) and sea urchins at six reef sites in 10 m of water in Bonaire were conducted in 2005 to monitor changes since they were last surveyed in 2003. Live coral averaging 47% cover and thin filamentous algal turfs averaging 37% cover dominate Bonaire's reefs. *Montastrea annularis* and *M. faveolata* were the two most abundant of the 18 stony coral species and the two hydrozoan (fire) coral species recorded. Seaweed remains rare on Bonaire's reefs comprising less than 2% cover. The herbivorous sea urchin, *Diadema antillarum* was also rare on Bonaire's reefs averaging only 0.027/m^2. There have been no significant changes in the abundance in any of the groups we quantified over the past two years but monitoring should continue for live coral, macroalgae and *Diadema* abundance at least.

Introduction

The so-called "coral reef crisis" (Bellwood et al. 2004) is primarily a crisis of reef corals. Over the past two decades the death rates of corals on many Caribbean reefs have exceeded their recovery rates (Connell 1997). As a result, corals no longer dominate most coral reef ecosystems. The decline of corals in these ecosystems is often accompanied with, or possibly caused by, an increase in macroalgae (Hughes 1994). Thus, it stands to reason that any attempt to monitor the health of a coral reef ecosystem should measure the abundance of reef corals and the large seaweeds (foliaceous macroalgae) that threaten them.

The abundance of these groups at any point in time is only the first step in monitoring coral reefs. It is most useful to know if coral abundance and macroalgae are increasing, decreasing or holding constant. To address this question requires monitoring patterns of abundance over a long enough period of time to determine trends over time.

This chapter quantifies the patters of abundance of reef corals and macroalgae on six monitored reef sites in Bonaire in March 2005. These groups as well as sea fans, sponges, other algal assemblages and sea urchins were quantified using methods identical to those used in 2003 in order to begin to monitor trends over time.

Given the potential negative impact macroalgae can have on reef corals, monitoring herbivory is critical for any monitoring plan (see Executive Summary). Other chapters focus on quantifying several different groups of herbivorous reef fish (see Brown and

Hansen). The only other group of important herbivores on reefs is sea urchins, particularly the long-spined black sea urchin, *Diadema antillarum* (see Smith and Malek this report; on sea urchin abundance in the near shore fringe between the coral reef and shore). In this chapter, the population densities of *Diadema* were quantified at each coral reef site at a depth of 10 m.

Materials and 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. Transect methods used were modified from the Atlantic and Gulf Rapid Reef Assessment (AGGRA) protocol (Steneck et al. 2003). Specifically, we measured the number of cm occupied by each organism group and all coral species along each transect. Macroalgal biomass is most critical and it was estimated from the calculated algal index as the product of percent cover multiplied by algal canopy height (in mm; Steneck and Dethier 1994, Kramer 2003).   We quantified three transects per reef site.

Abundances of four species of sea urchins (*Diadema antillarum* , *Tripneustes ventricosus, Echinometra lucunter* and *E. viridis* were quantified in accordance with AGRRA protocols buy searching a one-meter path on either side of the 10 m transect tape (i.e. a total of 20 m^2 were surveyed for each transect).

Results

Live coral dominates Bonaire's reefs (Fig 1.). Live coral cover was 47% varying only slightly among reef sites (ranging from 55% at Forest to 40% at Karpata). Thin veneers of filamentous algal turfs were the next most abundant group occupying 39% cover on Bonaire's reefs. The turf canopy height was low averaging only 1.1 mm ($\pm$ 0.1 SE). The remaining groups were moderately rare (less than 10% cover) or less and included gorgonians, sponges and coralline algae (Fig. 1) or very rare (less than or equal to about one percent cover) including macroalgae, erect articulated algae and noncoralline crustose algae (Fig. 2).

Coral

Gorgonians & Sponges

Coralline Algae

Turf Algae
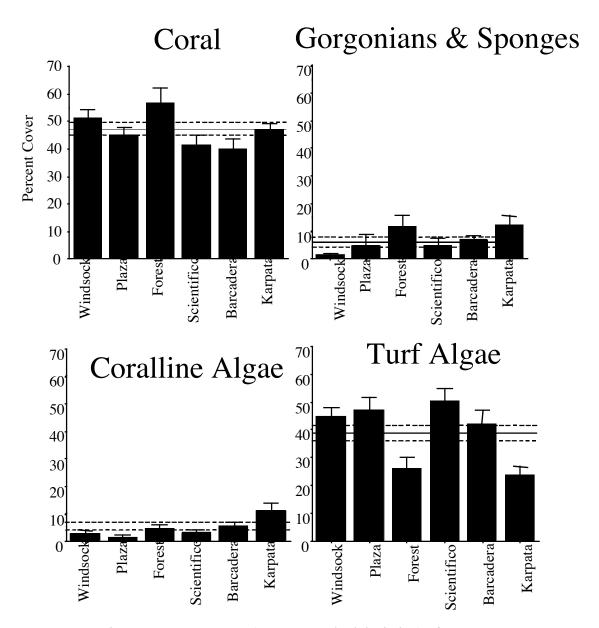
Figure 1. Percent cover (mean ± standard deviation) of stony corals, gorgonians, sponges, coralline and turf algae in Bonaire in 2005. Solid horizontal lines show mean values, dashed lines indicate ± 1 standard error.

Macroalgae were rare at most sites (Fig. 2). The average algal index, which reflects the biomass of algae on the reefs, was 12.9. This places the algal biomass on Bonaire's reefs among the lowest 7% in the Caribbean compared to 91 reef sites studied in the recent Atlantic and Gulf Reef Rapid Assessment (AGRRA; Lang 2004). The Caribbean algal index was more than an order of magnitude greater than Bonaire and averaged 138 (± 5.9 SE) with a maximum of 927.
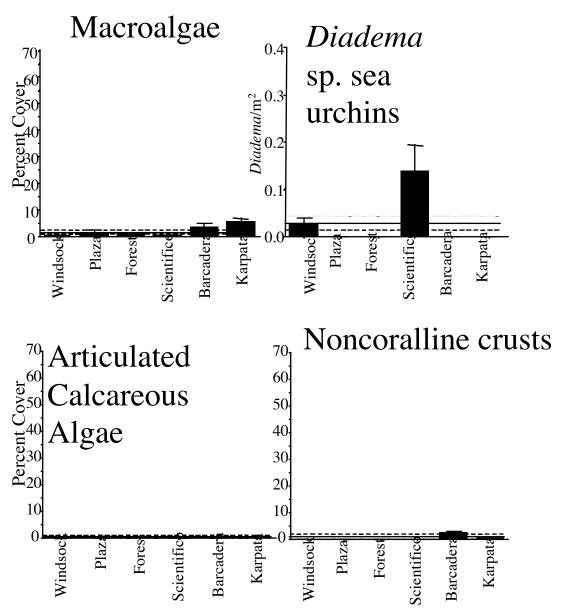
Figure 2. Percent cover (mean ± standard error) of macroalgae, noncoralline crust, articulated calcareous algae and *Diadema* abundance in Bonaire in 2005. Solid horizontal lines show mean values among all sites, dashed lines indicate ± 1 standard error. Note that the abundances of articulate and noncoralline crusts are so low that they are almost undetectable.

Two species of sea urchins were recorded in the surveys but they were relatively rare and thus unimportant to Bonaire's reefs at 10 m depth. The black long-spined sea urchin, *Diadema antillarum* was the most abundant urchin but it remained below detectable levels at four of our six reef sites (Fig. 2). The highest population density of 0.15 urchins/m^2 found at Reef Scientifico (Fig. 2) was more than two orders of magnitude lower than population densities reported prior to the 1984 *Diadema* die-off. Based on the six sites we studied, the average population density of *D. antillarum* in Bonaire in March

of 2005 was 0.027/m^2 ± 0.013 SE. A total of four individuals of *Echinometra viridis* were recorded (average density 0.008/m2) at two sites therefore this species has little functional importance to Bonaire's reefs at this time.

Bonaire's reefs are dominated by *Montastrea annularis* and *M. faveolata* (16 and 10% cover, respectively; Fig. 3). The remaining reef builders included 16 species of stony corals and two species of hydrozoan fire corals (*Millepora* spp, Fig. 3). The rank order of coral abundance in 2005 compares well with that reported in 2003 (see Bonaire Report 2003). This demonstrates species level stability in coral abundance over the years since the last survey and it attests to the repeatability of this method of measuring coral abundance.
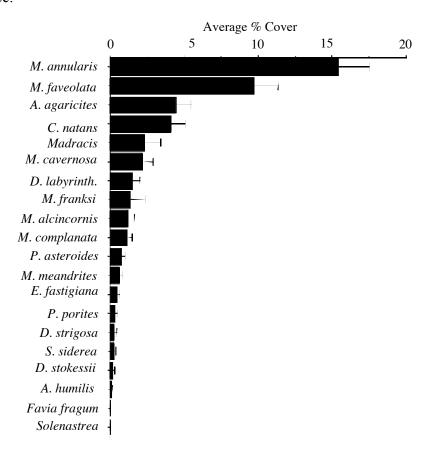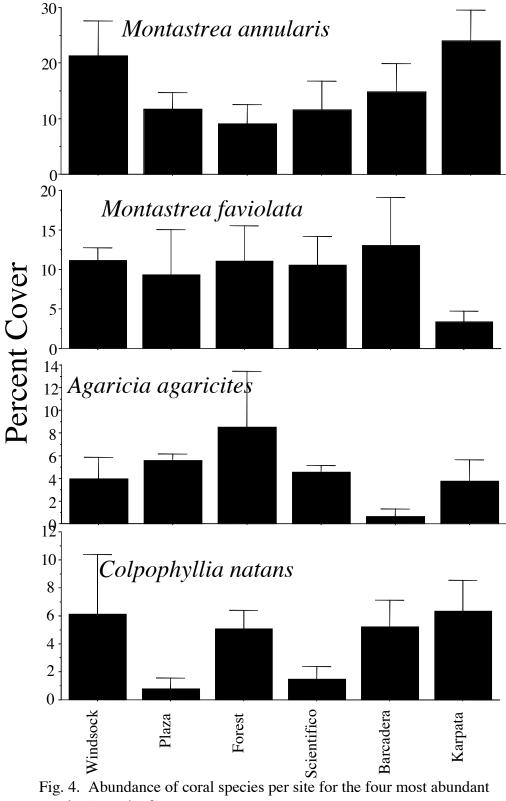
Figure 3. Percent cover (mean ± standard error) of stony corals from all sites pooled in 2005.

The abundance of some of the eight most abundant corals varied considerably among sites (Figs. 4 and 5). *Montastrea annularis* and *M. faviolata* were abundant at all sites except for a significant decline in the latter at Karpata. Three species reached their highest abundance at the Forest site on Klein Bonaire (i.e., *Agaricia agaricities, Madracis mirabilis* and *Millepora alcicornis)*. Most patterns of abundance varied without trend with the possible exception of *Diploria labyrnthaformis* that generally increased in abundance from south to north reaching its highest abundance at Karpata (Fig. 5).

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Fig. 4. Abundance of coral species per site for the four most abundant species (see Fig. 3)
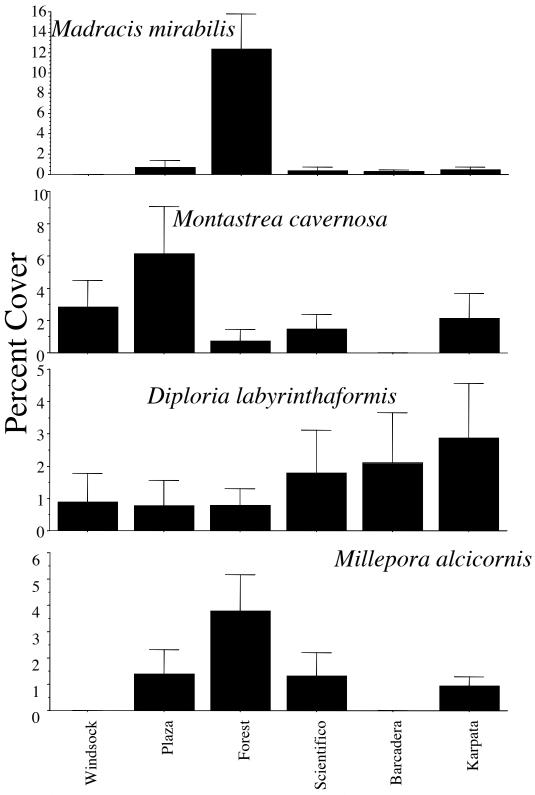
Fig. 5. Abundance of coral species per site for the 5th through 8th r most abundant species (see Fig. 3)

Discussion

Healthy reefs were traditionally described as having abundant live coral and little to no macroalgae (Darwin 1909, Steneck 1988, Hughes 1994). This changed in recent years when most Caribbean reefs "phase-shifted" to macroalgal dominance and now have only about 10% live coral (Gardner et al. 2003). Bonaire's reefs are different. They remain coral dominated (up to 50% live cover) and macroalgae remains rare (Fig. 1).

There is a clear inverse relationship between macroalgal and coral abundance (Williams and Polunin 2001, Kramer 2003). Several studies using manipulative experiments concluded that macroalgae competes with, and reduces the fitness of, stony corals with which they are in contact (Lewis 1986, Hughes 1994, McCook 1999, McClanahan et al. 2001). Thus it is possible that the absence of macroalgae may contribute to the high cover of live coral. It also holds that coral recruitment is higher on reefs with low algal biomass (see Brown and Arnold, this report).

The relative absence of macroalgae is probably due to high rates of herbivory on Bonaire's reefs. While other studies in this report examined grazing fish, this chapter quantified the abundance of the sea urchin, *Diadema antillarum,* because its abundance is increasing throughout the Caribbean and some studies have seen improvement in reef condition scale with the grazing activity of this urchin (Edmunds and Carpenter 2001). However, *Diadema* remains too rare to have a functional impact as an herbivore in this system. Its density should continue to be monitored. Much higher densities have been found in shallow non-reef sites in Bonaire (see Smith and Malek's chapter in this report).

Monitoring Reef Health Using Coral and Macroalgae

Together, the coral and macroalgal abundance indicate Bonaire's reefs are healthy. These two indicators remain similar to those reported in 2003. These reef attributes should be monitored at these same sites reported here over time to determine if significant and troubling trends are occurring.

It is also useful to monitor the rates and causes of mortality in adult and newly recruited corals. The best way to monitor the former is by using the Atlantic and Gulf Reef Rapid Assessment protocol (AGRRA). The methods and procedures have been refined and it remains the only species-based assessment protocol in the Caribbean. AGGRA includes methods of quantifying recent and past mortality events, and it trains participants how to identify and quantify physiological stress and death from bleaching and diseases. The protocol measures algal abundance in ways identical to what is reported here. The key advantage to the AGRRA protocol is that it has been applied to nearly 30 reef sites throughout the Caribbean and thus allows direct comparisons between conditions in Bonaire vs. those found elsewhere in the Caribbean.

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Chapter 2: Patterns in distribution, abundance and body size of carnivorous and herbivorous reef fish populations on Bonaire

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Abstract

Visual census techniques were used to survey the abundance, distribution and body sizes of reef fish at six sites in Bonaire, March 2005. Data were compared to a survey conducted in 2003 on the same six sites. Damselfish, *Stegastes* spp. dominated the reefs in terms of population density, whereas scarids dominated in terms of biomass. Biomass of important algae-removing herbivores, the parrotfish, has significantly decreased since 2003. There were more smaller-bodied parrotfish observed in 2005, but fewer larger (>20 cm) parrotfish. A measure of herbivory, rates of bites taken of algae surfaces on the reef are high on Bonaire. Average bite rates for the grazing fish was lowest at Forest, despite high biomass and densities of these fish at this site. No statistical significance in biomass or density of carnivorous reef fish was found between the six sites in 2005 but overall biomass of all carnivorous reef fish was highest at Reef Scientifico, and lowest at Karpata. Carnivorous and herbivorous fish populations are robust in Bonaire compared to many other locations in the Caribbean (Kramer 2003) and most of the biomass consists of fairly large-sized snappers and grunts. There has been an increase in biomass of snappers, but significant decreases in the biomass of serranids (groupers and seabass) are seen between 2003 and 2005. Of particular concern is the significant decline in the abundance of large-bodied groupers and scarids, two groups of fish that play a very important ecological role on the reefs. The Bonaire monitoring program is important to eventually understand the effect of a fish protection area on the abundance and sizes of ecologically important reef fish in Bonaire.

Introduction

Coral reefs worldwide are in a rapid decline (Bryant *et al*. 1998; Bellwood *et al*. 2004). In the Caribbean, macroalgal phase-shifts have occurred on most reefs in large part due to the loss of herbivorous reef fish populations that serve a vital ecological role in keeping macro and turf algal biomass low, thereby increasing the survivorship of corals (Sammarco and Carleton 1981; Hughes 1994; Kramer 2003). Heavy fishing pressure on these reefs have denuded populations of fish and invertebrates and have had far-reaching consequences in the food web structure, often causing changes in species composition in an area, and creating an unstable at-risk coral reef ecosystem (Hughes 1994; Pauly *et al*. 1998).

World fisheries have reduced the abundance and body size of fishes (Steneck 1998; Jackson *et al*. 2001). Large predator fishes are often targeted by fisheries due to their size

and high market value, followed by herbivorous fish as populations of large predators are removed. Even artisanal fishing can have a large impact on the abundance of large fishes in reef systems (Hawkins and Roberts 2004). Jennings and Polunin (1996) found that reef fish communities can significantly change by removing only 5% of the fish biomass from the top trophic level. Many of the largest carnivorous fishes found in reef systems, like groupers and snappers, are extremely vulnerable to overfishing because of their low growth rates and length of time to reach maturity (Sala *et al.* 2001). These fishes also aggregate to spawn and are easily caught with hook and line or by spear fishing, making them an easy target for the fisheries industry (Sala *et al.* 2001).

In the last decade, carnivorous fish have declined and herbivorous fish have increased on Bonaire (Steneck and McClanahan 2003). Establishing no-take reserves or Fish Protection Areas (FPAs) as proposed for the Bonaire National Marine Park may help the conservation and protection of reef ecosystems. There is evidence that target species like groupers and snappers increase in abundance within no-take reserves compared to fished areas (Roberts and Polunin 1991; Polunin and Roberts 1993; Russ and Alcala 1989 and 1996, Russ 2002; Roberts *et al*. 2001). Another potential ecological advantage of these protected areas is the maintenance of spawning-stock biomass within the FPAs. It is believed that there is a spillover effect to the surrounding reef system, which can supply adjacent fishing areas and enhance the yield (Johnson *et al*. 1999; McClanahan and Mangi 2000; Roberts *et al*. 2001). Finally, it may also be more inexpensive to establish and monitor a FPA in comparison to traditional catch-oriented fishing management tools (Bohnsack 1993).

This report provides information on key ecological reef fish populations which contributes to long-term monitoring activities of coral reef ecosystem status on Bonaire. Herbivorous and predatory reef fish were surveyed in Bonaire in 2003 to establish a baseline for fish abundance in areas that were considered for the establishment of a fish protection area (Steneck and McClanahan 2003) and surveys were repeated in March 2005. This information is useful for assessing the impact FPAs will have on key reef fish assemblages and any cascading effects on algae and coral community structure of the reefs.

Methods

Abundance and sizes of carnivorous and herbivorous reef fish were surveyed using visual census techniques at six sites in Bonaire including (from south to north): Windsock, Plaza, Forest (Klein Bonaire), Reef Scientifico, Barcadera, and Karpata. Survey methods used in these studies replicate a study done in March 2003 (Paddack *et al.* in Steneck and McClanahan 2003). Transect surveys were conducted at 10 m depth using SCUBA. Abundance and sizes of carnivorous reef fish were recorded in transects 40 meters long and two meters wide (80 m^2) and herbivorous fish in transects 25m long and 2m wide (50 m^2). Six to eight surveys were conducted at each site (total +640 m^2/site). A clear plastic ruler marked with 1cm intervals affixed to the end of a 1m pvc rod marked in 10 cm intervals was used to estimate fish length and transect width as the 25 meter transect tape

was laid out behind the diver. The size of each fish to the nearest centimeter was recorded, and in post-analysis, fish length was converted to biomass using length-weight conversions provided by Bohnsack and Harper (1988) and those found in www.FishBase.org (Froese and Pauly 2005).

The major herbivorous fish encountered in this survey included fish of the family Scaridae (parrotfish), Acanthuridae (surgeonfish), Pomacentridae (damselfishes) and Kyphosidae (chubs). Appendix A at the end of this report provides a list of the species surveyed. Prevalent predators found in Bonaire were surveyed, which included 29 carnivorous species belonging to nine different families. The carnivorous fish families surveyed included: Aulostomidae (trumpetfish), Carangidae (jack), Haemulidae (grunt), Labridae (wrasse), Lutjanidae (snapper), Muraenidae (Moray), Serranidae (grouper & seabass), Sphyraenidae (barracuda), Synodontidae (lizardfish) (Appendix B).

In addition to density and abundance surveys, bite rates were measured of herbivorous fish. A $1m^2$ area was randomly chosen at 10 meters depth on the reef and five-minute observations were made of the number of bites taken by pomacentrids, scarids, and acanthurids. The species and size of the fish with corresponding bite counts was recorded.

The data were examined for homogeneity of variance and normality and density data was transformed as necessary (log transformation) to meet assumptions required for analysis of variance (ANOVA). Single factor ANOVA's were used to test for differences among sites for the most recent survey done in March, 2005 (_=0.05). Two-way ANOVA's were run to determine significant differences in fish biomass and density between sites and among seasons.

Results

Herbivore Density
Forest, Klein Bonaire (ANOVA: $F_{5,37}$=3.935, P=0.0058) had the highest densities of all of the herbivorous fish surveyed in March, 2005 (Fig. 1). This is consistent with the results of the survey done in March, 2003, where Paddack *et al.* also found herbivorous fish densities to be significantly higher at Forest (Steneck and McClanahan 2003). Territorial damselfish made up the highest proportion of herbivores (Fig. 1) and their density varied considerably between sites, most notably the difference is seen at Forest, Barcadera and Karpata, with Forest significantly higher than the other sites (ANOVA: $F_{5,37}$=5.989, P=0.0003). Although the density of the other herbivores, those which remove a substantial amount of algal biomass in their feeding activity of which *Scarus* spp. was the most dominant, appears to be low at Barcadera relative to the other sites surveyed, there were no significant differences in density of this group of herbivorous fish between any of the sites.

March 2005 Density of Herbivorous Fish
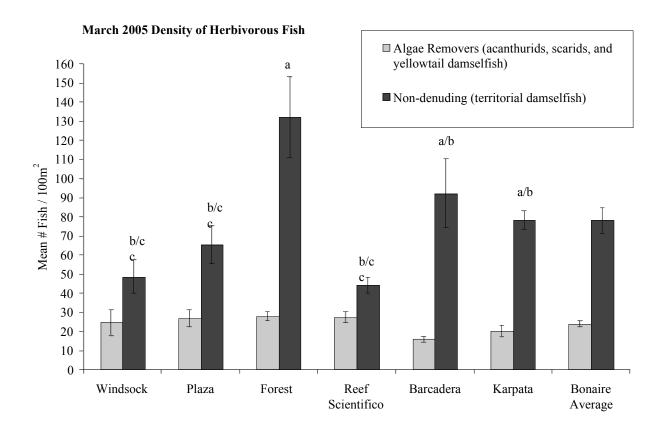
Figure 1. Density the two major functional groups of herbivores; those that remove a substantial amount of algal biomass in their grazing on the reef (surgeonfish, parrotfish and the yellowtail damselfish) and those which are non-denuding of algal biomass but which exclude others from their territories (primarily three-spot and longfin damselfish, at 10 m depth). The density of the algae removers was not significantly different between sites and similarities of the density of territorial damselfish between sites are indicated by the letters. Error is represented as one ± standard error.

Herbivore Biomass

Biomass of all the algae removing herbivores did not differ significantly among sites in March, 2005, as was found in the March 2003 survey. This group did have a lower biomass at Windsock than elsewhere (ANOVA: $F_{5,37}=5.412$, P=0.0007). Also, the non-denuding damselfish had a lower biomass at Reef Scientifico and higher biomass at Barcadera compared to the other sites (ANOVA: $F_{5,37}=14.144$, P=0.0000) (Fig. 2).

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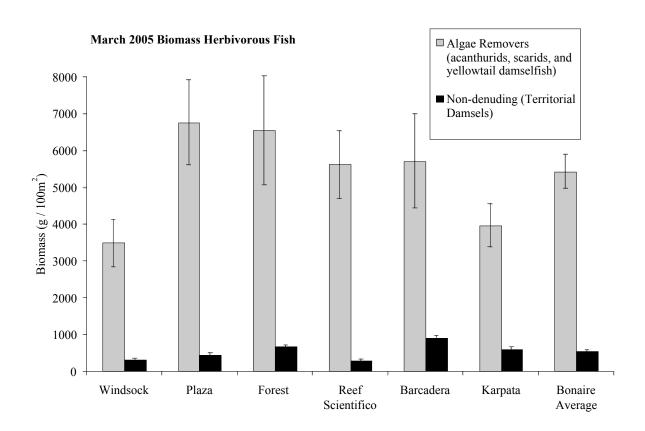
Figure 2. Biomass the two major functional groups of herbivores; those that remove a substantial amount of algal biomass in their grazing on the reef (surgeonfish, parrotfish and the yellowtail damselfish) and those which are non-denuding of algal biomass but which exclude others from their territories (primarily three-spot and longfin damselfish, at 10 m depth). The biomass of the algae removers was not significantly different between sites except for a lower biomass at Windsock. The biomass of territorial damselfish was significantly higher at Barcadera and lower at Reef Scientifico than elsewhere. Error is represented as one ± standard error.

2003 and 2005 Scarid Biomass
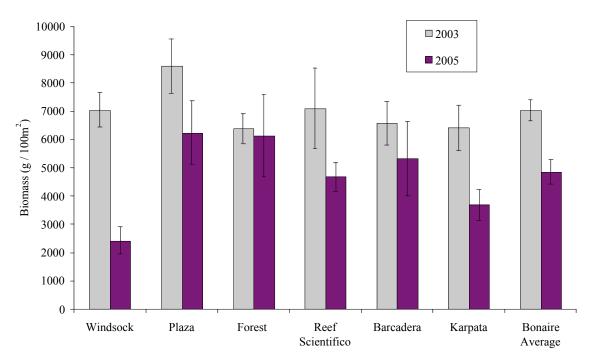
Figure 3. Biomass the dominant herbivore on the reefs, parrotfish. There is a significant overall decrease in the biomass of scarids from 2003 to 2005. Error is represented as one (±) standard error.

Total biomass was dominated by scarids at all sites (Fig. 2). However, compared to 2003, scarid biomass has decreased (Fig. 3). A two-way ANOVA between sites and years show this decrease in biomass is significant (2-way ANOVA: $F_{5,70} = 15.17$, p=0.000). More small-bodied parrotfish were observed in 2005 than 2003, but there is a decline in the frequency that large (>20 and >30 cm) parrotfish are seen (Fig. 4).
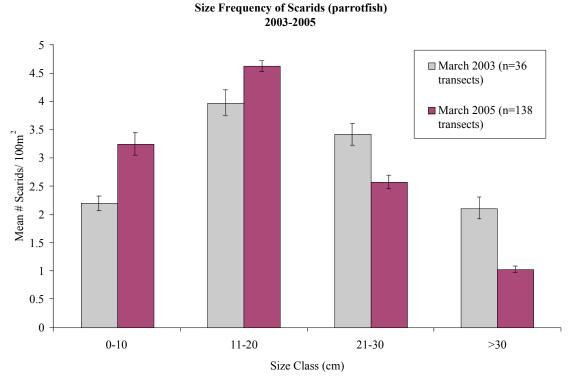
Figure 4. Frequency of observations of different sized parrotfish in 2003 and 2005. More small-bodied parrotfish were observed in 2005 than 2003, but there is a decline in the frequency that large (>20 and >30 cm) parrotfish are seen.

Grazing on the Reef

Average bite rates of parrotfish (Fig. 5) was lowest at Forest than the other sites, even though this difference was not significant (ANOVA: $F_{5,457}= 1.89$, p=0.09). Although scarids are generally more abundant at Plaza and Forest (Fig. 3, 2005 data) there does not seem to be a clear relationship in overall density of grazers and rate of feeding at these sites (Fig. 1 and 5).

Bite Rates of Grazers
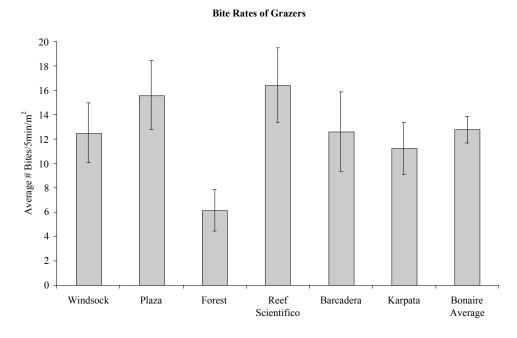
Figure 5. Bite rates of parrotfish at different sites on Bonaire. Data combined from observations made Summer 2004, November 2004 and March 2005. Error is represented as one (±) standard error.

Density Carnivores
Density of the three most common predatory fish families, the grunts, snappers, and groupers did not significantly differ between the six sites (ANOVA: $F_{4, 31} = 0.701$, P = 0.597). However, the mean density of carnivorous fish was highest at Reef Scientifico (24.59 fish per 100 m^2) and lowest at Karpata (7.97 fish per 100 m^2) (Fig. 6). Figure 7 illustrates mean densities for the two most important carnivores (the piscivores, or fish-eating fish) from 2003 and 2005. There was no significant difference between years of the snappers (p=0.07), but the overall density of groupers increased significantly from 2003 to 2005 (ANOVA: $F_{5,31}= 31.04$, p<0.000) (however, biomass decreased, next section).

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2005 Density of The Three Most Common Predatory Fish Families
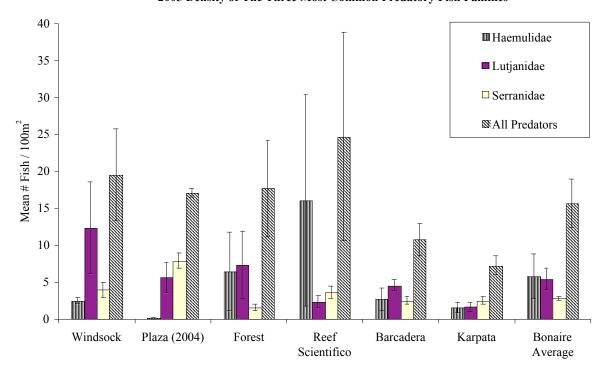
Figure 6. Density the three most common predatory fish family and all predators combined. Plaza was not sampled in March 2005, however representative samples were made four months prior to this survey and are displayed here. Error is represented as one ± standard error.

2003-2005 Density of Snappers (Lutjanids) and Groupers (Serranids)
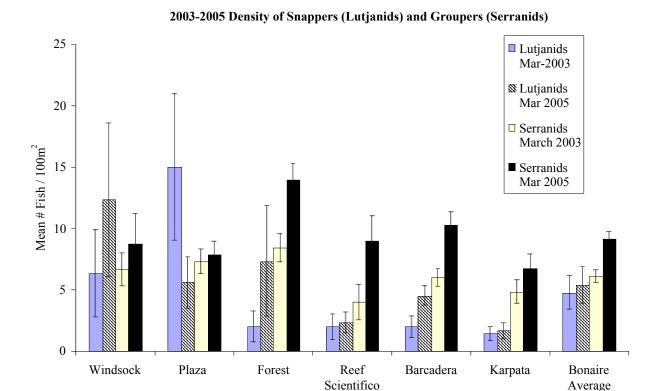
Figure 7. Density of two important carnivorous reef fish families in Bonaire 2003 and 2005. Error is represented as one ± standard error.

Biomass Carnivores

Biomass of carnivores did not significantly differ between five sites (ANOVA: $F_{4,54}$ = 1.364, P = 0.259). Lutjanids made up the largest proportion of total biomass of the surveyed carnivorous reef fish (2.65 ± 0.79 kg/100m^2) followed by haemulids (0.82 ± 0.27 kg/100m^2) and serranids (0.33 ± 0.06 kg/100m^2) (Fig. 8).

The mean values for two important piscivore families in 2003 and 2005 were compared (Fig. 9). There were increases in biomass of lutjanids (ANOVA: $F_{5,60}$ =4.13, p=0.047) but significant decreases in biomass of serranids was seen between 2003 and 2005 (ANOVA: $F_{5,60}$= 7.87, p=0.000). Particularly, declines in the abundance of large (>20 and >30cm) groupers can be seen in Figure 10.

2005 Biomass of The Three Most Common Predatory Fish Families

Figure 8. Biomass of the three most common carnivorous families in Bonaire, March 2005. Error bars are standard errors.

2003-2005 Biomass of Snappers (Lutjanids) and Groupers (Serranids)
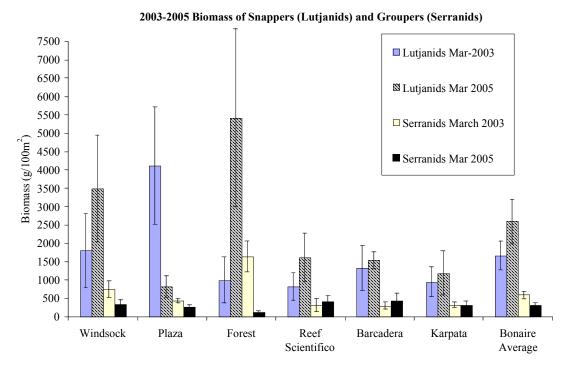
Figure 9. Biomass of two important carnivorous reef fish families in Bonaire 2003 and 2005. Error is represented as one ± standard error.

Size Frequency Serranids (groupers)
2003 - 2005
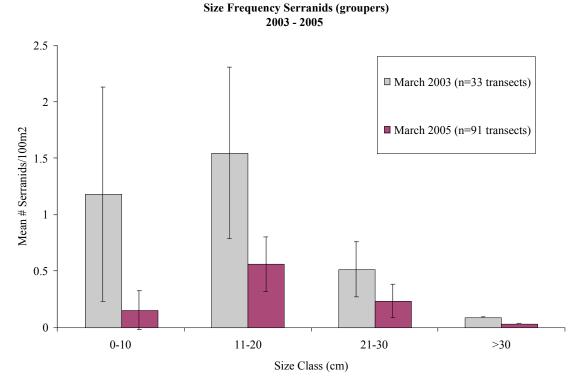
Figure 10. Abundance of different size classes of groupers found on Bonaire's reefs from 2003 to 2005. Error is represented as one ± standard error.

Discussion

Predators

Density of carnivorous reef fish did not differ significantly between the six different sites surveyed this year. Mean density was highest at Reef Scientifico and lowest at Karpata. Although there are similarities between density and biomass of predators, caution has to be taken when using biomass and densities of individual species in relation to their impact on the reef system. The bluestriped grunt has the highest density but is only ranked 3rd with regards to biomass. On the other hand, Schoolmaster is only ranked 5th with regard to density, but accounts for the largest biomass of any family on the reef. A side-by-side comparison of the predator fish families shows that the biomass of lutjanids increased from 2003 to 2005. In contrast, serranids decreased from 2003 to 2005. The biomass of serranids was noticeably higher in 2003 at Windsock and Forest compared to 2005

Predation is recognized as a key structuring process in reef systems (Jennings and Polunin 1997), and is how energy is transferred between upper trophic levels (Parrish *et al.* 1985). However, the ecological role of carnivorous reef fish is complex and still poorly understood (Hixon 1997; Pennings 1997), mostly due to the inherent difficulties of studying predator-prey interactions on a large scale (Hixon 1991; Caley 1993) and

because large predators have been extirpated from most reefs (Steneck and Sala 2005). Much of the biomass of carnivorous reef fish on Bonaire reefs consist of fairly large-sized snappers, like schoolmasters and mahogany snapper. This is an important observation because it is these fish that are targeted first if fishing pressure increase. These predators are important piscivores and their food includes a variety of fishes including damselfish and scarids (Randall 1967). Type and size of prey consumed vary with size and species of the predator (Doherty and Sale 1985) and a shift in predator size, biomass and species may therefore affect the structure and abundance of prey consumed. Fishes in the families reported here are important carnivores on the reef and gut content analysis has shown that other fish (of particular note are *herbivorous* fish) is a part of their diet (Randall 1967). .

Carnivorous fishes' important role in reef systems becomes evident when studying areas with heavy fishing pressure. The removal of carnivorous fishes can relax the trophic cascade reaction altering the community structure of the entire ecosystem. One example involves the role of carnivorous reef fish in controlling the density of damselfish (Hixon and Beets 1993; Connell 1996; Hixon 1997; McClanahan 2005). Damselfish maintain territories which they defend vigorously from invasion from other reef fish, including herbivorous fishes (Brawley and Adey 1997 and see Fig. 11). The reduced grazing pressure within the damselfish territory allows for higher algal biomass, which can smother corals and reduce coral settlement rates (see Arnold *et al.* this report). Removal of carnivorous reef fish could increase the abundance of damselfish and damselfish territories and indirectly cause higher algal biomass and reduced coral cover. This would be an example of top-down control (consumer dominated) by carnivorous reef fish.
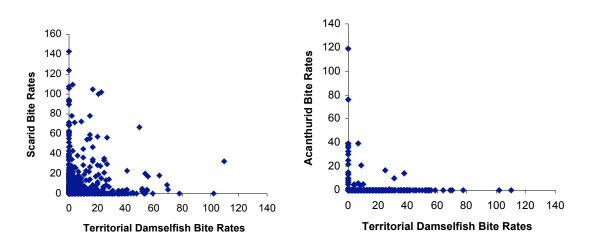
Figure 11. Bite rates of acanthurids (right) and scarids (left) as a function of damselfish interaction strength represented as damselfish bite rates (x-axis). There is an inverse relationship of acanthurids and scarid feeding relative to the territoriality of damselfish.

Herbivores

The bite rates of scarids at the different reefs (Figure 5) suggest that feeding rates differ among sties. The different biomass and densities of scarids at different sites does not seem to provide any association to differences seen in bite rates. Forest, for example has the lowest bite rates yet in March 2005, was the site of one of the highest densities and biomass of scarids (Fig.3). Importantly, there may be a correlation between the density and therefore the effectiveness of territorial damselfish suppressing the feeding ability of other algae removing fish (see Fig. 11). At Forest, there is a significantly higher density of the damselfish where there is also a low rate of herbivory.

Conclusion

Herbivorous fish play a major ecological role on coral reefs in keeping macroalgal abundance low and providing suitable substrate for coral recruitment, settlement, growth and survivorship (Sammarco and Carleton 1981). Territorial damselfish will negatively affect feeding of acanthurids and scarids (Fig. 11). The lower feeding observed at Forest (Fig. 4) may be explained by one or two factors; a relatively higher biomass and density of predators at this site that might be suppressing the activity of these fish, or the high density (over 100 fish / 100 m^2) and biomass of damselfish at Forest. Other studies have suggested that damselfish populations are controlled by predatory fish (Hixon and Beets 1989).

Very little information is available of the population dynamics of territorial damselfish occupying Bonaire's reefs in response to changes in other fish populations particularly of their predators, the serranids (groupers), lutjanids (snappers) and other piscivores such as the trumpet fish or sand diver. Possible correlations of changing predatory fish populations and the variation of *Stegastes* spp. densities and biomass between sites and among seasons seen in this study will provide vital evidence to the importance of managing both predatory *and* herbivorous reef fish and avoiding a commonly-occurring macroalgal phase-shift on Bonaire's reefs. However, a strong case for this already exists with evidence that Bonaire's reefs are in a better state compared to other reefs in the Caribbean, owed largely to the fact that large parrotfish are still abundant on these reefs (Kramer 2003 and unpub. dat.). However, a strong word of caution should be heeded that the ecosystem is at risk with the loss of large-bodied parrotfish over the last two years (Fig. 4).

It is important to carry on the monitoring program of the Bonaire reefs in order to continue the conservation efforts and ensure that Bonaire's reefs stay healthy in the future.

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Chapter 3: Status of the sea urchins *Diadema antillarum, Echinometra lucunter* and *Tripneustes ventricosus*

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Abstract

An urchin and macroalgal abundance survey was added to the reef monitoring assessment in March 2005 to assess the natural populations of several urchin species present on the reefs of Bonaire. We surveyed live urchin and macroalgal abundance at six sites on the leeward side of Bonaire. *Diadema antillarum, Echinometra lucunter* and *Tripneustes ventricosus* were enumerated if present on the reef flat at each site using a $1m^2$ quadrat. Percent macroalgal cover was estimated for every quadrat. *Tripneustes* was only found at Reef Scientifico with a site density of 0.24 ($\pm$ 0.65) urchins/m^2. *Echinometra* was found only at Forest, on Klein Bonaire, with a site density of 1.09 ($\pm$ 2.91) urchins/m^2. *Diadema* was found at measurable densities at three sites (Plaza, Reef Scientifico, and Karpata). Urchin abundance in Bonaire was comparative with densities of our species found elsewhere. Macroalgal coverage was recorded at four of six sites, with several sites significantly different. Low macroalgal coverage compared to other reefs around the Caribbean suggests Bonaire's reefs are in good condition.

Introduction

Extensive research of coral reefs in the Caribbean has illustrated the gradual phase shift from coral dominance among reef systems to one that is dominated by a variety of macroalgal species over the last 30 years. Hurricane Allen in 1981 assisted the destruction of coral cover in the Caribbean by damaging the fast growing, yet fragile Acroporids (Woodley *et al*. 1981; Hughes 1994). Unfortunately for the already injured coral reefs in the Caribbean, a massive mortality event of the long-spined sea urchin, *Diadema antillarum* in 1983 along with a history of overfishing on many islands contributed to the completion of the macroalgal phase shift. *Diadema* was a key algal grazer, and with the loss of both urchin and fish grazers, the functional herbivore guild was removed from the reef system. Examples of this new reef state can be seen around the Caribbean (Hughes 1994; Woodley 1999; Haley & Solandt 2001; Miller *et al*. 2003). Slowly, *Diadema* populations are recovering from their 97% population crash (Miller *et al*. 2003); however densities are still lower than the pre-morality event with patchy distribution. Without substantial grazing by herbivorous fish or urchins, the macroalgal phase of coral reefs may remain for years to come.

Bonaire has escaped the severe macroalgal phase shift that occurred throughout the Caribbean following the *Diadema* die-off. Ongoing reef monitoring in Bonaire has provided time series data on different aspects of reef health. The healthy populations of

herbivorous fish, such as parrotfish, surgeonfish, and damselfish (scarids, acanthurids and pomacentrids, respectively) compete amongst themselves for algae on Bonaire's reefs in the absence of significant urchin densities. Thus, the herbivorous functional guild is composed mostly of herbivorous fish, and algal productivity on most of Bonaire's coral reefs is grazed by this diversity of fish, independent of urchin densities.

The presence of either urchin or herbivorous fish on coral reefs in Bonaire impacts both directly and indirectly on coral reef health and coral recruitment. . Experiments have shown that the removal of *Diadema* from an area can cause a reduction in the settlement of coral larvae (Sammarco 1980). The urchins on reefs in Bonaire include *Diadema*, *Echinometra lucunter* and *Tripneustes ventricosus*. *Diadema* is known for controlling algae, but it has been suggested that *Tripneustes* can also decrease macroalgal productivity and invade territories once occupied by *Diadema* (Hendler *et al.* 1995; Moses & Bonem 2001). *Echinometra* is an algal grazer but also impacts the reef through bioerosion.

Urchins impact reef communities in differing ways, primarily through contributing to an overall grazing pressure. The purpose of introducing an urchin and macroalgal abundance survey into the reef monitoring program was to provide baseline data on populations of these organisms. Data collected over time may assist in discovering trends, patterns or processes that are occurring within the reefs. We predicted that *Tripneustes* and *Echinometra* density would be low, in part due to the predicted low macroalgal coverage on the coral reefs. Because of the abundance of herbivorous fish on Bonaire, the loss of *Diadema* may not have as large of an impact on the reefs as elsewhere in the Caribbean. Past research in Bonaire determined *Diadema* is very rare at 5-10 m and below, and some recovery of *Diadema* would be expected to occur in the shallow coastal zones of Bonaire's reefs. Observing the changes of *Diadema* abundance in Bonaire may help determine the effects of recovery.

Study Species

Tripneustes ventricosus is a large white-spined urchin that can attain a maximum diameter of 150 mm. The species inhabits grassy areas with sandy bottoms, but also can be found in reefs consisting of rocks or rubble from depths of 0 to 55 m. Due to their persistent grip, they can live in high wave energy zones (Hendler *et al.* 1995).

Echinometra lucunter can also attain a maximum size of 150 mm. Their appearance varies, having a reddish test with red to black stout spines. Capable of withstanding the energy in surf zones, they prefer limestone reef rock or shallow fore reef habitat. They can withstand strong surf zones due to a thick test. *Echinometra* will feed on drifting, attached and boring algae. *Echinometra* may excavate carbonate reef rock for food and shelter using their teeth and thick spines (Hendler *et al.* 1995).

Diadema antillarum is commonly known as the long-spined urchin, often has long, sharp black spines. This highly active urchin used to occur in large numbers, with densities as

high as 20 individuals per square meter (Scoffin *et al.* 1980). Full grown adults can reach as large as 500 mm, sometimes with spines up to four times the length of the test (Hendler *et al.* 1995). Studies have shown that algal turf actively grazed by *Diadema* can be 2 to 10 times more productive than ungrazed turf (Williams and Carpenter 1988). So while *Diadema* is a major herbivore, it also plays an important role in overall reef productivity.

Methods

Six sites, pre-selected for other studies on Bonaire on the leeward side of the island, were surveyed for urchin and macroalgal abundance: Windsock, Plaza, Forest on Klein Bonaire, Reef Scientifico, Barcadera, and Karpata. The surveillance of urchins was a subset of a larger reef flat assessment project (see Bowdoin and Wilson, this report). At each site, five transects perpendicular to the shore were sampled every 25 meters (for a total of 100m of shoreline). The distance from shore to the reef flat was measured from along each transect, and water depth was recorded at the end of the reef flat.

Once the site baseline map was produced, the survey was conducted at three reference points within each marker transect: 1) reef edge, 2) mid-reef and 3) nearshore reef. Five quadrats were haphazardly placed at each reference point for a total of 75 quadrats per site (5 markers, x 3 reference points, x 5 quadrats), with over 300 random quadrat samples all together. Depth was also estimated for each reference point. On sampling days, Karpata and Barcadera had rough wave action, limiting sampling. At Karpata, urchin and macroalgal densities could only be assessed for three of the five transects, and only at the reef edge and mid-reef locations (n=30). Only the mid-reef and reef was sampled at Barcadera (n=50).

When an urchin was encountered in a quadrat, it was identified to species level and measured to the nearest centimetre in test diameter. Percent macroalgae (excluding turf algae) was estimated for each quadrat. Urchin density was later calculated for each site, along with urchin size frequency. Sites with macroalgae were compared using a t-test to determine significant differences.

Results

Of the six sites surveyed, *Tripneustes ventricosus* were recorded only at Reef Scientifico with a site density of 0.24 ($\pm$ 0.65) urchins/m^2 (Fig. 2). Two individuals were observed at Karpata outside our quadrat locations. The distribution of *Tripneustes* was patchy, with most of the animals being enumerated in the shallow sections of the reef, on rock, in high energy zones. *Echinometra* were observed at only Forest, with a recorded density reaching 1.09 ($\pm$ 2.91) urchins/m^2 for the site (Fig. 1). Considering only the shallow zone, density was higher (3.28 ($\pm$ 4.33) urchins/m^2) due to the concentration of animals in this zone.
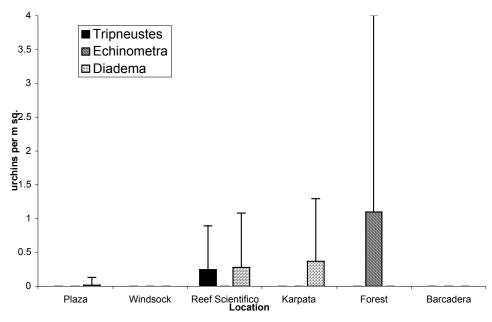
Figure 1: Urchin abundance per square meter for all six locations. Standard deviation is indicated by error bars.

Macroalgal abundance was observed and recorded at three of the six sites. At Windsock, the percent cover of macroalgae was 5.09% ($\pm$ 6.92) m^{-2}, while Karpata and Forest were higher with 7.73% ($\pm$ 10.76) and 10.2% ($\pm$ 19.77) m^{-2}, respectively (Fig. 2). Windsock was significantly different from Forest, but not Karpata. Karpata and Forest were not significantly different from each other.
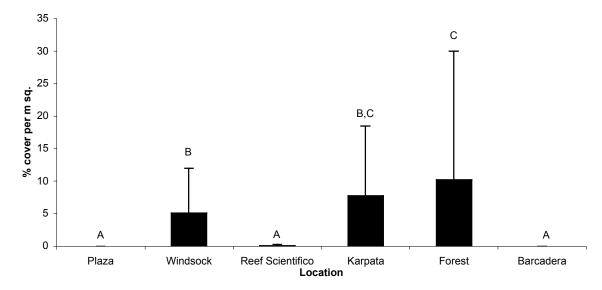
Figure 2: Macroalgal percent coverage per square meter for all six sites. Standard deviation is indicated by error bars. Also shown, are the significant relationships among the sites.

Size distribution of urchins show a distinct trend within each species. Figure 4 illustrates that the population of *Echinometra* is composed of small individuals ranging in size from 1 to 5.5 cm (Fig. 3a), while *Tripneustes* had larger individuals, ranging from 5 to 10 cm (Fig. 3b). *Diadema* were found in sites varying from 1cm to 12 cm individuals (Fig. 3c).
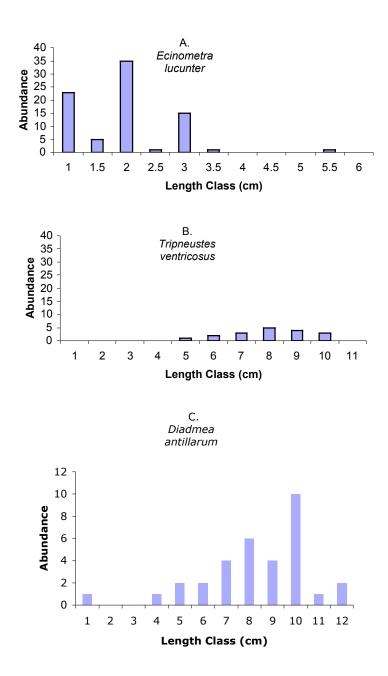
Figure 3: Size frequency of *Echinometra lucunter* (A), *Tripneustes ventricosus* (B), and *Diadema antillarum* (C). Data was pooled for all six sites.

A compilation of studies on *Tripneustes* and *Echinometra* densities in the Caribbean can be seen in Table 1 with sources listed. More reported densities were found for *Tripneustes*. However, our calculated density falls within the ranges of other sources.

Table 1: Urchin densities found in the Caribbean. All reported in m^2.

Location	*Tripneustes*	*Echinometra sp.*	Source
Bonaire	**0.24**	**1.09**	**This paper**
Bermuda	1.2	-	Tertschnig 1984
St. Croix			
Tague Bay	0.007	0.171	Miller *et al.* 2003
Tague Bay	0.5 - 1	-	Tertschnig 1989
Jamaica			
Discovery Bay	0.17 - 2.35	-	Haley & Solandt, 2001
Discovery Bay	0.15	2.3	Hendler *et al.* 1995
Discovery Bay	1.8		Woodley *et al.* 1999

Discussion

The area of the sites surveyed ranged from 4 to 6.8 km^2 in this study. Survey observations from all six sites in Bonaire indicate that urchin populations are extremely low and often patchy. Macroalgal coverage was also very low and patchy, unlike reefs found in Jamaica and St. Croix (Aronson & Precht 2000; Haley & Solandt 2001; Edmunds & Carpenter 2001). Both *Tripneustes ventricosus* and *Echinometra* were only seen in recorded numbers at one site each. *Diadema* remains relatively rare in Bonaire, and some sites where it is relatively abundant; there was a 0% macroalgae cover (Fig. 1 and 2).

With the disappearance of urchin herbivores, fish have taken over the role as dominant forager (Carpenter 1988). Urchins may not be necessary in Bonaire to keep reef algal biomass in check. With such low abundance of macroalgae on reefs, the urchin population may be resource limited.

Low population densities may be hindering successful reproduction of urchins. External fertilization requires a certain density of individuals to be in relatively close contact to allow successful interaction between gametes. If this density is not attained, then expelled gametes float away with currents (Moses & Bonem 2001). *Echinometra* seen in the surf zone of Forest would suggest viable density structure, but the size frequency from observed individuals suggests these animals were still juveniles. *Tripneustes* observed in the shallow zone of Reef Scientifico appeared to be of adult size. With optimal conditions, these urchins may become reproduce successfully.

Thirty four species of fish eat urchins in the Caribbean. These urchin predators include triggerfish, grunts, jacks and wrasses (Hendler *et al.* 1995). Queen Triggerfish (*Balistes*

vetula) can be a prominent foe for urchins; however, in Bonaire sightings have been extremely rare for this species.

Echinometra was only found on the reef at Forest. The density of this urchin was higher than both *Tripneustes* and *Diadema*. However, the impact of this urchin is two fold. Algal grazing by *Echinometra* is minimal, but its ability to excavate reef rock is not. Echinoids are responsible for more than 90% of the bioerosion in Caribbean waters. Erosion of carbonate rock produces free sediment, causing a change in reef structure (Hendler *et al.* 1995). Bioerosion by Echinometra is density dependent. Bioerosion was not assessed for this study, but other investigators have reported estimates for sites around the Caribbean. Notably, sediment from such bioerosion can reach 3.9 kg/m^2 in the US Virgin Islands and 7 kg/m^2 in Bermuda (Hendler *et al.* 1995). *Echinometra* population at Forest may be too low to produce enough free sediment in to the system. Yet, it may be worthwhile to monitor this species for bioerosion effects.

According to Moses and Bonem (2001), *Tripneustes* are capable of controlling algae on reefs. *Tripneustes* are proficient feeding on the larger, older macroalgae, without being greatly affected by the algae's chemical defences. This allows *Tripneustes* to graze on the older algal species, producing bare zones. *Diadema* prefer grazed zones with softer algal species and newly settled recruits. Thus, *Tripneustes* may facilitate the dispersal of *Diadema* by clearing old macroalgae away and initiating food supply preferred by *Diadema*. *Tripneustes* may also aid in *Diadema* larval recruitment, as *Diadema* require grazed substrate for settlement, as do corals (Edmunds & Carpenter, 2001; Miller *et al.* 2003). *Tripneustes* was found in association with *Diadema* at Reef Scientifico (M. Smith, pers. ob.). However, due to a lack of macroalgal zones in Bonaire, this facilitative association may not be present on the reefs we surveyed.

Macroalgal abundance was low in Bonaire compared with other reefs within the Caribbean (Steneck and McClanahan 2003). A shift from macroalgae to turf algae in Bonaire may be maintained by the heavy foraging capacity of the herbivorous fish. Since *Diadema* is recovering throughout the Caribbean (Aronson and Precht 2000), it and other herbivorous urchins should be monitored to assure Bonaire reefs maintain their current well grazed and resilient state.

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Chapter 4: Coral Recruitment and the Role of Territorial Damselfish

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Abstract

Results of this study support the hypothesis of increased turf algal abundance and reduced settlement within damselfish territories. After one year, spat density was significantly greater on plates outside of damselfish territories, with 73% settling outside of territories. Settling corals were found to settle preferentially on the inducer coralline crustose alga, *Titanoderma prototypum* (36%), as well as on bare terracotta (37%). Additionally, settlement declined on caged plates following increased occlusion by turf algae, mimicking the trend of reduced larval availability to subcryptic habitats that threatens macroalgal overgrown areas of the Caribbean. This research illustrates the need for reductions in hook and line fishing on Bonaire by demonstrating an indirect trophic cascade effect, reduced herbivory, of overfishing predators.

Introduction

Macroalgal phase shifts (sensu Hughes 1994) jeopardize reef resilience by suppressing coral recruitment. The idea of reef resilience refers to the ecosystem's ability or the rate at which it is able to recover following disturbances of various severities (Boesch 1974). Areas of high algal biomass are poor nursery habitats for settling corals (Birkeland 1977). These areas in which post-settlement survival is low are common in the Caribbean. Since the biomass of macroalgae correlates inversely with the biomasss of herbivorous fishes (Williams and Polunin 2001), Bonaire's coral reefs should be receptive to settling corals (i.e. have high recruitment potential; sensu Steneck and Dethier 1994) because herbivore densities are high and macroalgal abundance is lowest in the Caribbean (Kramer 2003). In fact, coral settlement was found to be nearly three times higher in Bonaire than at four other regions of the Caribbean (Steneck *et al.* 2004), and population densities of juvenile corals to be significantly greater than in Mexico (Slingsby and Steneck 2003) and Belize (see Brown and Arnold, this report). Nevertheless, other changes in fish communities are cause for concern. In the last decade, fishing pressure on Bonaire's reefs has caused declines in large predatory fish (Steneck and McClanahan 2003). Previous studies suggest predation may be important in structuring the distribution and abundance of damselfish populations (Hixon and Beets 1993; Graham *et al.* 2003,). Damselfish exclude herbivorous fishes from their territories (see Brown and Hansen, this report), thereby creating patches of higher algal biomass and potentially lower coral recruitment. Thus, an indirect trophic cascade effect of overfishing predators may be reduced herbivory leading to reductions in coral recruitment.

This study examines the role of these territorial damselfish in controlling the recruitment potential of reefs on Bonaire. By negating the positive effects of grazing fish, I hypothesized territorial damselfish would increase turf algal abundance creating unsuitable habitats for coral settlement. Analysis of results from the first year of study support this theory, showing damselfish create micropatches of elevated algal abundances and lower abundances of juvenile corals.

Materials and Methods

In March, 2004, 240 terracotta coral settlement plates were deployed on six of Bonaire's reefs (methods of Mundy 2000), both inside and outside of damselfish territories at a depth of 10 m. The sites are, from north to south, Karpata, Barcadera, Reef Scientifico, Forest (on Klein Bonaire), Plaza, and Windsock. Damselfish territories were determined through observations of both three-spot and longfin damselfish over 3 minute intervals. In June, 2004, six plates at each site were affixed with galvanized wire mesh (6.35 mm) cages to mimic the inhibitory effects of algae on coral recruitment microhabitats. These simulated damselfish gardens test the hypothesis that anything that reduces water flow, reduces larval availability, thereby reducing settlement densities.

The plates were monitored four times throughout the year (June 2004, August 2004, November 2004, and March 2005). Half of the plates from each site, including all caged plates, were analyzed under the microscope for newly settled corals and their subsequent survival relative to the successional community states that may positively or negatively impact recruitment. Newly settled corals, or spat, are coral larvae that have recently attached themselves to the substratum. The larvae then metamorphose, defined as a developmental event following attachment consisting of the differentiation and calcification of the septal ridges (Morse *et al.* 1988). A newly settled coral larvae is said to have undergone recruitment, or become a "recruit", if it has survived metamorphosis and remains part of the population until noted by an observer (Keough and Downes 1982).

The subset of plates analyzed were transported in seawater, censused microscopically, and returned to the reef within six hours. The plate undersides only were analyzed for spat. Numerous studies have observed that juveniles are most often found on the undersides of surfaces. Specifically, Raimondi and Morse (2000) reported that given the choice *Agaricia humilis* will orient on the underside of surfaces, and Steneck *et al.* (2004) found 85% of spat in a Caribbean wide study to settle on the undersides of settlement plates. Thus, in this study, the focus was purely on plate undersides. Every spat on the plate was identified to genus, determined to be dead or alive, measured, and mapped for its location on the plate as well as its settlement substrate. The location of *Titanoderma prototypum* was also mapped on the plate underside. All 240 plate tops and undersides were photographed underwater to monitor for succession of fowling species. Percentage coverage of encrusting biota on plate undersides was determined from these pictures. Thus, time series data on recruitment, growth, and mortality in reference to the succession of fouling organisms was accumulated and analyzed.

In addition to monitoring the plates, factors known to impact coral recruitment, such as live coral cover, algal abundance, and the presence of inducer species were examined at the six survey sites. The density of juvenile corals was determined at each site according to the methods described in Chapter 7 under *Juvenile Coral Demography Transects*. Juvenile corals included those with a diameter of 40 mm or less (Bak & Engel 1979).

Results

Preliminary surveys of average turf algal biomass and densities of juvenile corals (≤40 mm in diameter) per m^2 inside and outside damselfish territories across all six sites are inversely correlated (Figure 1 a&b).

a.

b.
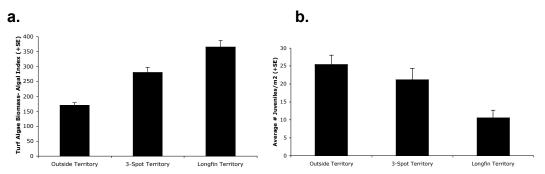
Figure 1 a&b. Average turf algal biomass and population density of juvenile corals per m^2 at six sites outside damselfish territories and inside 3-Spot and Longfin damselfish territories.

One-hundred-thirteen spat were found on 120 tiles. Forest and Barcadera had the highest cumulative coral settlement rates of all six sites over the course of the year since the plates were deployed in March, 2004. (Figure 2). The recruits were primarily of the genus, *Agaricia* (85%) and *Porites* (10%), with the remaining percentage unidentified. Coral recruitment on plates outside of damselfish territories was higher (average of 1.36 +/- .40 SE spat per plate) than on plates inside of damselfish territories (average of .51 +/- .13 SE spat per plate) (Figure 3).
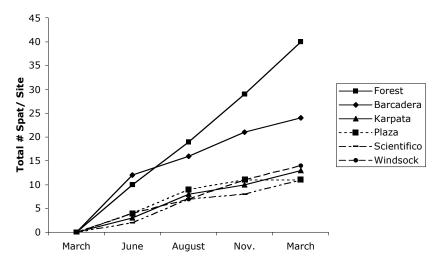
Figure 2. Cumulative number of newly settled corals over time
(excluding post-settlement mortality).
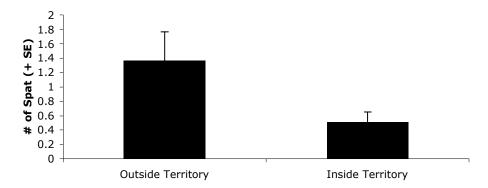
Figure 3. Average number of spat found per plate outside and inside
of damselfish territories.

The majority of new recruits settled on bare terracotta or the crustose coralline algae,
Titanoderma prototypum, with 37 and 36% of settlement occurring on these preferred
substrates, respectively (Figure 4). The remaining 4% settled on recruit killers inimical
to settlement such as sponges or bryozoans.
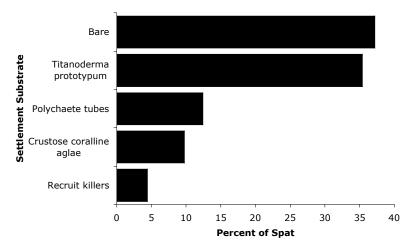
Figure 4. Preferred settlement substrates for coral recruits across all sites.

Turf algae fouled the cages following their deployment in June. As fouling increased, settlement to the undersides of plates covered with cages declined (Figure 5). Settlement on caged and uncaged plates remained virtually equal through August when algal fouling was undetectable. However, by November, algal growth on cages was noticeable and settlement on caged plates was down, and by March, while settlement remained fairly constant on uncaged plates, it decreased further on plate undersides occluded by fouled cages.
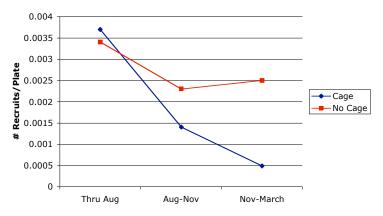
Figure 5. Coral settlement since June 2004 on caged plates vs. uncaged plates.

Over time, settlement and survivorship also declined as fouling organisms colonized the plates. The June cohort consisted of the greatest number of settlers, followed by the August cohort. The number of new settlers in November and March declined (Figure 6). Rates of post settlement mortality were also found to be highest amongst the November cohort, indicated by the steep slope in Figure 6, with a mortality rate of 23%/month.
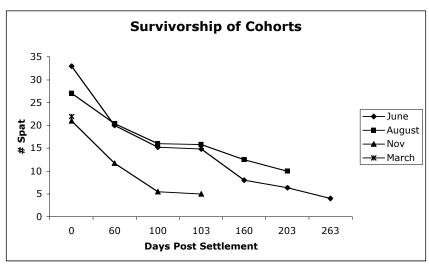
Figure 6. Survivorship of total number of spat found in June, August, and November over time since settlement.

Discussion

Coral recruitment is regulated sequentially by three factors: 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). Coral larvae undergo a sequence of behavioural 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 will be induced to metamorphose and settle (Morse et al 1988). Lab studies have supported the hypothesis that larval selection and survival is enhanced by the crustose coralline algae, *Titanoderma prototypum* (Harrington *et al.* 2004). Furthermore, for some time, researchers have equated coralline abundance with a higher recruitment potential of the benthos (Edmonds and Carpenter 2001, Steneck *et al.* 2004). Thus, presence of high abundances of *T. prototypum* in Bonaire likely increase settlement in well grazed areas by facilitating step two (propensity to settle) of the three-step process to coral recruitment. However, high populations of damselfish on the island increase turf algal biomass and decrease larval availability to the benthos, thereby limiting settlement within their territories. The results of this study support the hypothesis that damselfish increase turf algal abundance and create habitats unsuitable for coral settlement. Figures 1 and 3 illustrate turf algal biomass inside of damselfish territories is inversely correlated to juvenile coral densities and recruitment is indeed greater outside of territories.

Of the one-hundred thirteen newly settled corals found on the undersides of 120 plates, the dominant spat (*Agaricia* and *Porites*) are brooding corals. Larvae released from brooding species are internally fertilized and immediately capable of settlement. This often results in brooded larvae settling in the immediate vicinity of the parent colony (Richmond 1997). Settlement of brooders occurring throughout the year, such as *A. humilis*, has been shown in previous studies and was reported on Curacao to be the most

common of any coral species (van Moorsel 1989). In November, following the annual mass spawning event in late August, the settlement plates were monitored for newly settled spawning species, but no spawning species were found. This was not surprising because broadcast corals, including all of the reef builders, rarely recruit in the Caribbean (Sammarco 1985).

Settling corals in Bonaire were found to settle preferentially on *T. prototypum* (36%) as well as bare terracotta (37%) (Figure 4). The apparent preference of spat for these early successional substrates correlates with the slight pattern of settlement and survivorship decline as time passed following deployment of bare plates.   Over the course of the year, the plates became increasingly fowled with heterotrophic successional species inimical to settlement and survival. This may explain the reduced abundance and survivorship of cohorts settling later in the year (Figure 6). More data is needed here to say for sure if this is a real trend or if mortality is just high during the first 100-150 days of life. A leveling off of the curves for the June and August cohorts around 150 days may suggest the attainment of a size refuge. Survival is not merely a function of the attributes of the settlement substrate, but of the ability to resist overgrowth by algae and encrusting invertebrates (Richmond 1997). As recruits grow, their mortality rates decline since they are less likely to be overgrown by competitors (Hughes and Jackson 1985).

Reduction in settlement on plates with cages only occurred after fouling of turf algae increased. The settlement decline on plates with cages was evident 6-10 months after the cages were placed (Figure 5). This trend of reduced larval availability to subcryptic habitats mimics that of recruitment in macroalgal overgrown areas of the Caribbean, or perhaps more specifically to the ability of damselfish to reduce the recruitment potential of the benthos via turf algae.

Previous studies point to the importance of maintaining populations of herbivorous fish (Bellwood *et al.* 2004). While Bonaire has intact herbivore populations, low macroalgae, and high coral cover, large predators have been declining (Steneck and McClanahan 2003). If large predators control damselfish abundance, then predator abundance may indirectly control the ability of coral reefs to recruit and recover from disturbances. In this event, it is critical to reverse the decline of predators, in addition to maintaining herbivore populations, in order to effectively manage the coral reefs of Bonaire.

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Chapter 5: Juvenile Corals and Seaweed: A Comparison Between the Reefs of Bonaire and Belize

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Abstract

In this study, two reef systems were surveyed for both juvenile coral density and macroalgae abundance. The reefs of Bonaire have relatively high densities of juvenile coral and low abundances of macroalgae. In contrast, the reefs surveyed in Belize are more representative of the rest of the Caribbean, where juvenile coral densities were low and macroalgae abundance was high. It appears that high macroalgal abundances reduce the recruitment potential for settling corals and therefore reefs with high macroalgae abundances may be less able to recover from disturbances. Given that most of the reefs throughout the Caribbean are suffering from low coral abundance and high macroalgae abundances, managers should aim to reduce macroalgae abundances in order to increase the recruitment potential for settling coral and the resilience of the coral reef ecosystem.

Introduction

Many coral reefs in the Caribbean have experienced dramatic declines in live coral cover in recent decades (Hughes 1994, Hughes and Tanner 2000, Steneck and McClanahan 2003, Gardner *et al.* 2003). The island of Bonaire, located 50 miles north of Venezuela, has escaped this decline and currently has some of the healthiest reefs in the Caribbean (Kramer, 2003). The abundance of both adult and juvenile corals on Bonaire's reefs is high, while macroalgae abundance, a stressor of reefs, is low. Reefs throughout the Caribbean, including those of Belize, have experienced declines in live coral abundance and increases in macroalgae (Aranson *et al.* 2004).

Studies have shown that macroalgae can stress reefs by shading and smothering both juvenile and adult corals (Lewis 1986, McClanahan *et al.* 1999, Kramer 2003). This hypothesis is supported by studies which have shown that reefs with high macroalgae are hostile to settling coral larvae because settlement sites are low and post-settlement mortality is high (Birkeland, 1977; Hughes, 1994). Such environments have a "low recruitment potential" (sensu Steneck and Dethier). If in fact macroalgae reduce the recruitment potential of reefs, it follows that reefs dominated by macroalgae will be less resistant to and less likely to recover from disturbances. This is likely a widespread problem for many reefs in the Caribbean, given the current domination of macroalgae on most of these reef systems (Kramer 2003).

The objective of this study is to quantify the abundance of juvenile corals and macroalgae to determine if the patterns between the two are consistent with the concept that seaweed is harmful to young corals. For this, we compare two regions with differing abundances of macroalgae. The reefs of Bonaire have the lowest cover of macroalgae in the

Caribbean, while the reefs of Belize have high algal abundance typical of the rest of the Caribbean (Steneck and McClanahan 2003, Kramer 2003). The underlying hypothesis is that juvenile coral will be more abundant in Bonaire than in Belize, given Bonaire's low cover of macroalgae.

Methods

The methods used for this survey are outlined in Chapter 7 of this report. At six sites in Bonaire and four sites in Belize, a $1/16m^2$ (25 cm X 25 cm) quadrat was placed every 2.5 meters along four ten meter transects by divers at a depth of 10m. In addition to the species and size of juvenile corals, the percent cover of macroalgae, turf algae, coralline algae, and live coral was also recorded within each quadrat. Juvenile corals are characterized by having a diameter of 40 mm or less (Bak & Engel 1979). Measurements of canopy height were recorded for macroalgae and turf algae. Algal abundance was measured as an "Algal Index" (AI) or the percent cover multiplied by the canopy height. The AI corresponds directly to algal biomass and is a better measure of abundance than percent cover alone. Data was analyzed to determine whether there were differences in juvenile coral and macroalgal abundance between sites and regions.

Results

The average cover of macroalgae was higher in Belize than in Bonaire (Figure 1), while the average density of juvenile corals was higher in Bonaire than in Belize (Figure 2).
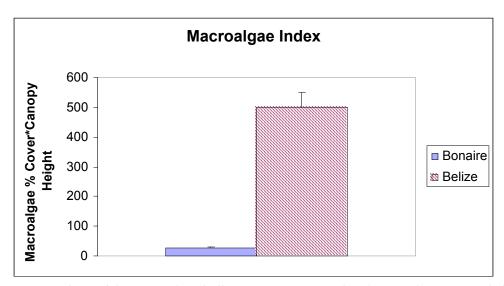
Figure 1. Comparison of the macroalgae indices (%cover macroalgae*macroalgae canopy height) from Bonaire and Belize.

Juvenile Coral Abundance
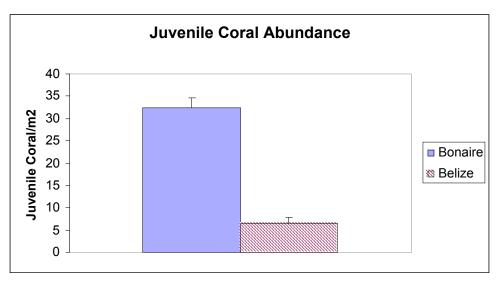
Figure 2. Comparison of the average juvenile coral abundance from Bonaire and Belize.

There is an inverse relationship between the population density of juvenile corals and the abundance of algae, measured as the algal index (Figure 3).

Bonaire and Belize Macro Algae/Juvenile Coral Interactions

$R^2 = 0.7285$
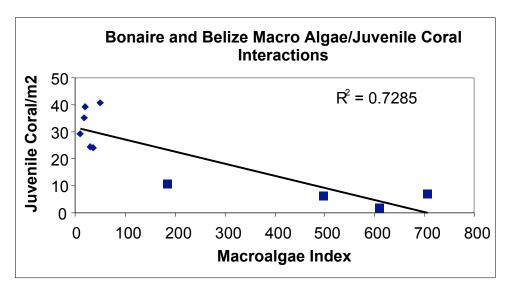
Figure 3. Average density of juvenile corals as a function of macroalgae index from sites in Bonaire (diamond data points) and Belize (square data points).

Our data from Bonaire indicate that when juvenile coral abundance is broken down by species, a few species of corals, such as *Agaricia agaricites* and *Porites astreoides* are strong dominants(Figure 5). The species composition and their relative abundances from this study are consistent with the data from the 2003 Bonaire report (Steneck and McClanahan, 2003, ch. 2). The rank order abundance population and species richness of juvenile corals recorded in 2005 (this study) was virtually identical to that found in 2003 (Slingsby and Steneck 2003, Begin and Stephenson 2003). This indicates that the

methods we used to record juvenile corals are repeatable and that the strength of interactions with macroalgae is strong and consistent.

Bonaire Coral Density by Species 2005
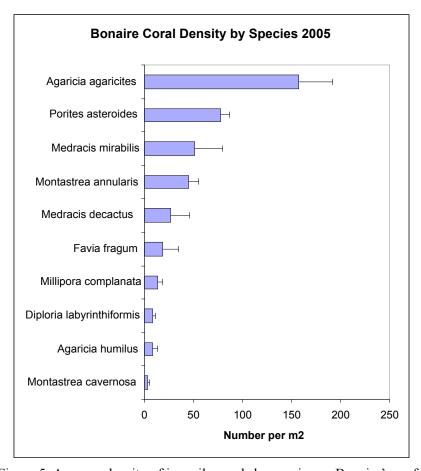
Figure 5. Average density of juvenile corals by species on Bonaire's reefs.

Discussion

The abundance of juvenile corals is currently much higher on the reefs of Bonaire than on the reefs of Belize. One possible explanation for this, which is supported by our pooled data from both regions, is that low abundances of macroalgae on Bonaire provide a favourable habitat for corals to settle and grow, while high abundances of macroalgae in Belize inhibit coral settlement and growth. The inverse relationship between macroalgae and juvenile coral is consistent with results from the previous Bonaire Report from 2003, which showed the same pattern with data from Bonaire and the Yucatan Peninsula in Mexico. A similar pattern was also documented in a time series spanning two decades in Jamaica (Hughes and Tanner 2000). During this time series a dramatic decline in live coral cover coincided with a substantial increase in macroalgal abundance.

The increase in macroalgal abundance throughout the Caribbean in recent decades is likely the result of a decrease in the abundance of herbivores present in most reef systems. Populations of herbivores such as parrotfish and the urchin *Diadema antillarum* have declined substantially due to overfishing and disease, respectively (Hughes and

Tanner, 2000). However, in degraded reefs where herbivory has recovered, so has coral recruitment (Edmunds and Carpenter 2001). For example, in Jamaica, increasing *Diadema antillarum* populations resulted in less macroalgae and significantly higher densities of juvenile corals. If the restoration of one species of herbivore can make a difference, managers throughout the Caribbean should work to restore herbivory, especially among fish populations.

Bonaire appears to be the exception to the rule when it comes to overall reef health in the Caribbean (Kramer 2003). However, if predatory fish are declining due to overfishing (Steneck and McClanahan 2003), and this trend continues as has happened elsewhere, herbivores may become more of a target for fishermen. Furthermore, if fish trap use increases, herbivorous fish will likely decline and macroalgae will increase. Considering that it is likely that it is the herbivorous fish that are responsible for Bonaire's low macroalgal cover, overfishing of these herbivores could have dramatic negative impacts on the reef.

Our data indicate that macroalgae regulates the recruitment potential for corals in reef ecosystems. Thus, it might be a good idea for managers on Bonaire and throughout the rest of the Caribbean to focus their efforts on restoring herbivore populations in order to reverse the trend of decreasing coral abundance. The resulting increase in live coral cover could potentially result in an overall rise in species diversity of a reef system, improving its resilience by increasing its tolerance to disturbance and its ability to recover (Bellwood *et al*. 2004). The importance of monitoring changes over time of both algae and coral abundance as management schemes are instated cannot be understated. Methodological approaches can be found in Chapter 7.

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Chapter 6: Spatial and temporal trends in nearshore benthic composition (1981 - 2005)

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Abstract

Bonaire is regarded as one of the healthiest Caribbean reefs and is well-suited for a study of nearshore benthic composition. From 1981-1983 F.C. van Duyl (1985) mapped the reefs of Bonaire. In March 2005, six sites were sampled and bottom type, ecologically dominant groups, and community types mapped. Most sites exhibited striking changes in nearshore benthic composition over the 20+ year period. Of the three reef zones described (inshore, midzone, and reef break), inshore and midzone areas were most different between 1985 and 2005. Considerable variation among sites exists. Only one site, Karpata, appeared to remain relatively unchanged over the 20+ year period. These results highlight the need for continued long-term reef monitoring and suggest Geographic Information Systems (GIS) as a practical tool to aid in management decisions.

Introduction

Most reefs in the Caribbean are in a state of decline, with percent live coral cover precipitously dropping over the past 30 years, while percent algal cover has steadily increased (for example, Hughes 1994). As such, the need to quantify, document, and communicate changes in coral reef ecosystems has recently received much attention (for example, Jameson *et al.* 2001; Asch and Turgeon 2003). Geographic Information Systems (GIS) is a practical tool that can be used to evaluate reef status and effectively communicate change (Garza-Perez *et al.* 2004; McKergow *et al.* 2005). Bonaire is the exception to this general trend of decline and is regarded by many as one of the healthiest of Caribbean reefs (Steneck and McClanahan 2004). As such, Bonaire is well-suited for a study of nearshore benthic composition.

From 1981-1983, Fleur C. van Duyl set out studying and mapping the reefs of Bonaire and Curacao. In creating a hand-drawn atlas of these reefs, her objectives were two-fold: (1) to test ecological and morphogenetic models of coral reef structure (Connell 1978; Adey 1978; Roberts 1974), and (2) to establish an inventory of the reefs that would serve as a tool for improved reef management. In March 2005, we set out to map the nearshore benthic composition at six sites on Bonaire: Karpata, Barcadera, Reef Scientifico, Forest on Klein Bonaire, Plaza, and Windsock. Our objectives were: (1) to create maps similar to those of van Duyl (1985) by using the same classification scheme, (2) to translate them into electronic form using GIS, and (3) to document changes to the reef over the past

20+years. Understanding such changes may be important in assessing reef health and may aid in current and future management decisions.

Methods

1981-1983 Mapping Effort
From 1981-1983, van Duyl (1985) created a series of maps describing the nearshore benthic composition of Bonaire using aerial photographs (~1:3700 scale) and ground-truthed with SCUBA using diver propulsion vehicles, and snorkeling. Nearshore mapping (7-15m water depth) described the bottom type (when live coral cover <10%), dominant benthic groups (7 total), and community types (a set of co-occurring species; up to 5 per group). Details and photographs are in van Duyl (1985). Mapping focused on ecologically dominant organisms. Maps were hand drawn (1:4000 scale), with each strip covering approximately 1600m lateral of reef area.

2005 Mapping Effort
Nearshore benthic composition was mapped at six sites in March 2005 (Fig. 1). For each site, at 25m intervals for 100m of shoreline, perpendicular transects were snorkelled and benthic composition type and respective distances recorded, until the reef break was reached (except for Barcadera where only 75m of shoreline was sampled). A Geographic Positioning System (GPS) (Garmin GPS map 176 C) established georeferenced points from which compass bearings were taken for each shore interval at each site. Zones of dominant bottom, group, and community types were determined using van Duyl's classifications with additional classification systems created for bottom types in 2005 (Table 1). Field maps were redrawn to scale using the "heads-up" digitizing method into electronic form using the GIS platform ArcView 3.0 (ESRI, RockWare, Inc. 1996) and edited to match colors and symbols with van Duyl's 1985 maps. Van Duyl's original maps were scanned and edited for comparison. Analyses of spatial trends through time were based upon visual inspection of the two maps for each site.

Results

A visual comparison between studies completed in 1985 (van Duyl) and this study showed dramatic differences in benthic composition for most sites. Bottom type, dominant benthic group, and community type were described from the inshore to the reef break.

Karpata
Van Duyl (1985) showed the inshore to include both shore zone and rubble bottom types. Head corals dominated the midzone, with isolated *Acropora cervicornis* and *A. palmata* communities. Along the reef break the head/foliate coral group (head corals and *Agaricia* with sea whips community), was abundant (Fig. 1).

Results from 2005 showed similar inshore trends to 1985 (Fig. 1, Fig. 7B). The inshore zone included both rubble and sand bottom types, but also included the foliate/finger

coral group (*Millepora complanata* and Porites-type communities). The sea whip group (sea whips dominated by *Pseudopterogorgia* spp. with sea fans of *Gorgonia* spp. and sea whips with head corals communities) dominated the midzone. The foliate/finger coral group (*M. complanata* and *Porites* communities) was also present in the midzone. Neither of these midzone groups was present in 1985. In addition, rubble and sand bottom types were found to dominate the midzone. As in 1985, a small patch of *A. palmata* occurred in the midzone. Along the reef break, the sea whip group (sea whips with head corals community) and the foliate/finger coral group dominated; both groups were not present in 1985 in this area.

Barcadera
Van Duyl (1985) showed the *A. palmata* group dominated the inshore at this site (Fig. 2). The *A. cervicornis* group dominated the midzone, while the head coral group (*Montastrea annularis* with sea whips community) dominated the reef break.

Spatial trends for the inshore and midzone environments in 2005 differed from those in 1985 (Fig. 2 Fig. 8C). In 2005, the inshore was dominated by rubble and the midzone by the *A. palmata* group (i.e. *A. palmata* and *M. complanata* community). The reef break was dominated by the head coral group (*M. annularis* with sea whips community), results consistent with the 1985 study. Also present near the reef break is an area of *A. cervicornis* rubble.

Reef Scientifico
Van Duyl (1985) describes an inshore area at Reef Scientifico dominated by sand with a patch of *A. palmata* (Fig. 3)*. A. cervicornis* dominates the midzone, while the head/foliate coral group (head corals and *Agaricia* spp. with sea whips community), dominate the reef break.

In contrast, we found in 2005 that "pavement" (consolidated coral rubble, Table 1) with areas of intertidal rocks dominated the inshore, while sand, rubble and sand, and the head coral group (*M. annularis* without sea whips community) dominate the mid-zone (Fig. 3, Fig. 8B). The sea whip group (sea whips and head corals community) dominated the reef break.

Forest, Klein Bonaire
Van Duyl (1985) described the inshore at Forest as mostly shore zone and sand (Fig. 4). The head coral group (*M. annularis* with sea whips community) dominated the midzone, along with small patches of *A. cervicornis*, sea whips, and rubble. The reef break was dominated by the head coral (*M. annularis* with sea whips community) and the head/foliate coral (head corals and *Agaricia* spp. with sea whips community) groups.

In 2005, inshore and midzone environments differed from those described in 1985 (Fig. 4, Fig. 8A). pavement dominated the inshore, while rubble and sand dominated the midzone. Small patches of the foliate/finger group (*M. complanata* community), the head coral group (*M. annularis* with sea whips community), and the *Acropora palmata* group were present in the midzone.

Plaza
Van Duyl (1985) described a shore zone environment at Plaza (18 Palms) with two discreet patches of *A. palmata* in the inshore (Fig. 5). The head coral (*M. annularis* with sea whips community) and *A. cervicornis* groups dominated the midzone. The head/foliate group (head corals and *Agaricia* without sea whips community) dominated the reef break.

All zones differed in 2005 as compared to 1985 (Fig. 5, Fig. 7A). pavement and associated macroalgae dominated the inshore zone. Discrete *A. palmata* patches were not observed in 2005 in this zone. The midzone was dominated by both rubble and rubble and sand with a large patch reef located in the center. The head coral (*M. annularis* with sea whips community) and the foliate/finger coral (*Millepora* spp.) groups divided the patch reef. Rubble extended to the reef break, with a small area of *A. cervicornis* and the head coral group (*M. annularis* with sea whips community) toward the northern margin.

Windsock
Van Duyl (1985) described the inshore as shore zone and sand (Fig. 6). The midzone was dominated by rubble with sand throughout, as well as by patches of *A. cervicornis, A. palmata* and the foliate/finger group (*Millepora* community). The head/foliate group (head corals and *Agaricia* with sea whips community) dominated the reef break.

In 2005, inshore and midzone environments were similar to 1985 (Fig. 6, Fig. 8C). pavement dominated the inshore, while rubble dominated the midzone. Patches of sand, the foliate/finger coral group (*M. complanata* community) and small areas of the head coral group (*M. annularis* community) were also present. Only rubble and sand dominated the reef break zone in 2005, differing from 1985 results.

Discussion

From 1981 to 2005, most sites exhibited striking changes in nearshore benthic composition in terms of bottom, dominant group, and community types. Of the three reef zones described (inshore, midzone, and reef break) inshore and midzone areas were most likely to depict different spatial patterns in 2005 than 1985, though considerable between-site variation exists. Only one site, Karpata, appeared to remain relatively unchanged over the 20+ year period.

Spatial analyses of the nearshore benthic composition from 1981-2005 show some important trends. All six sites observed by van Duyl (1985) contained *A. cervicornis* or *A. palmata*. *Acropora* assemblages tend to dominate areas of high prevailing wave energy but less frequent storm disruption in both the inshore and midzone (Hubbard 1997). By 2005, *Acropora* species covered considerably less nearshore area. For example, Barcadera was dominated between 1981 and 1983 in both the inshore and midzone areas by vast *Acropora* assemblages. However, in 2005, only rubble left by *A. palmata* was recorded inshore (Fig. 7), while *A. palmata* and large areas of *A. cervicornis*

rubble were observed in the midzone. These observations are consistent with the chronology of white band disease of the early 1980's that killed most *A. cervicornis* and *A. palmata* throughout the Caribbean (Aronson 2001; Steneck and McClanahan 2004).

All six sites have more rubble than they did 20+ ago. While rubble was observed only at Windsock and Karpata between 1981 and 1983, all sites contained rubble bottom-type in 2005. For example, Reef Scientifico (Don's Habitat), Plaza, Windsock, and Forest all showed large areas of rubble in the inshore and midzone areas (Figures 3-6). It is highly likely that the increase in rubble is due to *A. cervicornis* and *A. palmata* mortality and subsequent breakage since the outbreak of white band disease.

The sea whip group's abundance increased from 1981-2005. Sea whips are often found in areas of low stony-coral cover and rubble bottom-type (van Duyl 1985). These results are consistent with the observed increase in rubble bottom-type over the same time period. While sea whips were present at all six sites, they were dominant only at Forest, between 1981 and 1983. By 2005 however, sea whips were found to dominate midzone communities and reef break zones at two sites, Karpata and Reef Scientifico. These two sites showed increases in amount of rubble bottom and decreases in amount of stony coral cover from 1981-2005.

The foliate/finger coral group also appears to have increased from 1981-2005. The group (containing *Agaricia*, *Madracis*, *Porites porites*, and *M. complanata* communities) was observed to dominate at only Windsock between 1981 and 1983. However, head coral dominance remained relatively unchanged between 1981 and 2005.   Van Duyl describes all six sites as having areas of head coral communities, with *M. annularis* being the most prevalent. Four out of six sites, including Barcadera, Plaza, Windsock and Forest, showed little change in the coverage of head corals (Figures 2, 4-6). In general, head corals tended to be found in the deeper waters of the midzone and reef break zones. This seems to support the general theory of morphological depth zones for corals (with increasing depth, growth forms change from branching types, to domes or massive corals, to plates) (Hubbard 1997; Graus and Macintyre 1976). Van Duyl's study was, however, initiated after the white-band induced Acropora die-off in Bonaire. Undoubtedly, branching corals were much more abundant in shallow zones in the past.

While our results are compelling, possible sources of error include: methods employed by van Duyl, synchronization between 2005 sites and van Duyl's 1985 maps, and visual accuracy while snorkeling. Most sites exhibited dramatic changes over the 20+ year time period. Our results highlight the need for continued long-term reef monitoring and suggest GIS as a practical tool to observe changes in reef communities over time and to aid in management decisions.

Table 1. A comparison of bottom types identified by van Duyl and this study.

Bottom Type	van Duyl (1985)	This study (2005)
Rubble Hard Bottom	Loose and cemented coral debris, hard bottoms, dead reef flats, and stands of dead *Acropora palmata* and head corals *in situ.*	NA
Shore Zone	Composite of sand, coral debris, beach rock, and hard bottoms that are partly covered with encrusting organisms.	NA
Rubble	NA	Largely unconsolidated coral rubble; individual skeletons still apparent.
Rubble and Sand	NA	Even mixture of rubble and sand.
Pavement	NA	Consolidated coral rubble.
Algae-covered Pavement	NA	Pavement covered by conspicuous, filamentous algae.
Intertidal Rocks	NA	Large intertidal boulders/rocks

Karpata
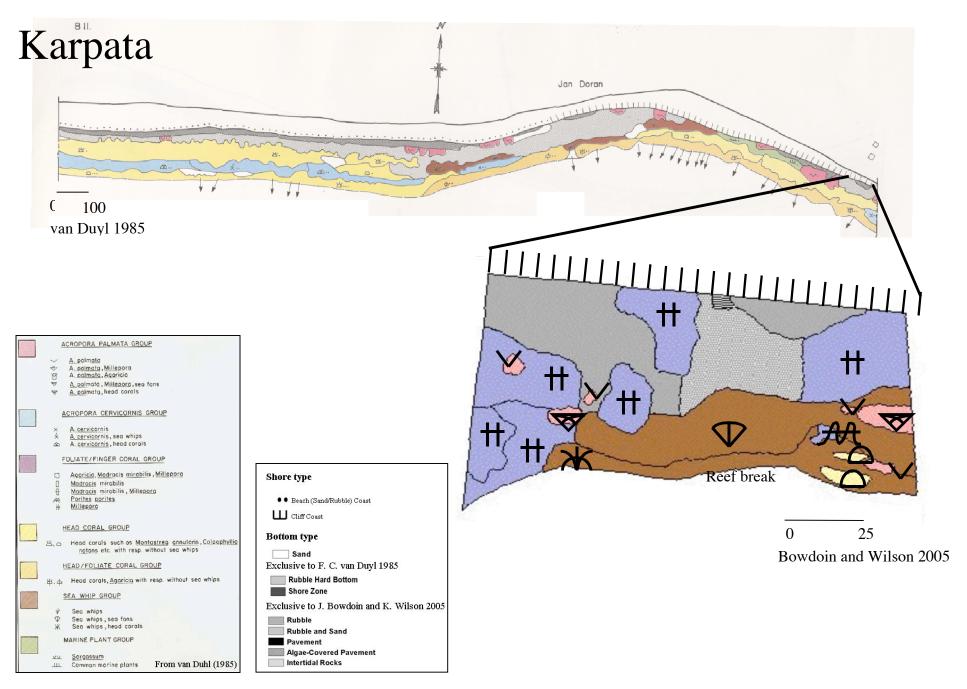
Figure 1. Maps of Karpata from 1985 (top) and 2005 (bottom) showing nearshore spatial trends in benthic composition.

Barcadera

B15.

Hilltop Hotel

Oil Slick Leap

0   100

van Duyl 1985

ACROPORA PALMATA GROUP
⌄ A. palmata
⌄ A. palmata, Millepora
⌄ A. palmata, Agaricia
⌄ A. palmata, Millepora, sea fans
⌄ A. palmata, head corals

ACROPORA CERVICORNIS GROUP
× A. cervicornis
⤬ A. cervicornis, sea whips
⌂ A. cervicornis, head corals

FOLIATE/FINGER CORAL GROUP
☐ Agaricia, Madracis mirabilis, Millepora
▯ Madracis mirabilis
⊞ Madracis mirabilis, Millepora
ᴪ Porites porites
ǂ Millepora

HEAD CORAL GROUP
⌂,⌂ Head corals such as Montastrea annularis, Colpophyllia natans etc. with resp. without sea whips

HEAD/FOLIATE CORAL GROUP
⌂,ǂ Head corals, Agaricia with resp. without sea whips

SEA WHIP GROUP
ᴪ Sea whips
ᴪ Sea whips, sea fans
⤬ Sea whips, head corals

MARINE PLANT GROUP
ᴠᴠ Sargassum
⊥⊥ Common marine plants

From van Duhl (1985)

Shore type

•• Beach (Sand/Rubble) Coast

⊔ Cliff Coast

Bottom type

☐ Sand
Exclusive to F. C. van Duyl 1985

▨ Rubble Hard Bottom

■ Shore Zone
Exclusive to J. Bowdoin and K. Wilson 2005

▨ Rubble

▨ Rubble and Sand

■ Pavement

▨ Algae-Covered Pavement

▨ Intertidal Rocks

Reef break

0   25

Bowdoin and Wilson 2005

Figure 2. Maps of Barcadera from 1985 (top) and 2005 (bottom) showing nearshore spatial trends in benthic composition.

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Reef Scientifico
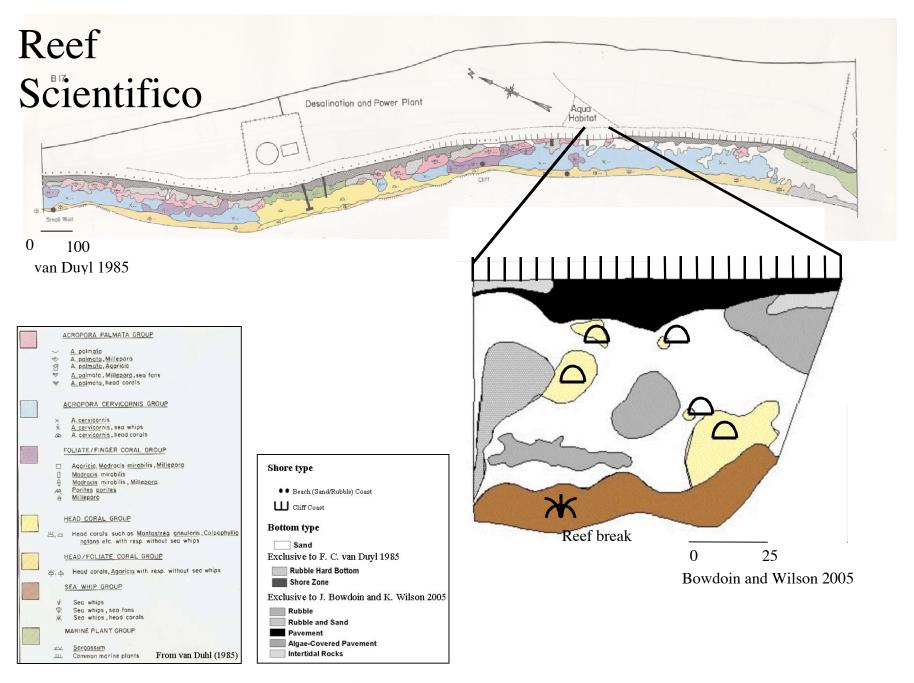
Figure 3. Maps of Reef Scientifico from 1985 (top) and 2005 (bottom) showing nearshore spatial trends in benthic composition.

Forest

van Duyl 1985

Reef break

Bowdoin and Wilson 2005

0   100

0   25

ACROPORA PALMATA GROUP

∪ A. palmata
♨ A. palmata, Millepora
☒ A. palmata, Agaricia
▽ A. palmata, Millepora, sea fans
▿ A. palmata, head corals

ACROPORA CERVICORNIS GROUP

× A. cervicornis
✕ A. cervicornis, sea whips
⌂ A. cervicornis, head corals

FOLIATE/FINGER CORAL GROUP

▢ Agaricia, Madracis mirabilis, Millepora
▯ Madracis mirabilis
╫ Madracis mirabilis, Millepora
⚭ Porites porites
╫ Millepora

HEAD CORAL GROUP

⛑,△ Head corals such as Montastrea annularis, Colpophyllia
notans etc. with resp. without sea whips

HEAD/FOLIATE CORAL GROUP

⛑,⌀ Head corals, Agaricia with resp. without sea whips

SEA WHIP GROUP

✦ Sea whips
▽ Sea whips, sea fans
✴ Sea whips, head corals

MARINE PLANT GROUP

∿∿ Sargassum
⫫ Common marine plants

From van Duhl (1985)

Shore type

•• Beach (Sand/Rubble) Coast
ШШ Cliff Coast

Bottom type

▢ Sand
Exclusive to F. C. van Duyl 1985
▨ Rubble Hard Bottom
▬ Shore Zone
Exclusive to J. Bowdoin and K. Wilson 2005
▨ Rubble
▨ Rubble and Sand
■ Pavement
▨ Algae-Covered Pavement
▢ Intertidal Rocks

Figure 4. Maps of Forest from 1985 (top) and 2005 (bottom) showing nearshore spatial trends in benthic composition.

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Plaza

Figure 5. Maps of Plaza from 1985 (top) and 2005 (bottom) showing nearshore spatial trends in benthic composition.

Windsock

van Duyl 1985

Reef break

Bowdoin and Wilson 2005

Figure 6. Maps of Windsock from 1985 (top) and 2005 (bottom) showing nearshore spatial trends in benthic composition.
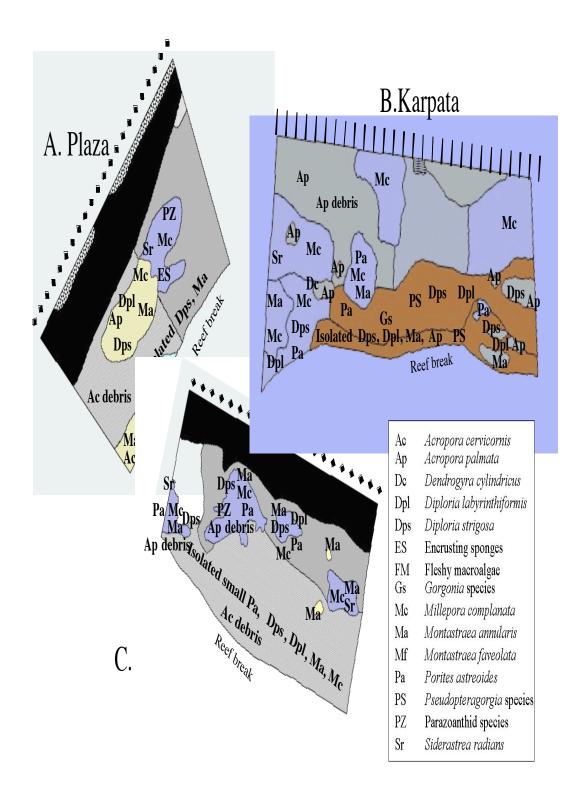
Figure 7. Maps of the 2005 study sites showing more detailed spatial trends in benthic composition.

B. Reef Scientifico

C. Barcadera

Ac	*Acropora cervicornis*
Ap	*Acropora palmata*
Dc	*Dendrogyra cylindricus*
Dpl	*Diploria labyrinthiformis*
Dps	*Diploria strigosa*
ES	Encrusting sponges
FM	Fleshy macroalgae
Gs	*Gorgonia* species
Mc	*Millepora complanata*
Ma	*Montastraea annularis*
Mf	*Montastraea faveolata*
Pa	*Porites astreoides*
PS	*Pseudopteragorgia* species
PZ	Parazoanthid species
Sr	*Siderastrea radians*
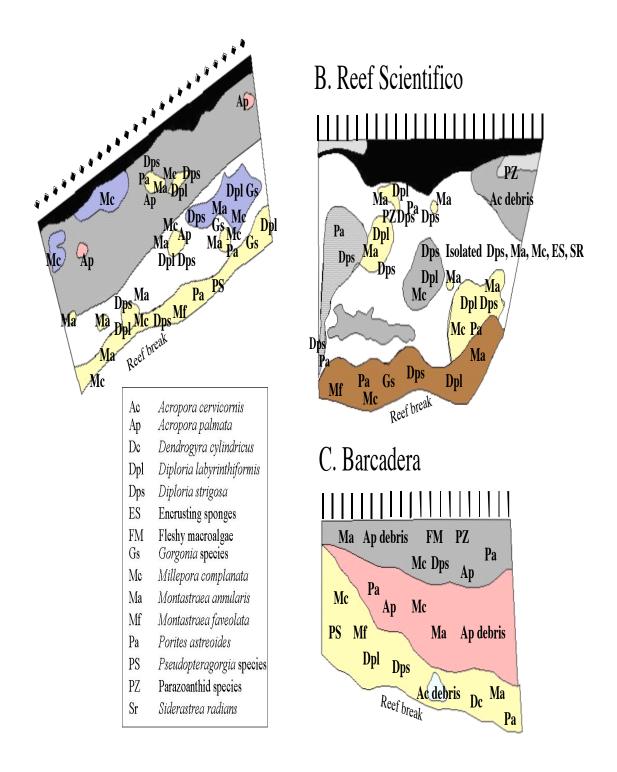
Figure 8. Maps of the 2005 study sites showing more detailed spatial trends in benthic composition.

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Chapter 7: Recent advances in Fish Protection Areas: Implementation, problems, and potential solutions

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Abstract

No-take reserves, or fish protection areas (FPAs), can increase fish biomass and species diversity within reserves and some in surrounding areas. Implementation of fish protection areas is a difficult job because it involves many different steps but one major determinant of the potential success of the reserve is community involvement. Reserves may not realize their objectives if legitimate needs of the local community are not considered. When community members are involved, there is a better chance for compliance and a greater likelihood that fish protection areas will succeed.

Introduction

Fish protection areas are one way to try to reverse the depletion of fish stocks around the world. The idea behind fish protection areas is that by setting aside part of an ecosystem where there is no or limited fishing, essential habitats for fish are protected, fish stocks may rebuild and increase the number of fish which can then be harvested (McClanahan and Arthur 2001; Halpern and Warner 2002; Sale *et al.* 2005). This form of fisheries management has been put into use in coral reefs because by protecting areas of reef, not only are fish populations protected, but many other associated animals essential for ecosystem functions, such as corals, are protected too. Several studies in recent years have evaluated fish protection areas in relation to coral reefs and several suggested how to improve protection and the production of fish from these areas. This chapter summarizes some of the recently published literature to determine if this management approach is still viable, and if it is, what impediments remain in their implementation.

Results from Fish Protection Areas

Most studies of reefs closed to fishing show an increase in the biomass of fished organisms in the area (Table 1). Polunin and Roberts (1993) showed that closing areas off Belize and Saba to fishing increased the biomass, size and abundance of many reef fish. Jennings and Polunin (1996) found that fish protection areas off Fiji showed increased biomass of large predators and a decrease in the number of large herbivores in reserves. Reefs off Kenya and Tanzania had an increase in the number of fish species on closed reefs versus those where fishing was allowed to occur (McClanahan and Arthur 2001). Fish protection areas off New Zealand showed increased numbers of lobsters and fish versus their unprotected equivalent areas (Shears and Babcock 2002). Arias-

González *et al.* (2003) found in protected areas off the Mexican Caribbean coast there was an increase in fish and lobster biomass, and Acosta and Robertson (2003) also saw an increase in lobster populations and biomass in reserves off Belize. Halpern and Warner (2003) after reviewing 80 reserves observed that biomass, density and diversity all increased with fish protection areas.

Some studies did not record positive effects of fish protection areas. In one case, after closure of a small reserve off Israel, the recruitment of the branching coral *Styophora pistillata* actually declined in an these areas closed to human use (Epstein *et al.* 2005). Rogers and Beets (2005) found that despite 50 years of closure, fish protection areas in US Virgin Islands show no difference between reserves and open areas. These two examples are very instructive about some limitation to the successful implementation of coral reef fish protected areas. First, the perceived management problem must result from fishing impacts and thus be treatable by the cessation of fishing. The first example illustrates this well. Most coral decline results from bleaching or disease which are not directly linked to fishing pressure. No-take reserves are incapable of halting much of the decline in live coral (Jameson *et al.* 2002; Bruno *et al.* 2001). The absence of PFA impact in the US Virgin Islands is probably related to the poor compliance in that region (Williams and Polunin 2000). These problems must be seriously considered before attempting to implement fish protection areas.

Positive effects commonly seen in fish protection areas is an increase in function at higher trophic levels of fish protection areas (Shears and Babcock 2002; Arias-González *et al.* 2003). The decline in trophic level function is one reason suggested by Pandolfi *et al.* (2005) that coral reefs have begun to transform to ecosystems dominated by macroalgae. When trophic levels function properly there are several ecologically equivalent species in the same functional group. When several different species do the same job on the reef, and a natural event causes the decline of one species, another species will continue its functional role. Otherwise, with a decrease in trophic level functions, the layers that protect the ecosystem from disaster have been lost. This stimulated several scientists to propose we manage for ecological functions, such as herbivory, at a function group level (Bellwood *et al.* 2004).

The decline in critical ecological functions is what happened in many Caribbean reefs as overfishing drastically decreased the biomass of larger herbivorous fish such as parrotfish. During this time the grazing sea urchin, *Diadema antillarum* increased until a pathogen caused its mass mortality. With the decline in *Diadema*, no other major herbivores were abundant enough to control macroalgal abundance (Hughes 1994).

Higher order carnivores, if not reproductively limited, usually increase most rapidly following the establishment of fish protection areas (McClanahan 2005). Several studies found that with increases in large-bodied carnivores, herbivorous sea urchin abundance declines (McClanahan 1995; McClanahan and Muthiga 1989). Shears and Babcock (2002) found that in fish protection areas off New Zealand lobster and fish populations increased while the population density of the urchin *Evechinus chloroticus* decreased. The decrease in the urchin populations appears to be due to predation from the now more

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abundant carnivorous fish and lobsters. Arias-González *et al.* (2003) also showed that reserves off Mexico not only had greater fish biomass but also an increase in the number of juvenile lobster, adding to the trophic structure of the ecosystem.

Implementation of Fish protection areas

For fish protection areas to provide the increase in organism numbers and diversity there needs to be community buy-in to establish areas where fishing in prohibited. This is usually not popular with fishing communities that rely on the reefs for their livelihood or for which fishing has been a long-standing tradition. In areas where governmental agencies create a fish protected area without any *input* from the community, usually there is no increase in fish populations because there has been no buy-in in the management of the area. In Honduras, the government established 25 fish protection areas without any input from the stakeholders. As a result, the only reserve that was successful was the Cayos Cochinos Biological Reserve where the Hondurian Navy patrols (Harbourne *et al.* 2001). Many local people near the reserves do not even know the reserves exist or what the consequences are of removing fish from the protected area. At Wakatobi National Park in Sulawesi, Indonesia, the government also established a fish protected area without input from the local Mola people. Over 95% of the Mola village population uses the reefs for income through fishing, coral mining, and live turtle trading. With little knowledge of regulations that restrict fishing activity and no input during the formation of the reserve, the majority of the community disapproved of any restrictions (Elliott *et al.* 2001). There also was much confusion on the part of the villagers about the rules and regulations of the reserve. The process of establishing the reserves was so flawed that it bred contempt among the villagers; so much so that when coral dynamiting occurred on the reefs, the villagers would not assist the police in catching those responsible because of the extreme distrust toward governmental police (Elliott *et al.* 2001).

The best way to go about establishing a fish protected area is to get the community involved (Brown *et al.* 2001; Jones 2002; Carter 2003). The initial step is to identify stakeholders who would be affected by the establishment of a fish protected area. Stakeholders may include scientists, political leaders, people from the fishing community, people from the surrounding community, and dive shops or tour operators. Since the primary regulatory action is to stop fishing in identified areas, the fishing community stakeholders will be most affected and should be included and actively involved at every step in the process. Often it is useful to bring all groups together and provide scientific information about the advantages to establishing a fish protected area. Proposed fish protected areas should also provide economic advantages, especially for the local fishing community which may depend on the reef for income (Jones 2002). While a fish protected area often provides an increase in tourism because increased biomass of large fish will draw divers and thus may provide increased income for local vendors and dive shops, this economic boost often does not translate to the fishing community. While the idea of preserving natural places is shared by many people in different communities around the world (Brown *et al.* 2001; Elliott *et al.* 2001), unless

there is compensation to the local community for the closure, then the community will not value the reserve.

In Tobago, a meeting about the establishment of Buccoo Reef Marine Park showed that the local community was interested in establishing the reserves but only if the increased tourism was kept to small local hotel and resorts which would benefit the local community. The establishment of large hotel chains would provide money to the chains not to the local community (Brown *et al.* 2001). Involvement of all stakeholders in the discussions of the creations of fish protected area improves the likelihood for the success of the reserve.

Several good examples of successful fish protection areas come from the Philippines, and many of these strategies apply to Bonaire. Fish protection areas have been established in the Philippines since the early 1980's and after the establishment of the reserves, an increase in both fish numbers and coral cover has occurred (White *et al.* 2002; Christie *et al.* 2002). There were several steps in the creation of the fish protected areas. The first was to obtain scientific information, then have meetings with the community to begin discussing the reserves. The next step, education, involved holding meetings to provide scientific information to the community and receive community feedback. When the marine reserve was established, managers began to get community people involved as rangers and other personnel working in the reserve. This linked the community to the management process and built confidence in the fish protected area process. Finally, the managers had meetings several years after the establishment to discuss problems and issues that had arisen with the development of the reserve (White *et al.* 2002). The involvement of the community in the decision to establish the reserve as well as educating and getting them involved in the fish protected area has made the reserve successful. When the community has a stake in the resource they become involved and work with the government to establish and comply with the guidelines of the reserves (Christie *et al.* 2002).

A similar positive experience of community involvement and compliance occurred in the Caribbean island of St. Lucia (Roberts *et al.* 2001). There, the initially reluctant fishing community became strong advocates for fish protected areas. However, this level of support was not received until after years of community organizing efforts, including establishment of fishermen's cooperatives, and many meetings raising awareness and a level of buy-in to the project. Fishermen worked closely with mangers and other stakeholders to establish marine use zones most appropriate to the needs of the island community (Goodridge *et al.* 1997). Additionally, a program to compensate fishermen most affected by displacement was necessary for the first year of closure, but eventually an increase in fish biomass inside the protected areas began to spill over to fishing areas, providing a higher catch per unit of fishing effort. In St. Lucia, the fish protection areas have been able to provide an alternative to unsustainable fishing practices, have reduced user conflict, and overall improved the marine environment of coastal areas (Kai Wulf, pers. comm.).

Problems with Fish protection areas

While there are some examples of well-run marine reserves in the world, many fish protection areas are considered "paper parks," where the government creates a fish protected area but no one follows the rules and no increase in fish biomass is seen after the creation of the reserve. This is the case in Honduras as mentioned before (Harbourne *et al.* 2001), in Indonesia (Elliott *et al.* 2001), and in territories of the United States. Two fish protection areas in the US Virgin Islands were established in the 1950's but they have not seen the expected increases in fish species (Rogers and Beets 2001). The suggested reason for the continued decrease in reef organism populations is that the reserves are too small (approximately 2500 ha of reserves) and the rules are too lenient. Traditional fishing practices, including rod and line or traps of "conventional Virgin Island designs" are allowed in the reserve but it is often difficult to tell if the equipment being used fits the regulations or not (Rogers and Beets 2001).

Regulation of fish protection areas is a common problem especially when the protected areas are not near a shore. Off the coast of Florida the US established a marine reserve to protect deep-water *Oculina* coral, but because of it is off shore it is difficult to protect and control. Boats and planes are used to patrol the areas but it is often difficult to determine if the boats in the protected area are fishing or not (Reed 2002). The problem of offshore enforcement is also seen in the Philippines. The Tubbataha Reef National Marine Park consists of two atolls but the community has trouble patrolling the reef because of its distance from the nearest island (White *et al.* 2002). DeMartini (2004) suggested that atolls are good candidates for fish protection areas because they are prime nursery habitat to for juvenile fish, but because atolls are not associated with an island they are politically difficult to regulate.

Another problem of regulation is the cost. Personnel must be paid to patrol the reefs and prevent outsiders some entering the reserve otherwise fishing will occur in the protected area. The cost of establishing and managing a fish protected area can be high although the majority of the cost is in the initial establishment (White *et al.* 2002). One way to lower patrolling costs is to get community members involved in the fish protected area. If the community polices the reserve then less money is needed for patrolling and it adds to the sense of pride in the fish protected area.

The politics of fish protection areas and the management of the reserves can be complicated because management can fall under several different agencies. In the United States the management of water quality, fisheries management, and coastal development all are the responsibilities of different agencies. Often there is not good communication between the agencies and this causes problems from fish protection areas because one agency is not responsible for the regulations (Lindeman *et al.* 2000; Duval *et al.* 2004).

Finally, fish protection will not necessarily protect corals in reef ecosystems. A major problem for coral reefs is global warming. Increasing sea surface temperature is correlated with bleaching; when temperatures get above the thermal threshold of the coral, bleaching occurs. West and Salm (2002) suggest that if coral preservation is the

goal of management, it might make sense to discover factors that help prevent bleaching and then creating fish protection areas where these factors are found. Examples of environmental factors they suggest that prevent bleaching include, upwelling zones, shaded areas, areas with high water flow, and saving corals that are acclimated to warmer water temperatures.   However, the resilience of reefs not only relies on an ecosystem's ability to resist a disturbance such as bleaching, but recovery from it. Intact fish communities can facilitate recovery. Palau in western Pacific suffered a 90% mortality event due to bleaching (Bruno *et al.* 2001) but has intact fishing communities due to good local management and FPAs (Johannes 2002). The reef has recovered completely and has newly pre-bleaching coral cover (Steneck unpublished data).

Recommendations for Fish Protection Areas
More research on fish protection areas should be conducted to assist scientists and managers understanding of the interactions that are occurring on coral reefs. Sale *et al.* (2005) point out five major gaps in the literature surrounding fish protection areas. The gaps include information about larvae dispersal, patterns of juvenile movement, the impact of fishing on the ecosystem, water mass movements in areas of fish protection areas and more examples of significant increases in fish populations resulting from fish protection areas. Lindeman *et al.* (2000) also discuss the need for more information on spawning behaviour and larvae movements to assist the agencies in making decisions on fish protection areas, particularly noted for groupers. Some researchers are beginning to answer some of the crucial questions for a better understanding of fish protection areas. Guichard *et al.* (2004) looked at larval transport and suggest that ocean currents and larval duration in the water column should influence the site selection for fish protection areas.

Area protection may constrict the area that is available for fishing. Support for such measures will likely be lacking from the very stakeholders from whom compliance is critical for the success of a fish protection area (Kaunda-Arara and Rose 2003). There must be a perceived or real spillover that benefits adjacent fishery communities. Having a program in place that document before and after catch per unit effort (CPUE) is an ideal way to monitor the success of a fish protection area as well as provide evidence of benefits to people whose livelihoods may be most at stake (Roberts and Polunin 1991).

International involvement in the formation of coral reefs is recommended and has communication between protected area mangers (Bellwood *et al.* 2004; Pandolfi *et al.* 2005). International involvement provides money and the ability for researchers to work out answers to the questions posed by Sale *et al.* (2005). Pandolfi *et al.* (2005) suggest increasing trophic levels on reefs so there are more interactions and more overlap of organisms in conformational groups. Bellwood *et al.* (2004) suggest that most fish protection areas are too small to provide the increases in fish numbers that the world is looking for. Increasing size the size of fish protection areas should increase the fish populations in the area of the reserve, but Agardy (2000) points out that each fish protected area is different and the results in one fish protected area will be different than in another fish protected area. Scientists and managers need more information to make the best informed decisions.

Conclusions

Fish protection areas usually increase the abundance and diversity of harvested species but many problems such as a lack of community buy-in prevents their effective deployment.   Ideally we should continue working on effective fish protection areas to fill our knowledge gaps so scientists and managers have a better understanding of the reefs and make better recommendations. The greatest way to help fish protection areas is to make sure that all stakeholders, especially from the fishing community, should be involved in the creation, design, and if possible, monitoring of fish protection areas. If fish protection areas increase the size and abundance of fish such that the community profits, then stakeholders will want to protect the reefs for their own reasons. Information on how the fish protection areas are changing should be regularly shared with the fishing community. This means both the good news and bad news is presented to fishers so they can make informed decisions about what to do next. A monitoring program that openly shared its findings will be viewed less suspiciously allowing the adaptive co-management process to develop the credibility and trust it must have to be durable. Science must merge with the needs of society if useful changes are to be made because only when society cares about the future of coral reefs will changes for the better occur.

Table 1. Review of recent studies done on fish protected areas showing the goal of studies, the results from the study and whether the goal of the study was fulfilled.

Study (Authors and Year)	Goals of the Study	Results of the Study	Was the Goal Fulfilled?
Acosta and Robertson (2003)	Did reserves act as refuge for two lobster species (*Panulirus argus* and *P. guttatus*)?	*Panulirus argus* populations increased 300% and biomass increased 2000% within the reserve, *P. guttatus* populations did not change	Yes
Arias-González *et al.* (2004)	Did trophic levels increase within the marine reserve?	Increase in both fish and lobster biomass	Yes
Halpern and Warner (2002)	Do reserves increase fish biomass quickly (1-2 years) or over a longer period of time (>10 years)?	Review of 80 marine reserves showed an increase in fish biomass within 2 years	Yes, but no long term data so species that did not response to the reserve may need longer period to increase than the studied period

Study (Authors and Year)	Goals of the Study	Results of the Study	Was the Goal Fulfilled?
Jennings and Polunin (1996)	Does fishing have an effect on the community of a fish protected area?	Increase in large carnivores within the protected area and a decrease in large herbivores	Yes, fishing does have an effect but it seems increased fish biomass occurred because of protection not from fishing
McClanahan and Arthur (2001)	Do fish protected areas off East Africa see increases in fish biomass?	Increase in fish biomass and diversity within the protected area	Yes
Polunin and Roberts (1993)	Does a fish protected area increase fish biomass?	Increased biomass and number of fish	Yes
Shears and Babcock (2002)	Are more trophic levels present within marine reserves?	Increase in fish and lobster populations within reserves, so an increase in trophic levels did occur	Yes
White *et al.* (2002)	Would no fishing around a Philippine island increase fish biomass?	Increased fish numbers and increased coral cover	Yes
Russ and Alcala (2004)	Is there an overall benefit to fisheries next to marine reserves in the Philippines?	Increased spillover over the past three decades	Yes
Epstein *et al.* (2005)	Would closure of a reef increase coral populations in a small protected area?	Increased number of corals but decreased growth and recruitment	No
Rogers and Beets (2005)	Are marine reserves around the US Virgin Islands increasing fish populations and coral cover	No differences in biomass of fish nor coral between protected areas and unprotected areas	No

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Chapter 8: Methods of Juvenile Coral Recruitment Monitoring

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Rational

Patterns of distribution and abundance of juvenile corals is a measure of coral recruitment. Corals become sexually mature at sizes above 40 mm in diameter, so quantifying the abundance of corals less than 40 mm in size is our estimate of coral that will recruit to adult populations if post-settlement mortality is relatively low. This protocol is designed to address two important objectives. OBJECTIVE ONE: Algal community structure and density of juvenile corals along set transects will be measured. Corals within the quadrats will be identified to species or genus and measured in size. OBJECTIVE TWO: On each transect, selected juvenile corals will be mapped and photographed to monitor their growth and survival over time. From these data, survivorship curves for juvenile corals will be determined which allow recruitment rates to adult populations to be determined.

Methods

Site selection:
Select a 10 m location on a target reef. Obtain high resolution GPS coordinates at the center of the reef site. For ease of relocating a site from a boat, use a weighted line with a toggle buoy to mark the precise coordinates of the set transects.

Establish four 10 m transects along the reef. The transects will be approximately parallel to shore in order to maintain a constant depth.

If possible, mark the start and finish points of the transects so repeated monitoring can be conducted at these locations over time. The coral settlement plates provide a means for marking permanent transects.

Objective 1: *Juvenile Coral Demography Transects:*

Along each of the four transects established using the method described above, regular quadrat sampling will be conducted to quantify the distribution, abundance and size of juvenile corals. For this, string a meter tape from the northernmost plate to the southernmost plate. Place a 25 cm X 25 cm quadrat at the 0, 2.5, 5, 7.5 and 10 m locations on the tape (i.e. 5 locations per transect). Randomly place the quadrat where corals or algae could recruit. Substrate with live invertebrates such as sponges, gorgonians and adult corals should be avoided (reject quadrats with > 25% live invertebrate cover).

Within each set quadrat, measure the size of each coral colony that is less than or equal to 40 m (long axis). Identify each coral to species if possible but at least to genus. In each quadrat visually estimate percent cover of turf algae, macroalgae, articulated algae, crustose corallines and non-coralline crusts (primarily *Peysonnelia*). Measure the average canopy height of macroalgae, turf algae, and articulated algae. Enter data using the excel data template provided (see Appendix A.). Note: Visual percent cover is more desirable than point-intercept or grided quadrats (see Dethier et al 1993).

Objective 2: *Coral Settlement Plates & Site markers for transects & monitored juvenile corals:*

To mark transects and specific locations as well as being able to monitor settlement and post-settlement survival, terra cotta coral settlement plates will be placed. The methods for placing terracotta settlement plates are detailed in Chapter 2.

Settlement plates should be 10 cm X 10 cm and approximately 1 cm thick. A 1/4" hole should be drilled in the center of each plate (use a masonry bit and a drill press). When dry, each plate should be numbered consecutively on the smooth underside of the plate with a permanent, waterproof pen (place the irregular surface facing up). Write the number above and below the hole, and cover the numbers with clear durable epoxy (West System 105 epoxy works well over a 3 – 5 year period). Also write the number of each plate in large numbers on the upper side of the plate and cover it with epoxy (this number will get covered as the plate gets colonized but when scraped, can serve well for initial orientation of transects).

The method for affixing plates is to hammer a plate into the reef into which a 1/4" vertical bolt is fixed. This works, but settlement plate loss is relatively high. A better method is to drill holes into dead coral and insert a plastic wall anchor into which a stainless steel bolt is screwed. This method holds plates for at least 3 – 4 years.

Place the first settlement plate at the beginning of the transect (northern end) and place the last one at the end of 10 m (southern end). The others should be places along the transect where substrate allows. It is a good idea to place plates within 25 cm of a juvenile coral for monitoring purposes. For photo orientation purposes, place the plate numbers so that they face you as you swim seaward down the transect.

Make maps of plate placement (including numbers) before leaving the station.

Monitoring Survivorship and Growth of Juvenile Corals

At each coral settlement plate, look for a juvenile coral within 25 cm (one quadrat length) of the plate. Record the plate number and whether the juvenile coral is to the right, above, left or below the plate using the shoreward to seaward orientation. Sketch the location of the coral in reference to the plate. If possible take a digital photograph of the plate and the quadrat (showing the plate number) in that same seaward orientation and

then take a close up photo of the recruit with a ruler scale next to the coral. Repeated photos of these corals will provide growth and death rates over time per species.

If a digital camera is not available, record the juvenile coral placement as described in the paragraph above, identify the coral to species, and measure the long axis of the coral.

Monitoring Frequency

The primary objective is to determine the distribution, abundance and size of juvenile corals at each reef site. For this, annual monitoring using the methods described above.

Annual monitoring should be conducted between May and August to maximize fair weather, minimize hurricane potential and to standardize annual patterns throughout the region.

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Appendix A. Average biomass, density, and fork length of herbivorous fish, Bonaire 2005

	Biomass (g per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Windsock						
Acanthurus bahianus	782.53	1368.47	8.67	14.46	14.88	1.64
Acanthurus chirurgus	0.00	0.00	0.00	0.00		
Acanthurus coeruleus	204.53	231.13	1.33	1.63	16.67	1.53
Kyphosus sectatrix	0.00	0.00	0.00	0.00		
Microspathadon chrysurus	70.56	78.25	1.00	1.10	13.33	0.58
Scarus coelestinus	0.00	0.00	0.00	0.00		
Scarus croicensis/iserti	68.91	106.76	0.67	1.03	14.00	0.00
Scarus guacamaia	0.00	0.00	0.00	0.00		
Scarus taeniopteris	853.75	739.44	6.33	4.97	14.80	5.75
Scarus vetula	695.12	380.74	2.00	1.26	27.30	4.76
Sparisoma aurofrenatum	257.08	298.80	2.67	3.01	15.94	0.92
Sparisoma chrysopterum	0.00	0.00	0.00	0.00		
Sparisoma viride	558.78	707.13	2.00	1.79	17.25	9.07
Stegastes diencaeaus	148.25	86.54	16.33	8.52	6.57	0.61
Stegastes leucostictus	0.00	0.00	0.00	0.00		
Stegastes planifrons	160.95	86.15	32.33	18.99	5.18	1.12
Acanthuridae	987.07	1304.54	10.00	13.97	15.56	1.81
Kyphosidae	0.00	0.00	0.00	0.00		
Pomacentridae	379.76	151.21	49.67	21.37	5.77	1.00
Scaridae	2433.65	1157.74	13.67	4.97	17.61	3.76
Denuding (Acanthurids, Microspathadon)	**1057.63**	**1318.28**	**11.00**	**14.24**	**14.86**	**1.14**
Excavating (Scarids)	**2433.65**	**1157.74**	**13.67**	**4.97**	**17.61**	**3.76**
Non-denuding (Territorial Damsels)	**309.20**	**137.89**	**48.67**	**21.30**	**5.58**	**1.01**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**3491.28**	**1581.82**	**24.67**	**16.72**		
Grand Total	**3800.48**	**1700.05**	**73.33**	**23.45**	**9.06**	**2.04**
Plaza						
Acanthurus bahianus	12.21	34.55	0.25	0.71	13.00	
Acanthurus chirurgus	245.97	324.67	1.75	2.25	15.67	1.89
Acanthurus coeruleus	213.28	186.94	1.50	1.41	16.00	1.87
Kyphosus sectatrix	0.00	0.00	0.00	0.00		
Microspathadon chrysurus	47.07	92.56	0.50	0.93	14.50	2.12
Scarus coelestinus	0.00	0.00	0.00	0.00		
Scarus croicensis/iserti	834.33	579.23	7.25	6.14	15.08	4.47
Scarus guacamaia	0.00	0.00	0.00	0.00		
Scarus taeniopteris	652.70	663.84	6.00	7.09	14.40	4.48
Scarus vetula	1815.39	1020.68	4.00	2.39	31.18	6.44
Sparisoma aurofrenatum	277.01	388.20	2.50	2.78	16.10	4.31
Sparisoma chrysopterum	123.59	349.56	0.25	0.71	30.00	
Sparisoma viride	2542.42	2026.96	3.00	2.14	29.98	5.29
Stegastes diencaeaus	353.56	112.30	43.50	16.24	6.19	0.85

Appendix A. Average biomass, density, and fork length of herbivorous fish, Bonaire 2005

	Biomass (g per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Plaza, cont.						
Stegastes leucostictus	0.00	0.00	0.00	0.00		
Stegastes planifrons	101.29	74.36	21.75	17.35	5.22	1.30
Acanthuridae	471.46	245.81	3.50	1.77	15.74	1.68
Kyphosidae	0.00	0.00	0.00	0.00		
Pomacentridae	501.93	156.53	65.75	28.61	5.99	0.94
Scaridae	6245.45	3155.94	23.00	11.66	19.64	2.54
Denuding (Acanthurids, Microspathadon)	**518.53**	**262.80**	**4.00**	**1.85**	**15.40**	**1.35**
Excavating (Scarids)	**6245.45**	**3155.94**	**23.00**	**11.66**	**19.64**	**2.54**
Non-denuding (Territorial Damsels)	**454.85**	**135.48**	**65.25**	**28.42**	**5.92**	**0.90**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**6763.98**	**3256.45**	**27.00**	**12.65**		
Grand Total	**7218.83**	**3237.64**	**92.25**	**34.96**	**9.78**	**1.63**
Forest, Klein Bonaire						
Acanthurus bahianus	0.00	0.00	0.00	0.00		
Acanthurus chirurgus	0.00	0.00	0.00	0.00		
Acanthurus coeruleus	205.46	258.03	1.50	1.77	15.25	1.04
Kyphosus sectatrix	0.00	0.00	0.00	0.00		
Microspathadon chrysurus	191.25	209.44	2.25	2.49	14.17	0.75
Scarus coelestinus	0.00	0.00	0.00	0.00		
Scarus croicensis/iserti	251.27	469.32	1.50	2.78	17.00	1.89
Scarus guacamaia	0.00	0.00	0.00	0.00		
Scarus taeniopteris	1086.45	309.89	14.00	8.07	13.45	5.85
Scarus vetula	1469.56	1322.05	3.50	2.78	27.88	3.97
Sparisoma aurofrenatum	121.15	190.30	0.75	1.04	19.00	4.36
Sparisoma chrysopterum	0.00	0.00	0.00	0.00		
Sparisoma viride	3220.71	3314.19	4.50	3.96	26.64	9.46
Stegastes diencaeaus	129.81	99.85	10.00	5.24	7.00	1.17
Stegastes leucostictus	0.00	0.00	0.00	0.00		
Stegastes planifrons	541.50	101.08	122.00	59.87	4.84	0.89
Acanthuridae	205.46	258.03	1.50	1.77	15.25	1.04
Kyphosidae	0.00	0.00	0.00	0.00		
Pomacentridae	862.56	182.66	134.25	59.34	5.26	1.04
Scaridae	6149.16	4135.34	24.25	6.88	16.92	5.15
Denuding (Acanthurids, Microspathadon)	**396.71**	**212.92**	**3.75**	**1.98**	**14.63**	**1.09**
Excavating (Scarids)	**6149.16**	**4135.34**	**24.25**	**6.88**	**16.92**	**5.15**
Non-denuding (Territorial Damsels)	**671.31**	**102.11**	**132.00**	**60.04**	**5.07**	**0.90**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**6545.87**	**4175.93**	**28.00**	**6.68**		
Grand Total	**7217.18**	**4182.38**	**160.00**	**62.97**	**7.34**	**1.93**

Appendix A. Average biomass, density, and fork length of herbivorous fish, Bonaire 2005

	Biomass (g per 100 m^2)		Density (# per 100 m^2)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Reef Scientifico						
Acanthurus bahianus	44.37	125.51	0.50	1.41	15.50	
Acanthurus chirurgus	73.63	148.55	0.50	0.93	16.00	4.24
Acanthurus coeruleus	153.00	229.75	1.00	1.51	16.33	1.53
Kyphosus sectatrix	628.98	1779.04	0.75	2.12	33.00	
Microspathadon chrysurus	32.50	60.18	0.50	0.93	13.00	0.00
Scarus coelestinus	0.00	0.00	0.00	0.00		
Scarus croicensis/iserti	112.67	198.50	1.25	2.12	12.78	0.69
Scarus guacamaia	0.00	0.00	0.00	0.00		
Scarus taeniopteris	1789.78	748.79	14.50	7.39	15.46	2.45
Scarus vetula	1520.08	995.55	4.75	3.20	26.24	5.28
Sparisoma aurofrenatum	276.66	241.83	2.25	1.98	17.53	3.43
Sparisoma chrysopterum	0.00	0.00	0.00	0.00		
Sparisoma viride	985.95	1213.66	2.25	2.25	22.10	7.28
Stegastes diencaeaus	209.25	118.37	26.00	11.36	5.47	0.98
Stegastes leucostictus	0.00	0.00	0.00	0.00		
Stegastes planifrons	73.80	57.61	18.25	8.31	4.36	1.21
Acanthuridae	271.00	248.95	2.00	1.85	16.20	1.60
Kyphosidae	628.98	1779.04	0.75	2.12	33.00	
Pomacentridae	315.55	196.30	44.75	11.85	5.13	1.09
Scaridae	4685.14	1430.56	25.00	8.42	18.12	2.94
Denuding (Acanthurids, Microspathadon)	**932.48**	**1818.34**	**2.50**	**2.07**	**17.25**	**4.71**
Excavating (Scarids)	**4685.14**	**1430.56**	**25.00**	**8.42**	**18.12**	**2.94**
Non-denuding (Territorial Damsels)	**283.05**	**146.09**	**44.25**	**11.54**	**5.06**	**0.99**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**5617.62**	**2596.26**	**27.50**	**8.19**		
Grand Total	**5900.67**	**2568.38**	**72.50**	**9.61**	**10.08**	**1.55**
Barcadera						
Acanthurus bahianus	0.00	0.00	0.00	0.00		
Acanthurus chirurgus	95.85	177.85	0.50	0.93	18.50	0.71
Acanthurus coeruleus	180.35	258.46	1.00	1.51	17.83	1.26
Kyphosus sectatrix	0.00	0.00	0.00	0.00		
Microspathadon chrysurus	115.47	76.96	1.50	0.93	13.67	1.03
Scarus coelestinus	0.00	0.00	0.00	0.00		
Scarus croicensis/iserti	230.76	322.25	0.75	1.04	25.00	2.00
Scarus guacamaia	0.00	0.00	0.00	0.00		
Scarus taeniopteris	672.07	490.39	4.50	2.78	16.24	4.77
Scarus vetula	1299.53	1023.33	3.00	1.85	28.67	4.44
Sparisoma aurofrenatum	115.45	169.48	0.75	1.04	19.00	2.65
Sparisoma chrysopterum	0.00	0.00	0.00	0.00		
Sparisoma viride	3006.30	3503.62	4.00	4.00	27.55	5.33
Stegastes diencaeaus	525.55	108.10	31.50	13.08	8.33	0.88

Appendix A. Average biomass, density, and fork length of herbivorous fish, Bonaire 2005

	Biomass (g per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Barcadera, cont.						
Stegastes leucostictus	0.00	0.00	0.00	0.00		
Stegastes planifrons	377.00	177.07	60.75	39.44	5.51	0.61
Acanthuridae	276.20	352.02	1.50	2.07	18.25	0.96
Kyphosidae	0.00	0.00	0.00	0.00		
Pomacentridae	1018.02	230.55	93.75	51.10	6.75	0.83
Scaridae	5324.11	3722.57	13.00	4.90	23.27	3.56
Denuding (Acanthurids, Microspathadon)	**391.67**	**397.13**	**3.00**	**2.62**	**15.29**	**1.50**
Excavating (Scarids)	**5324.11**	**3722.57**	**13.00**	**4.90**	**23.27**	**3.56**
Non-denuding (Territorial Damsels)	**902.54**	**232.78**	**92.25**	**51.21**	**6.61**	**0.81**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**5715.78**	**3615.31**	**16.00**	**4.14**		
Grand Total	**6618.33**	**3608.58**	**108.25**	**53.63**	**9.29**	**2.40**
Karpata						
Acanthurus bahianus	0.00	0.00	0.00	0.00		
Acanthurus chirurgus	26.84	75.92	0.25	0.71	14.00	
Acanthurus coeruleus	95.27	182.60	0.75	1.49	15.25	1.06
Kyphosus sectatrix	0.00	0.00	0.00	0.00		
Microspathadon chrysurus	149.12	235.34	1.75	2.92	14.42	0.63
Scarus coelestinus	0.00	0.00	0.00	0.00		
Scarus croicensis/iserti	55.28	156.34	0.25	0.71	21.00	
Scarus guacamaia	0.00	0.00	0.00	0.00		
Scarus taeniopteris	864.69	327.06	10.25	4.33	12.71	4.60
Scarus vetula	377.31	535.78	1.00	1.51	28.67	4.04
Sparisoma aurofrenatum	238.22	220.29	1.75	1.67	18.50	2.83
Sparisoma chrysopterum	0.00	0.00	0.00	0.00		
Sparisoma viride	2160.16	1262.66	4.25	2.71	26.10	6.04
Stegastes diencaeaus	187.79	177.44	14.00	9.86	7.49	1.58
Stegastes leucostictus	0.00	0.00	0.00	0.00		
Stegastes planifrons	425.41	139.31	64.25	16.05	5.45	0.30
Acanthuridae	122.11	182.38	1.00	1.51	14.83	1.04
Kyphosidae	0.00	0.00	0.00	0.00		
Pomacentridae	762.33	365.86	80.00	13.01	5.94	0.82
Scaridae	3695.66	1539.82	17.50	7.54	16.68	2.97
Denuding (Acanthurids, Microspathadon)	**271.23**	**319.85**	**2.75**	**3.54**	**14.58**	**0.70**
Excavating (Scarids)	**3695.66**	**1539.82**	**17.50**	**7.54**	**16.68**	**2.97**
Non-denuding (Territorial Damsels)	**613.21**	**186.58**	**78.25**	**13.63**	**5.77**	**0.61**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**3966.89**	**1670.66**	**20.25**	**8.24**		
Grand Total	**4580.10**	**1703.16**	**98.50**	**12.82**	**7.86**	**1.28**

Appendix A. Average biomass, density, and fork length of herbivorous fish, Bonaire 2005

	Biomass (g per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Bonaire Average						
Acanthuridae	362.87	560.83	2.96	5.70	15.98	1.69
Kyphosidae	109.39	741.91	0.13	0.88	33.00	
Pomacentridae	651.34	338.38	79.26	46.00	5.81	1.06
Scaridae	4856.48	2984.56	19.65	8.90	18.75	4.10
Denuding (Acanthurids, Microspathadon)	**574.58**	**920.89**	**4.22**	**5.89**	**15.34**	**2.23**
Excavating (Scarids)	**4856.48**	**2984.56**	**19.65**	**8.90**	**18.75**	**4.10**
Non-denuding (Territorial Damsels)	**549.02**	**266.80**	**78.00**	**45.77**	**5.67**	**0.99**
Algae Removers (acanthurids, scarids, and yellowtail damselfish)	**5431.06**	**3097.80**	**23.87**	**10.35**	**17.05**	**1.32**
Grand Total	**5980.08**	**3126.66**	**102.00**	**47.37**	**8.90**	**2.01**

Appendix B. Average biomass, density, and fork length of predatory fish, Bonaire 2005

	Biomass (kg per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Windsock - 10 m						
Anisotremus surinamensis	0	0	0		0	0
Aulostomus maculatus	0.03	0	0.18		42	0
Bodianus rufus	0.03	0.07	0.36		13.5	3.54
Bothus lunatus	0	0	0		0	0
Caranx latus	0	0	0		0	0
Caranx ruber	0	0	0		0	0
Epinephelus cruentatus	0.34	0.1	3.93		16.36	4.78
Epinephelus fulvus	0	0	0		0	0
Epinephelus guttatus	0	0	0		0	0
Epinephetus adscensionis	0	0	0		0	0
Gymnothorax sp.	0.06	0	0.18		55	0
Haemulon carbonarium	0	0	0		0	0
Haemulon flavolineatum	0.35	0.22	2.5		17	5.13
Haemulon sciurus	0	0	0		0	0
Hypoplectrus sp	0	0	0		0	0
Lutjanus apodus	0.61	0.42	1.43		26	9.55
Lutjanus cyanopterus	0	0	0		0	0
Lutjanus griseus	0	0	0		0	0
Lutjanus jocu	0	0	0		0	0
Lutjanus mahogoni	2.44	0.08	10.18		23.61	2.9
Lutjanus synagris	0	0	0		0	0
Mycteroperca bonaci	0	0	0		0	0
Mycteroperca tigris	0	0	0		0	0
Mycteroperca venenosa	0	0	0		0	0
Ocyurus chrysurus	0.41	0.37	0.71		32.25	8.5
Scorpaena plumieri	0	0	0		0	0
Serranus tigrinus	0	0	0		0	0
Sphyraena barracuda	0	0	0		0	0
Synodus intermedius	0	0	0		0	0
Aulostomidae	0.03	0	0.18		42	0
Carangidae	0	0	0		0	0
Haemulidae	0.35	0.22	2.5		17	5.13
Labridae	0.03	0.07	0.36		13.5	3.54
Lutjanidae	3.47	0.2	12.32		24.39	4.89
Muraenidae	0.06	0	0.18		55	0
Serranidae	0.34	0.1	3.93		16.36	4.78
Sphyraenidae	0	0	0		0	0
Synodontidae	0	0	0		0	0
All Predators	**4.27**	**0.2**	**19.46**		**22.06**	**7.16**

Appendix B. Average biomass, density, and fork length of predatory fish, Bonaire 2005

	Biomass (kg per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Forest - 10 m						
Anisotremus surinamensis	0.59	0	0.31		42	0
Aulostomus maculatus	0.16	0.12	1.09		35.43	13.55
Bodianus rufus	0.23	0.57	0.31		26	7.07
Bothus lunatus	0	0	0		0	0
Caranx latus	0	0	0		0	0
Caranx rubber	0.1	0.09	0.94		18.5	3.67
Epinephelus cruentatus	0.11	0.06	1.56		16	3.83
Epinephelus fulvus	0	0	0		0	0
Epinephelus guttatus	0	0	0		0	0
Epinephetus adscensionis	0	0	0		0	0
Gymnothorax sp.	0	0	0		0	0
Haemulon carbonarium	0	0	0		0	0
Haemulon flavolineatum	0.08	0.27	0.31		20.5	9.19
Haemulon sciurus	0.51	0.04	5.78		16.38	1.71
Hypoplectrus sp	0	0	0		0	0
Lutjanus apodus	3.05	0.42	2.5		40.25	5.47
Lutjanus cyanopterus	0.27	0	0.16		45	0
Lutjanus griseus	0.72	0.27	1.09		34.57	5.26
Lutjanus jocu	0	0	0		0	0
Lutjanus mahogoni	1.17	0.05	3.44		27.09	1.48
Lutjanus synagris	0	0	0		0	0
Mycteroperca bonaci	0	0	0		0	0
Mycteroperca tigris	0	0	0		0	0
Mycteroperca venenosa	0	0	0		0	0
Ocyurus chrysurus	0.17	0	0.16		43	0
Scorpaena plumieri	0	0	0		0	0
Serranus tigrinus	0	0	0		0	0
Sphyraena barracuda	0	0	0		0	0
Synodus intermedius	0	0	0		0	0
Aulostomidae	0.16	0.12	1.09		35.43	13.55
Carangidae	0.1	0.09	0.94		18.5	3.67
Haemulidae	1.18	0.4	6.41		17.83	6.02
Labridae	0.23	0.57	0.31		26	7.07
Lutjanidae	5.39	0.5	7.34		33.4	7.41
Muraenidae	0	0	0		0	0
Serranidae	0.11	0.06	1.56		16	3.83
Sphyraenidae	0	0	0		0	0
Synodontidae	0	0	0		0	0
All Predators	**7.16**	**0.5**	**17.66**		**25.42**	**10.59**

Appendix B. Average biomass, density, and fork length of predatory fish, Bonaire 2005

	Biomass (kg per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Reef Scientifico - 10 m						
Anisotremus surinamensis	0	0	0		0	0
Aulostomus maculatus	0.12	0.01	0.63		43.75	0.96
Bodianus rufus	0.67	1.01	0.78		24.4	11.37
Bothus lunatus	0	0	0		0	0
Caranx latus	0	0	0		0	0
Caranx ruber	0.88	0.5	0.94		36.33	7.66
Epinephelus cruentatus	0.41	0.13	2.66		20.06	5.41
Epinephelus fulvus	0	0	0		0	0
Epinephelus guttatus	0	0	0		0	0
Epinephetus adscensionis	0	0	0		0	0
Gymnothorax sp.	0.04	0	0.16		50	0
Haemulon carbonarium	0	0	0		0	0
Haemulon flavolineatum	0.14	0.06	1.56		15.2	5.12
Haemulon sciurus	1.58	0.11	14.53		17.14	2.94
Hypoplectrus sp	0	0	0		0	0
Lutjanus apodus	0.82	0.62	1.09		31.86	10.76
Lutjanus cyanopterus	0	0	0		0	0
Lutjanus griseus	0	0	0		0	0
Lutjanus jocu	0	0	0		0	0
Lutjanus mahogoni	0.26	0.26	0.47		31.67	6.11
Lutjanus synagris	0	0	0		0	0
Mycteroperca bonaci	0	0	0		0	0
Mycteroperca tigris	0	0	0		0	0
Mycteroperca venenosa	0	0	0		0	0
Ocyurus chrysurus	0.51	0.18	0.78		35.2	3.49
Scorpaena plumieri	0	0	0		0	0
Serranus tigrinus	0	0	0.94		5.67	0.82
Sphyraena barracuda	0	0	0		0	0
Synodus intermedius	0.04	0	0.16		30	0
Aulostomidae	0.12	0.01	0.63		43.75	0.96
Carangidae	0.88	0.5	0.94		36.33	7.66
Haemulidae	1.72	0.11	16.09		16.95	3.23
Labridae	0.67	1.01	0.78		24.4	11.37
Lutjanidae	1.59	0.44	2.34		32.93	7.82
Muraenidae	0.04	0	0.16		50	0
Serranidae	0.41	0.13	3.59		16.3	7.95
Sphyraenidae						
Synodontidae	0.04	0	0.16		30	0
All Predators	**5.46**	**0.35**	**24.69**		**20.32**	**9.04**

Appendix B. Average biomass, density, and fork length of predatory fish, Bonaire 2005

	Biomass (kg per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Barcadera - 10 m						
Anisotremus surinamensis	0.07	0	0.16		28	0
Aulostomus maculatus	0.01	0.03	0.31		23	7.07
Bodianus rufus	0.28	0.34	0.31		28.5	3.54
Bothus lunatus	0	0	0		0	0
Caranx latus	0	0	0		0	0
Caranx ruber	0.11	0.12	0.31		28	2.83
Epinephelus cruentatus	0.16	0.06	1.56		18.2	3.71
Epinephelus fulvus	0.06	0	0.16		29	0
Epinephelus guttatus	0	0	0		0	0
Epinephetus adscensionis	0	0	0		0	0
Gymnothorax sp.	0	0	0		0	0
Haemulon carbonarium	0.19	0.12	0.47		28	2.65
Haemulon flavolineatum	0.15	0	1.88		15.58	1.83
Haemulon sciurus	0.07	0	0.16		28	0
Hypoplectrus sp.	0.01	0.01	0.47		8.33	2.52
Lutjanus apodus	0.62	0.16	1.56		27.6	3.84
Lutjanus cyanopterus	0	0	0		0	0
Lutjanus griseus	0	0	0		0	0
Lutjanus jocu	0	0	0		0	0
Lutjanus mahogoni	0.67	0.12	2.66		23.76	3.99
Lutjanus synagris	0	0	0		0	0
Mycteroperca bonaci	0	0	0		0	0
Mycteroperca tigris	0.21	0	0.16		45	0
Mycteroperca venenosa	0	0	0		0	0
Ocyurus chrysurus	0.2	0.49	0.31		33.5	10.61
Scorpaena plumieri	0	0	0		0	0
Serranus tigrinus	0	0	0.16		6	0
Sphyraena barracuda	0.13	0	0.16		50	0
Synodus intermedius	0	0	0		0	0
Aulostomidae	0.01	0.03	0.31		23	7.07
Carangidae	0.11	0.12	0.31		28	2.83
Haemulidae	0.48	0.15	2.5		18.69	5.85
Labridae	0.28	0.34	0.31		28.5	5.66
Lutjanidae	1.49	0.19	4.53		25.76	5.08
Muraenidae	0	0	0		0	0
Serranidae	0.44	0.33	2.5		17.94	9.7
Sphyraenidae	0.13	0	0.16		50	0
Synodontidae	0	0	0		0	0
All predators	**2.93**	**0.27**	**10.78**		**22.75**	**8.14**

Appendix B. Average biomass, density, and fork length of predatory fish, Bonaire 2005

	Biomass (kg per 100 m²)		Density (# per 100 m²)		Fork length (cm)	
	mean	SD	mean	SD	mean	SD
Karpata - 10 m						
Anisotremus surinamensis	0	0	0		0	0
Aulostomus maculatus	0.12	0.14	0.78		37.2	112.54
Bodianus rufus	0.37	0	0.16		39	0
Bothus lunatus	0	0	0		0	0
Caranx latus	0	0	0		0	0
Caranx ruber	0.29	0.18	0.47		33	3
Epinephelus cruentatus	0.37	0.12	2.5		19.38	6.34
Epinephelus fulvus	0	0	0		0	0
Epinephelus guttatus	0	0	0		0	0
Epinephetus adscensionis	0	0	0		0	0
Gymnothorax sp.	0	0	0		0	0
Haemulon carbonarium	0	0	0		0	0
Haemulon flavolineatum	0.18	0.11	1.25		18	4.99
Haemulon sciurus	0.18	0.23	0.47		26.33	6.43
Hypoplectrus sp.	0	0	0		0	0
Lutjanus apodus	0.81	0.29	0.63		41.5	3.32
Lutjanus cyanopterus	0	0	0		0	0
Lutjanus griseus	0	0	0		0	0
Lutjanus jocu	0	0	0		0	0
Lutjanus mahogoni	0.36	0.08	1.09		26.57	2.82
Lutjanus synagris	0	0	0		0	0
Mycteroperca bonaci	0	0	0		0	0
Mycteroperca tigris	0	0	0		0	0
Mycteroperca venenosa	0	0	0		0	0
Ocyurus chrysurus	0.16	0	0.16		42	0
Scorpaena plumieri	0	0	0		0	0
Serranus tigrinus	0	0	0.16		6	0
Sphyraena barracuda	0		0		0	0
Synodus intermedius	0.06	0.07	0.31		14.5	3.54
Aulostomidae	0.12	0.14	0.78		37.2	112.54
Carangidae	0.29	0.18	0.47		33	3
Haemulidae	0.37	0.18	1.72		20.27	6.39
Labridae	0.37	0	0.16		39	0
Lutjanidae	1.33	0.5	1.88		32.83	490.77
Muraenidae	0	0	0		0	0
Serranidae	0.37	0.12	2.66		18.59	6.95
Sphyraenidae	0	0	0		0	0
Synodontidae	0.06	0.07	0.31		14.5	3.54
All Predators	**2.9**	**0.46**	**7.97**		**25.84**	**10.56**

Appendix C. Juvenile Coral Demography Template

Date:										
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										
Corallines										
Turf										
T-CH (mm)										
Macro.										
M-CH (mm)										
NCC										
Art										
A-CH (mm)										
M. annularis										
Agaricia spp.										
Porites ast.										

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										
Corallines										
Turf										
T-CH (mm)										
Macro.										
M-CH (mm)										
NCC										
Art										
A-CH (mm)										
M. annularis										
Agaricia spp.										
Porites ast.										

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										
Corallines										
Turf										
T-CH (mm)										
Macro.										
M-CH (mm)										
NCC										
Art										
A-CH (mm)										
M. annularis										
Agaricia spp.										
Porites ast.										