



*A REPORT ON THE STATES OF THE CORAL REEFS
OF BONAIRE WITH ADVICE ON THE ESTABLISHMENT OF
FISH PROTECTION AREAS*

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Table of Contents and Contributing Authors

	Page
Executive Summary	
Robert S. Steneck and Tim McClanahan	3-14
Chapter 1: Patterns of abundance: coral, sea fans, seaweed and sea urchins Anne Simpson and Robert S. Steneck	15-21
Chapter 2: Abundance and species composition of juvenile corals Chantale Bégin and Elizabeth Stephenson	22-30
Chapter 3 : Reef fish populations: distribution, abundances and size structure Michelle Paddack and Shawn M. Shellito	31-39
Chapter 4: Juvenile corals and seaweed Shauna Slingsby and Robert Steneck	40-42
Chapter 5: Depth zonation of seaweed, nutrient concentrations and grazing T. R. McClanahan, S. Jones and R. Steneck	43-48
Chapter 6: The fishing community, marine protected areas and fish protected areas Darcie A. Couture and Benjamin Baron-Talre	51-57
Chapter 7: Diver tourists: the aesthetic and economic value of fish protected areas Sheril Kirshenbaum	58-62
Appendix A: Average density, fork length, and biomass of herbivorous fish	63-69
Appendix B: Average density, fork length, and biomass of carnivorous fish	70-79

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To all we are grateful.

Executive Summary

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Introduction:

Bonaire has long been considered to have amongst the healthiest reefs of the Caribbean. However, at the 2002 Annual Meeting of Pew Fellows for Marine Conservation in Bonaire, several scientists with a long history of research on Bonaire's coral reefs, expressed concern over the future of the island's reefs. Specifically, they identified the decline in large predatory fish such as groupers as a noticeable change during the past decade. They suspected that this change resulted from increased fishing pressure on Bonaire's reefs. They also suggested the Bonaire authorities take action to protect the reef-fish stocks.

In response to those concerns, officials of the Bonaire Marine Park consulted with scientists and fishermen on Bonaire to explore the possibility of establishing fish protected areas (FPAs), as a way to protect the reef fish stocks. If FPAs improve both fish stocks and the condition of the coral reef, all stakeholders will profit. If fish stocks increased significantly in FPAs, a "spill over" of these fish to adjacent fished areas would be expected. Also, fish that perform important ecological functions could improve the quality of the coral reef ecosystem. Therefore, areas protected from fishing should have healthier coral reefs, which would also improve the island's valuable ecotourism businesses.

The Pew Fellows program funded a research project designed to identify potential FPAs. The Bonaire Marine Park authority, in consultation with the local fishing community would determine the location and size of the FPAs. To monitor the effects of fish protection areas so fishing impacts can be isolated from other factors (such as natural changes, shore-based impacts or affects of scuba divers), an equal number of similar reef sites were selected for study, with half closed to fishing while half remaining open (as "control" reefs).

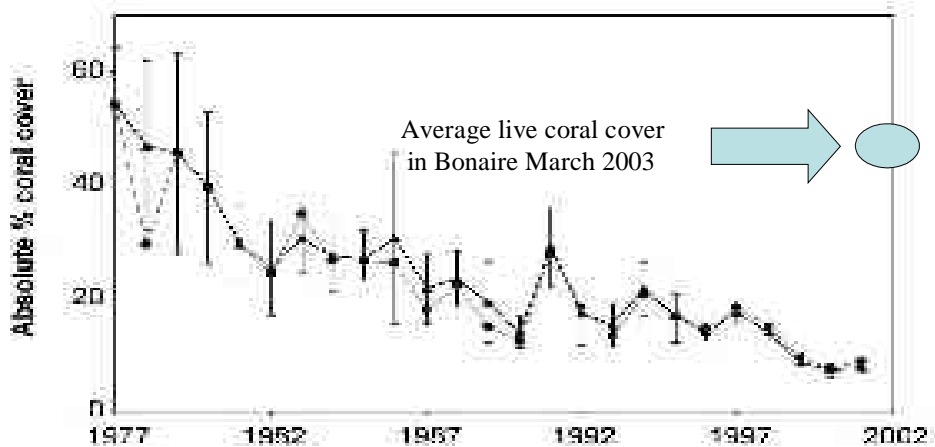
This report reviews the status and recent trends of coral reefs in the Caribbean and Bonaire. It identifies the key features of healthy reefs and how Bonaire's reefs compares with those elsewhere in the Caribbean. The seven chapters go into scientific detail on factors contributing to the condition of Bonaire's reefs as of March and April 2003. Special focus will be on factors that threaten reef health or are critical to reef resilience such as seaweed overgrowth, nutrient inputs from land and the ecology of juvenile corals. The report concludes with chapters on the

socioeconomic effects of Bonaire’s coral reefs on the fishing and diving industries that depend on them.

Declines in Coral Reefs of the Caribbean: Bonaire is the Exception

Coral reefs throughout the Caribbean are in a serious state of decline. Since 1977, live coral cover declined 90% from an average cover of 50% to less than 10% (Figure 0.1; Gardner 2003). Bonaire’s reefs are an exception. An assessment of Caribbean reefs conducted between 1998 and 2000, determined that Bonaire’s reefs had the highest abundance of live coral, and the lowest abundance of harmful seaweed (known as “macroalgae”) which are capable of smothering corals (Figure 0.2; Kramer 2003). Further, in the recently completed Atlantic and Gulf Reef Rapid Assessment (“AGRRA”), an index of reef health was developed based on 13 independent variables such as live coral cover, rates of coral mortality, prevalence of coral disease, macroalgal abundance, and herbivore abundances. Based on the AGRRA assessment, Bonaire had the highest index of reef health in the Caribbean (Kramer 2003).

Fig. 0.1. The average percent decline of live coral cover throughout the Caribbean based on 263 reefs



sites in 65 separate studies (from Gardner et al 2003). The circle represents the average live coral cover recorded in Bonaire in March of 2003.

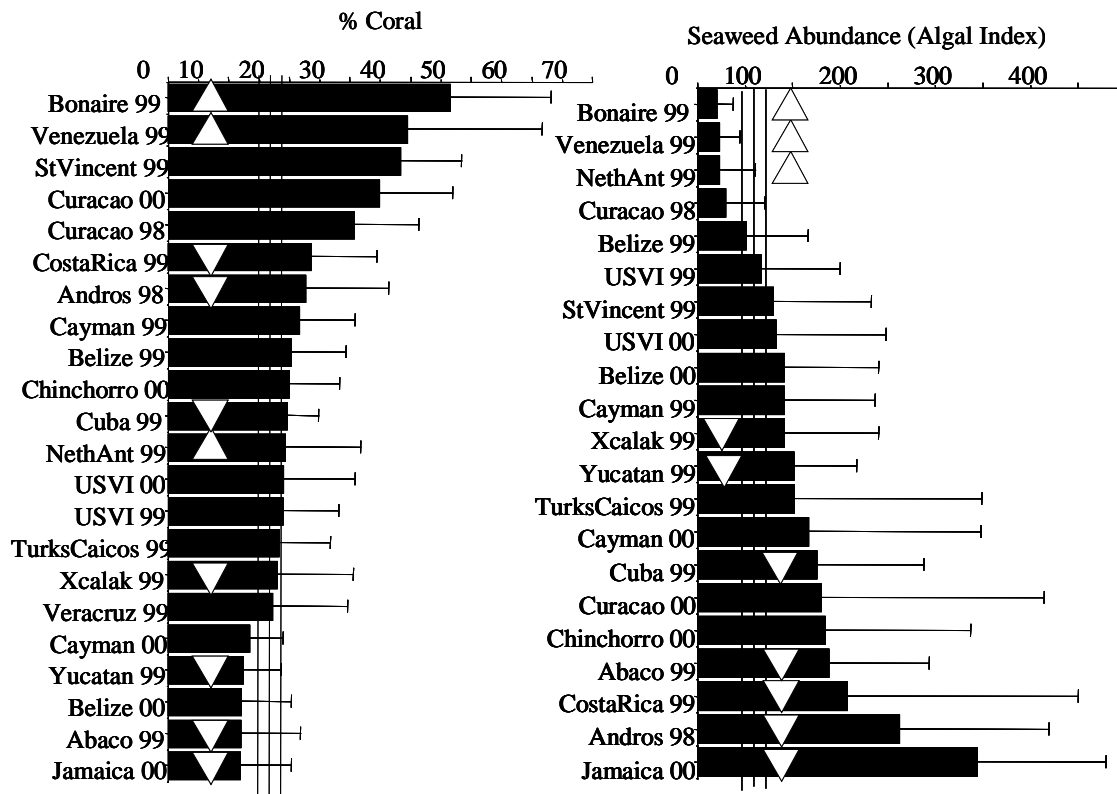


Figure 0.2. The average coral and algal abundance in 17 reef systems distributed throughout the Caribbean (From the AGRRA database, Kramer 2003). Bonaire’s coral cover was highest and its seaweed abundance (Algal Index) was lowest. Average and standard error across all reefs are represented by three vertical lines. Reefs health classification based on 13 AGRRA indicators use up-pointing triangles (△) for good condition and down-pointing (▽) for poor condition (Kramer 2003).

Causes of coral reef decline: The Manageable vs. Unmanageable

There is a growing realization that while coral reefs are highly diverse, they are also highly fragile ecosystems. In recent years coral reef deterioration resulted from coral bleaching, outbreaks of disease, sedimentation from runoff, pollution and blooms of seaweed. Of these, coral bleaching, disease and an increase of seaweed growth on reefs account for the vast majority of documented coral mortality. Much is known about the factors that contribute to the decline of coral reefs but only a few of these factors such as fishing can be locally managed.

Climate Effects: Coral bleaching occurs when sea temperatures become unusually warm causing corals to expel the tiny plant “symbionts” that live within their tissues providing food and giving color to the corals. As a result, corals turn white but they will recover fully if the bleaching duration is short. If the warm water persists, so will the bleaching until the coral dies. Vast areas of the Indian Ocean, tropical Pacific and Caribbean suffered lethal bleaching as a result of unusually warm water temperatures that occurred in 1998.

Atmospheric carbon dioxide is accumulating in the atmosphere due to the burning of fossil fuels. This carbon dioxide creates an acid in the ocean that dissolves limestone. Since coral skeletons are limestone, there is growing concern that the increase of carbon dioxide may make it harder for corals to make their skeleton. It is possible that the extra energy corals must spend to calcify makes them more susceptible to diseases. Over the past two decades the frequency and diversity of diseases have increased in unprecedented proportions.

Biological Effects: Coral diseases can be localized and minor, or at a very large scale with significant impacts to coral cover on reefs. In the early 1980s, white-band disease attacked and killed elkhorn and staghorn corals (*Acropora palmata* and *A. cervicornis*) throughout the Caribbean. Within a decade, the most abundant coral species in the Caribbean had become rare. In Bonaire, the elkhorn and staghorn corals that once grew close to the shore, died as a result of this disease leaving a largely coral-free zone between the current coral reef and the shore.

In 1983 and 1984 another disease struck the Caribbean but this time it affected the dominant seaweed grazing sea urchin *Diadema antillarum*. The disease was first observed in Panama and quickly it spread throughout the Caribbean killing well over 95% of this sea urchin population. As a result of this decline, macroalgae abundance on many reefs dramatically increased. The increase in macroalgae was most noticeable where overfishing had removed other grazing parrotfish and surgeonfish. For example, in Jamaica where the fringing reef area is small relative to the great number of fishermen, overfishing had occurred long ago, first on most carnivorous fish (such as groupers, snappers and triggerfish) and then on herbivorous fish such as parrotfish. By the early 1980s, the sea urchin had become the only important grazer keeping harmful algae closely cropped and thus allowing the remaining corals to grow and young coral to become established. Although there was a slight rise in macroalgal abundance prior to the mass mortality of the herbivorous sea urchin (Figure 0.3), the algal cover increased more than 60% following the *Diadema* die-off.

Coral *Jamaica* Macroalgae

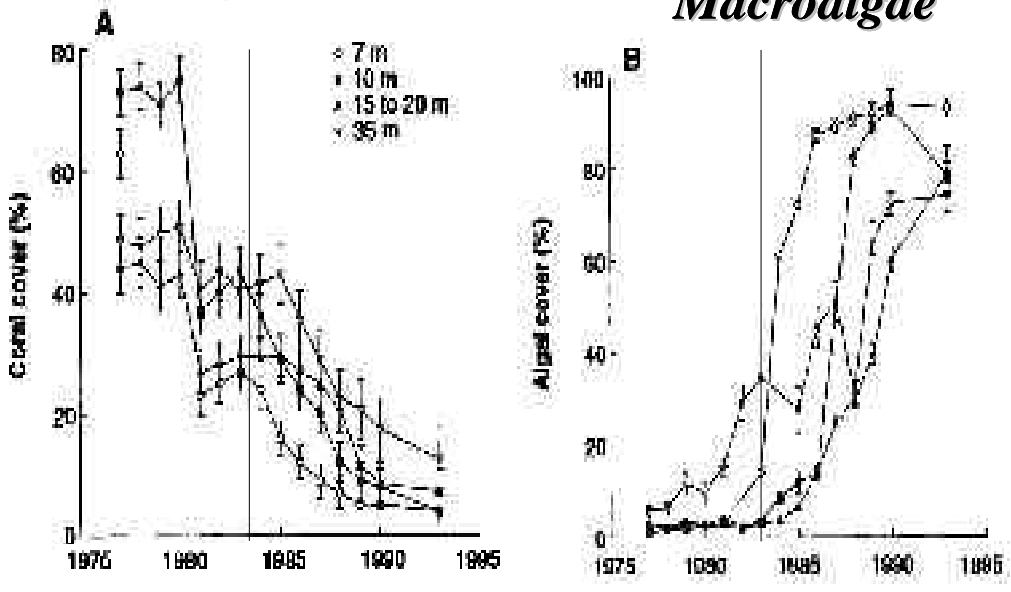


Figure 0.3. The decline of coral and the increase in macroalgae (seaweed) over two decades (Hughes 1994). The vertical line represents the timing of the mass mortality in the grazing sea urchin *Diadema antillarum*.

When macroalgae becomes abundant, it can overgrow and kill corals directly. There is also evidence that abrasion from macroalgae can stress corals by interfering with the feeding activity of coral’s delicate tentacles. Studies have also shown that macroalgae “carpets” on coral reefs can prevent juvenile corals from surviving on reefs.

The increase in macroalgae throughout the Caribbean is alarming. All of the seven most degraded reefs in the Caribbean were identified as having above average macroalgae abundance (see Fig. 0.2). The most degraded reefs, such as Jamaica, had the highest algal abundance. Conversely, the three reefs identified as being in best condition in the Caribbean all had the lowest abundance of algae of those studied (Figure 0.2).

Conditions that limit algae abundance contribute to the health of coral reefs. Seaweed growth results from elevated nutrient levels, reduced herbivory, or a combination of the two. Most experimental studies that manipulated both nutrients and herbivory found the strongest algal response resulted from changes in grazing pressure. However, interactions between the two processes are likely such that under conditions of high nutrients, higher rates of herbivory may be required to keep algal abundance low.

The functional role of carnivorous fish on coral reefs is less well documented. Several studies have shown them to control the abundance of prey such as sea urchins. Less well understood is the role of carnivorous fish in controlling the abundance of territorial damselfish. Highly aggressive territorial damselfish keep other herbivores from their grazing range and thus function as an herbivore-exclusion cage. If declining numbers of carnivores is resulting in an increase in damselfish, then the reef could become as overgrown with algae as have others that lost their herbivorous fish.

Much of the decline in reef health probably results from the cumulative impacts of several of these factors. For example, when corals die from bleaching or disease, their surfaces become available for algal colonization and this increases the surface area on which grazers can feed. As a result, grazing pressure per area declines because the same numbers of bites from resident herbivores are spread over a larger area. Such declines in grazing often result in increases in seaweed abundance on the reef, which in turn, can reduce the recruitment of juvenile corals (Chapter 4) thus perpetuating the degraded state.

What's manageable: The factors on which humans have the greatest influence, such as any shift in fish abundance and composition, nutrient loading and other sources of pollution, are often also those that are most easily managed. The currently healthy reefs of Bonaire could degrade if important conditions on the reef change. The management actions to halt these possible causes of deterioration in the coral reefs would include the establishment of FPAs and means to control runoff from land.

Summary Results 2003:

The Biological Status of the Coral Reefs of Bonaire & Socioeconomic Implications

In March and April of 2003, teams of researchers studied the coral reefs of Bonaire to establish the baseline conditions that currently exist and against which trends can be determined and future changes from fish protection areas be assessed. Six study sites were chosen with advice from the Bonaire Marine Park. They represent a range of comparable reefs minimally affected by the 1999 Hurricane Lenny. The sites selected for this study were: Windsock, Plaza, Forest on Klein Bonaire, Scientifico, Barcadera and Karpata (Fig. 0.4). When feasible, parallel studies were conducted at 5 and 10 m depths, however, only the latter depth had fully developed reefs at all sites. The study was designed to quantify the patterns of abundance of the dominant reef organisms as well as to study the processes that control their abundances or threaten their stability. This was done to establish a baseline and to determine if significant differences exist among any of the study sites that would make them a poor choice as a FPA. We also examined some socioeconomic factors related to fishing and scuba diving activities if FPAs are established in Bonaire.

Figure 0.4 Map of Bonaire, Netherlands Antilles, showing the location of sites sampled in 2002 and 2003. 1 Karpata; 2 Oil Slick Leap; 3 Barcadera; 4 Reef Scientifico; 5 Forest on Klein Bonaire; 6 Plaza, 7 Windsock.



Patterns of dominance in corals, algae, and fishes

Bonaire's reefs are currently in good condition. Stony corals dominate Bonaire's reefs with most of the sites averaging 50 and 46 percent cover at 5 and 10 meter depths respectively (Chapter 1; Figure 0.1). The next most abundant groups were small, close-cropped turf algae (32 and 34%) and calcareous coralline algae (11 and 10%) at the two depths. Harmful seaweed "macroalgae" were rare. These results compare well with past studies conducted on Bonaire's reefs (Figure 0.2; Kramer 2003). Sponges and gorgonian corals (sea whips and sea fans) together comprised only about 3% of the substrate at both depth. None of the major groups varied significantly among sites.

The dominant corals were the mountainous star corals, *Montastraea annularis* and *M. faveolata* at both 5 and 10 m depths (Chapter 2) which is typical of Caribbean reefs since the staghorn coral mass mortality of the 1980s. The juvenile corals, however, were strongly dominated by species of *Agaricia* and to a lesser extent *Porities astreoides*, and noticeably not the *Montastraea*

species that dominate the reef. Juvenile coral densities did not vary significantly among sites (Chapter 2).

The fish fauna on Bonaire’s reefs is rich but in recent years its declining trend in predator abundance is disturbing. Seaweed-eating parrotfish are the most abundant fish group averaging over 6000 g per 100 square meters of reef (Chapter 3). This is beneficial to the reefs because parrotfish, along with surgeonfish, are the dominant herbivores on Bonaire’s reefs. The fish community structure overall did not differ greatly among sites, although the biomass of certain carnivorous fish was variable among sites, especially at 10 meter depths. Sites with reportedly lower fishing pressure over the past decade such as Forest on Klein Bonaire, had greater densities of large carnivores such as groupers and snappers. Only at such sites were these predators the second most abundant fish group by mass (Chapter 3).

Over the past decade, the abundance of predatory fishes such as groupers and snappers declined dramatically, whereas the abundance of herbivorous fishes increased (Figure 0.5). Hook and line selectively catches carnivores and only they decreased in number. The decline in large predators may have contributed to the increase in herbivores but it could have also contributed to an increase in territorial damselfish (such as dusky and threespot damselfish of the genus *Stegastes*; Hixon and Carr 1997, Chapter 3). On all reefs, damselfishes were most abundant (in terms of number of fish per 100 square meters). Territorial damselfish can interfere with the important grazing activity of parrotfish and surgeonfish (Russ 1987; discussed further below).

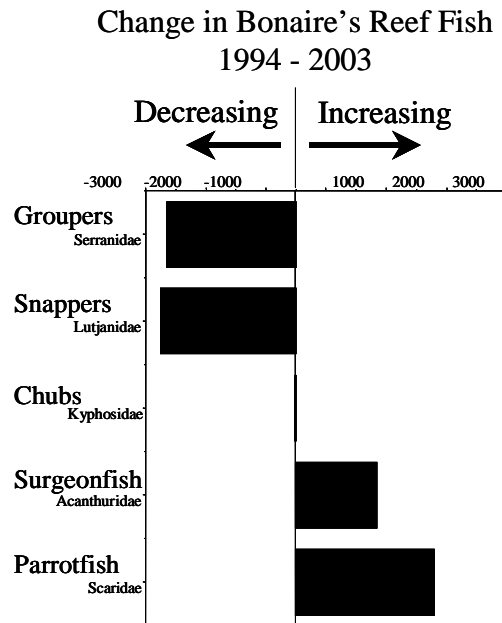


Figure 0.5. Changes in Bonaire’s reef fish fauna biomass (grams/100 m²) between 1994 and 2003. 1994 data are from Dr. Callum Roberts and were published in Hawkins et al 1999; 2003 data are from Chapter 3. Note the rapid decline in groupers and snappers over the past decade.

The decline of large predators was recent and most rapid between the period of 1994 (data of Hawkins et al 1999) to 1999 (AGRRA data; Chapter 3). This decline may have resulted from the rapid overfishing of large predators. The remaining smaller predators such as coneys, hinds and grunts are less preferred by the fishing community and may be more resilient to decline than are large snappers and groupers.

Recreational scuba diving was suspected by local fishermen to be a cause for the decline in predatory fish in recent years. However, in a recent study that examined Bonaire's reef with and without recreational scuba diving concluded that: "*Diving had no significant effect on reef fish communities*" (Hawkins et al 1999).

Potential structuring processes (nutrient concentrations, herbivory and coral recruitment)

Some of Bonaire's reefs have high levels of nutrients (Chapter 5), but presumably sufficiently high rates of grazing to prevent macroalgal blooms. The low abundance of macroalgae in turn results in a reef habitat that promotes coral recruitment and thus provides the system with high resilience.

Nutrient levels were surprisingly high at one site (Reef Scientifico; Chapter 4). Specifically, phosphate compounds (PO_4) that are commonly thought to be the most limiting nutrient on coral reefs were found to exceed a dangerously high concentration (greater than 0.20 mg/l) at that site. Other nutrients such as nitrogen compounds of nitrates, nitrites and ammonia were below average levels for coral reefs (McClanahan 2002) and below levels thought to stimulate algal growth (Lapointe 1997). Water sampling should be continued to determine if the values we found represent average levels of nutrients on the reef.

Significantly, the elevated levels of nutrients at Reef Scientifico were not accompanied by elevated abundances of macroalgae (Chapter 2). This may be because herbivores keep new algal growth cropped to low levels. Other studies have concluded that herbivory may be the primary controlling factor of macroalgal abundance on coral reefs and it often swamps the affects of variations in nutrient levels (Miller et al 1999, Hughes et al 1999).

Herbivory is almost exclusively from fish (*Diadema* sea urchins are rare and thus ecologically unimportant). Bite rates from grazing fishes averaged 313 bites per meter square per hour from four sites for parrotfish and surgeonfish combined. This is nearly twice the rate reported recently for Yucatan coast of Mexico (Steneck and Lang 2003). The high population density of large parrotfish also suggests Bonaire's reefs may be frequently grazed (Chapter 3). In contrast to the high bite rates and herbivore biomass, the rates of grazing on transplanted pieces of algae were surprisingly low at all depths (Chapter 5). The low attack rates on these algae may be because macroalgae are so rare on Bonaire's reefs (Chapter 1) that the fish simply did not target them as food over the short duration of this experiment (Chapter 5). Despite the overall low levels of herbivory, patterns with depth were evident and these may explain the elevated macroalgal abundance at 25 to 40 meters depth. Specifically, grazing frequency declined with depth and was undetectable below 25m. In contrast, nutrients did not change over the 40 m

depth transect studied (Chapter 5). Because the nutrients needed for seaweed growth were present at depths below 25 m but herbivory was functionally zero, seaweed abundance increased (Chapter 5).

Juvenile coral densities were greatest at sites having the lowest abundance of macroalgae (Chapter 4). This pattern was most striking when low juvenile coral densities from Mexico, where algae were abundant, were compared with Bonaire, where algae are rare (Chapter 4). Other studies have shown that when herbivory increases causing macroalgae to decline, that juvenile coral densities increase as well.

Overall it appears that the health and resilience of Bonaire's coral reefs relies on the effectiveness of herbivores to keep macroalgae low. This may be especially important at sites such as Reef Scientific where nutrient levels were found to be dangerously high. If territorial damselfish are becoming more abundant due to the loss of predators and the damselfish activity is reducing the effectiveness of herbivorous fish (Chapter 3), then Bonaire's reefs could become overgrown by macroalgae as so many others have throughout the Caribbean (Fig. 0.1).

Socioeconomic implications:

The sustainability of reef fish stocks is income security for the local fisheries and other industries that depend upon them. The rapid decline in commercially important fishes (Figure 0.5) could be reversed if some reefs are protected from fishing ("Fish Protected Areas"). Fish protected areas have been shown to benefit carnivorous reef fish (Chapter 6). As populations increase they "spill-over" to adjacent fishing grounds where they are caught. Several studies have found this to be an effective way to maintain a regular income for local fisheries.

Dive operations represent another economic stakeholder group in Bonaire. There are 14 dive operations that employ over 100 people who serve over 60,000 visitors annually. The estimated gross dive-generated revenue for Bonaire in 2000 was about \$34 million. Because large predatory fish (groupers in particular) are attractive and draw divers, they are worth 20 times more alive than when they are harvested (Chapter 6). Divers who were surveyed in Bonaire said they came to Bonaire because of its excellent reefs and most mentioned fish abundance as one of the key attractive features they look for when diving on coral reefs (Chapter 7).

It appears the FPAs would have value both as a means of stabilizing fish stocks for Bonaire's fishing industry and improving the attractiveness for the dive industry. We also believe carnivores may help control damselfish populations which could show to be harmful on reefs if they are not controlled.

Recommendations

Bonaire's reefs are healthy but possibly at risk due to recent fishing pressure on them. Large predatory fish such as groupers have declined rapidly in recent years. We recommend Fish Protection Areas be established and monitored to see if fish abundances increase in the FPA

areas as well as adjacent fished regions. We recommend that fish catches be recorded scientifically (but confidentially) so catch rates around the reserve can be monitored. Further we recommend monitoring corals, algae, sea urchins, nutrients and rates of herbivory inside FPAs and identical reefs open to fishing. Particular attention should be given on changes in fish species composition, body size and the functional role specific fish play in coral reef systems. For example, functionally important predators (such as groupers), herbivores (such as parrotfish) and territorial damselfish abundances should be monitored.

Further, we recommend FPAs be established scientifically so we can document changes that result from the cessation of fishing as opposed to other possible changes to the reefs. Thus we suggest three FPA reefs and three “control” reefs (where fishing is allowed) be established as soon as possible (three allow averages to be calculated). Since most of the reefs are not currently significantly different from one another (Chapters 1 – 5), any consistent changes in the three FPAs relative to the three control areas will be attributable to change in fishing pressure.

In order to effectively monitor the changes a FPA has on the reef, the Pew Fellows program would continue to examine the sites. We suggest the fishing community as well as the scuba diving industry be informed and encouraged to participate in the monitoring and research activities. Stakeholder involvement in the implementation of a FPA is as important to its success as is the involvement of the Marine Park authority. A strategic plan should be made for these newly established areas in conjunction with the Marine Park’s objectives to help guide these actions with long-term goals. The researchers involved in this project, the park managers, and the stakeholders would all work closely to ensure the protected area goals are reached.

Literature Cited

Gardner, T. A., Cote, I. M., Gill, J. A., Grant, A., Watkinson, A. R. 2003. Long-term region-wide declines in Caribbean corals. *Science Express*. www.sciencexpress.org. 17 July2003.

Hawkins, J. P, Roberts, C. M. van’t Hof, T., DeMeyer, K., Tratalos, J. and Aldam, C. 1999. Effects of recreational scuba diving on Caribbean coral and fish communities. *Conservation Biology*. 13: 888-897.

Hixon, M. A., and Carr, M. H. 1997. Synergistic predation, density dependence and population regulation in marine fish. *Science*. 277: 946- 949.

Hughes, T., Szmant, A., Steneck, R. Carpenter, R., Miller, S. 1999 Algal blooms on coral reefs: what are the causes? Critique of: “Nutrient Thresholds for Eutrophication and Macroalgal Overgrowth of Coral Reefs in Jamaica and Southeast Florida: by B. E. Lapointe (*Limnol. Oceanogr.* 42: 119 - 1131). *Limnol. and Oceanogr.* 44: 1583 – 1586

Kramer, P. A. 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997 – 2000). *Atoll Research Bulletin* 496: 1 – 58.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms in coral reefs in Jamaica and southeast Florida. *Limnol. & Oceanogr.* 42: 119 - 1131.

Miller, M. W., M. E. Hay, et al. 1999. "Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs." *Limnol. & Oceanogr.* 44(8): 1847-1861.

Russ, G. 1987. Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? *J. Exp. Mar. Biol. Ecol.* 110: 1 – 17.

Slingsby, S. N. 2003. Patterns of association and interactions between juvenile corals and macroalgae in the Caribbean. MS thesis. University of North Carolina at Wilmington.

Chapter 1: Patterns of abundance: coral, sea fans, seaweed and sea urchins

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Abstract

A survey of the abundance of live coral, sea fans (known as gorgonians) and sponges, seaweed (known as macroalgae), at six reef sites in Bonaire was conducted in 2002-2003. The primary objectives of the survey were to (1) characterize key components of reef structure at potential control and Fish Protected Area (FPA) sites and (2) establish a baseline on which to gauge the long-term impacts of the proposed FPAs. Transects surveys were conducted at both 5 and 10 m depths for all proposed sites with the exception of Windsock and Plaza where only 10 m transects were completed. There were no significant differences in live stony coral or macroalgal percent cover for a given depth between survey sites, however the abundance of gorgonians/sponges and coralline algae differed significantly among several sites at both 5 m and 10 m. Bonaire's reefs exhibited significantly greater cover of live coral at 5 m and 10 m compared to other reefs in the Caribbean such as the Bahamas, and non-marine protected areas (MPA) in Belize, and the Yucatan. Macroalgal abundance was significantly lower in Bonaire compared with other reefs in the Caribbean including the non-MPAs in the Bahamas, and MPAs in the Bahamas, Belize, and the Yucatan. Because high macroalgal abundance on reefs is associated with coral mortality and reduced recruitment, the comparatively low percent cover of macroalgae and corresponding high percentage of live coral cover in Bonaire suggests that these reefs are less degraded than elsewhere in the Caribbean.

Introduction

There is evidence that many coral reefs throughout the Caribbean are in a state of decline due to the combined effects of natural and anthropogenic disturbances (Hughes 1994). Over the past several decades, major shifts in the structure of reef communities have been recorded in numerous locations, such as Jamaica, where the combined effects of hurricane damage, reef diseases, and intense overfishing, have resulted in a system with less than 5% live coral cover and greater than 90% cover of fleshy macroalgae (Hughes 1994). Such rapid deterioration of many Caribbean coral reefs created the impetus for conservationists and resource managers to develop and implement management strategies aimed at reducing the impacts of human activities on reefs.

The creation of the Bonaire Marine Park in 1991 was one such effort to reduce the impact of human activities on the coral reefs of Bonaire, N.A. Recreational SCUBA divers must adhere to strict rules designed to minimize the impact of diving on the reefs within the park, and are required to pay a fee to dive within the park. This money goes to funding conservation-oriented

research, as well as management and enforcement activities. Spear and trap fishing are illegal within the Bonaire Marine Park however, hook and line fishing is still permitted. There is evidence that fishing pressure in the park has increased in recent years. Increased fishing pressure has been associated with the decline in both diversity and size of predatory reef fishes, such as groupers within Bonaire Marine Park (Figure 0.5; Callum Roberts, personal communication Oct. 2002). In an effort to reduce fishing pressure and mitigate the chance of possible overfishing, park managers, in consultation with fishing and diving industry representatives, are planning to establish small, no-take zones called Fish Protected Areas (FPAs) where fishing will not be permitted. The effects of FPAs on predatory reef fish populations and reef community structure as a whole will be assessed using data collected in a before-after control-impact (BACI) experiment. Data presented in this chapter constitute initial (before) sampling of the abundance of important reef habitat components (such as live coral and macroalgae) in control sites and potential FPA sites prior to a closure to fishing in the latter areas.

The cessation of fishing at the FPA sites in Bonaire may have indirect effects on patterns of live coral and macroalgal cover that are difficult to predict. For example, in a proposal to help establish and monitor the effects of FPA's on Bonaire's reefs, R. Steneck and T. McClanahan suggested that algal biomass might increase at FPA sites if grazing pressure was reduced due to increased predation on herbivorous fishes by higher numbers of predatory fishes. Since patterns of live coral and macroalgal abundance are important indicators of the general state of reef health, it is crucial to monitor the impact of management measures, such as the establishment of FPAs on these key components of reef habitat. It is also useful to monitor the abundance of other major reef components such as coralline algae, which may act as a catalyst for coral recruitment, and gorgonians and sponges, which contribute to overall habitat structural complexity on the reef.

Materials and methods

Surveys of stony coral, gorgonian/sponge, coralline and macroalgal cover were conducted utilizing a modified protocol developed for Atlantic and Gulf Rapid Reef Assessment (AGGRA) (Steneck et al. 2003). Abundances of *Diadema antillarum* were also recorded in accordance with AGGRA protocols. Data for each reef component surveyed (except *Diadema*) were analyzed by transect depth using a one-way analysis of variance (ANOVA) to test for differences in percent cover between sampling sites in Bonaire. Differences in percent cover of stony corals and macroalgae between Bonaire and other Caribbean reefs were analyzed using ANOVA and Tukey post-hoc tests. Additionally, gorgonian abundance measurements were made by recording the number of colonies (by genera) in 1 m² quadrats spaced at 2.5 m intervals on either side of a 10 m transect line.

Results

There were no significant differences in percent cover of live stony coral or macroalgae between surveyed sites at either 5 m or 10 m depth (Figure 1.1). Overall, macroalgal cover was low and

live coral cover was high. In contrast, significant differences in gorgonian, sponge, and coralline algal cover were present between several sites (Figure 1.2). At 5 m, gorgonian and sponge cover was similar at Karpata and Forest (Klein Bonaire). These sites differed significantly ($p < 0.05$) from Plaza and Barcadera where no gorgonian and sponge cover was recorded at 5 m depth. No significant differences in sponge & gorgonian cover were apparent at 10 m depth. Coralline algae cover was not significantly different between sites at 5 m depth; however, at 10 m depth, coralline algal cover was significantly lower at Windsock compared to Forest (Klein Bonaire) and Karpata. Overall, cover of gorgonians & sponges appeared to be more constant between sites at 10 m than at 5 m depth while coralline algal cover was fairly consistent between sites at both 5 m and 10 m, with the exception of lower cover at Windsock.

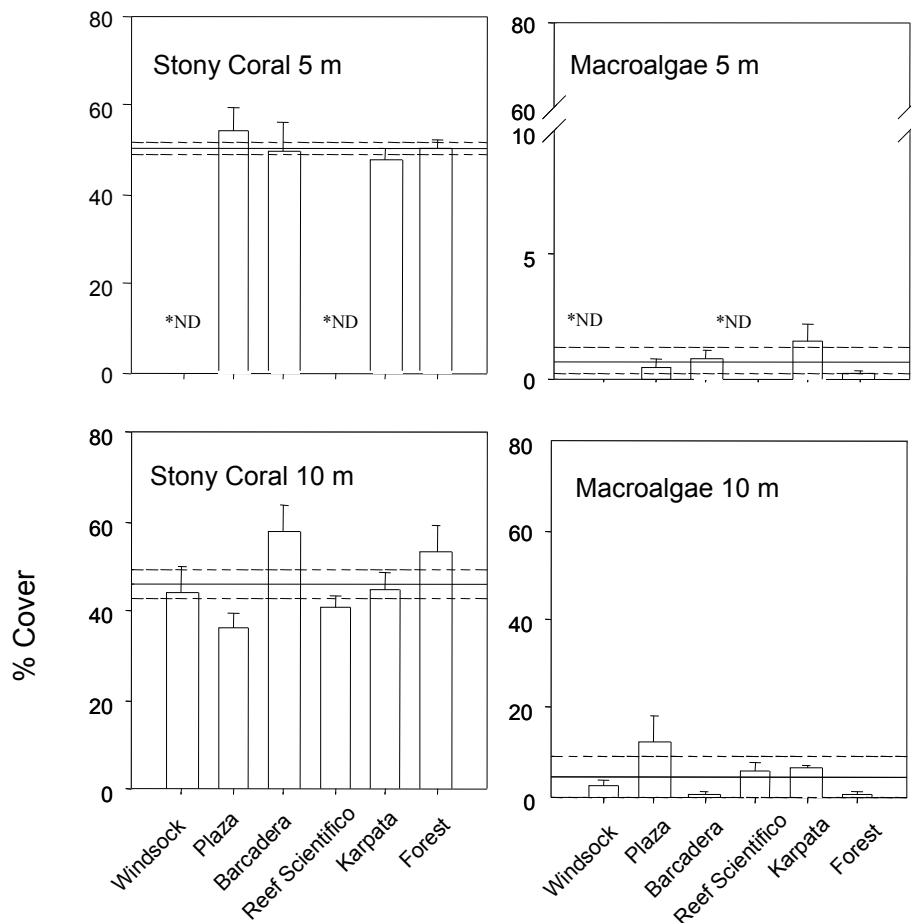


Figure 1.1. Percent cover (mean \pm standard deviation) of stony corals and macroalgae at 5 m and 10 m depth at potential FPA sites in Bonaire. Surveys were conducted in 2002-2003. Solid horizontal lines show mean values, dashed lines indicate ± 1 standard error.

Surveys of gorgonian abundance revealed several patterns. The genera *Plexaura* appeared to be the numerically dominant group on reefs in Bonaire in March 2003 (Figure 1.3). Karpata exhibited both the highest density and diversity of gorgonians compared with other survey sites

whereas Windsock (10 m) appeared to have the lowest overall densities. Note that figures 1.2 and 1.3 appear to show contradictory information for Barcadera (5 m), only because data for percent cover and gorgonian abundance (quadrats) were collected from different transects. Reefs of Bonaire were compared with other reefs systems with fishing (i.e., “control”) and without fishing (i.e., MPAs). Live coral cover was significantly greater in Bonaire compared to other coral reefs in the Caribbean including: Belize (control areas), Bahamas (control and MPA areas), and the Yucatan (at 10 m only) (Figure 1.4). Moreover, Bonaire’s reefs had significantly lower percent cover of macroalgae than reefs in Belize (control areas 10 m only), the Bahamas (control and MPA areas) and the Yucatan (10 m only) (Figure 1.4).

Densities of the herbivorous sea urchin *Diadema antillarum* varied from 0.22 ± 0.7 per m^2 at 5 m to 0.24 ± 0.8 per m^2 at 10 m depth. These densities were not significantly different from other Caribbean reefs examined in this paper.

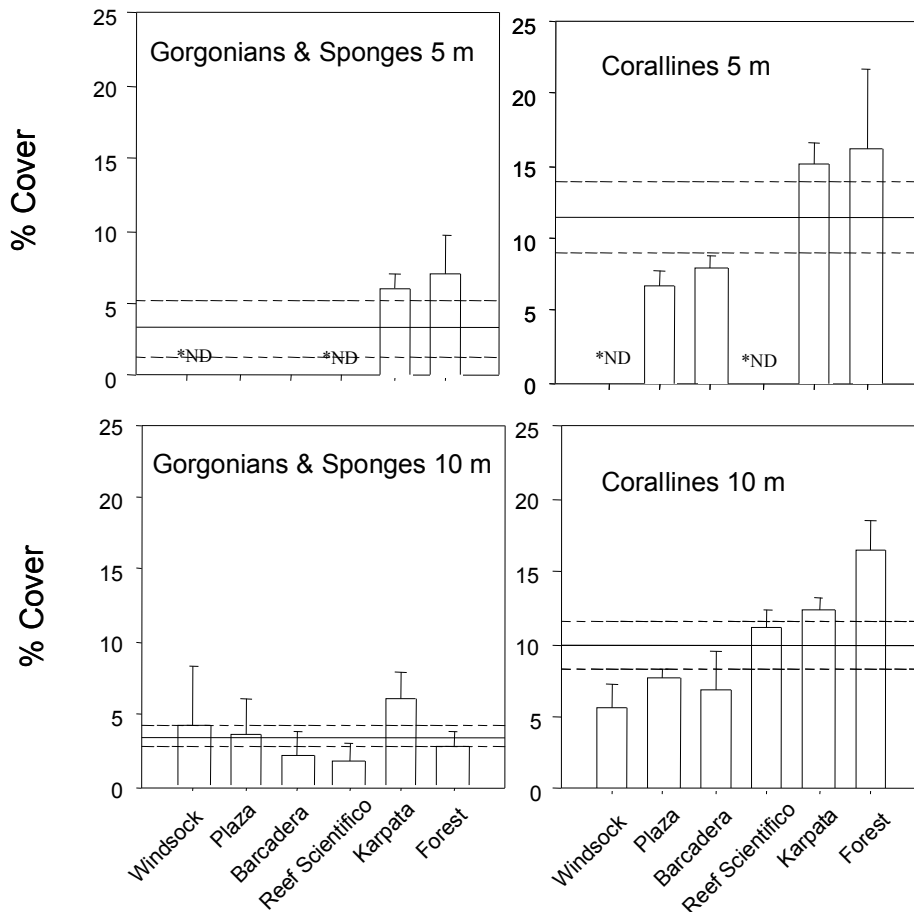


Figure 1.2. Percent cover (mean \pm standard deviation) of gorgonians & sponges and coralline algae at 5 m and 10 m depth at potential FPA sites in Bonaire. Surveys were conducted in 2002-2003. Solid horizontal lines show mean values, dashed lines indicate ± 1 standard error.

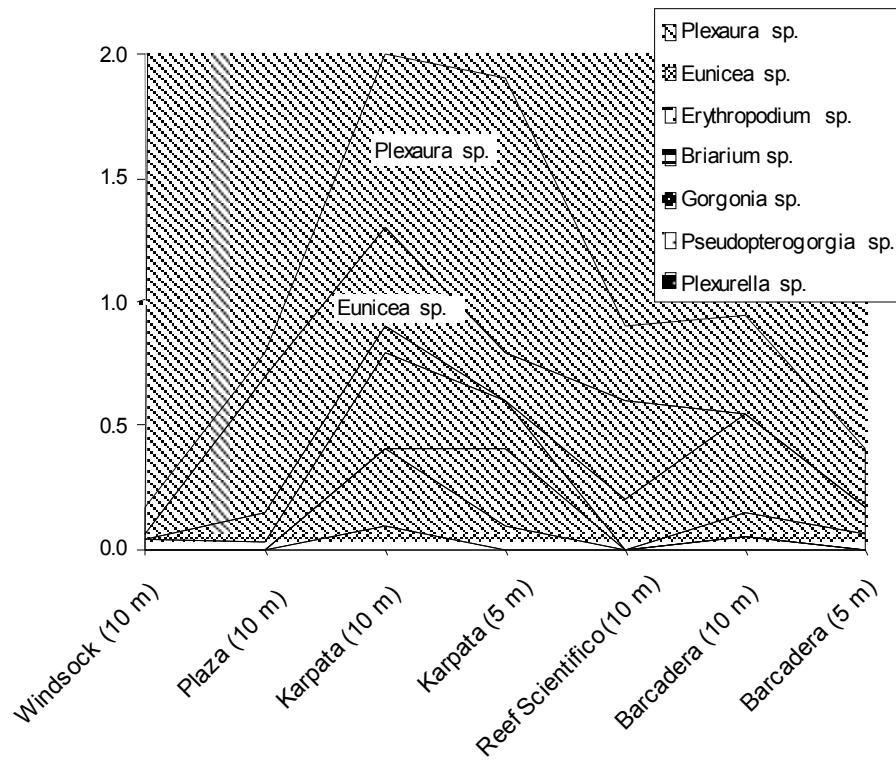


Figure 1.3. Dominant genera of reef gorgonians at proposed FPA sites in Bonaire (March 2003).

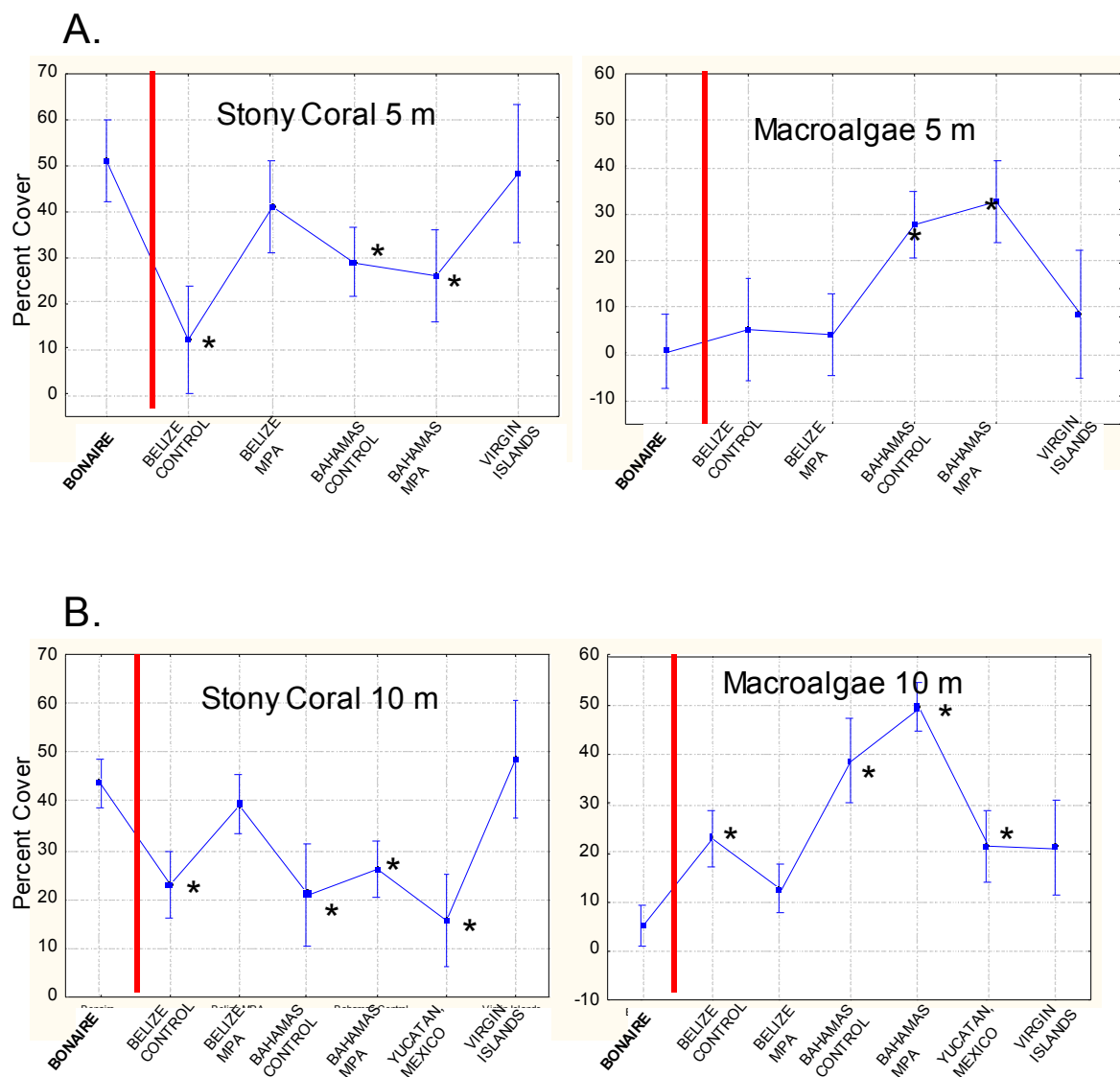


Figure 1.4. Comparison of live stony coral and macroalgal cover at (A) 5 m and (B) 10 m depth from various Caribbean reefs surveyed from 2002-2003. Asterisk symbols indicate significant differences (ANOVA $p < 0.05$) in cover compared Bonaire's reefs. Error bars show 95% confidence intervals.

Discussion

Surveys of live coral and macroalgae at proposed FPA sites in Bonaire revealed that there were no significant differences in the percent cover of either reef component between sites. This finding is favorable for the possible future implementation of Fish Protection Areas (FPAs) at several sites.

Significant differences in gorgonian and sponge percent cover among sites will not affect the ability to monitor the effects of FPAs on overall state of reef “health”. Although gorgonian communities have been shown to exhibit zonation patterns with depth (Kinzie 1973), relationships between gorgonian and sponge abundance and the overall state of reef “health” have not been documented. Significant differences in coralline algae between sites may suggest differences in the intensity of parrotfish or urchin grazing. Some species of coralline algae have been shown to induce coral settlement (Morse et al. 1988) and thus may be important for reef regeneration. The abundance of juvenile corals was surveyed at all sites (see Chapter 2) and will continue to be monitored to assess the impact of FPAs on coral recruitment.

Compared to other several other Caribbean reefs, Bonaire overall showed a higher live coral cover and correspondingly low macroalgal cover, suggesting these reefs are in better condition than most Caribbean reefs. It is possible that the high reef quality in Bonaire results from the limits to fishing that result in high densities of herbivorous fishes (Chapter 5) that help to control the settlement and growth of macroalgae.

References

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.

Kinzie, R.A. 1973. The zonation of West Indian gorgonians. *Bulletin of Marine Science* 23(1): 93-155.

Morse, D.E., Hooker, N., Morse, A.N.C., Jensen, R.A. 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. *Journal of Experimental Marine Biology and Ecology* 116:193-217.

Steneck, R.S., Ginsberg, R.N., Kramer, P., Lang, J., and Sale, P. 2003. Atlantic and Gulf Rapid Reef Assessment (AGRRA): a species and spatially explicit reef assessment protocol. 9th International Coral Reef Symposium. Bali, Indonesia. Nov. 2000.

Chapter 2: Abundance and species composition of juvenile corals

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Abstract

Surveys of adult and juvenile corals were conducted at six sites in Bonaire to quantify species diversity and abundance and provide data on these reefs prior to the potential establishment of Fish Protected Areas. Reefs surveyed were characterized by high coral coverage and were dominated by mound corals (most importantly the *Montastrea annularis* complex). There were no differences in adult coral communities among sites. There were differences in juvenile coral density between reefs with Forest, a site on Klein Bonaire, having a lower density than Plaza and Windsock. Mean density of juveniles was relatively high and species richness was high compared to other Caribbean locations. *Agaricia* sp. and *Porites astreoides*, both brooders, were the most abundant juvenile corals.

Introduction

In the past few decades, there has been a decline in the health of corals across the Caribbean. Some of the factors responsible for this decline include overfishing, coral disease, coral collection, bleaching events, hurricanes and the large-scale reduction in herbivory due to the die-off of the black urchin *Diadema antillarum* and hurricanes (Hughes 1994). Coincident with the degradation of reefs has been a marked decline in coral recruitment (Connell 1997). Possible reasons for declining recruitment are reduced fecundity of adult colonies and a loss of suitable substrate for larval settlement (Hughes and Tanner 2000). On many Caribbean reefs, there has been a substantial reduction of available settlement substrate due to a phase-shift to macroalgal dominance (Hughes 1994).

Coral recruitment is vital to the recovery and long-term survival of a reef (Kojis and Quinn 2001). Therefore, given all the threats to reef health, it is important to monitor the rate of recruitment on reefs, in order to assess their potential resilience. A better understanding of patterns and processes in the early life history of corals is crucial to understanding the ecology and to predict the future of coral reefs.

A study of juvenile coral abundance and diversity was conducted in Bonaire. The purpose of this study was to generate baseline data to compare to surveys that will be taken after the closure. Thus, the effect of area closure on adult coral species composition and on juvenile abundance and diversity can be monitored. The specific goal was to determine the population density of juvenile corals on a per-reef scale so reef resilience can be monitored. This large-scale measurement of coral recruitment is likely to differ from smaller scale measurements of coral density on particular substrata (see Chapter 1 on algal-coral densities). Overall, six sites were surveyed to allow continued monitoring of sites that are proposed for protection as well as sites

where fishing will be allowed. This type of replicated Before After Controlled Impact (BACI) design has been shown to be an effective way to assess impacts on reef communities of management actions such as those proposed for Bonaire (Underwood 1992).

Materials and Methods

Adult corals

Three 10-meter transects were placed on hard substratum on the reef (avoiding sand channels and patches) at standard depths of 5 m and 10 m. Six sites were sampled (Windsock, Plaza, Reef Scientifico, Klein Bonaire, Karpata and Barcadera), which correspond to the sites used in other chapters of this report (see map, Figure 0.4). Species-specific abundance of stony (scleractinian) corals and the reef-building fire corals (hydrozoans such as *Millepora* sp) were quantified by measuring the length of their live tissue along the transect line (to the centimeter) following the topography of the reef. Thus, the summed length of corals for any given linear meter will add up to more than that length.

Juvenile corals

A belt of 0.5 m on each side of the transect (total area 10 m² for each transect) was carefully surveyed for juvenile corals. We followed Rogers et al. (1984) for the operational cut-off of juvenile corals as those less than 4 cm in colony diameter. Juveniles were identified to the lowest possible taxon, counted and assigned to the appropriate 1 cm size-class. Colonies < 4 cm that were clearly the product of fragmentation of larger colonies were omitted from these surveys in order to assess new recruitment (as in Rogers et al. 1984).

Data analysis

Differences in abundance of juvenile corals between sites were tested using a one-way ANOVA. Differences in community composition were analyzed with non-metric multi-dimensional scaling (MDS), using Bray-Curtis similarity and square root transformations, followed by the ANOSIM permutation test (Clarke 1993).

Results

Adult coral colonies

Species composition for adult corals varied significantly with depth (ANOSIM, $P < 0.01$). The *Montrastrea annularis* complex (*M. annularis*, *M. faveolata* and *M. franksii*) was by far the dominant coral, and both *M. annularis* and *M. faveolata* were slightly more abundant on shallow (5m) reefs (Figure 2.1). *Millepora* sp, *Madracis* sp., *Colpophyllia* sp. and *Agaricia* sp. were also common at both depths. There were no significant differences in adult coral species composition among sites surveyed (ANOSIM $P = 0.27$).

Juvenile corals

Total reef-wide density of juvenile corals (all species and all size classes combined) averaged 2.92 juveniles/m² across all sites. There was no significant difference in density of juveniles between shallow (5 m) reefs (3.1 juv/m²) and deep (10 m) reefs (2.68/m²). The species composition also did not change significantly (ANOSIM, P = 0.065) with depth.

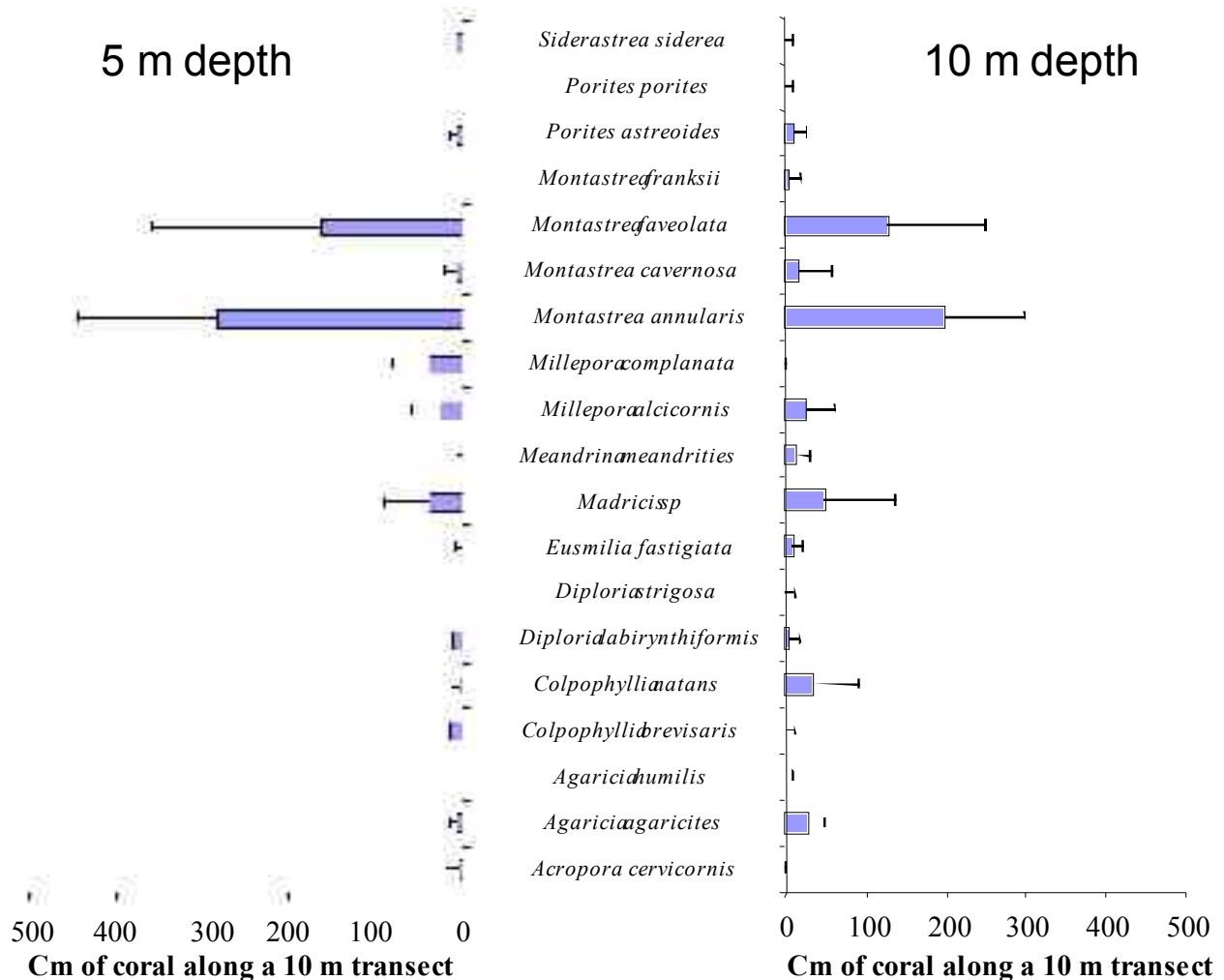


Figure 2.1. Abundance of adult coral colonies at 5m(left) and 10m (right) across all sites (mean ± standard deviation)

There were significant differences in juvenile abundance among sites (one-way ANOVA, $F_{5,54} = 3.16$, $P = 0.014$), with Plaza showing the highest reef-wide densities, followed by Windsock, Karpata, Reef Scientifico, Barcadera and Klein Bonaire. *A posteriori* SNK test showed Plaza and Windsock have significantly higher juvenile densities than Klein Bonaire (Figure 2.2). The composition of the juvenile coral assemblage also varied significantly among sites (ANOSIM, $P < 0.001$), although clear distinctions between sites were not obvious (MDS, Figure 2.3). The SIMPER analysis indicated that 50% of the difference between Klein Bonaire and Windsock and

Plaza can be attributed to lower densities of *Madracis* sp., *Monstrastrea annularis* and *Porites astreoides*. Densities of *Agaricia* sp. juveniles at Klein Bonaire (1.32 juv/m²) was between those at Windsock (1.02/m²) and at Plaza (2.12/m²).

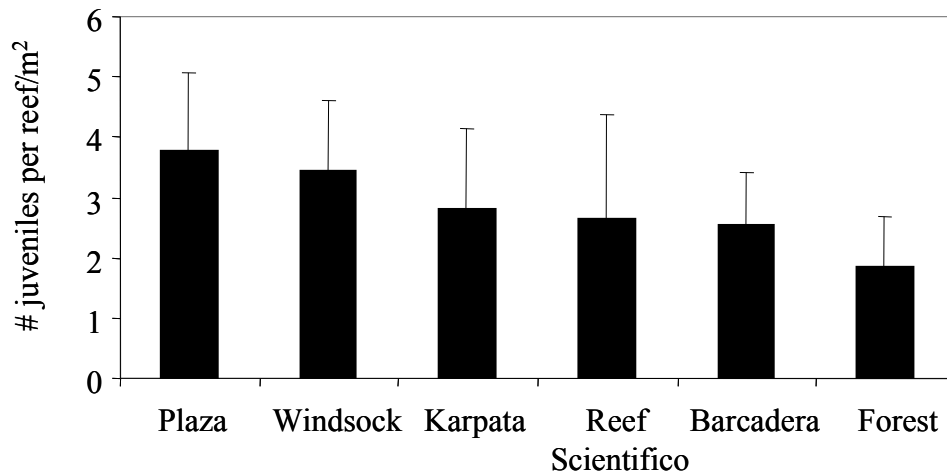


Figure 2.2. Density of juvenile coral at each of 6 sites surveyed (Mean \pm standard deviation). Forest and Windsock do not differ significantly from each other, and Karpata, Reef Scientifico, and Barcadera do not differ significantly from each other.

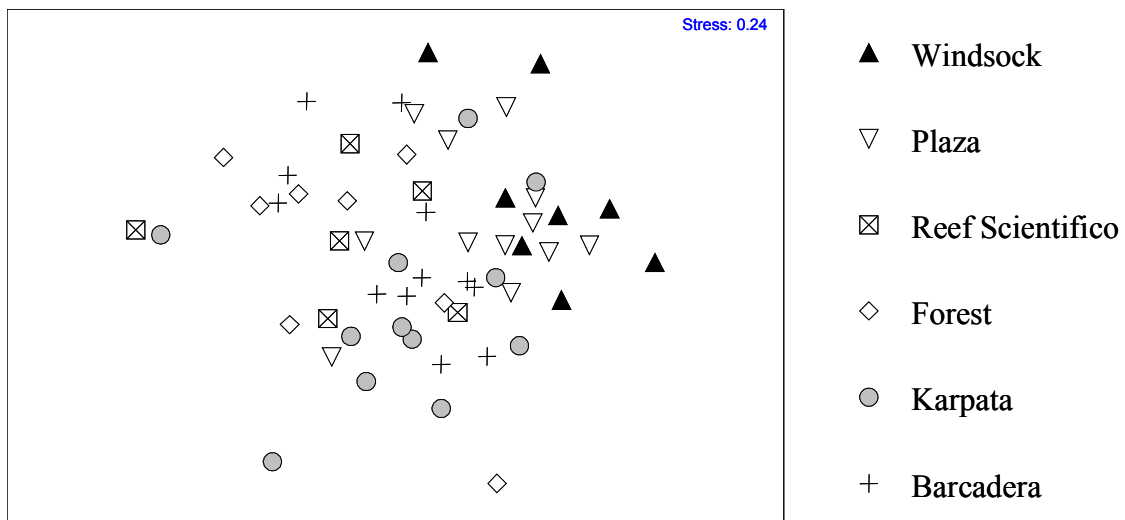


Figure 2.3. Non-metric multidimensional scaling plot of juvenile coral abundance. The closer two sites are on the plot, the more similar their juvenile coral communities.

Overall, sixteen taxa of juveniles were recorded. Of these, *Agaricia* sp. was by far the most abundant, followed by *Porites astreoides*, *Madracis* sp., *Montastrea annularis* complex and the hydrozoan *Millepora* sp. (Figure 2.4). *Diploria* sp., *Montastrea cavernosa*, *Colpophyllia* sp., *Eusmilia fastigiata*, *Siderastrea siderea* and *Meandrina meandrites* were also present at densities greater than 0.02/m². There was no significant correlation between abundance of juveniles and abundance of adults (Pearson correlation, $P > 0.05$), that is, the species that were most abundant as juveniles were not those most abundant as adults.

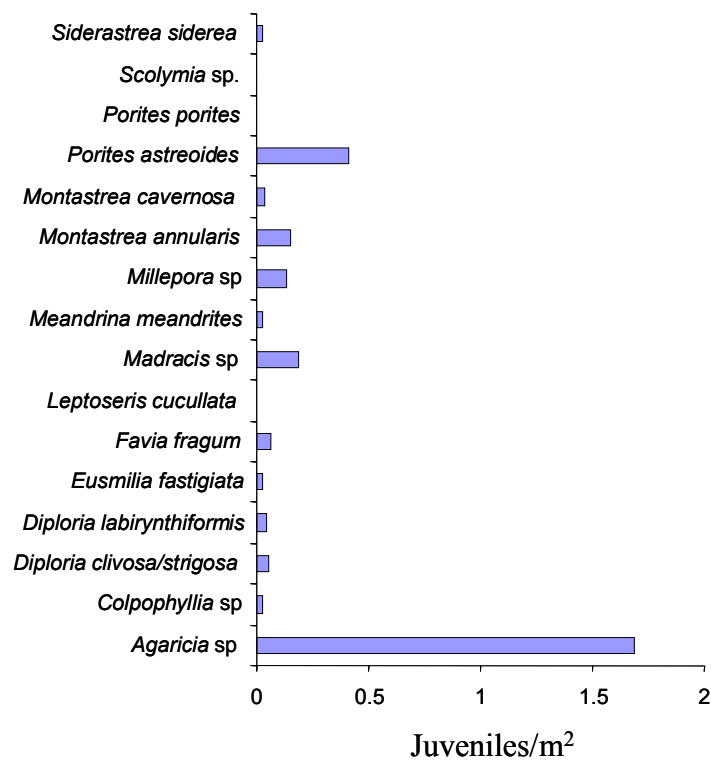


Figure 2.4. Mean density of juvenile corals across depths and sites

Discussion

Characterization of Bonaire corals

The Bonaire reefs surveyed were dominated by the *Montastrea annularis* complex. Branching corals were much less abundant, and of those *Madracis* sp. were the most important. *Acropora* sp. were present in very low abundance. Since there were no differences in species composition for adult corals among sites, any differences in community in a site after the establishment of a no-take zone should be the effect of the closure.

In contrast to adult corals, juvenile corals were significantly different among sites in both abundance and species composition. Klein Bonaire had lower densities of juveniles than both Windsock and Plaza, which may reflect either a lower availability of settlement substrate or a lower supply of coral spat.

Agaricia sp. was by far the most abundant juvenile coral. This same characteristic was observed in Bonaire in the late 1970s (Bak and Engel 1979) as it has elsewhere in other Caribbean islands, both in the past and today (Rogers et al, 1984, Chiappone and Sullivan 1996, Edmunds 2000). The high abundance of *Agaricia* spp. juveniles probably relates to its productive mode (brooding) and high reproductive output of this coral (Bak and Engel 1979). The second most abundant species of juvenile coral (*Porites astreoides*) is also a brooder (Richmond and Hunter 1990, Richmond 1997), and a species that is commonly found both as a juvenile and as an adult throughout the Caribbean (Rogers et al 1984, Edmunds 2000).

The results from this survey are similar to the surveys conducted in 1974 in Bonaire (Bak and Engel 1979). The most striking difference is the near absence of *Leptoseris cucullata* (= *Helioseris cucullata*) in our surveys, whereas this was the third most abundant species of juvenile corals in 1974. Adult colonies of *L. cucullata* were never recorded on the transects in this study, and it may be that a low abundance of adults in Bonaire results in poorer recruitment for this brooder. The abundance of *L. cucullata* has declined in other parts of the Caribbean (Hughes 1985) and it may be that the density of adult colonies in Bonaire is lower now than it was in the 1970s. Also, the elkhorn coral, *Acropora palmata*, was present in low densities in 1974 but was not recorded in our surveys in 2003. Conversely, we observed a higher relative abundance of *Montastrea annularis* and *Madracis* sp. than that observed in 1974.

The lower abundance of juveniles at Forest on Klein Bonaire was evident among both brooding (e.g., *Porites astreoides*, *Madracis* sp.) as well as broadcasting (e.g., *Montastrea annularis*) corals (Richmond and Hunter 1990). This suggests that substrate availability, rather than lowered supply of larvae, regulates juvenile densities when measured at a reef-wide scale. This is supported by the high densities of juveniles found on turf-covered substrates between live corals (see Chapter 4 on coral/algal interactions). Measurements of juvenile density per available recruitment substrate differ significantly from those measured for the entire reef, because with the first method quadrats that fell in sand or over 100% live coral were relocated. This may explain that the Forest site on Klein Bonaire has the highest density of adults of all sites. Thus the Forest site may receive a high number of coral larvae (resulting in high spat density) but the high coral cover, and thereby low substrate availability, results in low overall density of juveniles. In fact, there is a negative correlation between the amount of substratum available for coral settlement (crustose coralline algae and turf) and the deviation between the two methods of quantifying juveniles. Thus, the lower the available recruitment substrate, the higher the deviation between the methods.

Comparison with other Caribbean islands

The method used in this study surveyed juvenile density over the entire reef. This method differs from other studies in which only suitable substrate was surveyed (see Bak and Engel 1979 and

Chapter 1 on coral/algal interactions). The mean density of juveniles found with this latter method appears higher than the densities found in our survey. Therefore, total juvenile densities were compared only to previous surveys conducted by Steneck and Bégin (in prep) in which identical methods were used.

The total density of juvenile corals was relatively high in Bonaire (2.92 juveniles/ m²) compared to other Caribbean islands (Figure 2.5). The juvenile density in Bonaire was greater than that found in St. Croix (1.24/m²) and Navassa (1.24/m²) but was less than the density found in St. John (5.08/m²).

As in St. John, St. Croix and Navassa (Steneck and Bégin in prep), the dominant coral juveniles in Bonaire were brooders, predominantly agaricids. The prevalence of *Agaricia* sp. may be due to large numbers of *A. agaricites* which are known to have a high recruitment rate (Bak and Engel 1979, Chiappone and Sullivan 1996). In Bonaire, *Porites astreoides* had the second highest juvenile density. This finding is similar to results from St. John and St. Croix.

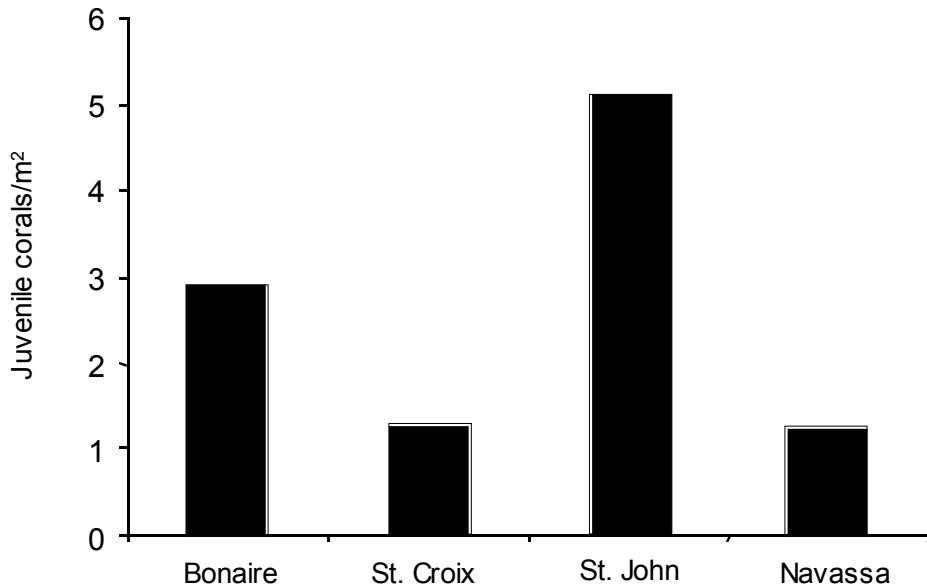


Figure 2.5. Comparison of juvenile coral density at Bonaire with three other Caribbean locations

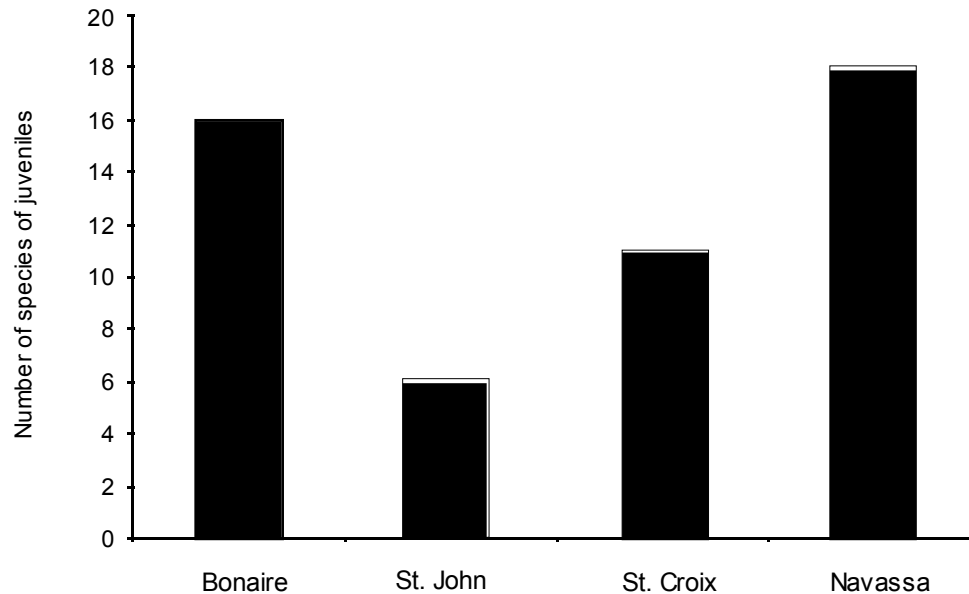


Figure 2.6: Comparison of species richness at Bonaire with three other Caribbean locations.

Some coral species that exhibit low recruitment elsewhere in the Caribbean have relatively high juvenile densities in Bonaire. The number of *Montastrea annularis* recruits was relatively high in Bonaire as it was in St. John (Steneck and Bégin, in prep.). No *M. annularis* juveniles were found in Navassa or in St. Croix (Bégin and Steneck 2003, Steneck and Bégin in prep). Additionally, several studies by Bak and Engel (1979), Rogers *et al* (1984) and Hughes and Tanner (2000) indicate that *M. annularis* usually exhibits a low rate of recruitment. Similarly, *Madracis* sp. had the fourth highest juvenile density in Bonaire (of 16 species recorded as juveniles). However, no *Madracis* sp. recruits were found in St. John and St. Croix and very few were found in Navassa (Bégin and Steneck 2003).

The species richness of juvenile corals in Bonaire (16 species) was high compared to St. John (11 species) and St. Croix (6 species) and was only slightly lower than the number of species found in Navassa (18) (Bégin and Steneck 2003) (Figure 2.6).

We also compared the relative abundance of adult corals colonies in Bonaire to other Caribbean sites. The most abundant adult species in Bonaire was *Montastrea annularis*. This is the dominant coral today throughout the Caribbean. Abundance of *M. cavernosa* was very low in Bonaire which contrasts with studies in St. John (Edmunds 2000) and St. Croix (Rogers *et al* 1984) in which this species was relatively common. Abundance of adult agariciids was also low in Bonaire. *Agaricia* sp. were found to be relatively abundant in St. John (Edmunds 2000), St. Croix (Rogers *et al* 1984) and Navassa (Miller *et al* in prep). The high number of juvenile agariciids in Bonaire, despite the low abundance of adults, may again be due to the fact that *A. agaricites* exhibits a high recruitment rate relative to its abundance on most reefs (Rogers *et al* 1984).

Conclusion

Reefs of Bonaire are characterized by high coral coverage and the species composition is comparable to most other Caribbean locations, with mound corals (most importantly the *Montastrea annularis* complex) dominating the community. All sites surveyed had similar adult coral communities. Juvenile corals were relatively abundant, and showed high species richness compared to other Caribbean islands. Density of juvenile corals varied among sites surveyed and appears to be related to the amount of substrate available for settlement rather than differences in the supply of coral spat. The dominant juvenile corals were brooding species (dominated by *Agaricia* sp. and *Porites astreoides*).

References

- Bak, R.P.M., Engel, M.S. 1979. Distribution, abundance and survival juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Marine Biology* 54: 341-352.
- Bégin, C.B., Steneck, R.S. 2003. The role of crustose coralline algae in coral settlement around Navassa Island. Pages 57-65 in M.W. Miller (Ed.) Status of reef resources of Navassa Island: Nov 2002. NOAA Technical Memorandum NMFS-SEFSC-501. 119 pp.
- Chiappone, M., Sullivan, K.M.. 1996. Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. *Bulletin of Marine Science* 58(2): 555-569.
- Clarke, K.R. 1993 Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.
- Connell, J.H., 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16, S101-S113.
- Edmunds, P.J. 2000. Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Marine Ecology Progress Series* 202: 113-124.
- Hughes, T. P. 1985 Life Histories and population dynamics of early successional corals. *Proceedings of the Fifth International Coral Reef Congress* 4, 101-106.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265.
- Hughes, T.P., Tanner, J.E. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81, 2250-2263.
- Kojis, B.L., Quinn, N.J., 2001. The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. *Bulletin of Marine Science* 69, 967-974.

Miller, M.W., Vermeij, M., Williams, D. and McClellan, D. (in preparation). Benthic habitats and community structure of Navassa. NOAA Technical Memorandum.

Richmond, R.H., Hunter, C.L. 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific and the Red Sea. *Marine Ecology Progress Series* 60: 185-203.

Richmond, R.H. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkland, C. (Ed.), *Life and death on coral reefs*. Chapman and Hall, New York, pp. 175-119.

Rogers, C.S., Fitz, H.C.I., Gilnack, M., Beets, J., Hardin, J. 1984. Scleractinian coral recruitment patterns at salt river submarine canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* 3, 69-76.

Underwood, A.J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, viable world. *Journal of Experimental Marine Biology and Ecology* 161(2): 145-178.

Chapter 3: Reef fish populations: distribution, abundances and size structure

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Abstract

Abundance and size structure of a subset of reef fishes (herbivores and carnivores) were measured at two depths (5 and 10 m) on each of the six survey sites. Parrotfish were the most abundant fish by mass. Damselfish were most abundant by population density. Carnivorous fishes were moderately abundant and greatest at the Forest site on Klein Bonaire. Density and biomass of herbivorous fishes did not differ among sites (with one exception), or between depths within sites. Carnivorous fish biomass was variable among areas, particularly among sites at 10 m depths. All sites had generally similar fish community structure. Rates of grazing were higher than other sites measured in the Caribbean. However, territorial damselfish had a marked negative affect on grazing parrotfish and surgeonfish.

Introduction

Interest in establishing Marine Protected Areas (MPAs) has been rising rapidly over the past decade as marine resource managers, scientists, and the public have become increasingly aware of the shortfalls of traditional marine resource management methods and the added stresses to near shore areas caused by growing human populations. However, many reserves have been established with unclear goals and management actions or plans, resulting in a lack of ability to demonstrate the effects of protection. This chapter provides baseline data on herbivorous and carnivorous fish populations on Bonaire in several areas that are being considered for the establishment of Fish Protected Areas. Such baseline data is crucial for both providing information necessary for establishing a reserve in the most appropriate area as well as for providing data that can be compared to over time in order to monitor the effectiveness of the marine reserve.

Methods

Transect surveys were conducted at six sites in Bonaire: Barcadera, Reef Scientifico, Karpata, Forest (Klein Bonaire), Plaza and Windsock. Surveys were conducted at 5 m and 10 m depths at all sites with the exception of Reef Scientifico where the 5 m depth lacked sufficient reef structure to be considered comparable to other sites. Abundance and sizes of herbivorous fishes and their potential fish predators were recorded along a minimum of five randomly placed 25 m long by 2 m wide transects at each depth. A clear plastic ruler affixed to the end of a 1-m rod was carried by the divers in order to measure transect width and fish length. The size of each fish counted was estimated to the nearest centimeter by a diver trained in fish size estimation. Fish

length was converted to biomass using length-weight regressions from Bohnsack and Harper (1988).

All predominant herbivorous and carnivorous fishes found within this region were surveyed. This included 21 herbivorous species contained within the following four families: Scaridae (parrotfishes): *Scarus iserti*, *Scarus guacamaia*, *Scarus coelestinus*, *Scarus taenopterus*, *Scarus coeruleus*, *Scarus vetula*, *Sparisoma rubripinne*, *Sparisoma chrysopterum*, *Sparisoma atomarium*, *Sparisoma aurofrenatum*, *Sparisoma viride*; Pomacentridae (damsel-fishes): *Stegastes planifrons*, *Stegastes dorsopunicans*, *Stegastes variabilis*, *Stegastes diencaeus*, *Stegastes leucostictus*, *Microspathadon chrysurus*; Acanthuridae (surgeonfishes): *Acanthurus bahianus*, *Acanthurus coeruleus*, *Acanthurus chirurgus*; and Kyphosidae (chubs): *Kyphosus sectatrix*. The following carnivorous fishes were also surveyed: Serranidae (bass and groupers): *Paranthias furcifer*, *Rypticus saponaceus*, *Serranus tigrinus*, *Hypoplectrus chlorurus*, *H. nigricans*, *H. puella*, *H. unicolor*, *Epinephelus cruentatus*, *E. guttatus*, *E. adscensionis*, *E. fulvus*, *Mycteroperca tigris*; Aulostomidae (trumpetfish): *Aulostomus maculatus*; Carangidae (jacks): *Caranx ruber*; Lutjanidae (snappers): *Ocyurus chrysurus*, *Lutjanus analis*, *L. mahogoni*, *L. apodus*, *L. griseus*; Synodontidae (lizardfish): *Synodus intermedius*; Scorpaenidae (Scorpionfish): *Scorpaena plumieri*; Muraenidae (morays): *Gymnothorax funebris*, *G. miliaris*, *Echidna catenata*; Sphyrinaeidae (barracuda): *Sphyrina barracuda*; Bothidae (flounder): *Bothus lunatus*.

Data were examined for homogeneity of variance and normality and transformed as necessary (log transformation needed for density data) to meet assumptions required for analysis of variance (ANOVA). Single factor ANOVA's were used to test for differences among sites at each depth and between depths at each site ($\alpha = 0.05$).

Results

Density

Densities of herbivorous fishes were not significantly different among sites at either the 5 or 10 m depth (ANOVA: 5 m: $F_{4,33} = 2.356$, $P = 0.074$; 10 m: $F_{5,30} = 0.999$, $P = 0.435$ [Figure 3.1, Appendix A]). Herbivorous fish density did not significantly vary between depths within each site with the exception of Forest (Klein Bonaire) where the density was significantly higher at the 10 m depth (ANOVA: $F_{1,12} = 10.125$, $P = 0.008$). This was likely a result of inconsistent reef structure at the 5 m depth (several breaks in the reef and large areas of sand). Damsel-fish made up the largest proportion of herbivores at all sites except at Plaza where scarids were slightly more abundant. In all other cases, scarids were the second-most abundant group of herbivores (Figure 3.1). Carnivorous fish density was much more variable among sites (Figure 3.1, 3.2). Carnivore density differed significantly among the 5 m sites and at the 10 m sites the differences were marginally non-significant (ANOVA: 5 m: $F_{4,31} = 3.061$, $P = 0.031$; 10 m: $F_{5,30} = 2.509$, $P = 0.052$). Carnivores were less abundant than damselfish and scarids at all sites (Figure 3.1). Serranids (hamlets, grouper, bass) were by far the most abundant of the carnivores, followed by snappers. However, the diversity of larger-bodied groupers was low; although fairly common, the tiger grouper (*Mycteroperca tigris*) was the only species of grouper observed on any of surveyed the Bonaire reefs.

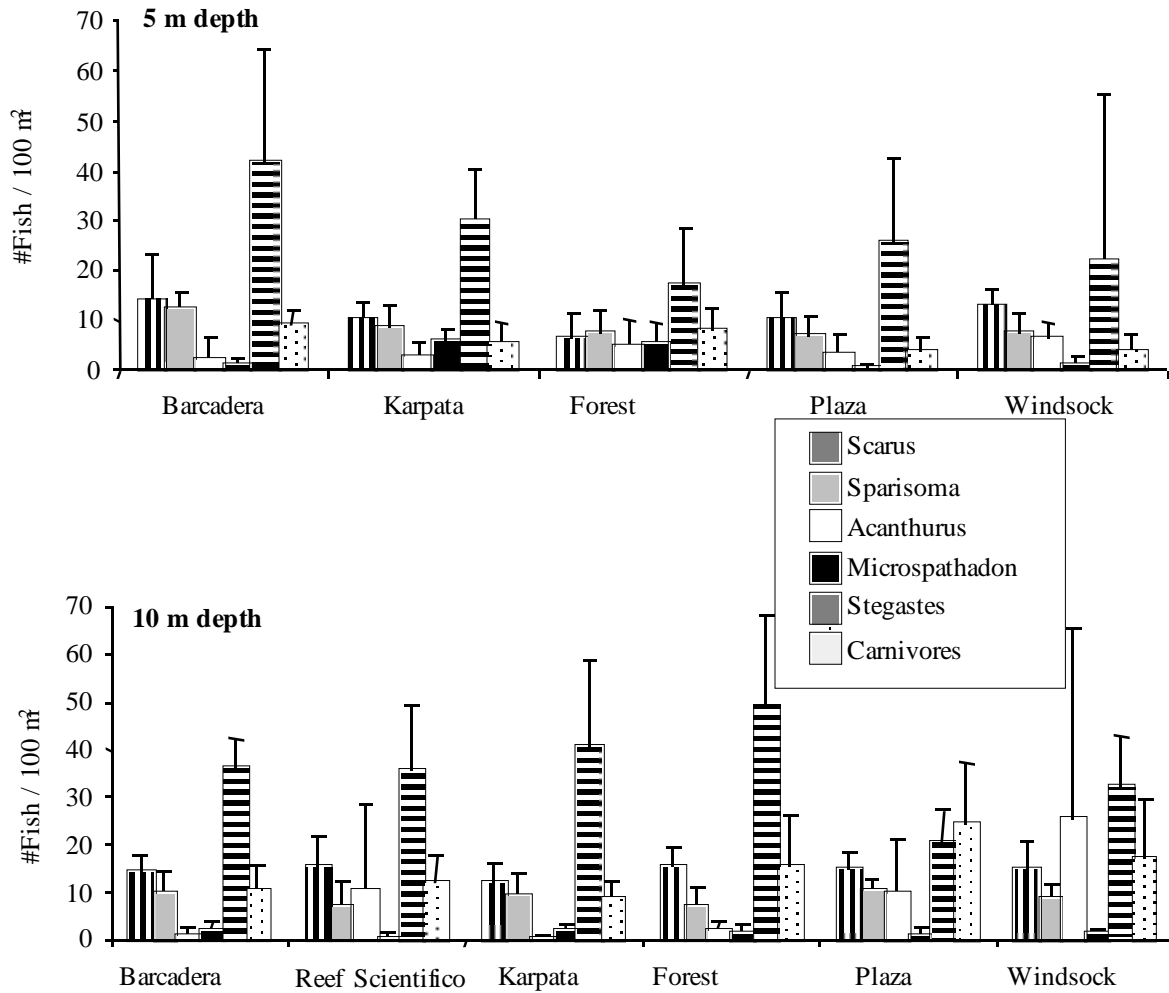


Figure 3.1. Density of fish at 10 m and 5 m sites, by family or group.

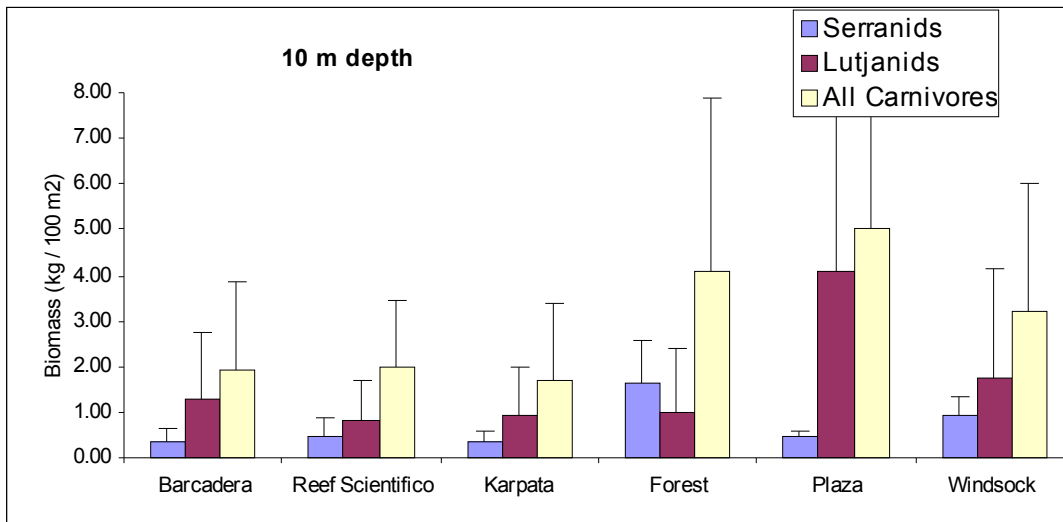
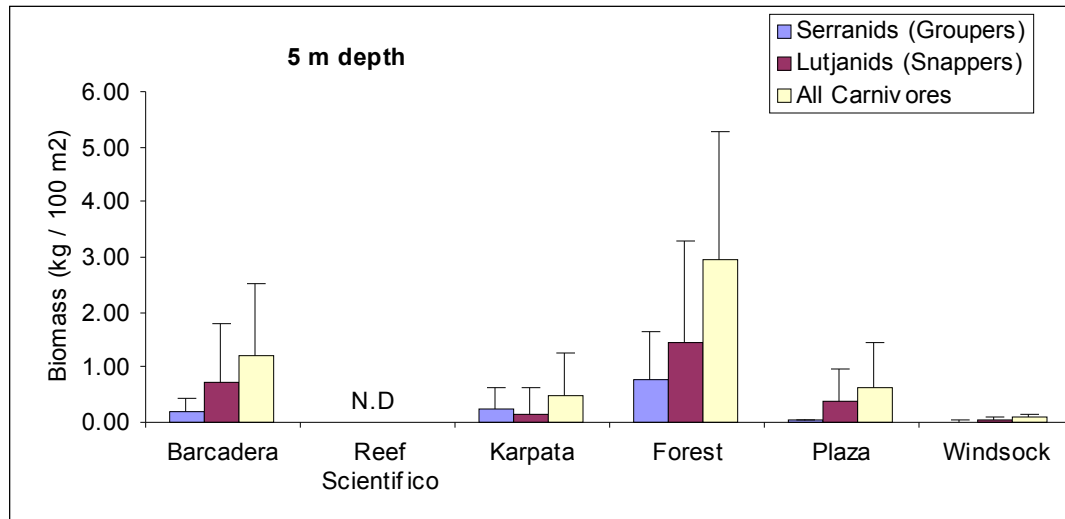


Figure 3.2 Density of select predator groups at 5m and 10m sites.

Biomass

As with density, biomass of herbivorous fishes did not significantly differ among sites at either depth (ANOVA: 5 m: $F_{4,33} = 1.232$, $P = 0.316$; 10 m: $F_{5,30} = 2.368$, $P = 0.063$ [Figure 3.3, Appendix B]). Biomass of carnivores was more highly variable and differed significantly among the sites at 5 meter depth but not at the 10 meter depth (ANOVA: 5 m: $F_{4,33} = 6.371$, $P = 0.001$; 10 m: $F_{5,30} = 1.681$, $P = 0.170$ [Figure 3.2, 3.3]). This was due to the high biomass of carnivores

at the 5 meter site at Forest (Klein Bonaire) and the extremely low values at Windsock (Figure 3.4). Within sites, herbivorous fish biomass differed between depths only at one site (Plaza [ANOVA: $F_{1,10} = 5.999$, $P = 0.034$]). Carnivorous fish biomass differed between depths at two sites, Karpata and Plaza (ANOVA: $F_{1,15} = 5.226$, $P = 0.037$; $F_{1,10} = 12.305$, $P = 0.006$; respectively). Lutjanids made up the largest proportion of biomass at each site (39-84% of the total biomass) at all sites but two. At Forest (Klein Bonaire, 10 meters) and Karpata (5 m), 50 % of the carnivore biomass was made up of serranids. This was driven by *Epinephelus cruentatus* (graysby) at Karpata and both *E. cruentatus* and *Mycteroperca tigris* (tiger grouper) at Forest (Figure 3.3). Total biomass was dominated by scarids at all sites (Figure 3.3).

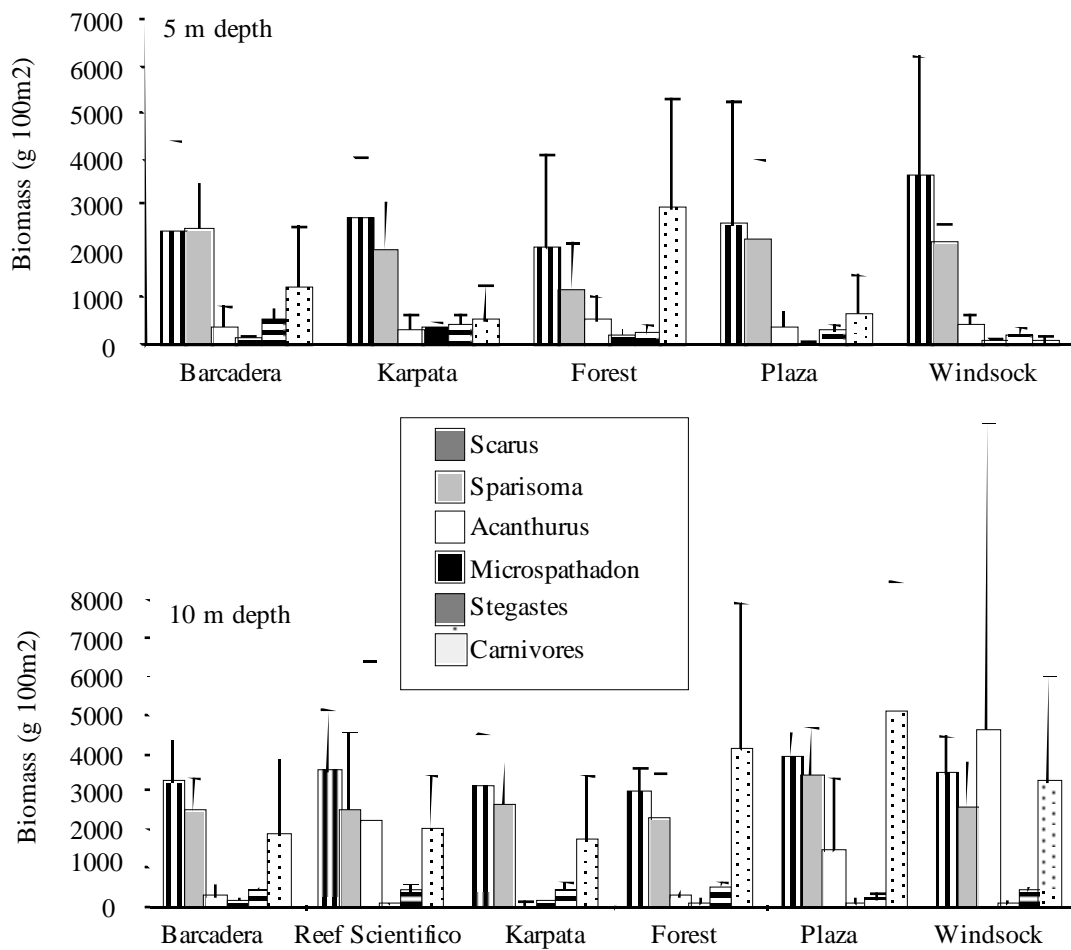


Figure 3.3. Average fish biomass per site, categorized by family or group.

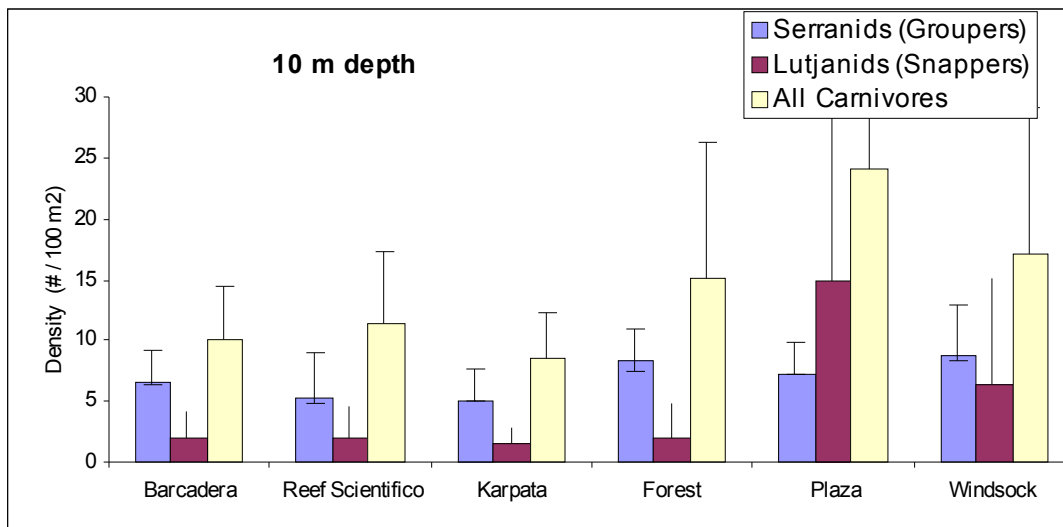
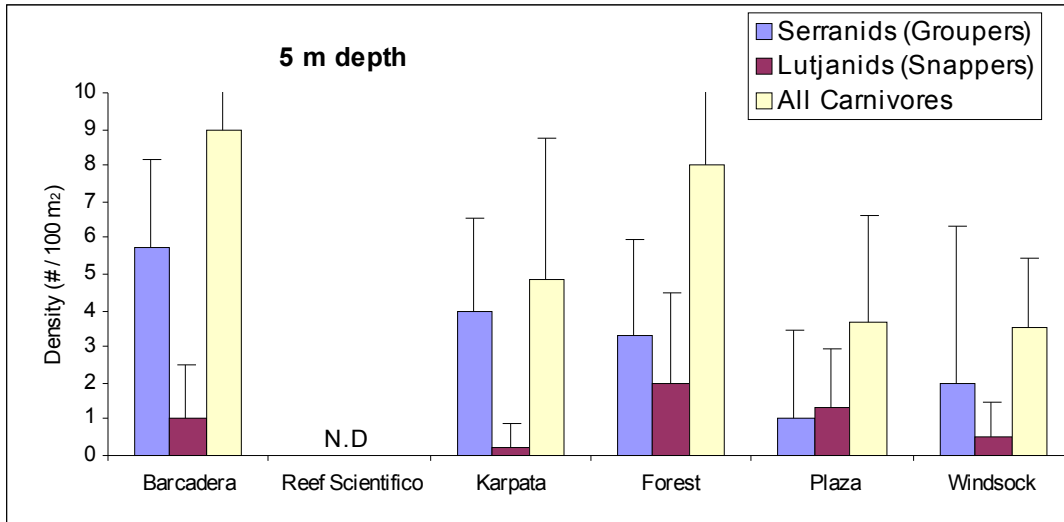


Figure 3.4. Average biomass of serranids (groupers), lutjanids (snappers), and all carnivores together.

Discussion

Bonaire reefs contain fairly robust fish populations relative to many other Caribbean reefs (Figure 3.5, 3.6). Overall, the differences in herbivorous fish density and biomass were small. However, both density and biomass of carnivorous fishes varied widely among sites, with very

low biomass on shallow areas of Karpata, Plaza, and Windsock (Figure 3.4). However, the deeper portions of those reefs contained higher numbers of carnivores, driving up the overall site average to become more similar to other sites. Each group of fish was well represented at each site and there was no single site that stood out in terms of having a particularly rich fish assemblage. However, Forest and Plaza each had greater biomass of carnivores than several other sites.

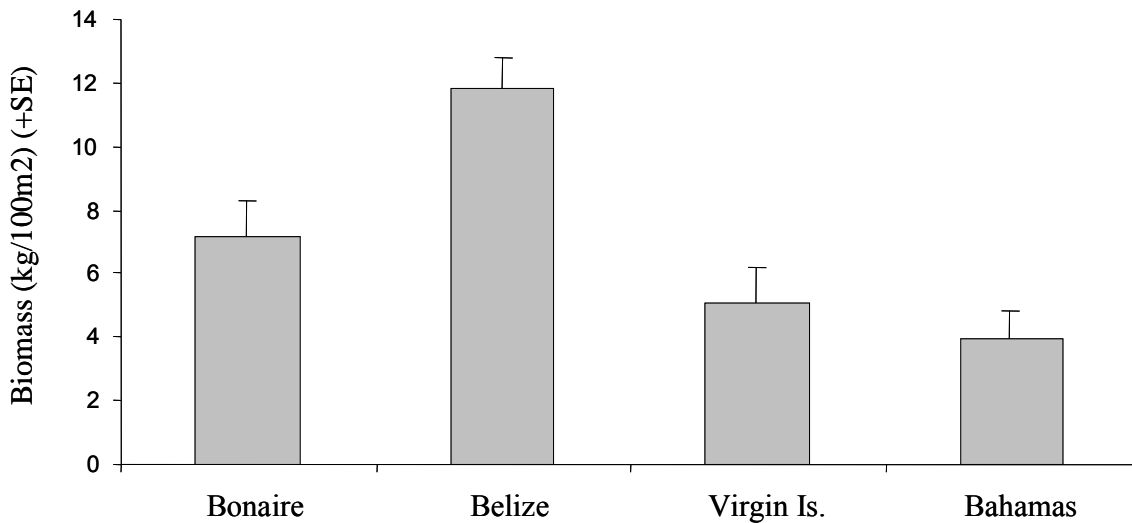


Figure 3.5. Regional comparison of herbivorous fish biomass.

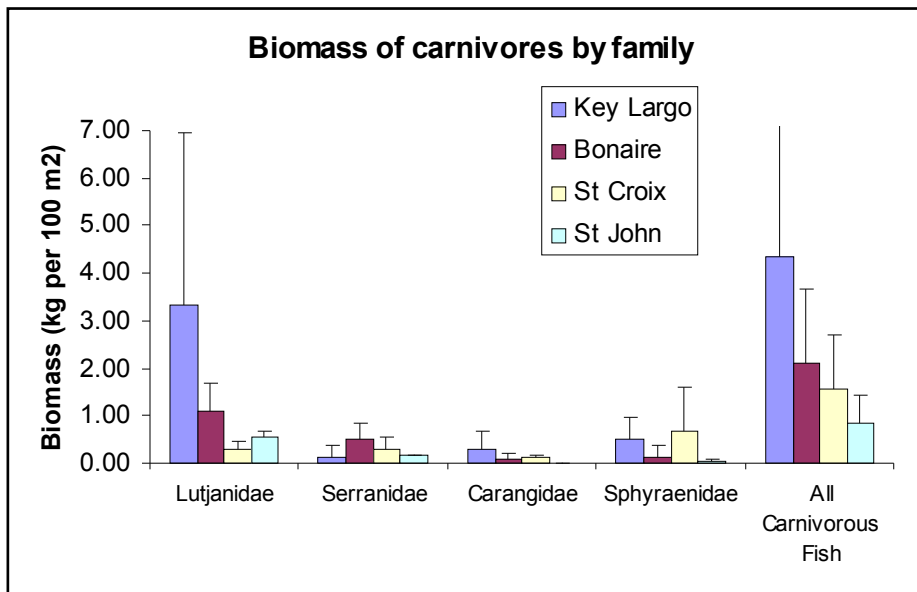


Figure 3.6. Regional comparison of select groups of carnivorous fish biomass.

Herbivory is almost exclusively from fish (*Diadema* sea urchins are rare and thus ecologically unimportant; see Chapter 1). Fish grazing was measured at three sites (Plaza, Reef Scientifico, and Barcadera) by quantifying the number of bites per square meter over five minute observation periods (methods of Steneck 1983). Bite rates from grazing fishes averaged 313 bites per meter square per hour for parrotfish and surgeonfish combined (from a total of 75 five minute bite observations). This is nearly twice the rate reported recently for Yucatan coast of Mexico (i.e. 175/m²/h Steneck and Lang 2003). The high population density of large parrotfish also suggests Bonaire's reefs may be frequently grazed (Figure 3.1).

Territorial damselfish are so aggressive they can function like biological cages (Hixon and Brostoff 1983). When we quantified bite rates, we observed meter square areas irrespective of what fish were present in the area. When all 75 bite surveys were plotted so both parrotfish and surgeonfish grazing was examined as a function of damselfish bites, a strong inverse relationship was evident (Figure 3.7). This suggests that parrotfish are deterred by damselfish grazing and surgeonfish are excluded by the small territorial fish. If damselfish are controlled by predatory fish as has been suggested (Hixon and Beets 1989), then the decline in predators (Fig. 0.5) could result in an increase in damselfish which could reduce herbivory and allow harmful macroalgae to increase.

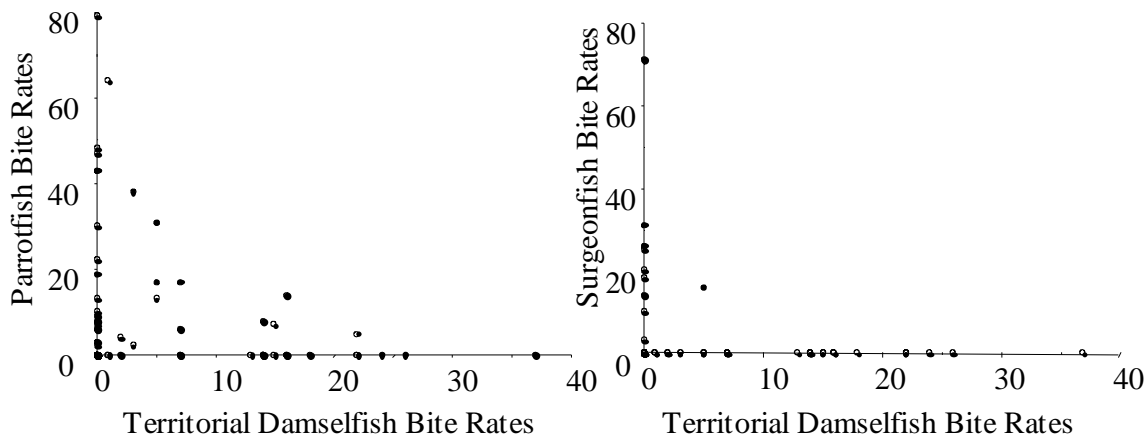


Figure 3.7. Bite rates from parrotfish and surgeonfish as a function of bite rates from damselfish.

When considering sites for potential marine reserve areas, there are several factors to consider. If goals are conservation-oriented (to protect a diverse and rich area) the species composition and diversity will be important factors. However, if management is directed toward a single species or group of marine organisms, then areas should be considered that are rich both in the species of concern and also habitat and food resources required by that organism. Reserves established with the goal of augmenting fisheries may have to consider placement more carefully in order to ensure that the reserve areas can be a source of spillover into fished areas. Many studies have

demonstrated that marine reserves can be effective in enhancing the density and biomass of fishes, and in some cases, have been successful in augmenting the fishing catches in nearby areas (Russ and Alcala, 1996). Baseline data such as we are providing here will provide an important barometer for the success of the reserves over time. The importance of public support for reserves cannot be underestimated, and baseline data gives the opportunity to evaluate the effectiveness and benefits of marine reserves over time.

References

Bohnsack, J.A., Harper, D.E. 1988. Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC 215:1-31.

Hixon, M. A. and Brostoff, W. N. 1983. Damselfish as keystone species in reverse: Intermediate disturbance and diversity of reef algae. *Science* 220: 511 – 513.

Hixon, M. A. and Beets, J. P. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44: 666 – 680.

Steneck, R. S. 1983 Quantifying herbivory on coral reefs: just scratching the surface and still biting off more than we al Reefs. *Symposia Series for Undersea Research*, Vol. 1.

Russ, G.R., Alcala, A.C. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132:1-9.

Chapter 4: Juvenile corals and seaweed

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Abstract

The density of juvenile corals is inversely correlated with the abundance of macroalgae. Bonaire has both high densities of newly recruited corals and low abundances of macroalgae. Coral reefs with little macroalgae have the highest recruitment potential for settling corals and thus the highest reef resilience following a disturbance.

Introduction

In a classic paper, Charles Birkeland (1977) observed that the recruitment of corals on the Caribbean coast of Panama was significantly higher than it was on the Pacific coast. Further, the pattern of settlement at these locations was greatest where algal growth was lowest. Other studies found that macroalgae can reduce coral recruitment, growth, fecundity and the cover of live coral tissue (Lewis 1986, Tanner 1995, Miller et al 1999). This is troubling because macroalgal abundance has increased on most reefs of the Caribbean (see the Executive Summary). If there is a general inverse relationship between macroalgal abundance and coral settlement densities, then whatever controls the abundance of algae is essentially controlling the recruitment of corals and the resilience of coral reefs.

Bonaire is known to have the lowest cover of macroalgae of any reef studied in the Caribbean (see Executive Summary; Kramer 2003). Does it also have higher than average rates of coral recruitment? To address this question, we quantified the density of newly settled corals on hard (non-living coral) substrata on the reefs of Bonaire. We also selected a reef complex in Akumal Mexico where identical measurements would allow us to compare settlement densities in habitats where macroalgae were abundant.

Methods:

At predetermined intervals (i.e. every 1 m), on a 10 m long transects, a 1/16 m² quadrat was placed. Within the quadrats the percent cover of macroalgae and density of juvenile corals, was recorded. A juvenile coral is one with a maximum diameter of less than 4 cm (Raimondi and Morse 2000). All sites shown in Figure 4.1 were surveyed.

Results:

The population density of newly settled corals was inversely correlated with the abundance of macroalgae. This held at both regions individually (Slingsby 2003) and when pooled across regions (Figure. 4.1).

Algal/juvenile coral interactions

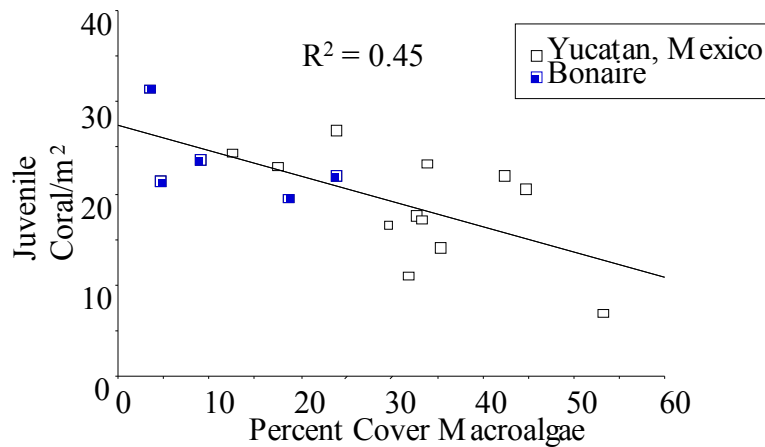


Figure 4.1. The density of juvenile corals as a function of percent cover of macroalgae. Data from a Yucatan reef in Mexico was pooled with the reefs of Bonaire.

While this cannot demonstrate that the absence of macroalgae will foster higher rates of coral recruitment, it is consistent with that hypothesis.

Discussion:

Jamaica is one of the best studied reef environments in the Caribbean. As late as the early 1980s it had a healthy coral reef with a high percent of live coral, a low abundance of macroalgae (Steneck 1994, Hughes 1994; Figure 0.3). Then during the 1980s macroalgae increased (probably due to insufficiently rates of grazing; Hughes 1994, Steneck 1994). That rise in macroalgae corresponded with a sharp decline in coral recruitment (Hughes 1999). The sudden mass mortality of the grazing sea urchin *Diadema antiillarum* in 1984 resulted in the most distinct increase in macroalgae throughout the Caribbean (Steneck 1994). In recent years this sea urchin population as begun to recover in Jamaica and as a result the macroalgal abundance has decline and juvenile coral densities have increased (Edmunds and Carpenter 2001).

Thus it appears that macroalgae is a regulator of the recruitment potential of the benthos for corals. Managers would do well to maintain reefs with low abundance of macroalgae in order to

keep coral recruitment high. High rates of coral recruitment are the best means of increasing the resilience of coral reefs following a disturbance.

References

Birkeland, C., 1977 The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits Proc. Third Int. Coral Reef Symposium 15-22

Edmunds, P. J. and R. C. Carpenter, 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. PNAS. 98: 5067-5071

Hughes, T. P. and J. E. Tanner, 2000. Recruitment failure, life histories and long-term decline of Caribbean Corals. Ecology. 81(8): 2250-2263

Lewis, S. M. 1986 The role of herbivorous fishes in the organization of a Caribbean reef community Ecological Monographs 56 183-200

Miller, M. W., Hay, M. E., Miller, S. L., Malone, D., Sotka, E. E. 1999. Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. Limn. Ocean. 44: 1847 – 1861.

Raimondi, P. T. and A. N. C. Morse, 2000. The Consequences of Complex Larval Behavior in a Coral. Ecol. 81: 3193-321

Chapter 5: Depth zonation of seaweed, nutrient concentrations and grazing

R. S. 1994

Is T.R. McClanahan¹ and S. Jones²

herbivore

loss more Coral Reef Conservation Project, Mombasa, Kenya

damaging the Wildlife Conservation Society, Bronx, NY

to reefs

than

Abstract

? Case

Hard coral, rugosity (reef complexity) and frondose algal cover were estimated along depth transects from 5 to 40 m on the leeward side of Bonaire in areas projected to be closed and Caribbean areas. We also measured inorganic nutrients of phosphorus and nitrogen and herbivory to determine the possible influence of these factors on benthic cover. There were systematic differences among sites in terms of benthic cover estimates and only weak relationships with depth for coral and bottom complexity. Frondose algae increased with depth, following zones, an intermediate depth zone of *Dictyota* and a deeper zone of *Lophora variegata*. Nutrient concentrations did not vary with depth or correlate with frondose algae or hard coral abundance. There were no differences among the study sites in terms of nutrient concentrations except for higher phosphates at Reef Scientifico and nitrates at Windsock, and the levels suggest some form of eutrophication. Herbivory was low for the *Lophora variegata* assay and restricted to the shallow depths of less than 20m. Frondose algae would appear to be more influenced by herbivory than inorganic nutrients.

m on

Global

Abstract

Coral

Nutrient influx in coral reefs from land sources is hypothesized to cause shifts in the balance of the coral reef community. With an anthropogenic increase of available nutrients in the waters, productivity of algae is expected to rise and increase algal cover and biomass unless herbivory can increase and compensate for the greater algal production. An increase in algal cover is expected to lead to a decline of live and healthy corals, and thus the decline of fish species associated with healthy coral reefs. The eutrophication of coral reefs has far reaching effects and is an essential consideration in management initiatives.

School of

When considering sites suitable to establish Fish Protected Areas, the general health of coral and reef areas should be documented and considered. Herbivore assays, nutrient analysis, and atmospheric cover and complexity measurements were conducted on each of the following four sites: Ric Oil Slick Leap, Reef Scientifico, Windsock, and The Plaza between April and May 2003 (see Science, Figure 0.4). We examined the relationship between coral cover, frondose algae, and herbivory contour complexity with depth and also measured inorganic nutrients and herbivory of *Micro* to determine the possible influences of these factors on each other.

Miami,

Florida.

Methods

Coral Cover and Complexity

A 10m chain transect was randomly placed perpendicular to the depth gradient in a straight line at 5m intervals to a maximum of 40m depth. The maximum depth was 40 m but less if the reef ended in a sand plan shallower than this depth. The length of the line that was intercepted by hard coral and frondose algae was measured to the nearest centimeter and the percentage cover of coral and alga were calculated as the fraction of this cover divided by the total length of the transect. Coral reef complexity (rugosity) was determined at each depth by pressing the chain along the bottom contour of the reef, measuring the distance that this 10 m line traveled along the bottom and dividing this distance into the 10 m length of the transect.

Nutrients

Water samples were collected along the reef contour at 10 cm above the reef surface in two 1 liter Ziploc plastic bags at 5 m depth intervals from the surface to 40m depth. The water samples were immediately returned to the laboratory and fully processed within five hours of collection. Water was analyzed for the following nutrients using Hach prepackaged reactants: phosphate (ascorbic acid method), nitrate (cadmium reduction method), nitrite (diazotization method), and ammonia (salicylate method). A Hach DR2400 spectrophotometer was used to determine light penetration after reaction with the chemicals. All glassware was thoroughly cleaned with a 10% hydrochloric solution and rinsed several times with the sample itself prior beginning the above-mentioned reactions.

Herbivore Assay

Several hundred blades of the frondose alga *Lobophora variegata* were collected at between 20 and 30 meters depth at Oil Slick Leap on the first day of the field expedition. Blades were collected of a standard size of between 10 and 20 cm² with round and entire margins on the blades edges. *L. variegata* blades were held in fresh saltwater and changed daily for no longer than four days. A single *L. variegata* blade was attached with a clothespin every meter on a 10m rope (N= 10 blades per assay). The ropes containing the assays were laid down at 5m intervals between 5 m and 30 m, and up to 40 m in the morning. Some reefs ended in a sand plain at 30 m and the assays were not laid at greater depths on these reefs. The assays were soaked for 6 hours before collection at which time each blade was examined for the presence of herbivore. If bite marks were evident on any particular blade, the percent consumed of each blade and the source of the herbivory (e.g. fish or urchin) was recorded. From this study the percentage of the assays bitten and consumed were estimated for each depth and site.

Results

Benthic cover

There are no differences in the cover of hard coral, benthic algae and rugosity or reef complexity between the four study sites. This is consistent with findings reported in Chapter 1 in this report. Hard coral cover increases with depth (F=5.6, $p < 0.023$) but the relationship is weak ($r^2 = 0.16$). There is no relationship with complexity and depth for the 5 to 40 m depth range studied. The frondose alga *Lobophora variegata* abundance increases with depth (F=7.6, $p < 0.01$) [Figure

5.1]) but the relationship is weak ($r^2 = 0.20$). *Lobophora* is most abundant at depths below 30 meters. The frondose alga *Dictyota* increases with depth but is most abundant at the intermediate depths between 15 and 30 meters.

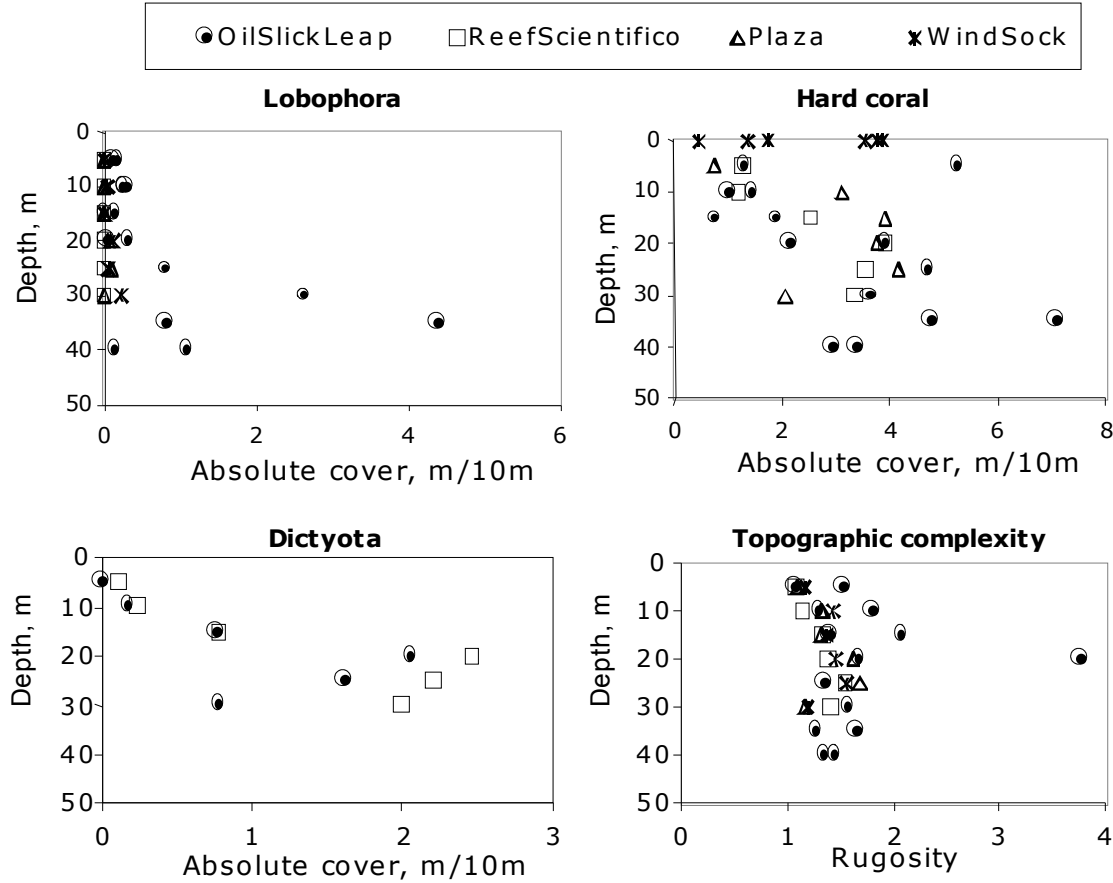


Figure 5.1. Cover of benthic macroalgae and rugosity measures at each of four sites

Nutrients

There are no significant relationships between depths and nutrient concentrations for any of the four measured nutrients (Figure 5.2). Ammonium (NH_3) is not different among sites. There are differences in the concentrations of other nutrients between study sites. Windsock had more nitrate NO_3 than all other sites but the other sites were not different from each other. Windsock and Reef Scientifico had the same concentrations of nitrite NO_2 and they were both higher than Plaza and Oil Slick sites, which did not differ. Phosphate, PO_4 is higher in Reef Scientifico than other sites and Windsock has higher phosphates than Oil Slick Leap. Consequently, Reef Scientifico and Windsock tend to be the most eutrophic, with high PO_4 at Reef Scientifico and high nitrogen at Windsock. There is no relationship between nutrient concentrations and frondose algae, coral cover or rugosity in the studied sites.

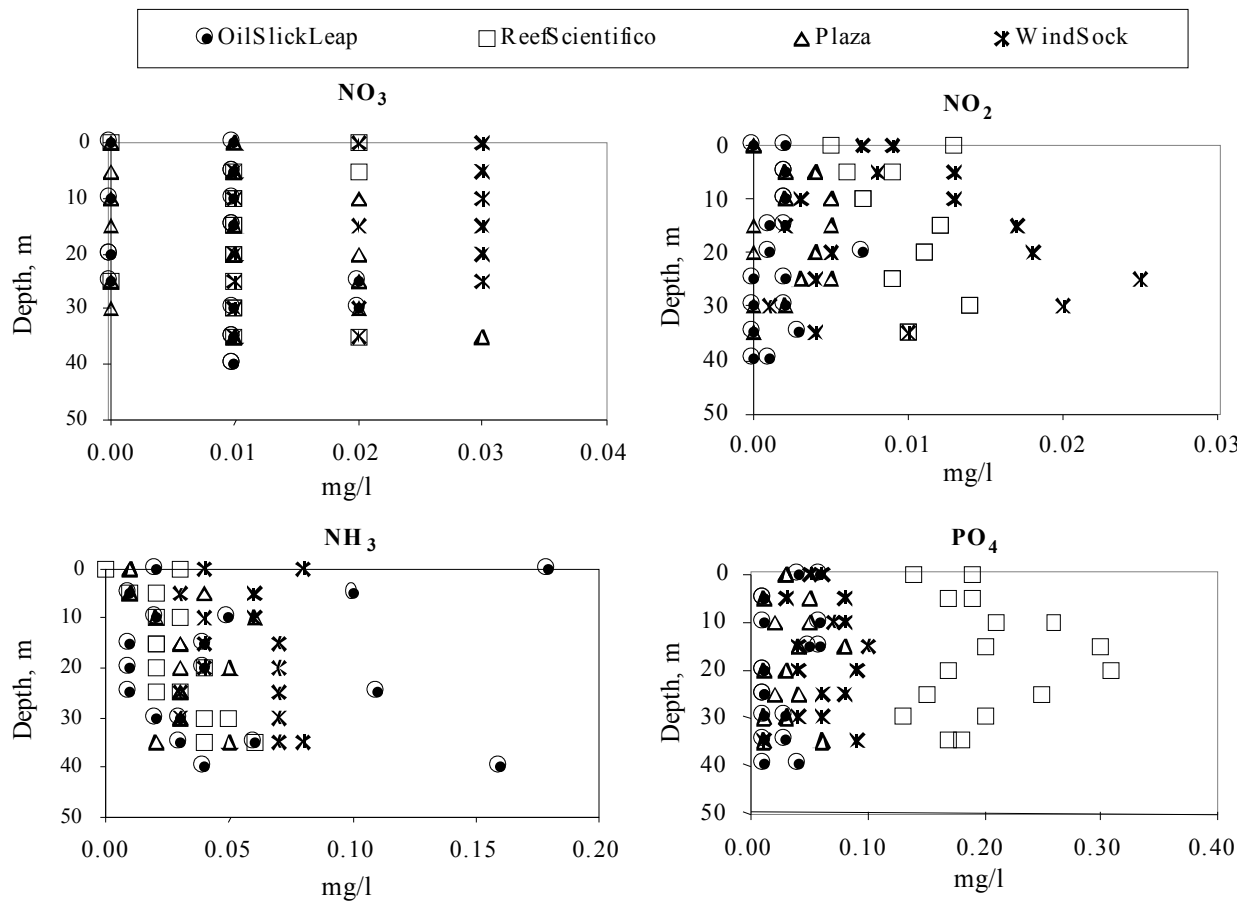


Figure 5.2 Nutrient concentrations at each of the four sites around Bonaire

Herbivory

Herbivory levels are low for this particular assay for the six-hour time period with only 7.4% fronds bitten and 1.4% of their surface area being eaten based on 231 assays (Figure 5.3). Herbivory was restricted to the top 20 meters of water depth and the percent bitten decreased with depth ($F=13.4$, $p < 0.0003$) but the relationship was quite variable ($r^2 = 0.05$). The amount eaten also decreased with depth ($F=7.2$, $p < 0.008$) but was, again, highly variable ($r^2 = 0.03$). There were no significant differences in the herbivory levels on this assay in the four studied sites. All bites were attributed to fish, largely parrotfish.

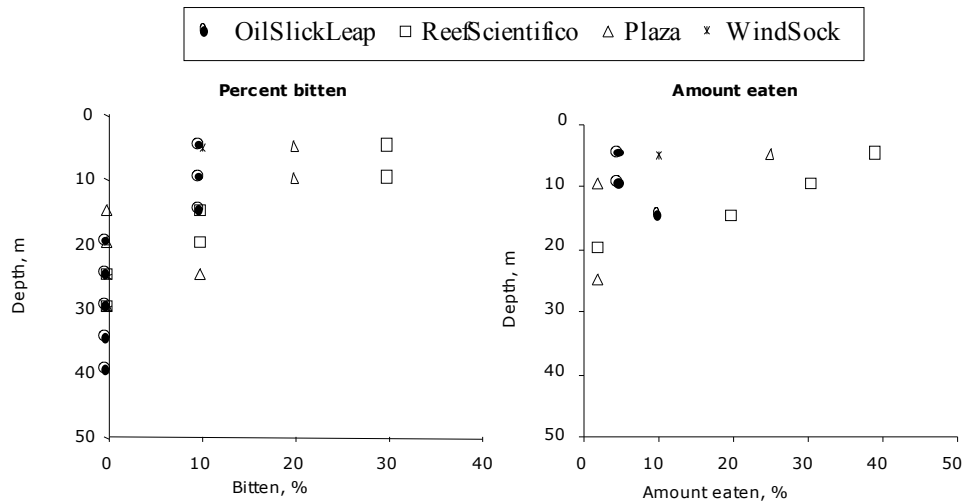


Figure 5.3. Amount bitten and eaten from the herbivory bioassay

Discussion

The lack of significant differences in benthic cover and rugosity suggest no reason to prefer one site to another for protective management based on these criteria. There is a need, however, to consider the diversity of the coral and other groups done in this study before the decision on closed areas is finalized. The similar initial conditions of the sites will allow for an easy test of the effects of protective management on these factors. Coral cover and rugosity are, however, likely to change slowly while frondose algae may change faster. Frondose algae may be expected to change in the course of 100 days while coral cover would require 2 or more years before any changes are expected upon implementation of the MPA.

There are differences in nutrient concentrations among sites but it is generally balanced in that one potentially protected (Reef Scientifico) and one control site (Windsock) have the higher nutrient concentrations, although Reef Scientifico differs most in terms of the PO_4 . The average level of nutrients for most of these reefs is typical for coral reefs based on comparisons with other studies. The two exceptions are the phosphates at Reef Scientifico and nitrates at Windsock, which are well above average and suggest some eutrophication. More studies over time and space in these sites may be required to determine how persistent these nutrients are and their source. The usefulness of this baseline data extends beyond determining the effectiveness of the proposed FPAs. It is a monitoring tool for other management initiatives such as development of the waste treatment facilities, nearshore development, and adoption of ecologically friendly landscaping.

Frondose algae would appear to be controlled by herbivory and not nutrients or light in these sites. Frondose algae cover increases with depth while herbivory decreases with depth.

Herbivorous fish were also found to not differ significantly between sites (Chapter 3). The findings here are consistent with others that found there is no significant difference of macroalgal abundance between survey sites (Chapter 1), maintaining the incidence of this pattern. There is no relationship with nutrient concentrations with depth and with frondose algal cover. There appears to be a zonation pattern with depth for the frondose algae, with *Dictyota* dominant in the intermediate 20 to 30 meter and *Lobophora* dominating the deeper 30 to 40 meter depths. It may be useful to use a more herbivore susceptible assay, such as *Padina*, in future herbivory assay studies, as *Lobophora* may be too resistant to herbivory for short-term experiments. Repeating this study with different assays or over a longer time is an additional priority prior to establishing the FPAs. Sampling the nutrients while monitoring temperature over a longer time scale would help determine if the differences between sites are of natural fluxuation or are in fact of anthropogenic sources.

Chapter 6: The fishing community, marine protected areas and fish protected areas

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Abstract

Fisheries management in coral reef environments can be a difficult task; there are typically many species involved, a large area of critical habitat, and multiple stakeholders interested in the development of policies. Designating a zone as a Marine Protected Area (MPA), an area in which fishing is restricted, can help to resolve these issues. There is scientific evidence that MPAs increase fish biomass and diversity both within and around the protected area. The process of designing and implementing MPAs should involve input from all of the stakeholders, but especially the fishing community who may more directly rely on the resources for their livelihoods or sustenance. Some of the most successfully managed coral reefs are due to marine tenure in which the fishing community takes responsibility for their fishing grounds through active involvement. In deciding to establish a fish protected area in Bonaire, these factors, along with evaluating the socioeconomic impact of the Fish Protected Areas, should be incorporated. The goal of the collaboration among the fishing community, the Marine Park, and the researchers is to create reefs that benefit everyone in Bonaire.

Introduction

Areas restrictive to fishing, generically defined as Marine Protected Areas (MPAs), have been established all over the world as a means of protecting and enhancing fish stocks. These areas can be large or small in scale, and may be established as isolated individual sites or as networks. The rules governing extraction from a MPA vary widely; such rules can include seasonal restrictions, gear restrictions, access restrictions, or any combinations of these rules. The most restrictive MPAs are “no-take” zones, where no extraction of any species is allowed under any circumstances. Several tangible benefits of MPAs have been documented in many areas, under various local circumstances. These benefits include increased biomass and species richness, “spillover effects” to adjacent areas, and the provision of benchmark sites that provide fisheries managers with a baseline by which to measure the effectiveness of various policies. The design of a MPA can be tailored to the needs and constraints of the local area. Size, biological and physical characteristics, rules for use, socioeconomic impact, funding structure, and enforcement issues should all be taken into consideration to provide for a successful area of protection.

Effectiveness of MPAs

Several studies on the impact of MPAs have demonstrated an improvement in the biomass and diversity of the fish stocks within the protected areas (Polunin and Roberts, 1993; Jennings et al. 1996; Luttinger, 1997; McClanahan et al. 1999). In the Seychelles, a study was conducted on

four different marine parks, ranging in size from about 1 to 11 km², all of which have been under protection since at least 1979. The regulations for these areas state specifically that reef habitats must not be damaged, and that fishes must not be captured; however, differences in the enforcement of these rules were evident. Two of the sites, Cousin Island Nature Reserve and Sainte Anne Marine National Park, were effectively protected, while the other sites, Baie Ternay Marine National Park and Curieuse Marine National Park, suffered from little enforcement and heavy poaching, in addition to subsistence fishing by locals. In practical terms, the last two sites can be considered unprotected, or poorly protected at best. Measurements of the mean biomass of sixteen families of diurnally active, reef-associated fishes showed a significant difference between the two effectively protected sites and the two poorly protected sites. Figure 6.1 compares areas of similar habitat (granitic reef), and it should also be noted that both of the well-protected sites were closer to the poorly protected sites than to each other, strongly suggesting that the enforced no-take rules are responsible for the higher biomass, rather than geographical fish distribution or recruitment (Jennings et al. 1996).

In southern Kenya and northern Tanzania, similar studies have been conducted comparing the fish diversity and biomass of protected patch reef and back reef areas with fished reef areas. McClanahan et al. (1999) determined that protected sites had 3.5 times the biomass of unprotected sites, and there was a 34-95% reduction in the numbers of species per transect in unprotected areas compared to protected areas. Figure 6.2 illustrates the difference in species richness for several major families at protected versus unprotected sites (McClanahan et al. 1999).

Spillover Effects

Some studies of existing MPAs have identified a “spillover effect”, by which the fish stocks in adjacent unprotected areas are enhanced (McClanahan and Mangi, 2000; Roberts et al. 2001). After a seven-year study at the Mombasa Marine Park and Mombasa Marine Reserve in Kenya, McClanahan and Mangi (2000) determined that there was a measurable spillover effect from the more protected southern area of the park, comparable to that of naturally protected deep windward reef edge. Total catch, mean size, and number of species of fish were measured at the north and south end of the park, and plotted against the distance from the park (Figure 6.3). At the north end, the reef is highly accessible to fishers and heavy use of pull seines is practiced. Pull seining is a highly effective method of removing fish of all sizes, and the results of the study may indicate that this gear reduces the evidence of spillover to a very small area, of perhaps only a few hundred meters from the border of the park. In the south, fishing gear is restricted to less effective “traditional” methods, including traps and hand lines, and the use of pull seines is banned. In this area, the spillover effect may extend as far as 2 km from the park border. (Figure 6.3, McClanahan and Mangi, 2000).

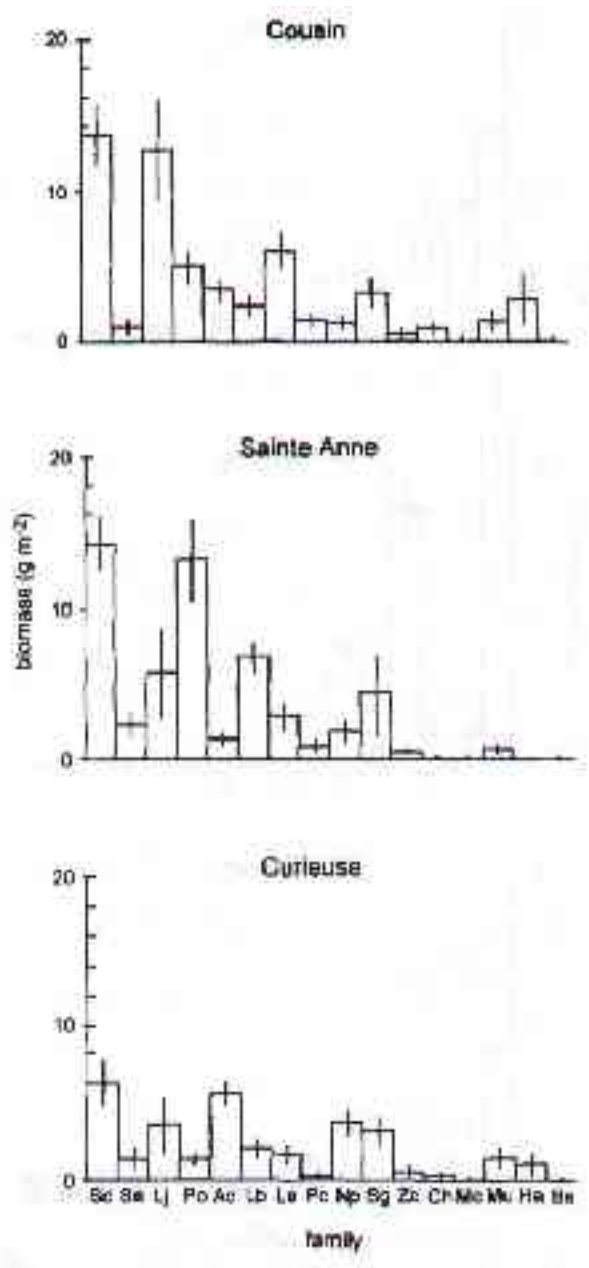


Figure 6.1. Mean biomass (\pm SE) of 16 families of diurnally active reef-associated fishes. Sc, Scaridae; Se, Serranidae; Lj, Lutjanidae; Po, Pomacentridae; Ac, Acanthuridae; Lb, Labridae; Le, Lethrinidae; Pc, Pomacanthidae; Np, Nemipteridae; Sg, Siganidae; Zc, Zanclidae; Ch, Chaetodontidae; Mc, Monacanthidae; Mu, Mullidae; Ha, Haemulidae; Bs, Balistidae. (Jennings et al. 1996).

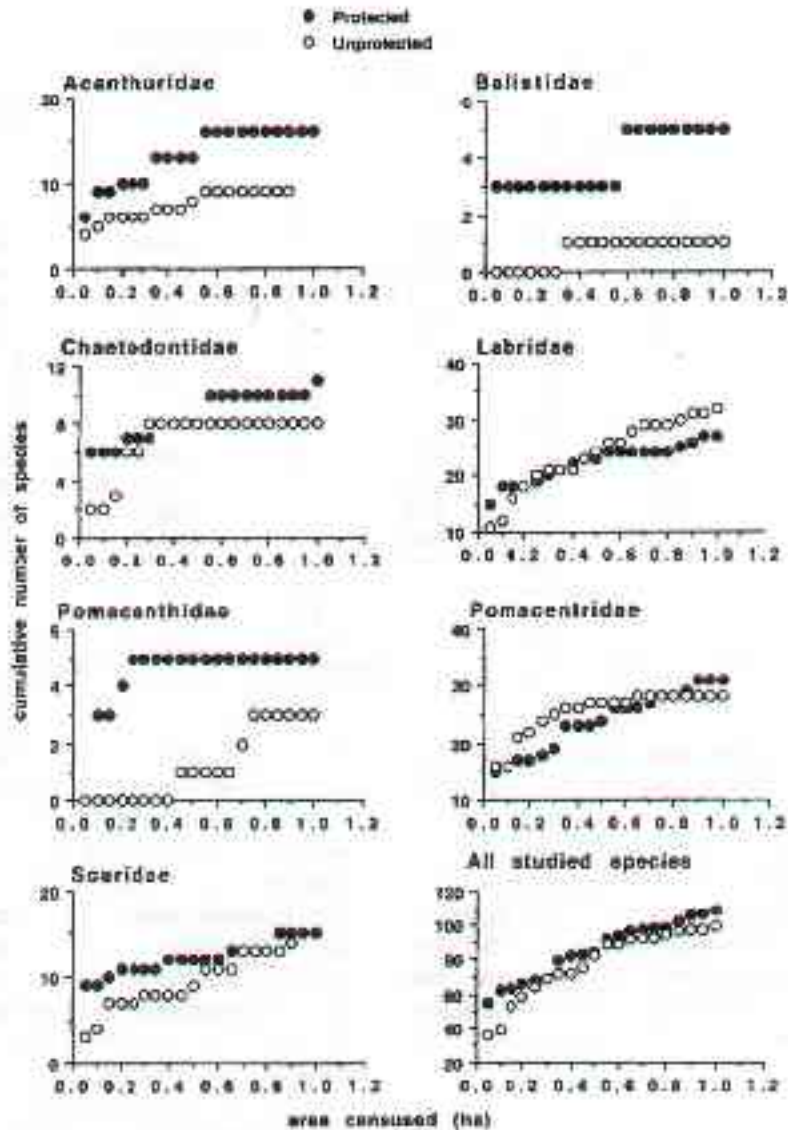


Figure 6.2. Species-area relationships comparing protected and unprotected reefs.(McClanahan et al. 1999).

Baseline Studies

Although any level of protection seems to result in measurable benefits in biomass and spillover of harvestable species of fish, no-take MPAs can provide the additional benefit of creating valuable benchmark sites for baseline data on fish stocks, allowing fisheries managers to separate human extractive impacts from natural oceanographic and ecological effects. Both single-species and multispecies models for management rely on a time series of survey data and catch-at-age

data. MPAs can be unexploited areas, against which fisheries managers can measure population changes and improve estimates of population parameters used in models (Murray et al. 1999).

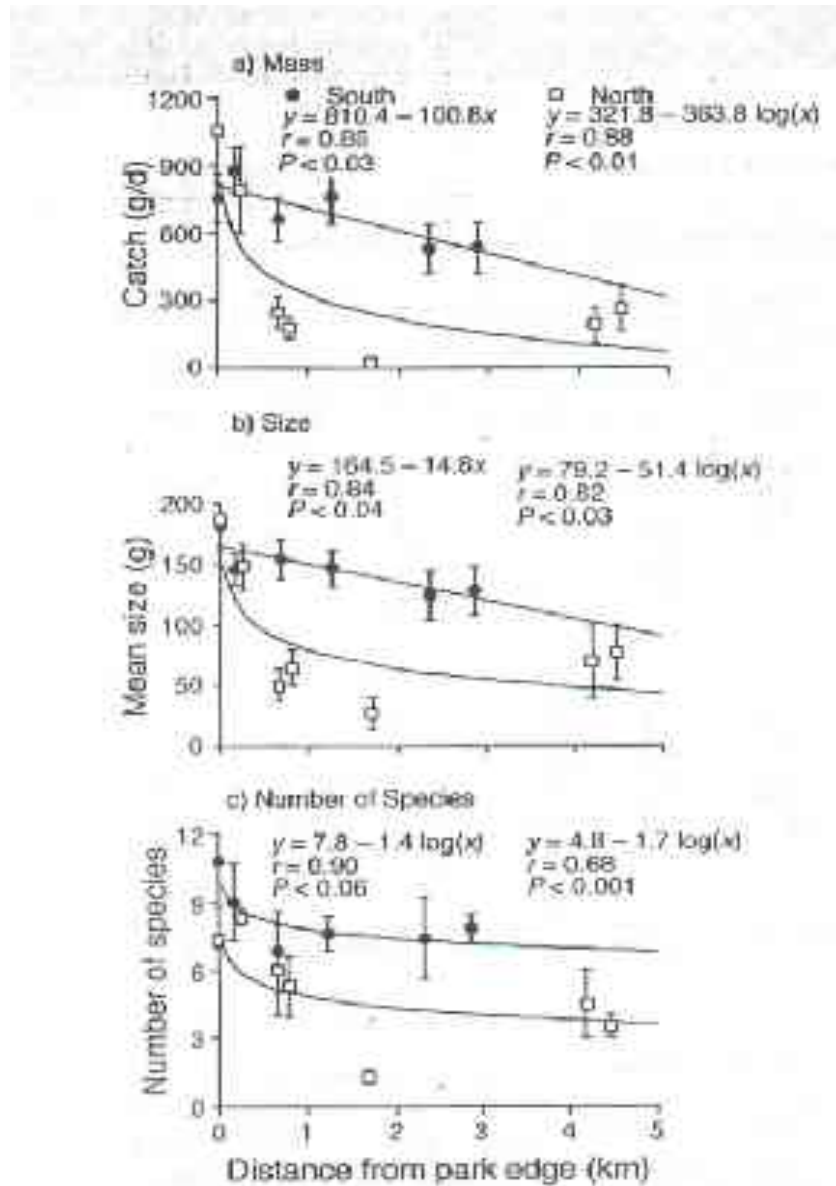


Figure 6.3. Total catch, mean size of fish, and number of species over a 14 day period as a function of the distance away from the park border. (McClanahan & Mungi 2000).

The Fishing Community and Fish Protected Areas

Marine Tenure and Community-Based Management

With evidence that MPAs, particularly no-take MPAs, are a successful tool in protecting and enhancing coral reef fisheries for both managers and fishermen (Jennings et al., 1996; Luttinger, 1997; McClanahan et al., 1999; McClanahan and Mungi, 2000), the question then becomes, what

is the process of implementing a MPA that will have some assurance of being successful? Resistance from the community to implementation of MPAs often arises when the goals and benefits (both economic and social) are not well articulated by those promoting their use and thus become difficult for the resource users to understand (Murray et al., 1999). With the key impediments to implementing marine reserves and protected areas being political in nature (Ogden, 1997), the success of the reserves will be dependant on the support and involvement with the stakeholders of the resource, especially the fishermen when no-take MPAs are being considered.

Recently, there has been a resurgence of community-based marine resource management (Birkeland, 1997b; Luttinger, 1997; WGESC, 1999; Brown et al., 2001; Johannes, 2002). Johannes (2002) believes that the success of many Oceania fisheries (isolated islands on which people depend on reef resources) is due in large part to community-based marine resource management. In such an arrangement, “customary marine tenure”, or the right to control access to and actions on one’s traditional nearshore fishing grounds, plays a crucial role. Customary marine tenure provides resource users the incentive to create and enforce rules that benefit and conserve the resource. In order to have sustainable coral reef fisheries, it has been suggested that it is essential that the resource users themselves have training, government support, and explicit legal authority to manage their resource (Birkeland, 1997b). Even the United States, notorious for its top-down style of resource management, is choosing to involve the relevant stakeholders of its coral reefs in the preparation of coral reef resource management plans (WGESC, 1999).

Scientific and ecological goals of the reef should be integrated with socioeconomic needs. The trade-off from fishing to tourism for some coral reef communities can be very large; therefore, consideration has to be given to how best preserve coral reefs communities in addition to maximizing commerce and income. In Bermuda, the Government offered large payments and gear compensations to fishermen in order to close the coral reefs to fishing in an attempt to stop reef deterioration. These same fishermen were then encouraged to use their boats for more lucrative endeavors in tourism (Birkeland, 1997a).

Implementing Fish Protection Areas in Bonaire: A Community Approach

Consideration is being given to establish no-take MPAs for the reefs in Bonaire. Elsmarie Beukenboom, the Director of STINAPA/Bonaire National Marine Park, believes that it is very important to work closely with the fishermen in establishing these no-take MPAs. Otherwise she does not see a successful implementation occurring. One of her first concerns is trying to erase the negative connotation of the “no-take” name for fishermen. Therefore, the name “fish protected” areas are being used instead of no-take MPAs. The Director also felt that the government of Bonaire employees should approach fishermen to discuss the implementation Fish Protected Areas, since this is their island and they have everything to gain or lose from the proposed no-take areas.

When interviewed by Ms. Beukenboom, most fishermen in Bonaire characterized fishing as becoming poorer over the past few years (meeting March 2003). There was general agreement among the fishermen that the number of fish, particularly large predatory fish, have been declining for a number of years. Some of the fishermen blamed the decline on the increase in divers and dive boats for scaring away the fish (Beukenboom, March 2003), however, most of

the fishermen did believe that if an area is not fished the fish will come back. The idea of Fish Protected Areas was presented to the fishermen and they agreed it is logical that if the areas are closed to fishing, fish number and size should increase, and eventually create a spillover effect (Beukenboom, March 2003). The importance of fostering an understanding with fishing community regarding the goals and benefits of the fish protected areas is crucial, because there will never be enough money to enforce a fish protected area if the fishing community is strongly opposed to it.

In the March 2003 discussion of what areas to make into fish protected areas, the fishermen and STINAPA considered closing the sites from Divi to Plaza and Playa Lechi to Black Durgon. The acceptance of these areas by the fishermen was partially due to the ongoing conflicts between the hotel dive operations and fishermen at these sites. One of the thoughts behind the selection of those areas by STINAPA was that the closing would help relieve this conflict. In addition, the hotel dive operators—the other stakeholder in the process—already want fishing to stop. In making these areas Fish Protected Areas, the hotel dive operators will closely watch fishing activities in front of their hotels. This will relieve some of the enforcement responsibilities from the already overextended STINAPA wardens.

Fish Protected Areas in Bonaire: A Socio-Economic Overview

Of the areas chosen for fishing closure fewer than 10 fishermen heavily fish those areas (Beukenboom, 2003). In fact, there are only about 20-30 commercial fishermen in Bonaire—only 5-10 subsist solely from fishing—and none of them solely fish the reefs proposed for closure (Beukenboom, pers. comm. 2003; DeMeyer, pers. comm. 2003). In contrast, there are 14 dive operations in Bonaire that employ about 100-120 people that serve around 60,000 visitors annually (Bonaire Home Page, 2003; DeMeyer, pers. comm. 2003). In 2000, an estimated \$34 million in gross dive-generated revenue was generated for Bonaire’s economy (DeMeyer, pers. comm. 2003). Economically, fish protected areas are valuable for everyone involved (Table 1).

Table 1. Value of fish protected areas

<i>For Fishermen</i>	<i>The less than 10 fishermen displaced from fishing in these areas will eventually profit from the increase in fish from spill-over.</i>
<i>For Divers</i>	<i>Divers are able to see bigger and more abundant fish.</i>
<i>For Bonaire</i>	<i>Fish are worth more when they are left alive than when they are extracted. For example, groupers are worth 20 times more when they are not extracted (Sala et al., 2001).</i>
<i>An increase in eco-tourism equals an increase in island revenue.</i>	

Fish Protected Areas in Bonaire: The Future

Additional meetings with fishermen are scheduled, particularly with those fishermen who are most impacted by the fish protected areas, to give them the opportunity to voice their opinions. One of the next steps is getting the establishment of Fish Protected Areas passed through the government, and the addition of the Marine Ordinance and strategic plan, which needs to be created in order to implement a Fish Protected Area (Schuit, pers. comm. 2003).

Thought should be given to how to assist those fishermen directly impacted by the proposed closures. Some ideas that were casually discussed were gasoline allowances to minimize the financial burden of displacement and asking the hotels to contribute money so those fishermen can purchase gear appropriate for pelagic fishing.

Continued study of the fish communities in Bonaire should allow fishermen and park managers to observe how the fish protected areas are progressing. Once or twice a year after the establishment of the fish protected areas a research team will come back to monitor the areas and collect information that will be shared with STINAPA and the fishing community. Working together, the fishing community, STINAPA, and the researchers can create conditions that benefit everyone in Bonaire.

References

- Beukenboom, C. E. 2003. Report on meetings held with fishing community on Thursday, March 13, 2003.
- Birkeland, C. 1997a. Symbiosis, fisheries and economic development on coral reefs. *Trends in Ecology and Evolution* 12(9): 364-366.
- Birkeland, C. 1997b. Implications for resource management. Pages 411-435. *In* Life and death of coral reefs. Editor C. Birkeland. Chapman & Hall. NY.
- Bonaire Home Page. 2003. www.geographia.com/bonaire.
- Brown, K., Adger, W.N., Tompkins, E., Bacon, P., Shim, D., Young, K. 2001. Trade-off analysis for marine protected area management. *Ecological Economics* 37:417-434.
- DeMeyer, Kali. 2003. Personal communication with creator of Bonaire National Marine Park and current head of the Bonaire branch office of The Coral Reef Alliance on April, 4 2003.
- Jennings, S., Marshall, S.S., Polunin, N.V.C. 1996. Seychelles' marine protected areas: comparative structure and status of reef fish communities. *Biological Conservation* 75: 201-209.
- Johannes, R.E. 2002. The renaissance of community-based marine resource management in Oceania. *Annual Review of Ecology and Systematics* .33: 317-340.
- Luttinger, N. 1997. Community-based coral reef conservation in the Bay Islands of Honduras. *Ocean and Coastal Management* 36(1-3):11-22.
- McClanahan, T.R., Muthiga, N.A., Kamukuru, A.T., Machano, H., Kiambo, R.W. 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biological Conservation* 89: 161-182.

McClanahan, T.R. and Mangi, S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* 10(6): 1792-1805.

Murray, S.N., Ambrose, R.F., Bohnsack, J.A., Botsford, L.W., Carr, M.H., Davis, G.E., Dayton, P.K., Gotshall, D., Gunderson, D.R., Hixon, M.A., Lubchenco, J., Mangel, M. MacCall, A., McArdle, D.A. Ogden, J.C., Roughgarden, J., Starr, R.M, Tegner, M.J., Yoklavich, M. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries Management* 24(11):11-25.

Ogden, J.C. 1997. Marine managers look upstream for connections. *Science* 278:1414-1415.

Polunin, N.V.C., Roberts, C.M.. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* (100): 167-176.

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R. 2001. Effects of marinereserves on adjacent fisheries. *Science* (294):1920-1923.

Rodriguez-Martinez, R., Ortiz, L.M. 1999. Coral reef education in schools of Quintana Roo, Mexico. *Ocean and Coastal Management* 42:1061-1068.

Sala, E., Ballesteros, E., Starr, R.M. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries*: 23-30.

WGESC (Working Group on Ecosystem Science and Conservation). 1999. Coral reef Protected areas: a guide for management. A presentation to the U.S. Coral Reef Task Force.

Chapter 7: Diver tourists: the aesthetic and economic value of fish protected areas

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Abstract

Marine Protected Areas (MPAs) offer numerous benefits and they are being established worldwide as a means of halting or reversing the degradation of marine ecosystems. Tropical MPAs may promote conditions that are attractive to dive tourists, but a systematic basis for assessing their effectiveness has been lacking. We interviewed 30 dive tourists in Bonaire to ascertain which reef attributes were most attractive to them. The two prime attributes were abundance of fish and corals. Divers were asked to compare the Bonaire reefs to those they had dived elsewhere. More than half considered the reefs in Bonaire superior to other locations. These findings, along with case studies in New Zealand, elsewhere in the Netherlands Antilles, and Jamaica, strongly suggest that management measures that enhance these attributes increase the attractiveness to dive tourists and thus could be economically important for Bonaire.

Introduction

Marine and terrestrial environments around the world are threatened by activities ranging from over-harvesting and habitat destruction to regional modification of food web relationships and climate. Marine Protected Areas are created for many reasons and in the Caribbean, but perhaps the greatest benefits are derived from tourism (Dixon et al. 1995). Bonaire is consistently ranked as the finest snorkeling and [scuba diving](#) destination in the Caribbean. Its entire coast is lined by narrow fringing coral reefs and a double reef complex is present and accessible in most of the southern sites on Bonaire's leeward side (Van Veghel 1997). There are 86 listed dive sites and 20 dive operations. Bonaire has a relatively arid climate and frequently calm seas that keep many reefs clear and diveable year round. Water temperatures average 78-84°F, with visibility often averaging over 30m. Because of these attributes, it is an ideal location for divers, ecotourists, and underwater photographers.

Bonaire's fish population is among the most diverse in the Caribbean. Nearly 2,000 fish surveys conducted there between December 1993 and July 1999 reported a total of 362 species from 77 sites surveyed (Pattengill- Semmens 2002). Recent research has found that Bonaire currently has relatively high coral cover and relatively low macroalgal abundance, which are attributes of a healthy reef (Steneck 2003). (see Chapter 1)

There has not been a great amount of research on whether MPAs are beneficial to the dive-tourism industry. If reef condition or particular fish fauna improve within a protected area, then it is possible that these locations would become more attractive to divers. The goal of this

investigation was to ascertain which reef attributes are most attractive to dive tourists and to determine how they feel reefs of Bonaire compare to those elsewhere. This study will also explore case studies in New Zealand, elsewhere in the Netherlands Antilles, and Jamaica to consider how marine reserves have influenced the attributes found to be most attractive to dive tourists as well as the socioeconomic impacts of MPAs.

Methods

Diver Preference Survey

The preferences of divers for important reef attributes were surveyed by interviewing tourist divers at four dive sites in Bonaire, Netherlands Antilles. Dive sites sampled included Windsock, Plaza, Habitat, and Karpata. Divers were selected at random as they emerged from the water. They were asked a series of questions about impressions of what they had seen. In total, 30 divers were interviewed during March 11-15, 2003. The principle question was ‘what are the most important features of the reef which you like to see on a dive?’ Respondent’s answers were categorized into nine categories: “fish abundance”, “colorful fish”, “large fish”, “coral abundance”, “coral color”, “unspoiled reef”, “clear water”, “other animals”, and “other”. Divers were allowed to list multiple attributes. In total, 67 replies were reported. Participants were also asked how Bonaire’s reefs compared to other areas where they had dived. Reefs were rated as “better”, “average”, “below average” and “different/does not compare”.

Data Analysis

The total number of responses for each category was divided by 67 to yield a percentage. Finally, a pie chart was created to illustrate the varied levels of the significance of different reef attributes to dive tourists. The same method was used to interpret reef comparison responses.

Results

“Fish abundance” was most frequently described by divers as the most important attribute of a reef (Figure 7.1). This factor accounted for 28% of responses. “Coral abundance” ranked second earning 16% of answers followed by “coral color” and “colorful fish” with 14% each. The remaining attributes “unspoiled reef”, “clear water”, “other animals”, and “other” each earned less than 10% of responses.

When divers compared quality of reefs dived that day to other sites, the majority felt that Bonaire’s reefs were superior to those dived in other parts of the world. They rated Bonaire’s reefs ‘better’ 57% of the time (Figure 7.2). Only 7% of divers considered Bonaire’s reefs ‘below average.’ The remaining participants felt that the reefs were ‘average’ (23%) or ‘different/could not compare’ (13%).

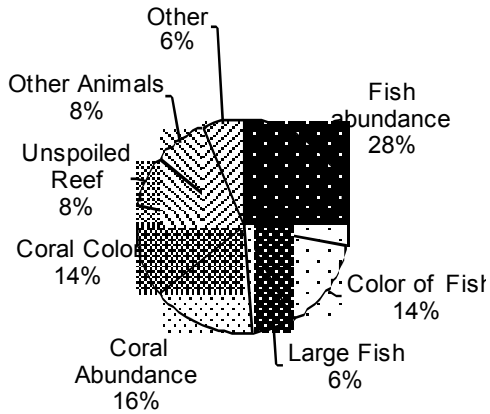


Figure 7.1. Most important reef attributes to divers on Bonaire's reefs

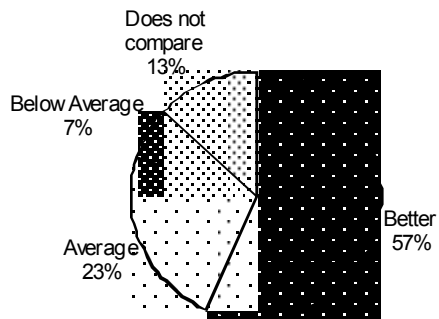


Figure 7.2. Divers' comparison of Bonaire's reefs to other reefs

Discussion

The results of the diver preference survey show that fish and coral abundance were the most important aspects of Bonaire's coral reefs to divers. These findings suggest that management measures enhancing these attributes would increase the attractiveness of areas to dive tourists. Because of the effort needed to implement marine reserves, there is a great social pressure to justify their implementation by considering the economic value of such a program. These

benefits may be better understood by considering the effectiveness of other marine reserves in increasing fish and coral abundance and concentrating on the way dive tourism in these areas has been affected.

There is considerable evidence that protecting areas from fishing leads to rapid increases in abundance, size, biomass, and diversity of animals (Roberts and Hawkins, 2000). Studies comparing protected and fished coral-reef communities of Saba Marine Park in the Netherlands Antilles found that after four years of protection, the abundance of fish susceptible to exploitation increased (Polunin and Roberts, 1993). The length and size of many species was also greater in the protected areas. Habitat data indicated that fishing effects are likely to have been the key factor in the differences observed between areas.

Economic and social benefits of marine protected areas have been documented. For example a marine reserve was established in Leigh, New Zealand in 1977... Ten years after its establishment, the tourist visitation rate had increased (Ballantine, 1987). By 1987, the Leigh reserve had almost complete support of the community due to both improved commercial fishing and tourism. A visitor survey revealed most individuals had come to the area because of its reserve status and they reported passing up other coastal areas where fishing was permitted in favor of visiting the protected reefs of Leigh. Many tourists also expressed support of setting up more marine reserves with similar no-take rules (Ballantine, 1987). The economic benefits of the Leigh marine reserve led to considerable political and public pressure to create many more such reserves.

Williams and Polunin (2000) studied whether high levels of fishing in Jamaica may reduce the appeal of its coral reefs. They concluded that, “where it can be achieved, total prohibition of fishing might be necessary for an area to achieve maximum appeal to divers.” Areas where protection from fishing is enforced remain attractive to tourist divers while unprotected areas have suffered dramatic reduction in fish biomass and diversity that reduce the aesthetic value for tourists (Williams and Polunin 2000).

Dive tourism is the foundation of Bonaire’s economy ([International Coral Reef Initiative 2003](#)) and Bonaire received about \$34,000,000 in diving revenue for the year 2001 (Kalli DeMeyer, personal communication 2003). However, the cost of sustainable management requires funding (McClanahan 1999). The Bonaire Marine Park authorities pioneered the implementation of a diver’s admission fee of \$10.00 that has allowed the Marine Park to become self-sufficient in covering its operational costs. Most divers we interviewed in past studies have been supportive of this fee because they believe it contributes to maintaining a healthy area to dive (Tourism Corporation of Bonaire 2003).

We considered how representative our surveys of dive tourists were likely to be of dive tourists generally. Although our sample size was limited, the respondents represented a wide range of ages and countries. Compared to the findings of dive tourist surveys in Jamaica, the same attributes - fish and coral abundance - were determined to have the highest significance to divers (Williams and Polunin 2000).

If no-take reefs in Bonaire respond the way others in the Caribbean have, then at the very least, large charismatic fish such as groupers that are currently targeted by fishers are likely to become more abundant and to attain greater sizes (Roberts et al. 2001). Closed areas with large charismatic fish may create a diving attraction, which has the potential to generate greater and more sustainable income than fishing. The findings of our diver survey in Bonaire suggest that Fish Protected Area management measures to enhance fish would increase the attractiveness of areas to dive tourists and possibly generate more revenue in the future.

References

Ballantine, W.J. 1987. "Marine Reserves: Lessons from New Zealand." *Progress in Underwater Science* 13:1-14

Dixon, J.A., Fallon, Scura, L. and van't Hof, T. 1995. Ecology and microeconomics as 'joint products': the Bonaire Marine Park in the Caribbean. In: *Biodiversity Conservation*, Perrings, C.A (ed), pp. 127-145. Amsterdam, Netherlands: Kluwer.

[International Coral Reef Initiative](http://www.icran.org/SITES/doc/bmp.pdf). 2003. Bonaire Marine Park [Online]. Available at <http://www.icran.org/SITES/doc/bmp.pdf>.

Pattengill-Semmens, C.V. 2002. The reef fish assemblage of Bonaire Marine Park: an analysis of REEF Fish Survey Project data. *Proceedings 53rd Gulf and Caribbean Fisheries Institute* 53:591-605

Polunin, N.V.C., Roberts, C.M. 1993. Greater Biomass and Value of Target Coral-Reef Fishes in Two Small Caribbean Marine Reserves. *Marine Ecology Progress Series* 100:167-176

Reef Environmental Education Foundation. 2003. Project Statistics Survey [Online]. Available at http://www.reef.org/data/GCFI_Bonaire.pdf

Roberts, Callum M. and Hawkins, Julie P. 2000. Fully-protected Marine Reserves: a guide. WWF Endangered Species Campaign, USA and Environment Department, University of York, YO10 5DD, UK

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R. 2001. Effects of Marine Reserves on adjacent fisheries. *Science* 294:1920-1923.

Tourism Corporation of Bonaire 2003. Bonaire: Dutch Caribbean [Online]. Available at <http://www.interknowledge.com/bonaire/>

Van Veghel, M. L. J. 1997. A field guide to the reefs of Curacao and Bonaire. 8th

International Coral Reef Symposium. 1: 223-234

Williams, I.D., Polunin, N.V.C. 2000. "Differences Between Protected and Unprotected Reefs of the Western Caribbean in Attributes Preferred by Dive Tourists." *Environmental Conservation*: 27(4):382-391

Appendix A. Average density, fork length, and biomass of herbivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
All Herbivores (w/o <i>S. partitus</i>)	73.00	30.37			6.32	3.14
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o <i>S. partitus</i>)	43.50	22.90			2.17	0.60
Scarid	26.75	10.69			9.78	5.38
Acanthurids	2.75	3.69			0.69	0.96
Don's Habitat - 10 m						
<i>Acanthurus bahianus</i>	0.67	1.03	20	4.24	0.13	0.22
<i>Acanthurus chirurgus</i>	0.00	0.00			0.00	0.00
<i>Acanthurus coeruleus</i>	10.00	17.89	19.77	2.69	2.05	4.27
<i>Kyphosus sectatrix</i>	0.00	0.00			0.00	0.00
<i>Scarus croicensis/iserti</i>	1.33	2.42	11.25	4.5	0.05	0.08
<i>Scarus taeniopterus</i>	9.00	3.95	14.19	4.45	0.48	0.23
<i>Scarus vetula</i>	5.33	3.27	30.13	4.56	3.00	1.47
<i>Sparisoma aurofrenatum</i>	3.00	2.10	18.44	1.74	0.32	0.21
<i>Sparisoma chrysopterus</i>	0.00	0.00			0.00	0.00
<i>Sparisoma viride</i>	4.33	4.08	28.38	7.51	2.20	1.98
<i>Microspathadon chrysurus</i>	0.67	1.03	15	0.00	0.07	0.10
<i>Stegastes diencaeus</i>	11.67	9.91	7.6	1.31	0.16	0.14
<i>Stegastes dorsopunicans</i>	1.33	3.27	8	2.16	0.02	0.05
<i>Stegastes leucostictus</i>	0.00	0.00			0.00	0.00
<i>Stegastes planifrons</i>	21.67	10.15	6.77	1.32	0.21	0.10
<i>Stegastes variabilis</i>	1.00	2.45	5.33	0.58	0.00	0.01
<i>Stegastes partitus</i>	124.33	35.52	4.86	1	0.37	0.10
All Herbivores (w/o <i>S. partitus</i>)	70.00	21.61			9.05	4.57
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o <i>S. partitus</i>)	36.33	13.35			1.67	0.39
Scarid	23.00	9.44			12.07	5.29
Acanthurids	10.67	17.51			4.35	8.41
Karpata - 10 m						
<i>Acanthurus bahianus</i>	0.00	0.00			0.00	0.00
<i>Acanthurus chirurgus</i>	0.00	0.00			0.00	0.00
<i>Acanthurus coeruleus</i>	0.29	0.76	16	0.00	0.03	0.08
<i>Kyphosus sectatrix</i>	0.00	0.00			0.00	0.00
<i>Scarus croicensis/iserti</i>	0.00	0.00			0.00	0.00
<i>Scarus taeniopterus</i>	6.57	2.99	15.61	5.52	0.48	0.27
<i>Scarus vetula</i>	5.43	2.51	28.63	5.69	2.70	1.08
<i>Sparisoma aurofrenatum</i>	2.57	0.98	18.78	2.95	0.30	0.09
<i>Sparisoma chrysopterus</i>	0.57	0.98	35.5	0.71	0.47	0.80
<i>Sparisoma viride</i>	6.29	3.90	21.18	10.26	1.88	0.69
<i>Microspathadon chrysurus</i>	2.00	1.15	15.14	1.46	0.21	0.11
<i>Stegastes diencaeus</i>	4.00	2.31	9.14	0.95	0.09	0.06
<i>Stegastes dorsopunicans</i>	0.29	0.76	10	0.00	0.01	0.02

Appendix A. Average density, fork length, and biomass of herbivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
<i>Stegastes leucostictus</i>	3.43	3.41	6.42	1	0.02	0.02
<i>Stegastes planifrons</i>	32.57	16.48	7	0.00	0.34	0.18
<i>Stegastes variabilis</i>	0.29	0.76	6.81	1.66	0.00	0.01
<i>Stegastes partitus</i>	88.57	29.00	4.7	0.93	0.24	0.05
All Herbivores (w/o <i>S. partitus</i>)	64.29	19.13			6.77	1.89
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o <i>S. partitus</i>)	42.57	18.57			1.83	0.46
Scarid	21.43	6.40			11.65	3.68
Acanthurids	0.29	0.76			0.06	0.16
Karpata - 5 m						
<i>Acanthurus bahianus</i>	0.60	1.35	18	4.36	0.09	0.19
<i>Acanthurus chirurgus</i>	0.20	0.63	23	0.00	0.05	0.17
<i>Acanthurus coeruleus</i>	2.00	2.67	14	3.53	0.17	0.24
<i>Kyphosus sectatrix</i>	0.00	0.00			0.00	0.00
<i>Scarus croicensis/iserti</i>	0.00	0.00			0.00	0.00
<i>Scarus taeniopterus</i>	5.40	3.27	14.26	6.18	0.34	0.20
<i>Scarus vetula</i>	5.40	1.90	26.63	7.41	2.36	1.24
<i>Sparisoma aurofrenatum</i>	3.00	3.30	14.07	4.79	0.17	0.26
<i>Sparisoma chrysopteron</i>	0.00	0.00			0.00	0.00
<i>Sparisoma viride</i>	5.60	2.46	22.39	9.74	1.82	0.94
<i>Microspathadon chrysurus</i>	5.80	2.20	15.28	3.13	0.69	0.27
<i>Stegastes diencaeus</i>	15.20	6.20	8.42	1.72	0.28	0.11
<i>Stegastes dorsopunicans</i>	1.00	1.41	8.4	1.14	0.02	0.02
<i>Stegastes leucostictus</i>	1.00	1.05	6.4	0.55	0.01	0.01
<i>Stegastes planifrons</i>	13.00	6.88	6.28	1.73	0.11	0.09
<i>Stegastes variabilis</i>	0.00	0.00			0.00	0.00
<i>Stegastes partitus</i>	144.20	58.99	4.34	1.08	0.32	0.12
All Herbivores (w/o <i>S. partitus</i>)	58.20	12.87			6.43	1.79
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o <i>S. partitus</i>)	36.00	11.96			2.85	0.77
Scarid	19.40	4.81			9.40	3.52
Acanthurids	2.80	2.70			0.61	0.60
Klein Bonaire, Forest - 10 m						
<i>Acanthurus bahianus</i>	0.80	1.10	16	1.41	0.07	0.10
<i>Acanthurus chirurgus</i>	0.00	0.00			0.00	0.00
<i>Acanthurus coeruleus</i>	1.60	0.89	17	0.82	0.21	0.12
<i>Kyphosus sectatrix</i>	0.00	0.00			0.00	0.00
<i>Scarus croicensis/iserti</i>	0.40	0.89	10		0.01	0.01
<i>Scarus taeniopterus</i>	10.00	3.74	13.48	5.52	0.53	0.18
<i>Scarus vetula</i>	5.20	1.10	27.77	6.07	2.41	0.50
<i>Sparisoma aurofrenatum</i>	2.80	1.79	15.43	3.1	0.18	0.14
<i>Sparisoma chrysopteron</i>	0.00	0.00			0.00	0.00

Appendix A. Average density, fork length, and biomass of herbivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Sparisoma viride	4.40	2.61	27	9.18	2.07	1.19
Microspathadon chrysurus	1.60	1.67	15.25	0.96	0.17	0.17
Stegastes diencaeus	3.20	3.63	8.75	0.71	0.06	0.07
Stegastes dorsopunicans	0.80	1.79	8	0.00	0.01	0.03
Stegastes leucostictus	0.40	0.89	6		0.00	0.00
Stegastes planifrons	45.20	16.35	6.71	1.42	0.44	0.08
Stegastes variabilis	0.00	0.00			0.00	0.00
Stegastes partitus	140.80	29.00	4.94	1.12	0.46	0.07
All Herbivores (w/o S. partitus)	76.40	16.64			6.61	0.76
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o S. partitus)	51.20	18.53			2.28	0.43
Scarid	22.80	5.02			10.38	1.47
Acanthurids	2.40	1.67			0.56	0.37
Klein Bonaire, Forest - 5 m						
Acanthurus bahianus	3.11	3.62	15.93	1.44	0.28	0.36
Acanthurus chirurgus	0.22	0.67	18		0.02	0.07
Acanthurus coeruleus	1.78	2.73	16.25	1.75	0.20	0.35
Kyphosus sectatrix	0.00	0.00			0.00	0.00
Scarus croicensis/iserti	0.22	0.67	12	0.00	0.01	0.02
Scarus taeniopterus	1.78	2.73	14.38	7.13	0.12	0.27
Scarus vetula	4.44	2.96	26.9	6.8	1.95	1.78
Sparisoma aurofrenatum	3.11	2.47	10.29	5.94	0.11	0.12
Sparisoma chrysopterus	0.22	0.67	29	0.00	0.10	0.29
Sparisoma viride	4.22	3.53	18.21	10.62	0.98	1.01
Microspathadon chrysurus	5.56	3.84	10.2	5.91	0.35	0.24
Stegastes diencaeus	7.33	6.00	6.94	2.03	0.09	0.09
Stegastes dorsopunicans	1.11	1.45	8.4	1.14	0.02	0.02
Stegastes leucostictus	0.00	0.00			0.00	0.00
Stegastes planifrons	8.44	5.90	7.21	1.79	0.10	0.08
Stegastes variabilis	0.00	0.00			0.00	0.00
Stegastes partitus	64.67	33.03	4.53	1.18	0.17	0.11
All Herbivores (w/o S. partitus)	41.56	18.49			4.50	2.39
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o S. partitus)	22.44	12.64			1.45	0.72
Scarid	14.00	8.12			6.53	4.90
Acanthurids	5.11	4.81			1.03	1.02
Plaza - 10m						
Acanthurus bahianus	3.00	2.76	15.11	3.02	0.25	0.24
Acanthurus chirurgus	0.33	0.82	25	0.00	0.12	0.29
Acanthurus coeruleus	6.67	9.69	18.1	3.58	1.10	1.84
Kyphosus sectatrix	0.00	0.00			0.00	0.00
Scarus croicensis/iserti	2.33	1.51	14.71	4.64	0.16	0.17

Appendix A. Average density, fork length, and biomass of herbivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Scarus taeniopterus	7.33	2.42	15.64	4.55	0.50	0.21
Scarus vetula	5.33	1.63	30.06	6.84	3.23	0.79
Sparisoma aurofrenatum	3.33	3.01	14.4	6.8	0.25	0.37
Sparisoma chrysopterum	0.00	0.00			0.00	0.00
Sparisoma viride	7.00	2.76	27.29	6.83	3.16	1.39
Microspathadon chrysurus	1.00	1.67	16	1	0.12	0.22
Stegastes diencaeus	9.00	3.29	6.7	1.77	0.09	0.04
Stegastes dorsopunicans	0.67	1.03	7.5	0.71	0.01	0.01
Stegastes leucostictus	1.33	1.63	7.5	0.58	0.01	0.02
Stegastes planifrons	9.00	6.66	7	1.59	0.10	0.08
Stegastes variabilis	0.33	0.82	4	0.00	0.00	0.00
Stegastes partitus	142.33	30.68	4.71	1.26	0.42	0.07
All Herbivores (w/o S. partitus)	56.67	7.76			9.52	1.71
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o S. partitus)	21.33	6.28			1.51	0.40
Scarid	25.33	5.01			14.59	2.93
Acanthurids	10.00	10.95			2.94	3.67
Plaza - 5 m						
Acanthurus bahianus	3.00	2.76	15.44	1.59	0.25	0.25
Acanthurus chirurgus	0.00	0.00			0.00	0.00
Acanthurus coeruleus	0.67	1.03	17.5	0.71	0.09	0.14
Kyphosus sectatrix	0.00	0.00			0.00	0.00
Scarus croicensis/iserti	1.33	1.63	21	4.24	0.23	0.36
Scarus taeniopterus	5.67	3.88	15.82	5.35	0.42	0.43
Scarus vetula	3.67	3.44	29.55	4.06	1.90	2.24
Sparisoma aurofrenatum	1.67	1.51	16.8	4.87	0.16	0.16
Sparisoma chrysopterum	0.00	0.00			0.00	0.00
Sparisoma viride	5.33	3.72	26.25	6.39	2.11	1.66
Microspathadon chrysurus	0.67	1.03	9	9.9	0.04	0.10
Stegastes diencaeus	12.00	5.66	6.25	2.47	0.12	0.08
Stegastes dorsopunicans	0.33	0.82	8	0.00	0.00	0.01
Stegastes leucostictus	1.33	3.27	8.75	1.71	0.02	0.06
Stegastes planifrons	12.00	12.71	5.78	1.85	0.09	0.09
Stegastes variabilis	0.00	0.00			0.00	0.00
Stegastes partitus	134.33	46.86	5.03	1.11	0.46	0.16
All Herbivores (w/o S. partitus)	47.67	24.44			5.91	4.66
Chubs	0.00	0.00			0.00	0.00
Damsels (w/o S. partitus)	26.33	16.94			1.47	0.57
Scarid	17.67	8.43			9.66	8.68
Acanthurids	3.67	3.44			0.69	0.67
Windsock - 10 m						
Acanthurus bahianus	3.33	2.42	15.2	2.7	0.28	0.22

Appendix A. Average density, fork length, and biomass of herbivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Acanthurus chirurgus	3.67	5.99	20.82	1.4	0.69	1.07
Acanthurus coeruleus	18.33	35.40	19.67	1.71	3.61	7.18
Kyphosus sectatrix	1.33	3.27	23	0.00	0.36	0.89
Scarus croicensis/iserti	5.00	3.03	12.47	1.41	0.25	0.25
Scarus taeniopterus	4.67	3.93	17.5	5.01	0.48	0.46
Scarus vetula	5.33	1.63	26.56	6.86	2.76	0.94
Sparisoma aurofrenatum	3.33	3.27	14.7	10.56	0.24	0.22
Sparisoma chrysopterus	0.33	0.82	26	6.02	0.10	0.25
Sparisoma viride	5.00	2.10	28.13	0.00	2.25	1.07
Microspathadon chrysurus	1.67	0.82	14	3.72	0.14	0.08
Stegastes diencaeus	8.67	3.93	6.04	1.97	0.07	0.04
Stegastes dorsopunicans	2.00	1.79	8.17	0.75	0.03	0.03
Stegastes leucostictus	1.33	1.63	7.5	0.58	0.01	0.02
Stegastes planifrons	20.33	8.14	7.2	1.75	0.25	0.11
Stegastes variabilis	0.00	0.00			0.00	0.00
Stegastes partitus	141.00	66.02	3.85	1.54	0.27	0.11
All Herbivores (w/o S. partitus)	84.33	48.49			11.80	7.20
Chubs	1.33	3.27			0.73	1.78
Damsels (w/o S. partitus)	34.00	9.96			1.56	0.23
Scarid	23.67	6.38			12.17	2.58
Acanthurids	25.33	40.33			9.15	15.98
Windsock - 5 m						
Acanthurus bahianus	6.40	2.97	13.69	2.3	0.39	0.23
Acanthurus chirurgus	0.00	0.00			0.00	0.00
Acanthurus coeruleus	0.00	0.00			0.00	0.00
Kyphosus sectatrix	0.40	0.89	40	0.00	0.60	1.34
Scarus croicensis/iserti	2.00	2.00	11.8	7.4	0.10	0.14
Scarus taeniopterus	3.20	4.15	14.25	2.71	0.15	0.15
Scarus vetula	8.00	4.69	26.3	7.14	3.38	2.75
Sparisoma aurofrenatum	2.40	2.19	16.83	0.98	0.18	0.17
Sparisoma chrysopterus	0.40	0.89	26	0.00	0.12	0.27
Sparisoma viride	4.80	2.28	26.67	3.73	1.86	0.38
Microspathadon chrysurus	1.60	1.67	11	5.23	0.10	0.12
Stegastes diencaeus	19.60	29.54	5.59	1.54	0.12	0.19
Stegastes dorsopunicans	0.40	0.89	5	0.00	0.00	0.00
Stegastes leucostictus	0.00	0.00			0.00	0.00
Stegastes planifrons	2.00	3.46	5.8	2.49	0.02	0.03
Stegastes variabilis	0.00	0.00			0.00	0.00
Stegastes partitus	87.20	88.06	2.86	0.91	0.06	0.05
All Herbivores (w/o S. partitus)	51.20	30.32			7.08	3.12
Chubs	0.40	0.89			1.20	2.68
Damsels (w/o S. partitus)	23.60	34.85			0.59	0.41
Scarid	20.80	5.93			11.59	5.28

Appendix A. Average density, fork length, and biomass of herbivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Acanthurids	6.40	2.97			0.78	0.46
Bonaire Average						
Acanthurus bahianus	1.84	2.64			0.16	0.23
Acanthurus chirurgus	0.38	1.89			0.08	0.35
Acanthurus coeruleus	3.84	11.99			0.67	2.48
Kyphosus sectatrix	0.14	0.96			0.07	0.43
Scarus croicensis/iserti	1.19	2.04			0.09	0.18
Scarus taeniopterus	6.30	4.34			0.38	0.29
Scarus vetula	5.11	2.71			2.51	1.53
Sparisoma aurofrenatum	3.03	2.37			0.20	0.20
Sparisoma chrysopterum	0.14	0.51			0.07	0.30
Sparisoma viride	5.68	3.18			2.02	1.19
Microspathadon chrysurus	2.51	2.65			0.24	0.26
Stegastes diencaeus	10.30	9.74			0.14	0.12
Stegastes dorsopunicans	1.00	1.60			0.02	0.03
Stegastes leucostictus	0.86	1.82			0.01	0.02
Stegastes planifrons	19.19	15.56			0.19	0.15
Stegastes variabilis	0.19	0.82			0.00	0.00
Stegastes partitus	121.84	57.85			0.31	0.15
All Herbivores (w/o S. partitus)	61.68	25.37			7.16	3.66
Chubs	0.14	0.96			0.14	0.85
Damsels (w/o S. partitus)	34.05	18.04			1.82	0.76
Scarid	21.43	7.75			10.56	4.78
Acanthurids	6.05	13.78			1.81	5.46

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Barcadera - 10 m						
Sphryaena barracuda	0.00	0.00			0.00	0.00
Bothus lunatus	0.00	0.00			0.00	0.00
Synodus intermedius	0.00	0.00			0.00	0.00
Aulostomus maculatus	1.33	1.63	31.25	6.29	0.11	0.17
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.67	1.03	16.00	0.00	0.04	0.06
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	3.00	2.10	16.22	5.29	0.26	0.26
Epinephalus fulvus	0.00	0.00			0.00	0.00
Hypoplectrus puella	0.33	0.82	10.00	0.00	0.01	0.01
Hypoplectrus unicolor	0.67	1.03	9.00	0.00	0.01	0.01
Hypoplectrus chlorurus	0.67	1.03	11.00	2.83	0.02	0.03
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	1.33	1.63	7.75	1.50	0.01	0.01
Mycteroperca tigris	0.00	0.00			0.00	0.00
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.00	0.00			0.00	0.00
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.67	1.03	24.00	2.83	0.16	0.26
Lutjanus apodus	1.33	1.63	36.00	2.00	1.12	1.32
Ocyrus chrysurus	0.00	0.00			0.00	0.00
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.33	0.82	60.00	0.00	0.16	0.40
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.00	0.00			0.00	0.00
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	6.67	2.42			0.34	0.29
All Jacks	0.00	0.00			0.00	0.00
All Snapper	2.00	2.19			1.28	1.46
All Morays	0.33	0.82			0.16	0.40
ALL PREDATORS	10.00	4.56			1.90	1.94
Barcadera - 5 m						
Sphryaena barracuda	0.00	0.00			0.00	0.00
Bothus lunatus	0.00	0.00			0.00	0.00
Synodus intermedius	0.50	0.93			0.09	0.25
Aulostomus maculatus	1.75	1.67	33.14	8.61	0.18	0.20
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.00	0.00			0.00	0.00
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	0.75	1.04	17.00	2.65	0.06	0.09

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Epinephalus fulvus	1.00	1.85	15.50	6.03	0.08	0.17
Hypoplectrus puella	0.50	0.93	10.00	2.83	0.01	0.02
Hypoplectrus unicolor	0.50	0.93	11.00	0.00	0.01	0.02
Hypoplectrus chlorurus	0.50	0.93	10.50	0.71	0.01	0.02
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	2.50	1.41	9.30	1.06	0.03	0.02
Mycteroperca tigris	0.00	0.00			0.00	0.00
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.00	0.00			0.00	0.00
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.00	0.00			0.00	0.00
Lutjanus apodus	1.00	1.51	33.75	4.79	0.72	1.09
Ocyrus chrysurus	0.00	0.00			0.00	0.00
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.00	0.00			0.00	0.00
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	5.75	3.11			0.20	0.22
All Jacks	0.00	0.00			0.00	0.00
All Snapper	1.00	1.51			0.72	1.09
All Morays	0.00	0.00			0.00	0.00
ALL PREDATORS	9.00	3.21			1.20	1.33
Don's Habitat - 10 m						
Sphryaena barracuda	0.00	0.00			0.00	0.00
Bothus lunatus	0.00	0.00			0.00	0.00
Synodus intermedius	0.67	1.63	31.00	1.41	0.20	0.48
Aulostomus maculatus	2.67	2.73	33.25	4.33	0.25	0.25
Scorpaena plumieri	0.67	1.63	27.50	3.54	0.29	0.71
Paranthias furcifer	1.33	1.03	18.25	2.36	0.13	0.11
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	2.33	2.66	19.57	4.65	0.31	0.45
Epinephalus fulvus	0.00	0.00			0.00	0.00
Hypoplectrus puella	0.00	0.00			0.00	0.00
Hypoplectrus unicolor	0.00	0.00			0.00	0.00
Hypoplectrus chlorurus	0.33	0.82	10.00	0.00	0.01	0.01
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	1.33	1.63	7.75	0.96	0.01	0.01
Mycteroperca tigris	0.00	0.00			0.00	0.00

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.00	0.00			0.00	0.00
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.67	1.63	25.00	0.00	0.18	0.44
Lutjanus apodus	1.00	1.67	28.33	5.77	0.44	0.70
Ocyrus chrysurus	0.33	0.82	32.00	0.00	0.17	0.41
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.33	0.82	15.00	0.00	0.00	0.00
Echidna catenata	0.33	0.82	35.00	0.00	0.03	0.06
All Serranids	5.33	3.72			0.45	0.44
All Jacks	0.00	0.00			0.00	0.00
All Snapper	2.00	2.53			0.79	0.92
All Morays	0.67	1.03			0.03	0.06
ALL PREDATORS	11.33	6.02			2.01	1.42
Karpata - 10 m						
Sphryaena barracuda	0.00	0.00			0.00	0.00
Bothus lunatus	0.29	0.76	37.00	0.00	0.28	0.74
Synodus intermedius	0.00	0.00			0.00	0.00
Aulostomus maculatus	1.43	1.90	27.20	4.38	0.08	0.10
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.29	0.76	22.00	0.00	0.05	0.12
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	2.57	1.51	18.89	3.37	0.29	0.17
Epinephalus fulvus	0.00	0.00			0.00	0.00
Hypoplectrus puella	0.29	0.76	10.00	0.00	0.00	0.01
Hypoplectrus unicolor	0.29	0.76	8.00	0.00	0.00	0.01
Hypoplectrus chlorurus	1.71	1.38	9.50	1.22	0.03	0.02
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	0.00	0.00			0.00	0.00
Mycteroperca tigris	0.00	0.00			0.00	0.00
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.29	0.76	20.00	0.00	0.03	0.09
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.00	0.00			0.00	0.00
Lutjanus apodus	0.57	0.98	37.50	3.54	0.55	0.96
Ocyrus chrysurus	0.86	1.57	30.33	5.51	0.39	0.83
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.29	0.76	25.00	0.00	0.01	0.02
Gymnothorax miliaris	0.00	0.00			0.00	0.00

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	5.14	2.54			0.37	0.22
All Jacks	0.29	0.76			0.03	0.09
All Snapper	1.43	1.51			0.93	1.05
All Morays	0.29	0.76			0.01	0.02
ALL PREDATORS	8.57	3.60			1.70	1.69
Karpata - 5 m						
Sphryaena barracuda	0.00	0.00			0.00	0.00
Bothus lunatus	0.00	0.00			0.00	0.00
Synodus intermedius	0.00	0.00			0.00	0.00
Aulostomus maculatus	0.67	1.00	36.67	11.55	0.09	0.18
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.00	0.00			0.00	0.00
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	1.78	1.86	16.75	4.80	0.14	0.22
Epinephalus fulvus	0.22	0.67	12.00	0.00	0.01	0.02
Hypoplectrus puella	0.00	0.00			0.00	0.00
Hypoplectrus unicolor	0.00	0.00			0.00	0.00
Hypoplectrus chlorurus	0.89	1.05	10.75	0.96	0.02	0.02
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.22	0.67	26.00	0.00	0.06	0.18
Serranus tigrinus	0.67	1.41	7.33	0.58	0.00	0.01
Mycteroperca tigris	0.22	0.67	23.00	0.00	0.03	0.10
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.00	0.00			0.00	0.00
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.00	0.00			0.00	0.00
Lutjanus apodus	0.22	0.67	35.00	0.00	0.15	0.49
Ocyrus chrysurus	0.00	0.00			0.00	0.00
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.44	0.88	22.50	3.54	0.01	0.02
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	4.00	3.87			0.26	0.36
All Jacks	0.00	0.00			0.00	0.00
All Snapper	0.22	0.67			0.15	0.49
All Morays	0.44	0.88			0.01	0.02
ALL PREDATORS	4.89	3.89			0.50	0.74
Klein Bonaire, Forest - 10 m						
Sphryaena barracuda	2.80	6.26	35.00	0.00	0.80	1.79
Bothus lunatus	0.00	0.00			0.00	0.00

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Synodus intermedius	0.00	0.00			0.00	0.00
Aulostomus maculatus	0.80	1.79	35.00	7.07	0.09	0.20
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.00	0.00			0.00	0.00
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	4.40	2.61	21.36	4.54	0.75	0.57
Epinephalus fulvus	0.40	0.89	15.00	0.00	0.02	0.05
Hypoplectrus puella	1.20	1.10	9.67	2.08	0.02	0.02
Hypoplectrus unicolor	0.40	0.89	8.00	0.00	0.00	0.01
Hypoplectrus chlorurus	0.80	1.10	12.50	3.54	0.03	0.05
Hypoplectrus nigricans	0.40	0.89	8.00	0.00	0.00	0.01
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	0.00	0.00			0.00	0.00
Mycteroperca tigris	0.80	1.10	41.00	1.41	0.81	1.12
Caranx sp.	0.80	1.79	25.00	0.00	0.20	0.44
Caranx ruber	0.40	0.89	20.00	0.00	0.05	0.11
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	1.60	2.61	26.50	4.20	0.53	0.86
Lutjanus apodus	0.40	0.89	40.00	0.00	0.46	1.02
Ocyrus chrysurus	0.00	0.00			0.00	0.00
unidentified moray	0.40	0.89	75.00	0.00	0.33	0.75
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.00	0.00			0.00	0.00
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	8.40	2.61			1.63	0.94
All Jacks	1.20	1.79			0.25	0.43
All Snapper	2.00	2.83			0.99	1.39
All Morays	0.40	0.89			0.33	0.75
ALL PREDATORS	15.20	11.01			4.09	3.77
Klein Bonaire, Forest - 5 m						
Sphryaena barracuda	1.33	3.32	35.83	2.04	0.41	0.96
Bothus lunatus	0.00	0.00			0.00	0.00
Synodus intermedius	0.00	0.00			0.00	0.00
Aulostomus maculatus	0.44	0.88	32.50	3.54	0.04	0.08
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.00	0.00			0.00	0.00
Epinephalus guttatus	0.22	0.67	15.00	0.00	0.01	0.03
Epinephalus cruentatus	0.89	1.45	19.00	3.37	0.10	0.16
Epinephalus fulvus	0.89	1.45	28.00	9.52	0.39	0.87
Hypoplectrus puella	0.00	0.00			0.00	0.00
Hypoplectrus unicolor	0.22	0.67	13.00	0.00	0.01	0.03
Hypoplectrus chlorurus	0.89	1.05	12.25	1.89	0.03	0.04

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	0.00	0.00			0.00	0.00
Mycteroperca tigris	0.22	0.67	40.00	0.00	0.21	0.62
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.89	2.03	25.25	6.50	0.27	0.55
Lutjanus griseus	0.89	1.76	31.50	4.04	0.44	0.93
Lutjanus mahogoni	0.22	0.67	30.00	0.00	0.10	0.30
Lutjanus apodus	0.44	1.33	40.00	0.00	0.51	1.52
Ocyrus chrysurus	0.44	1.33	40.00	0.00	0.41	1.22
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.00	0.00			0.00	0.00
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	3.33	2.00			0.75	0.91
All Jacks	0.89	2.03			0.27	0.55
All Snapper	2.00	2.45			1.45	1.84
All Morays	0.00	0.00			0.00	0.00
ALL PREDATORS	8.00	4.80			2.93	2.36
Plaza - 10 m						
Sphryaena barracuda	0.33	0.82	40.00	0.00	0.14	0.35
Bothus lunatus	0.33	0.82	30.00	0.00	0.17	0.41
Synodus intermedius	0.67	1.63	29.00	1.41	0.16	0.40
Aulostomus maculatus	0.33	0.82	27.00	0.00	0.02	0.04
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.00	0.00			0.00	0.00
Epinephalus guttatus	0.33	0.82	13.00	0.00	0.01	0.03
Epinephalus cruentatus	4.00	2.53	16.67	4.50	0.34	0.26
Epinephalus fulvus	0.00	0.00			0.00	0.00
Hypoplectrus puella	1.00	1.10	11.33	3.21	0.03	0.05
Hypoplectrus unicolor	0.33	0.82	12.00	0.00	0.01	0.02
Hypoplectrus chlorurus	0.33	0.82	9.00	0.00	0.00	0.01
Hypoplectrus nigricans	0.33	0.82	7.00	0.00	0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	0.67	1.03	8.00	0.00	0.01	0.01
Mycteroperca tigris	0.33	0.82	20.00	0.00	0.03	0.08
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.00	0.00			0.00	0.00
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	13.33	14.79	24.45	0.88	3.41	3.91
Lutjanus apodus	1.67	1.51	27.40	4.28	0.65	0.64
Ocyrus chrysurus	0.00	0.00			0.00	0.00

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.00	0.00			0.00	0.00
Echidna catenata	0.33	0.82	30.00	0.00	0.02	0.04
All Serranids	7.33	2.42			0.44	0.16
All Jacks	0.00	0.00			0.00	0.00
All Snapper	15.00	14.57			4.07	3.93
All Morays	0.33	0.82			0.02	0.04
ALL PREDATORS	24.00	13.08			5.01	3.46
Plaza - 5 m						
Sphryaena barracuda	0.00	0.00			0.00	0.00
Bothus lunatus	0.00	0.00			0.00	0.00
Synodus intermedius	0.67	1.63			0.12	0.28
Aulostomus maculatus	0.67	1.03	37.50	3.54	0.09	0.14
Scorpaena plumieri	0.00	0.00			0.00	0.00
Paranthias furcifer	0.00	0.00			0.00	0.00
Epinephalus guttatus	0.00	0.00			0.00	0.00
Epinephalus cruentatus	0.00	0.00			0.00	0.00
Epinephalus fulvus	0.33	0.82	15.00	0.00	0.02	0.04
Hypoplectrus puella	0.33	0.82	10.00	0.00	0.01	0.01
Hypoplectrus unicolor	0.00	0.00			0.00	0.00
Hypoplectrus chlorurus	0.00	0.00			0.00	0.00
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	0.33	0.82	11.00	0.00	0.01	0.02
Mycteroperca tigris	0.00	0.00			0.00	0.00
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	0.00	0.00			0.00	0.00
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.67	1.03	23.50	4.95	0.16	0.28
Lutjanus apodus	0.67	1.63	26.50	4.95	0.23	0.58
Ocyrus chrysurus	0.00	0.00			0.00	0.00
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.33	0.82	35.00	0.00	0.03	0.06
Gymnothorax miliaris	0.00	0.00			0.00	0.00
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	1.00	1.10			0.03	0.04
All Jacks	0.00	0.00			0.00	0.00
All Snapper	1.33	1.63			0.40	0.56
All Morays	0.33	0.82			0.03	0.06
ALL PREDATORS	3.67	2.94			0.65	0.79

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Windsock - 10 m						
<i>Sphryaena barracuda</i>	0.33	0.82	32.00	0.00	0.07	0.18
<i>Bothus lunatus</i>	0.00	0.00			0.00	0.00
<i>Synodus intermedius</i>	0.33	0.82	24.00	0.00	0.05	0.11
<i>Aulostomus maculatus</i>	0.33	0.82	22.00	0.00	0.01	0.02
<i>Scorpaena plumieri</i>	0.00	0.00			0.00	0.00
<i>Paranthias furcifer</i>	2.00	3.35	17.00	4.65	0.18	0.31
<i>Epinephalus guttatus</i>	0.00	0.00			0.00	0.00
<i>Epinephalus cruentatus</i>	5.00	2.10	18.87	6.76	0.73	0.54
<i>Epinephalus fulvus</i>	0.00	0.00			0.00	0.00
<i>Hypoplectrus puella</i>	0.33	0.82	10.00	0.00	0.01	0.01
<i>Hypoplectrus unicolor</i>	0.00	0.00			0.00	0.00
<i>Hypoplectrus chlorurus</i>	0.33	0.82	11.00	0.00	0.01	0.02
<i>Hypoplectrus nigricans</i>	0.33	0.82	10.00	0.00	0.01	0.01
<i>Rypticus saponaceus</i>	0.00	0.00			0.00	0.00
<i>Serranus tigrinus</i>	0.67	1.03	9.00	1.41	0.01	0.01
<i>Mycteroperca tigris</i>	0.00	0.00			0.00	0.00
<i>Caranx sp.</i>	0.00	0.00			0.00	0.00
<i>Caranx ruber</i>	1.00	1.10	28.00	6.24	0.40	0.57
<i>Lutjanus griseus</i>	0.00	0.00			0.00	0.00
<i>Lutjanus mahogoni</i>	4.00	8.00	25.58	2.57	1.18	2.35
<i>Lutjanus apodus</i>	2.00	3.10	22.50	6.12	0.48	1.07
<i>Ocyrus chrysurus</i>	0.33	0.82	25.00	0.00	0.09	0.21
unidentified moray	0.00	0.00			0.00	0.00
<i>Gymnothorax funebris</i>	0.00	0.00			0.00	0.00
<i>Gymnothorax moringa</i>	0.00	0.00			0.00	0.00
<i>Gymnothorax miliaris</i>	0.00	0.00			0.00	0.00
<i>Echidna catenata</i>	0.00	0.00			0.00	0.00
All Serranids	8.67	4.32			0.93	0.43
All Jacks	1.00	1.10			0.40	0.57
All Snapper	6.33	8.71			1.75	2.42
All Morays	0.00	0.00			0.00	0.00
ALL PREDATORS	17.00	12.18			3.21	2.79
Windsock - 5 m						
<i>Sphryaena barracuda</i>	0.00	0.00			0.00	0.00
<i>Bothus lunatus</i>	0.00	0.00			0.00	0.00
<i>Synodus intermedius</i>	0.00	0.00			0.00	0.00
<i>Aulostomus maculatus</i>	0.00	0.00			0.00	0.00
<i>Scorpaena plumieri</i>	0.00	0.00			0.00	0.00
<i>Paranthias furcifer</i>	0.00	0.00			0.00	0.00
<i>Epinephalus guttatus</i>	0.00	0.00			0.00	0.00
<i>Epinephalus cruentatus</i>	0.00	0.00			0.00	0.00

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Epinephalus fulvus	0.00	0.00			0.00	0.00
Hypoplectrus puella	0.00	0.00			0.00	0.00
Hypoplectrus unicolor	0.00	0.00			0.00	0.00
Hypoplectrus chlorurus	0.00	0.00			0.00	0.00
Hypoplectrus nigricans	0.00	0.00			0.00	0.00
Rypticus saponaceus	0.00	0.00			0.00	0.00
Serranus tigrinus	2.00	0.00	7.75	1.50	0.01	0.01
Mycteroperca tigris	0.00	0.00			0.00	0.00
Caranx sp.	0.00	0.00			0.00	0.00
Caranx ruber	1.00	2.00	12.00	0.00	0.02	0.04
Lutjanus griseus	0.00	0.00			0.00	0.00
Lutjanus mahogoni	0.50	1.00	16.00	0.00	0.03	0.07
Lutjanus apodus	0.00	0.00			0.00	0.00
Ocyrus chrysurus	0.00	0.00			0.00	0.00
unidentified moray	0.00	0.00			0.00	0.00
Gymnothorax funebris	0.00	0.00			0.00	0.00
Gymnothorax moringa	0.00	0.00			0.00	0.00
Gymnothorax miliaris	0.50	1.00	25.00	0.00	0.01	0.02
Echidna catenata	0.00	0.00			0.00	0.00
All Serranids	2.00	0.00			0.01	0.01
All Jacks	1.00	2.00			0.02	0.04
All Snapper	0.50	1.00			0.03	0.07
All Morays	0.50	1.00			0.01	0.02
ALL PREDATORS	3.50	1.91			0.07	0.09
Bonaire All Site Average						
Sphryaena barracuda	0.42	2.04			0.12	0.58
Bothus lunatus	0.06	0.33			0.04	0.26
Synodus intermedius	0.25	0.88			0.05	0.21
Aulostomus maculatus	0.97	1.54			0.09	0.16
Scorpaena plumieri	0.06	0.47			0.02	0.20
Paranthias furcifer	0.36	1.18			0.03	0.11
Epinephalus guttatus	0.06	0.33			0.00	0.01
Epinephalus cruentatus	2.17	2.32			0.25	0.36
Epinephalus fulvus	0.31	0.93			0.06	0.32
Hypoplectrus puella	0.33	0.75			0.01	0.02
Hypoplectrus unicolor	0.22	0.63			0.00	0.01
Hypoplectrus chlorurus	0.64	1.00			0.01	0.03
Hypoplectrus nigricans	0.08	0.40			0.00	0.00
Rypticus saponaceus	0.03	0.24			0.01	0.07
Serranus tigrinus	0.83	1.29			0.01	0.01
Mycteroperca tigris	0.14	0.51			0.09	0.39

Appendix B. Average density, fork length, and biomass of carnivorous fish on six reefs in Bonaire in March, 2003.

	Density		Fork length		Biomass	
	(# per 100 m ²)		(cm)		(kg per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Caranx sp.	0.06	0.47			0.01	0.12
Caranx ruber	0.31	0.99			0.07	0.27
Lutjanus griseus	0.11	0.66			0.05	0.34
Lutjanus mahogoni	1.78	5.85			0.46	1.54
Lutjanus apodus	0.83	1.53			0.48	0.94
Ocyrus chrysurus	0.19	0.76			0.11	0.51
unidentified moray	0.03	0.24			0.02	0.19
Gymnothorax funebris	0.03	0.24			0.01	0.11
Gymnothorax moringa	0.06	0.33			0.00	0.02
Gymnothorax miliaris	0.11	0.46			0.00	0.01
Echidna catenata	0.06	0.33			0.00	0.02
All Serranids	5.17	3.50			0.47	0.60
All Jacks	0.36	1.08			0.09	0.29
All Snapper	2.92	6.22			1.10	1.86
All Morays	0.28	0.70			0.04	0.22
ALL PREDATORS	10.19	8.55			2.03	2.39