

*Status and Trends of
Bonaire's Coral Reefs,
2009*

& Need for Action

2009



2007



2004



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Executive Summary:

Status and Trends of Bonaire's Reefs & Need for Immediate Action

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Overview and conclusion

In 2005 STINAPA requested we provide advice on how to monitor Bonaire's coral reefs (Steneck and McClanahan 2005). Our advice was 1) keep it simple and 2) keep it focused on known drivers and indicators of coral reef health. We emphasized four key drivers, coral cover, algal abundance, herbivory and coral recruitment, as the best combination for monitoring the health and resilience of coral reefs (i.e., Hughes et al 2005, Mumby and Steneck 2008). Further, we suggested that the current status of any variable is less important than its trend over time.

We applied our trend analysis for five time intervals (1999, 2003, 2005, 2007, and 2009) at six monitoring sites (Windsock, 18th Palm, Forest, Reef Scientifico, Barcadera and Karpata). We found negative trends in three of the four key variables (underlined in Fig 1), and additional negative trends in five other variables. In total, eight of the nine monitored variables (we did not monitor nutrients) showed negative trends (listed in Fig. 1). We detected no positive trends. The increase in algal abundance is most troubling. These results suggest that the risk of collapse of Bonaire's reefs is increasing and warrants increasing protection of herbivorous fishes and reducing nutrient discharge.

Suggested Approach to Monitor Coral Reefs

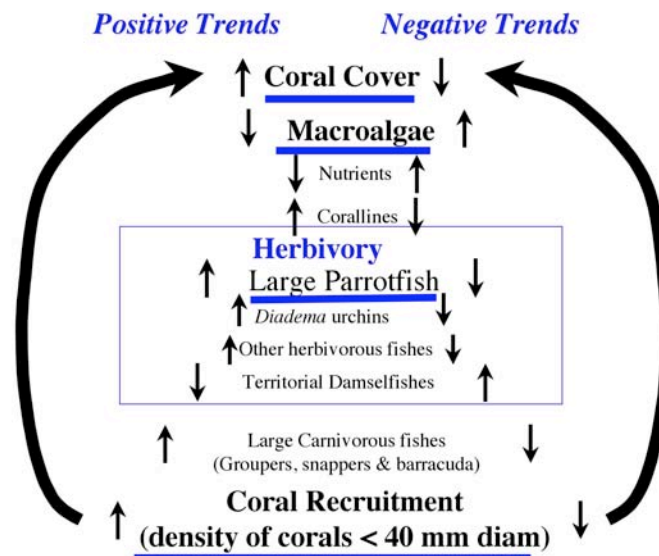


Fig. 1. List of variables to monitor to detect positive (left arrows) and negative (right arrows) trends. Key variables are underlined. Drivers for most variables are listed below those variables. (from Steneck and McClanahan 2005)

Monitoring Rationale and Results

Of the 10 variables proposed for monitoring coral reefs (Fig. 1, Steneck and McClanahan 2005), four are “*key variables*” that either drive or indicate the health of coral reefs. Coral cover defines the physical and ecological structure of this ecosystem. Macroalgae drives and indicates reef health. No algal dominated coral reef has ever been described as healthy. The two primary factors driving macroalgal abundance are herbivores and ambient nutrients. Evidence is strongest that herbivores play the greatest role in driving algal abundance (reviewed in Mumby and Steneck 2008).

While overall coral abundance remains stable on Bonaire, macroalgae (harmful to reefs) and coralline algae (helpful to reefs) are increasing and decreasing in abundance respectively (Fig. 2). Macroalgae, and dense filamentous turf algae, inhibit coral settlement and can kill corals, whereas some species of coralline algae have been shown to facilitate the settlement and recruitment of reef corals (Harrington et al 2004).

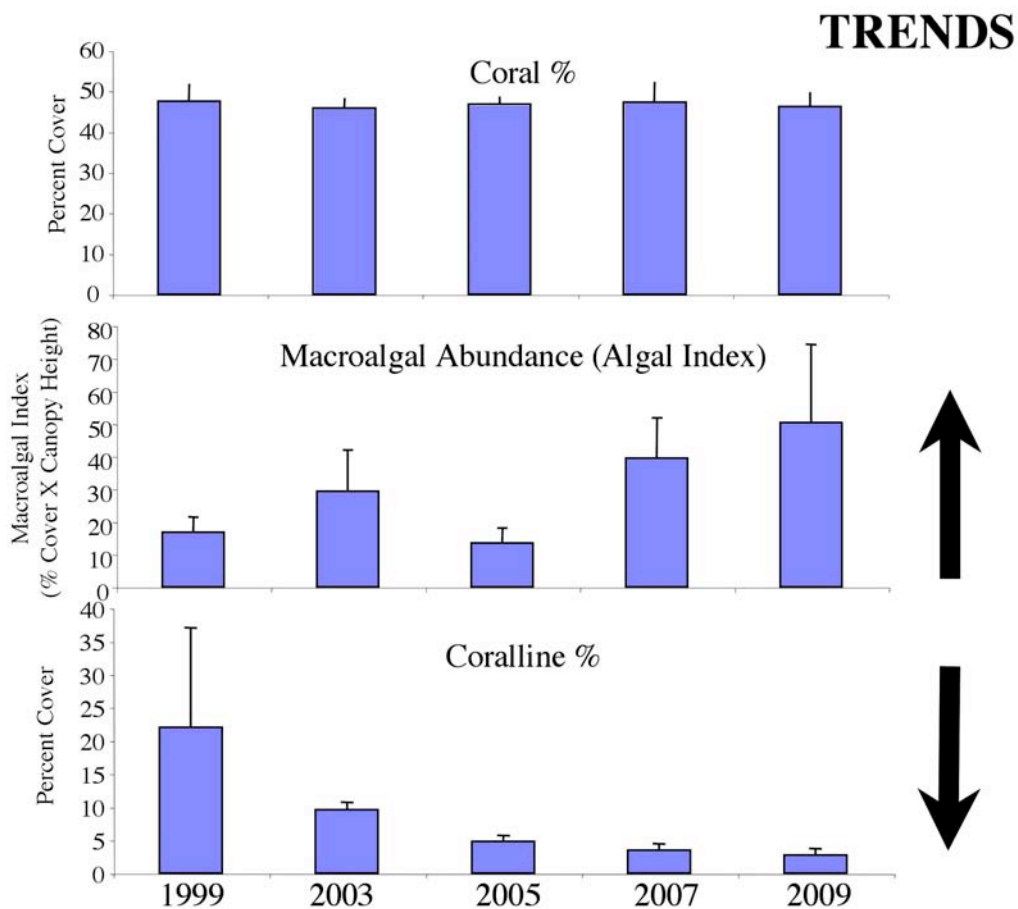


Fig. 2. Monitoring results 1999 – 2009 for coral, macroalgae and coralline algae (from Steneck and Arnold 2009, Ch. 1). Significant trends are indicated by the up arrows (i.e., increasing) and down arrows (i.e., decreasing).

We did not monitor nutrient levels in Bonaire. However, recent studies indicate that nutrient levels are dangerously high in some areas (Ramon de Leon personal communication). Few

studies have shown a clear relationship between nutrient levels and algal abundance. This is most likely due to the countervailing effects of herbivory on most of the world's coral reefs (Diaz-Pulido and McCook 2003). However, declining herbivory is clearly evident among herbivorous fishes (Fig. 3, Jaini 2009, Ch. 3). Specifically, the population density of scarid parrotfishes and their bite rates are both declining (Fig. 3). Additionally, populations of the herbivorous sea urchin, *Diadema*, that had increased from 1999 to 2005 have since declined to very low abundance (Steneck and Arnold 2009, Ch. 1). Although the recent *Diadema* decline could have been the result of Tropical Storm Omar, even when this species was at its recent peak abundance (2004), its population density was still too low to be effective in reducing seaweed.

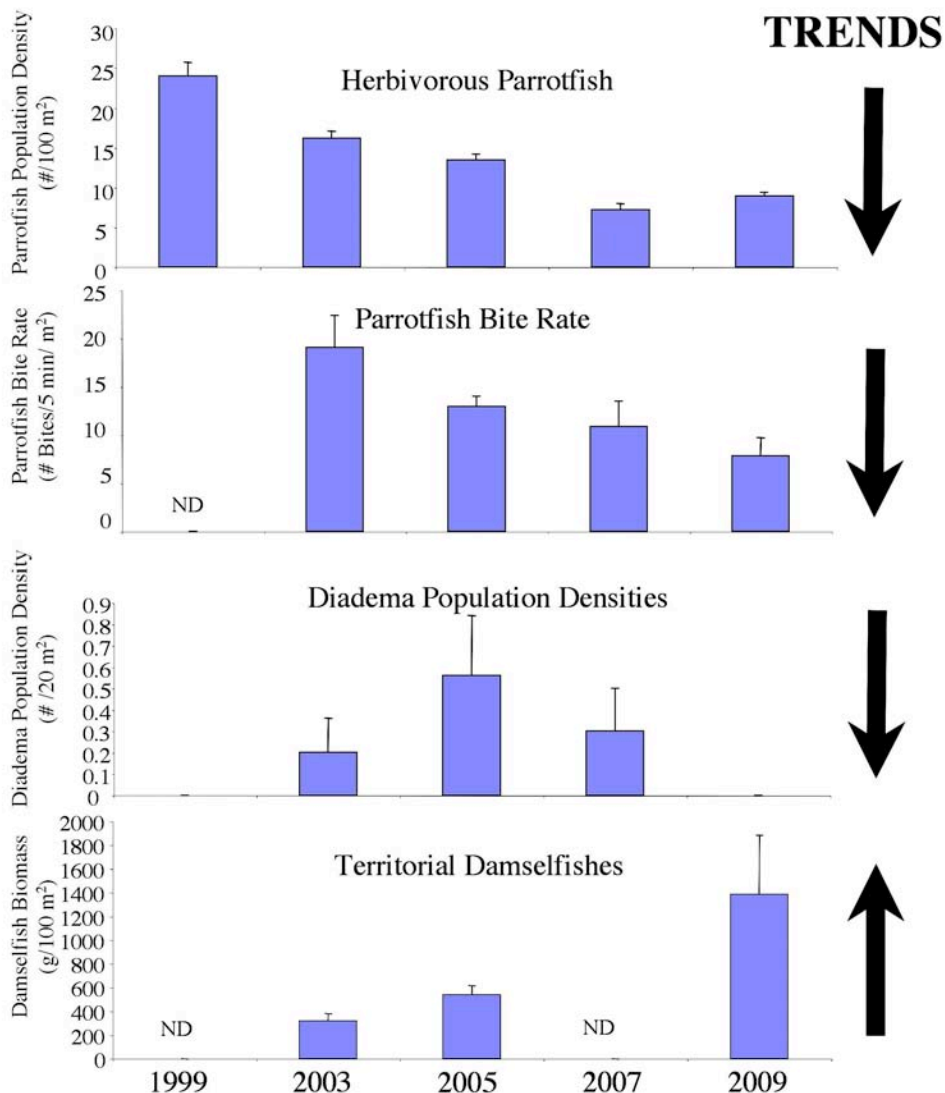


Fig. 3. Trends in herbivory. Parrotfish abundance, bite rate and *Diadema* abundance all scale positively with herbivory. Damselfish scale negatively. Arrows indicate trend. Data from Chapters 1 (Steneck and Arnold 2009), 2 (Eldridge 2009), 3 (Jaini 2009), and 4 (DeBey and Steneck 2009).

To exacerbate the decline in effective herbivory is the rise in damselfish populations. Territorial damselfishes can interfere with the grazing activity of tangs and parrotfishes (Jaini 2009, Ch 3).

Therefore, the increasing abundance of damselfish (Fig. 3) is a negative trend for the health of Bonaire's reefs. One of the strongest suspected links is the role of predatory fishes in controlling the abundance of territorial damselfish. For example, McClanahan 2005 studied how coral reefs changed in Belize following the establishment of no-take reserves. The strongest positive effect was among fish predators and the strongest negative effect was among damselfishes. That decline in damselfishes as predator abundance increased corresponds well with several other studies showing predator control of damselfish abundance (e.g., Almany 2004).

Predatory fish that eat other fish (especially preying on damselfish) and were found in fish surveys in Bonaire include: trumpetfish, bar jack, schoolmaster snapper, tiger grouper, graysby, coney, cubera snapper, mahogany snapper, black grouper and barracuda. Their population densities dropped in half from 2003 and 2009 (Fig. 4).

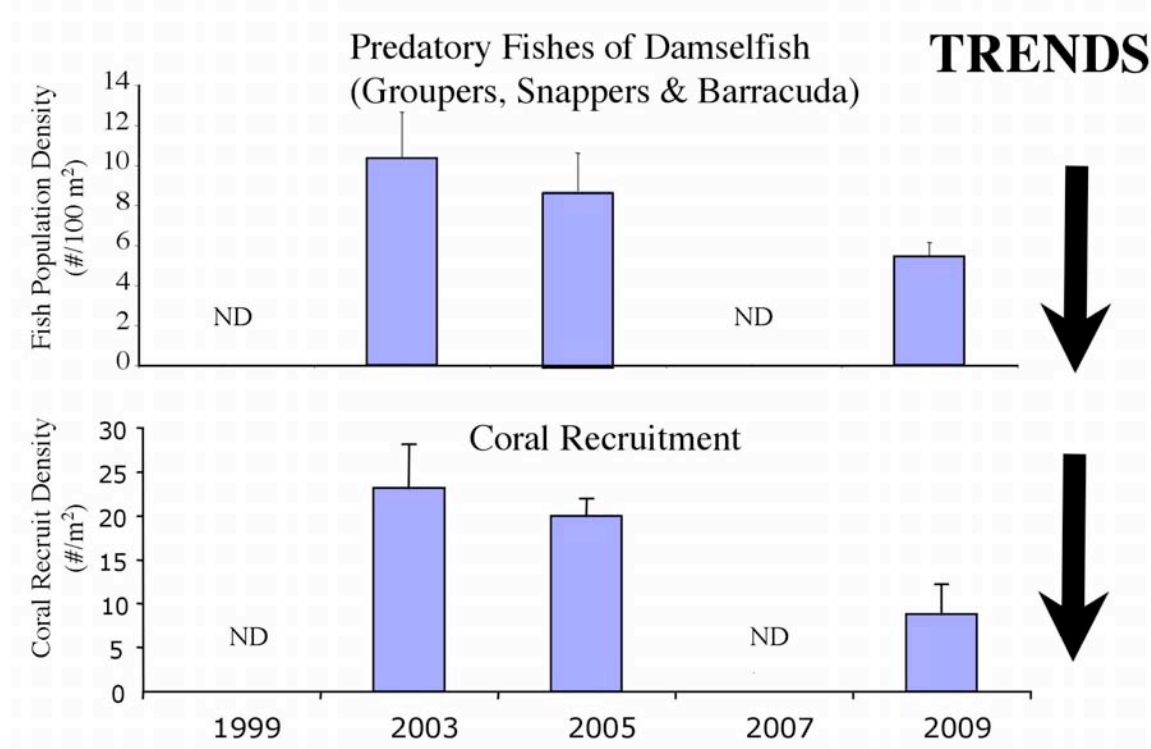


Fig. 4. Trends in predatory fishes that are known to or suspected to eat damselfishes. Data from AGRRA 1999, Bonaire Reports 2003, 2005 and 2009). Population densities of coral recruits (corals less than 4 cm in diameter) (Ch. 1; Steneck and Arnold 2009).

Coral recruitment in 2009 was significantly lower than what was recorded in 2003 and 2005. 2007 data are lacking for coral recruitment, so it's possible that the 2009 decline could have resulted from unusual destruction caused by Tropical Storm Omar in October, 2008.

By applying the trend results (i.e., the arrows in Figs. 2 – 4) together with the predictions in the suggested approach to monitoring coral reefs (Fig. 1; Steneck and McClanahan 2005), we see that the preponderance of trends are negative for Bonaire's coral reefs (Fig. 5).

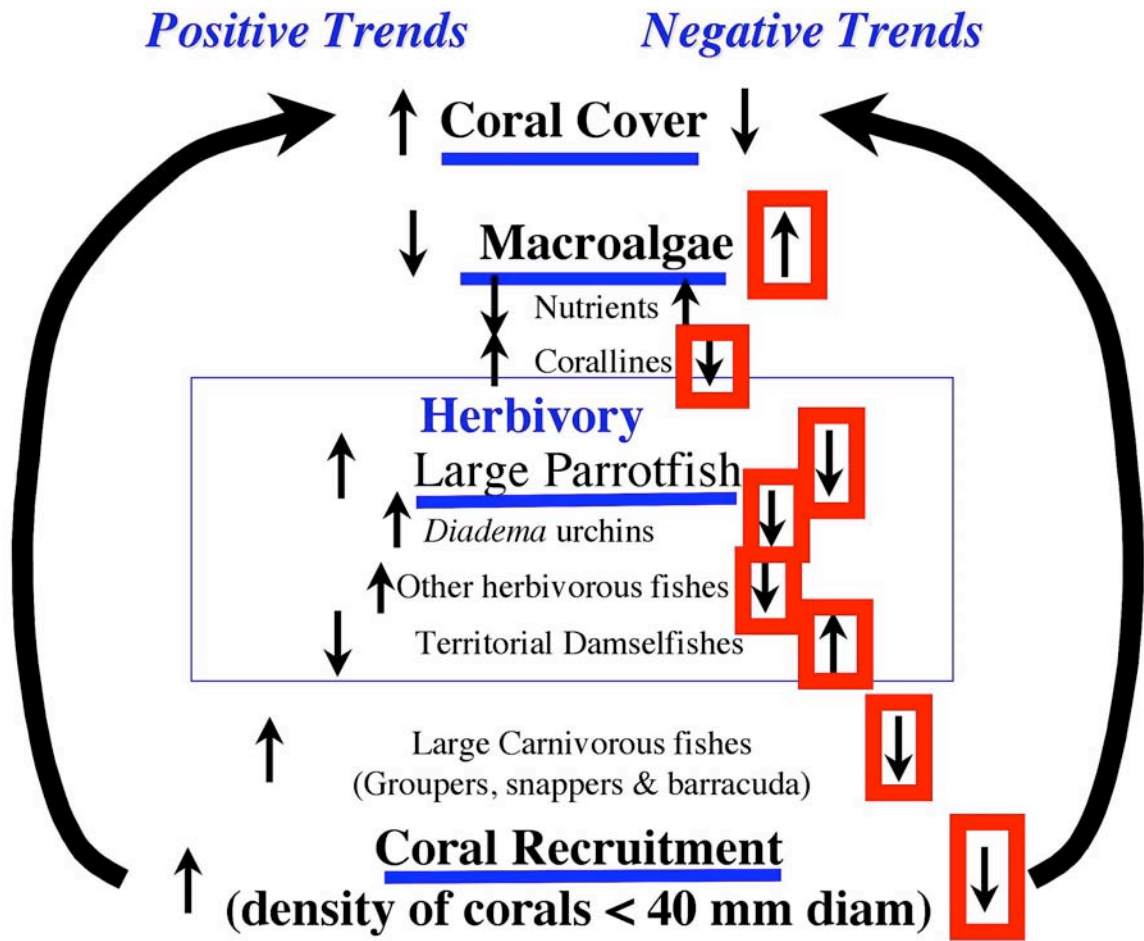


Fig. 5. The interpreted monitoring protocol. Where clear trends were found (Figs. 2 – 4 and Eldridge 2009), they were surrounded by a red box. Note that no significant positive trends were found. No data were presented for nutrients or other herbivorous fishes. Only coral cover shows no trend all.

Conclusion

Coral reefs are complex biological systems prone to sudden change (Scheffer et al 2001). Given the clear trends in dangerous directions, immediate management actions should be taken. We suggest the greatest effort be placed in fisheries management. All herbivorous fishes (parrotfishes and tangs) should be protected. A moratorium on all other fishing on the reefs until the current threat stabilizes should also be considered.

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Chapter 1: Patterns of abundance in corals, seaweeds, sea urchins and juvenile corals in Fish Protection Areas and Controls: baseline data for monitoring

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Abstract

Surveys of the abundance of live stony coral, seaweed (known as macroalgae), sea urchins and juvenile corals were quantified at four Fish Protection Areas (FPA) sites and at five sites open to fishing (control sites). All were in 10 m of water and five of the sites have been monitored every other year since 2003. The FPA and control sites differed significantly at this initial period. Specifically, live coral and coralline algae were more abundant at control sites (50% and 4 % cover respectively) while macroalgae was less abundant. Sea urchins were also slightly more abundant but still at very low population densities (at 0.4 urchins/20 m²). In contrast coral and coralline algae were less abundant at the FPA sites (40% live coral, 1.7% coralline algae). Macroalgae were more abundant and sea urchin less abundant (0.2 urchins/20 m²) than at the control sites. While the FPA and control site baseline differences were not expected, they still provide a proper baseline against which future change will be measured.

Introduction

Live reef corals define the structure and functioning of coral reef ecosystems. Many coral reefs have become seaweed or algal dominated, but so far, the reefs of Bonaire maintain relatively high coral cover, low algal abundance and relatively high coralline algal abundance (Kramer 2003, see Bonaire Reports for 2003, and 2005 on file with STINAPA).

Declines in coral abundance is often accompanied with, or possibly caused by, an increase in macroalgae (Hughes 1994, Mumby and Steneck 2008). Conversely, calcareous algae facilitates settlement and metamorphosis of some baby corals (Raimondi and Morse 2000, Ritson-Williams et al 2009). Therefore, monitoring inhibitory fleshy algal abundance and facilitating coralline abundance can gauge the health of coral reefs and their ability to recover following a mortality event.

What controls the abundance of macroalgae and coralline algae has received considerable attention over the past few decades. Most studies have shown that herbivory from scraping herbivores such as parrotfishes and sea urchins controls algal abundance much more strongly than does nutrient abundance (McCook 1999, Williams and Polunin 2001, Kramer 2003, and Mumby and Steneck 2008). Other studies have indicated that herbivores facilitate coralline algal abundance (van den Hoek 1969, Steneck 1986, 1988, 1997, Steneck and Dethier 1994, Edmunds and Carpenter 2001).

Thus observing increases or stasis in coral abundance, coralline algae and scraping herbivores indicates a relatively healthy condition. Whereas increases in macroalgae indicate an unhealthy

trend. To determine reef health requires monitoring patterns of abundance over a long enough period to detect significant trends over time.

Overfishing on coral reefs is an ever-present concern. In Bonaire, Fish Protection Areas were established in 2007 to create effective oases where fishing pressures are absent and fish stocks can recover. To determine if those areas also adopt healthier conditions, baseline studies were initiated in 2008, prior to significant changes which can be observed two or more years following instatement of a protected area.

Materials and Methods

The distribution and abundances of major reef-occupying groups such as stony coral, macroalgae, sea urchins and juvenile corals were quantified using 10 m long line transects placed on reefs (methods of Benayahu and Loya 1977; Kramer 2004) at 10 m depth at each of our nine study sites (Listed in Fig. 1). Algae were subdivided into functionally important groups (see Steneck and Dethier 1994) such as crustose coralline, articulated coralline, foliaceous macroalgae (hereafter: “macroalgae”) and noncoralline crusts. Transect methods used were modified from the Atlantic and Gulf Rapid Reef Assessment (AGGRA) protocol (Steneck et al. 2003). Specifically, we measured the number of cm occupied by each organism group and all coral species along each transect. Macroalgal biomass is most critical and it was estimated from the calculated algal index as the product of percent cover multiplied by algal canopy height (in mm; Steneck and Dethier 1994, Kramer 2003). We quantified three transects per reef site.

Abundances of four species of sea urchins (*Diadema antillarum*, *Tripneustes ventricosus*, *Echinometra lucunter* and *E. viridis*) were quantified in accordance with AGGRA protocols by searching a one-meter path on either side of the 10 meter transect tape (i.e. a total of 20 m² were surveyed for each transect).

Juvenile coral densities were also censused along a 10 m transect tape at a depth of 10 m, recording the number of juvenile corals (less than or equal to 40mm in max diameter) in a 1/16 m² quadrat. The quadrat was placed at the 0, 2.5, 5, 7.5, and 10 m marks along the transect on "available substrate" or substrate upon which a coral larva might settle (i.e.- not an area with live coral, sand, etc.).

We present data for the Fish Protection Areas (FPA) and control sites. However, two of the FPA sites (Plaza and Científico) and three of the control sites (Windsock, Barcadera and Forest) are the sites we have monitored since 2003. At those sites, ceramic plates mark specific transect areas so all of our monitoring is along nearly fixed transects. In most cases, the transect falls no more than 0.5 m from the transect locations of previous years.

Results

Live coral remains the single most abundant component of Bonaire’s reefs (Fig 1.). Live coral cover at all nine sites averaged 41.9%. The coral cover was higher at the Control sites than the FPA sites (Fig. 1). A total of 19 species were recorded. However, by far, the dominant corals

were star corals of the genus *Montastraea*. The two most abundant species was, *M. annularis* and *M. faveolata* at 12.6 and 10% cover of the reef, respectively. The next two most abundant taxa were *M. cavernosa* and *Agaricia agaricites* at 3.5 and 2.6% of the reef surface area, respectively.

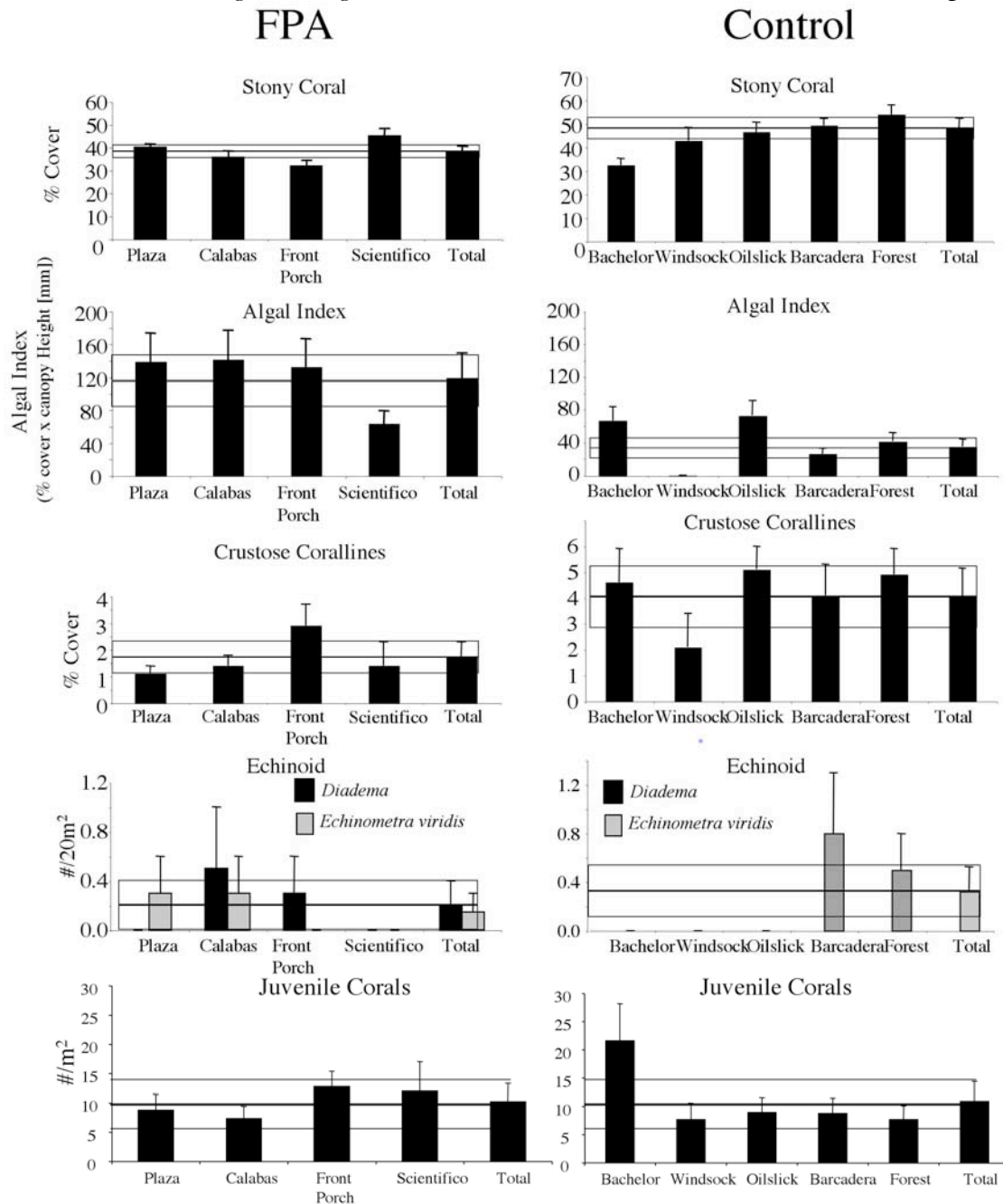


Fig 1. Percent cover of major reef components in FPA and Control Sites and population densities of sea urchins.

Turf algae was the second most abundant component of the reef comprising 37.9 % of the reef surface with an average canopy height of 2.0 mm. This represents an increase in the canopy height of almost a mm from the average in 2007 of 1.1 mm (± 0.1 SE).

Macroalgal cover was 10.7% for all nine sites. The algal index (percent cover x canopy height) reflects algal biomass (Steneck and Dethier 1994). The Control sites had significantly lower algal abundance than did the FPA sites (Fig. 1)

Crustose coralline algae was significantly more abundant among the Control than the FPA sites (Fig. 1). However coralline abundance among all nine sites was only 3% cover.

Herbivorous sea urchins were relatively rare and ecologically unimportant. Among all nine sites studied, the average population density of the black long-spined sea urchin, *Diadem antillarum* was 0.1 per 20 m² survey area (or 0.005 per m²). The most abundant sea urchin was *Echinometra viridis* with a population density averaging 0.23 per 20 m².

Overall, the density of juvenile corals on Bonaire in 2009 was greatly reduced compared to previous monitoring years. This decline was consistent across FPA (average 10.23 juvenile corals per m²) and Control sites (average of 10.94 juvenile corals per m²). In previous years, the average number of juvenile corals hovered around 20 per m². The island-wide decline is very pronounced, but due to a lack of data taken from consistent methodology in 2007, we are unable to rule out sedimentation caused by Tropical Storm Omar in October of 2008 as the source of mortality.

Discussion

Healthy reefs were traditionally described as having abundant live coral and little to no macroalgae (Darwin 1909, Steneck 1988, Hughes 1994). This changed in recent years when most Caribbean reefs “phase-shifted” to macroalgal dominance and now have only about 10% live coral (Gardner et al. 2003). Bonaire’s reefs are different since corals remain the most abundant living component of the reef and macroalgae are relatively rare (Fig. 1).

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

The relatively low abundance of macroalgae is probably due to the relatively high rates of herbivory on Bonaire’s reefs (see Jaini 2009, in this report). While other studies in this report examined grazing fish, this chapter quantified the abundance of the sea urchin, *Diadema antillarum*, because its abundance is increasing throughout the Caribbean and some studies have seen improvement in reef condition scale with the grazing activity of this urchin (Edmunds and Carpenter 2001). However, *Diadema* remains too rare to have a functional impact as an herbivore in this system. Its density should continue to be monitored. Much higher densities have been found in shallow non-reef sites in Bonaire (see Prendiville 2009 chapter in this report).

FPA and Control Baseline Data

Since the Fish Protection areas were first established in 2008, no change due to that management action would be expected at this time. However, to determine change in highly complex ecosystems, a “before and after controlled impact” (BACI) design is necessary. BACI designs first establish a baseline against which change due to the manipulation is quantified. In this case, the control sites have higher coral and coralline abundance and lower algal abundance than the FPA sites. It will be against this baseline that future change will be assessed.

The larger picture of reef health in Bonaire is covered in the Executive Summary (Steneck and Arnold, 2009).

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Chapter 2: Herbivorous fishes: Patterns of distribution, abundance, body size and trends over time in Bonaire

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Abstract

Eight coral reef sites were surveyed in March 2009 off the western shore of Bonaire to collect data on the abundance and biomass of algal removing herbivorous fish. Populations were compared between the recently designated no-take Fish Protected Areas (FPAs) and control sites as a baseline for future monitoring. The herbivorous fish population of Bonaire has been surveyed and quantified over the past seven years. Analyses of patterns in scarid and acanthurid populations monitored at five study sites from 2003 to 2009 indicate a significant decline in density and biomass of these critical functional families. This study also analyzed developmental data of initial and terminal phase scarids. One interesting baseline difference was that the initial phase scarids in the FPAs had greater density and smaller sizes than in the control sites.

Introduction

This report quantifies the distribution and abundance of herbivorous fish in Bonaire. Fish herbivory is a critical function for the control of algal biomass and the maintenance of healthy coral reefs. Macroalgae overgrowth smothers and kills corals. The distribution and abundance of herbivores, such as parrotfish, can prevent a shift to a macroalgal dominated phase and hasten recovery of a damaged coral reef to a healthy state (Mumby *et al.* 2007)).

In January 2009, Bonaire created two Fish Protected Areas on the west coast of Bonaire. The FPAs extend from the shore to a depth of 200 feet. Within the FPAs fishing is prohibited, except for pelagic baitfish. The legislative intent was to provide habitat where important herbivorous benthic species, such as parrotfish, can attain their maximum size and maturity (STINAPA 2009). Larger and older fish lay more eggs, and provide a “spillover effect” of mature fish into adjoining fished zones (Johnson *et al.* 1999; McClanahan and Mangi 2000; Roberts *et al.* 2001). This report compares scarid density, biomass, size and phase between treatments.

Since 2003, herbivorous fish have been monitored at five sites: the four control sites of this study and FPA site, Reef Scientifico. Trends over time include surveys from March 2003, 2005 and 2007 (Paddack *et al.* 2003, Brown and Hansen 2005, and Mumby pers comm). The historical trend shows a pattern of significant decline in abundance of the major algal removing species.

Ratios of scarid phases and sizes may be an early indicator of environmental stress from overfishing, or competitive interactions caused by limited resources on the reef (Bruggeman *et al.* 1996). Reef fish specialize in foraging or grooming specific coral, algae and plants. They may also selectively focus on materials based on abundance, competition, and qualitative conditions. Reef health is therefore tied to these aspects of scarid populations (Mumby and Wabnitz 2001,

Steneck 2009). Scarid ratios by phase and maturity are reviewed and compared for significant differences.

Methods

Visual census surveys of eight sites were conducted in March 2009 off Bonaire's west coast, four in Fish Protected Areas (F) and four control sites (C). Sites from south to north were Windsock (C), Eighteenth Palm (F), Calabas (F), Forest on Klein Bonaire (C), Front Porch (F), Reef Scientifico (F), Barcedera (C), and Oil Slick Leap (C).

Transect dimensions were 30 m x 4 m (120 m²). Using SCUBA, eight transects were surveyed at each site at a depth of 10 m. For each transect a 30 m pre-measured tape was laid out on the substrate. The diver swam back at an elevation of 1-2 meters above the substrate, recording data for each herbivorous fish within 2 m on either side of the tape.

Using standardized survey methods the diver recorded data for initial and terminal phase Scaridae (parrotfish), Acanthuridae (surgeonfish), Pomacentridae (damselfish) except *Stegastes partitus*, and *Kyphosus sectatrix*. Data recorded on each fish included species, size (length to the cm), and developmental phase (scarids). To calibrate the size of fishes observed, the diver practiced estimating sizes of dimensional fish drawings underwater. In post-analysis, length was converted to biomass using allometric relationships specified in Bohnsack and Harper (1998), or if not available there then www.FishBase.org (Froese and Pauly 2009).

Results

Algal Removing Fish

Algal removing herbivorous fish graze and consume a substantial amount of algal biomass. Functional algal removers recorded were initial and terminal phase scarids, acanthurids, and *Microspathodon chrysurus* (yellowtail damselfish). Sites are shown south to north, including Forest on Klein Bonaire (Fig. 1 and Fig. 2). Significant variation among sites were found for fish biomass (ANOVA: $F_{7,64}=2.19$, $P=.04$), but not density. Mean biomass of algal removing fish in the FPAs was 4742 g/100m² and 6072 g/100m² in the control sites.

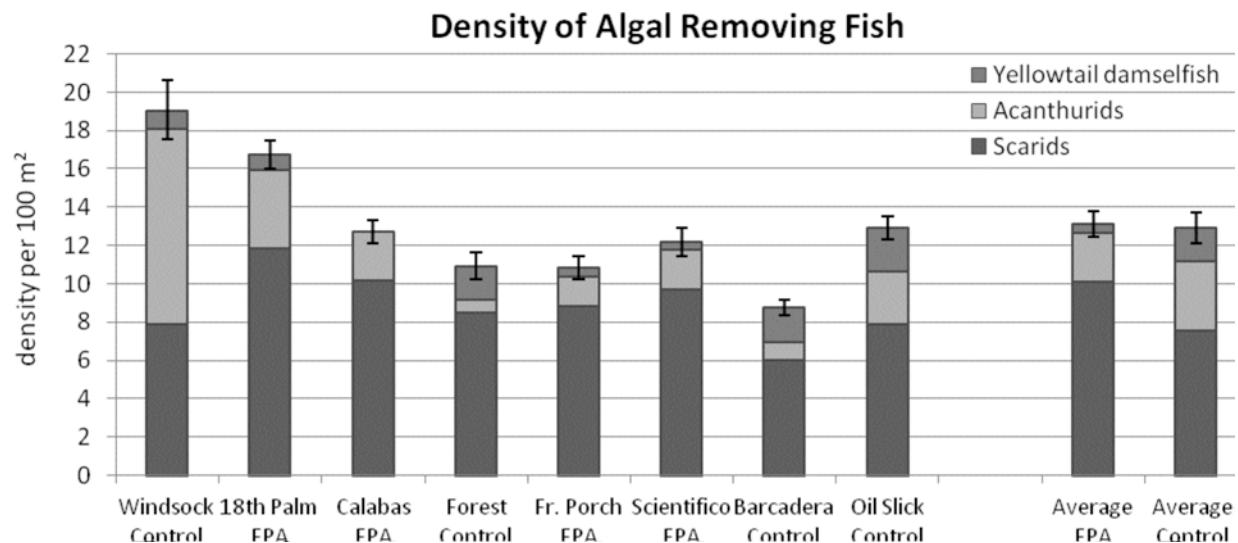


Figure 1. Density of algal removing herbivorous fish. Error is one \pm standard error.

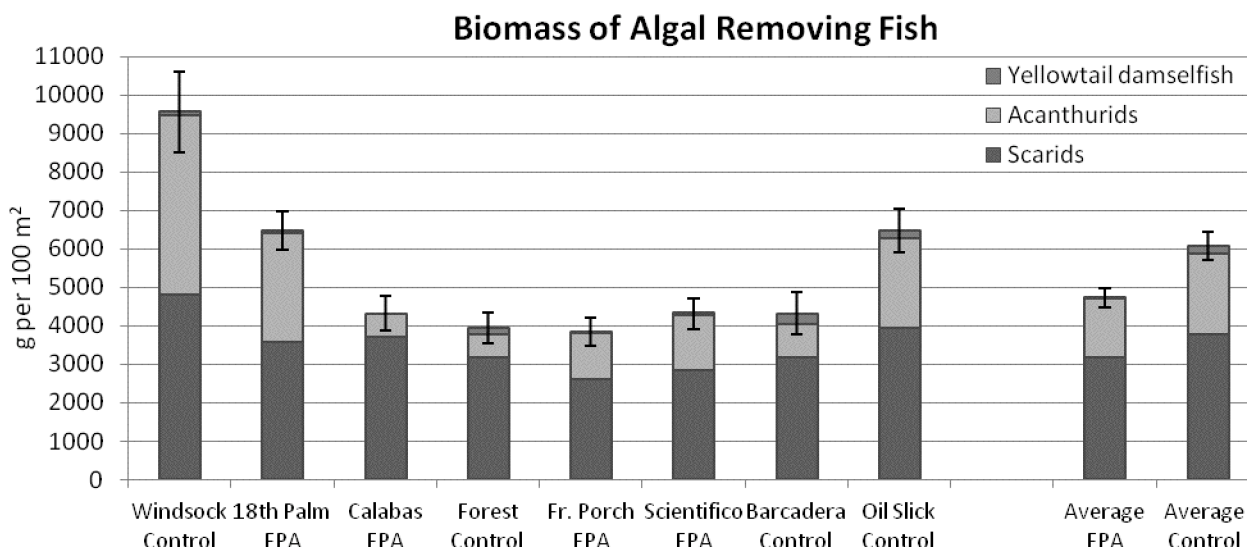


Figure 2. Biomass of algal removing herbivorous fish. Error is one \pm standard error.

Herbivorous Groups

Non-denuding territorial damselfish selectively trim and defend a small algal patch. These small fish aggressively protect their patch from the larger marauding macroalgal denuding herbivores (Hixon and Beets 1989). The role of the scarid family as a keystone taxa is an ecological determinate of reef health (Paine 1995). The combined acanthurids and yellowtail damselfish group are grouped to indicate their impact as the remaining herbivorous fishes. One-way ANOVA analyses presents significant variation among fish groups by both density ($F_{2,23}=10.34$, $P=7.50 \times 10^{-4}$) and biomass ($F_{2,23}=27.06$, $P=1.54 \times 10^{-6}$).

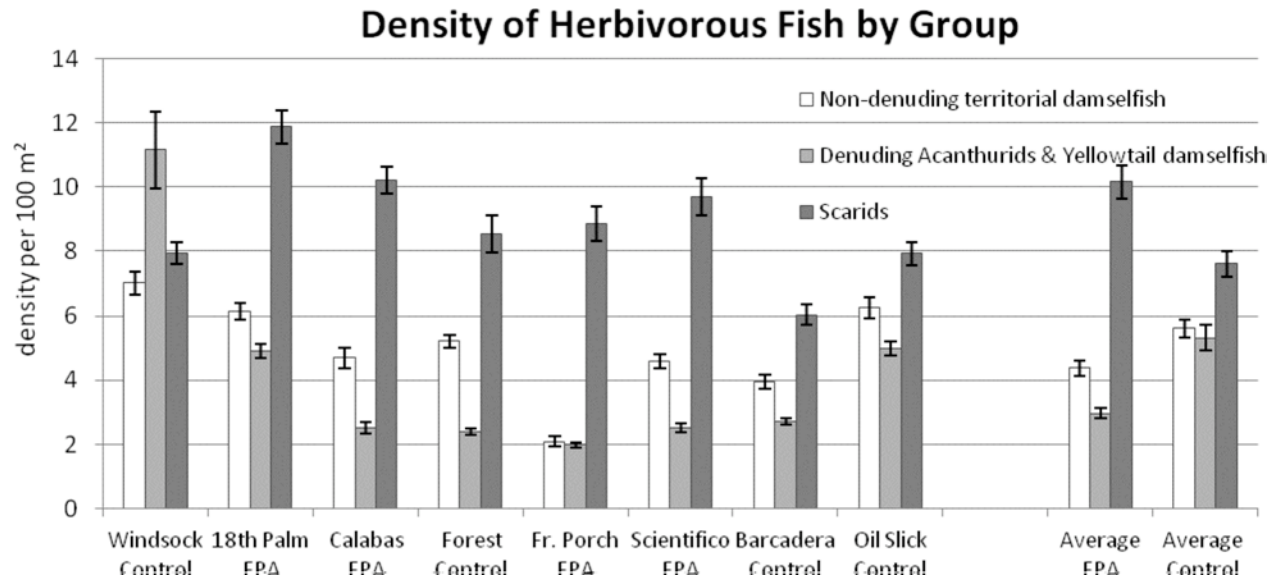


Figure 3. Comparative density of herbivorous fish groups. Error is one \pm standard error.

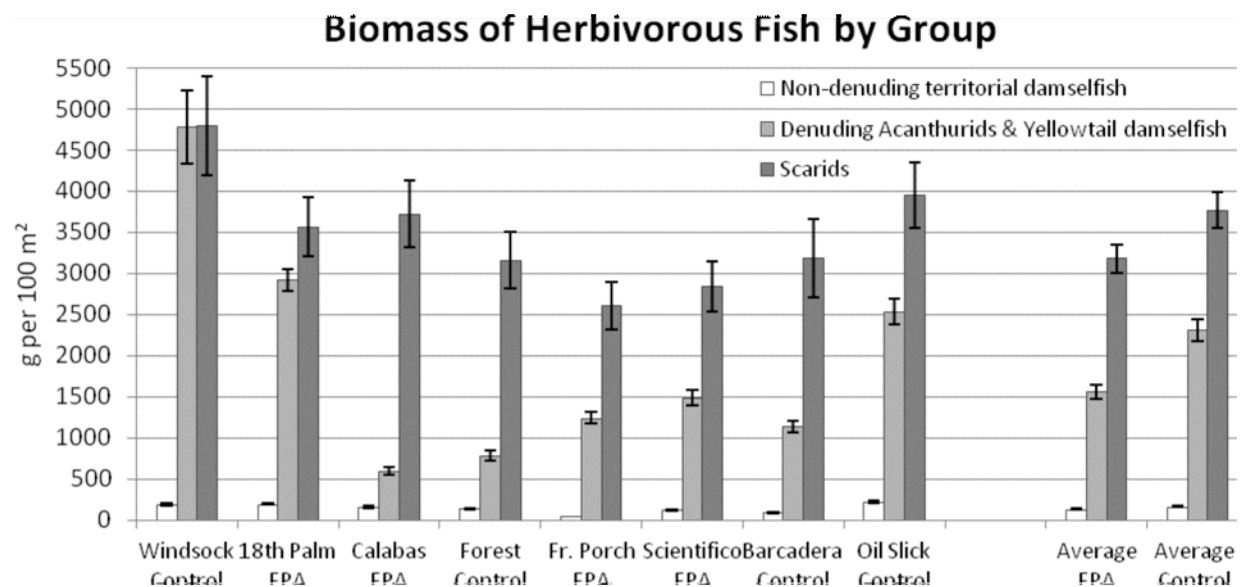


Figure 4. Comparative biomass of herbivorous fish groups. Error is one \pm standard error.

Trends over Time

Scarid surveys for this study included only initial and terminal phase scarids (juveniles were not surveyed). 2007 data is shown as recorded without juvenile scarids. *Data from 2003 and 2005 were adjusted to remove juvenile scarids by deducting the ratio (32%) and mean biomass (3 g) of juvenile scarids derived from the data of a 2005 site.

The density of acanthurids and scarids from 2003-9 shows a pattern of significant decline (ANOVA: $F_{3,39}=4.94$, $P=.006$) (Fig. 7). This trend is amplified by the significant reduction of scarids (ANOVA: $F_{3,19}=14.20$, $P=6.56\text{-}5$) (Fig. 5). Acanthurid abundance does not show variation, but their biomass is has significant variation with an increasing trend over the last five years (ANOVA: $F_{3,19}=3.27$, $P=.05$) (Fig. 6 and Fig. 9). Of particular importance is the extreme variation in scarid biomass (ANOVA: $F_{3,19}=20.60$, $P=9.66\text{-}6$). The reduction of scarid biomass outweighs any improvement contributed by acanthurids. Combined biomass of the two families continues in a significant downward trend over time (ANOVA: $F_{3,39}=4.12$, $P=.01$) (Fig. 10).

Distribution of acanthurids and scarids from 2003 to 2009 also exhibit a consistent trend of decreasing density and biomass along a south to north axis. This pattern is driven by the high abundance of acanthurids at Windssock and Eighteenth Palm (Fig. 6).

Scarid Phase and Size in Fish Protected Areas and Control Sites

Comparisons of scarids by developmental phase and site type are presented in Fig. 11-16, App. B and App. C. Density of initial phase scarids was 64% higher in the FPAs than the control sites (Fig. 11 and Fig. 12). Greatest abundance was noted for *Scarus* initials within the FPAs (App. B). Two-way ANOVA analysis demonstrated significantly greater biomass by genera (*Scarus* and *Sparisoma*) and site type, with overall ANOVA values of $F_{15,127}=10.52$, $P=6.00\text{E-}5$ (App. B). Terminal phase scarid biomass in the FPAs (1958 g/100²) was 28% less than in the controls (2712 g/100²). Greatest biomass was represented by terminal phase males at Windssock (Fig. 13, Fig. 14, App. C).

Scarid size was significantly different between FPAs sites (mean 23.9 cm) and control sites (mean 27.6 cm), ANOVA: $F_{7,63}=6.18$, $P=.004$. Initial phase scarids in the FPAs had a mean size of 20.7 cm, while initials in the control sites were 24.0 cm. Initials also had significant variation in size (ANOVA: $F_{7,63}=5.72$, $P=.005$) (Fig. 15 and Fig. 16).

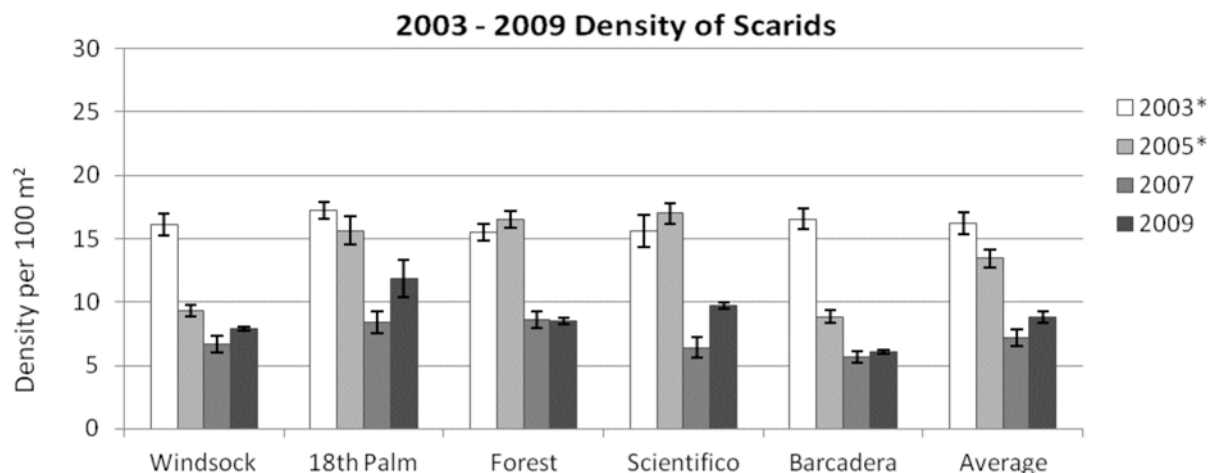


Figure 5. Scarid densities at five sites 2003 – 2009. Error is one \pm standard error.

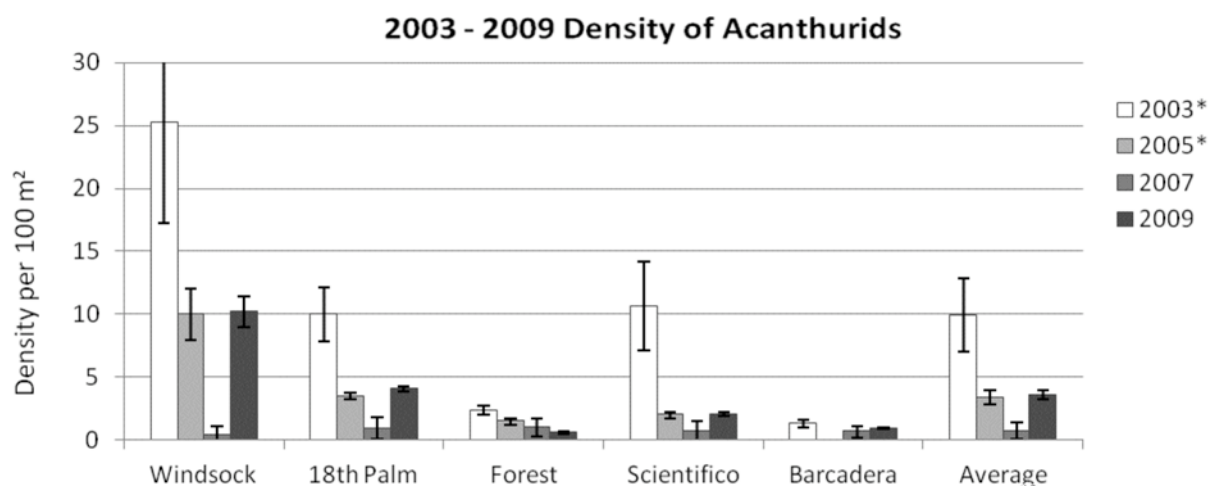


Figure 6. Acanthurid densities at five sites 2003 – 2009. Error is one \pm standard error.

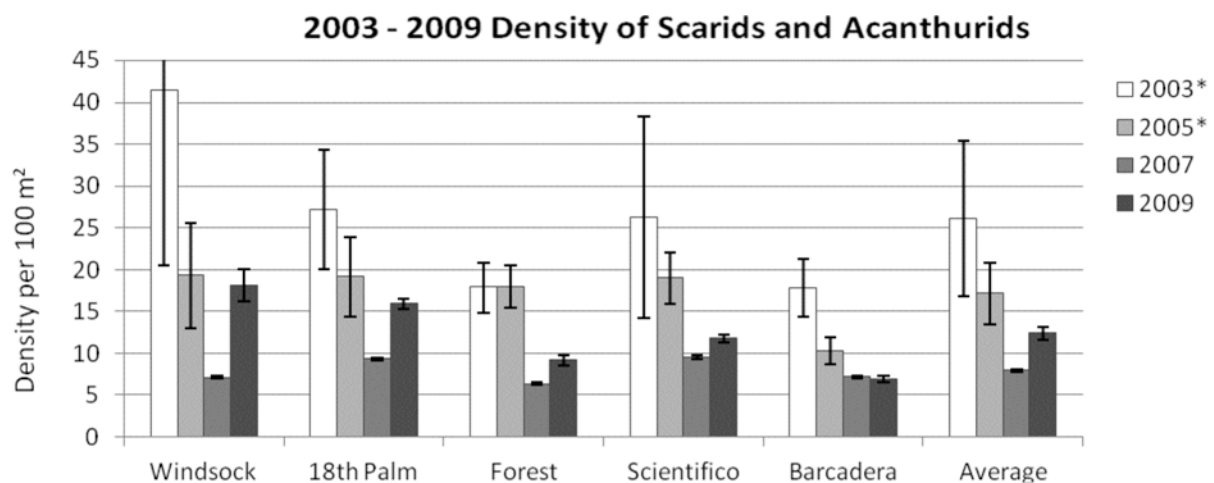


Figure 7. Combined scarid and acanthurid density 2003 – 2009. Error is one \pm standard error.

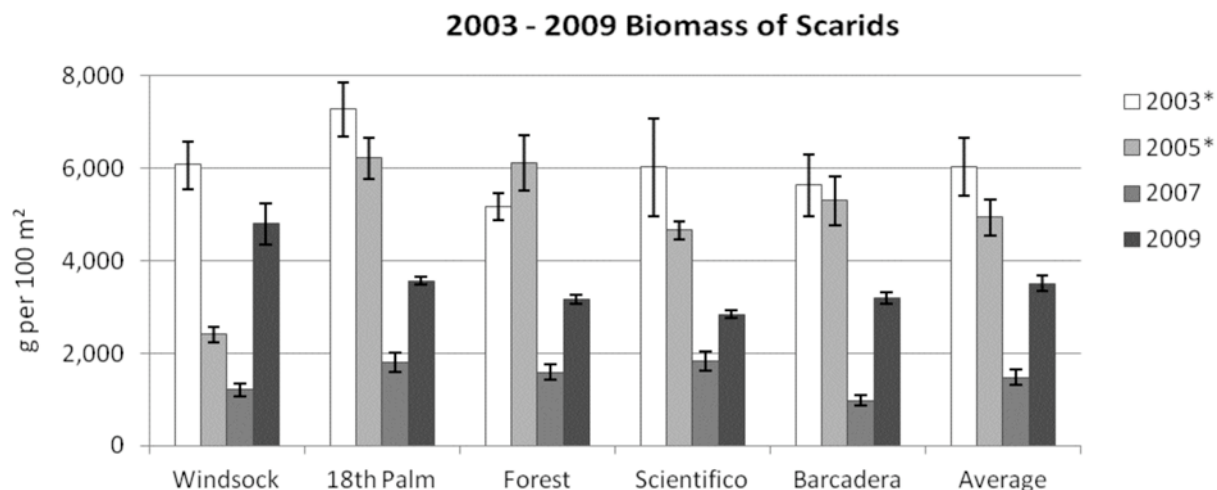


Figure 8. Scarid biomass at five sites 2003 – 2009. Error is one \pm standard error.

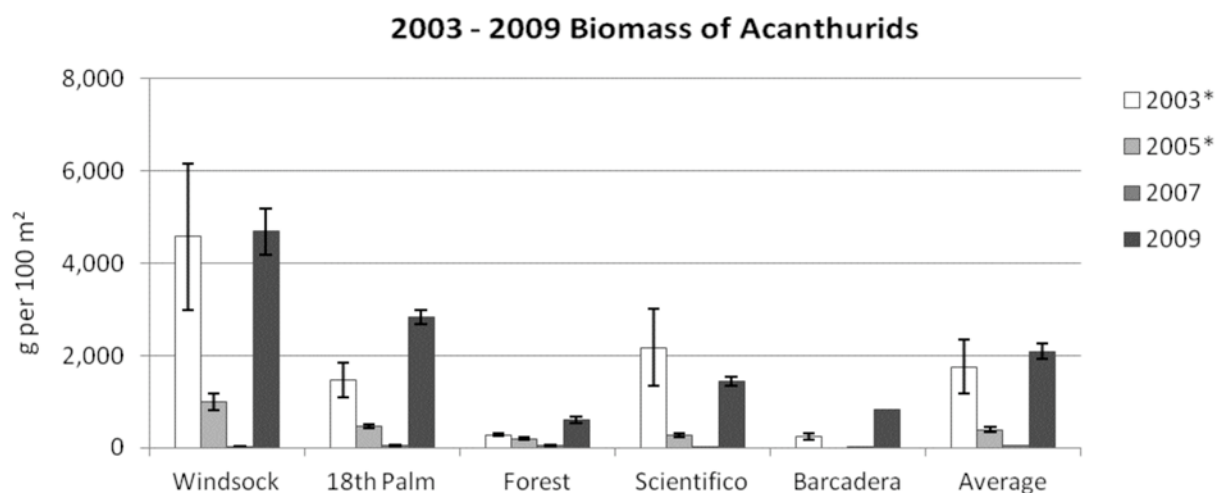


Figure 9. Acanthurid biomass at five sites 2003 – 2009. Error is one \pm standard error.

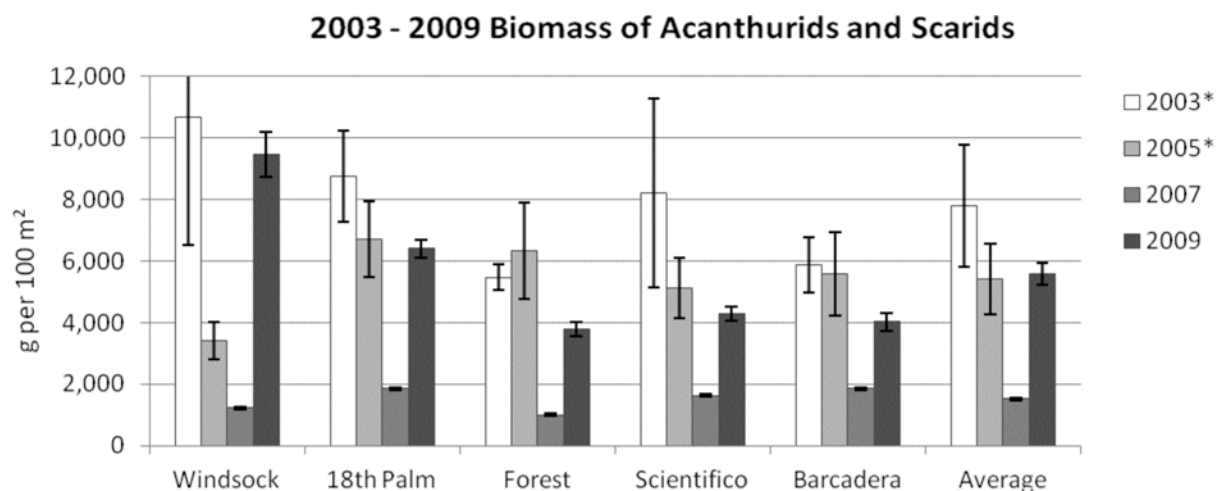
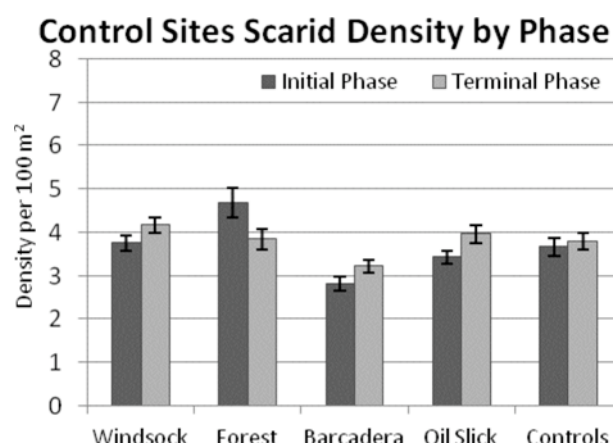
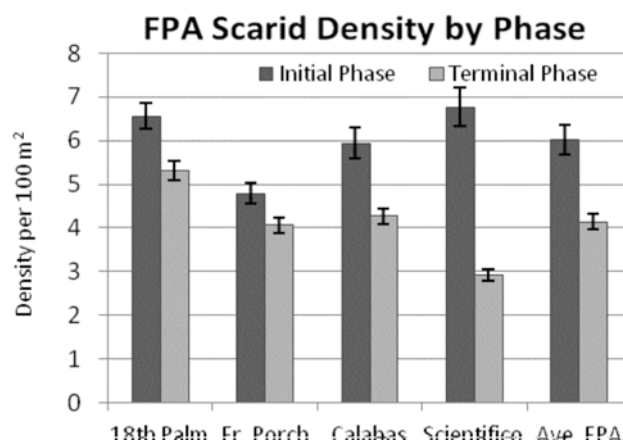
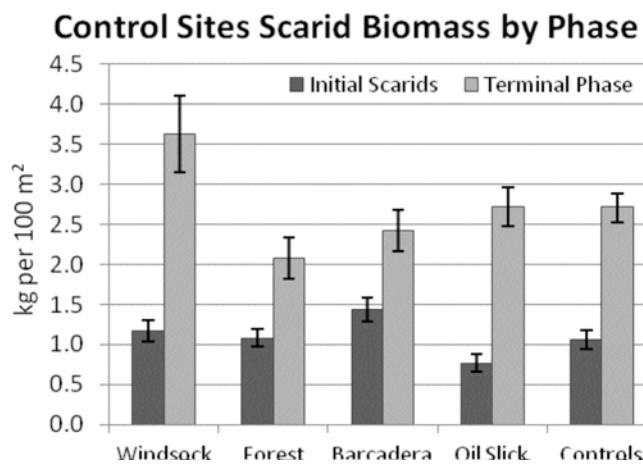
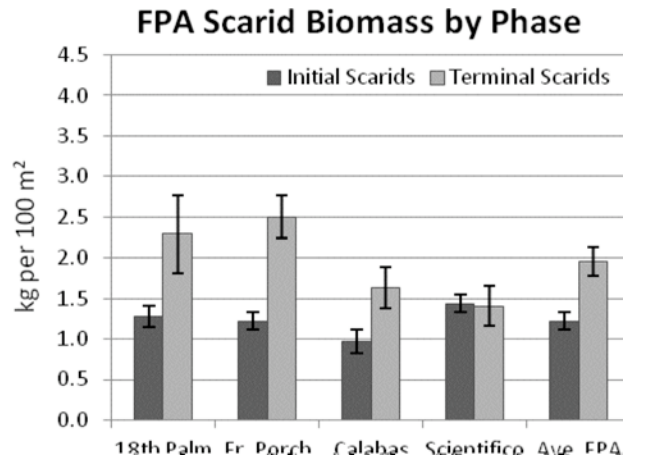


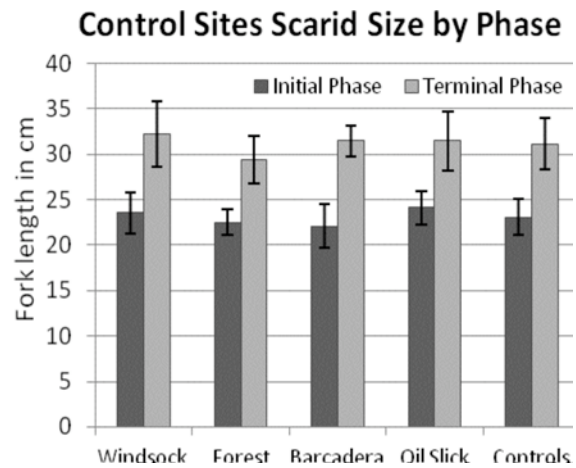
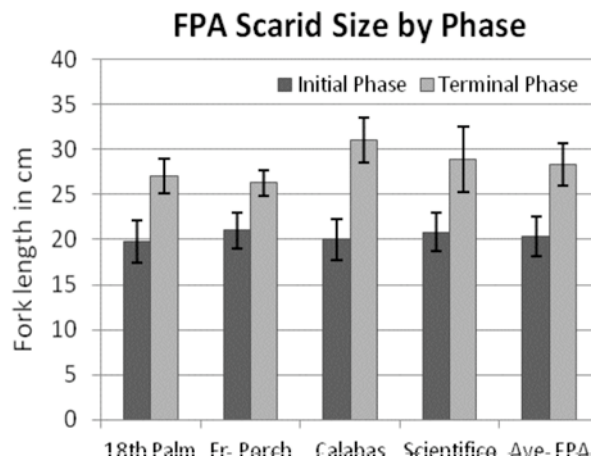
Figure 10. Scarid and acanthurid biomass 2003 – 2009. Error is one \pm standard error.



Figures 11 and 12. Scarid population densities in FPAs and controls subdivided by developmental phase. Error is one \pm standard error.



Figures 13 and 14. Scarid population biomass in FPAs and control sites subdivided by developmental phase. Error is one \pm standard error.



Figures 15 and 16. Mean sizes of scarids in FPAs and control sites subdivided by developmental phase. Error is one \pm standard error.

Discussion

The distribution of algal removing herbivorous fish in Bonaire plots a U-shaped curve, peaking in the south and north. The dominant reef fish family, *Scaridae*, play a disproportionately large role in sustaining herbivorous biomass. Over time, abundance of the most effective algal removers, scarids and acanthurids, has decreased. Scarid abundance is highest in the FPAs, which harbor 64% more initial phase scarids than controls, and a significantly greater proportion of females and smaller (younger) fish.

Reef health can be measured by the ability of a reef to resist environmental stress. Desirable characteristics include maintaining coral cover during phase shifts, and the ability to rapidly regenerate following catastrophically destructive events, such as a hurricane (Knowlton 1992, Lesser 2004). On Bonaire, these two factors of coral reef resilience are directly correlated to the herbivorous fish that feed on the macroalgae (Hughes 1994, Bellwood *et al.* 2004). Since the rapid and weedy growth of macroalgae easily outpaces the rate of coral growth, herbivorous fish, particularly scarids, are key indicators of a reef's resilience to withstand long-term phase shifts and short-term catastrophic events (Mumby and Edwards 2007).

Windsock had the highest density and biomass of herbivorous fish, which is consistent with the low algal index cover concurrently recorded in this report by Steneck (2009). The biomass of algal removing fish in control sites was 128% greater than the FPAs. High herbivorous biomass appears linked to their low algal index (Mumby and Edwards 2007, Steneck 2009). This is indicative of the scarid role in controlling macroalgal.

The herbivores most highly targeted by fishers are large terminal scarids. Although their density is effectively equal among treatments, 4 per 100 m², biomass of terminals in the fished controls is 38% greater (considerably more meat per catch). While the FPAs are less productive for fishers, they foster a greater abundance and ratio of initial phase scarids (females and immatures). This evidence suggests these sites are preferred nursery and transitional habitats. As a before and after controlled impact experimental design, it is too soon to judge the effectiveness of the FPAs. However, this baseline analyses may help assess future trends, effectiveness and selection of FPAs (Roberts *et al.* 2001).

Critical habitat provides protection for species at vulnerable points in their life cycle, or during catastrophic events. The concept of ecosystem connectivity comprises habitat for larval nurseries, juveniles, transitionals, and connective corridors in-between. By protecting additional habitat types known to provide reef system connectivity, Bonaire's algal removing fish and corals would both benefit. Mangroves and sea grass beds are preferred nurseries and sheltering areas for many species, including scarids. Expansion and protection of mangroves and sea grass beds would be excellent additions to Bonaire's fish protected areas (Mumby and Steneck 2008).

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Chapter 3: Herbivory on Bonaire's reefs: Spatial and temporal trends in species and group specific grazing frequencies.

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Abstract

Herbivores are key components of coral reef ecosystems. Rates of herbivory are a factor of the number of herbivores present, the percent grazable substrate and the strength of interactions among herbivores and their environment. This study quantified bite rates of herbivorous fish found on the leeward reefs of Bonaire to understand the spatial and temporal trends in grazing frequency. By far parrotfish (Scaridae) were the most important herbivores at 10m depth. Majority of the scarid bite rates consisted of bites from small or medium sized, juvenile or initial phased princess parrotfish (*Scarus taeniopterus*) and were positively density dependent. Analysis of bite marks on coral settlement plates provides evidence for a competitive interaction between *Scarus* sp. and *Sparisoma* sp. On average there were territorial damselfish present in more than 80% of the quadrats surveyed and this had an adverse effect on the bite rates of scraping (scarids) and denuding herbivores (acanthurids and yellow tail damselfish). The significant decline in Scarid bite rates from 2005 to 2009 is a cause of concern and this report stresses the need to understand the mechanisms that have lead to the decline of scarid bite rates in order to prevent a phase shift of a coral dominated system to a macroalgal dominated one. A year since the establishment of Fish Protected Areas (FPA) in Bonaire, this study also compared bites rates within FPA and outside of them and found no significant difference between the two. This study sets the grazing frequency baseline for future studies on the effectiveness of the established FPAs in Bonaire.

Introduction

Herbivory is a key ecological driver responsible for maintaining low algal biomass in coral reef ecosystems (Mumby and Steneck 2008). In the Caribbean, the importance of vertebrate herbivores (scarids and acanthurids) became evident after the mass mortality (1983-84) of the then hyperabundant herbivorous sea urchin, *Diadema antillarum*, when the shift from coral to macroalgal systems was less severe (if at all) for reefs with intact grazing fish populations (Williams and Polunin 2001). Evidence for the fact that herbivory exerts the dominant impact on macroalgal abundance (Mumby and Steneck, 2008) can be found in large scale correlative studies that have shown an inverse relationship between macroalgal abundance (biomass or macroalgal index) and herbivorous fish abundance (biomass or density) (Williams and Polunin 2001, Kramer 2004). Additional evidence comes from manipulative studies that have caused experimental phase shifts from coral dominated to algal dominated systems by the simple exclusion of herbivorous fish (Hughes et al. 2007). In absence of herbivores, heavily fished reefs (e.g. Jamaica) shift to macroalgal reefs (Williams and Polunin 2001), thus highlighting the importance of maintaining healthy herbivorous fish populations for reef resilience through effective management and regulation.

Herbivorous fish can differ significantly in their impact on algal communities and thus are functionally divided into Scrapers (Excavators), Denuders and Non-denuders (sensu Steneck 1988). Deep grazing parrotfish (Scaridae) fall under the “Scraping or Excavating” functional group and have the greatest impact on algal biomass, where as on the other hand “Denuders” such as acanthurids and certain pomacentrids (e.g. blue tang, *Acanthurus coeruleus* and the yellowtail damselfish, *Microspathodon chrysurus*) are only able to significantly impact algal assemblages at high population densities. Most pomacentrids (e.g. Damselfish, *Stegastes* sp.) have a limited ability to reduce algal biomass and fall under the “Non-denuding” herbivore functional group (Steneck 1988). Most pomacentrids within the non-denuding herbivore group are territorial grazers that maintain and defend their territories against other herbivores thereby reducing the grazing impact of scrapers (excavators) and denuders inside and in close proximity to their territories (Steneck 1988, Hixon 1997). In addition to these three main herbivore functional groups, certain authors have tried to classify scarid species as “Scrapers” or “Excavators” based on morphological and behavioral differences. “Scrapers” tend to produce scraping bites that consist of two parallel shallow grooves and the length of a groove is ten times its width (Bellwood and Choat 1990). On the other hand “Excavators” produce bite scars that have 4-6 deep grooves and the length of the groove is twice its width (Bellwood and Choat 1988). Depending on the species, size and stage, Streelman et al. (2002) identified most *Sparisoma* sp. to be excavating. Where as, *Scarus* sp. were defined to be a scraping species with smoother teeth and weaker jaws and musculature (Bellwood and Choat 1990, Bruggeman et al. 1994, Streelman et al. 2002). The smaller scrapes of scrapers tend to be rapidly reoccupied by algae via vegetative regrowth but the deeper larger scars produced by excavators, that tend to not only remove the algae but also some of the substrate beneath them, remain clear for several days until algae recruits to the scar (Bruggeman et al. 1994, Bonaldo and Bellwood, 2009). There is a fine line between scrapers and excavators which is often crossed at small and very large sizes of *Sparisoma* and *Scarus* (Bonaldo and Bellwood 2008, in situ observations).

In this study herbivore grazing frequencies (bite rates) were quantified on the shallow reefs (10m) of Bonaire, Netherland Antilles. In the beginning of 2008, the national parks foundation of Bonaire, STINAPA, closed off two areas on the leeward side to bottom fishing (STINAPA). Study sites were chosen based on availability of past survey data and new sites were added to monitor the effects of the Fish Protected Area (FPA). These sites going from South to North include: Bachelor’s beach^c, Windsock^c, Eighteenth Palm^f, Calabazas Reef^f, Front Porch^f, Reef Scientifico^f, Barcadera^c, Oil Slick Leap^c, Karpata^c and Forest (regional control site on Klein Bonaire)^{c1}. Spatial or temporal differences in bite rates can be either due to changes in the grazable substrate (decline in coral cover or other algal inhibiting substrates, Mumby and Steneck 2008) or changes in herbivore abundance or changes in the strength of ecological interactions that may have a direct or indirect impact on herbivory (e.g. inter or intraspecific competition, territoriality, habitat effects etc.). Thus to better understand herbivory on Bonaire’s reefs multiple variables such as species specific bite rates, herbivore size and life stage, substrate type, bite topography and presence of territorial damselfish were recorded. Additionally, bite marks found on coral settlement plates were also analyzed to test for competitive interactions between *Scarus* sp. and *Sparisoma* sp.

¹ c = control site, f = FPA site. FPA established in 2008

Materials and Methods

Bite rate data was collected on the leeward reefs of Bonaire, Netherlands Antilles from March 3rd to March 13th 2009. For each site at a depth of 10m (± 0.5 m), a minimum of seven 1 m² quadrats with an epilithic algal cover greater than 60% were chosen and observed for 5 minutes each. During the 5 minutes, the number of bites taken within the quadrat was recorded along with the herbivore species, life stage (juvenile phase, initial phase, and terminal phase) and size (total length). Type of substrate topography (high or low) was recorded for the bites. Additionally, algal canopy height, time of day, presence and absence of territorial damselfish were also recorded. The data was entered into excel and was analyzed using excel and Systat 12.

In addition to this in-situ observational study, bite marks found on coral settlement plates from past experiments were also analyzed. The plates that were analyzed were from PED and PED control treatments² deployed in March of 2007 and recovered in March of 2008. Coral settlement plates (Arnold and Steneck 2007) were acid washed and scrubbed to remove crustose coralline algae. Parrotfish bite marks were easily visible on the terracotta plates and were measured and counted under the microscope. *Scarus* and *Sparisoma* bite marks were identified based on in situ observations and published studies (Bellwood and Choat 1989, Streelman et al. 2002, Bonaldo & Bellwood 2009). When visual identifications didn't produce any clear trends due to the high number of questionable marks, we used the ratio between length and width of the mark to determine if it was a scraper (e.g. *Scarus*) or excavator (e.g. *Sparisoma*) (Bellwood and Choat 1989, Streelman et al. 2002). Bellwood and Choat (1989) found that on average the length to width ratio was 10 for scrapers and 2 for excavators. The length to width ratio frequency distribution of the plate bite data set showed nodes around these values with a cut off around 6, thus in the dataset anything above or equal to a ratio of 6 was considered a scraper (i.e. *Scarus*) and anything below was considered an excavator (i.e. *Sparisoma*).

Results & Discussion

The average hourly bite rate observed in Bonaire was 120 bites / m² (Figure 1a). Herbivorous fish species that were observed biting algal substrate include; queen parrotfish (*Scarus vetula*), princess parrotfish (*Scarus taeniopterus*), striped parrotfish (*Scarus isteri*), stoplight parrotfish (*Sparisoma viride*), redband parrotfish (*Sparisoma aurofrenatum*), blue tang (*Acanthurus coeruleus*), yellowtail damselfish (*Microspathodon chrysurus*), longfin damselfish (*Stegastes dieneaeus*), three-spot damselfish (*Stegastes planifrons*) and bicolor damselfish (*Stegastes partitus*). Scarids were the dominant herbivore group observed in Bonaire (Figure 1b). Denuding (acanthurids and yellowtail damselfish) and non-denuding (damselfish) fish species constituted a very small portion of the total bites observed (Figure 1c&d).

² The parrotfish exclusion device treatment (referred to as a "PED") consisted of a stainless steel matrix of 12, 6 inch stainless steel bolts protruding up from a star-like stainless steel base, designed to impede large parrotfish from grazing around the edges of the coral settlement plates. The PED controls were identical to the PED except the 6 inch bolts were missing to allow herbivores of all sizes access to the settlement plate.

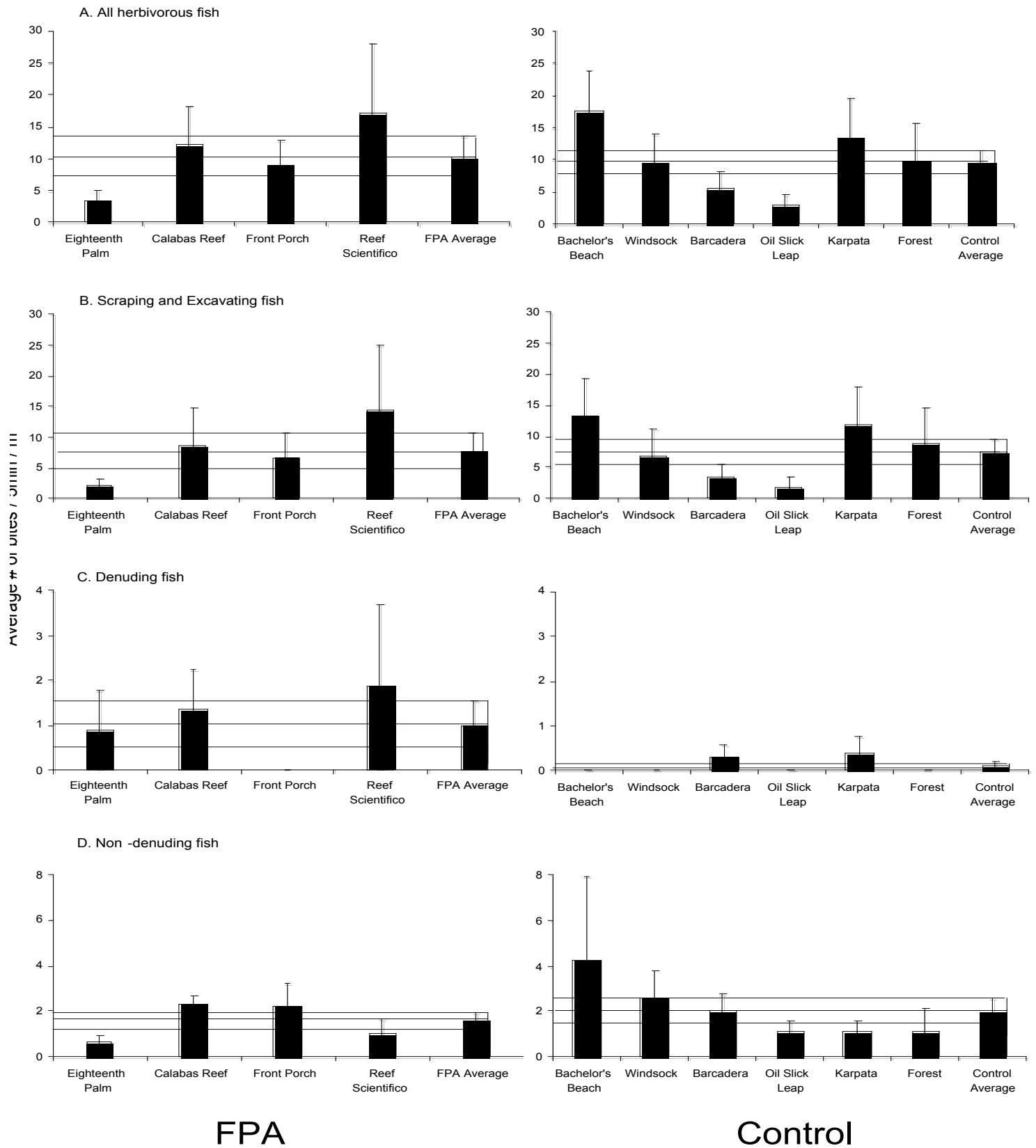


Figure 1. Average # of bites / 5min / m² at the study sites, the graphs on the left show FPA sites where as the graphs on the right contain control sites. Sites are arranged from South to North (L to R). a) Bite rates of all herbivores (Scaridae, Acanthuridae and Pomacentridae), b) Bite rates of Scrapers and Excavators (Scaridae), c) Bite rates of Denuders (Acanthuridae and yellowtail damselfish) and d) Bite rates of Non-denuders (Pomacentridae). Error bars denote \pm standard error. Horizontal lines indicate the error and the mean of the average bite rates for control or FPA sites for each graph. Note the change in scale of y axis among groups.

Impact of territorial damselfish on grazing frequency of scrapers, excavators and denuders

Territorial damselfish were present in more than 60% of the quadrats at each site (Figure 2a) and this seemed to have an adverse effect on the bite rates of scrapers, excavators and denuders, where sites with a lower percent of damselfish present had higher bite rates and vice versa (e.g. Reef Scientifico and Oil Slick Leap, Figure 2b).

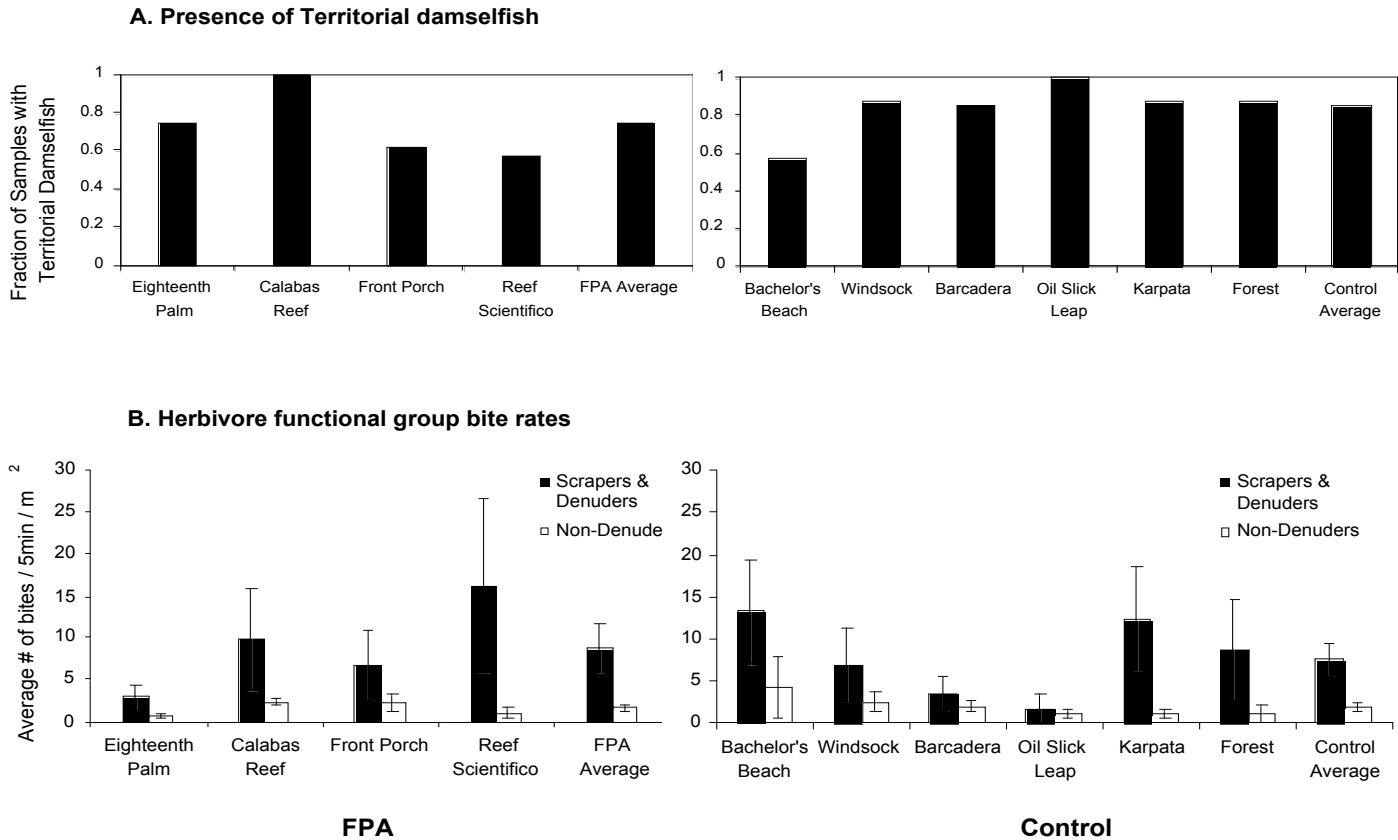


Figure 2. a) Fraction of quadrats with territorial damselfish per site b) Bites rates (Average # of bites / 5min / m²) of scraping & denuding (scarids, acanthurids and yellowtail damselfish) and non-denuding (pomacentrids) fish as a function of site (Error bars denote \pm standard error). The graphs on the left contain the FPA sites while those on the right have the control sites both going from South to North.

By altering algal succession territorial damselfish (pomacentrids) are able to establish and maintain distinct filamentous algal mats on reefs which in turn have higher rates of primary productivity and local species diversity (Hixon 1997). Even though territorial damselfish may have a positive effect on local species diversity and algal productivity within their territories, an abundance of damselfish can be quite detrimental to coral reefs. Damsel fish can effectively reduce scarid and acanthurid bite rates by their aggressive territorial behavior (Steneck 1988, Fig. 2, 3 & 4). Thick algal turfs that are maintained in damselfish territories trap sediment and exclude growth of corallines (Steneck 1997) and thus are areas of lower coral recruitment (Arnold and Steneck 2007).

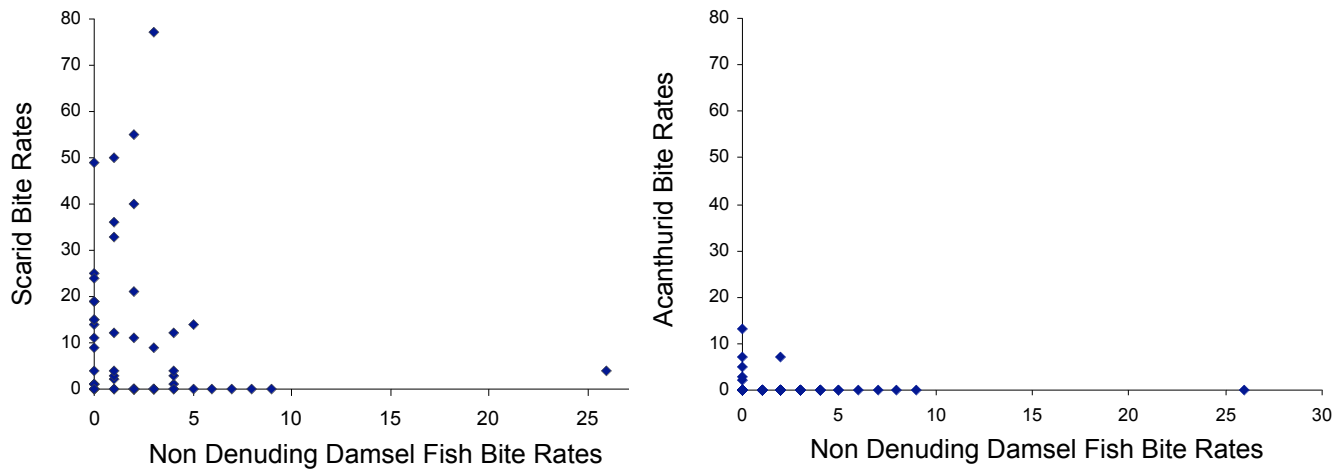


Figure 3. Average Bite rates (# of bites / 5min / m²) of scarids (left) and acanthurids (right) as a function of damselfish bite rates (# of bites / 5min / m²).

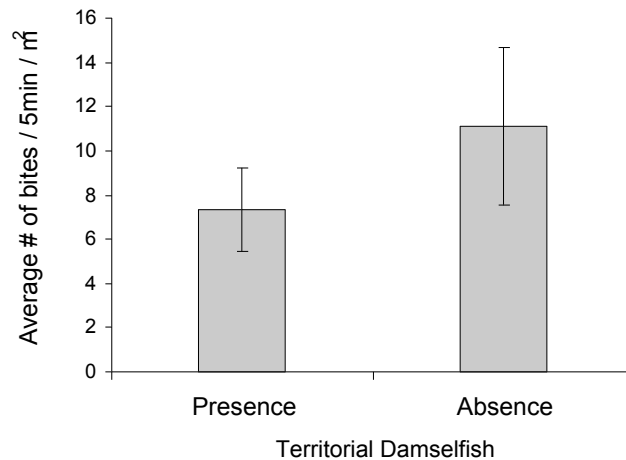


Figure 4. Bite rates (Average # of bites / 5min / m²) of scrapers, excavators and denuders (scarids, acanthurids and yellowtail damselfish) in the presence and absence of Territorial damselfish (x-axis).

Even when reefs have high abundances of scarids and acanthurids, their denuding effect on algae may be suppressed in the presence of territorial damselfish ($p=0.376$, Figure 4) which in turn suppress coral recruitment making reefs more vulnerable (Arnold and Steneck 2007). Thus, monitoring damselfish numbers is important to determine the health of coral reef ecosystems, the hyperabundance of which may be indicative of a decline in predator abundances.

Herbivory in Scaridae

Scarids are the dominant reef herbivores in terms of population density, biomass and grazing intensity (Steneck 1988, Mumby 2006, Bonaldo and Bellwood 2008, Figure 1). In the absence of parrotfish grazing, benthic algal biomass increases thereby reducing the propensity of coral larvae to settle to the substrate. Understanding where parrotfish target their grazing effort helps us understand the dynamic between parrotfish grazing and coral settlement. There was a

significant difference between bites on high (convex or flat) substrates than low (concave) ($p=0.00$) for the Scaridae family, the genus *Scarus* and the genus *Sparisoma* (Figure 5) thus indicating that rather than freeing up coral settlement habitat (topographic lows and on the under sides of reef structures), parrotfish grazing increases the propensity of coral to settle due to the relative low algal biomass. In order to observe the differences in bite topography observed by Bellwood and Choat (1990) and *Sparisoma* Bruggemann et al. (1994), one would have to distinguish between convex and flat surface as *Scarus* has been known to shown no preference between the two where as *Sparisoma* seems to feed primarily on convex surfaces.

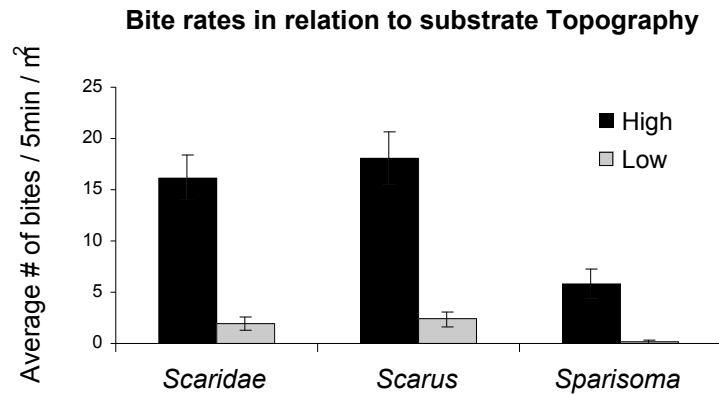


Figure 5. Scarid bite rates (Average # of bites / 5min / m²) in relation to substrate topography (High = Convex or flat and Low = Concave). Error bars denote \pm standard error.

When scarid bite rates are separated according to size, stage and species, it is evident that most scarid bites come from small or medium sized, juvenile or initial phase, *Scarus taeniopterus* (Figure 6). The scarid bite rate patterns observed here relate well to those observed by Steneck (2009) concerning the benthic algal index (percent cover multiplied by the canopy height) and percent cover of crustose corallines. At high grazing frequencies benthic algae are maintained at low levels as observed in Reef Scientifico (Figure 6 and Steneck 2009). Similarly larger and older *Scarus vetula* and *Sparisoma viride* species may be responsible for the low algal index and or high coralline cover observed in Front Porch, Barcadera and Oilslick Leap despite the relatively low grazing frequency (Figure 6 and Steneck 2009).

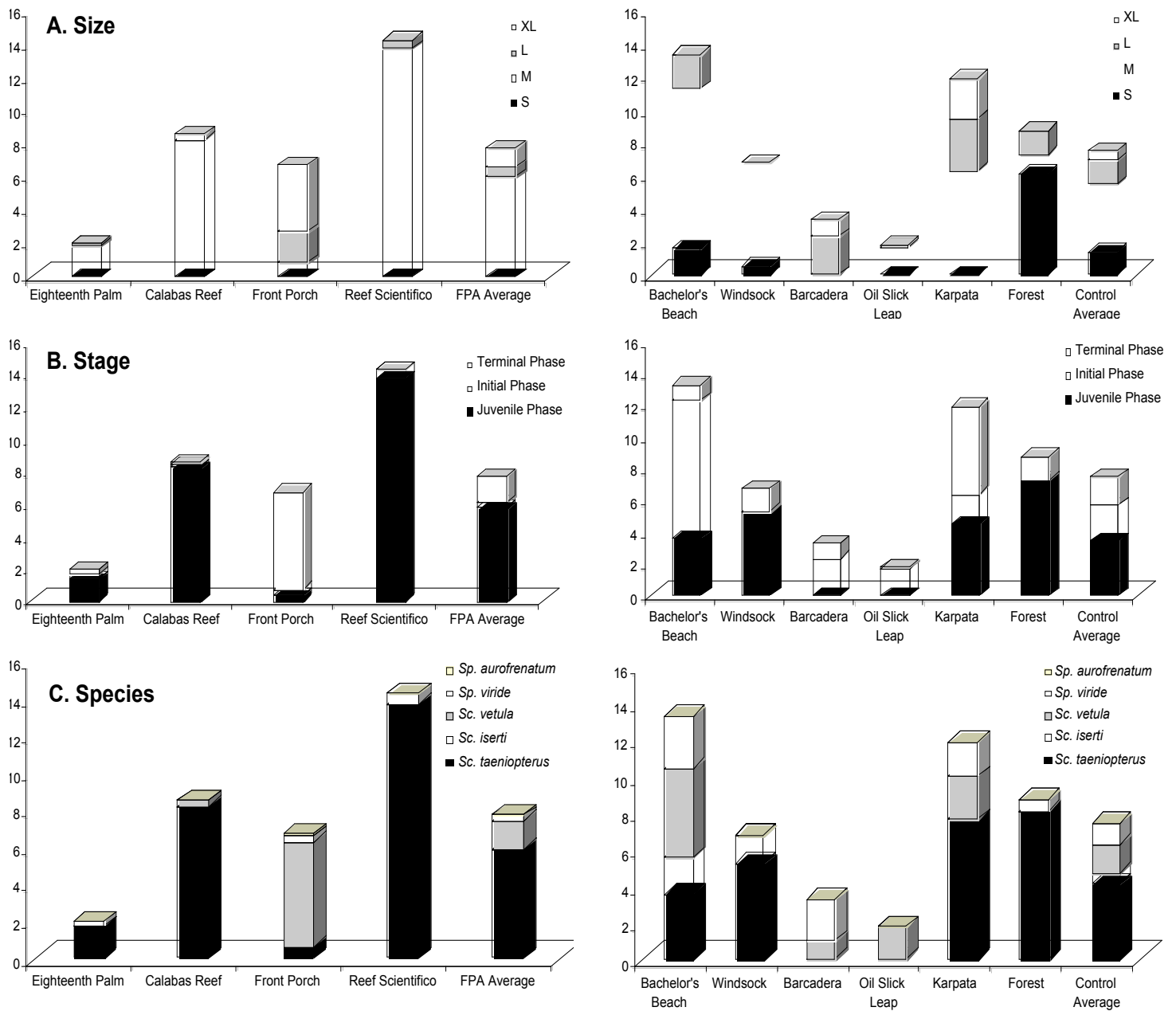


Figure 6. Scarid bite rates as a proportion of fish a) Size b) Life stage and c) Species. Average bite rates (# of bites / 5min / m²) on y-axis and sites on x-axis. Graphs on the left contain the FPA sites whereas graphs on right contain control sites, all sites range from South to North (L to R). *Sparisoma aurofrenatum* bite rates were observed in front porch only. Scarid size classes: S <13cm; M 13-20cm; L 21-30cm; XL >31cm Total Length (TL) based on TL of species from Humann and DeLoach, 2002.

The observed patterns of species specific bite rates (Figure 6) raises the question of connection between bite rates and population densities (Figure 7). A significant positive density dependent relationship between scarid species bite rates and their population density was observed for princess parrotfish (*Scarus taeniopterus*, $R=0.825$, $p=0.012$, Figure 7). Absence of a similar relationship between other species of scarids may be due to the lack of bite rate data present for

them (Figure 7). Although not significant ($p \approx 0.3$), negative correlations between population density and bite rates were found for queen parrotfish (*Scarus vetula*) and stoplight parrotfish (*Sparisoma viride*) and these might indicate the occurrence of competition in these grazing species as highlighted by other studies (Mumby and Wabnitz, 2002). Scarid bite rates are dominated by *Sc. taeniopterus* (Figure 6c), most of which were small or medium in size and in their juvenile or initial phase of development (Figure 6a & b). Higher abundances of smaller scarid species (*Sc. iserti* and *Sc. taeniopterus*) in comparison to the larger ones (*Sc. vetula* and *Sparisoma viride*) should be of concern to managers due to the lower consumption of algae (grazing intensity) offered by smaller scarids.

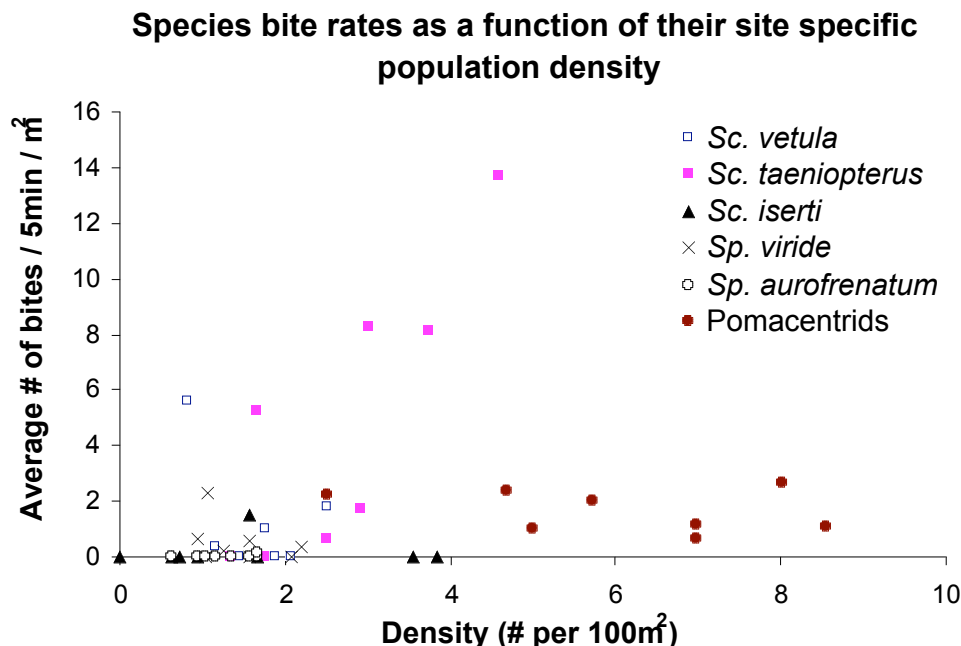


Figure 7. Relationship between species bite rates and density. Density data from Appendix A (Eldridge, 2009). Significant positive correlation between *Scarus taeniopterus* bite rates and density ($R = 0.825$, $p = 0.012$). All other species specific correlations were not significant.

Analysis of coral settlement plates for grazer bite marks helps provide insight into the interactions between herbivores. In 2007, settlement plates were deployed under various treatments (as explained under methods) to see the impact of herbivore exclusion on coral settlement and subsequent recruitment. Interestingly in Bonaire, Coral settlement (# of SPAT per plate) didn't differ between PED plates and PED control plates in comparison to other areas (Figure 8, Arnold unpublished data). The Parrotfish Exclusion Devices (PED) didn't seem to work in Bonaire, the initial increase in benthic algal abundance within PEDs may have attracted parrotfish that live in a low algal biomass ecosystem like Bonaire. The bite marks on plates were measured and recorded by Steneck and Mumby in 2008 (unpublished) and showed that PED (P) plates had more bites than naked (N) or PED control (PC) plates (Figure 9). Most bites were small to medium in size.

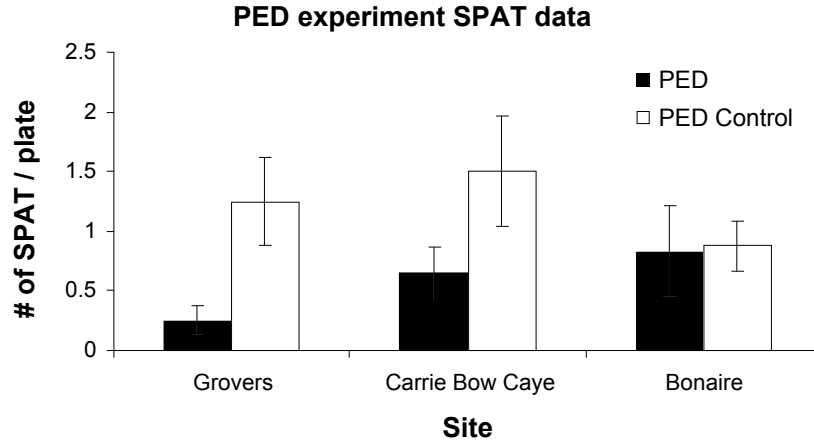


Figure 8. Average # of coral SPAT per settlement plate observed in Grovers, Carrie Bow Caye and Bonaire on PED and PED control treatments. Plates were deployed in March 2007 and retrieved in March 2008. Error bars denoted ± 1 SE. (Arnold, unpublished data)

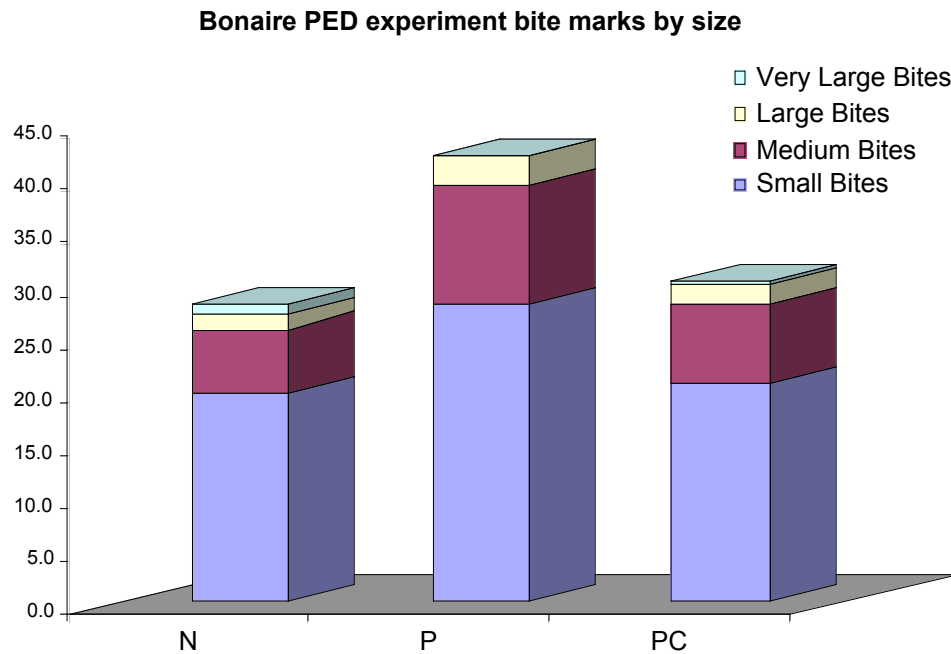


Figure 9. Average # of bite marks separated by size observed on Naked (N), PED (P) and PED control (PC) treatments in Bonaire. Plates were deployed in March 2007 and retrieved and analysed in March 2008. (Steneck and Mumby, unpublished data).

I used a subset of the plates analyzed by Steneck and Mumby (unpublished, Figure 9) and measured and identified the bites based on the criteria mentioned in the methods. Interestingly PED plates had more *Scarus* bites than *Sparisoma* bites ($p=0.002$), but there were no observable differences between the two in PED control plates (Figure 10). This may indicate a competitive interaction between the two, niche partitioning or that PEDs are better able to exclude *Sparisoma* sp. than *Scarus* sp. As a scraper *Scarus* may occupy a different niche than *Sparisoma* (excavator), for instance, studies have shown adult *Sparisoma viride* to graze on convex surfaces

and *Scarus vetula* to graze on flat surfaces (Bellwood and Choat 1990, Bruggemann et al. 1994). This evidence of interspecific competition and the fact that PEDs aren't able to completely exclude parrotfish is a sign of a healthy reef with surplus grazing.

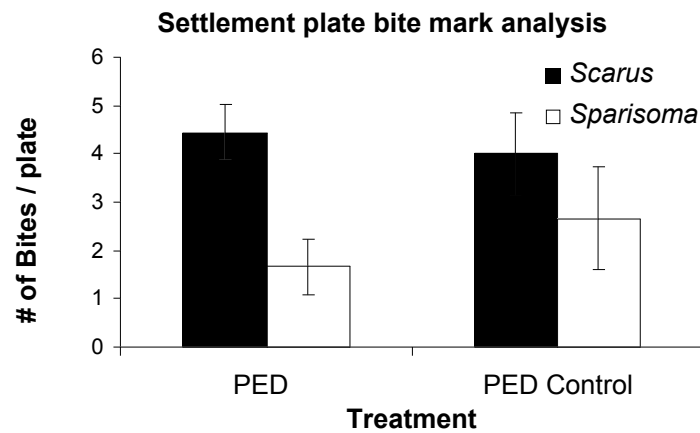


Figure 10. Average number of bites observed on PED and PED control plates. Bites identified as those of genus *Scarus* or *Sparisoma* using the length to width ratio. ($L/W < 6$ *Sparisoma*, $L/W \geq 6$ *Scarus*) based on Bellwood and Choat, 1990. Error bars indicate \pm SE. Significant difference between the numbers of *Scarus* vs. *Sparisoma* bites found on PED plates ($p=0.002$). Non-significant difference found in PED control ($p=0.21$).

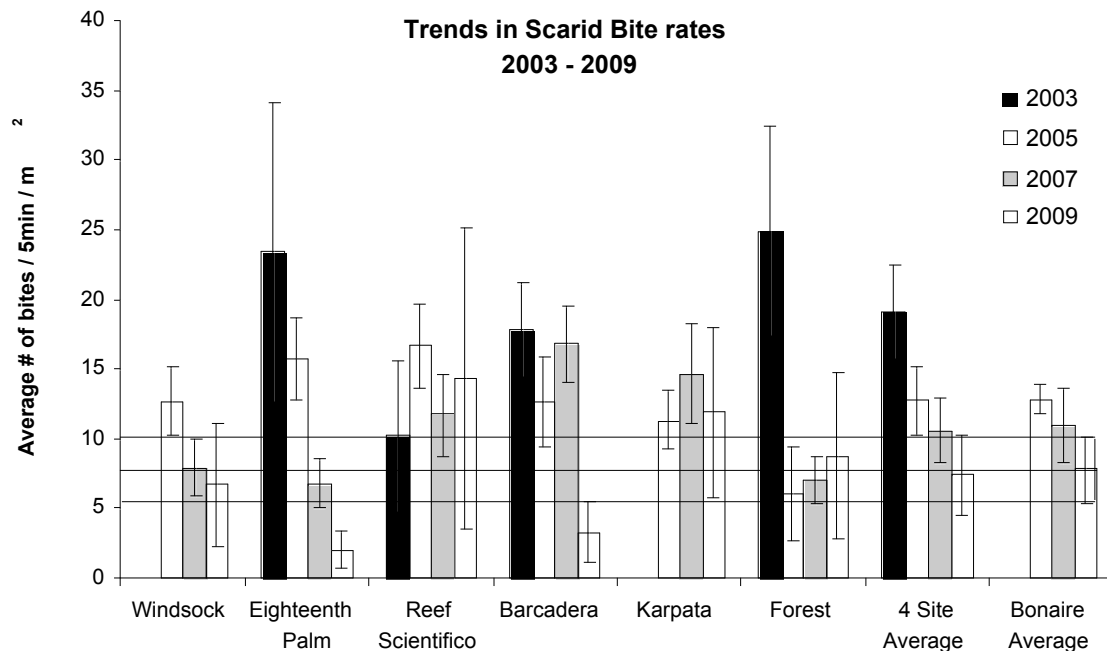


Figure 11. Spatial and Temporal trends in Scarid bite rates (Average # of bites / 5min / m^2). Error bars indicate \pm Standard error. Horizontal lines indicate the error and the mean of the average Bonaire bite rates for 2009. The four site average includes Eighteenth Palm, Reef Scientifico, Barcadera and Forest for all years. Bonaire average represents the mean of Windsock, Eighteenth Palm, Reef Scientifico, Barcadera, Karpata and Forest for, 2007 and 2009. Significant decline in average Bonaire bite rates from 2005 to 2009 ($p=0.034$). Data sources: 2003 (Steneck, unpublished data), 2005 (Brown and Hansen, 2005) and 2007 (Alvarado et al., 2007).

Scarid bite rates (Average # of bites / 5min / m²) have been monitored on the reefs of Bonaire since 2003 (Figure 11). For 2003 we have data for Eighteenth Palm^f, Reef Scientifico^f, Barcadera^c and Forest^c (Steneck, unpublished data). For 2005 and 2007 we have data for Windsock^c, Eighteenth Palm^f, Reef Scientifico^f, Barcadera^c, Oil Slick Leap^c, Karpata^c and Forest^c³ (Brown and Hansen, 2005 and Alvarado et al. 2007). There was a significant decline in average scarid bite rates from 2005 to 2009 for the above mentioned sites (p=0.034). The four site (Eighteenth Palm^f, Reef Scientifico^f, Barcadera^c and Forest^c) average showed a significant (p=0.027) decline from 2003 to 2009 (Figure 11). Eighteenth palm showed site specific significant declines from 2003 and 2005 to 2009 (p=0.000), and from 2007 to 2009 (0.009). Barcadera also showed a significant decline from 2003 and 2007 to 2009 (p=0.001), and 2005 to 2009 (p=0.005, Figure 11). The highest bite rates in Bonaire were recorded on Forest in 2003, since which forest has shown a significant (p=0.031) decline to present day levels (Figure 11). The significant decline in the Bonaire average of scarid bite rates from 2005 to 2009 (Figure 11) should be of concern to managers. Decline in bite rates of scarids (dominant scrapers and excavators on coral reefs) can lead to an increase in benthic macroalgae (Williams and Polunin, 2001, Kramer, 2004, and Hughes et al. 2007) and once a system shifts from coral dominated to algal dominated reefs its recovery can be almost impossible. The overall decline in Bonaire and the site specific decline in Eighteenth Palm and Forest could be due to changes in scarid abundances as documented by Eldridge (2009), changes in grazeable percent cover of the reef (Steneck 2009) or changes in the strength of the interactions between organisms that may affect grazing frequency (competition and territorial damselfish, Figure 2 & 7).

Spatial trends in bite rates: Control vs. FPA

There was no significant difference between average herbivore bite rates (average # of bites / 5min / m²) in sites outside of the FPA (Control) when compared to sites inside the FPA (Figure 1a). A year after implementation, the fish protected areas don't seem to have any affect on herbivorous fish bite rates when compared to the control areas (Fig. 1, 2 & 6). An increase in fish abundance and ecosystem health after the closure of an area may not be immediate, for example in a marine reserve in the Phillipines it took a few years for the positive affects on fish abundances to occur (Russ and Alcala, 1999). At a lower confidence level of 90% we can conclude that there is a significant difference (p=0.074) between Acanthurid bite rates within the FPA as compared to outside, however these denuders have a minor impact on algal biomass (Figure 1c). With the implementation of FPAs one expects an increase in fish abundance and density (Mumby and Steneck, 2008), but this result should be taken with caution. Due to high level of variability that stems from the highly mobile nature of Acanthurid schools, the observed difference may be due to sampling error. And this precaution is further stressed by the data presented by Eldridge (2009) where acanthurid abundance within FPA was less than that outside. FPAs in Bonaire require regular monitoring to determine their effectiveness. The areas that were designated as FPAs were chosen based on the three criteria: significant coral coverage, ease of monitoring and limited use by fishermen (STINAPA), and thus a significant effect due to release from fishing pressure in Bonaire FPAs will take longer to occur in comparison to an FPA that is established in an area of heavy fishing pressure. Other than the obvious effects of changes in herbivorous fish population densities, the observed spatial trends in herbivorous fish bite rates inside and outside FPAs may be attributed to factors such as habitat differences, differences in

³ c = control site, f = FPA site. FPA established in 2008

the strength of interactions between various herbivores (territorial, schooling and non-schooling herbivores) or large scale regional trends.

In conclusion, Bonaire seems to have a healthy herbivorous fish population which maintains reef algae at low levels. Scarids are the dominant consumers of benthic algae; unfortunately this group has been showing a steady decline in bite rates since 2005. An increase in prevalence of territorial damselfish may be causing the decline in scarid bites which in turn increases benthic algal biomass and reduces coral recruitment. Established Fish Protected Areas (FPA) pose the potential of controlling pomacentrid (damselfish) density by creating a safe haven for larger predators.

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Chapter 4: Patterns of Distribution, Abundance and Size Structure of Bonaire's Predatory Reef Fish

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Abstract

Predatory fish were surveyed at ten sites on Bonaire's leeward reefs. Predatory fish populations have remained stable since 2003, however some heavily fished predatory fish have declined. Snapper (*Lutjanidae*) biomass and density is significantly lower than reported in 2003, 2005 and 2007. Grouper (*Serranidae*) density and biomass has also declined significantly since 2003. Grunts (*Haemulidae*) have increased in biomass and density at all sites except at Eighteenth Palm (Dive Site # 32). The decline of Bonaire's snappers and groupers is important and should be monitored. Baseline data for newly established FPA (Fish Protected Area) and control sites reveal higher than average abundance of grunts in the control and higher than average snappers in FPA.

Introduction

Large predatory fish have and continue to be chronically overexploited by humans in most marine ecosystems (Jackson et al. 2001). The loss of predators on coral reefs can directly alter community functioning, such as predator-prey interactions and indirectly influence community structure and biodiversity (Dulvy 2004). Management efforts that encourage the diversity and abundance of marine predators are essential for marine conservation purposes and for promoting the resilience of coral reefs faced with increasing disturbance through climate change (Bellwood 2004). This chapter describes the status of Bonaire's predatory fish populations and compares the current abundance and distribution of predators with past monitoring data from 2003, 2005 and 2007. We also provide baseline data for the newly established fish protection and control areas. The ultimate goal of this work is to help elucidate the broader ecological trends occurring on Bonaire's reefs with respect to predatory fish with the ultimate intent of guiding future marine protection strategies.

Methods

Location

Predator abundance (population density and biomass) was obtained by conducting underwater surveys at ten different sites along Bonaire's leeward reefs. Of these ten sites, six were surveyed in 2003, 2005 and 2007 including (from south to north): Windsock (Dive Site # 33), Eighteenth Palm (Dive Site #32), Forest on Klein Bonaire (Dive Site N), Reef Scientifico (Dive Site #25). All previous data were included in past Bonaire reports available via STINAPA (Steneck et al. 2003, 2005, 2007).

In 2009 four additional monitoring sites were added to the reef monitoring efforts to establish a baseline for an ongoing Before-After-Control-Impact (BACI) study. A BACI compares differences in the ecological characteristics of a particular marine reserve before and after its establishment. The purpose of a BACI is to identify a quantifiable ecological benefit associated with marine protection.

As such, in 2008, based on the findings and recommendations of the 2007 Bonaire Monitoring Report (Steneck et al. 2007) fish protection areas (FPA) were established at the following locations (from south to north): Bachelor's Beach (southern control site, Dive Site # 18), Calabas Reef (southern FPA site, Dive Site #31), Front Porch (northern FPA site, Dive Site # 28) and Oil Slick Leap (northern control site).

In summary, the complete order of all sites surveyed in March of 2009 is the following (from south to north): Bachelor's Beach, Windsock, Eighteenth Palm, Calabas, Forest, Front Porch, Reef Scientifico, Barcadera, Oil Slick Leap and Karpata. Note that previous reports had called the "Eighteenth Palm" site "Plaza" because of the name of the hotel in front of the monitoring site.

Survey Methods

Fish surveys were conducted by SCUBA at 10 meters depth at all ten locations aforementioned. Survey methods used in this chapter replicate those from previous Bonaire reports. The abundance, sizes and species of predators were recorded while swimming 30 meter long and 4 meter wide transects (total area = 100 m²), delineated by a 30 meter transect tape. Transects were replicated 16 times without overlap at all sites except Karpata and Bachelor's Beach where only 8 transects were completed. Predator size was recorded to the nearest centimeter and was converted to biomass using length-weight conversions from Bohnsack and Harper (1988) and those found in www.FishBase.org (Froese and Pauly 2005).

Results

Species

The most common predatory fish families that were surveyed included: *Aulostomidae* (trumpetfish), *Carangidae* (jack), *Haemulidae* (grunt), *Labridae* (wrasse), *Lutjanidae* (snapper), *Muraenidae* (Moray), *Serranidae* (grouper & seabass), *Sphyrnaeidae* (barracuda), *Synodontidae* (lizardfish). The thirty predatory fish species surveyed in 2005 were also surveyed in 2009. Appendix D at the end of this report lists the average biomass, density and fish length of all species surveyed at all 10 monitoring sites.

Overall predator densities (number per 100 m²) have remained constant among all sites (Fig. 1). Predator density was highest at Windsock with an average of 24 predators per 100 m² and lowest at Eighteenth Palm with an average of 8 predators per 100 m². Predator Biomass has also remained constant (Fig. 1-2). Biomass was highest at Barcadera with an average of 8,417 grams per 100 m² and lowest at Eighteenth Palm with an average of 1,929 grams per 100 m².

Trends in Population Density of All Predators 2003-2009

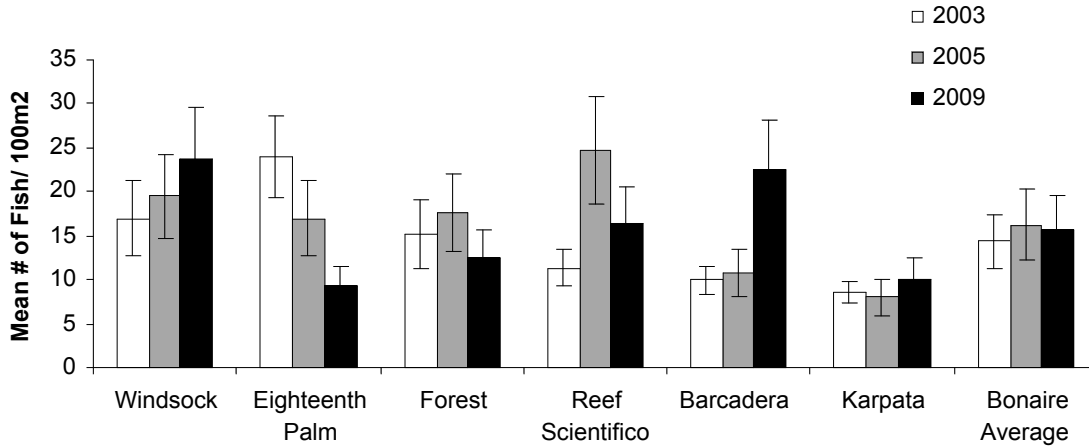


Figure 1. Average population density of all 30 species surveyed in 2003, 2005 and 2009. Monitoring data from 2007 was not included because not all 30 predator species were recorded. Error is represented as \pm one standard error.

Trends in Biomass of All Predators 2003-2009

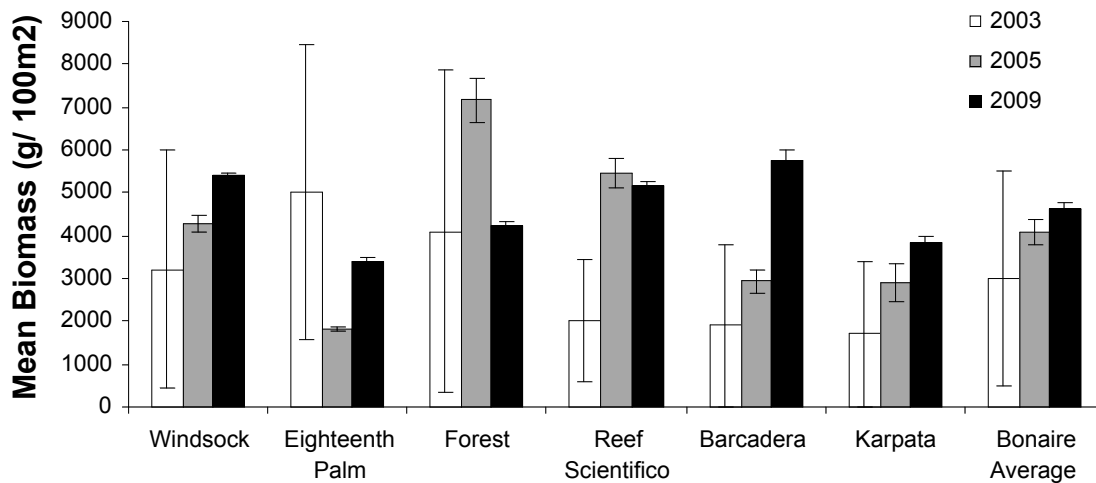


Figure 1-2. Average biomass of all 30 species surveyed in 2003, 2005 and 2009. Monitoring data from 2007 was not included because not all 30 predator species were recorded. Error is represented as \pm one standard error.

Predator Families

The three most common predatory fish families were snappers (*Lutjanidae*), groupers (*Serranidae*) and grunts (*Haemulidae*). Grunts were by far most abundant followed by snappers and groupers (Fig. 2)

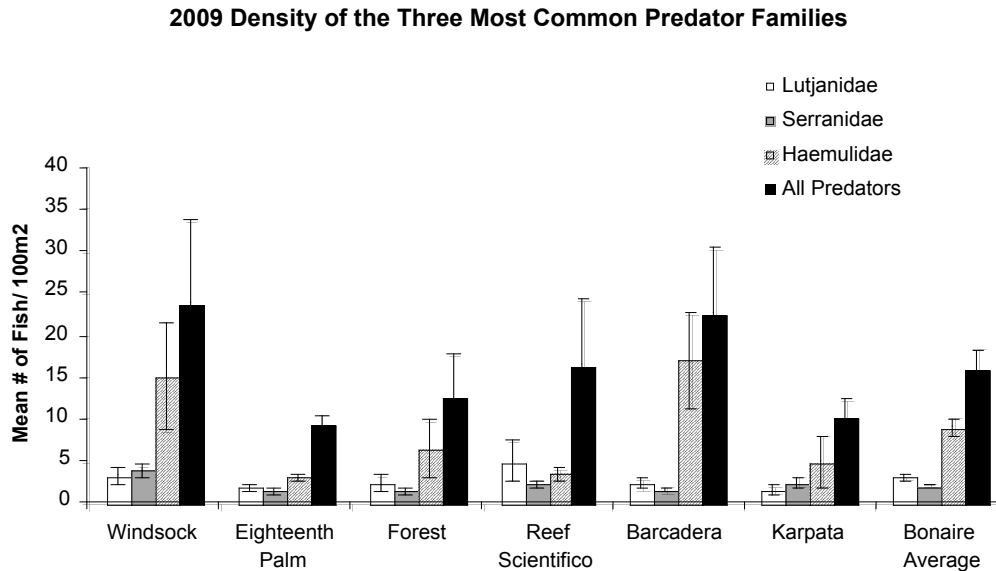


Figure 2. Average population density for all common predator families including snappers (*Lutjanidae*), groupers (*Serranidae*) and grunts (*Haemulidae*) surveyed in 2009. Error is represented as \pm one standard error.

Snappers (*Lutjanidae*)

Species surveyed belonging to the snapper family included: schoolmaster (*Lutjanus apodus*), mahogany snapper (*Lutjanus mahogoni*), yellow-tail snapper (*Ocyurus chrysurus*), cubera snapper (*Lutjanus cyanopterus*), mangrove snapper (*Lutjanus griseus*), dog snapper (*Lutjanus jocu*) and lane snapper (*Lutjanus synagris*).

Although snapper density and biomass had been relatively constant throughout Bonaire from 2005 to 2007, they declined significantly in 2009 (Fig. 3, Fig. 4). In 2009, yellowtail snapper biomass was highest at Barcadera (1,904 g/ 100m²) and lowest at Eighteenth Palm (873 g/100m²). Yellowtail snapper densities were highest at Reef Scientifico (5 individuals/ 100m²) and lowest at Karpata and Eighteenth Palm (2 individuals / 100m²).

Trends in Snapper (*Lutjanidae*) Biomass 2003-2009

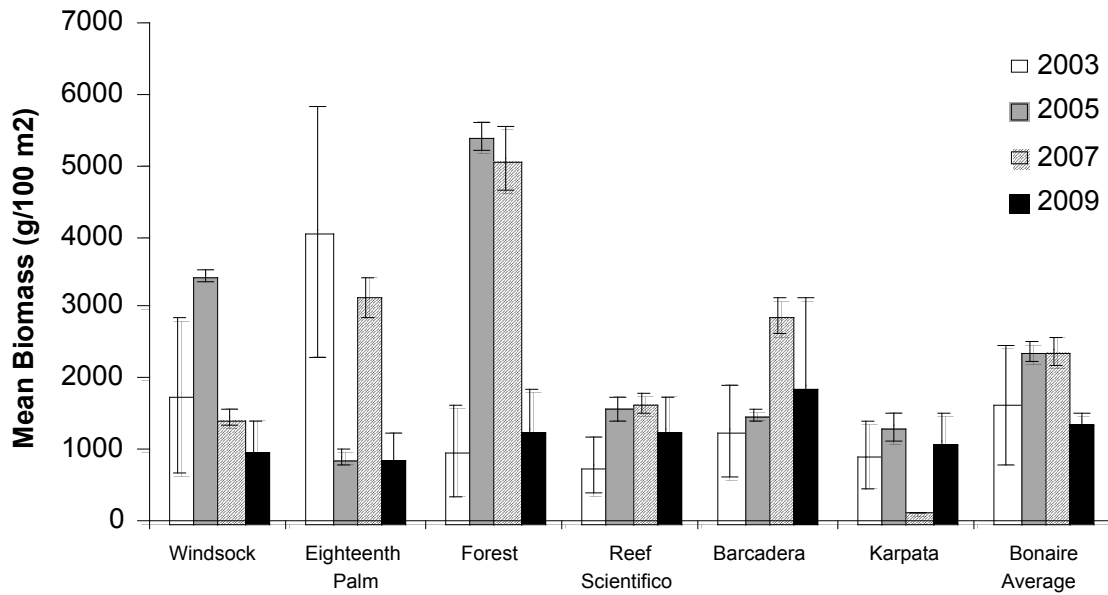


Figure 3. Average biomass for snappers (*Lutjanidae*) at all monitoring sites from 2003 to 2009. Error is represented as \pm one standard error.

Trends in Population Density of Snappers (*Lutjanidae*) 2003-2009

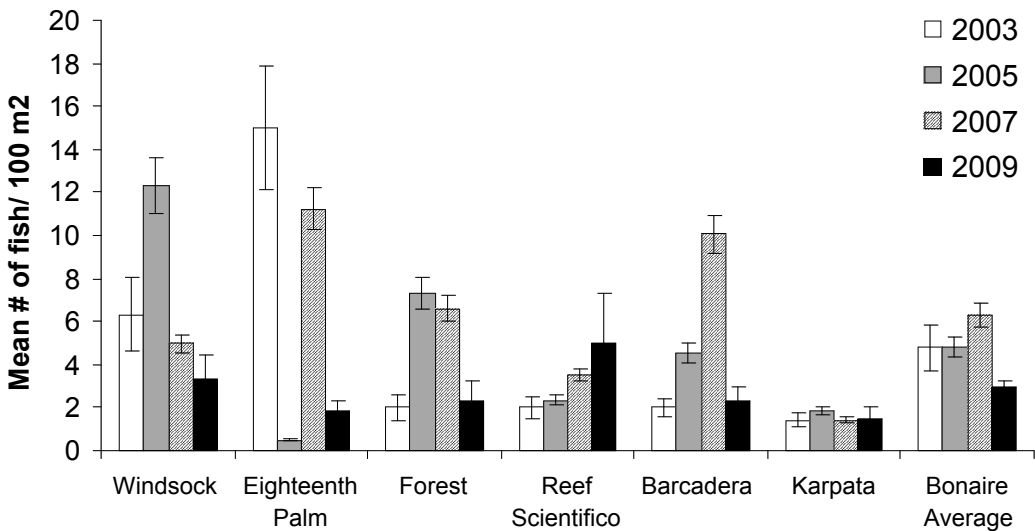


Figure 4. Average population density for snappers (*Lutjanidae*) at all monitoring sites from 2003 to 2009. Error is represented as \pm one standard error.

Groupers (Serranidae)

Grouper species surveyed included black grouper (*Mycteroperca bonaci*), tiger grouper (*Mycteroperca tigris*), yellowfin grouper (*Mycteroperca venenosa*) and harlequin bass (*Serranus tigrinus*).

Since 2003 grouper biomass and density has decreased (Fig. 5, Fig. 6). This disparity could be explained by an increase in larger size classes for groupers greater than 20 cm in length (Fig. 7) and will be described further in the discussion. Grouper biomass was highest at Karpata (881 g/ 100m²) and lowest at Eighteenth Palm (112 g/ 100m²). Grouper density was highest at Windsock (4 individuals/ 100m²) and lowest at Eighteenth Palm and Forest (1 individual/ 100m²).

Trends in Grouper (Serranidae) Biomass 2003-2009

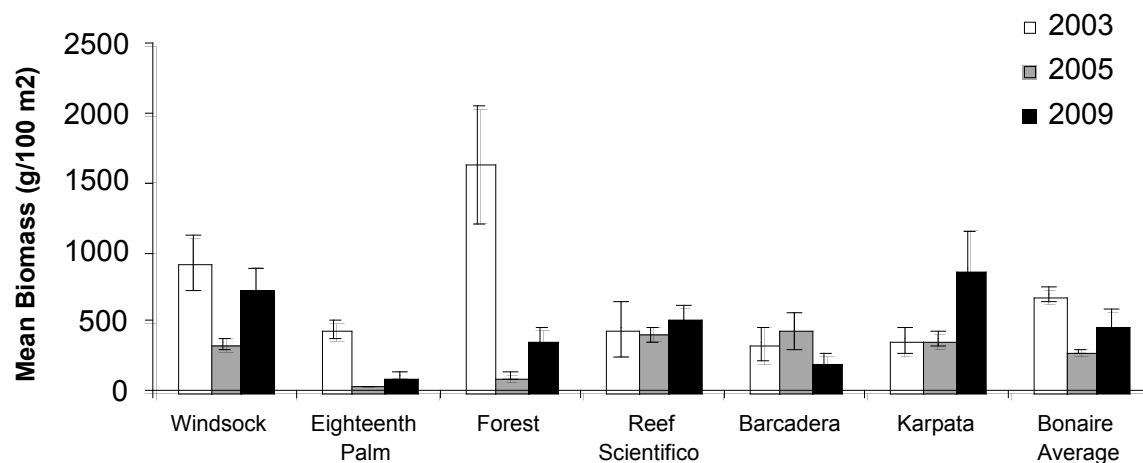


Figure 5. Average biomass for groupers (*Serranidae*) at all monitoring sites from 2003 to 2009. Values for grouper biomass in 2007 are not included because groupers were not recorded in 2007. Error is represented as \pm one standard error.

Trends in Population Density of Groupers (*Serranidae*) 2003-2009

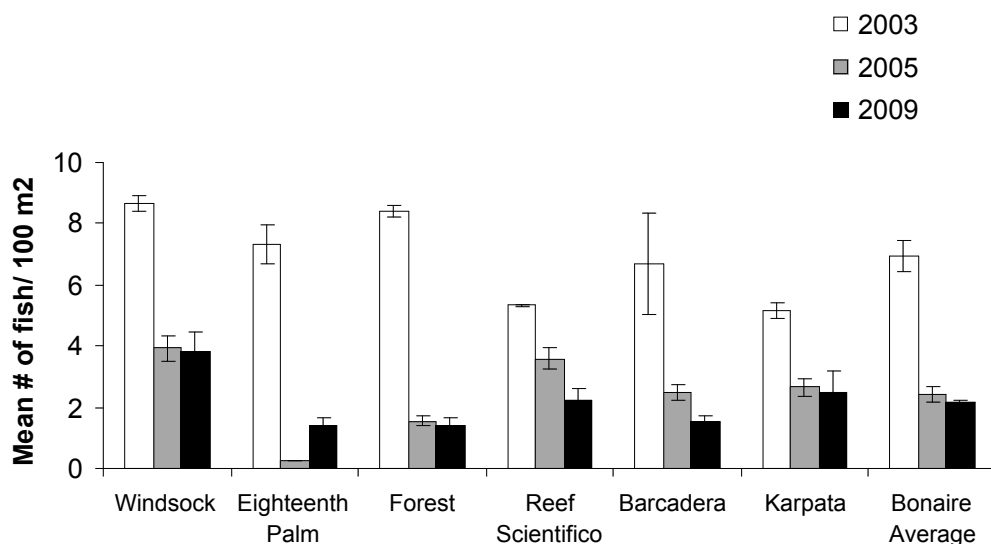


Figure 6. Average population density for groupers (*Serranidae*) at all monitoring sites from 2003 to 2009. Values for grouper density in 2007 are not included because groupers were not recorded in 2007. Error is represented as \pm one standard error.

Size Frequency for Serranids (groupers) 2003- 2009

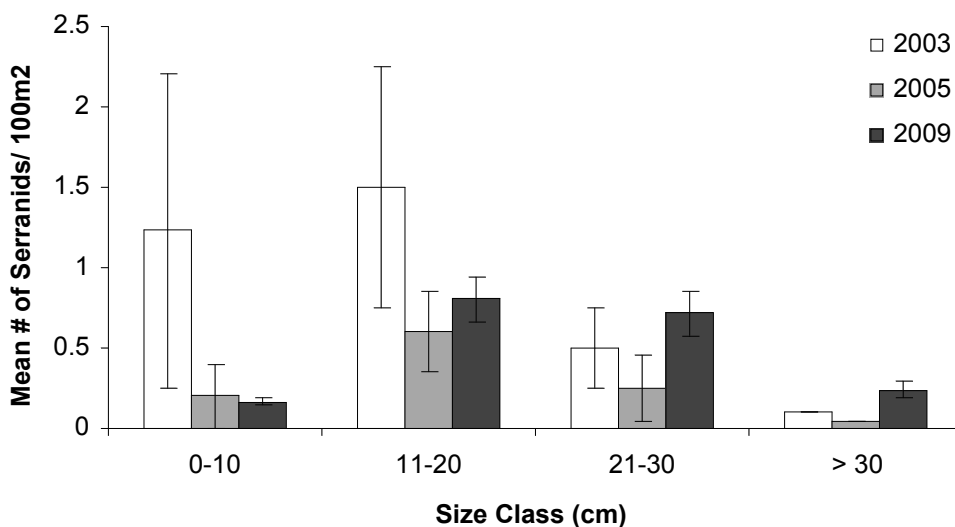


Figure 7. Abundance of different size classes of groupers on Bonaire from 2003 to 2009. Values for grouper size class in 2007 are not included because groupers were not recorded in 2007. Error is represented as \pm one standard error. Error values are not available for 2003, 2005, > 30 cm size class.

Grunts (Haemulidae)

Grunt species that were surveyed included Caesar grunt (*Haemulon carbonarium*), French grunt (*Haemulon flavolineatum*) and Bluestriped Grunt (*Haemulon sciurus*). Grunts have consistently increased in biomass and density at all sites since 2005, with the exception of Eighteenth Palm (Fig. 8, Fig. 9).

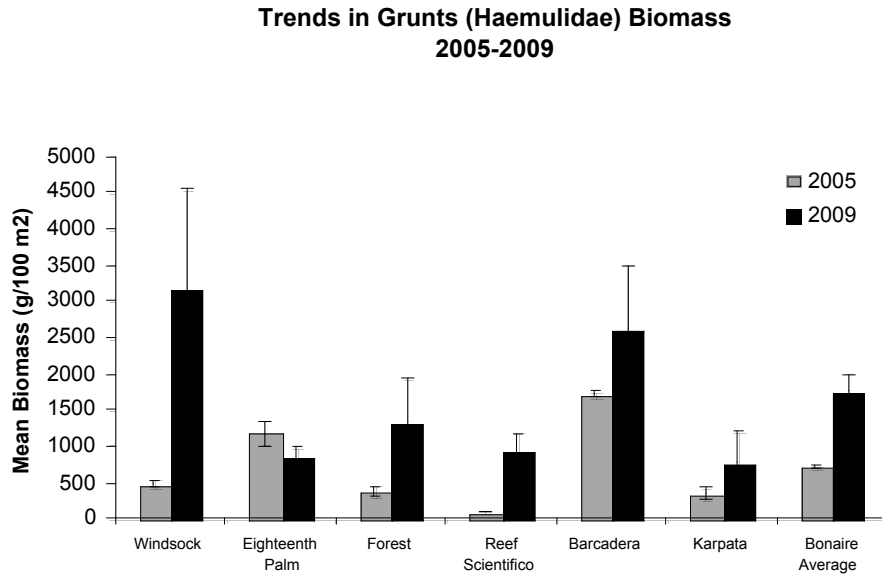


Figure 8. Average biomass for grunts (*Haemulidae*) at all monitoring sites from 2003 to 2009. Values for grunt biomass in 2003 and 2007 are not included because grunts were not recorded during those years. Error is represented as \pm one standard error.

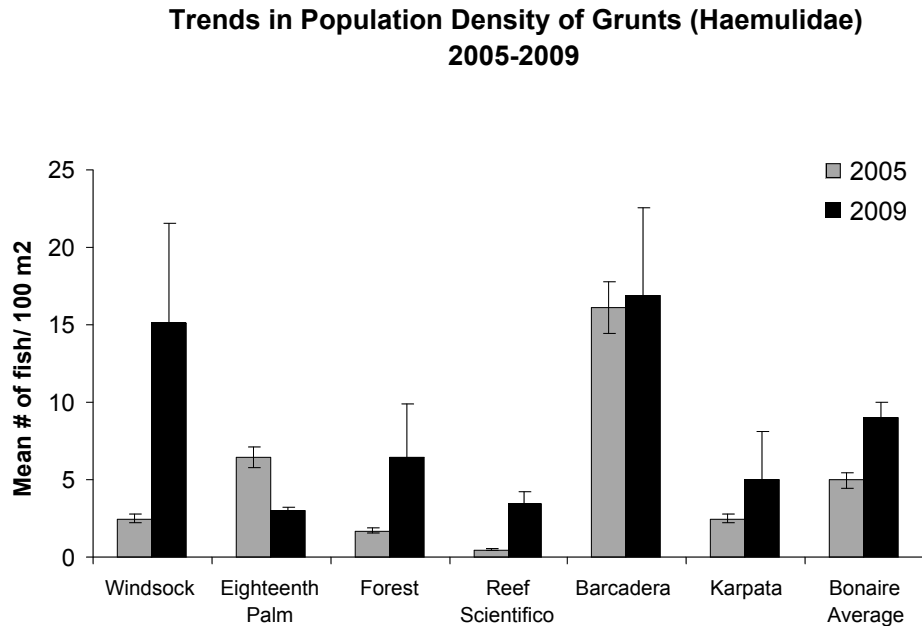


Figure 9. Average population density for grunts (*Haemulidae*) at all monitoring sites from 2003 to 2009. Values for grunt density in 2003 and 2007 are not included because grunts were not recorded during those years. Error is represented as \pm one standard error.

Predators Targeted by Fishing

Specific predatory fish species that are commonly targeted by fishing include graysbies (*Epinephelus cruentatus*) and yellowtail snapper (*Ocyurus chrysurus*) (Nenadovic, 2007).

Yellowtail snapper biomass has increased significantly since 2003 (Fig. 10). Its abundance was highest at Karpata (1,560g / 100 m²) and lowest at Barcadera (303g / 100 m²). Yellowtail biomass was also significantly higher at Karpata than any other monitoring year and significantly lower at Barcadera than in 2007.

Graysby density has increased significantly in Bonaire since 2003. However, there is no trend in graysby biomass (Fig. 12).

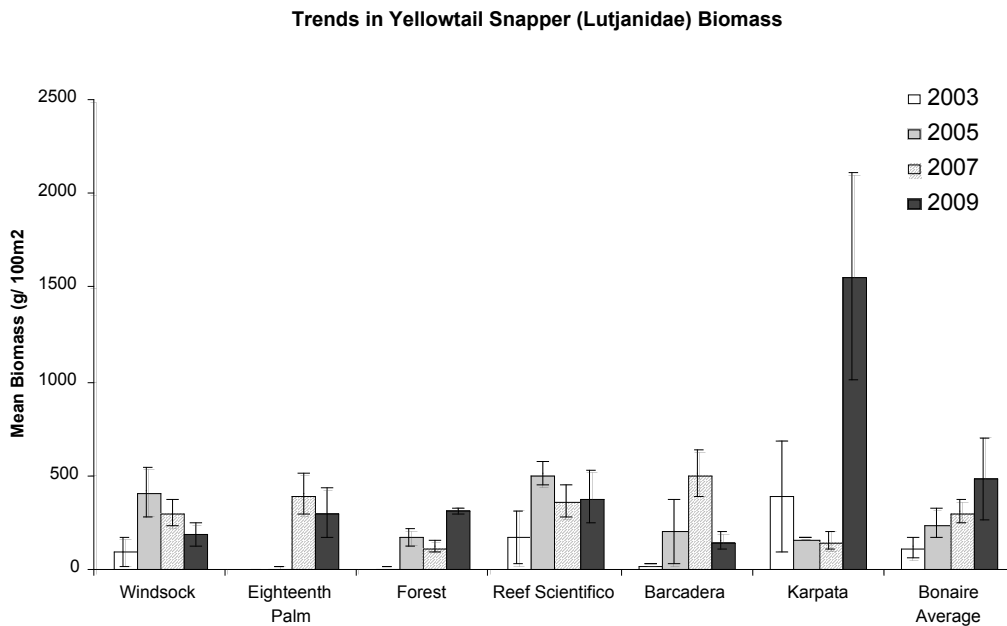


Figure 10. Average biomass for yellowtail snapper (*Ocyurus chrysurus*) from 2003 to 2009. Error is represented as \pm one standard error.

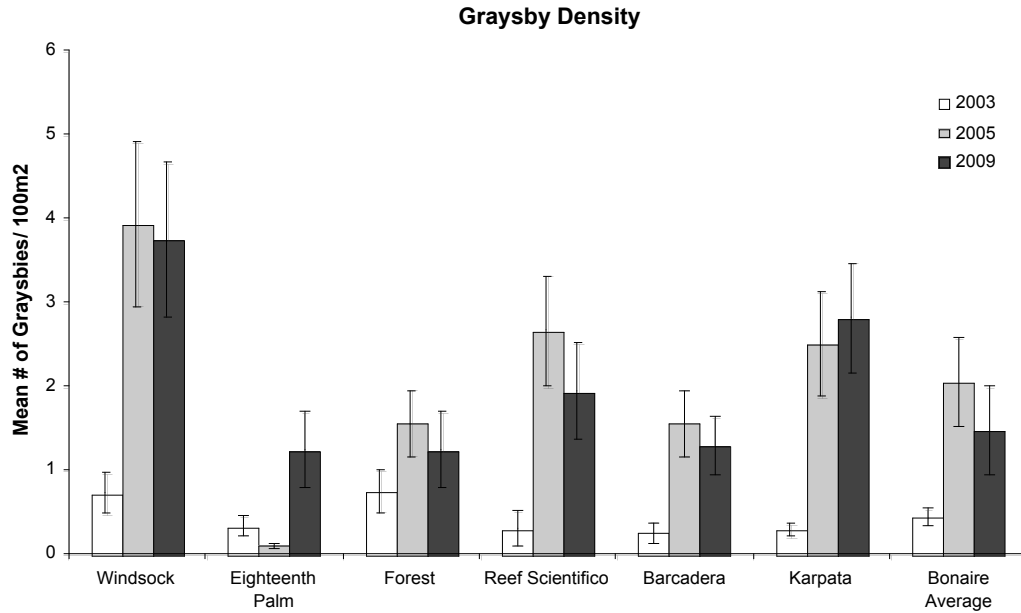


Figure 11. Average population density for graysby (*Epinephelus cruentatus*) from 2003 to 2009. Values for graysby density in 2007 are not included because they were not surveyed in 2007. Error is represented as \pm one standard error.

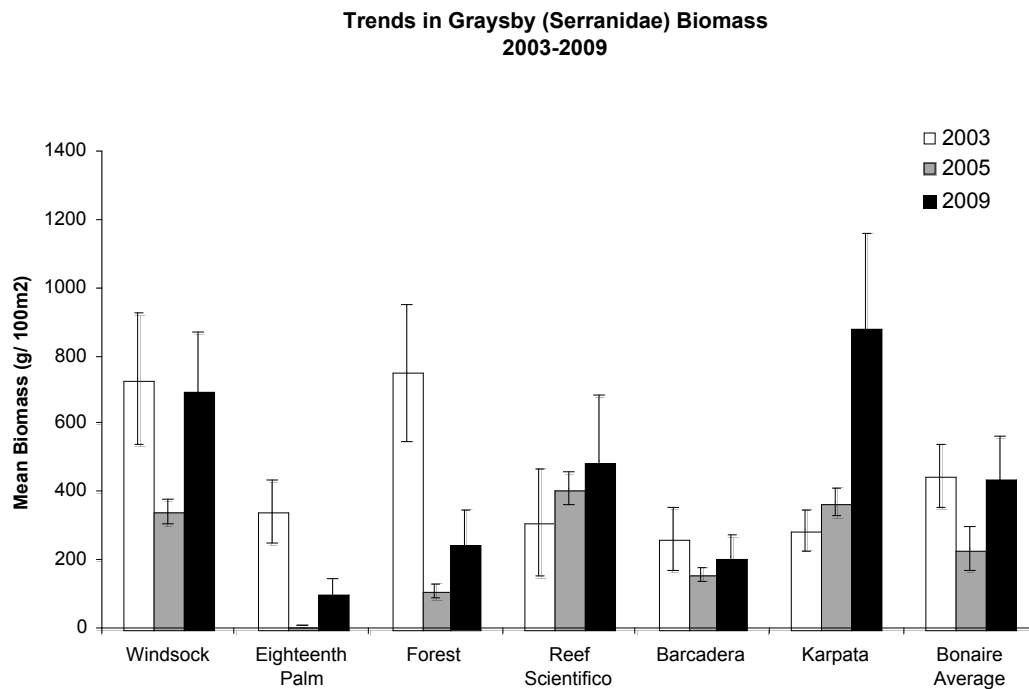


Figure 12. Average biomass for graysby (*Epinephelus cruentatus*) from 2003 to 2009. Values for graysby density in 2007 are not included because they were not surveyed in 2007. Error is represented as \pm one standard error.

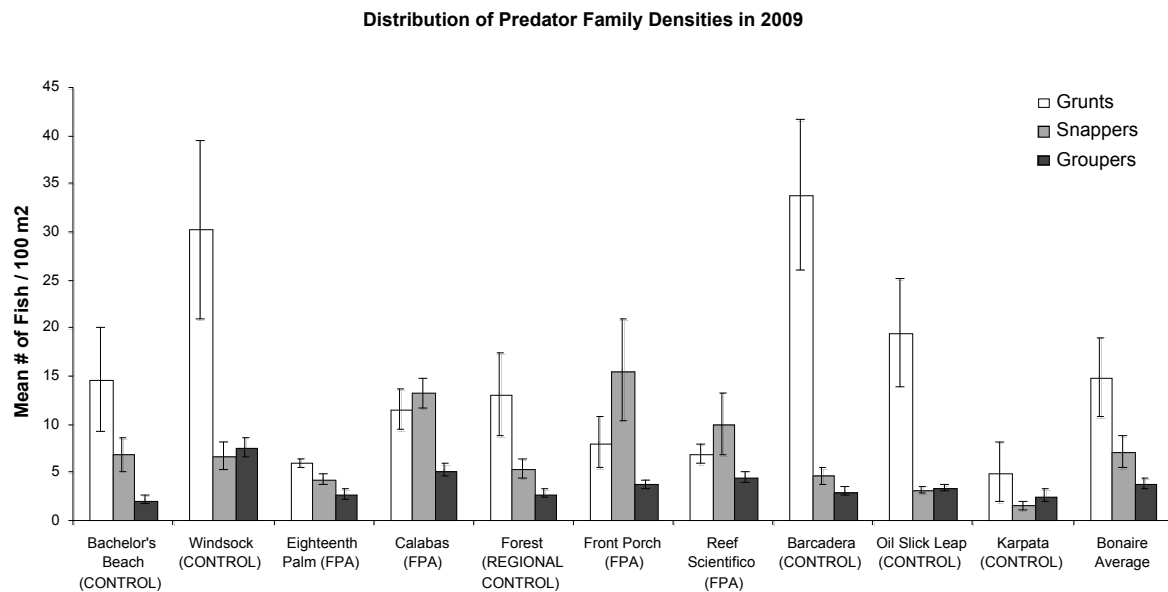


Figure 13. Average density for snappers, grunts and groupers in 2009. This graph includes new monitoring sites which were established as fish protection areas (FPA) in 2008. Error is represented as \pm one standard error.

Discussion

The 2003 monitoring report described Bonaire's predator populations as more robust than other regions in the Caribbean (Paddock 2003). The 2009 results demonstrate that while predator abundance is increasing for some species, such as yellowtail snapper (Fig. 10), and in some locations, such as Windsock and Barcadera (Fig. 1), Bonaire is also experiencing chronic declines in other predators, such as groupers (Fig. 6) and sites such as Eighteenth Palm (Fig. 1). This chapter serves as a guide for future marine management strategies by identifying the most vulnerable predator species and highlighting specific sites as priorities for protection.

Predator Families

Of the most common predator families, grunts are increasing in abundance while snappers and groupers are not. Grunts are not typically targeted by fishing activities which could explain why grunt populations continue rise. The decline in grouper and snapper abundance could also complement the noticeable increase in grunts. As more groupers and snappers are fished off the reefs, more resources become available for competing grunt species.

Snappers and groupers are targeted by fishing practices (Nenadovic, 2007) and are most likely the reason for apparent declines in both predator families (Fig. 3, Fig. 6). Graysby, a small species of grouper, also referred to as "Burunchi" by local Bonaireans is a heavily sought after fish species (Nenadovic, 2007) and fishing could cause this species to decline (e.g. Fig. 11).

However, the apparent increase in grouper biomass is at odds with an observed decrease in grouper density. These conflicting trends are partially elucidated by the analysis of size class trends (Fig. 7). It is possible that while groupers have continued to be fished on Bonaire's reefs, the groupers that have not been removed have grown larger and effectively increased in biomass. In other words, Bonaire has fewer groupers than it did in 2003 but these remaining groupers are older and therefore larger.

Grunts are predators but they are not targeted by the fishery. We would not expect an FPA-control effect with them.

Average yellowtail snapper biomass appears to be higher than previous years and this is due to the abundance of yellowtails recorded at Karpata. Without Karpata, the Bonaire average would be reduced to 265 g / 100m² rather than 481 g / 100 m², which would have reduced the Bonaire average to below 2007 levels.

Fish Protection Areas

In addition to continuing the Bonaire monitoring effort the 2009 survey also serves as baseline for tracking the effectiveness of the fish protection areas (FPAs) established in 2008. FPAs at Eighteenth Palm, Calabas, Front Porch and Reef Scientifico were designated based on recommendations from previous reports. This report is the first of a series of reports that will continue to assess the effectiveness of these FPAs (Fig. 13).

What the 2009 report does indicate is that the FPAs have yet to show clear increases in biomass and density of predatory fish, particularly for monitoring sites such as Eighteenth Palm and Reef Scientifico (Fig. 1, Fig. 13). However, only one year has passed since the FPAs were implemented and the 2011 monitoring report will undoubtedly provide better evidence on the long term effectiveness of these FPAs. It will be critical to closely monitor Eighteenth Palm where predator abundance is already low and still declining (Fig. 1, Fig. 2).

Nevertheless, there were more grunts in the control sites and more snappers in the FPA sites in 2009. It is unlikely these were the result of the FPA affects. Trends of these and other species will be very interesting to follow.

Conclusion

Predators are key ecological drivers of coral reefs by maintaining diversity and resilience of reefs (Bellwood et al. 2004, McClanahan 2005, Sandin et al. 2008). Bonaire's predatory fish abundance is continuing to decline at some sites since monitoring efforts began in 2003. It will be important to track the effectiveness of the recently established FPAs and revise management strategies accordingly. Graysbies and yellowtail snapper continue to be harvested at an unsustainable rate and if effective protection is not implemented these species could be extirpated from sites such as Eighteenth Palm and Barcadera where densities continue to decline.

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Chapter 5: The abundance of the seas urchins *Diadema antillarum*, *Echinometra lucunter*, *Echinometra viridis*, and *Tripneustes ventricosus* in shallow reef zones of Bonaire

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Abstract

In March 2009, additional sites were added to the reef monitoring assessment due to the implementation of fish protected areas. Population densities of *Diadema antillarum*, *Echinometra lucunter*, *Echinometra viridis*, and *Tripneustes ventricosus* were determined at nine sites on the leeward side of Bonaire, N.A. *Diadema* and *E. viridis* were encountered at five of the nine sites, while *E. lucunter* was found at seven of the nine sites. Only one *Tripneustes* individual was encountered. It was located at Bachelor's Beach. This is a drastic change from 2007 results. *E. lucunter* densities have increased significantly at Barcadera, Eighteenth Palm, Windsock, and Forest since 2007. There was no significant change in the abundance of *Diadema*.

Introduction

The Caribbean has been undergoing a change from coral-dominated systems to algal-dominated systems over the past few decades. Disturbance from Hurricane Allen, a reduction in parrotfish, and a mass mortality of the sea urchin *Diadema antillarum* are all contributing factors to this phase shift (Hughes 1994). The mass mortality of *Diadema* led to the discovery of its ecological importance as an algal grazer (Mumby et al 2006). They feed on algal turf and a significant increase in macroalgae occurred after the die-off (Hendler et al 1995). *Diadema* is important to the resilience of coral reefs, especially during severe disturbances such as high hurricane frequencies, overfishing of parrotfish, and changing nutrient levels.

Bonaire is one of the few places in the Caribbean that has escaped the phase shift to algal dominated ecosystems after the *Diadema* die-off (Smith and Malek 2005). Bonaire has an abundance of herbivorous fishes that compete for algae. Thus, algae on Bonaire's reefs are maintained even without high populations of *Diadema* and the functional group of herbivores for Bonaire is not dependent on urchins.

Among the sea urchins, *Diadema* is considered to be the principal algae grazer in the Caribbean. *Tripneustes ventricosus*, *Echinometra lucunter*, and *Echinometra viridis* are three other urchin species that are found in the Caribbean and also help maintain reef health. *T. ventricosus* also grazes on algal turf, but on a smaller scale. The *Echinometra* spp. graze on algae, but also maintain reef health through bioerosion. *E. lucunter* grazes heavily on drift algae (Haley and Solandt 2001). *E. viridis* may be important for grazing when *Diadema* is not present because it may inhabit where *Diadema* used to be since it no longer has to compete with *Diadema*, which is known to act aggressively towards it (Shulman 1990).

This study looks at the population densities of sea urchins in the shallow lagoon areas of Bonaire's reefs. In 2008, the Bonaire government implemented two fish-protected areas (FPAs). One FPA is located off the southern part of the island, while the other is located off the northern part. Both are located on the leeward side of the island. As a result, sites inside and outside of the FPAs were monitored during this study. Thus, study sites and methods have slightly changed from those used in 2005 and 2007 (Smith and Malek 2005; Cameron and Brodeur 2007). Karpata was not monitored in this study, but five new sites were added.

Study Species

While past studies have only included three species of urchins, this study includes four – *Tripneustes ventricosus*, *Echinometra lucunter*, *Echinometra viridis*, and *Diadema antillarum*.

Tripneustes ventricosus has a dark brown test with white spines. It is a large urchin, growing up to 150 mm in test diameter (Moore 1966). They usually live between two and three years, but environmental factors can affect their lifespan. Their preferred habitat is grassy areas covering sandy bottoms, or among reefs, rocks, and rubble. *T. ventricosus* is capable of inhabiting high wave energy areas (Hendler et al 1995).

Echinometra lucunter is a smaller urchin with a black to red test and long, sharp spines. One of their common names is the rock-boring urchin because they are bioeroders and create their own shelters by eating rocks and coral. They prefer shallow areas, and can withstand the high wave energy of the tidal zone (Hendler et al 1995). *E. lucunter* is slow-growing and long-living, with an average lifespan of over ten years (Ebert et al 2008).

Echinometra viridis usually has a red test with blunter spines than those of *E. lucunter*. There is also a distinctive white ring around each of the spines. Like *E. lucunter*, they live in shallow waters, are able to withstand high wave energy, and are important bioeroders (Griffin 2003). *E. viridis* and *E. lucunter* individuals can coexist in close proximity to each other. (McCartney and Lessios 2002).

Diadema antillarum, commonly referred to as the long-spined urchin, is a large urchin with a black test and long, very sharp black spines. As a juvenile, the spines are white or black and white (Sterrer 1986). They can grow up to 500 mm including the spine, which can be up to four times the length of the test (Hendler et al 1995). *Diadema* can have a lifespan of up to six years, but their lifespan is closely related to temperature, thus causing populations in warmer climates to have a quicker rate of development and shorter lifespan (Grzimek 1972). Preferred habitats include areas in which they can hide under or in, such as corals or artificial structures. *Diadema* is especially important as an herbivore that helps prevent coral-dominated areas from undergoing a phase shift to algal-dominated ecosystems, but also helps the overall reef health by grazing turf algae. Williams and Carpenter (1988) stated that studies have shown that grazed algal turf is two to ten times more productive than ungrazed algal turf.

Methods

Nine sites on the leeward reefs of Bonaire, N.A., five of which were previously selected for monitoring, were surveyed for sea urchin abundance: Oil Slick Leap, Barcadera, Reef Scientifico, Front Porch, Calabas Reef, Eighteenth Palm, Windsock, Bachelor's Beach, and Forest. Smith and Malek (2005) and Cameron and Brodeur (2007) refer to the study site Eighteenth Palm as Plaza. All surveyed areas were 50m² transects. Two transects were surveyed at each site, with the exception of Scientifico and Barcadera which only had one transect each. The entire area was scanned for urchins. Each urchin encountered was identified to species level. Individual *Diadema* and *Tripneustes* were measured for test size while *Echinometra* species were counted per meter square using one meter square quadrats.

Results

Of the nine sites surveyed, only one *Tripneustes ventricosus* individual was recorded. It was found at Bachelor's Beach (Figure 1). This is a significant change from 2005 and 2007, when measurable population densities were found at Reef Scientifico. *Diadema* population densities ranged from 0 to 0.24 urchins/m² (± 0.10), with the highest density at Reef Scientifico (Figure 1). *Diadema* populations did not have any significant changes from previous studies. Both *Echinometra* species were found in very concentrated areas, inhabiting only a small portion of the area surveyed at each site. The highest population densities for *E. lucunter* and *E. viridis* were 0.57 (± 0.22) and 0.34 (± 0.20) urchins/m², respectively, at Forest (Figure 2). In comparison to data in the 2005 and 2007 Bonaire Reports, population densities for *Echinometra lucunter* were significantly higher in 2009 at Barcadera, Eighteenth Palm, Windsock, and Forest (Smith and Malek, Figure 1, 2005; Cameron and Brodeur, Figure 2, 2007).

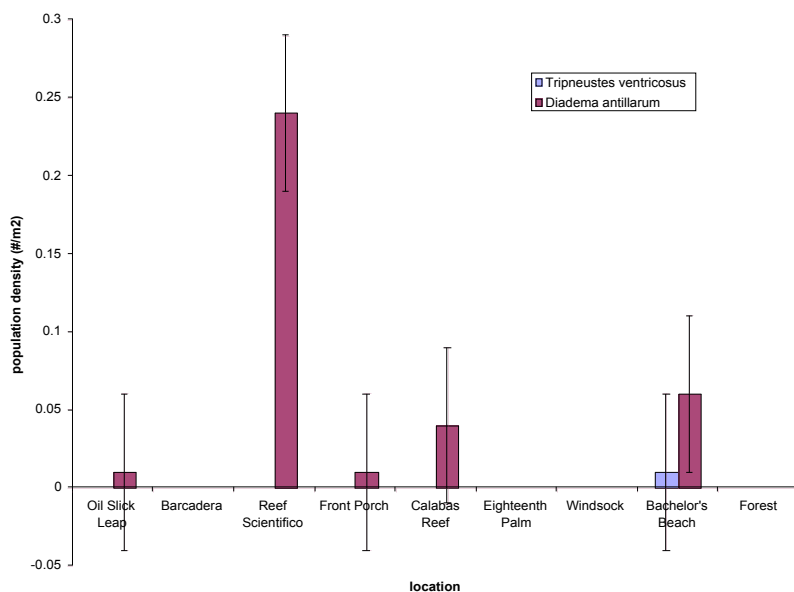


Figure 1. Abundance of *Diadema antillarum* and *Tripneustes ventricosus* per meter square for all nine sites. Standard deviation is indicated by error bars.

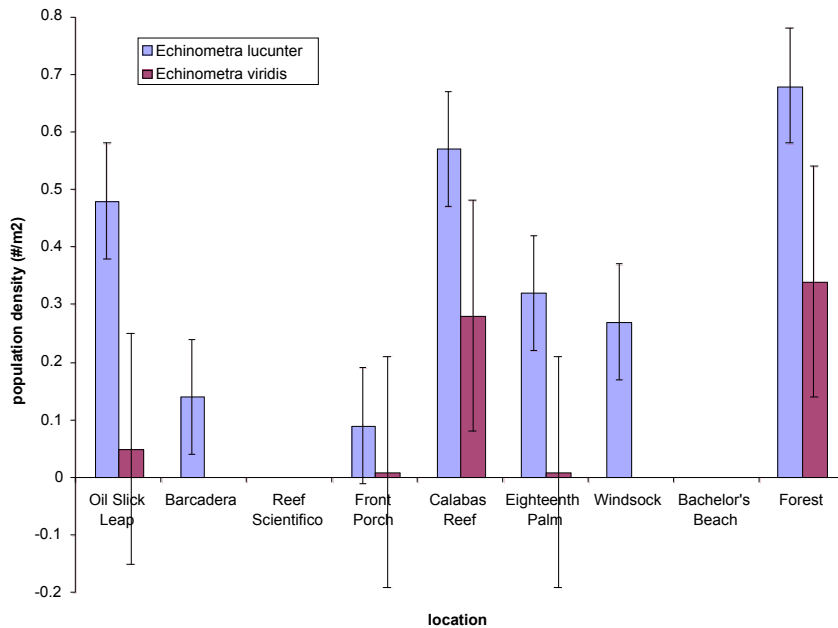


Figure 2. *Echinometra lucunter* and *Echinometra viridis* abundance per square meter for all nine sites. Standard deviation is indicated by error bars.

The abundance of *Diadema* by test size indicates that the majority of individuals are from four to five centimeters in diameter (Figure 3). Data included in the 2005 Bonaire Report indicated that the majority of individuals were greater than eight centimeters in diameter, and in the 2007 Bonaire Report that the majority of individuals were between three and four centimeters in diameter, suggesting differences between all three studies.

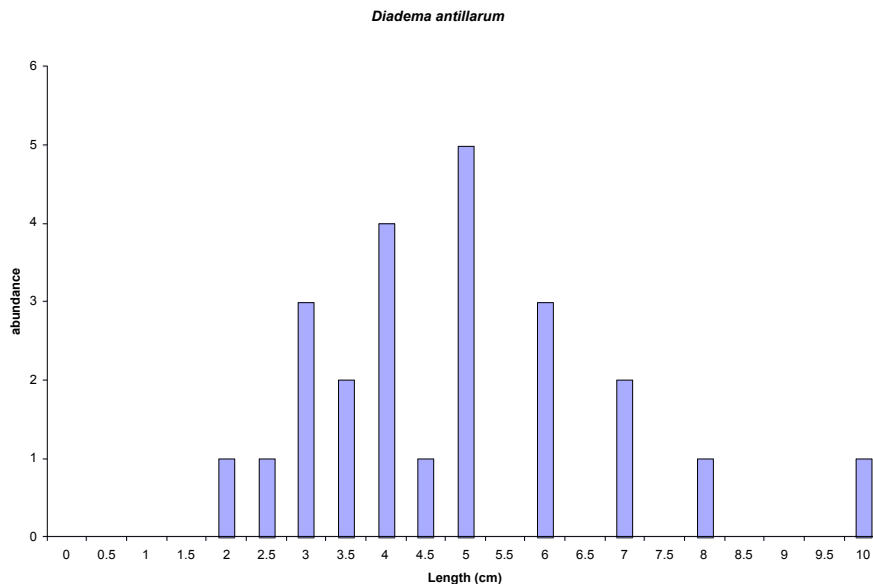


Figure 3. *Diadema antillarum* abundance by size frequency. Data from all nine sites was combined.

Discussion

Observations at all nine sites indicate that population densities for all urchin species surveyed are low and patchy (Figure 1, 2). This is similar to results found in 2005 and 2007. Comparisons between FPA sites and control sites were difficult because there seems to be little evidence supporting correlation between population densities protection status of the site. The FPA areas were implemented within the past year, leaving little time for changes to occur. More time is needed to determine if FPA sites are beneficial to population densities.

Diadema populations have not decreased significantly, but total numbers are much lower than those totaled in 2005 and 2007. This is possibly a result of Hurricane Omar, which brought destruction to Bonaire in October 2008. The shift in the majority of test sizes between all three studies could possibly be a result of a new generation. Grzimek (1972) states that *Diadema* have a lifespan of about six years, but there is heavy reliance on food and temperature. Thus, warmer waters lead to shorter lifespans. The time between the 2005, 2007, and this report's results is approximately the same as one lifespan.

Echinometra lucunter population densities increased at Barcadera, Eighteenth Palm, Windsock, and Forest since 2007. Even though it is believed that sea urchins are not important herbivores for Bonaire's reefs because of the abundance of herbivorous fish (Carpenter 1988), an increase in sea urchin population densities may suggest an improvement in reef health.

Echinometra viridis abundance was added to the sea urchin survey during this study. The population densities were extremely low in comparison to those found at Puerto Rico (Griffin 2003). The populations were measurable at several sites and should continue to be included in future reports.

The low and patchy population densities of sea urchins does not appear to be an issue for the reefs of Bonaire since there is an abundance of herbivorous fish. Recent studies have shown a decline in parrotfish populations, though. If this trend continues, and sea urchin populations, especially *Diadema*, do not increase, the reefs will become algal-dominated from lack of grazing.

In addition to being important grazers, Echinoids are also important bioeroders, accounting for over 90% of bioerosion in the Caribbean (Hendler 1995). Echinoid bioerosion is considered important for reefs as a limiting factor in growth, and it plays a role in community structure by heavily influencing newly settled coral spat (Mokady et al 1996).

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Chapter 6: Abundance of initial stage and juvenile parrotfish in shore habitats of Bonaire reef

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Abstract

In March 2009, the spatial patterns of fish-habitat interactions were assessed in the back reef of Bonaire, Netherlands Antilles. Microhabitats were characterized and quantified for four fish protection areas (FPA) and four control sites. In each of the sites, *Sparisoma viride*, *Scarus vetula*, and *S. taeniopterus*, were also quantified. This study indicates that each site was composed of different microhabitats, size (area), types and arrangement of microhabitats vary among sites and these changes influence the patterns of fish abundance. Sites containing more complex structures yielded higher fish abundance and when the microhabitats were separated by sand or cemented benthos they attracted less fish. This study also demonstrated that the complex structured microhabitats of FPA sites consist mostly of dead *A. palmata* piles suffering from erosion, suggesting that this progressive lost of habitat could have consequences for the conservation of the herbivorous parrotfishes.

Introduction

Nearshore habitats such as seagrass beds, mangroves, algal flats and lagoonal reef patches are shown to be unique environments that provide shelter, food, movement corridors for many coral reef organisms, including fish species (Ogden, 1997; Acosta, 1999; Mumby et al., 2004). The presence, abundance and distribution of these are suggested to influence the distribution and abundance pattern of fish and other organisms in the marine environment (Ogden, 1997). In particular, back- reef habitat is shown to offer abundant microhabitats providing refuge shelter and foraging areas that attract different species of juvenile fishes, including scarid species (Mateo and Tobias, 2001). In this respect the complexity of substrate (McCormick, 1994) or architecture (Hacker and Steneck, 1990) of the habitat is suggested to be a key determinant to its suitability.

On the other hand, back reefs are shown to be important habitat for young herbivorous parrotfish (Garpe and Öhman, 2003), who have recently drawn the attention of researchers and managers of coral reef ecosystems because of their role in controlling algal biomass that threaten the ecological balance or resilience of these systems (Hay, 1997; Hixon, 1997; Graham et al., 2006). Understanding the demographic dynamics of herbivores fish populations has progressively become a research priority for reef ecologists.

This study evaluates patterns of abundance for the initial phase and juvenile stage of three species of parrotfishes (*Sparisoma viride*, *Scarus vetula*, *S. taeniopterus*) in the back reef habitat along the coast of Bonaire. The study describes the spatial pattern of fish – habitat interactions for established fish protection areas (FPA), and compares these to control sites. This analysis provides information that may be useful for the fish protection initiative in Bonaire.

Methods

Four FPA (18th Palm, Calabas, Sunset (also called Front Porch), Scientifico) and four control sites (Windsock, Oil Slick, Barcadera, Forest) situated on the leeward coast of Bonaire were sampled. At each site, two 50 x 50 m² (100 m² per sample site) quadrats were measured perpendicular to the shore line. In each of the plots, substrate types (microhabitats) were identified, described, and measured. With the aid of snorkel, stoplight (*S. viride*), queen (*S. vetula*), and princess (*S. taeniopterus*) were visually censused for each sample site, recording the substrate type at their location.

Results

Nearshore benthic composition

Sampled sites of microhabitats found in Bonaire's back reef were characterized as: remnant reef (patches of mostly dead *Acropora palmata* colonies, live colonies were rare), rubble & sand (these were patches of sediment and rubble of *A. cervicornis* of different degrees of decomposition), reef edge (where our transects met or covered the reef break- these areas were dominated by live head corals and gorgonians of different densities), sand (an area of reef flat dominated by sand), cement (pavement of fossilized carbonate material), rocky area (piles of shore rocks or round shaped calcareous material), artificial structure (one selected site contained piles of concrete blocks, possible remnant of a dock), cliff (fossilized carbonate cement wall that continues making up a portion of the reef flat) (Bruggeman et al., 1994; Bowdoin and Wilson, 2005). These microhabitats can be grouped in two general categories, topographically complex substrate, such as remnant reef, artificial structure, cliff, reef edge, and rocky areas and less structured microhabitats, such as cement, sand, and rubble & sand.

Sampled sites were composed of some combination of the described microhabitats, and the proportion and arrangement (contiguous or separate) were different within and between sites (Table 1 in Annex). There is also a difference in the distribution of topographically complex substrates and less structured microhabitats between FPAs and control sites. Remnant reef, rocky area, reef edge, and cliff together comprised the largest proportion (65.4 %) of the total area of the control sites (Fig. 1). While FPA sites were dominated by rubble & sand, sand, and cement, which comprised almost 70% of the benthic composition, and substrates that provided more complex structure (remnant reef, artificial structure, and rocky area) comprised only 30% of these areas (Fig 1).

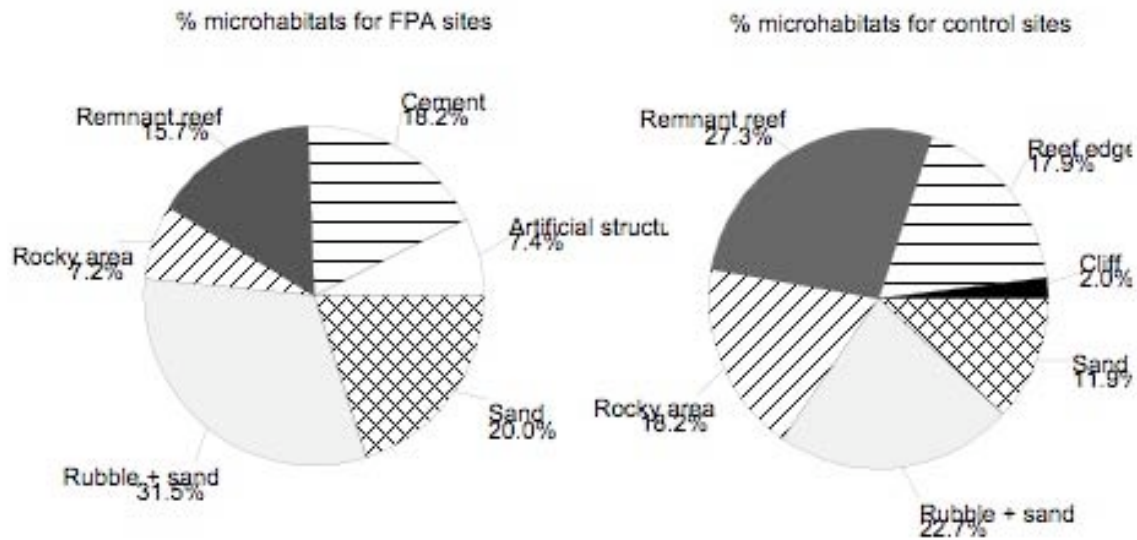


Figure 1. Comparison of microhabitat types among FPA and Control sites.

Fish distribution and abundance

In general, total abundance of initial phase and juvenile parrotfishes show a skewed preference for microhabitats with more complex structure in comparison to those of less complex structure. Remnant reef, cliff, artificial structure, and reef edge attract the highest abundance of fish compared to the other microhabitats (Fig. 2).

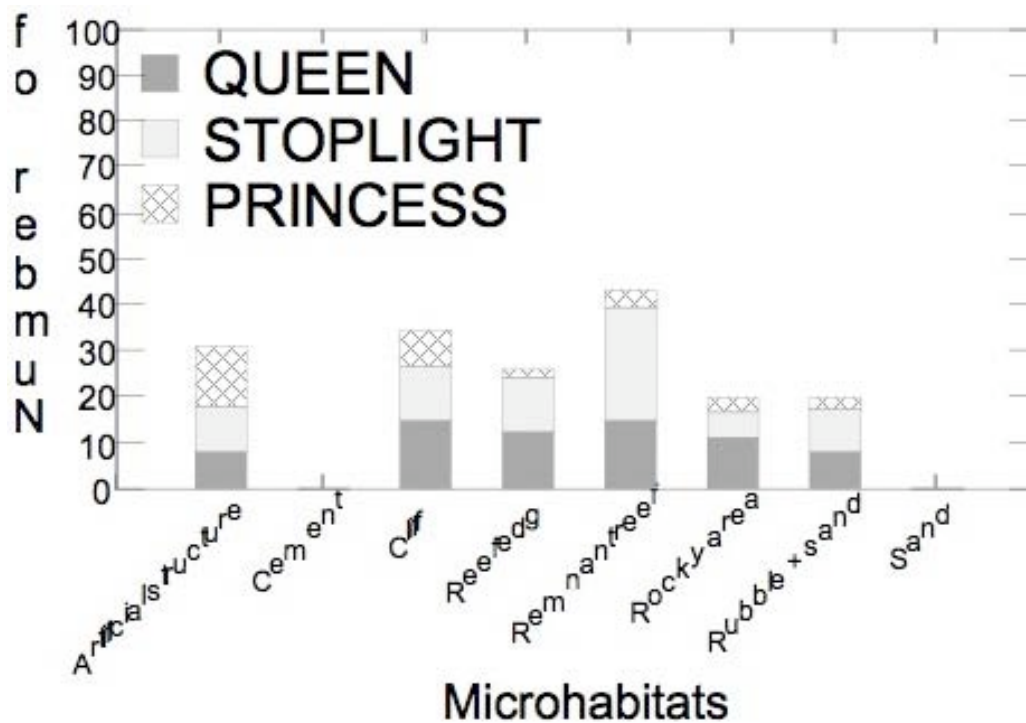


Figure 2. Comparison of fish abundance in different microhabitats.

However, at a finer scale, fish abundance is dependent on the abundance and arrangement of microhabitats contained within a site. In this respect, FPA sites Scientifico and Sunset show a higher abundance of fish as opposed to 18th Palm and Calabas Reef (Fig. 3). These differences are influenced by the characteristics of the microhabitats. Scientifico is comprised of a large remnant reef (47% of the total area) combined with a large patch of *A. cervicornis* rubble & sand (45%), and a little patch of sand (8%). Sunset, however, contained a large sand lagoon (64% of the area), but also contained the only artificial structure sampled in this study. Although small in area (6%), it was highly attractive to fish (Fig. 3). The artificial structure together with an adjacent large rocky area (25% of the total sample site) explains its fish abundance. While 18th Palm and Calabas each contained a small remnant reef (9% and 4%, respectively), small rocky areas (2% and 6%, respectively) combined with large sand lagoon (23%) in the case of Plaza, cement (49% and 30%, respectively), although large *A. cervicornis* rubble (17 and 60 % respectively) that are potential feeding areas, they yielded low abundance of fish (Fig. 3).

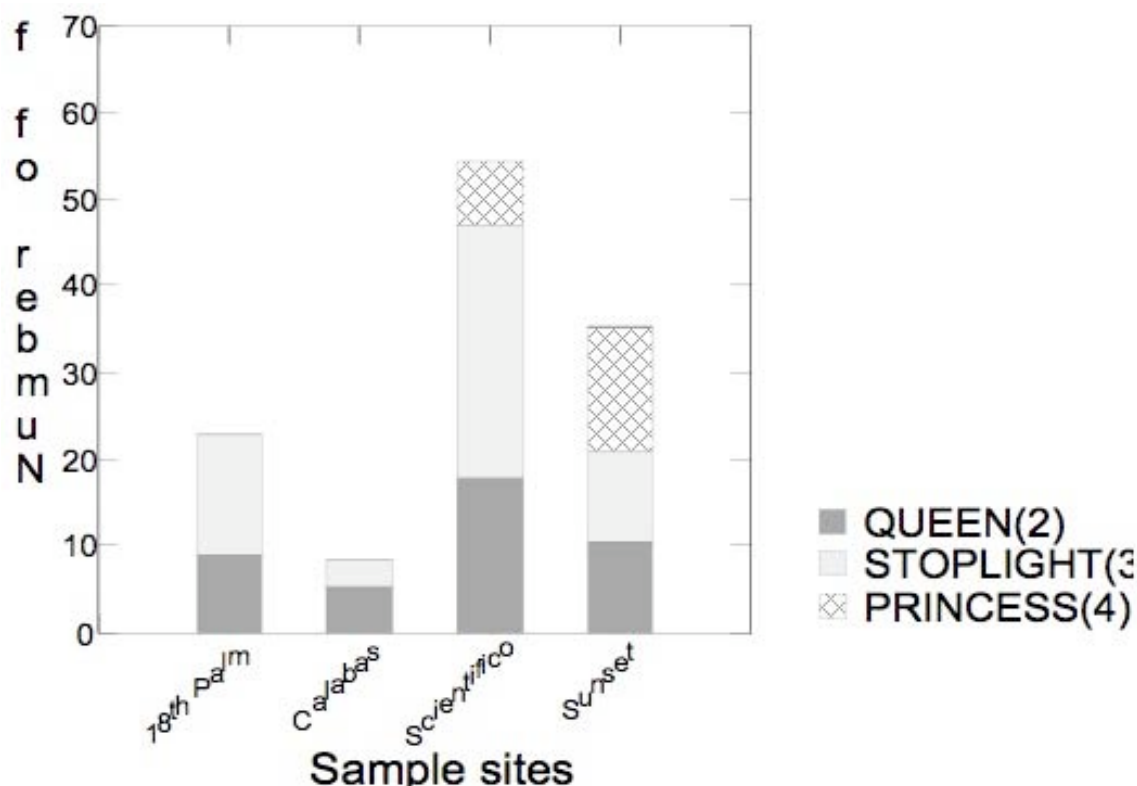


Figure 3. Comparison of fish abundance among FPA sites.

A more balanced distribution of microhabitat and fish abundance was observed in the control sites. For instance, Forest was composed of 34% reef edge, 37% rocky areas, and 28% sand lagoon. It is important to note that in a portion of this site the rocky area was continuous to the reef edge. Windsock was comprised of a large remnant reef (54%), a large *A. cervicornis* rubble patch (45%), and just 1% sand. Oil Slick contained a similar abundance of fish and was composed of a cliff (wall with large holes) that was highly attractive to fish, and adjacent to the

reef edge. On the other hand, Barcadera, with less fish abundance, was composed of a large sand lagoon comprising 47% of the area, located between a rocky shore comprising 43%, and a slim strip of reef edge that covered a remaining 10% of the sample site (Fig. 4).

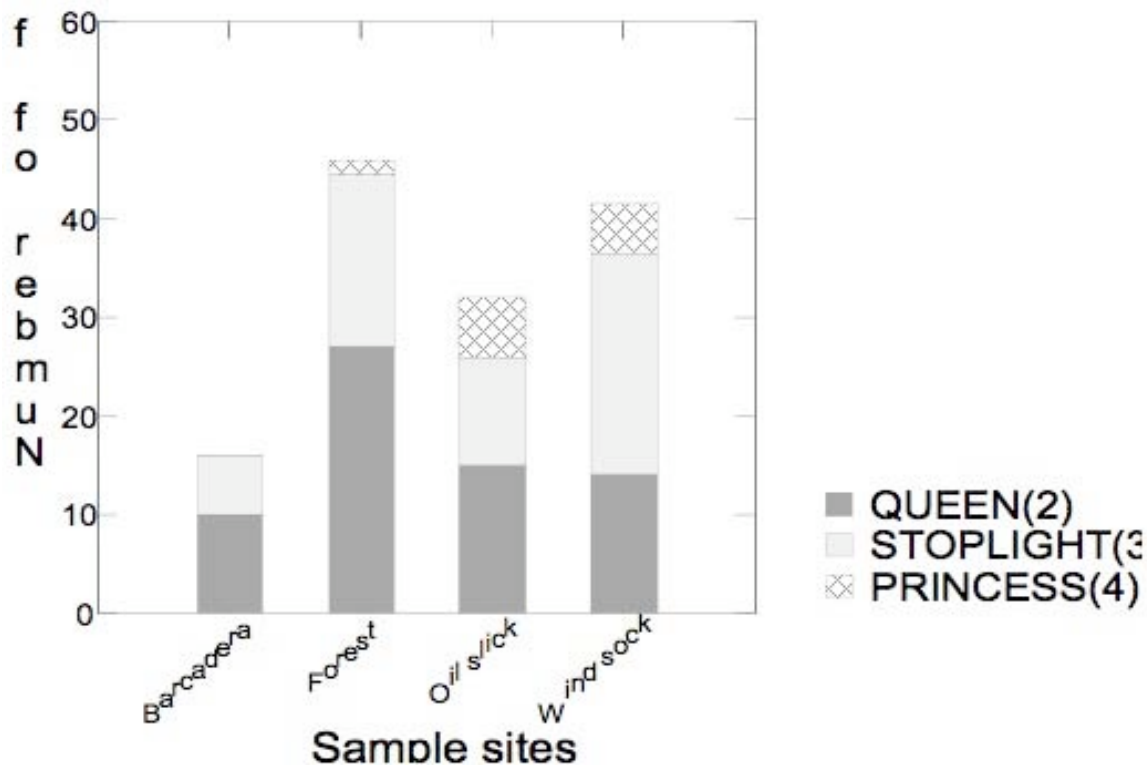


Figure 4. Comparison of fish abundance among Control sites.

Discussion

The general tendency for higher fish abundance to occur in remnant reef, artificial structure, cliff, and reef edge compared to medium abundance in rocky area, rubble & sand; and absent in bare sand and cement, suggests that physical structures with higher topographical complexity (Öhman, 2003) attract juvenile parrotfish more than those of lesser complexity. Complex structured habitats provide better shelter from predation for juvenile fishes and other organisms, when compare to less structured ones (Mateo and Tobias, 2001; Garpe and Öhman, 2003; Graham et al., 2006).

The synergy between complex structured shelter, food availability, and habitat connectivity may provide a more detailed explanation of the differences in pattern of abundance among sites. Although this study did not measure food abundance or availability, we observed intense grazing behavior in every location where juvenile fish were found, suggesting that food was a reason why they were present (Öhman and Garpe, 2003). This synergetic effect may also explain the importance of microhabitat arrangement in the sampled sites. In this regard, we observed sample sites with large remnant reef seemed to combine well with large *A. cervicornis* rubble patches where fish were also observed intensely feeding (Scientifico site in Table 1). While areas with

larger *A. cervicornis* rubble but very little complex remnant reef or other complex structured shelter (Calabas) attracted lower fish abundance (Table 1 in Annex). Another perspective of the habitat arrangement that may facilitate their use is their connectivity. In this respect, we observed that most combination of higher complex habitat structure (remnant reef) with lower complex habitat (that had presence of fish) hosted higher abundance of fish, were contiguous or connected, while a combination of habitats of intermediate complexity (rocky areas and reef edge) both separated by large sand lagoons yielded lower fish abundance (Table 1 in Annex).

The spatial and temporal trend in nearshore benthic composition of the Bonaire back reef was assessed by Bowdoin and Wilson (2005) who reported a large decline in live coral patches (changes in nearshore benthic composition). Our findings of complex structured shelter composed mostly of dead *A. palmata* colony and large patches of *A. cervicornis* rubble, are consistent with their reports, suggesting that these back reef habitats are severely degraded and decreasing, especially for the fish protection sites. The progressively degrading nursery habitat could represent a limiting attribute of the reef, which could result in a threat for viable populations of parrotfish in the long run (Graham et al., 2006).

The artificial site proved to host a higher abundance of juvenile parrotfish, comparable or higher than other natural microhabitats evaluated in this study (Fig. 2). Whether this improvised artificial reef enhanced new production of fish by improving survivorship, or just aggregating individuals from the surrounding area was not addressed in this study, however, in the absence or due to the lost of natural reef, a artificial reef could enhance fish production (Car and Hixon, 1997). In this case, artificial habitats could be an alternative that FPA management authorities may consider to evaluate, especially for those areas where natural habitats are degraded and continue to be highly disturbed.

Conclusion

The balance between microhabitat attractive to fish and its arrangement in the sites sampled, determined the pattern of juvenile parrotfish abundance and distribution. It is shown here that the shallow back reef is an important environment for at least part of the life cycle of three species of parrotfish in Bonaire. These microhabitats could have significant implication for conservation and management of these important herbivores (Mateo and Tobias, 2001; Mumby et al., 2004). In such case, the increasingly degrading back reef habitat of Bonaire could become a limiting factor to parrotfish distribution and abundance (Öhman and Garpe, 2003; Jonse, 2004). Management may need to revise its strategy of fish protection areas due to diminishing back reef nursery habitats (Bowdoin and Wilson, 2005). Control sites seem to have more promising back reef microhabitats for the protection of juvenile parrotfish.

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Annex

Table 1: Habitat type and area for all sites sample

Sample sites	Remnant reef	Reef edge	cliff	artificial	Rubble sand	sand	cement	Rocky area
Wind sock (c)	2,707 (54%)				2,243.83 (45%)	49.17 (1%)		
Plaza (FPA)	461.69 (9%)				867 (17%)	1,106.19 (23%)	2,450 (49%)	115.1 (2%)
Calabas (FPA)	200 (4%)				2,990 (60%)		1,510 (30%)	300 (6%)
Sunset (FPA)				287.3 (6%)		3,182.70 (64%)	270 (5%)	1,260 (25%)
Scientific (FPA)	2,379.27 (47%)				2,245 (45%)	375.73 (8%)		
Barcadera (c)		200 (10%)				909.5 (47%)		838 (43%)
Oil slick (c)		2,518 (93%)	200 (7%)					
Forest (c)		1,713 (35%)				1,420.00 (28%)		1,867.00 (37%)

Chapter 7: Non-indigenous and nuisance species in Bonaire National Marine Park

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Abstract

Invasive and nuisance species are characterized by their rapid colonization of new areas and unusual abundances that may trigger impacts over native species. The habitat and abundances of the orange cup coral, *Tubastrea coccinea*, an old invasive from the Indo-Pacific, and the native tunicate, *Trididemnum solidum*, were investigated. *Tubastrea* was found in low abundances at all sites of the Bonaire National Marine Park, predominantly at shallow reefs, at approximately 1 m depth, living on vertical surfaces over remnant reef, cliff, and other hard substrates. It also prefers shadowed areas or caves. A combination of intrinsic (organism) and extrinsic (environmental) characteristics drive the invasion of *Tubastrea* in the Caribbean. Some of these characteristics include mode of reproduction, high growth rate independent of light (intrinsic), lack of space competitors, and no predators (extrinsic). *Trididemnum* was absent from the monitoring sites but abundant in the northern region of the island. At all sites, neither *Tubastrea* nor *Trididemnum* seems to have strong interactions with native species. This study serves as a baseline for these species to be monitored over time.

Introduction

Non-native species that spread widely beyond the location of initial establishment, become locally abundant, or spread into natural areas, are referred to as invasive (Lodge et al., 2006). Invasions are determined by the characteristics of the receiving environment (extrinsic) and the characteristics of the organisms itself (intrinsic). Ecosystems that have reduced biodiversity, are under stress from environmental degradation and climate change, or have a lack of predators and competitors appear to be more vulnerable to invasions. Species with tolerances to broad ranges of temperatures or salinities, generalist with their prey, or with special reproductive features often characterize invaders. When a species succeeds and becomes invasive, the effects can be devastating on native ecosystems. Invasive species can rapidly and seriously degrade wild ecosystems by altering natural processes, changing the structure and function of many natural ecosystems (Carlton and Ruiz, 2005). At the same time, invasive species have been identified as one of the major causes of global change (Vitousek et al., 1997) and the cause of economic losses in environmental damages and associated control costs, impacting negatively other segments of the economy (Pimentel et al., 2005). No type of organism, habitat or biogeographic region is immune to invasive species (Steneck and Carlton, 2001). The number of invasive species in the Caribbean is generally thought to be low. However, several conspicuous invasive species such as the orange cup coral, *Tubastrea coccinea*, and more recently the highly invasive and harmful lionfish, *Pterois volitans* (Albin and Hixon, 2008), have spread throughout the region.

The aim of this study is to report the presence, abundances and habitat preferences of invasive and nuisance species in the Bonaire National Marine Park. Special attention was given to the orange cup coral, *Tubastrea coccinea*, and the tunicate *Trididemnum solidum*, and their interactions with native species.

Tubastrea coccinea

The orange cup coral, *Tubastrea coccinea*, is a small, encrusting colonial azooxanthellate and ahermatypic scleractinian coral. It is characterized by “brilliant red to orange or yellow polyp clumps that often form hemispherical mounds.” (Humann and DeLoach, 2002). *Tubastrea coccinea* is native of the Indo-Pacific and Indian Ocean. It has been reported in Australia (Cairns, 2004), Hong Kong (Lam et al., 2008), and Japan. Indeed, *Tubastrea* is pantropical cosmopolite (Cairns, 1994 in Glynn et al., 2008) because nowadays it is also present in the Caribbean and Equatorial Eastern Pacific, including Southern Brazil (Paula and Creed, 2005), Hawaii, Gulf of California (Humann and DeLoach, 2003), and the Galapagos (Witman and Smith, 2003). In the Caribbean, it was first recorded in 1943 in Puerto Rico and Curacao (Cairns, 2000 in Humann and DeLoach, 2002) and its introduction pathway is believed to be the ship’s hull fouling. After its first introduction, it spread throughout the Caribbean, Gulf of Mexico and coast of Brazil possibly carried in hulls or mobile platforms. According to Fenner and Banks (2004), *T. coccinea* was first observed in Florida in 2001 and at the Flower Garden Bank in 2002. To reach the current distribution within the Caribbean, Gulf of Mexico, and Florida could have taken about 60 years (Fenner and Banks, 2004).

Tubastrea coccinea prefers shaded areas in a wide range of environments, from pilings under docks, to caves in shallow reefs, to undercut faces and walls on deeper reefs (Humann & DeLoach, 2002). Vermeij (2006) reported that *T. coccinea* showed marked preference for the underside of the artificial panels at recruitment. The same study also reported that *T. coccinea* showed higher recruitment percentages at 12 m, compared to 30 m. In Hong Kong, *T. coccinea* was found in two dark and shallow caves at depths ranging from 9 to 20 m (Lam et al., 2008). According to Fenner and Banks (2004) from studies in Florida and the Gulf of Mexico, artificial structures are “clearly preferred habitat,” since in each area they are found first on some artificial structures.”

The orange cup coral, *T. coccinea* is a brooder, releasing planula larva. Paz-Garcia et al. (2007) described their larvae as a “brilliant yellow color” that measured between 3 to 5 mm. In the Gulf of California, the planulation was observed in the summer or fall when surface water was 25°C or higher. They also pointed out that *Tubastrea coccinea* becomes sexually active at very early age and part of their population is hermaphroditic.

Trididemnum solidum

Trididemnum is a colonial mat-like tunicate that overgrow corals. Colonies of this leathery tunicate encrust large areas of a reef, possibly overgrowing or killing the corals (Humman and DeLoach, 2002). According to MacGrath and Peachey (2008) the growth rate of *T. solidum* is “much higher than scleractinian corals and so overgrowth of live tissue is common and typically results in bleaching.”

Methods

To detect the presence of *Tubastrea coccinea* and *Trididemnum solidum* in the fore reef, 50 m long transects at 10 meters depth and parallel to the coast were conducted using scuba diving. All colonies at both sides of the transect (1 meter to each side) were measured to the nearest millimeter using a ruler. Given that the presence of both species was low and zero, respectively in all stations, extra underwater surveys of the shallow areas were also conducted using scuba and/or snorkeling. These shallow surveys were conducted charting two transects perpendicular to the coast, and measuring all colonies to the nearest millimeter in one meter stations to both sides of the transect. The depth was measured using a measuring tape and the inclination was recorded subjectively estimating the angle. In addition, the type of substrate was also recorded using an ad-hoc scale that classified the substrates as: DAP, for dead *Acropora palmata*; BOU, for boulder or rocks; CLF, for cliff; CON, for concrete or artificial structures; and BLK, for the calcareous block at the shallowest area of some of the sites.

The abundance of *Tubastrea coccinea* per site and depth was calculated using the mean abundances of the stations at same depth standardized to square meter. For the analysis of the substratum preference and inclination, the total abundance of colonies per site was averaged.

Results

Tubastrea was found at 10 meters depth only at Oil Slick Leap and Forest but at very low abundances. *Trididemnum* was not recorded at any of the 10 m stations, nor was it found at the shallow transects. On the contrary, *Tubastrea* was found in all shallow transects, with a maximum near $50 \text{ cm}^2 \text{ m}^{-2}$ in Oil Slick Leap (Fig. 1). The lowest abundance of *Tubastrea* was recorded at Calabas Reef, at $1 \text{ cm}^2 \text{ m}^{-2}$. The geographic pattern of *Tubastrea* shows a decreasing abundances from north to south sites, with and moderate increase at Windssock (Fig. 1).

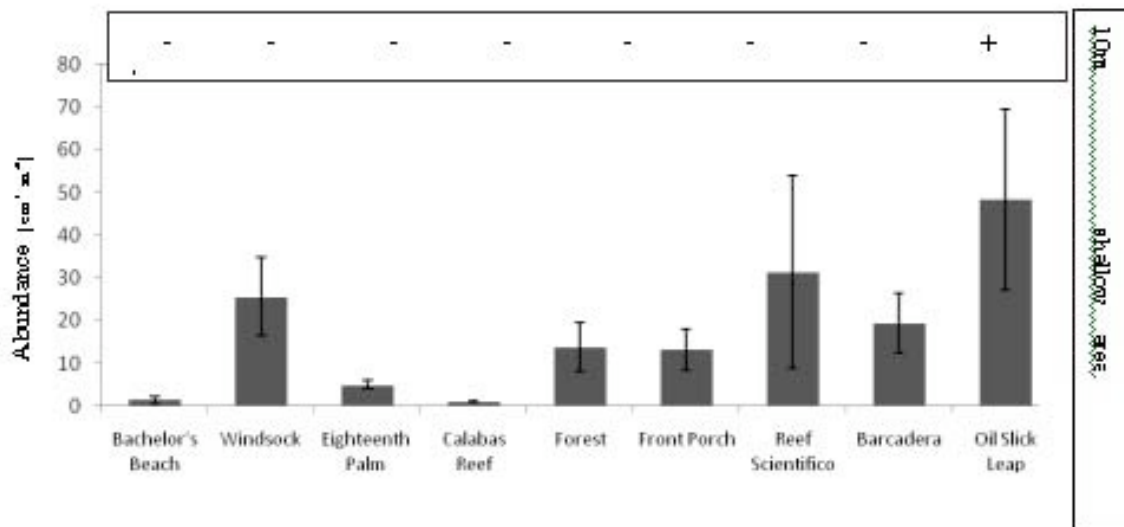


Fig. 1. Mean abundance of *Tubastrea coccinea* in shallow zones of Bonaire sites. The box in the upper area represent the presence (+) or absence (-) of *Tubastrea* at 10 m transects. The values of the abundances at 10 m are anecdotal (very low).

Tubastrea was more abundant at shallow areas, especially below 2.25 m depth (Fig. 2). The maximum mean abundance of *Tubastrea* by depth was $44.57 \text{ cm}^2 \text{ m}^{-2}$ at 1.01-1.25 m depth. The absolute maximum abundance per site was $251.77 \text{ cm}^2 \text{ m}^{-2}$ at Oil Slick Leap at the same depth. The same site registered the single presence of *Tubastrea* at 3.01-3.25 m and 6.01-6.25 m depths. *Tubastrea* was never seen exposed to the air at the shallowest depth of 0.00-0.25 m.

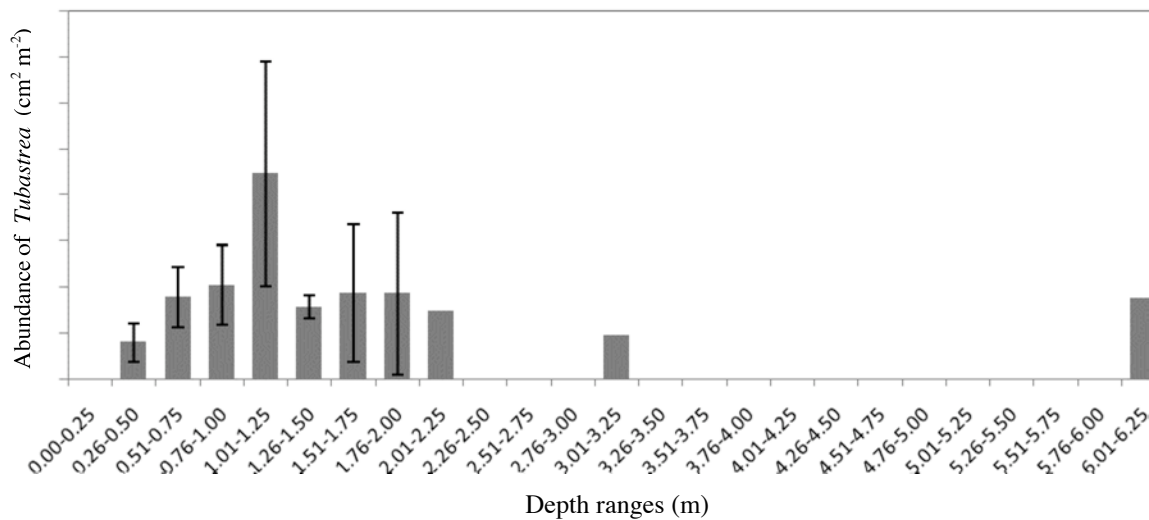


Fig 2. Abundance of *Tubastrea coccinea* with depth. Values represent mean abundances per 0.25 ranges depths.

Tubastrea colonies were found over hard substrates of different slopes. However, the colonies preferred nearly vertical angles, primarily the 60.1-90 angles, and secondly the 90.1-120 angles. The third most preferred angle was the 150.1-180 slopes that are upsides of hard substrates.

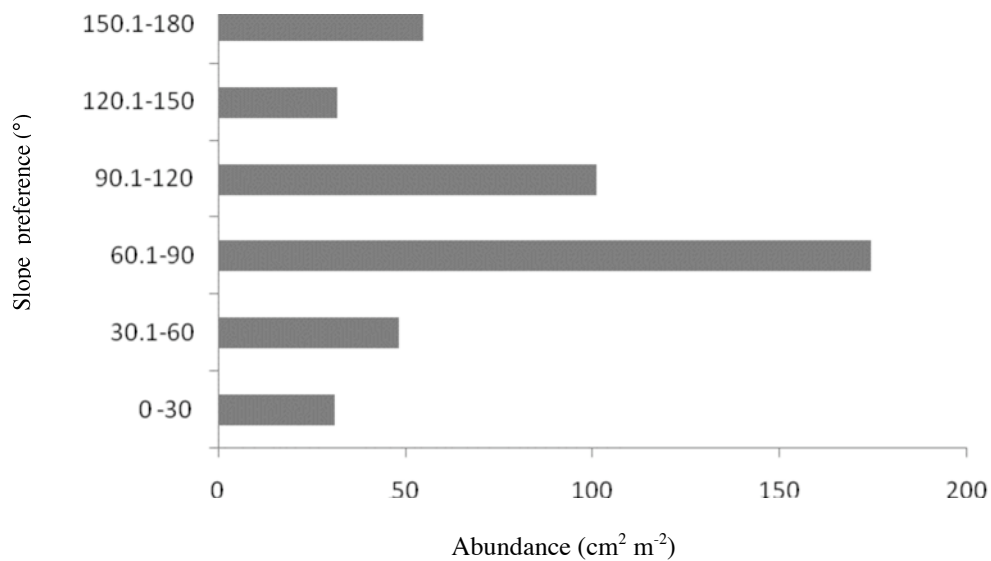


Fig 3. Slope preferences of *Tubastrea* over hard substrates.

Tubastrea hard substrate preference was non-specific (Fig. 4). In the northern most sites, most colonies were found over the cliff wall at the breaking zone. At Front Porch, an important part of the colonies were found over concrete artificial substrates, and at Calabas Reef exclusively at the edge of the calcareous block. However, at almost all sites (except Calabas Reef), *Tubastrea* was found growing on dead *Acropora palmata*, which were characterized by their irregular, upward and branching shapes. This substrate was especially abundant at Reef Scientifico, Eighteen Palm, Bachelor's Beach and Forest. The second most common substrate but in lower percentages were boulders (Fig. 4).

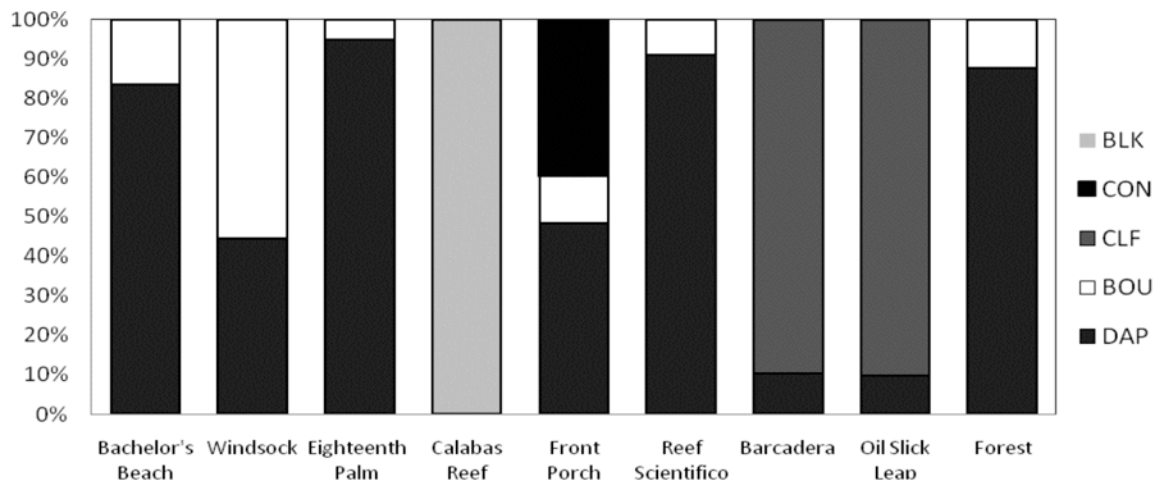


Fig. 4. Substratum preferences (%) of *Tubastrea coccinea* at nine sites. In parenthesis the total coverage of *T. coccinea* per site in cm² m⁻². DAP: dead *Acropora palmata*; BOU: boulder; CLF: cliff; CON: concrete structures; and BLK: calcareous shallow block.

Discussion

Tubastrea is rare and lives in shallow waters, primarily over vertical hard substrate. In Bonaire, it is more abundant at the northern sites on the leeward shores with the greatest abundance at Oil Slick Leap. *Tubastrea* was relatively rare despite the availability of hard substrate at all sites. The abundances of *Tubastrea* seems to be correlated to the type of habitat of the different sites. In fact, *Tubastrea* was primarily found in vertical substrates of shallow areas. For example, the highest abundances of *Tubastrea* were found in sites with cliffs or concrete walls, followed by sites with other abundant hard substrates such as rocks or remnant corals. On the contrary, the lowest abundances were found in sites with predominance of soft substrates or flat, hard substrates. Visual observations also report high abundances of *Tubastrea* on artificial hard substrates, especially over pillars of docks and piers.

Tubastrea orientation could explain the south to north increase in abundance (for a more detailed description of the shallow habitats see Chp. 6, Chang, 2009). The branching architecture of *Acropora* offered suitable microhabitat and was commonly occupied by *Tubastrea*. It is possible that higher abundances of Acroporids could lead to increasing abundances of *Tubastrea* in the future.

The data of this study show that the coral *Tubastrea* is a shallow and solitary species found in low abundances. According to Paula & Creed (2005) in southern Brazil, where the introduction is more recent, *Tubastrea* is more abundant between 0.1 to 0.5 m. The same authors report similar slope preferences (81-100°) and that *Tubastrea* was found mostly in density classes of 1 to 5 individuals. In the Galapagos Islands it was found only in low abundances, representing less than 5% percent cover in Rocas Gordon, Santa Cruz Island at 12 m depth (Witman & Smith, 2003).

The introduction of *Tubastrea* to Bonaire occurred more than 50 years ago. The first report was from nearby Curacao. This may imply that the distribution and local abundances of *T. coccinea* are relatively stable in space and time, meaning that it may be as abundant as it will become. It is likely that the colonization phase had finished.

The interactions between *Tubastrea* and native species are not clear. The literature reporting impacts over native species is restricted to the study by Creed (2006) which reported that in Iha Grande, Brazil, *T. coccinea* and *T. tagusensis*, caused necrosis or deformations of the endemic scleractinian coral *Mussismilia hispida*. Creed argues that both invaders are “competitively dominants and can reduce or exclude the native corals.” However, in Bonaire there is no evidence of strong interactions of *Tubastrea* over native species. According to Parker et al. (1999), in order to assess the impacts of invaders on a geographic scale, three main factors should be considered: the total area occupied, abundance, and some measure of the impact per individual. Based on these factors, the assessment of the impacts of the invasive *Tubastrea* are not high. First, *Tubastrea* is not locally abundant (dominant) in any site, habitat or substrate in the sites surveyed, and, on the contrary, only found at low densities. In addition, it is virtually absent at the deeper fore reef. Second, the colonies edges do not overlap nor interact with other benthic species, and it is found as a solitary species. However, it is important to monitor this apparent inoffensive state over time to assess the long term impacts and possible adaptations of

Tubastrea to changing environments, especially under possible phase shifts regimes witnessed in other coral reefs in the Caribbean or climate change scenarios.

A combination of intrinsic (organism) and extrinsic (environment) characteristics are driving the invasion of *Tubastrea coccinea*, making it a successful colonizer of benthic habitats of tropical areas. First, *T. coccinea* can survive independent from the presence of light which contributes to its colonization of dark or shadowed areas, caves, or undersides of substrates. Second, the study by Marshall (1996) demonstrated that *Tubastrea* has similar growth rates to zooxanthellae corals. Third, its preference of artificial substrates (Vermeij, 2006) may enhance the spread within the first introduced area as hull fouling or mobile platforms. Finally, from the reproductive point of view, *T. coccinea* becomes sexually active at a very early age, is a brooding hermaphrodite, and may be reproductively active year round with adequate environmental conditions. From the extrinsic point of view, some of the drivers are the habitat preferences of *Tubastrea* that do not seem to overlap with other native species, and the apparent lack of predators.

Finally, the absence of the encrusting tunicate *Trididemnum* in the monitored sites does not imply its absence in other areas of the island. Indeed, according to STINAPA staff, *Trididemnum* is locally abundant in the northern part of the island. This was confirmed by diving in two northern sites where *Trididemnum* mats covered important areas of hard substrates or coral colonies, directly interacting and competing with native corals for space. Some of these mats were tagged and photographed to assess their growth and colonization rates in a future study.

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Chapter 8: A comparison of 1998 bleaching events in Bonaire and Belize

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Abstract

The bleaching events of the past few decades have gone beyond previous events in intensity, expanse, and frequency. In 1998 much of the Caribbean experienced massive bleaching due to the combination of rising world temperatures and the El Niño event. It also suffered disturbances from massive storms. Belize was one of the areas particularly hard hit, whereas Bonaire was not and has remained much less affected by the current warming trend. This study utilizes the Coral Reef Temperature Anomaly Database (CoRTAD) from the National Oceanographic and Atmospheric Administration (NOAA) along with ReefBase records of bleaching events to compare the different trends of warming and bleaching during 1998. The overall thermal stress appeared to be far lower in the Bonaire region, even though sea surface temperatures spiked during the summer months. This difference in accumulated thermal stress, using degree-heating weeks, may reflect the lower intensities of bleaching that occurred in Bonaire. Additionally, the data suggest different threshold temperatures for bleaching for the two regions, with that threshold temperature being lower for the Bonaire than the Belize region. These data, along with continued predictions for future warming, can serve as a warning sign for preventative action to preserve Bonaire's coral reefs.

Introduction

The events of 1997-98 marked a significant change in the world's coral reefs. The combination of the El Niño event and the warming temperatures created an expansive bleaching event that affected 16% of the world's coral reefs (Wilkinson 2000). This sort of mass bleaching event was the largest, with no such mass events reported prior to the 1980s (Glynn 1993). Corals have shown some limited short-term resistance to elevated water temperatures (Bellwood et al. 2006), but the estimates of continued, long-term warming (Hoegh-Guldberg 1999; Donner et al. 2005) have created rising concern on the effects of bleaching on coral reefs and their surrounding communities. Due to corals' habitat being near their upper limits of their temperature ranges, for both reproductive and somatic growth advantages (Rosen 1981), the rising temperature trends put them even closer to their lethal limits.

Bleaching results from the expulsion by the coral hosts of their symbiotic zooxanthellae, photosynthetic algae that can reside both within the corals and free-living in the environment, in response to an environmental stress. These levels can vary seasonally, so the expulsion must be in response to a specific stressor in order to be considered coral bleaching (Fitt et al. 2000). Suharsono et al. (1993) indicated that the housing of these symbionts placed additional stress on the host, as elevated seawater temperatures more easily stressed symbiotic anemones than aposymbiotic anemones of the same population. The use of temperature reflects the possible role it plays in this relationship (Rosen 1981), although bleaching can be a result of various stressors,

including pollutants or extremes in salinity or light irradiance (Brown 1997). Although this relationship between the coral and the zooxanthellae can increase the effects of an environmental stress on the coral, the additional resources, which can be between 50-95% of the algae's photosynthetic products (Trench 1971; Muscatine 1990), increase the growth capacity of the coral hosts. Thus the potential effects of increased frequency and intensity in bleaching events can impact the survivorship and extent of corals and coral reefs.

Although previous studies on major bleaching events found a lack of statistically significant evidence that high water temperatures primarily caused the massive bleaching events (Atwood et al. 1992), more recent evidence, especially with the 1997-98 bleaching event, has pointed to maximum seawater temperatures as the major factor behind coral bleaching (Hoegh-Guldberg 1999; Bak et al. 2005; Sheppard and Rojja-Nieto 2005). With both remote-sensing and *in situ* observation methods, the ability to monitor the seawater temperatures over time allows for monitoring of possible bleaching events. The National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch monitors the levels of Degree Heating Weeks (DHWs), which convey the accumulation of thermal stress experienced by the corals within the previous twelve consecutive weeks (Wilkinson and Souter 2008). The NOAA Coral Reef Watch relays Satellite Bleaching Alerts when these values reach certain thresholds, indicating that bleaching is likely or nearly imminent. Additionally, the NOAA Coral Reef Temperature Anomaly Database (CoRTAD) documents past temperature data to further study these happenings (for a complete list of all acronyms used, see Table 1).

Within the Caribbean, the 1997-98 El Niño event brought temperatures to 31.5°C, well above the normal maximum of 29°C (Aronson et al. 2000). The area had suffered previous massive bleaching events in the 1980s and most recently in 1995, with the 1995 bleaching event being more severe in the north and the 1998 bleaching event more severe in the south (Goreau et al. 2000). The 1998 bleaching event in Belize was a 3000-year event with complete bleaching reaching large, plate- and head-forming species (Aronson et al. 2000). Combined with the devastation of Hurricane Mitch (Wilkinson 2000), the corals in southern Belize suffered 75% mortality rates. In contrast, the island of Bonaire, part of the Netherlands Antilles, has suffered far less mortality and bleaching. In 1998 the area suffered only from 15% mortality through September, at which time 100% of the *Agaricia* species bleached (Wilkinson 1998); however, no other species within the area bleached in similar water temperatures and conditions. Although there is evidence for different bleaching susceptibilities among species (Williams and Bunkley-Williams 1990; Bruno et al. 2001), the area overall has been far less susceptible to bleaching events.

This study looks at the 1998 bleaching events that occurred in Bonaire and off the coast of the Stann Creek district in Belize. By comparing the timing of the bleaching events to records of sea surface temperature (SST), sea surface temperature anomalies (SSTA), and the degree heating weeks of SSTA (SSTA_DHW) and thermal stress anomaly (TSA_DHW), this study hopes to find some evidence for the differences in the bleaching events, in not only their number but severity, for these two regions.

Methods

The National Oceanographic and Atmospheric Administration's (NOAA) Coral Reef Temperature Anomaly Database (CoRTAD) team provided the data for this study, which are approximately 4.5-km resolution data. The entire set of data, available at a weekly resolution, are accessible online (<http://www.nodc.noaa.gov/SatelliteData/Cortad/>) in a hierarchical data format (*.hdf). In order to bring these three-dimensional data (latitude, longitude, and time) into ArcGIS 9.2 (2006) for spatial analysis, the NOAA team formatted the data into a network common data format (netCDF or *.nc) (T. Brandon, personal communication, 25 February, 2009). The data included a 3 X 2 rectangle around the first Bonaire site from 12.151146°N, -68.358437°W in the upper northwest corner to 12.1072°N, -68.270546°W in the lower southeast corner (Figure 1). A 4 X 4 square bounded the second Bonaire site, with points from 12.2830°N, -68.2705°W in the upper northwest corner to 12.2390°N, -68.2266°W in the lower southeast corner. The area for southern Belize was much larger, ranging from 16.8973°N, -88.1782°W in the upper northwest corner to 16.7216°N, -88.0464°W in the lower southeast corner, centering a 3 X 3 grid on each of the 1998 bleaching sites (Figure 2). A total of eight bleaching sites occurred in the Belize area dataset in 1998; however, this study focused on only four of these occurrences. The study used the data sets FilledSST and SSTA for the 1998 year, along with the SSTA_DHW and the TSA_DHW data for the specific bleaching event. TSA represents the weekly SST minus the maximum weekly climatological SST, taking into account the past temperature regime of the area. NOAA's Coral Reef Watch program uses the TSA_DHW in its assessment of potential bleaching levels.

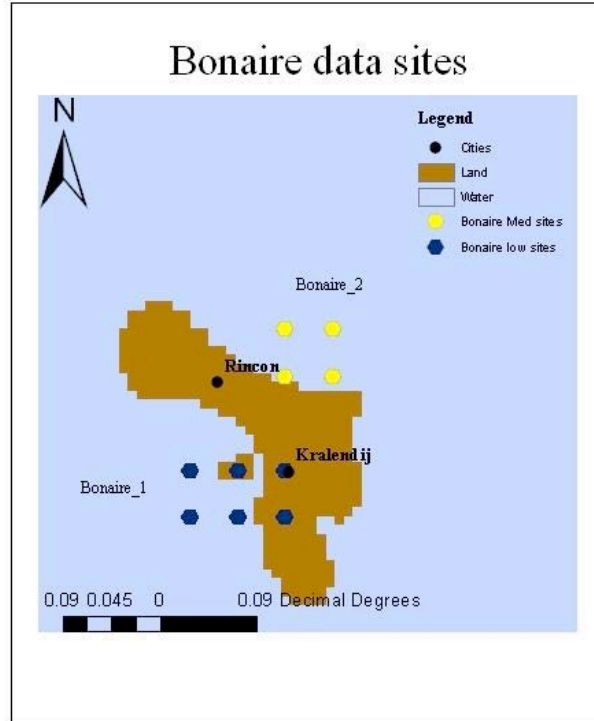


Figure 1. CoRTAD data sites within the Bonaire region for both the medium and low bleaching events.

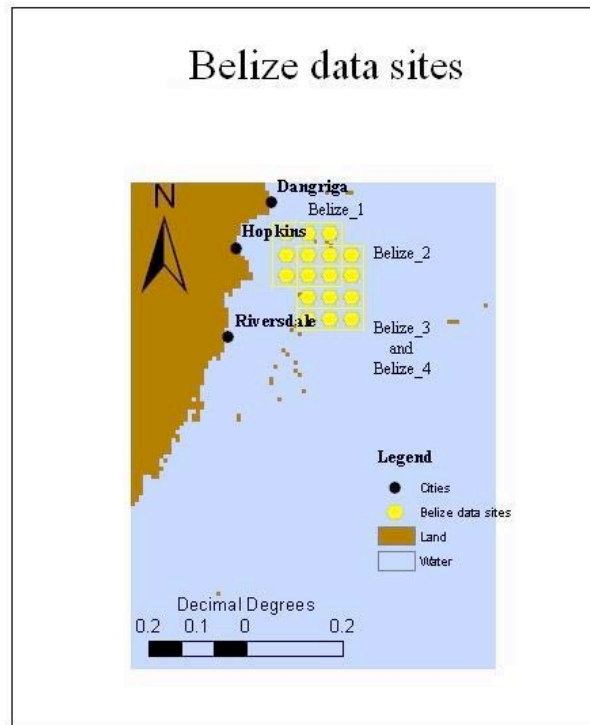


Figure 2. CoRTAD data sites within the Belize region for all four bleaching events. The outlines of the different sites are marked in yellow and named.

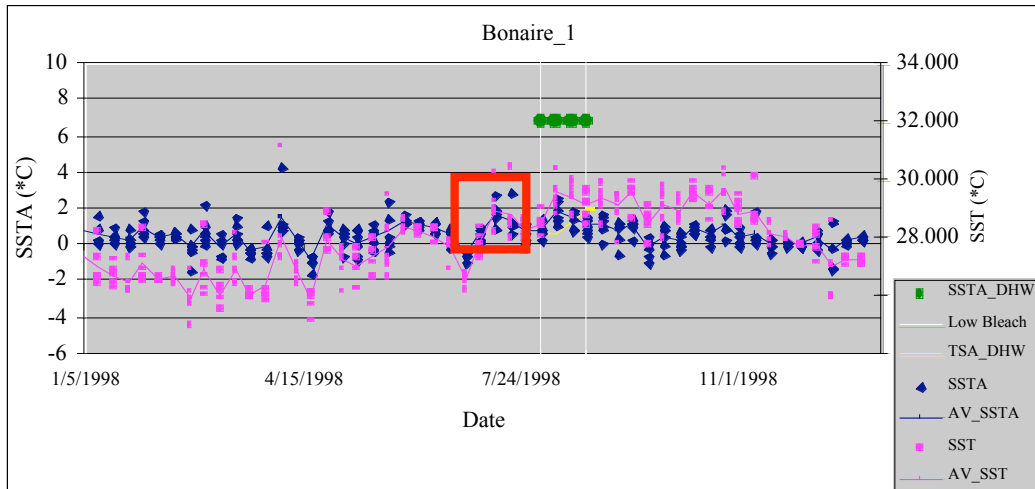
ReefBase, a non-profit organization that gathers and freely dispenses information regarding coral reef ecosystems, provided the records of bleaching events through their ReefGIS database, with coral reef locations provided by the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC). This database catalogs bleaching events, according to severity, location, and timing, adding notes regarding that bleaching event. The time resolution of these data is monthly, limiting the analysis to this time step. This study plotted these data, along with the CoRTAD data, in Microsoft Excel (2003) across the 1998 time span.

Results

Both Bonaire bleaching events occurred early in the year in August (Table 2). The event on the leeward side of the island (Bonaire_1) had a severity rating of low, whereas the event on the windward side of the island (Bonaire_2) had a severity rating of medium. Concerning the low bleaching event Bonaire_1, one of the six locations showed much higher temperatures in mid-July, just prior to the event (Figure 3a, red box). These elevated temperatures may have caused enough of a thermal stress to trigger the bleaching event; however, the data prior to that time period showed relatively low or negative anomalies, except for an errant point in April. Both during and after the bleaching event, both SST and SSTA values showed elevated levels, but the ReefBase dataset recorded no bleaching events for the rest of 1998 in that area. The SSTA_DHW averaged 6.77°C-degree heating weeks and the TSA_DHW averaged 1.05 °C-degree heating weeks during the month of the bleaching event.

Concerning the medium severity bleaching event Bonaire_2, the heightened SSTA and SST values began during the end of August, as evidenced by the quick increase in the SSTA_DHW line (Figure 3b). This increase, which raised the SSTA_DHW levels from just over 2°C- degree heating weeks to over 4°C- degree heating weeks, likely denotes the onset of the bleaching event. Additionally, the TSA_DHW values rose from 0°C- degree heating weeks to 0.33°C- degree heating weeks, values not generally consistent with bleaching events. However, ReefBase rated the severity of this event higher than the other Bonaire August bleaching event. Again, as with the other bleaching event in Bonaire, SST and SSTA spikes occurred after the recorded bleaching event, although no additional events appeared in the database

a.



b.

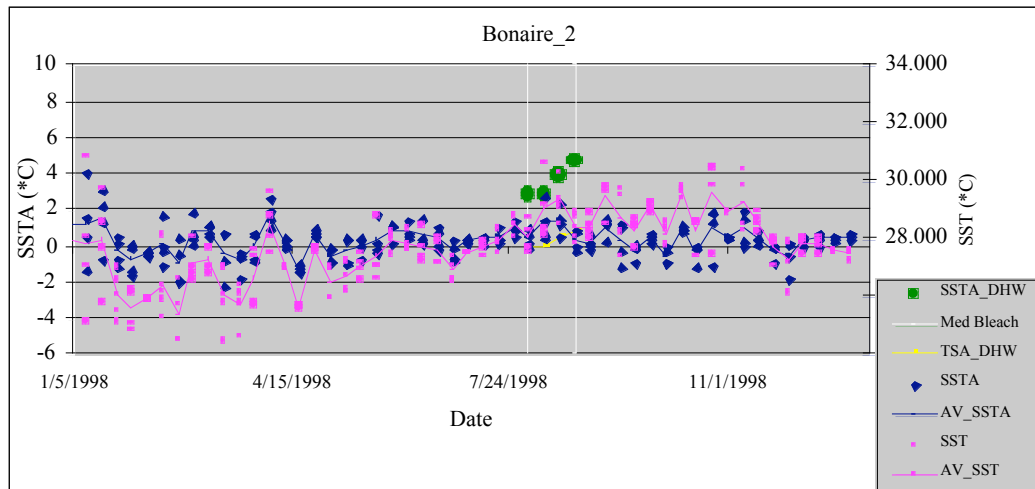


Figure 3. Sea surface temperature (SST; magenta dots), Sea surface temperature anomaly (SSTA; dark blue dots), Sea surface temperature anomaly degree heating weeks (SSTA_DHW; dark green circles), Thermal stress anomaly degree heating weeks (TSA_DHW; yellow line), along with average SST (AV_SST; magenta line), average SSTA (AV_SSTA; dark blue line), and marking of time period for bleaching event (vertical lines) for Bonaire_1 (a) and Bonaire_2 (b). The red box for site Bonaire_1 (a) denotes the two peaks in temperature in July.

The dataset contained evidence for one other bleaching event in 1998 that occurred to the south of the study area in September. The ReefBase dataset indicated that this event was of medium severity; however, it was outside the range of data provided from the CoRTAD dataset (Figure 4).



Figure 4. Bonaire's 1998 bleaching event sites denoted by intensity, color-coded circles (blue = low, yellow = medium, red = high).

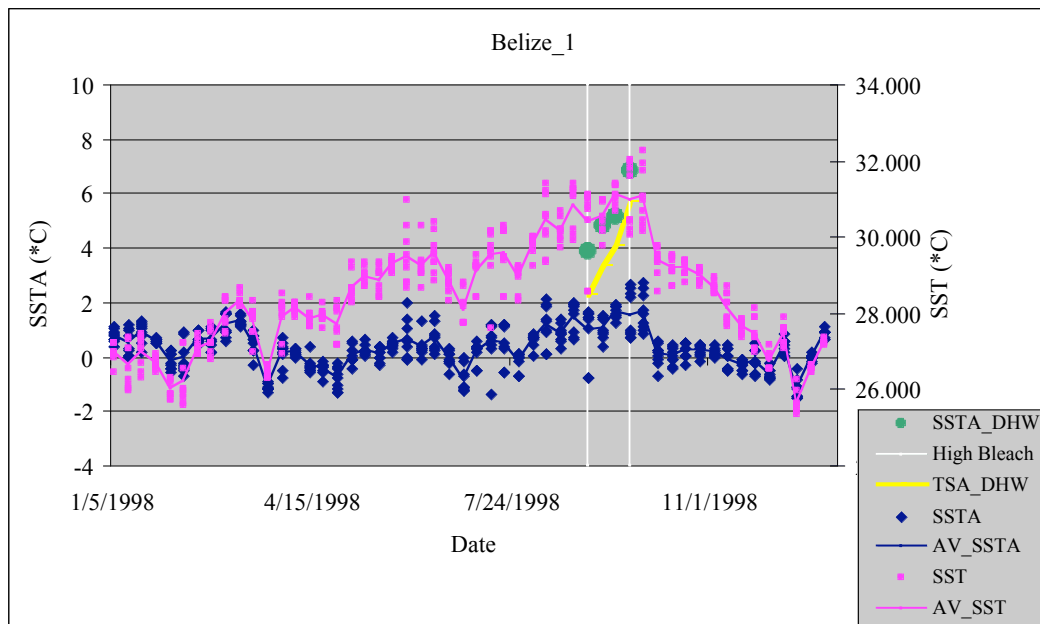
Two high severity bleaching events occurred in September 1998 in the Belize study area, Belize_1 and Belize_2. Both of these events showed similar trends, with steadily increasing SST and SSTA values beginning in April and peaking during the bleaching event in September (Figures 5a and 5b). The SSTA_DHW data revealed the large quick increase that occurred throughout September, with the highest values occurring at the end of the month. The SSTA_DHW absolute values for site Belize_1 were much higher than the values for site Belize_2, whose values were more similar to that of the medium-severity bleaching event in Bonaire (Table 2). The TSA_DHW values showed a similar trend to the SSTA_DHW values, ramping up throughout the month and ranging between 2-6°C- degree heating weeks for site Belize_1 and between 0-4°C- degree heating weeks for site Belize_2.

The next two events occurred in the same area and were likely related. The first, a medium bleaching event (Belize_3) that occurred in October, followed heightened SST and SSTA values in September (Figure 5c). Although by October the SST and SSTA values had dropped, both the SSTA_DHW and TSA_DHW values remained high, indicating the accumulated levels of thermal stress that had built up in the area. The SSTA_DHW values were above 8°C- degree heating weeks for the entire month and the TSA_DHW values stayed constant at 7.825°C-

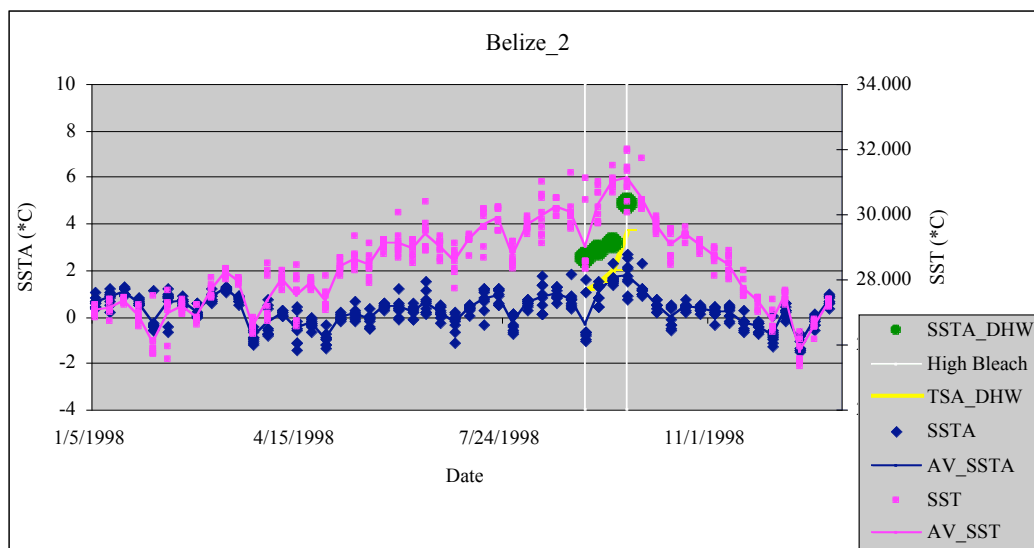
degree heating weeks, both of which were higher than the values that triggered the severe bleaching events in September. This timing of heightened DHW values, occurring at the end of September and beginning of October, may indicate that the bleaching events occurred during that time boundary.

A November low bleaching event (Belize_4) followed the October medium bleaching event Belize_3 in the exact same area, possibly indicating that the two events were related. During this time both the SST and SSTA values continued to drop, which supports a lower intensity bleaching event (Figure 5d). Additionally, the SSTA_DHW and TSA_DHW values dropped but were still in the range to initiate bleaching events.

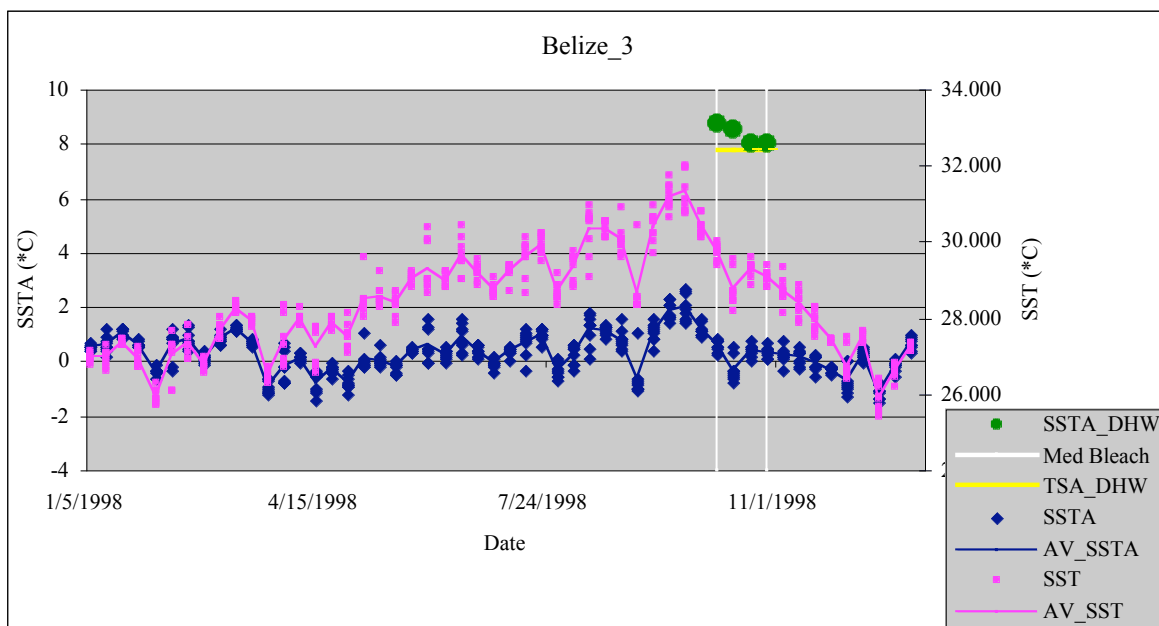
a.



b.



c.



d.

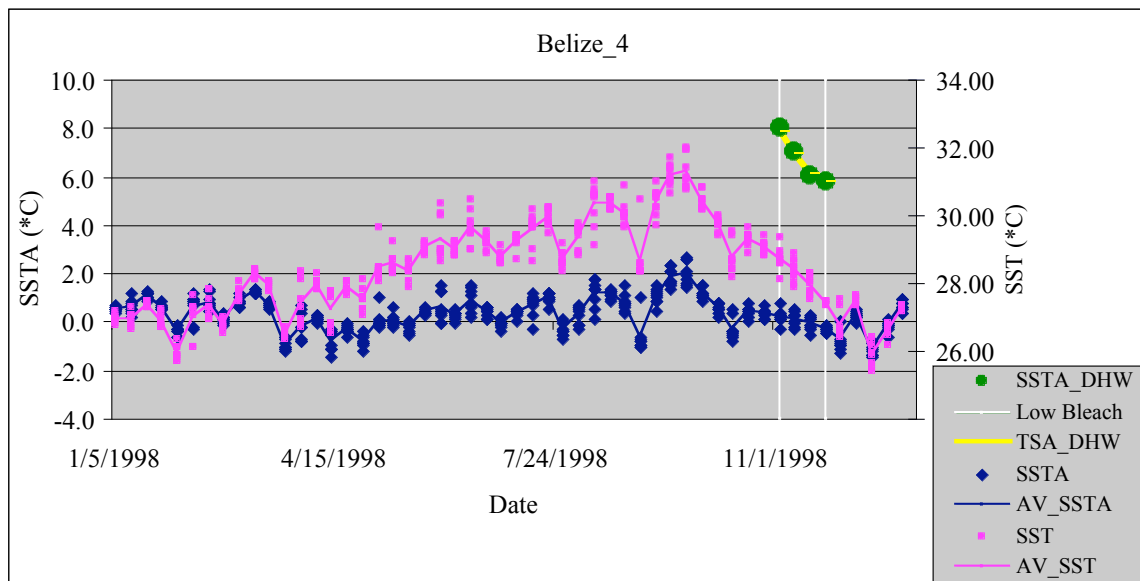


Figure 5. SST (magenta dots), SSTA (dark blue dots), SSTA_DHW (dark green circles), TSA_DHW (yellow line), along with AV_SST (magenta line), AV_SSTA (dark blue line), and marking of time period for bleaching event (vertical lines) for Belize_1 (a), Belize_2 (b), Belize_3 (c), and Belize_4 (d).

Discussion

The data for the Bonaire and Belize bleaching events revealed the heightened temperatures that occurred before and during the events. Brown (1997) used a much longer time span to look for threshold levels of thermal stress for Phuket and Tahiti. This study looked only at the year's

worth of temperature data to find differences among the two contrasting areas. Belize suffered from high levels of mortality during the 1998 year, which resulted not just from bleaching and thermal stress but also from the extreme rain from Hurricane Mitch (Wilkinson 2000). Bonaire, in contrast, has been relatively immune to the bleaching events, suffering fewer events and lower mortality (Wilkinson 1998). The 1998 year provided an opportunity to examine both areas during the height of bleaching.

The Belize area showed higher susceptibility to the accumulated DHW, as similar values provoked more intense bleaching events in Belize than in Bonaire. The high bleaching events in Belize had SSTA_DHW maxima of 6.81°C- and 4.83°C- weeks, which were within a 2°C range of the 6.77°C- degree heating weeks SSTA_DHW maximum for the Bonaire low bleaching event and the 4.67°C- degree heating weeks maximum for the medium bleaching event. However, the difference may lie in the TSA_DHW, a measure of accumulated thermal stress. The high bleaching events in Belize had maxima of 3.67°C- and 5.73°C- degree heating weeks (TSA_DHW), whereas the low bleaching event in Bonaire had a maximum of 1.84°C- degree heating weeks and the medium bleaching event had a maximum of 0.86°C- degree heating weeks. It is this accumulated stress that may show the differences in the levels of bleaching between the two areas, with the accumulated stress being far less within the Bonaire than within the Belize region.

The graphs may indicate a further conclusion for different threshold temperatures. Within the Belize region, the average SST temperatures had to peak and remain over 30°C for a few weeks before any of the bleaching events occurred. This value was only 29°C for the Bonaire region. These differences may indicate a potential warning sign, in that the Bonaire region has been subject to less thermal stress but lower temperatures may induce bleaching.

The ability to predict and track bleaching events can act as a warning sign for global changes to coral reef communities (Hughes 2000). The community structure can change post-bleaching, depending on the levels of bleaching and the recovery of the corals (Diaz-Pulido and McCook 2002). Graham et al. (2006) noted that a loss of structure due to bleaching mortality was a main driver in the loss of species, taxonomic, and functional diversities in reef ecosystems. As bleaching mortality can peak several months after the bleaching event (Goreau et al. 2000), continued monitoring is necessary to track the full impacts of bleaching events.

The use of the DHW tracking allows for early warnings to reef managers to watch for signs of bleaching, but the methods for determining the level of bleaching on a universal scale still need to be developed. McWilliams et al. (2005) pointed out that the severity of the 1999 bleaching events was only second to the 1998 bleaching events, yet the 1999 mass bleaching received little attention as it came right after the most extensive bleaching event in history. This relative comparison did not befit the 1999 events' absolute level of impact. With decreased reproductive capacity in bleached corals (Szmant and Gassman 1990) and even extinctions possible due to bleaching (Glynn and de Weerd 1991), the need to track and assess the damages is evident.

The increased bleaching events, in frequency and intensity, result from larger-scale, climatic changes that require a more holistic, world-scale approach to the problem. Corals have the potential to acclimate to the new conditions, but the changes have been so rapid and prevented

such acclimation (Hoegh-Guldberg 1999). With climate models indicating continued rises in temperature and consequently increased intensity and frequency of bleaching events, the future does not look promising (Hoegh-Guldberg 1999; Donner et al. 2005). Additional stressors from both anthropogenic and natural sources further hamper the ability of corals to recover from thermal bleaching events (Kleypass et al. 1999; Wilkinson 2000; Hughes et al. 2007). The recognition that the warming has reached the Netherland Antilles has occurred (Global warming is here 2009) and with it must come increased awareness and utilization of the many tools for monitoring and tracking bleaching events.

Acronym	Meaning
NOAA	National Oceanographic and Atmospheric Administration
CoRTAD	Coral Reef Temperature Anomaly Database
UNEP-WCMC	United nations Environment Programme World Conservation Monitoring Center
SST	Sea surface temperature
AV_SST	Average sea surface temperature
SSTA	Sea surface temperature anomaly
AV_SSTA	Average sea surface temperature anomaly
DHW	Degree heating weeks
SSTA_DHW	Sea surface temperature anomaly degree heating weeks
TSA_DHW	Thermal stress anomaly degree heating weeks

Table 1. List of acronyms used throughout this paper.

Area	Date	Severity	SSTA_DHW				TSA_DHW			
			Week 1_Av	Week 2_Av	Week 3_Av	Week 4_Av	Week 1_Av	Week 2_Av	Week 3_Av	Week 4_Av
Bonaire_1	August 1998	Low	6.77	6.77	6.77	6.77	0.54	0.54	1.28	1.84
Bonaire_2	August 1998	Medium	2.83	2.83	3.85	4.67	0.00	0.00	0.47	0.86
Belize_1	September 1998	High	3.84	4.82	5.15	6.81	2.24	3.33	4.08	5.73
Belize_2	September 1998	High	2.57	2.87	3.19	4.83	1.12	1.41	2.03	3.67
Belize_3	October 1998	Medium	8.78	8.53	8.02	8.02	7.83	7.83	7.83	7.83
Belize_4	November 1998	Low	8.02	7.01	6.06	5.77	7.83	6.94	6.09	5.82

Table 2. The two study sites from Bonaire along with the four study sites from Belize and their respective bleaching severities and DHW values.

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Overfishing and coral reefs

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Abstract

Overfishing has been found to be a significant contributor to the decline of coral reef ecosystems. Overfishing may reduce herbivory or predation, triggering trophic cascades. Ultimately, overfishing may lead to phase shifts in reefs, often resulting in an alternative stable states dominated by macroalgae. In recent years, management efforts have focused primarily on establishing marine protected areas. While these refuges offer some utility, additional measures need to be implemented to protect the long-term viability of coral reef ecosystems. The persistence of coral reefs depends on research and management activities that address key ecological drivers and promote resilience.

Introduction

Coral reefs are rich and diverse ecosystems on which hundreds of millions of people directly depend. Coral reefs sustain diverse fishery resources and provide valuable ecosystem services, such as shoreline protection. In the past, coral reefs were viewed as highly stable ecosystems, with changes occurring on the scale of millennia (Mumby and Steneck 2008). Recently, the paradigm has shifted and the prevailing notion is that reefs are fragile and dynamic systems. Coral reefs are particularly vulnerable to climate change and ocean acidification (Hoegh-Guldeurg et al. 2007) as well as overfishing.

As the burgeoning world population struggles to feed itself, overexploitation of fishery resources is increasingly widespread. Many people in tropical areas rely on reef fish as their primary source of protein. The populations of most countries with coral reefs are projected to double within the next 50 years (McManus 1997). Newton et al. (2007) found that 55% of coral reef fisheries are already been fished in an unsustainable manner- a situation that is likely to worsen.

Overfishing is a broad term which may be defined in a variety of contexts. Pauly (1994) noted a series of stages of overfishing: growth, recruitment, biological, ecosystem, economic, and Malthusian. This paper will define overfishing as the exploitation of fishery resources that result in deleterious effects to an ecosystem.

Importance of herbivory on healthy reefs

In healthy reef ecosystems, a high abundance of herbivorous organisms, such as scarids and urchins, maintain low algal biomass (Hughes et al. 2007). This preserves habitat complexity in the form of cracks and crevices, which are crucial to successful coral recruitment. Healthy, live corals create and maintain a complex, three-dimensional habitat. This structure provides refuge

for countless reef organisms, including Scarids and urchins. This positive feedback loop promotes the health (Mumby and Steneck 2008) and resilience (Mumby 2006, Hughes et al. 2007) of coral reef ecosystems.

Changes on the reef

Although people have exploited and degraded the fishery resources of coral reefs for millennia, the situation has become increasingly dire in recent years. Since the industrial revolution, the population of the earth in tropical regions has grown exponentially. Concurrent with the industrial revolution, new fishing gear was developed which radically improved the efficiency of fishing operations, and ushered in an era of commercial fishing. Furthermore, the social structure of coastal communities in many areas has changed significantly. Whereas community-based management dominated artisanal fisheries in the past, in many areas market pressures and poverty are causing reef organisms to be exploited at an increased rate, often with little regard for the future (Cinner and McClanahan 2006).

In the early stages of reef fisheries, predators such as sharks and groupers are typically harvested (McManus 1997, Bellwood et al. 2004). Depletion of reef predator populations can trigger trophic cascades resulting in changes to the community structure. Dulvy et al. (2004) found that exploitation of predatory reef fish lead to dramatic increases in the abundance of coral-eating starfish. Consequently, coral cover declined and the abundance of filamentous algae rose considerably.

As time progresses, mounting economic pressures often force fisherman to target other species at lower trophic levels, including grazers such as parrotfish (Bellwood et al. 2004). On many reefs, fishing has reduced grazers levels below levels which are critical to the health of the reef. When grazers are removed, macroalgae rapidly spreads (Hughes et al. 2007) and the growth, fecundity, and recruitment of corals are impaired (Birkeland 1977, Hughes et al. 2007). A phase-shift to a macroalgal community typically results, in turn leading to further declines in fishery resources (Done 2004).

Additionally, with the rise of global trade and cheap transportation, new markets have developed for reef organisms which were previously unprofitable to harvest. In some locales, reef fishes and invertebrates are collected for the rapidly growing international pet trade (Cinner and McClanahan 2006). In the Galapagos, a short-lived and ill-fated fishery developed for sea cucumbers. This novel fishery, fueled by Asian demand and facilitated by cheap transportation, quickly overexploited sea cucumber stocks in just a few years.

Coral reef fishes tend to be long-lived, and as such are easily overfished. In some species, recovery may take years to recover from overfishing. For example, the goliath grouper was widely overharvested in the Caribbean until recently. In parts of their range, harvest has been eliminated, yet even years later stocks are only marginally improved.

Fishing impacts the size structure of fish communities on coral reefs. Reef fishes are not equally vulnerable to exploitation (Jennings et al. 1999). Larger fish are typically more visible, more valuable, and often easier to capture. In the short run, size-selective mortality shapes the community structure and regulates trophic interactions. Importantly, herbivorous fishes graze at

different efficiencies. Grazing rates are generally a function of size, life stage, and species (Mumby 2006). Large parrotfish are especially important in maintaining levels of herbivory which prevent a transition to an algal reef. If intraspecific size-selective mortality persists over time, changes in genetic structure may occur, thus potentially altering the function of a species within a community.

Furthermore, many fisheries result in a considerable amount of bycatch and other waste. McManus (1997) reports that common fishing practices such as the use of explosives, poisons, or trawls typically result in the death of many fishes which are not recovered. Additionally, these techniques destroy live corals, reducing the complex architecture that fosters rich fish communities (McManus 1997).

Jamaica: a case study in coral reef collapse

In the second half of the last century, Jamaican reefs underwent a dramatic phase shift. In 1980, Jamaican reefs appeared healthy and had an abundance of live coral, though they were subject to heavy fishing pressure (Koslow et al. 1994). On mid-depth reefs, algal cover was minimal despite intense fishing pressure, likely as a result of robust urchin populations (Morrison 1988, Liddell and Ohlhorst 1992). An intense hurricane struck the reefs and reduced Coral cover by approximately half (Mumby et al. 2007). Over the next several years, the reefs showed signs of recovery. In 1983, a broad-scale mortality event decimated populations *Diadema antillarum* throughout the Caribbean (Hughes et al. 1985, Carpenter 1990). This die-off, coupled with depleted parrotfish populations as a result of overfishing, reduced herbivory below a critical threshold. Within a decade, Jamaican reefs were dominated by macroalgae and coral cover was minimal (Mumby et al. 2007). While overfishing may not have been the sole factor in the demise of Jamaican reefs (Hodgson 1994), it reduced the resilience of the reef and ultimately contributed to the development alternate stable state.

Management choices and changes

Coral reefs are in an increasingly perilous situation. A suite of threats ranging from local overfishing to global climate change threaten to vitality of these important ecosystems. Reef managers are tasked with maintaining healthy ecosystems while staying within socioeconomic constraints.

In the past several decades, marine protected areas have been the primary conservation tool employed by reef managers. In essence, marine protected areas provide a zero harvest refuge, allowing fishes to grow to maturity. The goal is that these areas generate surplus recruitment which then improves adjacent fisheries. In recent years, this phenomenon has been documented on a number of reefs (Roberts et al. 2001, Russ et al. 2003), though it may not be immediately apparent (McClanahan and Mangi 2000). Increases in fish biomass as a result of marine protected areas can lead to trophic cascades which promote coral recruitment (Mumby et al. 2007). The effectiveness of marine protected areas is a function of the vagility and fecundity of exploited organisms and the size of the reserve. Graham et al. (2008) found that while marine protected areas maintain high fish biomass, they offer little protection against large-scale

disturbances. Due to trophic interactions, marine protected areas may also exert unforeseen impacts on nonfishery species (Hixon and Beets 1993).

Fisheries policies need to take into account the importance of herbivory on reefs (Mumby and Steneck 2008). While marine protected areas have received considerable interest from researchers and managers, comparatively little has been done to examine the effects of fisheries policies (Mumby and Steneck 2008). Modifying harvest regimes to minimize impact on herbivory may promote the health and resilience of reef ecosystems.

In other ecosystems, fish stocking is widely used to maintain fish stocks at desired levels. Future research may want to examine the viability of using stocking as a means to maintain populations of coral reef fishes. If feasible, such an approach would provide jobs in coastal communities while reducing strain on reef communities. Fish stocking raises other concerns, such as the spread of pathogens and contamination of local gene pools. These risks should be weighed against the danger of the reef shifting to an alternative stable state dominated by macroalgae. Unfortunately, a recent attempt to artificially increase populations of herbivorous fishes at several small reefs in Hawaii was largely unsuccessful (Conklin and Stimson 2004), but further trials may prove more successful.

McManus (1997) advocates the use of integrated coastal zone management (ICZM) for the conservation of reef ecosystems. This holistic type of approach attempts to balance the needs of coastal communities with wise use of fishery resources. If executed successfully, such an approach results in a sustainable fishery for the community which meets human objectives while maintaining ecological integrity. ICZM approaches are not easy, but offer hope for the future.

Conclusion

Overfishing is a complex and often politically loaded issue, particularly when placed in the context of other global-scale threats to coral reefs. In the future, fishing and other consumptive activities should be balanced with the needs of the entire ecosystem (Mumby 2006). Overfishing is just one component of a suite of serious threats challenging the viability of coral reef ecosystems. Sea level rise, climate change, mangrove destruction, and ocean acidification pose significant danger to the persistence of coral reef communities. These global scale phenomena are often impractical for reef managers to address. Consequently, reef managers should seek to maximize resilience, which can in part be attained by maintaining surplus herbivory.

Certainly, the bold management changes which are needed will not be easy. However, existing research and management initiatives have proved largely inadequate (Birkeland 2004, Mumby and Steneck 2008). The welfare of millions of people in tropical communities depends heavily on the integrity of coral reefs (Whittingham et al. 2003). As such, it is imperative that action of unprecedented scope and magnitude is implemented to preserve coral reef ecosystems and the welfare of the people who depend on them. Future coral reef management initiatives will need to place more emphasis on the management of human activities, since our activities can and do have a profound effect on the viability of coral reef ecosystems (Bellwood et al. 2004).

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Chapter 10: Factors affecting macroalgal abundance on coral reefs: A global review

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Abstract

I review recent literature from around the world pertaining to factors controlling macroalgal abundance on coral reefs, specifically the top-down effects of herbivory and bottom-up effects of nutrients and their relative importance, and assess the quantity and quality of studies. Nineteen of 33 studies address both herbivory and nutrients as potential drivers, but one quarter of the studies conclude either herbivory or nutrients is the only controller of macroalgal abundance without addressing the other. Only 6 of 33 studies provide robust support for their findings, and 5 of these conclude that herbivory is relatively more important than nutrients in controlling macroalgal abundance on reefs. None of the 33 studies provide robust support for nutrients as the main driver of macroalgae. Many studies demonstrate complex interactive or situation-specific effects of both top-down and bottom-up drivers.

Introduction

Coral reefs represent some of the most diverse and socioeconomically important ecosystems worldwide (Hughes 1994; Knowlton 2001a; Koop *et al.* 2001). Despite this, coral reefs around the world are becoming increasingly threatened by a variety of factors, most of which are anthropogenic in origin, such as bleaching events associated with global warming, increased atmospheric CO₂, and diseases (Knowlton 2001a), among others. Perhaps two of the factors most highly touted as being harmful to reefs today are the overfishing of key herbivorous grazers and the input of excess nutrients into these ecosystems, through such mechanisms as deforestation and agriculture, physical destruction of reef framework, and pollution (Hughes 1994; Knowlton 2001b; Koop *et al.* 2001). It is thought that alterations to these two factors – herbivory and nutrient availability – may act indirectly to harm coral reefs by changing the relative success of macroalgal coral competitors (Knowlton 2001b).

Macroalgae, or seaweeds, represent one of three main types of epilithic algal cover found on coral reefs and are usually large, frondose vegetation of either fleshy or calcareous form (Lapointe 1997). Williams and Polunin (2001) describe what is becoming a familiar scenario on coral reefs around the world today; one where reef systems once dominated by corals have rapidly entered a state of macroalgal dominance. Once macroalgal cover increases to a certain amount on a reef, short-lived, small corals can become excluded and the growth and recruitment of larger, longer-lived corals can become compromised (Hubbard 1997). The space liberated by out-competed corals can then become filled by more macroalgae, further promoting its dominance, which can then lead to a ‘phase shift’ within such reef systems. Perhaps one of the most dramatic and well documented cases of such a phase shift has occurred in Jamaica (Hughes 1994; Woodley 1999; Williams and Polunin 2001). Here, coral abundance declined from over

50% to less than 5% cover in about 20 years, resulting in more than 90% of Jamaican reefs becoming covered by fleshy macroalgae (Hughes 1994).

Indeed, there exist three general schools of thought among researchers regarding the coral-macroalgae dynamic. The first proposes that nutrients act in a bottom-up fashion as the main driver of macroalgal abundance on coral reefs. The second school points towards herbivory as being the main driver, by exerting a top-down control upon macroalgal abundance. The last school of thought ascertains that some combination of nutrients and herbivory acts to control the extent of macroalgal abundance on coral reefs. The third scenario seems the obvious explanation, however there remains much controversy in the field today surrounding the extent to which each factor contributes to the coral-macroalgal dynamic on reefs and how they may (or may not) interact with one another (Knowlton 2001b).

Methods

I therefore attempted to critically review a variety of recent works pertinent to this issue and to assess the strength of each argument here; with the overarching goal of clarifying the relative importance of macroalgal herbivory and the amount of nutrients available within the system on the abundance of macroalgae on coral reefs around the world.

Results

I reviewed 33 studies addressing the importance of either herbivory, nutrients, or both with respect to reef macroalgal abundance, spanning a total of 23 years (Table 1). The studies carried out experiments in a range of reef types (barrier, bank barrier, fringing, patch, and atoll) from many geographical areas of the world including the Caribbean (Belize, Jamaica, Florida, Barbados, Grand Cayman, Cuba, Bahamas, Honduras), the Pacific (Hawaii, Guam, Australia), and the Indian Ocean (Kenya). There was a diverse array of approaches employed to study the subject, including: experimental manipulation *in situ*, experimental manipulations in the lab, observations, reviews, natural experiments, meta-analyses, and modeling.

Most experimental studies that assessed the importance of herbivory on macroalgal abundance manipulated grazing by scarids (parrotfish), acanthurids (surgeonfish), pomacentrids (damselfish), or *Diadema antillarum*, by either herbivore exclusion cages or natural experiment. Most of the experimental studies that assessed the importance of nutrients on macroalgal abundance involved manipulations of dissolved inorganic nitrogen and soluble reactive phosphorous followed by measurements of any changes in benthic algal or coral cover, often by functional group.

The robustness of a study's findings was evaluated based on some of the following criteria: manipulative > observational, *in situ* > laboratory, herbivory and nutrients addressed > herbivory or nutrients addressed.

Of the 33 studies, 3 addressed only nutrients, 11 addressed only herbivory, and 19 addressed both nutrients and herbivory. Eight studies concluded that either herbivory or nutrients were the controlling factor on macroalgal abundance without looking at the other factor, while 10 studies experimentally manipulated herbivory and nutrients in the field simultaneously. I determined that 6 of the 33 studies provided strong evidence for their findings, while 14 provided evidence of intermediate strength, and 13 were deemed weak.

Of the 6 most robust studies, 5 concluded that herbivory was the main factor affecting macroalgal abundance and 1 found that herbivory and nutrients were both important, but interacted in complex ways depending on algal functional group (Smith *et al.* 2001). Of the 13 weakly supported studies, 7 concluded that herbivory was the main driver of, or had an influence on, macroalgal abundance, while the other 6 found nutrients to be important. Overall, 20 studies found herbivory to be the most important factor controlling macroalgal abundance, while only 6 studies found nutrients to be the main controller. The remaining 7 studies presented seemingly inconclusive results or concluded that herbivory and nutrients may have interacted or had situation-specific effects on macroalgae.

Discussion

There is little doubt within the scientific community that the health of coral reef ecosystems worldwide has become threatened by an increase in macroalgal abundance due to anthropogenic factors. However, these causative factors, namely the decrease in herbivory due to overfishing or disease and the input of excess nutrients from land, have been rather hotly debated and remain so today. The ongoing scientific dispute between Lapointe (1997; 1999), an advocate for nutrients as the primary controller of reef macroalgal abundance, and Hughes (1999), an advocate for herbivory as the main controller of macroalgae, highlights this controversy and raises questions about the relative importance of top-down and bottom-up drivers on macroalgal abundance on coral reefs.

The three general schools of thought regarding the control of macroalgal abundance on coral reefs are that (1) nutrients act from the bottom up to drive macroalgae, (2) herbivory acts in a top-down fashion to control macroalgae, and that (3) some combination of the two acts to ultimately drive macroalgal abundance. I found each to have received ample attention in the literature. Littler and Littler (1984) began to address the issue with the development of the Relative Dominance Model (RDM); a paradigm predicting the predominant benthic cover of coral reefs based on levels of herbivory and nutrients in the system. This idea accepted both factors as important and the idea of a paradigm has been a persistent trend in the literature since (Szmant 2002; Littler *et al.* 2006). A dichotomy soon evolved however, as Lapointe (1997; 1999; 2004) adopted this paradigm in his work to support his conclusions that nutrients are the most important driver of macroalgal abundance and that a critical nutrient threshold exists for coral reefs, above which nutrient limited macroalgae will become dominant over corals. Proponents of the top-down theory, such as Hughes (1994; 1999, 2007), began looking at the dramatic phase-shift in the Caribbean that corresponded with ‘natural’ reductions in herbivory from the massive 1983 *D. antillarum* die-off to demonstrate the greater importance of top-down effects on macroalgal abundance. The combination and relative importance of both herbivory and nutrients

as drivers then began to draw attention, as is evident from the nearly two-thirds of the studies examined here that addressed both factors (Table 1). Indeed, 5 of the 7 studies reviewed from the past 5 years manipulate both factors and admit to some combination of the two acting to drive macroalgal abundance or species composition (Table 1).

While this review is by no means exhaustive, currently the best supported argument for the control of macroalgal abundance on coral reefs is that herbivory is the primary driver with nutrients playing a lesser role. Five of the 6 robust studies and 20 out of all of the studies support this argument. Notably, several studies elucidate more complex interactions among these top-down and bottom-up forces on reef macroalgae and benthic community structure. In a robust study by Smith *et al.* (2001), experiments performed in Hawaii demonstrated that herbivory and nutrient effects were varied among fleshy and calcareous algal functional groups, and that elevated nutrients and reduced herbivory had synergistic effects. Burkepile and Hay (2006) put forth an extensive factorial meta-analysis assessing over 50 studies objectively and found herbivory to be the main driver of macroalgal abundance on coral reefs, while nutrients were relatively less important with effects likely dependant on the inherent productivity of the system. They specifically suggest that nutrients will have a greater bottom-up effect in lower productivity temperate reef systems than in more highly productive tropical systems. Experimental manipulations in Australia by Diaz-Pulido and McCook (2003) highlighted the greater relative importance of herbivory, particularly with respect to macroalgal recruitment. In another recent review Szmant (2002) similarly provided strong support for herbivory as the main driver of macroalgal abundance on reefs on a global scale, while noting the case-specific and local importance of nutrients in situations such as sheltered bays. Clearly, evidence to date points toward the relatively greater importance of top-down vs. bottom-up macroalgal controls, but potentially complex and variable effects from alterations of both factors apparently exist.

As coastal human populations continue to grow, and climate change persists, associated anthropogenic effects on coral reefs around the world will undoubtedly intensify. Therefore this review points out what is now becoming a more urgent need for further clarification of the effects, mechanisms and interactions of anthropogenically-induced changes in the top-down and bottom-up forces affecting coral reef ecosystems. While herbivory was widely found to play a key role in controlling the dominance of macroalgae on coral reefs, there seems to be a deficiency of robust experiments performed in the field that simultaneously address the relative importance of top-down and bottom-up drivers of macroalgal abundance. Factors other than herbivory and nutrients, such as coral-algal competition dynamics and disturbance-recruitment-recovery processes, should also be documented further in the literature (Diaz-Pulido and McCook 2003). Effective manipulations of herbivory and ecologically relevant nutrients, such as those employed by McClanahan *et al.* (2005), should continue to be investigated in concert, with the ultimate goal of providing more conclusive evidence regarding the importance of factors affecting macroalgal abundance on coral reefs and how they interact.

My findings suggest that in order to mitigate potential future shifts from coral-dominated to macroalgae-dominated reefs, such as the dramatic phase-shift seen in Jamaica (Hughes 1994; Woodley 1999; Knowlton 2001a), management strategies should begin by focusing on the replenishment and protection of herbivorous fish stocks on coral reefs. Results suggest that maintaining grazing may be a key factor in preventing macroalgal dominance on reefs. This is

somewhat encouraging since such fishing management strategies can be applied worldwide at local levels, can be implemented on relatively short time scales (compared to issues like climate change), and they offer visible indicators of effectiveness and tangible results.

Table 1. Review of studies pertaining to the effects of herbivory and/ or nutrients on macroalgal abundance on coral reefs. Study location, reef type, and organism(s) are noted when possible. A brief summary of macroalgal driver(s) assessed, methodology used, and major conclusions are given for each study. Relative strength of evidence used to draw conclusions from is assessed subjectively for each study. Criteria for robustness included: manipulative > observational, *in situ* > laboratory, herbivory and nutrients addressed > herbivory or nutrients addressed.

Study (Authors and Year)	Study Type	Geographic Area	Reef Type	Organism(s)	Macroalgal Driver(s) Assessed	Methods Overview	Conclusions	Strength of Evidence	Justification
Littler and Littler (1984)	Proposal of hypothetical model	n/a	n/a	n/a	Nutrients and Herbivory	Thought exercise used to develop a paradigm	Herbivory as primary driver, nutrients secondary	Weak	Do not present any experimental or observational evidence to support model.
Lewis (1986)	Observational and Experimental; <i>in situ</i>	Belize	Back Reef of Barrier Reef	<i>Acanthuridae</i> (surgeonfish), <i>Scaridae</i> (parrotfish); algal turfs, crustose coralline algae, corals, macroalgae	Herbivory	Herbivorous fish densities visually assessed, grazing intensity determined. Herbivore exclusion cages used in the field to determine the role of herbivory in the maintenance of algal turf-dominance. Macroalgae transplants used to determine effects of herbivorous fish grazing on macroalgal biomass.	Herbivory as primary driver	Intermediate	Conclude herbivory is important in controlling macroalgal biomass and distribution using correlations and experimental field manipulations, but do not address nutrients.
Hughes (1994)	Observational	Jamaica	All that are/ were present	Large predatory fish (<i>Lutjanidae</i> (snappers), <i>Carangidae</i> (jacks), <i>Ballistidae</i> (triggerfish), and <i>Serranidae</i> (groupers)); Herbivorous fish (parrotfish, surgeonfish); <i>Diadema antillarum</i>	Herbivory	Information from long-term monitoring of Jamaican coral reef degradation was integrated and assessed. Human population growth, over fishing, coral and macroalgal cover, and <i>D. antillarum</i> populations were compared over time.	Herbivory as primary driver	Intermediate	Conclude herbivory is important in controlling macroalgal cover using correlations and observations from the field. Drastic, well-documented, natural 'experiment', but do not address nutrients.
Stimson <i>et al.</i> (1996)	Experimental; <i>in situ</i> and in laboratory	Hawaii	Patch and Fringing Reefs	<i>Dictyosphaeria cavernosa</i>	Nutrients and Herbivory	Benthic cover, irradiance, temperature and nutrient levels were estimated, and <i>D. cavernosa</i> growth rates were determined. Herbivore exclusion cages used in the field to assess grazing susceptibility. Effect of temperature and nutrient enrichment on <i>D. cavernosa</i> growth rates assessed in the lab. Nutrients around <i>D. cavernosa</i> determined <i>in situ</i> . Sediment cores from the field used in the lab to determine temperature effects on nutrient regeneration.	Nutrients as primary driver, Herbivory secondary	Weak	Some indirect support for nutrients as main driver of abundance for one macroalgal species through correlation and lab experiments. Focus on sediment nutrient regeneration not on role of nutrients from runoff. Experimental evidence for herbivory as driver of <i>D. cavernosa</i> abundance, but conclude herbivory controls macroalgal biomass while nutrients control productivity.

Table 1 (continued)

Lapointe (1997)	Observational and Experimental; <i>in situ</i> and in laboratory	Jamaica; Florida	Fringing reefs (Jamaica); Offshore reefs (Florida)	<i>Chaetomorpha linum</i> , <i>Halimeda opuntia</i> , <i>Sargassum polyceratum</i> , and <i>Lobophora variegata</i> (Jamaica); <i>Codium isthmocladum</i> (Florida)	Nutrients	Near-bottom nutrient concentrations and salinity measured. Nutrient enrichment bioassays performed in the lab and photosynthetic capacity and efficiency measured. Alkaline phosphatase assays (presumed gauge of P-limited productivity of macroalgae), tissue C:N:P ratios (to compare nutrient limitations), and tissue nitrogen isotopes (to assess contribution of nitrogen from natural vs. waste groundwaters) were determined.	Nutrients as primary driver; Nutrient threshold exists	Weak	Some circumstantial observational and manipulative lab evidence for nutrients controlling macroalgal abundance of two species. Only look at abiotic parameters. Conclude (through correlation) that nutrient limitation or excess above a universal threshold determines macroalgal abundance, but do not address herbivory.
Miller and Hay (1998)	Experimental; <i>in situ</i>	Florida	Fore Reef of Barrier Reef	Macroalgae (<i>Dictyota spp.</i> , <i>H. opuntia</i> , <i>Hypnea spp.</i> , <i>Lauencia spp.</i> , red filamentous, <i>Coelothrix</i> , <i>Galaxaura</i> , <i>Aphiroa</i> , <i>Styopodium</i>); Corals (<i>Porites divaricata</i> , <i>Porites porites</i> , <i>Cladocora arbuscula</i> , <i>Siderastrea radians</i> , <i>Manicina sp.</i>); Fish (stoplight parrotfish, redband parrotfish)	Herbivory	Exclusion cage experiments in the field with preplanted macroalgae or initially clean substrate and transplanted pieces of coral. Coral remaining, bite scars, algal cover, coral growth, and macroalgal species composition determined.	Herbivory may be a driver	Weak	Conflicting experimental evidence: macroalgal abundance significantly affected by grazing, abundance had no effect on coral growth, when macroalgae was already present coral growth was inhibited. Emphasize negative effects of two herbivore species on coral. Did not address nutrients.
Hughes <i>et al.</i> (1999)	Critical Review of Lapointe (1997)	Jamaica; Florida	Fringing reefs (Jamaica); Offshore reefs (Florida)	<i>C. linum</i> , <i>H. opuntia</i> , <i>S. polyceratum</i> , and <i>L. variegata</i> (Jamaica); <i>C. isthmocladum</i> (Florida)	Nutrients and Herbivory	Validity of Lapointe (1997) study assessed. Applicability of methods and data interpretation were questioned. Discrepancies among results and text highlighted. Alternative explanations for results given where applicable. Predicted herbivory was driver of macroalgal abundance.	Herbivory as primary driver	Intermediate	Compelling arguments for why nutrients were the primary macroalgal driver. Do not provide enough strong evidence for herbivory as main driver.
Lapointe (1999)	Rebuttal to Critical Review by Hughes <i>et al.</i> (1999)	Jamaica; Florida	Fringing reefs (Jamaica); Offshore reefs (Florida)	<i>C. linum</i> , <i>H. opuntia</i> , <i>S. polyceratum</i> , and <i>L. variegata</i> (Jamaica); <i>C. isthmocladum</i> (Florida)	Nutrients and Herbivory	Refuted criticisms made by Hughes <i>et al.</i> (1999) and presented some additional data (biomass changes in a macroalgal species following nutrient enrichment, biomass losses from grazing, macroalgal growth enhancement from nutrient enrichment) and literature used to defend position.	Nutrients as primary driver, Herbivory secondary	Weak	Additional data provided was synthesized from different studies, little attention given to top-down controllers. Seem to revise their original conclusion to include the role of herbivory.

Table 1 (continued)

Woodley (1999)	Review	Jamaica	Fore Reef of Fringing reefs	<i>D. antillarum</i> ; <i>Tripneustes ventricosus</i>	Herbivory	Variety of studies looking at top-down effects of echinoid grazers on macroalgal abundance synthesized and applied to Jamaican phase-shift example.	Herbivory as primary driver, nutrients may be a driver	Intermediate	Top-down effects found to be main driver. Evidence presented shows striking differences in macroalgal cover inside and out of grazing patches. No manipulations performed, nutrients not addressed. Two patches were in close proximity (presumably exposed to similar nutrient conditions) so conclusion supported.
Miller <i>et al.</i> (1999)	Experimental; <i>in situ</i>	Florida	Fore Reef of Barrier Reef	Frondose macroalgae (<i>Dictyota</i> sp., <i>Lauencia</i> sp.); filamentous cyanobacteria (<i>Scytonema</i> sp.); algal turfs; crustose corallines	Nutrients and Herbivory	Manipulated grazing (exclusion cages) and nutrient levels in the field. Tested a novel method to provide long-term nutrient enrichment <i>in situ</i> . Algal cover and biomass determined at four algal functional groups.	Herbivory as primary driver; Nutrients unimportant	Strong	Experimental manipulation in the field used to assess the relative importance of nutrient levels, herbivory, and any interactions between the two. Approach gives strong support for conclusions that herbivory is main driver of macroalgal abundance, while nutrients have little or no effect.
Thacker <i>et al.</i> (2001)	Experimental; <i>in situ</i>	Guam	Patch Reef	Macroalgae (<i>Dictyota bartayresiana</i> , <i>Padina tenuis</i> , <i>Halimeda</i> spp., <i>Tolypocladia glomerulata</i> , <i>Rosenvingea</i>); filamentous cyanobacteria (<i>Tolypothrix</i> sp., <i>Oscillatoria</i> spp.)	Nutrients and Herbivory	Manipulated grazing (exclusion cages) and nutrient levels in the field. Changes in macroalgal and cyanobacteria abundance, biomass, and palatability assessed.	Herbivory as primary driver; nutrients may be a driver	Strong	Experimental manipulation in the field to assess relative importance nutrients and herbivory, and any interactions between the two. Approach gave strong support for finding that herbivory is main driver of macroalgal abundance, while nutrients are not.
Smith <i>et al.</i> (2001)	Experimental; <i>in situ</i>	Hawaii	Fringing reef	Fleshy algae; calcareous algae; microinvertebrates (crustaceans, polychaetes, gastropods)	Nutrients and Herbivory	Manipulated grazing and nutrient levels in the field using artificial tile surfaces, exclusion cages, and nutrient enrichment. Changes in fleshy, calcareous and total algal biomass and sediment determined and an inventory of small invertebrates was taken.	Herbivory and nutrients as functional group-specific drivers; interaction effects	Strong	Experimental manipulation in the field to assess relative importance of nutrients and herbivory, and any interactions between the two. Approach gave strong support for finding that nutrients and herbivory affect relative dominance of fleshy and calcareous algae, and can interact to produce greater effects.
Stimson <i>et al.</i> (2001)	Observational and experimental; <i>in situ</i> and in laboratory	Hawaii	Patch, fringing and barrier reefs	Macroalgae (<i>D. cavernosa</i> , <i>Acanthophora specifera</i> , <i>Gracilaria salicornia</i> , <i>Kappaphycus alvarezii</i> , <i>Padina japonica</i>); Fish (parrotfish, surgeonfish)	Nutrients and Herbivory	Tested hypotheses for why macroalgae has remained dominant over coral on reefs in a once eutrophic bay, despite a drop in discharge (are nutrients levels still high enough to support dominance, or has herbivorous fish abundance declined?). Assessed changes in <i>D. cavernosa</i> distribution and abundance, herbivore biomass, macroalgae cover and patterns of grazing on macroalgae determined by manipulations in the field (exclusion cages). Herbivore preference for macroalgae in the area examined in the lab.	Herbivory as primary driver; nutrients secondary	Intermediate	Experimental manipulation in the field and the lab to assess grazing parameters. Did not experimentally manipulate nutrients. Much support for their finding that herbivory is drives macroalgal abundance, and all evidence for nutrients being secondary, is correlative and site-specific.

Table 1 (continued)

McClanahan <i>et al.</i> (2001a)	Experimental; <i>in situ</i>	Belize	Patch reefs of atoll	Macroalgae (<i>Halimeda</i> spp., <i>Geldiella</i> spp., <i>Sargassum</i> spp., <i>Turbinaria</i> spp.), <i>Lobophora</i> spp.), coralline algae, algal turf, coral, fish (<i>parrotfish</i> , wrasses, <i>surgeonfish</i>), sea urchins	Herbivory	Experimentally reduced macroalgal abundance in the field in fished and unfished areas. Patch reefs as replicates and controls. Looked at changes in algal and coral cover, fish abundances, and herbivory rates via herbivory assays.	Herbivory may be a driver	Weak	Effectiveness of experimental manipulation of herbivory in the field based on premise that fish protection zones actually result in higher rates of herbivory. Do not address nutrients as a potential driver of macroalgal abundance. Findings did not show herbivory acting predictably to control macroalgal abundance. Seems more applicable in assessing effectiveness of fishing- relating reef management strategies. Hurricane disturbance early in study possibly confounded results.
McClanahan <i>et al.</i> (2001b)	Observational and natural experiment; <i>in situ</i>	Kenya	Back reef lagoons of fringing reef	Fleshy algae, turf algae, coral, fish (<i>surgeonfish</i> , <i>parrotfish</i>), sea urchins	Herbivory	Recorded changes in coral composition, cover and bleaching, algae cover, and estimated herbivory indirectly before and after the 1998 coral bleaching event in the field, within and outside of marine protected areas.	Herbivory may be a driver	Weak	Use of the marine protected areas to assess effects of herbivory on macroalgal dominance based on assumption that herbivory was dependent on fishing protocols. Proxy of herbivore consumption used to draw conclusions from. Effects of herbivory on macroalgal dominance were inconsistent. Role of nutrients was not addressed.
Lirman (2001)	Observational and experimental; <i>in situ</i>	Florida	Patch and bank barrier reefs	Coral (<i>Siderastrea</i> <i>sideria</i> , <i>P.</i> <i>astreoides</i> , <i>Montastraea</i> <i>faveolata</i>); macroalgae (<i>Halimeda</i> spp., <i>Dictyota</i> spp.); filamentous algae; calcareous algae; corticated terete algae	Herbivory	Assessed how coral and algae interact by measuring coral contact with algae. Used herbivore exclusion cages and algal additions in the field to determine effects of herbivory and algal abundance on coral growth and mortality.	Herbivory as primary driver	Intermediate	Experimental manipulations in the field to assess effects of herbivory on algal functional group dominance. Found significant increases in algal biomass in the absence of grazing. Did not address nutrients.
Williams and Polunin <i>et al.</i> (2001)	Observational; <i>in situ</i>	Jamaica; Barbados; Belize; Grand Cayman; Cuba	n/a	Algae (macroalgae, crustose, turf); fish (<i>parrotfish</i> , <i>surgeonfish</i>); <i>D.</i> <i>antillarum</i> ; coral	Herbivory	Assessed percentage benthic and algal cover (by functional group and species), herbivorous fish biomass, and <i>D. antillarum</i> abundance at locations throughout the Caribbean. Included both heavily- and lightly-fished reefs.	Herbivory as primary driver; but interaction effects with amount of coral cover	Intermediate	Correlative approach with data derived from a large- scale census to support their conclusion. Did not address role of nutrients in controlling macroalgae.

Table 1 (continued)

Williams <i>et al.</i> (2001)	Experimental; <i>in situ</i>	Belize	Fore reef of barrier reef	Coral; coralline algae; turf algae; fleshy macroalgae; blue-green algae; fish (parrotfish, surgeonfish, damselfish)	Herbivory	Simulated manipulation of coral cover using inert tiles. Assessed changes in macroalgal cover, herbivorous fish biomass and feeding rates (bite rates) to test hypothesis that macroalgal abundance reaches a threshold, as a side effect of decrease coral cover, and where control by herbivorous fish is overwhelmed.	Herbivory as primary driver; but effects are subject to a threshold	Intermediate	Experimental manipulation in the field to assess effects of herbivory on algal dominance and idea that algal cover threshold exists (even on lightly-fished reefs) above which herbivores cannot exert sufficient top-down control. Provide relatively strong evidence for conclusions. Use of tiles may not adequately represent coral cover, or may have introduced unknown variables. Did not assess nutrients.
Koop <i>et al.</i> (2001)	Experimental; <i>in situ</i>	Australia	Patch reefs of Great barrier reef	Coral; epilithic algae; encrusting algae; macroalgae; clams; stromatopods; fish (parrotfish, damselfish); phytoplankton	Nutrients	Manipulated nutrient levels (low- and high-nutrient additions) in patch reefs to assess changes in many reef-related factors, both abiotic (nutrient uptake by reef and organisms, N-fixation, C-production, nutrient ratios) and biotic (coral growth, repair, reproduction, stress, bioerosion, grazing), over two years.	Nutrients unimportant at community level; but may be a driver at organism level	Intermediate	Manipulations of nutrients in the field over a long period to assess changes in many reef-related parameters (incl. macroalgae). Present good evidence for conclusion that nutrient addition does not result in macroalgal dominance. Did not manipulate herbivory, so other explanations for their findings possible.
Knowlton (2001a)	Review	Caribbean	All that are/ were present	<i>D. antillarum</i>	Herbivory	Variety of studies looking at effects of drastic changes in <i>D. antillarum</i> grazing (1983 mass mortality) on macroalgal abundance synthesized. Evidence suggesting the beginning of recovery of <i>D. antillarum</i> in the Caribbean was presented.	Herbivory as primary driver	Intermediate	Summarized correlative evidence from a natural experiment to support their conclusion that herbivory is main controller of macroalgal abundance. Did not thoroughly address other potential driving factors like nutrients. However, changes in macroalgal abundance were drastic and widespread across the Caribbean.
Knowlton (2001b)	Review	n/a	n/a	Macroalgae (<i>D. cavernosa</i>); <i>D. antillarum</i> ; <i>Acanthaster planci</i> (crown-of-thorns starfish); snails (<i>Drupella</i> spp.); ascidians (<i>Trididemnum solidum</i>)	Nutrients and Herbivory	A few case studies looking at results of natural experiments altering herbivory or nutrient levels, and their effects on macroalgal abundance and reef community structure in various locations were synthesized.	Herbivory as primary driver; nutrients secondary	Weak	Summarized correlative evidence from a few natural experiment case studies documenting dramatic changes in either nutrients or grazing (but not both) to support conclusion that herbivory is the main controller of macroalgal abundance.

Table 1 (continued)

Szmant (2002)	Review	n/a	n/a	Macroalgae and other functional groups; corals; herbivorous fish; grazers (<i>D. antillarum</i>)	Nutrients and herbivory	Extensive analysis and synthesis weighing the evidence presented by studies performed worldwide that assessed the extent of a variety of top-down and/or bottom-up controls on macroalgal abundance on reefs was performed.	Herbivory as primary driver; importance of nutrients case-specific and mostly localized	Strong	Experimental manipulations not performed by investigator, but presented a compelling and critical analysis of findings (from manipulative, observational, <i>in situ</i> and laboratory studies) worldwide to support conclusion that nutrients are only important in certain locations (i.e. sheltered bays), are not solely responsible for macroalgal dominance, and other anthropogenic factors (i.e. changes in herbivory linked to fishing) more important globally.
McClanahan et al. (2002)	Experimental; <i>in situ</i>	Belize	Patch reefs of atoll	Fish (parrotfish, damselfish, surgeonfish); fleshy macroalgae; turf algae; coralline algae; calcareous algae; coral (<i>Acropora cervicornis</i> , <i>Acropora palmata</i>)	Nutrients and herbivory	Manipulated herbivory (cages excluding large herbivores), P levels, and mimicked changes in coral cover (added portions of live coral) in small-scale field experiments using patch reefs as replicates. Assessed changes in algal biomass, cover, species colonization and composition, and fish species abundance and herbivory on experimental dead coral plates.	Nutrients unimportant; herbivory as possible species-specific driver	Weak	Manipulations of both herbivory and nutrients in the field. Did not alter nitrogen and used cages excluding only large herbivores. Herbivory never completely prevented and species-specific effects and interactions could have confounded results. Inconclusive evidence presented.
Diaz-Pulido and McCook (2003)	Experimental; <i>in situ</i>	Australia	reef slope on Great barrier reef	Macroalgae (<i>L. variegata</i> , <i>S. fissifolium</i>); fish (surgeonfish, parrotfish, damselfish, <i>Siganidae</i> (rabbitfish))	Nutrients and herbivory	Manipulated nutrient and herbivory levels in the field and assessed changes in density and growth of recruits of two ecologically variable macroalgae species, and effects of herbivory on recruit density and size.	Herbivory as primary driver of macroalgal recruitment; nutrients secondary	Strong	Manipulations of nutrients and herbivory in the field provided fairly strong support for finding that top-down control is more important to macroalgal growth and recruitment than addition of nutrients.
McClanahan et al. (2003)	Experimental; <i>in situ</i>	Belize	Patch reefs of atoll	Fish (wrasses, parrotfish, damselfish); fleshy algae; coralline algae; turf algae; coral (<i>P. asteroides</i> , <i>P. porites</i> , <i>P. furcata</i>)	Nutrients and herbivory	Manipulated nutrients and herbivory (exclusion cages) in the field and assessed changes in algal biomass, cover, and taxonomic composition, herbivory rates, coral survival, color, endosymbiont composition, and density using dead coral plates in each treatment.	Herbivory as primary driver; nutrients possible driver but effects variable	Intermediate	Manipulations in the field of both nutrients and herbivory to support their finding that herbivory is primary controller of macroalgal abundance. However, supporting results varied with taxa and focused on brown frondose algae. Effects of nutrient were highly variable.
Wolanski et al. (2003)	Observational; modelling	Australia (primarily)	Great barrier reef (primarily)	Macroalgae; herbivorous fish	Nutrients and herbivory	Several correlative and modelling exercises to assess effects of run-off (ie: nutrient input) and other watershed-related factors in the great barrier reef. Assumed that coastal addition of nutrients would result in reef degradation, manifested as increased macroalgal abundance.	Nutrients as primary driver; herbivory unimportant in this case	Weak	They modelled reef health using proxies, and correlative circumstantial evidence was used to support the role of anthropogenic nutrient inputs on reef health (nutrients not directly measured). Many statements and conclusions seem unsupported by literature.

Table 1 (continued)

Boyer <i>et al.</i> (2004)	Experimental; <i>in situ</i>	Honduras	Reef slope of fringing reef	Macroalgae (<i>Acanthophora spicifera</i>)	Nutrients and Herbivory	They manipulated nutrient concentrations (nitrogen and phosphorus) in the tissue of a species of macroalgae on a small-scale in three reef-related habitats (coral, seagrass bed, mangrove) and assessed the effects of this enrichment on herbivore consumption and preference, by looking at changes in algal biomass in treatments.	Herbivory as primary driver; nutrients secondary	Intermediate	Indirect evidence that herbivory will exert a greater control on macroalgal abundance than nutrients by determining that nutrient increases lead to compensatory increases in herbivory. Did not manipulate herbivory, focus is on one macroalgal species, and relative importance of each driver depends on habitat used.
Lapointe <i>et al.</i> (2004)	Experimental; <i>in situ</i>	Bahamas	Patch reef (part of substrate gradient)	Macroalgae (<i>Laurencia intricata</i> , <i>Digenea simplex</i> , <i>Microdictyon marinum</i> , <i>Cladophora catenata</i>); fish (parrotfish, surgeonfish); queen conch (<i>Strombus gigas</i>); sea hare (<i>Aplysia dactylomela</i>)	Nutrients and Herbivory	Manipulated herbivory (exclusion cages and grazer addition) along a 'natural' nutrient gradient emanating from the discharge point of a tidal mangrove creek towards an offshore patch reef. Assessed nutrient effects on grazing rates and preferences, algal biomass changes, algal species composition, algal nutrient ratios, and macroalgae/coral cover.	Nutrients as primary driver; herbivory controls species composition	Weak	Results are essentially correlative. No physical manipulation of nutrients levels. Based conclusion that nutrients are primary determinant of macroalgal dominance on premise that nutrient levels followed a specific gradient. Nutrient measurements were taken sporadically over years, not ensuring the same gradient existed throughout experiment. Universal statements based on circumstantial evidence from a site-specific situation.
Lesser (2004)	Review	n/a	n/a	n/a	Nutrients and herbivory	Recent studies from around the world pertaining to the top-down (herbivore) and bottom-up (nutrient) control of macroalgal abundance were summarized and compared briefly.	Herbivory as primary driver; nutrients secondary	Weak	Relatively limited synthesis (a section within the review) of recent studies assessing importance of either nutrients, herbivory, or both, on macroalgal dominance of reefs. Conclude that herbivory is relatively more important than nutrients as controller of macroalgal abundance.
McClanahan <i>et al.</i> (2005)	Experimental; <i>in situ</i>	Belize	Patch reef of atoll	Algae (turf, coralline, brown frondose); corals (<i>Diploria labyrinthiformes</i> , <i>P. furcata</i>); small fish (damselfish, wrasses, parrotfish)	Nutrients	Manipulated inorganic and organic nutrient levels in the field, alone and in concert, in the absence of herbivory by large fish (cages throughout). Assessed changes in algal species composition, functional group biomass, cover, growth rate, coral survival and coloration, and the prevalence of small herbivorous fish.	Nutrients as driver; but effects dependent on nature of nutrient (organic vs. inorganic) and their interaction	Intermediate	Manipulations in the field provide fairly strong support for conclusions that nutrients are a driver of algal abundance, and effects vary based on organic or inorganic inputs. Inorganics increase algal turf while organics reduce small herbivores (presumably grazing). Both nutrient types interact to increase turf biomass further. Conclusion that inorganics inhibit macroalgae challenge studies claiming increased inorganics lead to increased macroalgal abundance. Did not address top-down control.

Table 1 (continued)

Burkepile and Hay (2006)	Meta-analysis	n/a	n/a	Tropical and temperate macroalgae; seagrass; benthic microalgae; various herbivores	Nutrients and herbivory	Factorial meta-analysis of many field experiments that manipulated herbivory and nutrient levels to assess effects on benthic primary producers in inherently low- or high-productivity systems.	Herbivory as primary driver; nutrients secondary; inherent productivity of the system matters	Strong	Strong evidence that herbivory is main driver of tropical macroalgal abundance (high-productivity system) by combining data derived from a large number of studies, over large geographical area, and using strict criteria for their analysis.
Hughes <i>et al.</i> (2007)	Experimental; <i>in situ</i>	Australia	reef crests of Great barrier reef	Large and small herbivorous fishes; corals; algae	Herbivory	Experimentally decreased large predator and herbivore fish biomass (exclusion cages to simulate overfishing). Assessed changes in abundance and species of herbivorous fishes, cover of fleshy macroalgae and corallines, coral cover and colony survivorship. Coral species identified and mapped over time to give recruitment and composition data. Coral tissue thickness (biomass and condition proxy) and reproductive output were determined.	Herbivory as primary driver	Intermediate	Support for herbivory as a driver of macroalgal abundance with experimental field manipulations. Did not address nutrients as a potential driver. Conclude their findings are applicable to climate change issues by assessing differences in coral parameters following the 1998 bleaching event, however time between the study and the bleaching brings this link into question.
Littler and Littler (2007)	Review	n/a	n/a	n/a	Nutrients and Herbivory	Recent studies from around the world pertaining to the top-down (herbivore) and bottom-up (nutrient) control of macroalgal abundance were summarized and their applicability to indications of reef health and management were discussed.	Nutrients as driver; herbivory as driver	Weak	Evidence from many studies supports their conclusions regarding reef health indicators, management strategies, and the relative importance of top-down and bottom-up controls. All evidence seems to be presented with the Relative Dominance Model (RDM) they themselves developed. Did not make conclusions as to which driver may be more important.

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Chapter 11: Ocean Acidification and the Future of Coral Reefs

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Abstract

The continued absorption of atmospheric carbon dioxide (CO₂) by the world's oceans will likely have deleterious consequences for coral reef ecosystems. An extensive literature review was conducted to investigate the known or expected patterns of acidification and the prospect for coral reefs. The rising number of publications over the past few decades demonstrates the scientific paradigm of climate change and the world's oceans is expanding to include acidification. Seawater chemistry is changing at an unprecedented rate and the potential impact on coral reefs is alarming. Acidification reduces calcification and/or growth rates in mesocosm studies simulating various Intergovernmental Panel on Climate Change (IPCC) CO₂ emission scenarios. Biogeochemical models demonstrate a similar reduction and predict the impact will worsen over time. Few studies have clearly demonstrated a negative impact on productivity, recruitment, disturbance resistance and/or resilience of coral reefs. Acidification's effect on coral reefs is expected to be exacerbated by other factors such as ocean warming and nutrients. More research is necessary to investigate acidification's primary and secondary impacts on coral reefs, chronic exposure, synergistic effects and the outlook for coral reefs. The uncertain future of coral reefs underscores the need to reduce CO₂ emissions and effective management strategies to strengthen coral reef resilience.

Introduction

Coral reefs are often considered the rainforests of the sea due to their high diversity and the millions of species associated with them (Knowlton & Jackson 2008). They are one of the most valuable and productive ecosystems in the world; however, coral reefs are vulnerable to overexploitation and disturbance (Birkeland 1997). The earth's atmosphere is changing due to increasing levels of anthropogenic CO₂ (Hughes et. al. 2003). Oceans act like a sink for atmospheric CO₂ (CO₂atm) and since the pre-industrial era approximately 1/3 of all of the CO₂atm released has been absorbed by the world's oceans (Sabine et. al. 2002, Sabine & Feely 2007). Absorption of CO₂atm reduces pH levels (i.e. ocean acidification) and the availability of calcium carbonate (CaCO₃). Coral reefs are biogenic structures that require CaCO₃ for growth and development (Kleypas et. al. 2006). Over the past few decades, scientists have become increasingly concerned about the unprecedented rate of changing seawater chemistry and the future of coral reefs (Caldeira & Wickett 2003, Hughes et. al. 2003, Ohde & Hossain 2004, Pandolfi et. al. 2005, Turley et. al. 2007, Andersson et. al. 2008, Thurber et. a. 2008, De'ath et. al. 2009). Climate mediated disturbances (e.g. acidification and warming) in concert with local effects will likely have a profound impact on the future of coral reef ecosystems.

Methods

An extensive literature review was conducted to determine the known or expected patterns of ocean acidification and how acidification impacts the processes driving those patterns. The primary focus of the search was on key reef-building organisms such as scleractinian corals and crustose coralline algae (CCA). Moreover, the measured and/or expected impact of acidification on calcification, growth rates, productivity, recruitment, disturbance resistance, and coral reef resilience was investigated. The search included the anticipated outlook for the future and the primary research needs in moving forward. The number of publications was plotted per year to investigate recent scientific trends.

Expanding the Climate Change Paradigm

Over the past few decades research has focused primarily on global warming's impact on coral bleaching and disease; however, publications addressing the "other CO₂ problem" (Doney et. al. 2009) and coral reefs are relatively recent. Since the early 1970s studies have explored the relationship between CO₂ and the saturation states of calcite and aragonite (Kleypas et. al. 2006), and as early as 1979 Smith and Roth demonstrated the calcification rate of red coralline algae varies with CO₂ concentrations, yet it was Smith and Buddemeir's 1992 review that sparked widespread concern over decreasing CaCO₃ saturation states and the future of coral reefs.

To investigate if this alarm triggered an increase in scientific publications on acidification and coral reefs, the Google Scholar search engine was utilized with the keys words "Coral AND Reef AND Acidification." Figure 1 illustrates a significant ($R^2 = 0.805$) increase in publications over time (1990-2008), with almost an order of magnitude increase from 1997-2008, suggesting the scientific focus regarding climate change and coral reefs is expanding beyond bleaching and disease to include the effects of ocean acidification.

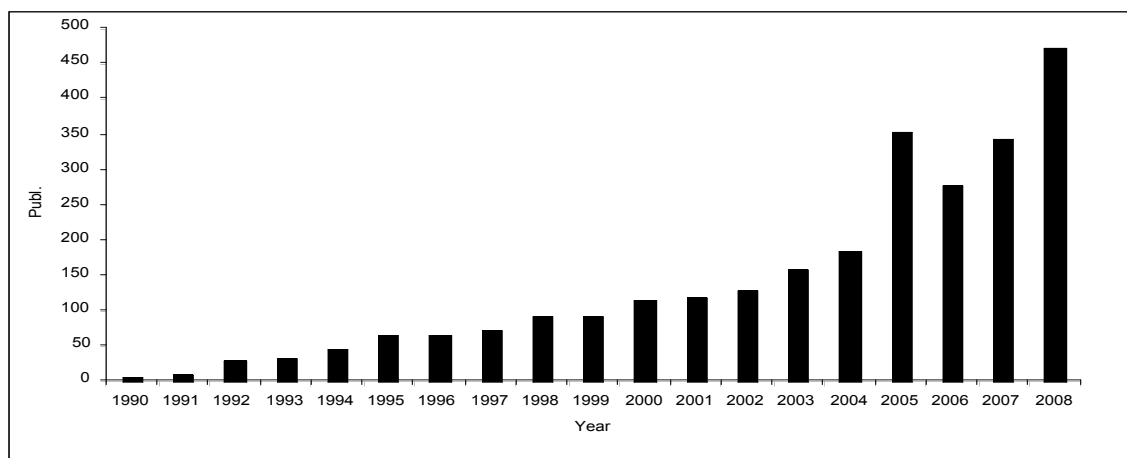


Figure 1. The number of publications per year centered on the topic: acidification and coral reefs. The steady rise in publications suggests the paradigm of climate change and the ocean is expanding to include acidification.

Changing Seawater Chemistry

Seawater chemistry is changing at an unprecedented rate (Caldeira & Wickett 2003, Pelejero et. al. 2005, Orr et. al. 2005, Turley et. al. 2007, IPCC 2007, Andersson et. al. 2008, De'ath et. al. 2009). pH levels have decreased since the preindustrial era and are expected to continue to decrease with rising CO₂atm (Table 1). Uptake of CO₂atm increases the concentration of aqueous CO₂, bicarbonate and H⁺ ions. Increasing H⁺ concentrations reduces pH and carbonate ion levels. Variations in carbonate ion concentrations largely determine the availability of CaCO₃, which formation and dissolution rates depend on the saturation state (<1 = undersaturation, >1 = supersaturation) (Doney et. al. 2009). Calcite and aragonite are the two major biogenic carbonate minerals generated by marine calcifying organisms and researchers use the aragonite saturation state (Ω_{arag}) as a proxy for carbonate, the limiting component of CaCO₃ (Guinotte & Fabry 2008).

Table 1. The known or suspected patterns of acidification and changing aragonite saturation horizons.

Known/Suspected Patterns	Study*	Findings	References
Oceans are becoming more acidic over time	F, B	PH has dropped 0.1 units since pre-industrial times	43, 72, 23, 70, 38, 36, 71, 12
	B	PH will drop 0.2-0.7 units from 1890-2100	35, 11, 72, 10, 8, 71, 12
Acidification is spatially variable; ASHs are shallowing	F, B	Uptake of CO ₂ is changing carbonate equilibrium, aragonite saturation horizons (ASH) are shallowing	25, 43, 5, 73, 34, 24, 30, 15, 23, 14, 9, 38, 36, 22
	B	ASHs are expected to change under different CO ₂ scenarios; ASH will continue to shallow over time and will impact coral reef distribution and abundance; high latitudes are most at risk	78, 44, 43, 42, 33, 62, 64, 23, 10, 32, 36, 12, 3, 76
* F=Field studies B= Biogeochemical modeling			

Ocean acidification is variable on a global scale and areas of aragonite undersaturation are expanding. Carbon chemistry and the aragonite saturation horizon (ASH), the depth where saturation state = 1, vary by ocean basin and Ω_{arag} is one of the factors limiting coral reef biogeography (Gattuso et. al 1998, Kleypas et. al 1999b, Kleypas et. al 2001, Guinotte et. al. 2006, Cao & Caldeira 2008). Ω_{arag} is a function of aqueous CO₂, H and temperature (De'ath et. al. 2009). Moreover, Ω_{arag} is typically higher in low-latitudes and in shallow, warm waters. Conversely, Ω_{arag} decreases at higher latitudes and with depth (Feely et. al. 2004). ASHs are shallowing and projections utilizing the IPCC “business as usual” CO₂ emission scenarios indicate zones of aragonite undersaturation will expand over time (Table 1). Biogeochemical models suggest the pre-industrial average tropical aragonite concentration was 4.6, it is currently 4.0, and is expected to drop to 2.8 by 2100 (Kleypas et. al. 2009).

Changing seawater chemistry is expected to impact the distribution and abundance of coral reefs. The depth of the ASH is important to marine calcifiers and determines the limit of CaCO₃ precipitation and dissolution (Guinotte & Fabry 2008). Continued absorption of CO₂atm may be promoting a “calcite sea,” changing the relative proportion of organisms depositing stable carbonate minerals (Andersson et. al. 2008). Decreasing Ω_{arag} will likely exacerbate other local and/or global stress experienced by coral reefs (Cao & Caldeira 2008). Deep water scleractinian

corals (typically occupying depths 200+ m) and/or high latitude corals are expected to be most at risk. These corals occupy water with slight carbonate supersaturation and are suspected to have an increased sensitivity to environmental variability (Guinotte et. al. 2006, Turley et. al. 2007, Andersson et. al. 2008). Moreover, it is predicted that 70% of scleractinian cold-water corals will occupy water undersaturated with aragonite by 2099 (Guinotte et. al. 2006). The earliest estimate for Ω_{arag} undersaturation in the southern ocean is 2030 (McNeil et. al. 2004).

The Impact of Ocean Acidification on Coral Reefs

Changing seawater chemistry is expected to have a profound impact on marine calcifying organisms associated with coral reefs such as scleractinian corals, CCA, *Millepora*, *Halimeda*, bivalves, echinoids, gastropods, lobsters, etc. An organism's tolerance to ocean acidification is likely species specific (Marubini et. al. 2003, Langdon & Atkinson 2005, Kurihara 2008) and acidification is thought to make creation of biogenic CaCO_3 more metabolically expensive for marine calcifying organisms (Guinotte et. al. 2006, Guinotte & Fabry 2008, Kurihara 2008). The primary focus of this discussion is on acidification's impact on reef-building scleractinian corals and CCA. The majority of marine calcifiers tested to date have been sensitive to even subtle changes in seawater chemistry, and most studies have focused on the calcification and/or growth response of coral reefs to changing seawater chemistry (Table 2).

Calcification and/or Growth Response

Ocean acidification impacts calcifying organisms' ability to secrete and accumulate carbonate during growth and development and it is largely assumed that Ω_{arag} drives coral calcification at the organismal level (Smith & Buddemeier 1992, 29, Marubini & Atkinson 1999, Marubini et. al. 2001, Marubini et. al. 2003, Marubini et. al. 2008). Mesocosm experiments demonstrate reduced calcification and/or growth rates with increased pCO_2 levels, decreased Ω_{arag} , carbonate ion concentrations and/or pH levels. CCA algae are sensitive to even subtle changes in seawater chemistry and some coral species are more responsive than others (Table 2). The underlying biological mechanism leading to reduced coral calcification and growth rates is likely mediated by a decrease in pH, carbonate or by a disruption in internal buffering leading to a change in carbon supply rather than the direct impact of CO_2 (Marubini et. al. 2008). Moreover, biogeochemical models predict decreases in calcification rates between 9-60% between 1880 (preindustrial era) and 2100 (Table 2).

The expected primary effects of reduced calcification are weaker skeletons, reduced accretion rates, and increased susceptibility to erosion (Kleypas et. al. 2009, Gattuso et. al. 1999). Calcification in corals is important to the health of coral reef ecosystems as many species associated with reefs depend on the structural complexity created by the calcareous skeletons (De'ath et. al. 2009). Acidification inhibits accretion and favors reef erosion leading to a reduction in structural stability (Kleypas et. al. 2001, Hoegh-Guldberg et. al. 2007). As seawater becomes increasingly undersaturated with respect to aragonite, shells and skeletons will become increasingly prone to dissolution (Feely et. al. 2004, Orr et. al. 2005, Kleypas et. al. 2006, Fine & Tchernov 2007, Silverman et. al. 2009, Andersson et. al. 2009). Reduced net vertical accretion will likely result in reef drowning and over time will favor faster growing, less skeletally dense coral species (Knowlton 2001). A significant reduction in coral carbonate production was demonstrated on China's Luhuitou fringing reef resulting in the rate of sea level rise surpassing the rate of reef accretion (Shi Qui et. al. 2009).

Reduced calcification may also lead to a competitive disadvantage for space and other resources (Kleypas et. al. 2009, Kleypas et. al. 2006, Guinotte et. al. 2006, Kuffner et. al. 2008, Andersson et. al. 2008). Rates of calcification and/or skeletal growth determine coral fitness and ecological success. Growth impacts a colony's ability to compete for light and space and to repair itself following disturbance (Langdon & Atkinson 2005). Larger colonies have a competitive advantage and a greater reproductive output compared to smaller colonies (Lirman 2000, Langdon & Atkinson 2005). Mesocosm experiments demonstrate a lower percent cover of CCA and an increase in non-calcifying algae suggesting acidification may accelerate the phase shift to fleshy algae observed on many reefs (Kuffner et. al. 2008).

Studies demonstrate the degree of sensitivity to acidification varies among species and can also be intensified by changes in temperature and nutrients (Table 2). Additionally, the response of coral reefs organisms to acidification may differ between life stages (Kurihara 2008). Paleo-records of massive coral colonies in the GBR demonstrate an unprecedented decrease in calcification rates over the last 400yrs which is likely due to the complex effects of reduced Ω_{arag} and other factors such as rising sea surface temperature (SST) and nutrients (Cooper et. al. 2008, De'ath et. al. 2009). Studies have demonstrated coral calcification response to increased pCO_2 is temperature dependent (Reynaud et. al. 2003); however, sensitivity has also been found to be similar across the normal temperature range (Langdon & Atkinson 2005). Similarly, warming exacerbates reduced calcification response in CCA (Anthony et. al. 2008). Nutrients may also increase coral sensitivity to changing Ω_{arag} (Marubini & Thake 1999). More information is needed to explain the differences among species, the effect on various life stages, and the impact of acidification in concert with other factors.

Impact on Other Processes

The effect of acidification reaches beyond reducing calcification/growth rates, and is expected to impact other important processes such as productivity and recruitment on coral reefs. Mesocosm studies demonstrate a mixed productivity and recruitment response of coral reefs to acidification (Table 3). Calcification and photosynthesis draw from the same internal pool of dissolved inorganic carbon (DIC) and are likely competing for a limited supply of DIC (Gattuso et. al. 1999, Langdon & Atkinson 2005). It is expected that reduced Ω_{arag} will require corals to invest more energy into calcification, diverting resources from other essential processes such as reproduction. Moreover, coral recruitment may be further hindered by reductions in CCA abundance, a key settlement substrate for corals (Hoegh-Guldberg et. al. 2007). Most studies to date have been short term, yet long-term exposure of coral reefs to acidification may have complex effects on reproductive success (Doney et. al. 2009).

Acidification is expected to affect coral reef disturbance resistance, yet few studies have been able to clearly demonstrate this. A few mesocosm studies have shown the combined stress of acidification, nutrients and elevated SST increases the incidence of coral disease.

Table 2. The impact of ocean acidification on calcification and/or growth rates of coral reefs.

Organism/System	Study *	Findings	Refs
Scleractinian Corals			
<i>Stylophora pistillata</i>	M		29
<i>Stylophora pistillata</i>	M	Response is temperature dependent. Sensitivity recorded at 28.3 C	69
<i>Stylophora pistillata</i>	M	Decrease in PH by 0.1 units resulted in a decrease in calc. and growth rate; calc. is C limited	57
<i>Acropora cervicornis</i>	M	Effect of pCO ₂ reduced growth rate and was > the impact of nutrients alone	68
<i>Acropora eurytoma</i>	M	55% decrease in calcification rates. Sensitivity to carbonate ion concentration rather than PH or C	74
<i>Acropora tenuis</i>	M	High CO ₂ levels disrupted growth after settlement, polyp endoskeleton malformed	48
<i>Porites astreoides</i>	M	78% reduction in post-settlement growth at mid and high pCO ₂ levels	1
<i>Porites porites</i>	M		61
<i>Porites lutea</i>	M		63
<i>Porites sp. (328 colonies)</i>	P		17
<i>Porites sp.</i>	P	21 % decline in calcification rates between 1988 and 2003 in the GBR	16
<i>Porites compressa</i>	M	Decrease in carbonate ion concentration resulted in decreased calcification rates	60, 59
<i>Porites compressa, M. capitata</i>	M, B	limited supply of DIC. Predict a 60% decrease in calc. rate (1890- 2065)	49
<i>Montipora capitata</i>	M	15-20% reduction in calcification rate	40
<i>A.intermedia, P. lobata</i>	M	~40% reduction in calcification rate; response enhanced by warming	4
<i>Oculina Patagonia, M. pharencis</i>	M	Corals lost their skeletons under low PH conditions (7.3-7.6); recalcified when returned to ambient levels	26
9 families, 17 coral genera	F	Luhuitou fringing reef, China. Decrease in reef carbonate production by 80-89% leading to reduced accretion rates which are lower than the rate of sea level rise	75
<i>A. verweyi, P. cactus, G. fascicularis, T. reniformis</i>	M	13-18% reduction in calc. rates, response to decreasing carbonate ion concn. is likely species specific	58
* M= Mesocosm Experiment, B= Biogeochemical/predictive modeling, P=Paleo Studies; F=Field Studies			

Table 2. continued.

Organism/System	Study *	Findings	Refs
Coralline Algae			
<i>Corallina pilulifera</i>	M	Increased CO ₂ , decreased PH inhibited calcification	27
<i>Bosniella orbigniana</i>	M	CO ₂ increased calcification rates	79
<i>Coralline</i> sp?	M	Increased CO ₂ inhibited growth	47
<i>P. onkodes</i>	M	High CO ₂ inhibited growth by 50%; impact exacerbated by warming	4
<i>L. pallescens</i> , <i>Hydrolithon</i> sp., <i>Porolithon</i> sp.	M	250% difference; change from positive to negative growth	
Coral Reef Community			
Coral Reef (Biosphere 2)	M, B	Calc. rates controlled by the ion concn. product of Ca ²⁺ and carbonate ion concn. rather than pH, pCO ₂ , or carbonate ion concn. alone; predict a 40% decrease in calcification rates between 1880-2065	51, 50
Coral Reef	B	Predict coral reef calcification may decline globally by 17-35% under doubled CO ₂ conditions	43
Coral Reef	B	Predicted 9–30% decrease in calcification rates between years 1990 and 2100	28
Coral Reef	F		77
Coral Reef	B	Coral reefs will likely stop growing and start dissolving when atmos. CO ₂ doubles	76
Coral Reef	B	Predict a 35% increase in calcification between 1890-2100; impact of SST in driving calc. rates outweighs reduced	62
Coral Reef	F	Coral reef accretion may be limited in high pCO ₂ conditions	56
Coral Reef	M	Net community calcification decreased; net accumulation to net loss of CaCO ₃ under double pCO ₂ conditions	2
Coral Reef	M, B	decrease by 21% by 2065	52, 53
* M= Mesocosm Experiment, B= Biogeochemical/predictive modeling, P=Paleo Studies; F=Field Studies			

Table 3. The impact of ocean acidification on other key coral reef processes

Processes	Organism/System	Study*	Findings	Refs
Productivity	Coral Reef Community	M	Net community primary production did not change significantly with respect to pCO ₂	52
	<i>Porites compressa</i> ; <i>M. capitata</i>	M	Increased CO ₂ increased net carbon production	49
	<i>Stylophora pistillata</i>	M	Productivity was insensitive to changes in PH & pCO ₂ levels	57
	<i>Stylophora pistillata</i>	M	Net photosynthesis increased with increased temp. & pCO ₂	69
	<i>Acropora eurytoma</i>	M	Reduced PH had no impact on photosynthesis	74
	<i>P. onkodes</i> , <i>A.intermedia</i> , <i>P. lobata</i>	M	Productivity reduced; CCA most sensitive to high CO ₂ ; impact exacerbated by warming; <i>Acropora</i> productivity enhanced at intermediate levels	4
Recruitment	<i>Porites astreoides</i>	M		1
	<i>Acropora tenuis</i>	M	High CO ₂ levels disrupted growth after settlement	48
	<i>Coralline sp.</i>	M	Increased CO ₂ inhibited recruitment rate; increase in non-calc. algae	47
	<i>M. capitata</i> , <i>P. damicornis</i> , <i>L. pallescens</i> , <i>Hydrolithon sp.</i> , <i>Porolithon sp.</i>	M	No significant impact on recruitment & reproduction	40
Disturbance Resistance	<i>Porites compressa</i>	M	Reduced PH, thermal and nutrient mediated stress induced herpes-like viral infection	80
	Coral Reef Community	M	Synergistic impact of increased temp. & low PH on white plague type II pathogen	67
	<i>P. onkodes</i> , <i>A.intermedia</i> , <i>P. lobata</i>	M	High CO ₂ induced bleaching, synergistic effect with warming to lower bleaching thresholds	4
	Coral Reef Community	B	Climate mediated acidification & warming reduce coral reef resilience; reduced diversity; reduced habitat complexity	36
	Coral Reef Community	F	Poorly cemented reefs are likely more susceptible to bioerosion	56
	<i>A. palifera</i> , <i>A. gemmifera</i> , <i>A. hyacinthus</i>	B	Expected increase in mechanical vulnerability; decreased diversity	55
* M= Mesocosm Experiment, B= Biogeochemical/predictive modeling, P=Paleo Studies; F=Field Studies				

Biogeochemical models predict the synergistic impact of ocean warming and acidification will result in increased bleaching, incidence of disease and bioerosion on coral reefs (Hoegh-Guldberg et. al. 2007). Acidification may lower bleaching thresholds of corals and any acclimation of corals to thermal stress may be offset by acidification (Anthony et. al. 2008). Moreover, CCA demonstrate a strong growth response to acidification and play an important role in coral reef wave-resistance and are instrumental in cementing the framework of coral reefs (Jokiel et. al. 2008). Typically, weaker skeletal density and poorly cemented reefs are more vulnerable to bioerosion and mechanical damage (Madin et. al. 2008, Manzello et. al. 2008). Mechanical damage may impact other processes as fragmentation of *Acropora palmata* following storms has been shown to increase mortality, decrease growth rates and reduce reproduction potential (Lirman 2000).

Eroding Resilience & the Uncertain Future of Coral Reefs

Ocean acidification will likely reduce coral reef resilience to local and/or global disturbances. The synergistic effects of acidification, rising SST, habitat destruction, pollution, etc. are expected to drive phase shifts to an alternative, less desirable states on coral reefs (Bellwood et. al. 2004, Pandolfi et. al. 2005, Knowlton 2001, Knowlton & Jackson 2008, Jackson 2008). Acidification will likely promote a shift to mechanically robust, smaller and morphologically simple corals resulting in reduced diversity and loss of functional redundancy which can have cascading ecosystem effects (Madin et. al. 2008). Ecological modeling predicts biodiversity and habitat complexity will decline, local and/or climate mediated stress will reduce reef resilience, driving coral reefs towards “the tipping point of functional collapse” (Hoegh-Guldberg et. al. 2007). Similarly, human impacts and habitat fragmentation undermines coral reef resilience and makes them vulnerable to future climate change (Hughes et. al. 2003). Local and global threats to coral reefs may be pushing coral reef ecosystems down the “slippery slope to slime” (Pandolfi et. al. 2005). Moreover, the synergistic impact of multiple variables and the loss of resilience will likely result in “ecological surprises” and shifting baselines (Knowlton 2001, Knowlton & Jackson 2008). Confronted with uncertainty, it is critical to manage reefs to improve resilience (Hughes et. al. 2003, Bellwood et. al. 2004, Pandolfi et. al. 2005, Knowlton 2001, Knowlton & Jackson 2008, Jackson 2008).

The ability of coral reefs to physiologically acclimate or genetically adapt to ocean acidification is unknown. Most studies to date have been short term (hours to weeks) and chronic exposure to acidification may induce either short term physiological acclimation or genetic adaptations not captured in mesocosm experiments (Kleypas et. al. 2009, Gattuso et. al. 1999, Doney et. al. 2009). Reef-building corals have low genetic diversity and long generation times making it unlikely they will adapt quickly enough to keep up with the unprecedented rate of changing seawater chemistry (Hughes et. al. 2003, Hoegh-Guldberg et. al. 2007). Paleo-records from Flinders Reef in the Coral Sea have demonstrated that the massive *Porites* coral has undergone large fluctuations in pH (~0.3 units) over the past 300 years (Pelejero et. al. 2005). The interdecadal pH cycle (~ 50 years) observed suggests that the *Porites* coral in this location is relatively well adapted to a wide range in pH and δ_{arag} . It is unclear how these organisms will react to longer term exposure to acidification and the unprecedented reductions in pH relative to historic levels.

One suggestion is corals may be able to alternate between soft-bodied and skeletal forms. Scleractinian corals exposed to low pH values changed their morphology by losing their skeleton and increasing biomass. These soft-bodied polyps regained their skeletons and reformed colonies once returned to ambient pH levels. Although corals may be able to persist under low pH conditions, the lack of skeletal complexity may cause major changes in coral reef structure and function (Fine & Tchernov 2007). Moreover, the overall fitness was likely reduced due to the loss of their protective skeleton (Doney et. al. 2009). More information is needed to determine if coral reefs will adapt given time (Langdon & Atkinson 2005, Kurihara 2008).

While it is widely recognized that local and/or global disturbances will continue to change coral reef ecosystems, coral reefs may face extinction. Climate mediated (e.g. warming and acidification) and local level disturbances threaten one third of reef-building corals with extinction (Carpenter et. al. 2008). In addition to the rapid, non-linear rates of change leading to sudden phase shifts, the synergistic effects of acidification, warming, habitat destruction, overfishing, pollution, etc. are paving the way for a mass extinction in the oceans with unknown consequences (Jackson 2008). The geological record supports that mass extinctions have created periods without living coral (reef gaps) which have taken millions of years to recover. These reef gaps are likely linked to CO₂atm levels and the availability of CaCO₃. The ocean responds gradually to atmospheric conditions and the Earth is “committed” to the process of acidification before its effects are obvious. An evolutionary solution to the unprecedented rate of changing seawater chemistry is unlikely and acidification has the potential to trigger the sixth great mass extinction event (Vernon 2008).

Concluding Remarks

A better understanding of how ocean acidification will impact the future of coral reefs is greatly needed. Studies should continue to explore the primary impacts of acidification, but also secondary impacts (e.g. increasing prevalence of disease and bleaching) which have strong demographic effects. There is a dearth of research concerning chronic exposure and the synergies among the various factors driving ecological change (Langdon & Atkinson 2005, Guinotte et. al. 2006, Kleypas et. al. 2006, Kurihara 2008, Jackson 2008, Guinotte & Fabry 2008, De’ath et. al. 2009). More research is needed to determine how acidification’s impact on phytoplankton and zooplankton populations will feedback to coral reefs (Guinotte et. al. 2006). Moreover, the ecosystem effects of acidification on higher tropic level organisms that depend on coral reefs for shelter and nutrition (Guinotte & Fabry 2008) and on functional groups that drive biogeochemical cycles (Zeebe et. al. 2008) has yet to be determined. Additionally, less is known about acidification’s impact on both calcifying and non-calcifying organisms throughout multiple life stages (Kurihara 2008, Zeebe et. al. 2008). Acidification will likely be a significant driver of coral reef degradation in the future. Reducing CO₂ emissions and managing reefs for improved resilience is critical to preparing for what lies ahead.

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Chapter 12: Creating a balance between tourism and coral reef sustainability: the effects of SCUBA diving on coral reef ecosystems worldwide.

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Abstract

Coral reefs are highly diverse yet fragile ecosystems. Many coral reefs are found near poorly-developed countries of low economic status, and tourism to these areas creates a necessary source of revenue through fishing, SCUBA diving, snorkeling, and other activities. There have been many studies documenting the detrimental effects of SCUBA diving on coral reef ecosystems. While many studies reveal *frequent* damage does occur, it does not usually translate to *extensive* damage of the reef. The amount of coral damage caused by divers is minute (4-5% mortality) compared to that caused by tropical storms (nearly 70%); however, there are important implications of diver-induced damage to the reef structure and ecosystem that need to be considered when implementing management strategies.

Introduction

Coral reefs are some of the most diverse ecosystems in the marine realm (Hawkins *et al.* 1999) and renowned for their beauty. Most coral reefs are located in warm, tropical waters between 30° N and 30° S latitudes (Achituv and Dubinsky 1990). Many studies worldwide have looked into the effects of different types of disturbances (both natural and anthropogenic) on reef ecosystems. This study will focus on the biological effects of diving on coral reef ecosystems.

Vacations to tropical areas containing corals reefs are popular among tourists. Many of these destinations are in less-developed countries and places that rely heavily on the economic benefits of this tourism. Barker and Roberts (2004) and Worachananant (2008) cited multiple studies on the economic benefits of tourism to areas that have coral reefs as ranging from \$2-682 million. Because reef tourism is often a major source of income to the areas they are found in (Gibson 1998), there is a need to emphasize the necessity of protecting these ecosystems. This is especially important for maintaining the long-term health of the reefs since tourists often only visit the reefs for a short period of time and may be causing high rates of damage that create long-lasting effects.

Reef degradation has been defined as a decrease in the amount of live stony corals present due to human activity such as diving (Hawkins *et al.* 1999). Divers cause damage through the collection of organisms, and spear fishing in particular can devastate reefs. Recreational divers collected organisms for many reasons, including as personal souvenirs, bait for fishing, aquarium trade, and for human consumption (Davenport 2006). While this still occurs in some areas, these practices are not as common today due to the relatively recent laws that prohibit the transport of reef organisms. Zakai *et al.* (2002) cited multiple sources concluding that currently, most of the damage inflicted by SCUBA divers is caused by bumping, breaking, and abrading corals

unintentionally during diving activities. This can happen during descent and while regulating buoyancy, by stepping directly on corals, kicking corals with fins, bumping into them with diving tanks and gear, and by using corals to maintain steadiness while taking photographs. Jameson *et al.* (1999) developed a Coral Damage Index (CDI) for reefs in the Red Sea to assess rates of diver-inflicted damage to reef structure and create a tool for better monitoring and prevention. Reefs containing 4% or more broken coral colonies or 5% or more coral rubble were classified as “hot spots” for further assessment and heightened monitoring. They compared data from intensively-dived Red Sea reefs to less-intensely dived Bonaire reefs and found a positive correlation between number of dives and percentage of damaged coral. In comparison, hurricanes and tropical cyclones produce varying degrees of damage to coral reef structures and have been found to cause from 30% to 67% immediate reduction in live coral on the Great Barrier Reef (Cheal *et al.* 2002). While damage cause by SCUBA diving may seem insignificant in comparison to that caused by storms, damage inflicted by divers can weaken the resilience of reefs to natural disturbances and lead to negative long-term effects (Hawkins *et al.* 1999). Therefore, it is important to accurately monitor and reduce diver impacts on coral reef ecosystems.

Effects of SCUBA diving on coral reef ecosystems

A search on Web of Science using the keywords ‘coral’ AND ‘reef’ AND ‘diving’ returned 24 references addressing the issue of how SCUBA divers affect coral reefs worldwide. All of those 24 sources concluded that recreational SCUBA divers had a detrimental effect on coral reefs (Table 1). Seventeen of those went on further to categorize the damage caused by divers specifically as broken corals (Table 2). Three references found that over time damage inflicted by divers led to changes in the coral community structure to favor faster-growing branching species over larger, mounding corals. Two studies showed that divers using underwater cameras, regardless of their level of diving expertise, caused more damage to corals than divers not taking photographs. However, three studies did find that when dive guides asked divers to avoid touching corals and then intervened underwater when divers bumped into corals helped in reducing the damage caused to corals by divers.

Table 1.	Positive Effect	Negative Effect
SCUBA diving on coral reefs	0	24

Table 1. From a Web of Science search using the keywords ‘coral’ AND ‘reef’ AND ‘diving,’ all 24 relevant sources returned determined that SCUBA diving had a detrimental effect on coral reefs.

Table 2.	Studies Citing a Specific Detrimental Effect
Broken Coral	17
Mixed Sediment	2
Changed coral speciation	3

Table 2. From a Web of Science search using the keywords ‘coral’ AND ‘reef’ AND ‘diving,’ 17 sources listed specific negative impacts caused by SCUBA diving on coral reef ecosystems.

The most commonly listed effects were coral breakage caused by bumping and stepping on corals, mixing of sediment around corals caused by fin kicks and walking, and a change in coral species present over time to favor faster-growing branching species over slower growing mounding corals.

Effects on reef fish communities

Wilson *et al.* (2006) found that depletion of corals from storms, bleaching, and disease leads to an overall decline in fish present at the reef, possibly due to mortality or relocation of fish as effects of habitat loss. This change in fish abundance is mainly seen in corallivores, but is present in all species relying directly on the reef for food or protection. Hasler and Ott (2008) saw no effect on fish species diversity or abundance due directly to the effects of SCUBA diving. They did note that there was a higher abundance of corallivorous fish at the reef crest than in other areas of the reef, possibly due to a higher proportion of branching corals present in that area. A higher abundance of surgeonfishes was hypothesized to be more influenced by higher levels of algae due to an *Acropora* die-off in the mid-1980s than by diving, and higher numbers of carnivorous fish could be attributed to divers feeding fish at some reefs (Hawkins *et al.* 1999), though the effects of this on community structures were not investigated in this study. On the other hand, Hawkins *et al.* (1999) found significantly more snappers, surgeonfish, and more fish overall for undived areas compared to dive sites. These studies suggest that breakage of corals by SCUBA diving, if widespread, may be indirectly influencing the community assemblages of reef fish by allowing for colonization of different species of corals and algae than were originally present, which may favor different functional assemblages.

Effects of sedimentation

Increased sedimentation caused by fin kicks leads to stress on corals as they have to increase metabolic costs to remove sediment from themselves, and the higher turbidity makes it harder to get sufficient sunlight for photosynthesis in the zooxanthellae (Nystrom *et al.* 2000). The highest rates of sedimentation occur at the entrance to dive sites, where divers are often still adjusting their buoyancy, and decreases with increasing distance from the entrance site (Hasler and Ott 2008).

Effects on coral community structure

In Bonaire Hawkins *et al.* (1999) studied differences in the coral community between protected sites with no diving allowed and sites that were heavily dived. They did not find significant differences in damage to corals, but noted more loose coral fragments in the diving sites. There was also higher coral cover overall in the protected sites with no diving, and a larger proportion of branching corals (and a higher number of species of corals) in the diving sites, though the total number of colonies per square meter was not significantly different between the protected sites and diving sites. While the proportion of mounding corals decreased at all sites, sites that experienced diving had a larger decrease in mounding coral cover. Abundance of soft corals and algae increased tremendously compared to stony corals in areas that contain heavy diving (Jameson *et al.* 2007). Unfortunately, diving areas dominated by branching corals suffer a higher rate of breakage because branching corals are more fragile than mounding corals

(Rouphael and Inglis 1997). Even when coral is not broken upon contact by divers, simply the stress caused by touching or abrasion of the organism can affect the coral's ability to recover from pathogens, disease, and natural disasters (Hall 2001; Hawkins *et al.* 1999; Hawkins and Roberts 1993).

Effects of diver behavior on damage rates

There have been several studies investigating whether the use of underwater cameras by divers increases the rate of damage caused to corals during dives. Multiple studies have found that divers using cameras caused more damage to corals than those not using cameras, though carrying a camera did not cause an increase in the number of contacts with the coral (Rouphael and Inglis 2001). Barker and Roberts (2004) found that camera use did lead to elevated rates of contact with the corals, and that this had no correlation with level of photographic skill.

Rouphael and Inglis (2001) also summarized multiple studies concluding that men had higher rates of contact and damage with corals while diving than women. Studies found this to be due to many factors, including women generally being more cautious (Rouphael and Inglis, 2001), men tending to be more adventurous than women (Hudgens and Fatkin 1985) and less likely to follow instructions (Vredenburg and Cohen 1993; Sirakaya, 1997), and men being more likely to ignore pre-dive briefings (Rutter and Giller 1984; Vredenburg and Cohen 1993).

Harriot *et al.* (1997) and Barker and Roberts (2004) found no effect of diving skill level on the number of contacts made with corals during a dive, indicating that as diving skill increases, rates of damage do not change or decrease. It has also been shown that diving at night leads to higher rates of contact and damage of corals than dives during daylight hours (Barker and Roberts 2004).

Prevention and management

Effects of educational briefings and intervention

Worachananant *et al.* (2008) investigated the effects of a pre-dive briefing, diver experience, camera use, and gender on rates of coral contact and damage. They found that significantly more divers that did not attend a pre-dive briefing caused damage to corals during their dives than those that did attend a briefing. The briefing contained information about the fragility of the ecosystem and the importance of not touching and damaging any living organisms, including the corals. Barker and Roberts (2004) tested the effects of a short, one-sentence pre-dive environmental briefing and found it to have no effect on the rates of divers contacting corals. They did find that actual intervention by the dive leader when divers came into contact with corals significantly reduced contact rates.

Diver carrying capacity

Zakai and Chadwick-Furman (2002) and Jameson *et al.* (1999) summarized diver carrying capacity as the maximum number of dives a site can support sustainably per year. They

specified three important variables that influence a sustainable diver carrying capacity in any area: 1) presence of vulnerable organisms, 2) levels of awareness of the environment and training of divers, 3) presence of additional anthropogenic stressors to the ecosystem. To further illustrate this point, some of the most heavily-dived reefs are found in the Red Sea and experience high levels of pollution and shoreline modifications, and it has been predicted that without changes in management these reef ecosystems will collapse within 20 years (Wilkinson 1993). Uyarra *et al.* (2009) and Tratalos and Austin (2001) identified the condition of corals as being one of the most important attributes of a positive diving experience by tourists, supporting the idea that decreasing the number of dives in a specific area (and thus reducing damage) will result in a more positive diving experience for future diving tourists.

Construction of artificial reefs

Stolk and Markwell (2007) and Treeck and Schumacher (1998) investigated the possible benefits of constructing artificial reefs as a way to preserve the natural reefs and control damage (and reverse/restore negative effects) caused by divers to these ecosystems. By introducing substrates that are conducive to coral settlement, current reefs may be expanded and the density of dives may be spread over a larger area, decreasing the likelihood of having areas with high rates of damage (Stolk and Markwell, 2007). Rinkevich (1995) also found that introduction of coral recruits to damaged reefs does allow for reef reconstruction and increase the genetic diversity of reefs. These findings indicate that the construction of artificial reefs and seeding damaged reefs with new recruits could help to create a sustainable form of SCUBA diving in coral reef ecosystems. Long-term studies of this approach, however, do not look as promising and this should not be viewed as an all-encompassing solution for ‘fixing’ broken reefs.

Other types of management

Many areas containing coral reefs have been established as marine protected areas. Some of these areas are zoned for different activities, some types of fishing are banned, and limits are placed on the number of dives allowed per site (Van’t Hof 1983; Zakai and Chadwick-Furman 2002). Because many of these areas economically depend on profits from diving tourism since fishing is often limited or banned in these areas, it is unreasonable to completely ban SCUBA diving. Places such as the Bonaire Marine Park have implemented a diving user-fee to help offset the detrimental effects of tourist SCUBA diving and other activities to the coral reefs (Van’t Hof 1983). While user fees may help to cover the costs of managing and patrolling coral reefs, there is still more that needs to be done to minimize the amount of damage caused by divers to reefs (Barker and Roberts 2004).

Concluding remarks

Coral reef diving can be a positive experience for many with minimal damage to the ecosystem. Damage to corals caused by careless and unknowing divers increases the coral’s vulnerability to diseases and further damage by storms, making it extremely important to reduce damage by divers. It is clearly important that steps need to be taken to reduce the impact of SCUBA diving on reefs by educating divers on the importance of preservation while continuing to draw a sustainable amount of ecotourism to coral reefs to financially support and protect these areas.

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Chapter 13: Valuing Coral Reef Ecosystems and Their Ecological Services: An Ecological Economics Approach

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Abstract

Ecology and economics have become increasingly interdependent as disciplines. With the rise of ecological and environmental economics, conservationists have new tools to advance both conservation and development objectives simultaneously. By valuing natural ecosystems in terms of the goods and services they provide, and evaluating the economic consequences of their decline, ecological economics can help us overcome the common-pool nature of these resources, bringing the aspirations of conservationists nearer to the realm of economic practicality. Among the ecosystems to which ecological economics has been applied, environmental concerns about the health of coral reefs are particularly urgent; at the same time, economic studies have shown that these ecosystems provide valuable services to human communities. Quantifying the ecosystem goods and services provided by these systems therefore constitutes an essential research priority. This paper summarizes recent research in this area and explains some of the issues involved.

Introduction

The first decade of the 21st century has seen steadily rising interest in the economic value of natural ecosystems and the services these ecosystems provide human societies. This interest has stimulated a growing body of interdisciplinary literature spanning the natural and social sciences, with the aim of reconciling the seemingly contrary goals of improving the material condition of human societies and maintaining well-functioning, biodiverse ecosystems. While many would argue that nature has an intrinsic value justifying its conservation on ethical or aesthetic grounds alone, both economists and ecologists have come to recognize that conservation is frequently also a concrete investment in the future. As natural ecosystems come under increasing anthropogenic stress from economic activity, the imperative has grown to assess the economic costs of ecosystem decline as well as the economic benefits that intact ecosystems provide. Incorporating this information into the cost-benefit calculations of economic planning promises a more rational, sustainable path of economic development if the necessary research can be done. Much of this research has focused on coral reef systems and the mangrove or seagrass ecosystems often associated with them. These extremely diverse ecosystems are both highly threatened and economically significant.

The economic discipline that attempts to evaluate the economic productivity of ecological systems is termed ecological economics. This field coalesced in the early 1990s largely around the work of economist Robert Costanza, with the founding of a journal bearing the discipline's name and subsequently influencing other transdisciplinary journals such as *Ecological Applications*. The concept of "ecosystem services" and the evaluation of these

services in monetary terms are central to ecological economics, and publication trends reflect an increasing awareness of the importance of these services. Publications referring to the value of ecosystem goods and services have increased according to a nearly exponential trend since 1991 (Figure 1a), and the issue was thrust into the forefront of scientific discourse with a seminal *Nature* paper by Costanza (1997) entitled *The Value of the World's Ecosystem Services and Natural Capital*. As of April 2009, this paper has received 1396 citations (Figure 2a) with a particularly noteworthy increase since 2005. It has provoked a great deal of discussion regarding the prospects, challenges, and ethical issues facing the field, spawning an entire special issue in *Ecological Economics* dedicated to its discussion (vol. 25, iss. 1). In 2002 the National Academy of Science responded by establishing a Committee on the Valuation of Ecosystem Services (Barbier and Heal 2006).

Studies of the ecosystem services of coral reefs and of their social importance also began to appear in the peer-reviewed literature starting in the mid to late 1990s. The application of ecological economic analysis to valuing coral reef ecosystems picked up around the same time and has also seen a marked increase in recent years (Figure 2 a and b).

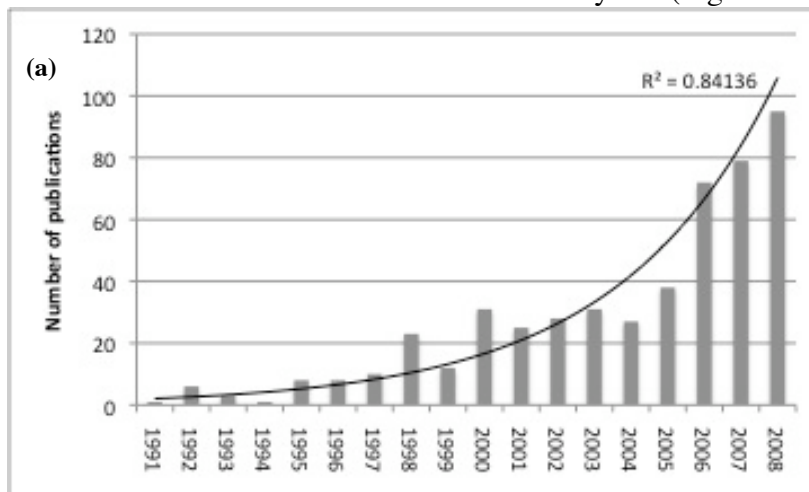


Fig. 1a. ISI Web of Science analysis of the number of publications referring to the valuation of ecosystem goods and services from 1991 to 2008. Search protocols: [ecosystem AND services AND value] OR [ecosystem AND goods AND value] OR [ecological AND services AND value] OR [ecological AND goods AND value].

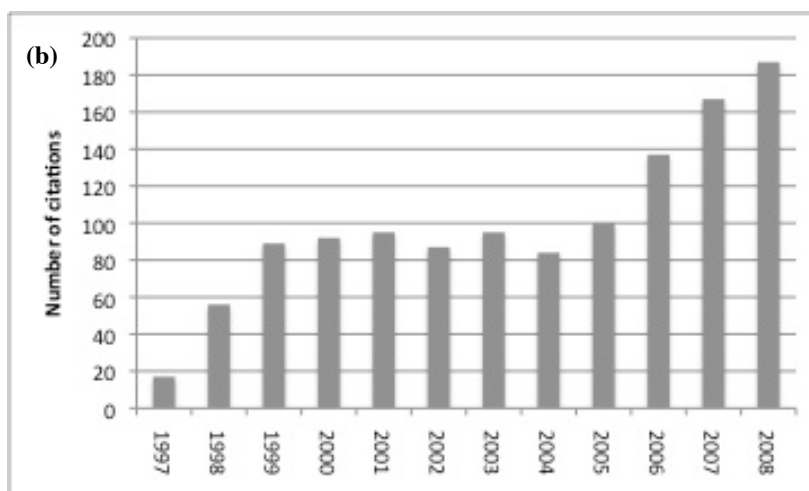


Fig. 1b. ISI Web of Science analysis of the number of citations referring to Costanza (1997) from 1997 to 2008.

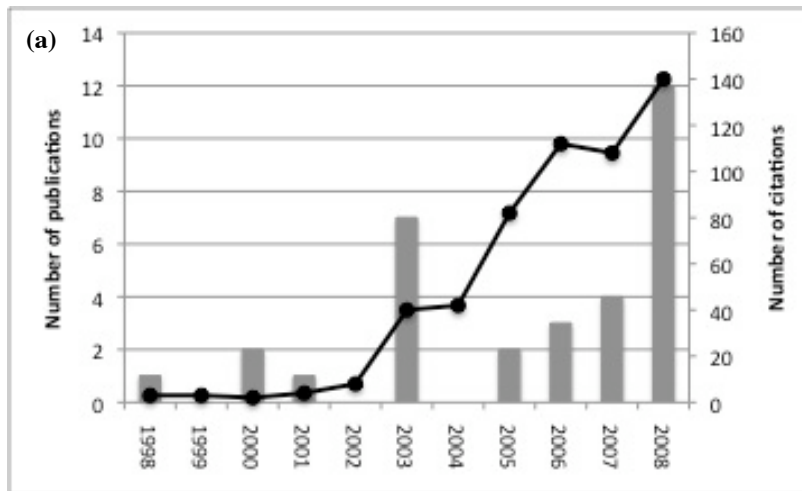


Fig. 2a. ISI Web of science analysis of the number of publications (histogram, left axis) and citations (line graph, right axis) referring to coral reef ecosystem goods and services between 1998 and 2008. Search protocols: [Coral AND reef AND ecosystem AND services] OR [Coral AND reef AND ecosystem AND goods].

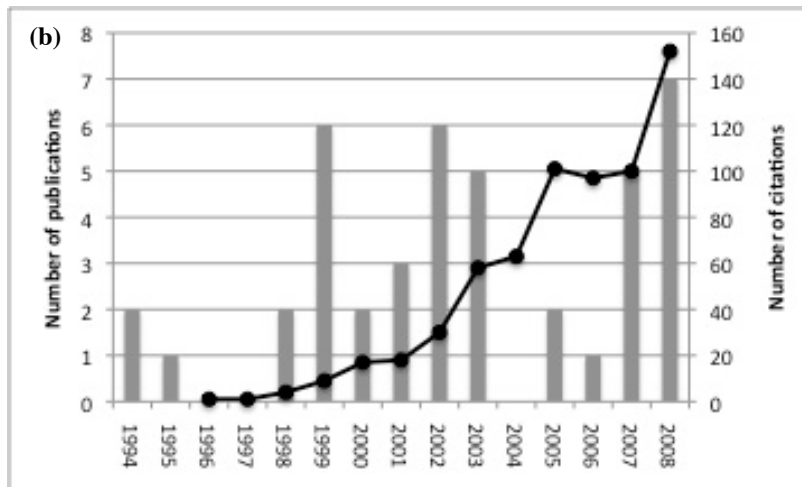


Fig. 2b. ISI Web of Science analysis of the number of publications (histogram, left axis) and citations (line graph, right axis) referring to the economic value of coral reef ecosystems. Search protocols: [Coral AND reef AND economic AND value] OR [Coral AND reef AND valuation] OR [Coral AND reef AND economic AND benefits] OR [Coral AND reef AND "ecological economics"].

Ecosystems services of coral reefs

An estimate by Cesar, Burke, and Pet-Soede (2003) places the global economic value of coral reefs at \$29.8 billion in benefits per year, divided into the four categories of tourism, fisheries, coastal protection, and biodiversity (Figure 3; see also table 1). However, this estimate may not even account for the full range of ecosystem services that reefs provide. The Millennium Ecosystem Assessment (2005) classifies ecosystem services into four general categories: (1) regulating services such as protection of shorelines, (2) provisioning services such as fish production, (3) cultural services such as tourism and recreation, and (4) supporting services such as nutrient cycling that are necessary for maintenance of the other services. Moberg and Folke (1999) elaborate on the ways these services are manifested in reef ecosystems, while also adding additional categories to this list. By acting as buffers against wave action, reefs protect shorelines from erosion. Important reef fisheries exist for fish, mussels, crustaceans, and seaweeds. In addition to these directed fisheries, Wood (2001) describes the trade in live reef fish for aquaria as a \$24-40 million industry. Unrepresented in economic analyses of reef

ecosystem services, but potentially highly significant, is the novel category of information services. As highly sensitive systems, reefs and their skeletons provide a long-term record of chemical and climatic conditions in the oceans, establishing a critical baseline against which to gauge more recent changes. By detoxifying or sequestering wastes and pollutants created by humans, reefs also perform an essential cleansing function in the marine environment. The many species found in reef ecosystems represent a valuable source of natural chemical products with potential pharmaceutical or other industrial applications. Additionally, the cultural and social practices of many indigenous communities have co-evolved with the biology of the reefs on which these societies depend for sustenance.

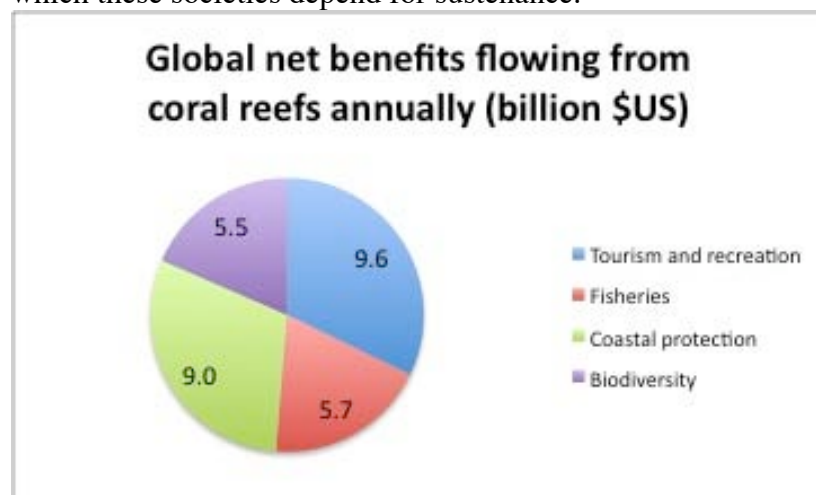


Fig. 3 Global annual benefit streams provided by coral reef ecosystems as estimated by Cesar, Burke, and Pet-Soede (2003). Major categories are tourism, fisheries, coastal protection, and biodiversity.

Potential net benefit streams of coral reefs per year, by region (million \$US)

	Southeast Asia	Caribbean	Indian Ocean	Pacific	Japan	USA	Australia	World
Reef area (km ²)	89,000	19,000	54,000	67,000	3,000	3,000	49,000	284,000
Fisheries	\$2,281	\$391	\$969	\$1,060	\$89	\$70	\$858	\$5,718
Coastal protection	\$5,047	\$720	\$1,595	\$579	\$268	\$172	\$629	\$9,009
Tourism/recreation	\$4,872	\$663	\$1,408	\$269	\$779	\$483	\$1,147	\$9,621
Biodiversity value	\$458	\$79	\$199	\$172	\$529	\$401	\$3,645	\$5,483
Total	\$12,658	\$1,853	\$4,171	\$2,079	\$1,665	\$1,126	\$6,278	\$29,830

Table 1. Potential net benefit streams per year of coral reefs by region, as calculated by Cesar, Burke, and Pet-Soede (2003).

As shown in Table 1, the greatest economic benefits from reef ecosystems are realized in Southeast Asia and Australia, reflecting the high biodiversity and relatively good condition of reefs in these regions. Accordingly, most studies quantifying these benefits have been performed on Indo-Pacific and Australian reefs. Their aggregate magnitudes can vary widely depending on the particular system and spatial scale considered, as shown in Table 2, from \$217,600 for the small mangrove-reef ecosystem of Rekawa, Sri Lanka to \$3.7 billion for the entire Great Barrier Reef of Australia. In addition to totals such as these, the economic value of coral reefs and their

associated nearshore ecosystems can also be expressed per unit area, both in aggregate and with respect to individual ecosystem services, as shown in tables 3 and 4, respectively.

Location	Annual Economic Value
Turks and Caicos Islands	\$47.3 million
Great Barrier Reef, Australia	\$3.7 billion
Phi Phi, Thailand	\$497.4 million
American Samoa	\$5.1 million (reefs)
American Samoa	\$750,000 (mangroves)
Mariana Islands	\$61.2 million
Guam	\$127.3 million
Hawaii	\$364.0 million
Indonesia	\$1.6 billion
Philippines	\$1.1 billion
Hon Mun MPA, Vietnam	\$6.2 million
Bonaire	\$19 million
Muthurajawela, Sri Lanka	\$8.1 million
Rekawa, Sri Lanka	\$217,600

Table 2. Total annual values of coral reef ecosystem services from various reef locations throughout the world. Data were summarized from Conservation International (2008).

Ecosystem	Location	Estimated Annual Value
Coral reefs	SE Asia region	\$231-\$2,700/ha
Coral reefs	Sri Lanka	\$130-\$44,040/ha
Coral reefs	Phi Phi, Thailand	\$15,118/ha
Coral reefs	Wakatobi National Park, Indonesia	\$121/ha
Coral reefs	South China Sea, Philippines	\$2,661.12/ha
Coral reefs	Olango Island, Philippines	\$383-634/ha
Coral reefs	Philippines (national average)	\$518.52/ha
Mangroves	Ras Mohammed Park, Egypt	\$91,000/ha
Mangroves	Nabq Protected Area, Egypt	\$24,000/ha
Mangroves	Rekawa, Sri Lanka	\$1,088/ha
Wetlands	Global average	\$2,800/ha
Wetlands	Muthurajawela, Sri Lanka	\$2,700/ha

Table 3. Estimated annual values per hectare of various coral reef and mangrove ecosystems throughout the world. Data were summarized from Conservation International (2008).

Ecosystem	Location	Ecosystem service	Estimated Annual Value
Coral reefs	Wakatobi National Park, Indonesia	Recreation	\$13.2/ha
Coral reefs	Wakatobi National Park, Indonesia	Recreation	\$13.2/ha
Coral reefs	Meso-American Barrier Reef	Fisheries	\$150-\$1,500/ha
Coral reefs	Wakatobi National Park, Indonesia	Fisheries	\$103.40/ha
Coral reefs	Wakatobi National Park, Indonesia	Coastal Protection	\$4.73/ha
Coral reefs	Sri Lanka	Coastal Protection	\$2,460-\$8,360/ha
Mangroves	Global average	Seafood (market value)	\$75-\$1,675/ha
Mangroves	Unites states (national average)	Fisheries	\$62/ha
Mangroves	Indonesia (national average)	Fisheries	\$600/ha
Mangroves	Gulf of Thailand	Fisheries	\$33-\$110/ha
Mangroves	Rekawa, Sri Lanka	Fisheries	\$493/ha
Mangroves	Matang, Malaysia	Fisheries	\$2,500/ha
Mangroves	Rekawa, Sri Lanka	Coastal Protection	\$300/ha
Lagoon	Rekawa, Sri Lanka	Fisheries	\$268/ha
Wetlands	Muthurajawela, Sri Lanka	Coastal Protection	\$1,800/ha
Wetlands	Muthurajawela, Sri Lanka	Recreation	\$20/ha

Table 4. Estimated annual values per hectare of ecosystem services provided by coral reef and mangrove ecosystems around the world. Data were summarized from Conservation International (2008).

An important caveat to remember when attributing these values is that the production of ecosystem services can be non-linear in character with respect to forcing factors or independent variables such as area. This adds an additional layer of complexity to ecological economics, as non-linearity in ecosystem services must be accounted for in order to avoid over- or under-valuing them and thereby to arrive at optimal policy decisions. For example, ecosystem services may show asymptotic behavior or thresholds over time and space, mirroring those seen in ecological processes such as population growth, predator functional responses, and species-area relationships (Koch et al. 2009). In such circumstances, valuing incremental changes in habitat characteristics becomes difficult. Incorporating these nonlinearities into future valuation studies is clearly a research priority in this field.

Analytical methods in ecological economics: Valuing ecosystem services

The value of some ecosystem services, such as tourism and fishery production, can be gauged by studying consumer preferences. Ecological economics has two principal tools to do this: contingent valuation and travel-cost methods. Contingent valuation directly asks people about their willingness to pay in exchange for a given availability of ecological goods and services. The responses are then combined with estimates of the number of stakeholders involved and used to construct economic models. Able quantify both use and non-use values of ecosystems, contingent valuation techniques estimate the consumer and producer surpluses (together, social surplus) that define these values. Figure 4 illustrates the basic concept of consumer and producer surpluses. The consumer surplus obtained from an economic activity is defined as the difference between what consumers would be willing to pay for each unit of a good or service (i.e. the consumer demand function) and what they actually pay (i.e. the equilibrium price level), integrated over all units of the good (Pendleton 1995). Similarly, the producer surplus of an

economic activity is defined as the difference between what producers would be willing to sell a service for (i.e. the producer supply curve) and the equilibrium price level, similarly integrated over all units. When discussing ecological services provided by nature, the emphasis, for obvious reasons, is on consumer surplus. However, producer surplus values can also be important when extending contingent valuation to industries indirectly dependent on the provision of these same services—for example, commercial establishments catering to eco-tourists. Figure 5 shows how a decline in the health of an ecosystem leading to a reduction in ecosystem services can shift either the demand or the supply curves for these services and for other economic activities dependent on them.

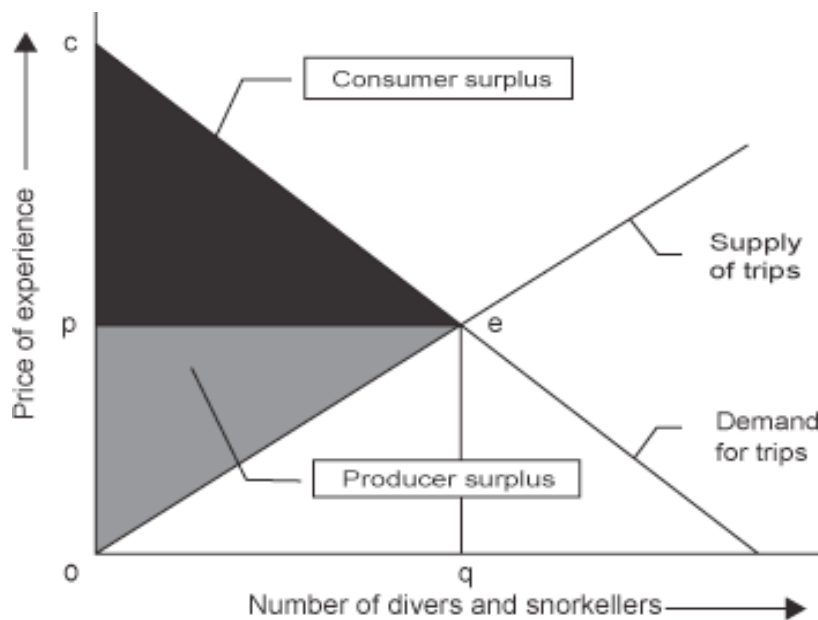


Fig. 4. Hypothetical consumer and producer surpluses associated with diving and snorkeling on a coral reef. The surplus consumers enjoy is the area under the demand curve above the equilibrium price up to the equilibrium number of divers or diving trips. The surplus producers enjoy is the area above the supply curve up to the equilibrium price and the equilibrium number of consumers. Producers may include tourism-related businesses or management authorities charging divers an entrance fee. Adapted from Cesar and van Beukering (2004).

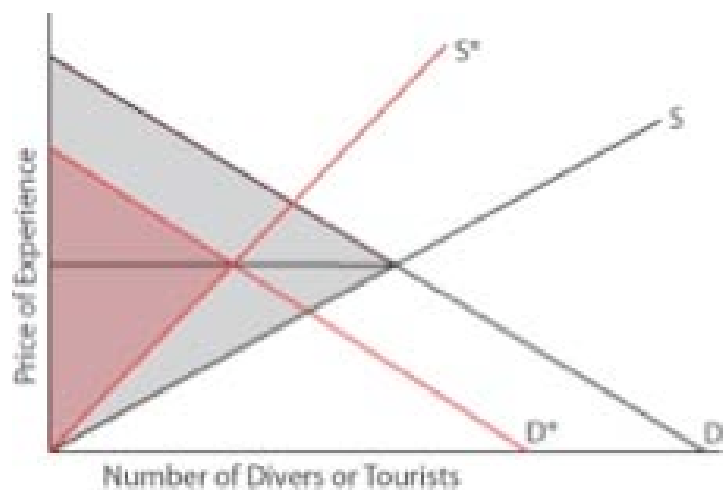


Fig. 5. The potential welfare impacts of a decrease in reef area, percent coral cover, or other ecological attributes that reduce the ability of a reef to supply ecological services and/or reduces the desirability of the services provided. The net social surplus (shaded area) combines consumer and producer surpluses, both of which are reduced by an inward shift of either the demand or the supply curve, or both.

Location	Type of user	Ecosystem good	Mean willingness to pay per visit	Total economic value	Type
Phi Phi, Thailand	Domestic	Biodiversity	\$7.17	\$147,000	Consumer surplus
Phi Phi, Thailand	International	Biodiversity	\$7.15	\$1.2 million	Consumer surplus
Anilao, Philippines	residents + non-residents	Tourism (diving)	\$3.70	\$95,000-\$116,000	Fee revenue
Mactan Island, Philippines	residents + non-residents	Tourism (diving)	\$5.50	\$850,000-\$1.0 million	Fee revenue
Panglao, Philippines	residents + non-residents	Tourism (diving)	\$3.40	\$3,500-\$5,300	Fee revenue
Bonaire	All visitors	Tourism (diving)	\$27.40	\$325,000	Consumer surplus
Hon Mun, Vietnam	Domestic	Tourism (diving)	\$3.10	\$128,245	Consumer surplus
Hon Mun, Vietnam	International	Tourism (diving)	\$3.90	\$114,945	Consumer surplus
MPAs in Florida, USA	All visitors	Tourism (diving)	\$25	\$93.0 million	Fee revenue
Buccoo Reef Park, Tobago	All visitors	Tourism (diving)	\$3.70-\$9.30	\$600,000-\$2.5 million	Consumer surplus
Seychelles Marine Parks	All visitors	Tourism (all)	\$12.20	\$88,000	Consumer surplus
Hanauma Bay, Hawaii	Snorkelers (all)	Tourism	\$2.69	\$125.2 million	Consumer surplus
Hanauma Bay, Hawaii	Divers (all)	Tourism	\$0.44	\$8.1 million	Consumer surplus
Pulau Payar Park, Malaysia	All visitors	Tourism	\$4.20	\$390,000	Fee revenue
Pulau Redang Park, Malaysia	All visitors	Tourism	\$3.00-\$4.40	\$373,900-\$545,100	Fee revenue

Table 5. Willingness of visitors to pay to gain access to various coral reef tourism destinations around the world. The economic value accruing from each user group's willingness to pay is also shown. Data were summarized from Conservation International (2008).

For many environmental services that consumers do not directly pay for, the equilibrium market price is zero, so the expressed willingness to pay to preserve these services gives a reasonable estimation of the consumer surplus derived from them. In the alternative, surveys of consumers' willingness to pay can be used to set appropriate entrance fees for marine parks and protected areas where extractive activities on reefs are disallowed. These fees can then be used to cover management, monitoring, and enforcement costs. It should be noted that individuals' responses to contingent valuation surveys may vary according to numerous socioeconomic factors, and these should be considered when extrapolating from a sample to a larger population of users (Seenprachawong 2004).

As an alternative to contingent valuation, the travel cost method considers the costs that users bear in order to gain access to ecosystem services, such as the costs of traveling to a destination, as an indication of the minimum value of those services (Seenprachawong 2004). If a demand function can be derived for a typical individual user based on varying levels of consumption (i.e. variable numbers of visits to a tourist destination) under different cost scenarios, then individual consumer surpluses can be aggregated across all users to estimate the immediate value of a particular ecosystem service. Table 5 summarizes the results of contingent valuation and travel cost studies that examined the willingness of stakeholders to pay in order to preserve the ecosystem services they obtained from coral reef systems.

Once basic data on consumer preferences and annual surpluses is available, ecological economists can move beyond quantifying the immediate benefits flowing from ecosystem services and begin to value future benefit streams by integrating them over time in terms of their equivalent net present value. This long-term valuation approach is critical when weighing the economic benefits realized through development or exploitation practices that may degrade ecosystems as against the long-run economic costs of such short-term overexploitation. In all such cases, different time horizons must be adjusted for to enable meaningful comparisons among alternative economic scenarios, hence the concept of net present value. When estimating the net present value (NPV) of any ecosystem, two parameters become critical: first, the term or finite time horizon over which benefits will be integrated; second, the discount rate applied over that term. NPV calculations are especially sensitive to the discount rate used. This parameter reflects the opportunity cost of an investment (in this case, forgoing the more immediate benefits of environmentally destructive economic activity in order to preserve ecosystem services) in terms of the interest rate that could be earned instead on an alternative investment over the time horizon considered. Formally, the net present value of an asset that pays benefits into the future can be stated as

net present value = $\sum_{i=0}^T \frac{\text{benefit}_i - \text{cost}_i}{(1 + \text{discount rate})^i}$ where T is the time horizon of discounting (Cesar and van Beukering 2004). Table 6 gives a sample of net present value estimates of the ecological services provided by various coral reef ecosystems throughout the world.

Location	Ecosystem good	Net Present Value	Discount Rate	Period
Portland Bight Protected Area, Jamaica	Tourism	\$11.0 million	10%	25 years
	Fisheries	\$19.0 million		
	Carbon sequestration	\$4.0 million		
	Coastal protection	\$366,000		
	Total	\$40.8-52.6 million		
Montego Bay, Jamaica	Tourism	\$315.0 million	15%	Indefinite
	Fisheries	\$1.3 million		
	Coastal protection	\$65 million		
	Biodiversity	\$19.6 million		
	Total	\$400 million		
Wakatobi National Park, Indonesia	Fisheries	\$2.2 million	10%	20 years
	Tourism	\$286,000		
	Total	\$2.6 million		
Bohol Marine Triangle, Philippines	Tourism	\$5,077,600	10%	10 years
	Fisheries	\$4,500,600		
	Total	\$11.54 million		
Bonaire	Tourism	\$180.0 million	10%	20 years
Bucco Reef Marine Park, Tobago	Tourism	\$9.1-\$18.7 million	10%	10 years
Leuser National Park, Indonesia	Total value	\$7.0-\$9.5 billion	4%	30 years
Surat Thani, Thailand	Total value	\$60,400	6%	30 years
Ream National Park, Cambodia	Total value	\$11.9 million	10%	20 years
Hawaiian Islands	Total value	\$10.0 billion	3%	50 years
Taka Bone Rate MPA, Indonesia	Total value	\$3.5-5.0 million	10%	25 years
South China Sea basin, Philippines	Total value	\$449 million	10%	20 years

Table 6. Net present value calculations associated with the ecological goods and services provided by various coral reef ecosystems. Data were summarized from Conservation International (2008).

Other more exotic methods also exist in ecological economics. For example, choice experiments can be used to examine how the willingness of individuals to pay for maintenance of ecosystem services changes according to the use to which those services will be put (Barbier 2007). The economics costs of replacing lost ecosystem services with equivalent artificial substitutes, such as replacing the coastal protection function of reefs with sea walls, shoreline buffers, and beach replenishment also can serve as a method of estimating their value. Ecological goods and services can also be included in models of production functions alongside conventional economic factors of production such as labor. In this latter case, ecosystem services are considered to support or make more productive other economic activities whose values are measurable directly. Input-output matrices incorporating ecological commodities can be used to describe the production process (Miller and Blair 1985).

Gustavson, Lonergan, and Ruitenbeek (2002) propose an Index of Captured Ecosystem Value as an alternative to market-based measures of the value of ecological services. Derived from information theory, the index utilizes the number of trophic links between individual pairs of species that are collectively involved in producing or sustaining a harvested natural resource. The authors argue that market prices do not reflect the actual amount of “ecosystem information” (analogous to natural capital) that goes into producing various commodities, using coral reef fisheries as an example. Different fishing technologies capture different amounts of ecosystem information or value.

Ruitenbeek et al. (1999) argue that certain conventional economic assumptions can lead to suboptimal policies. Conventional cost-benefit calculations conceptualize management actions intended to reduce environmental impacts as a series of cumulative, stepwise environmental benefits with steadily increasing implementation costs. These costs and benefits can be valued independently from each other, and management steps are to be taken in monotonic sequence up to some level of acceptable cost. However, because coral reefs are complex systems, these authors contend that management interventions act in non-monotonic ways to produce complex dose-response functions that do not align with the classical cost-benefit model. Nevertheless, rigorous tools for cost-benefit analysis are necessary, so in place of the classical model they suggest an approach based on fuzzy sets to capture these complex dose-response functions. The authors develop a model and apply it to economic and investment policies for Montego Bay, Jamaica involving eight possible management measures. Their results suggest that while a 20 percent improvement in coral abundance over a “base case” scenario would be possible for a cost of \$153.4 million over 25 years by taking all eight actions, a 10 percent improvement would be possible at a cost of only \$12 million over the same period with only three actions—a possibility that conventional cost-benefit modeling would not have detected.

Various criticisms have been leveled against the conventional methods of ecological economics, revealing both limitations and areas for future research. In a commentary on Costanza’s 2007 paper in *Nature*, Serafy (1998) outlines several of these. First and most significantly, the methods used to value ecosystem services pose a significant danger of “double counting” when the values of different services are tallied together. An ecological input already “counted” according to its contribution to one type of ecosystem service may not subsequently be available to be counted toward provision of another service. In addition, aggregating the values of many services in order to inform policy tends to produce values with very broad ranges, unavoidably

detracting from their worth. Third, it is often difficult to distinguish “functions” from “services” in deciding what should be valued.

Spash (2002) criticizes contingent valuation by suggesting that the surveys it relies on are likely to “form” as well as to “inform” the stated preferences they elicit, in effect biasing the results by virtue of the very techniques used to obtain them. For individuals with strong preexisting conservation convictions, the specific information and “if-then” scenarios contained in contingent valuation surveys may inflate the stated willingness to pay above expected pre-survey levels, thereby introducing a systematic bias into the sample. At the same time, the same information may also change, or help “form,” the stated positions of individuals without strong preexisting convictions, introducing a second type of bias in the fraction of respondents who express a willingness to pay. Both these effects were observed to be highly significant in two studies (one in Jamaica, one in Curacao) that specifically examined the role of contingent valuation surveys in modifying respondents’ attitudes toward coral reef ecosystem protection.

In spite of all these caveats and alternative approaches, Barbier (2003) defends ecological economics, arguing that it has an integral role to play in sustainable development, particularly where poverty is a constant problem. If development is to proceed in a way that meets the needs of the present without compromising the ability of future generations to meet their own needs, a portfolio of economic assets must be actively managed and enhanced over time. The goal of ecosystem-based management is also served by quantifying the functions within an ecosystem, including their values to humans.

Applying ecological economics to reef ecosystems: Tourism and recreation

The spectacular biodiversity of coral reefs draws many divers and snorklers to destinations where reefs can be found. However, it is important to understand the extent to which the ecological health and condition of reefs actually influences tourists’ behavior and preferences, thereby dictating the value of these ecosystems as recreational attractions. A number of studies have used contingent valuation to shed light on this problem. Wielgus et al. (2003) found that divers at Israel’s Eilat Coral Beach Nature Reserve were willing to pay an additional \$2.60 per dive for each additional unit of a biological index that was a composite of (1) the density of fishes and corals per square meter of reef and (2) the genus richness of the reef. Visibility also elicited a positive willingness to pay of \$1.20 per additional meter. In this study, three sites were selected and ranked as either high, low, or medium in quality according to the value of the biological index for each. These sites were videotaped, and the tapes shown to a sample of divers at the reserve. In addition, different levels of visibility were also videotaped. From these alternatives, the authors identify three scenarios offering divers different levels of surplus. A 25 percent increase in both the biological index and visibility nets a \$600,519 consumer surplus, a 25 percent increase in the index and a 50 percent increase in visibility nets a \$1,331,604 surplus, and restoration of reefs to a “pre-damage” level of quality using 1963 as a baseline nets a surplus of \$2,856,463.

A very similar study was conducted in Bonaire by Parsons and Thur (2008) using the criteria of visibility, species diversity, and percent coral cover. The authors used contingent valuation to estimate the willingness of U.S. visitors to pay various hypothetical diving fees given three other

diving options. Various survey respondents were told that they could pay a dive tag price ranging from \$50 to \$250 and continue diving at Bonaire, or else choose to dive at a different location whose quality was either “good,” “medium,” or “poor” relative to Bonaire. Based on the results, table 7 shows the alternative scenarios and the value that would be lost, assuming quality at Bonaire were to decline to each of the three poorer levels. Estimations of the total asset value lost assumed a 3 percent discount rate and either a constant number of users or a 2 percent annual rate of growth in the number of divers visiting Bonaire.

Attribute	Level of environmental quality			
	Poor	Medium	Good	Bonaire
Coral cover	5%	20%	30%	35%
Species diversity	50 fish 10 corals	125 fish 25 corals	225 fish 40 corals	300 fish 45 corals
Visibility	20 feet	50 feet	75 feet	100 feet
Associated loss per user	\$192	\$142	\$45	-
Total asset value lost (constant user base)	\$179.0 million	\$132.0 million	\$45 million	-
Total asset value lost (2% annual growth in users)	\$538.0 million	\$398.0 million	\$126.0 million	-

Table 7. Hypothetical scenarios of environmental degradation in Bonaire and the resulting welfare losses, as estimated by Parsons and Thur (2008) using contingent valuation methods.

Most studies of the economic value of reefs with respect to tourism are conducted to evaluate the economic benefits of protected areas such as those in Bonaire. However, Pendleton (1995) criticized studies like the ones above for failing to distinguish between the value of a recreational activity or resource and the value of the protection it receives *per se*. According to this line of argument, the methodology used in such studies implicitly assumes that the entire benefit stream would immediately be lost without the protection. Instead, the value of a protected area is not simply users’ willingness to pay, but the difference between the net economic benefits with and without protection, i.e. the avoided losses in value that result from protection, minus the costs of that protection. In essence, valuing protected areas *per se* requires estimating the shift in the recreation demand curve that would otherwise occur. Applying this approach to Bonaire, the author estimates that net annual benefits from diving tourism in 1991 accruing locally to Bonaire were \$7,924,000 to \$8,799,000, with a total consumer surplus of \$19,184,000. The difference between these results and those of another study by Dixon et al. (1993) was attributed to the later study’s approximate inclusion of shadow prices in the calculation of net revenues arising from protection. In any case, Bonaire Marine Park was still found to be economically justified.

However, not all diving tourist destinations necessarily rely on healthy reefs. Carr and Heyman (2009) demonstrate this fact by contrasting tourism in Jamaica with tourism in Antigua and Barbuda. They characterize Jamaica as a “discount destination” that has marketed itself effectively to large numbers of tourists in spite of ecological degradation. From 1977 to 1993, live coral cover in Jamaica fell from 52 percent to 3 percent. At the same time, 66 percent of tourists to Jamaica lacked an understanding of “biodiversity” as applied to coral reefs, yet the island relies on tourism for 31 percent of its GDP. By contrast, Antigua and Barbuda instead markets itself as a higher-end destination catering to relatively fewer travelers who tend to be more interested in diving on healthy reefs. Tourism directly accounts for 21 percent of its GDP, and 75 percent when tourism-related industries are also considered. However, with signs of declining finfish stocks, these islands may be in danger of following the “Jamaica path.”

Brander, van Beukering, and Cesar (2007) performed a meta-analysis of coral reef recreation literature and concluded that greater standardization and better reporting of methodologies are needed in the future. Out of 166 studies, only 52 contained adequate information on the characteristics of the study area, the sample size, and the frequency of non-responses in surveys to enable comparison via meta-analysis. Furthermore, a cross-validation analysis of the data suggested that “value-transfer,” or the extrapolation of valuation estimates to sites not directly evaluated, tends to be more error-prone than most policy-making contexts would find acceptable. Yet facilitation of value-transfer is a major objective of ecological economic valuation studies. With regard to those studies among which comparisons were possible, the meta-analysis showed that the area of dive sites was positively related to recreational value per user, while the number of visitors showed a negative relationship. Divers are clearly sensitive to crowding and to the scope of reef areas. Contingent valuation tended to produce lower value estimates than other methods. Strong effects of both authorship and methodology were observed. Interestingly, biodiversity did not significantly explain variation in values.

Applying ecological economics to reef ecosystems: Fisheries

Fishing pressure on coral reefs has risen over time, sometimes dramatically. Figure 6 gives trends in both the number of fishermen and in landings per km² of coral reef averaged over 16 countries for the years 1970 to 2000 (data from Sadovy 2005). Figures 7 and 8 provide trends for individual countries. Birkeland (1997) notes that world coral reefs can sustain an annual yield of perhaps 20-35 million metric tons. However, yield per unit of gross primary productivity for reef systems is 10 to 60 times less than that for the Peruvian upwelling system. Still, Moberg and Folke (1999) note that the catch from reef areas constitutes around 10 percent of global fish consumption and up to 25% of fishery catch in developing regions. Souter (2000) observes that reef fisheries provide vital protein to a billion people in Asia. Globally, coral reefs may be able to provide a maximum sustainable yield of 1.5 million tons of fish per year, or 0.2 kg of seafood per capita per year (Hulm and Pemetta 1993). Tables 4 and 6 above provide various estimates of the value of coral reef fisheries around the world.

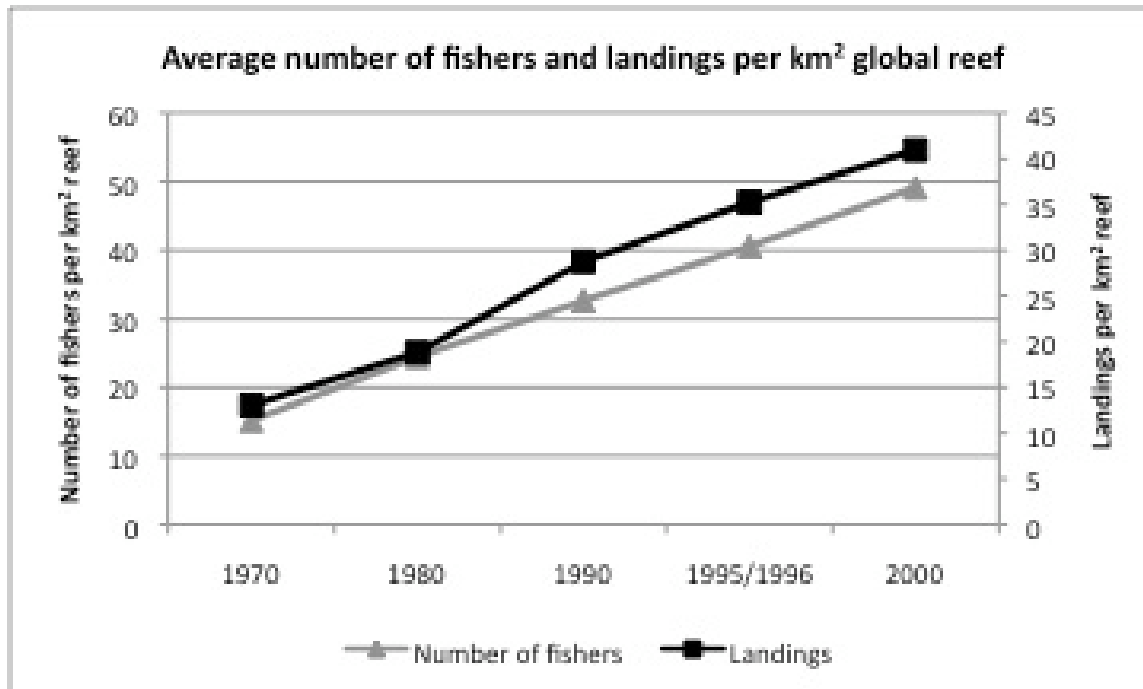


Fig. 6. Trends in the mean number of fishers and mean landings (in metric tons) per square kilometer of reef seen in a global survey encompassing the coral reefs of 16 countries. Data were collected for the years 1970, 1980, 1990, 1995 or 1996, and 2000. Countries in the survey were: Aruba, Bahamas, Barbados, Fiji, Indonesia, Jamaica, Maldives, Martinique, New Caledonia, Papua New Guinea, Philippines, Puerto Rico, Samoa, Solomon Islands, St. Lucia, Tonga. Data were obtained from Sadovy (2005).

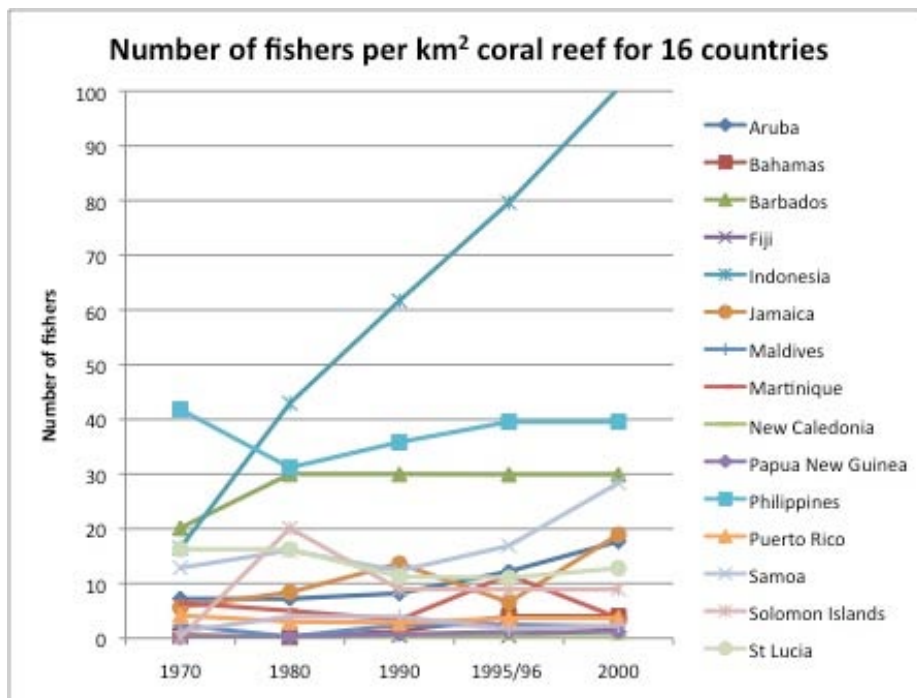


Fig. 7. Trends in the number of fishers per square kilometer of reef in each of the 16 countries surveyed by Sadovy (2005).

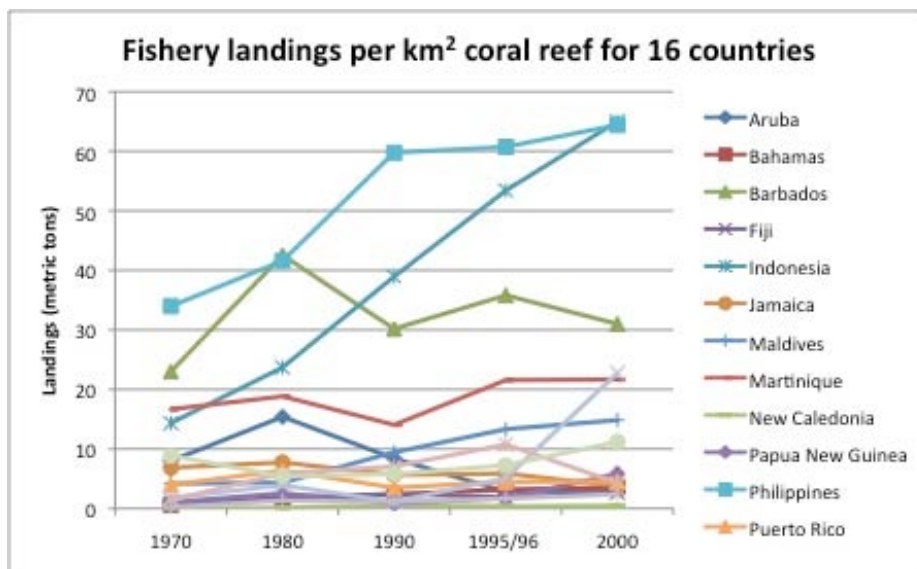


Fig. 8. Trends in fishery landings per square kilometer of reef in each of the 16 countries surveyed by Sadovy (2005).

Mangroves, which are often functionally interconnected with coral reefs (Mumby et al. 2004), have been shown to increase fishery yields in the Gulf of California by \$25,149 km⁻¹ (Aburto-Oropeza et al. 2008). The relationship tends to be proportional to the length of mangrove fringe, which acts as an estuarine nursery for harvested species. The value of this service over the six-year administrative timeframe set by the Mexican government is 200 times higher than the Mexican National Forest Service's official value of \$1,200 ha⁻¹, showing how undervalued

ecosystem services can be in some cases. Loss of one ha of these mangroves would lead to a loss of \$605,290 over 30 years with a 5 percent discount rate.

Barbier (2000) and Barbier and Strand (1998) address a few key theoretical issues involved in quantifying the economic value of ecosystems with regard to fishery production. Though applied to mangroves, their analysis readily extends to coral reefs as well. Specifically, the relevant economic model depends critically on whether the fishery is open-access or managed. Figure 9 describes the economic impact of a decline in coral cover as manifested in an open-access fishery. Under open-access conditions, entry into the fishery can continue until all economic rents are dissipated—that is, average costs would increase as catch per unit effort declined until the ex-vessel price of fish became equal to the average cost per unit catch. Consequently, producer surplus (i.e. that which accrues to fishers) is reduced to zero and only consumer surplus determines the value of the fishery. In this case, if the fish productivity of a reef is reduced by ecological degradation (due, for example, to increasing macroalgal dominance, loss of physical reef structure, or a reduction in fractional coral cover that reduces CPUE at all catch levels), the average cost curve for the fishery will shift upward. This is depicted as a shift from AC_1 to AC_2 in Figure 9. The consequent loss to consumer surplus will be the reduced area under the consumer demand curve at the new equilibrium price and level of catch, represented by the shaded area.

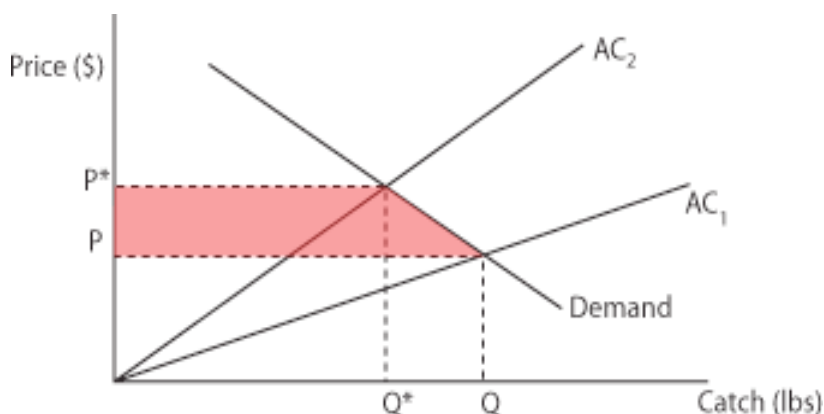


Fig. 9. The welfare impact of coral reef degradation upon an open-access fishery. Destruction of coral habitat leads to reduced fish productivity, thereby increasing the average cost function for the fishery from AC_1 to AC_2 . Consumer surplus, the integral of the difference between the market demand curve and the equilibrium price, is reduced by the amount represented by the shaded area as price rises from P to P^* . Adapted from Barbier (2000).

In an optimally managed fishery, the economic situation is different. Economic rents are maximized rather than dissipated, so that fishing effort equates marginal costs with consumer demand—the classic economic formula for profit maximization. The value of the fishery is therefore fully captured by producer surplus. In this situation, the relevant economic impact of a change in the productivity potential of a reef ecosystem with respect to fish lies in the resulting shift in the marginal, rather than the average, cost curve for the fishery. Marginal costs become steeper in a degraded ecosystem, shifting from MC_1 to MC_2 in Figure 10. Consequently, total economic welfare declines by the area of the shaded region. While few fisheries, and fewer still on coral reefs, could be described as “optimally managed,” many managed fisheries are likely to be hybrids of these two economic cases.

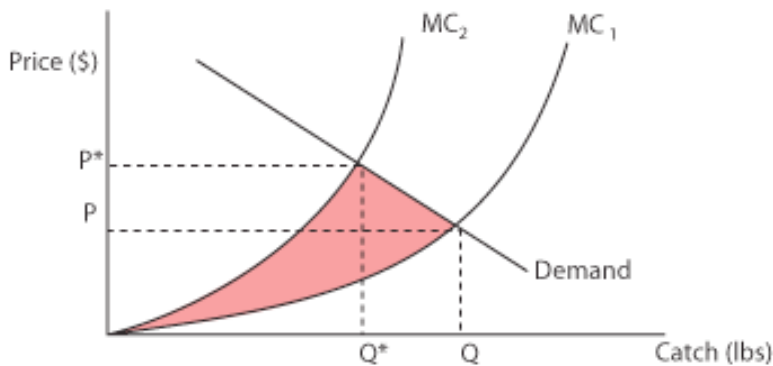


Fig. 10. The welfare impact of coral reef degradation upon an optimally managed fishery. Under optimal management, equilibrium catch is determined by the intersection of marginal cost with the demand curve. As habitat degradation reduces fishery productivity, marginal costs increase from MC_1 to MC_2 . Social surplus, the integrated difference between the market demand curve and the marginal cost curve up to the equilibrium price P , decreases by the amount represented by the shaded area as price rises from P to P^* . Adapted from Barbier (2000).

It is worth examining an interesting pattern found by Cinner et al. (2009) regarding the relationship between fish biomass and socioeconomic development in fishing communities. These authors found that fish biomass tended to be an inverted “U” shaped quadratic function of an index of community socioeconomic development (Figure 11). This pattern corresponds to the environmental Kuznets curve hypothesis, which states that ecological degradation initially increases with development and per capita wealth before eventually improving as affluence is increasingly attained. Similar relationships have appeared for deforestation, sulfur dioxide air pollution, and fecal coliform in rivers, among other parameters related to environmental quality (Shafik 1994). Various ideas have been advanced to explain this empirical relationship. Generally speaking, at low levels of development, little exploitation of the environment occurs. As development proceeds, it tends to occur at the expense of the environment. However, increasingly wealthy societies may be able to substitute more environmentally destructive techniques of production for less environmentally destructive ones. At the same time, the demand for a quality environment may increase as people are increasingly able to afford such a “luxury.” The composition of the economy could also change. In terms of reef fisheries, Cinner et al. (2009) suggest that reduced subsistence dependence on marine resources combined with increasing access to engines and spearguns leads to overexploitation at the intermediate stage of development. When high levels of development are attained, effective government, adoption of less damaging gear and fishing techniques, employment opportunities in non-extractive sectors, and an increase in non-extractive resource uses such as tourism contribute to improvements in fish biomass.

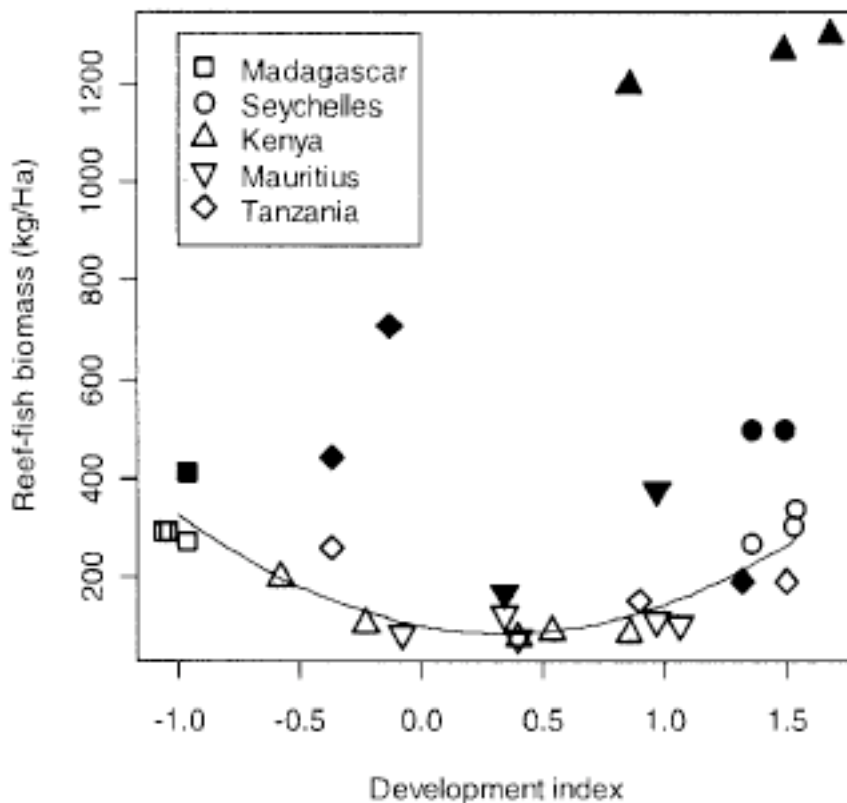


Fig. 11. The biomass of reef fish in protected sites and fished sites along a gradient of economic development. Protected sites: filled symbols. Unprotected sites: open symbols. The line represents a quadratic regression curve through the protected sites, suggestive of an “environmental Kuznets-curve” relationship between development and fish biomass on coral reefs.

Reproduced from Cinner et al. (2009).

Another possible explanation for the relationship the authors observed could be the decline in customary fisheries management institutions that often occurs as economic development initially proceeds (Cinner, Sutton and Bond 2007). Population growth, access to commercial markets, and the availability of more efficient fishing technology at intermediate levels of development stress and often undermine traditional forms of community-based common-property resource management such as periodic closures and locally restricted access, leading to overexploitation of fish stocks. At higher levels of income, efforts may be made to reinstitute similar institutions.

Applying ecological economics to reef ecosystems: Coastal protection

Regulating services provided by coral reefs include protection of coastline from storm surge and wave erosion and replenishment of beaches through production of sand. Mangroves, often found in association with reefs, stabilize sediments, reducing soil erosion and maintaining water quality (UNEP-WCMC 2006). White, Vogt and Arin (2000) estimated that Philippine coral reefs provided \$5000 to \$25,000 per km², while Costanza et al. (1997) estimated that the annual mean benefits of shoreline protection around the world could be as high as \$275,000 per km². In Sri Lanka, many beaches are particularly erosion-prone (UNEP-WCMC 2006), leading to a cost of \$1,230,000 to \$4,180,000 to replace the coastal protection function of degraded reefs with artificial structures. This unusually high value contrasts with that found in the Philippines, where shorelines are typically not as erosion-prone.

Cesar (1996) distinguishes three categories of Indonesian reefs in terms of the coastal protection value each offers. Reefs adjacent to sparsely populated agricultural areas typically provide \$829

per km by protecting coastal agricultural production from erosion. Reefs adjacent to densely populated areas can be worth \$50,000 per km based the cost of replacing housing and roads that would otherwise be lost to storm surges. Where tourism is important, reefs help maintain sandy beaches that would otherwise cost \$1 million per km to keep intact. In a similar classification scheme, Burke and Maidens (2004) relate the value of reef-related shoreline protection in the Caribbean to the level of shoreline development. Their classification is given in table 8 below.

Level of Shoreline Development	Definition of Development	Percent of Coastline	Value for shoreline protection services (\$ per km of coastline)	Total value (million \$ US)
Low	< 100 people within 5 km	29	2,000-20,000	10-30
Medium	100-600 people or a dive center within 5 km	27	30,000-60,000	120-150
High	> 600 people within 5 km	44	100,000-1,000,000	620-2000
TOTAL		100	2,000-1,000,000	750-2180

Table 8. Economic values of shoreline protection services offered by Caribbean reefs with respect to nearshore development intensity. Data from Burke and Maidens (2004).

However, much of the evidence attesting to the coastal protection value of reefs tends to be anecdotal. Areas of Orissa, India forested by mangroves suffered less damage during a 1999 cyclone than did unforested areas, and similar experiences have been reported in Vietnam (UNEP-WCMC 2006). Considerable dispute has taken place surrounding the role of reefs and mangroves in mitigating the effects of the 2003 Indian Ocean tsunami. At Hikkaduwa, Sri Lanka, reefs were in better condition than elsewhere, and waves were only 2-3 meters high, as compared with 10 meters where reefs were extensively damaged (UNEP-WCMC 2006).

Koch et al. (2009) found that the net present value of mangrove coastal protection services varied non-linearly with respect to a number of ecological and geographic factors. Values were variable over time according to tidal fluctuation on daily time scales, and on annual and interannual scales according to the density of mangroves and the biomass of accumulated detrital plant material. Similarly, variability in values was seen over space as a function of habitat quality, mangrove species assemblages and relative abundances, forested area, and latitude. The authors conclude that these variables should be incorporated into the planning process for mangrove restoration projects in order to achieve maximum benefits. Elaborating on this theme, Barbier et al. (2008) found that the aggregate value of 10 km² of mangroves in Thailand is maximized when 2 km² is converted to shrimp aquaculture and the rest left intact to provide coastal protection. This outcome contrasts with the “all or none” outcomes that obtain from linear assumptions about ecosystem value and provides a more equitable solution among stakeholders.

Applying ecological economics to reef ecosystems: Biodiversity and bioprospecting

The high levels of biodiversity in coral reefs likely hold many compounds with potential pharmaceutical or industrial applications. High taxonomic diversity translates to a high diversity of metabolites. 60 percent of anticancer and anti-infective drugs have been either derived from or modeled on natural products (Cragg et al. 1998). At the phylum level, diversity in coral reefs

is several times higher than in rainforests (Adey et al. 2000) and most coral reef species have not yet been identified (Reaka-Kudla 1997). Moreover, corals produce many secondary metabolites and chemical defenses that they use in competition for space on reefs (Fenical 1996), offering many potential opportunities for drug discovery. However, the rate of reef degradation is outstripping the rate at which species can be assayed for natural products of interest (Adey 2000). The large investment and lengthy development process for drugs also tend to create high financial risks that dampen exploration in this area. Nevertheless, the potential value of coral reef biodiversity to medicine may be high. Adey (2000) argues that aquaculture technologies exist which could permit mass culture of reef organisms for their secondary compounds without damaging reefs.

Ruitenbeek and Cartier (1999) constructed a model of hypothetical bioprospecting in Montego Bay, Jamaica to estimate the potential value of the site's pharmacological potential. Site-specific cost information was collected and combined with success rates and benefit values typical of other bioprospecting projects in the Caribbean. When valuing coral reefs for the pharmacological potential of their biodiversity, one critically important parameter is "ecosystem yield" as controlled by the species-area relationship and the possible sample yield from the reef. The species-area relationship exerts a controlling influence on the expected rates of success, with more specious areas more likely to yield successes as well as higher values. A second important parameter is rent distribution, a policy variable describing how benefits are distributed among parties involved in the enterprise. Controversy over rent distribution has led to the demise of other bioprospecting projects (Dalton 2000), and along with intellectual property concerns represents a significant institutional barrier to efforts of this kind. Thirdly, the extent of system complexity in the form of interdependence in discoveries and ecosystem yields must be considered in models.

The model of Ruitenbeek and Cartier (1999) placed bioprospecting values at \$2600 per sample with a typical success rate of 1 in 30,000 samples. Net values range from \$66 million to \$70 million depending on the amount of reef stress that occurs over a 16 year sampling program. This translates to values of \$530,000/ha or \$225,000/% coral abundance.

The imperative of ecological economics for coral reefs: Threats and challenges to reefs

Coral reefs have come under threat on multiple fronts, and many have already been significantly degraded. It is therefore imperative that an economic accounting be made of what is at risk, and what has already been lost. Overfishing on many Caribbean reefs has led to a phase shift in ecosystem state from coral-dominated to algal-dominated systems (Knowlton 1992). Global warming, combined with increasing frequency and intensity of climatic fluctuations, threatens corals worldwide with bleaching, as was experienced in 1998 during a particularly strong el Niño when a global mass bleaching event occurred (Souter and Linden 2000). White band, black band, and other coral diseases have also increased, especially in Caribbean corals (Harvell et al. 1999). Increased sedimentation arising from land-use practices also represents a significant threat (Cortes and Risk 1985). Cyanide and blast fishing add yet another source of disturbance (Pet-Soede, Cesar, and Pet 1999). Figure 12 shows the percentages of coral reefs in four threat categories as estimated by Wilkinson (2000).

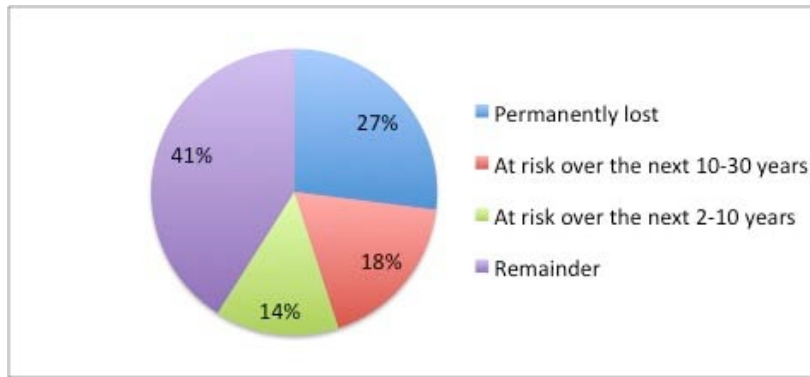


Fig. 12. Percentage of world coral reefs in each threat category, as estimated by Wilkinson (2000).

Warren-Rhodes, Sadovy and Cesar (2003) illustrate the unsustainability of many coral reef fisheries using the concept of marine ecological footprints (MEFs). An MEF refers to the marine ecosystem area required to sustainably support the consumption habits of a population of users. This area is related to the biocapacity or productivity of the ecosystem, or the amount of productive ecosystem area available per capita. A reef fish fishery is unsustainable if the MEF of its users exceeds what its biocapacity can sustain. Taking the assumption that per capita coral reef seafood consumption is 10 percent of total seafood consumption in Southeast Asian economies, and 25 percent in the Indo-Pacific, these authors calculate that Indo-Pacific MEFs exceed regional biocapacity by more than 2.5 times. In a similar analysis, Newton et al. (2007) conclude that an additional 75,031 km² of reef area would be needed to supply sustainable catches at current levels. They note that this area is 2.7 times the size of the Great Barrier Reef. The result of this overfishing through time has been the successive collapse of more and more reef taxa, both fish and invertebrates. Worm et al. (2006) predicted the global collapse of all currently fished taxa by 2048 based on historic trends, with 38 percent of all taxa currently collapsed. This trend toward collapse has occurred in both species-poor ecosystems and species-rich ecosystems such as coral reefs (Figure 13a), although declines have been steeper in the former. These collapses have serious implications for ecosystem resilience and redundancy, and for the maintenance of ecosystem services.

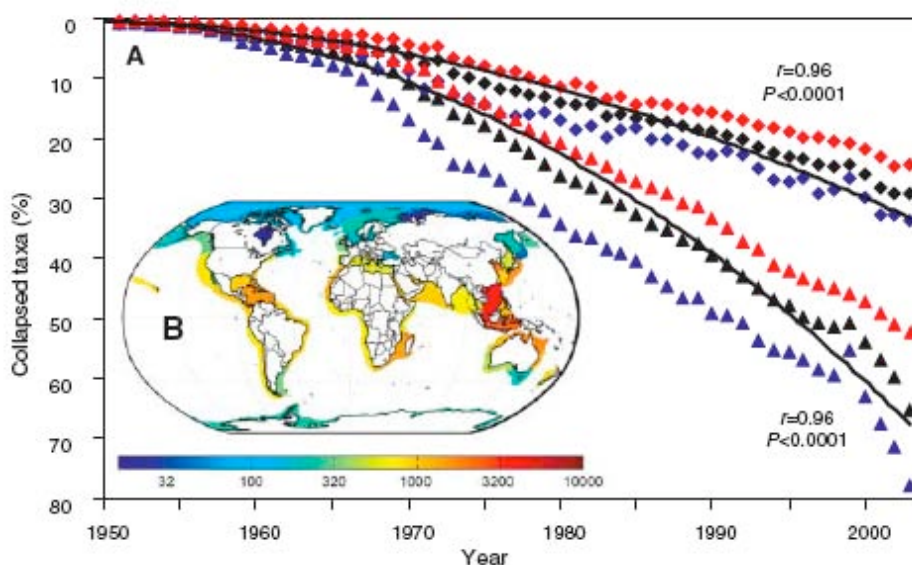


Fig. 13. (A) Global trajectories of collapsed taxa in large marine ecosystems as defined by Worm et al. (2006). Diamonds represent collapses by year, triangles cumulative collapses. Data are shown for all regions (black), species-poor regions (blue) and species-rich regions (red). (B) Species richness of large marine ecosystems, showing high biodiversity in tropical reef regions.

Reproduced from Worm et al. (2006).

A particularly serious threat to reefs may be ocean acidification due to increased atmospheric carbon dioxide concentrations. Brander et al. (2009) estimated the potential economic impact of ocean acidification on coral reefs by combining a meta-analysis of valuation studies with projections based on IPCC scenarios and a logistic model of reef decline with increasing ocean acidity. The authors assumed that the equation $R_t = \frac{\gamma A_t}{1 + \gamma A_t}$ describes the change in reef cover with ocean acidity, with R being the change in reef area since pre-industrial times, A is the change in ocean acidity (in pH) over the same period and γ is a parameter describing the impact of acidification on reefs. This equation was combined with regional reef values per unit area derived from meta-regression of 45 valuation studies to predict the economic losses associated with acidification. The equation was parameterized using the four IPCC SRES scenarios, yielding projected losses under each scenario. Figure 14 illustrates the economic damage expected to occur per year under each IPCC scenario as a result of decreases in reef area due to ocean acidification.

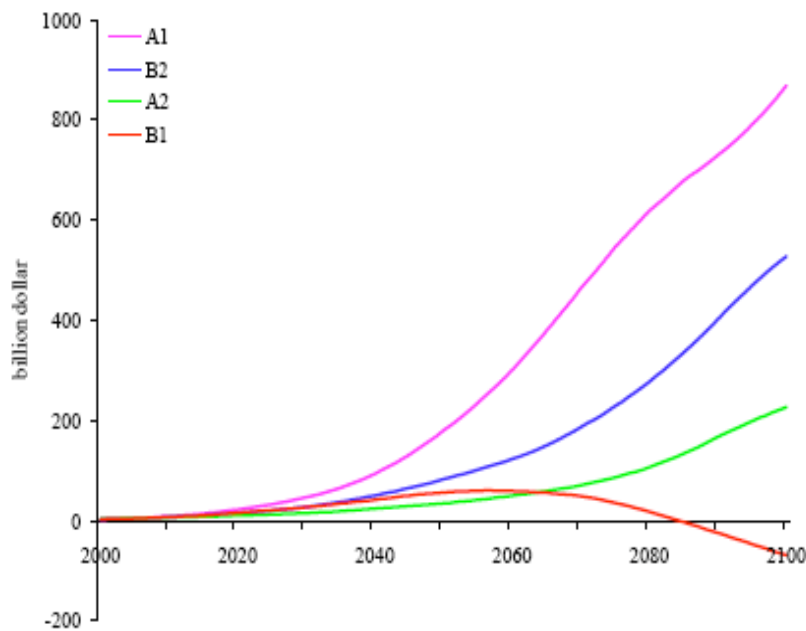


Fig. 14. The annual economic damages of ocean-acidification-induced coral reef area loss, as projected for the four IPCC future scenarios. A1: Globalization, with emphasis on human wealth; economic convergence among regions. A2: Regionalization, with emphasis on human wealth; technological change slower and more fragmented. B1: Globalization, with emphasis on sustainability and equity; reductions in material intensity and rapid change toward a service economy. B2: Regionalization, with emphasis on sustainability and equity; intermediate levels of economic development.

Reproduced from Brander et al. (2009).

By examining *ReefBase/RAMP* data, Pollnac et al. (2000) found that the healthiest coral reefs in the Philippines were characterized by higher fisher densities and greater recent increases in population density. These results seemed initially surprising given that overfishing and high terrestrial inputs of sediment and nutrients are primary causes of reef health decline. However, the authors explain that higher populations of resource users tend to be found where resources are more plentiful at any one time and move from resource-poor to resource-rich areas. Seen in this light, the empirical relationship the authors found only underscores the need for economically informed, sustainable management of fragile coral reef resources.

If the goods services provided by reef ecosystems are to be sustained, they must be valued, both aesthetically and economically. Collaboration among economists and ecologists is essential to this task, and the responsibility to manage these systems sustainably extends to all stakeholders. Even those who benefit only indirectly from reef ecosystems have a stake in their conservation. Ecological economics offers a powerful tool for bringing together the often-conflicting goals of economic development and conservation. However, if this promise is to be realized, it is a field that must be pursued with urgency given the current coral crisis, and its recommendations must inform policy at all levels wherever coral reefs are concerned.

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Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Windsock (Control)						
<i>Acanthurus bahianus</i>	7.19	16.32	26.72	3.30	2981.30	6588.09
<i>Acanthurus chirurgus</i>	1.35	3.83	23.00	0.00	354.56	1002.83
<i>Acanthurus coeruleus</i>	1.67	2.31	24.25	1.68	1346.04	2196.56
<i>Microspathodon chrysurus</i>	0.94	1.13	15.00	0.00	94.42	113.83
<i>Scarus iserti</i>	1.56	1.75	21.78	6.62	266.88	347.26
<i>Scarus taeniopterus</i>	1.67	1.09	21.93	5.35	305.58	358.83
<i>Scarus vetula</i>	1.46	1.24	42.89	10.78	2378.97	1744.29
<i>Sparisoma aurofrenatum</i>	0.94	1.13	22.17	6.14	190.11	241.23
<i>Sparisoma chrysotermum</i>	0.10	0.29	34.00	0.00	73.98	209.26
<i>Sparisoma rubripinne</i>	0.63	1.46	30.30	3.25	397.16	988.08
<i>Sparisoma viride</i>	1.56	1.21	33.50	4.69	1183.09	938.33
<i>Stegastes diencaeus</i>	4.48	3.70	9.60	1.01	130.90	112.61
<i>Stegastes leucostictus</i>	1.88	2.17	8.80	0.98	48.08	63.88
<i>Stegastes planifrons</i>	0.73	0.94	8.58	2.59	12.36	15.78
Acanthuridae	10.21	9.73	25.49	2.90	4681.89	4025.93
Pomacentridae	8.02	2.86	10.50	2.88	285.77	94.11
Scaridae	7.92	1.30	29.36	10.68	4795.78	1126.98
Denuding ²	11.15	9.54	22.57	5.41	4776.31	3527.66
Excavating ³	7.92	1.30	29.36	10.68	4795.78	1126.98
Non-denuding ⁴	7.08	2.90	9.10	1.49	191.35	88.03
Algal removers ⁵	19.06	5.46	26.96	9.68	9572.1	2065.04
Windsock Total	26.15	4.96	22.70	11.42	9763.44	2065.04

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Eighteenth Palm (F.P.A.)						
<i>Acanthurus bahianus</i>	2.50	1.99	28.68	2.39	1290.44	961.98
<i>Acanthurus chirurgus</i>	0	0			0.00	0
<i>Acanthurus coeruleus</i>	1.56	1.51	25.00	0.00	1544.31	1488.90
<i>Microspathodon chrysurus</i>	0.83	1.09	14.80	0.45	81.92	110.04
<i>Scarus iserti</i>	3.85	2.59	18.76	4.48	585.76	502.69
<i>Scarus taeniopterus</i>	2.92	0.77	20.25	2.53	379.51	180.34
<i>Scarus vetula</i>	1.88	1.16	32.80	4.82	1367.94	1116.45
<i>Sparisoma aurofrenatum</i>	1.56	1.21	20.85	5.36	322.61	332.55
<i>Sparisoma chrysopteron</i>	0.42	0.63	26.33	6.81	153.46	249.52
<i>Sparisoma rubripinne</i>	0	0			0.00	0
<i>Sparisoma viride</i>	1.25	1.09	30.25	2.40	757.78	694.87
<i>Stegastes diencaeus</i>	4.38	1.82	10.43	1.06	145.31	68.29
<i>Stegastes leucostictus</i>	1.67	1.26	9.72	2.24	44.33	40.56
<i>Stegastes planifrons</i>	0.10	0.29	10.00	0.00	2.84	8.03
Acanthuridae	4.06	1.77	27.15	2.59	2834.75	1197.24
Pomacentridae	6.98	2.15	11.29	2.49	274.40	83.70
Scaridae	11.88	1.74	24.62	7.00	3567.06	677.59
Denuding ²	4.90	1.74	23.51	6.19	2916.68	1100.16
Excavating ³	11.88	1.74	24.62	7.00	3567.06	677.59
Non-denuding ⁴	6.15	2.18	10.12	1.58	192.48	75.33
Algal removers ⁵	16.77	1.74	24.28	6.73	6483.73	856.05
Eighteenth Palm Total	22.92	1.85	21.29	8.36	6676.21	788.94

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	Mean	SD	mean	SD	mean	SD
Calabas Reef (F.P.A.)						
<i>Acanthurus bahianus</i>	1.56	2.01	22.26	5.91	324.56	386.94
<i>Acanthurus chirurgus</i>	0.21	0.39	25.00	7.07	86.37	196.11
<i>Acanthurus coeruleus</i>	0.73	1.44	15.67	7.23	185.49	496.37
<i>Microspathodon chrysurus</i>	0.00	0.00			0.00	0.00
<i>Scarus iserti</i>	3.54	2.74	21.15	5.08	765.37	518.74
<i>Scarus taeniopterus</i>	3.02	2.04	25.38	5.69	600.66	305.44
<i>Scarus vetula</i>	1.15	1.33	35.77	4.08	1108.34	1443.68
<i>Sparisoma aurofrenatum</i>	1.04	1.46	25.88	4.73	441.45	679.55
<i>Sparisoma chrysopterus</i>	0.10	0.29	25.00	0.00	27.91	78.93
<i>Sparisoma rubripinne</i>	0.31	0.62	24.50	6.36	114.34	275.95
<i>Sparisoma viride</i>	1.04	0.86	27.28	10.48	659.49	779.07
<i>Stegastes diencaeus</i>	4.17	3.09	10.79	1.40	136.45	88.81
<i>Stegastes leucostictus</i>	0.31	0.43	13.00	1.73	19.15	28.09
<i>Stegastes planifrons</i>	0.21	0.39	8.50	3.54	4.39	10.45
Acanthuridae	2.50	1.49	20.96	6.75	596.42	377.12
Pomacentridae	4.69	2.52	10.94	4.18	159.99	72.36
Scaridae	10.21	1.91	25.96	7.29	3717.56	762.04
Denuding ²	2.50	1.47	20.96	6.75	596.42	336.40
Excavating ³	10.21	1.91	25.96	7.29	3717.56	762.04
Non-denuding ⁴	4.69	2.56	10.94	2.18	159.99	79.47
Algal removers ⁵	12.71	1.81	24.71	7.42	4313.99	664.52
Calabas Reef Total	17.40	1.99	21.57	8.79	4473.98	605.74

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Front Porch (F.P.A.)						
<i>Acanthurus bahianus</i>	0.83	0.63	29.83	0.41	478.69	354.31
<i>Acanthurus chirurgus</i>	0.00	0.00			0.00	0.00
<i>Acanthurus coeruleus</i>	0.73	0.94	25.00	0.00	720.68	927.40
<i>Microspathodon chrysurus</i>	0.42	0.45	15.00	0.00	41.97	44.86
<i>Scarus iserti</i>	1.67	1.89	19.74	3.04	318.78	423.17
<i>Scarus taeniopterus</i>	2.50	1.00	20.25	1.54	300.71	148.09
<i>Scarus vetula</i>	0.83	0.89	25.80	8.17	311.13	342.71
<i>Sparisoma aurofrenatum</i>	1.67	1.41	21.80	2.67	317.84	282.87
<i>Sparisoma chrysopteron</i>	0	0			0.00	0
<i>Sparisoma rubripinne</i>	0	0			0.00	0
<i>Sparisoma viride</i>	2.19	2.18	32.60	4.31	1357.38	1062.15
<i>Stegastes diencaeus</i>	1.88	1.32	9.58	1.17	49.40	37.98
<i>Stegastes leucostictus</i>	0.21	0.59	7.00	0.00	2.18	6.15
<i>Stegastes planifrons</i>	0	0			0.00	0
Acanthuridae	1.56	0.77	27.90	2.51	1199.37	627.33
Pomacentridae	2.50	1.28	11.32	3.13	93.54	36.19
Scaridae	8.85	1.58	23.74	6.23	2605.85	614.74
Denuding ²	1.98	0.75	24.21	6.40	1241.34	563.22
Excavating ³	8.85	1.58	23.74	6.23	2605.85	614.74
Non-denuding ⁴	2.08	1.31	9.21	1.44	51.58	31.51
Algal removers ⁵	10.83	1.46	23.89	6.22	3847.19	594.00
Front Porch Total	12.92	1.43	21.91	7.69	3898.77	543.64

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Reef Scientifico (F.P.A.)						
<i>Acanthurus bahianus</i>	0.94	1.29	29.38	0.95	528.58	738.72
<i>Acanthurus chirurgus</i>	0.52	1.17	27.88	1.24	292.99	686.65
<i>Acanthurus coeruleus</i>	0.63	1.16	25.00	0.00	617.73	1143.80
<i>Microspathodon chrysurus</i>	0.42	0.63	15.00	0.00	41.97	63.45
<i>Scarus iserti</i>	0.73	0.94	21.58	6.29	121.46	162.04
<i>Scarus taeniopterus</i>	4.58	3.15	21.76	5.43	625.39	349.84
<i>Scarus vetula</i>	1.35	1.40	31.40	3.21	935.58	1181.53
<i>Sparisoma aurofrenatum</i>	1.35	1.09	21.54	3.49	325.31	469.31
<i>Sparisoma chrysotermum</i>	0.10	0.29	30.00	0.00	49.75	140.71
<i>Sparisoma rubripinne</i>	0	0			0.00	0
<i>Sparisoma viride</i>	1.56	0.53	28.81	4.85	783.93	349.08
<i>Stegastes diencaeus</i>	3.23	1.37	9.46	1.58	95.29	68.04
<i>Stegastes leucostictus</i>	0.52	0.62	10.25	0.96	14.93	16.30
<i>Stegastes planifrons</i>	0.83	1.34	6.92	1.01	7.56	11.98
Acanthuridae	2.08	1.17	27.58	2.16	1439.29	852.84
Pomacentridae	5.00	1.64	10.14	2.74	159.75	57.19
Scaridae	9.69	2.04	25.11	6.03	2841.41	605.30
Denuding ²	2.50	1.15	24.44	5.98	1481.26	760.03
Excavating ³	9.69	2.04	25.11	6.03	2841.41	605.30
Non-denuding ⁴	4.58	1.66	9.16	1.75	117.79	56.40
Algal removers ⁵	12.19	1.84	24.93	5.96	4322.67	661.63
Reef Scientifico Total	16.77	1.79	20.99	8.64	4440.46	604.16

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Barcadera (Control)						
<i>Acanthurus bahianus</i>	0.31	0.62	30.00	0.00	183.77	364.62
<i>Acanthurus chirurgus</i>	0.21	0.59	35.00	0.00	240.40	679.97
<i>Acanthurus coeruleus</i>	0.42	0.77	25.00	0.00	411.82	762.54
<i>Microspathodon chrysurus</i>	1.77	2.06	18.26	3.04	297.00	294.99
<i>Scarus iserti</i>	0.63	1.24	17.00	0.00	53.67	107.05
<i>Scarus taeniopterus</i>	1.35	1.25	22.72	3.80	217.58	203.48
<i>Scarus vetula</i>	1.77	1.13	34.17	4.63	1740.03	1913.77
<i>Sparisoma aurofrenatum</i>	1.15	1.25	18.58	3.06	123.84	125.13
<i>Sparisoma chrysopteron</i>	0.10	0.29	34.00	0.00	73.98	209.26
<i>Sparisoma rubripinne</i>	0.10	0.29	31.00	0.00	60.45	170.98
<i>Sparisoma viride</i>	1.07	1.15	36.70	5.93	915.30	1189.48
<i>Stegastes diencaeus</i>	2.50	2.36	9.24	1.17	65.11	78.03
<i>Stegastes leucostictus</i>	1.04	1.24	8.77	1.13	21.07	25.55
<i>Stegastes planifrons</i>	0.42	0.45	8.50	0.58	7.21	7.92
Acanthuridae	0.94	0.64	29.00	4.18	835.99	606.59
Pomacentridae	5.73	1.70	13.00	4.57	390.38	187.99
Scaridae	6.04	1.14	27.81	8.59	3184.85	1013.20
Denuding ²	2.71	0.69	23.63	6.63	1133.00	541.03
Excavating ³	6.04	1.14	27.81	8.59	3184.85	1013.20
Non-denuding ⁴	3.96	1.74	8.86	.99	93.38	52.02
Algal removers ⁵	8.75	1.04	26.68	8.24	4317.84	871.89
Barcadera Total	12.71	1.25	21.79	10.66	4411.22	786.49

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Oil Slick Leap (Control)						
<i>Acanthurus bahianus</i>	1.04	1.53	28.83	4.82	664.97	1022.53
<i>Acanthurus chirurgus</i>	0	0			0.00	0
<i>Acanthurus coeruleus</i>	1.67	2.09	25.00	0.00	1647.27	2064.96
<i>Microspathodon chrysurus</i>	2.29	2.08	14.88	0.31	225.60	206.75
<i>Scarus iserti</i>	0.94	1.13	19.92	0.69	134.69	168.51
<i>Scarus taeniopterus</i>	1.77	1.81	21.48	2.61	254.73	255.75
<i>Scarus vetula</i>	2.50	1.26	31.77	6.18	1732.30	1063.54
<i>Sparisoma aurofrenatum</i>	0.63	0.74	21.75	3.86	151.59	231.86
<i>Sparisoma chrysopterus</i>	0	0			0.00	0
<i>Sparisoma rubripinne</i>	0	0			0.00	0
<i>Sparisoma viride</i>	2.08	0.77	33.09	6.66	1673.98	987.11
<i>Stegastes diencaeus</i>	4.90	2.38	10.18	0.96	164.50	95.34
<i>Stegastes leucostictus</i>	1.15	1.09	11.70	3.03	57.27	75.56
<i>Stegastes planifrons</i>	0.21	0.59	7.50	0.00	2.53	7.15
Acanthuridae	2.71	1.80	26.92	3.76	2312.24	1446.97
Pomacentridae	8.54	2.49	11.84	2.71	449.89	144.61
Scaridae	7.92	1.35	26.97	7.46	3947.29	906.91
Denuding ²	5.00	1.75	21.76	6.77	2537.83	1273.02
Excavating ³	7.92	1.35	26.97	7.46	3947.29	906.91
Non-denuding ⁴	6.25	2.54	10.53	2.15	224.29	96.14
Algal removers ⁵	12.92	1.47	25.34	7.58	6485.12	1048.13
Oil Slick Leap Total	19.17	1.85	21.83	9.22	6709.41	952.88

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Forest (Control)						
<i>Acanthurus bahianus</i>	0	0			0.00	0
<i>Acanthurus chirurgus</i>	0	0			0.00	0
<i>Acanthurus coeruleus</i>	0.63	0.86	25.00	11.18	617.73	852.54
<i>Microspathodon chrysurus</i>	1.77	1.37	14.54	0.64	162.17	124.38
<i>Scarus iserti</i>	0	0			0.00	0
<i>Scarus taeniopterus</i>	3.75	3.39	23.12	5.54	658.80	456.80
<i>Scarus vetula</i>	2.08	0.77	32.03	5.07	1601.84	1240.64
<i>Sparisoma aurofrenatum</i>	1.67	1.00	22.65	3.76	348.27	213.57
<i>Sparisoma chrysopteron</i>	0	0			0.00	0
<i>Sparisoma rubripinne</i>	0.10	0.29	24.00	0.00	27.60	78.05
<i>Sparisoma viride</i>	0.94	0.94	29.17	7.48	523.29	620.72
<i>Stegastes diencaeus</i>	1.88	1.24	11.13	1.90	68.98	41.88
<i>Stegastes leucostictus</i>	0.73	1.13	10.13	2.02	30.60	63.40
<i>Stegastes planifrons</i>	2.60	1.63	8.27	1.46	39.80	27.35
Acanthuridae	0.63	0.86	20.00	11.18	617.73	556.50
Pomacentridae	6.98	1.48	10.87	2.80	301.56	88.12
Scaridae	8.54	2.01	26.41	6.47	3159.79	751.36
Denuding ²	2.40	0.89	17.02	7.64	779.90	483.36
Excavating ³	8.54	2.01	26.41	6.47	3159.79	751.36
Non-denuding ⁴	5.21	1.51	9.71	2.11	139.39	47.58
Algal removers ⁵	10.94	1.91	23.89	7.92	3939.69	674.93
Forest Total	16.15	1.77	19.40	9.38	4079.07	611.57

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix A. Average density, fork length, and biomass of herbivorous fish in Bonaire, March 2009

Species ¹	Density (# per 100 m ²)		Fork Length (cm)		Biomass (g per 100 m ²)	
	mean	SD	mean	SD	mean	SD
Bonaire Averages						
<i>Acanthurus bahianus</i>	1.80	3.05	25.09	2.33	823.53	1303.22
<i>Acanthurus chirurgus</i>	0.29	0.75	22.18	1.66	121.79	320.70
<i>Acanthurus coeruleus</i>	1.00	1.38	23.74	2.51	886.38	1241.64
<i>Microspathodon chrysurus</i>	1.05	1.10	15.35	0.63	118.13	119.79
<i>Scarus iserti</i>	1.61	1.54	19.31	6.61	280.83	278.68
<i>Scarus taeniopterus</i>	2.70	1.81	21.28	5.73	417.87	282.32
<i>Scarus vetula</i>	1.56	1.15	33.30	9.24	1397.02	1255.83
<i>Sparisoma aurofrenatum</i>	1.25	1.16	21.80	4.92	277.63	322.01
<i>Sparisoma chrysopteron</i>	0.10	0.23	28.25	6.51	47.39	110.96
<i>Sparisoma rubripinne</i>	0.14	0.33	29.45	4.18	74.94	189.13
<i>Sparisoma viride</i>	1.45	1.09	31.27	7.56	981.78	827.60
<i>Stegastes diencaeus</i>	3.42	2.16	10.05	1.28	106.99	73.87
<i>Stegastes leucostictus</i>	0.94	1.07	9.92	1.51	29.70	39.94
<i>Stegastes planifrons</i>	0.64	0.70	8.32	1.31	9.59	11.08
Acanthuridae	3.09	2.28	25.62	4.51	1814.71	1211.32
Pomacentridae	6.05	2.02	11.03	2.94	264.41	95.53
Scaridae	8.88	1.63	25.05	8.81	3477.45	807.26
Denuding ²	4.14	2.25	22.26	6.47	1932.84	1073.11
Excavating ³	8.87	1.63	25.05	8.81	3477.45	807.26
Non-denuding ⁴	5.00	2.05	9.71	1.71	146.28	65.81
Algal removers ⁵	13.02	2.09	25.09	7.47	5410.29	959.10
Bonaire Total	18.02	2.11	21.43	9.27	5556.57	869.81

¹ Species surveyed but not observed: *Stegastes fuscus*, *Stegastes variabilis*, *Kyphosus sectatrix*, *Scarus coeruleus*, *Scarus coelestinus*, and *Scarus guacamaia*

² Denuding (Acanthuridae, *M. chrysurus*)

³ Excavating (Scarids)

⁴ Non-denuding (*Stegastes*)

⁵ Algal removers (Acanthuridae, *M. chrysurus*, Scarids)

Appendix B. Density and fork length of initial and terminal phase Scarids in Bonaire, March 2009

Species	Initial Density 100m2	Initial Density SD	Term. Density /100m2	Term. Density SD	Initial Av. FL (cm)	Initial Av. FL SD	Term. Av. FL (cm)	Term. Av. FL SD
Windsock (Control)								
<i>Scarus iserti</i>	1.46	1.98	0.10	0.35	18.57	6.44	32.00	
<i>Scarus taeniopterus</i>	0.42	0.53	1.25	1.20	19.00	2.45	24.33	5.22
<i>Scarus vetula</i>	0.63	1.16	0.83	0.53	30.17	1.53	47.75	11.01
<i>Sparisoma aurofrenatum</i>	0.42	0.93	0.52	0.74	23.00	0.71	19.80	6.48
<i>Sparisoma chrysopterus</i>	0.10	0.35	0.00	0.00	34.00			
<i>Sparisoma rubripinne</i>	0.10	0.35	0.52	1.77	28.00		32.60	
<i>Sparisoma viride</i>	0.63	0.71	0.94	0.99	29.50	1.64	35.67	7.07
Scarus Total	2.50	0.55	2.19	0.58	21.54	6.57	33.62	11.94
Sparisoma Total	1.25	0.26	1.98	0.38	27.58	4.53	30.68	8.42
Windsock Total Scarids	3.75	0.46	4.17	0.45	23.56	5.93	32.23	9.69
Eighteenth Palm (FPA)								
<i>Scarus iserti</i>	2.19	3.11	1.67	2.33	14.67	3.35	24.25	2.66
<i>Scarus taeniopterus</i>	1.77	1.13	1.15	0.92	17.94	2.45	23.82	4.27
<i>Scarus vetula</i>	0.94	0.64	0.94	1.13	29.44	5.74	34.89	6.19
<i>Sparisoma aurofrenatum</i>	0.73	0.83	0.83	1.07	18.14	2.20	23.75	5.55
<i>Sparisoma chrysopterus</i>	0.21	0.46	0.21	0.46	19.00	2.83	32.50	2.12
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00				
<i>Sparisoma viride</i>	0.73	0.83	0.52	1.19	29.14	2.30	32.00	1.53
Scarus Total	4.90	0.64	3.75	0.38	18.68	7.76	26.78	6.27
Sparisoma Total	1.67	0.37	1.56	0.36	23.06	6.12	27.67	4.91
Eighteenth Palm Total Scarids	6.56	0.79	5.31	0.57	19.79	6.30	27.04	5.13
Calabas Reef (FPA)								
<i>Scarus iserti</i>	2.50	3.07	1.04	1.04	15.21	5.18	30.10	3.39
<i>Scarus taeniopterus</i>	1.67	2.62	1.35	1.19	19.38	2.24	28.38	5.04
<i>Scarus vetula</i>	0.73	1.13	0.42	0.76	32.00	1.73	43.50	4.04
<i>Sparisoma aurofrenatum</i>	0.21	0.46	0.83	1.60	19.50	0.71	28.88	0.19
<i>Sparisoma chrysopterus</i>	0.00	0.00	0.10	0.35			25.00	
<i>Sparisoma rubripinne</i>	0.10	0.35	0.21	0.71	20.00		29.00	
<i>Sparisoma viride</i>	0.73	0.83	0.31	0.52	26.00	9.90	38.67	6.11
Scarus Total	4.90	0.89	2.81	0.48	19.13	8.74	31.26	8.28
Sparisoma Total	1.04	0.32	1.46	0.32	24.10	3.62	30.71	5.83
Calabas Total Scarids	5.94	0.92	4.27	0.47	20.00	5.99	31.07	6.60

Appendix B. Density and fork length of initial and terminal phase Scarids in Bonaire, March 2009

Species	Initial Density /100m2	Initial Density SD	Term. Density 100m2	Term. Density SD	Initial Av. FL (cm)	Initial Av. FL SD	Term. Av. FL (cm)	Term. Av. FL SD
Front Porch (FPA)								
<i>Scarus iserti</i>	1.04	1.67	0.63	1.04	15.50	2.68	27.00	5.57
<i>Scarus taeniopterus</i>	1.77	1.13	0.73	1.13	19.41	1.54	22.57	1.91
<i>Scarus vetula</i>	0.31	0.52	0.52	1.06	24.67	10.21	26.20	6.35
<i>Sparisoma aurofrenatum</i>	0.63	1.04	1.04	1.28	19.50	3.77	22.60	2.39
<i>Sparisoma chrysopterus</i>	0.00	0.00	0.00	0.00				
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00				
<i>Sparisoma viride</i>	1.04	1.67	1.15	1.19	29.10	4.10	31.82	6.97
Scarus Total	3.13	0.73	1.88	0.10	18.63	4.60	25.06	2.36
Sparisoma Total	1.67	0.51	2.19	0.63	25.50	6.79	27.43	6.52
Front Porch Total Scarids	4.79	0.65	4.06	0.45	21.02	5.29	26.33	3.82
Reef Scientifico (FPA)								
<i>Scarus iserti</i>	0.52	1.19	0.21	0.46	18.20	0.24	25.00	8.49
<i>Scarus taeniopterus</i>	3.44	4.16	1.15	1.60	17.03	2.66	27.18	5.36
<i>Scarus vetula</i>	0.94	1.13	0.42	0.76	30.11	2.35	36.25	2.52
<i>Sparisoma aurofrenatum</i>	0.83	0.76	0.52	0.74	20.38	3.08	25.40	5.11
<i>Sparisoma chrysopterus</i>	0.00	0.00	0.10	0.35			30.00	
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00				
<i>Sparisoma viride</i>	1.04	0.71	0.52	0.74	26.60	5.95	32.00	2.31
Scarus Total	4.90	1.58	1.77	0.49	19.66	7.24	29.06	6.93
Sparisoma Total	1.88	0.55	1.15	0.27	23.83	4.40	28.82	12.61
R. Scientifico Total Scarids	6.77	1.17	2.92	0.38	20.82	5.65	28.96	9.58
Barcadera (Control)								
<i>Scarus iserti</i>	0.63	1.49	0.00	0.00	17.00			
<i>Scarus taeniopterus</i>	0.31	0.74	1.04	1.04	17.00		23.80	3.37
<i>Scarus vetula</i>	1.15	1.06	0.63	0.89	30.36	2.40	43.50	10.48
<i>Sparisoma aurofrenatum</i>	0.63	1.16	0.52	0.52	14.67	4.40	21.00	2.55
<i>Sparisoma chrysopterus</i>	0.00	0.00	0.10	0.35			34.00	
<i>Sparisoma rubripinne</i>	0.00	0.00	0.10	0.35			31.00	
<i>Sparisoma viride</i>	0.10	0.35	0.83	1.31	22.00		38.25	6.18
Scarus Total	2.08	0.42	1.67	0.52	24.35	7.72	31.19	5.97
Sparisoma Total	0.73	0.30	1.56	0.35	15.71	5.19	31.73	3.38
Barcadera Total Scarids	2.81	0.42	3.23	0.40	22.11	6.28	31.45	4.34

Appendix B. Density and fork length of initial and terminal phase Scarids in Bonaire, March 2009

Species	Initial Density /100m2	Initial Density SD	Term. Density 100m2	Term. Density SD	Initial Av. FL (cm)	Initial Av. FL SD	Term. Av. FL (cm)	Term. Av. FL SD
Oil Slick Leap (Control)								
<i>Scarus iserti</i>	0.73	1.13	0.21	0.46	19.43	0.50	22.50	2.12
<i>Scarus taeniopterus</i>	0.73	1.36	1.04	0.89	19.00	1.28	23.10	4.60
<i>Scarus vetula</i>	0.73	0.93	1.25	0.76	28.42	6.07	35.25	6.53
<i>Sparisoma aurofrenatum</i>	0.31	0.52	0.31	0.74	19.00	1.00	26.67	1.41
<i>Sparisoma chrysopterus</i>	0.00	0.00	0.00	0.00				
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00				
<i>Sparisoma viride</i>	0.94	0.35	1.15	0.74	27.78	5.51	37.91	4.25
Scarus Total	2.19	0.00	2.50	0.55	23.46	5.32	29.13	13.93
Sparisoma Total	1.25	0.44	1.46	0.54	25.58	6.21	35.50	7.34
Oil Slick Leap Scarids	3.44	0.38	3.96	0.56	24.13	4.91	31.47	8.54
Forest (Control)								
<i>Scarus iserti</i>	0.00	0.00	0.00	0.00				
<i>Scarus taeniopterus</i>	2.40	3.48	1.35	1.41	17.43	2.80	29.77	2.87
<i>Scarus vetula</i>	1.35	0.74	0.73	0.64	28.08	3.92	39.57	9.68
<i>Sparisoma aurofrenatum</i>	0.21	0.46	1.46	1.16	20.00	2.83	22.29	3.99
<i>Sparisoma chrysopterus</i>	0.00	0.00	0.00	0.00	24.00			
<i>Sparisoma rubripinne</i>	0.10	0.35	0.00	0.00	24.00		47.33	
<i>Sparisoma viride</i>	0.63	0.89	0.31	0.52	21.28	5.90	37.33	5.13
Scarus Total	3.75	1.20	2.08	0.68	22.76	7.53	33.20	7.19
Sparisoma Total	0.94	0.27	1.77	0.69	22.32	2.01	24.94	7.95
Forest Scarids	4.69	0.90	3.85	0.64	22.51	3.71	29.41	7.09
Bonaire Averages								
<i>Scarus iserti</i>	1.13	0.86	0.48	0.60	16.29	4.48	26.43	5.21
<i>Scarus taeniopterus</i>	1.56	1.06	1.13	0.20	18.07	3.42	25.70	5.32
<i>Scarus vetula</i>	0.85	0.32	0.72	0.29	29.36	6.22	38.31	10.05
<i>Sparisoma aurofrenatum</i>	0.49	0.24	0.76	0.37	19.03	3.82	23.62	4.72
<i>Sparisoma chrysopterus</i>	0.04	0.08	0.07	0.08	24.00	8.89	30.80	3.70
<i>Sparisoma rubripinne</i>	0.04	0.05	0.10	0.18	24.00	4.00	31.50	1.69
<i>Sparisoma viride</i>	0.73	0.30	0.72	0.35	27.43	6.41	35.31	6.37
Scarus Total	3.54	0.36	2.33	0.33	20.36	7.00	29.73	9.10
Sparisoma Total	1.30	0.34	1.64	0.38	24.03	6.80	29.51	7.71
Bonaire Ave. Scarids	4.84	0.56	3.97	0.38	21.33	7.13	29.64	8.54

Appendix C. Biomass of initial and terminal phase Scarids in Bonaire, March 2009

Windsock Scarids	Initial /100 m2	Initial SD	Terminal /100 m2	Terminal SD	Total /100 m2	Total SD
<i>Scarus iserti</i>	206.38	256.79	60.50	205.35	266.88	416.71
<i>Scarus taeniopterus</i>	41.76	58.10	263.82	398.65	305.58	430.59
<i>Scarus vetula</i>	368.33	696.86	2010.64	1791.88	2378.97	2093.15
<i>Sparisoma aurofrenatum</i>	96.41	214.40	93.70	184.99	190.11	289.48
<i>Sparisoma chrysopteron</i>	73.98	251.11	0.00	0.00	73.98	251.11
<i>Sparisoma rubripinne</i>	44.26	150.21	352.91	1197.80	397.16	1185.70
<i>Sparisoma viride</i>	336.08	387.06	847.01	990.25	1183.09	1125.99
Scarus	616.47	442.27	2334.96	1479.77	2951.44	1704.55
Sparisoma	550.74	289.06	1293.61	844.87	1844.35	956.62
Windsock Scarids	1167.21	361.31	3628.57	1179.97	4795.78	1352.38
Eighteenth Palm Scarids						
<i>Scarus iserti</i>	131.49	222.88	454.27	669.79	585.76	603.23
<i>Scarus taeniopterus</i>	156.11	123.99	223.40	258.48	379.51	216.41
<i>Scarus vetula</i>	509.42	332.79	858.52	1381.30	1367.94	1339.74
<i>Sparisoma aurofrenatum</i>	82.48	119.50	240.13	408.26	322.61	399.06
<i>Sparisoma chrysopteron</i>	24.27	57.56	129.18	291.06	153.46	299.42
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sparisoma viride</i>	371.95	429.40	385.84	857.32	757.78	833.84
Scarus	797.02	313.52	1536.18	917.11	2333.20	971.41
Sparisoma	478.70	280.14	755.15	502.70	1233.85	576.71
Eighteenth Palm Scarids	1275.73	304.94	2291.33	729.17	3567.06	813.11
Calabas Reef Scarids						
<i>Scarus iserti</i>	237.34	438.75	528.03	607.88	765.37	622.48
<i>Scarus taeniopterus</i>	178.93	257.83	421.73	476.13	600.66	366.53
<i>Scarus vetula</i>	445.82	766.34	662.52	1390.08	1108.34	1732.41
<i>Sparisoma aurofrenatum</i>	25.94	57.94	415.51	797.77	441.45	815.45
<i>Sparisoma chrysopteron</i>	0.00	0.00	27.91	94.72	27.91	94.72
<i>Sparisoma rubripinne</i>	15.78	53.57	98.56	334.52	114.34	331.14
<i>Sparisoma viride</i>	312.45	501.23	347.04	600.94	659.49	934.89
Scarus	862.09	526.57	1612.28	885.52	2474.38	1067.45
Sparisoma	354.18	288.27	889.01	540.31	1243.19	685.50
Calabas Reef Scarids	1216.27	420.70	2501.30	726.72	3717.57	914.45

Appendix C. Biomass of initial and terminal phase Scarids in Bonaire, March 2009

Front Porch Scarids	Initial /100 m2	Initial SD	Terminal /100 m2	Terminal SD	Total /100 m2	Total SD
<i>Scarus iserti</i>	72.29	77.99	246.49	468.06	318.78	507.80
<i>Scarus taeniopterus</i>	186.45	138.49	114.26	177.01	300.71	177.71
<i>Scarus vetula</i>	112.03	241.75	199.11	377.19	311.13	411.25
<i>Sparisoma aurofrenatum</i>	85.06	141.41	232.78	346.75	317.84	339.44
<i>Sparisoma chrysopteron</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sparisoma viride</i>	516.09	611.83	841.29	849.75	1357.38	1274.58
Scarus	370.77	169.82	559.86	352.15	930.63	373.69
Sparisoma	601.15	396.41	1074.07	605.13	1675.22	924.32
Front Porch Scarids	971.92	317.62	1633.92	510.55	2605.85	737.69
Reef Scientifico Scarids						
<i>Scarus iserti</i>	54.24	124.73	67.22	185.08	121.46	194.45
<i>Scarus taeniopterus</i>	295.91	329.35	329.47	430.13	625.39	419.81
<i>Scarus vetula</i>	499.37	663.74	436.22	854.76	935.58	1417.84
<i>Sparisoma aurofrenatum</i>	134.90	151.49	190.41	448.96	325.31	563.18
<i>Sparisoma chrysopteron</i>	0.00	0.00	49.75	168.85	49.75	168.85
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sparisoma viride</i>	450.99	428.07	332.94	470.02	783.93	418.90
Scarus	849.52	470.71	832.90	570.27	1682.43	919.83
Sparisoma	585.89	311.47	573.09	356.24	1158.99	511.38
Reef Scientifico Scarids	1435.42	392.49	1406.00	462.61	2841.41	726.36
Barcadera Scarids						
<i>Scarus iserti</i>	53.67	128.46	0.00	0.00	53.67	128.46
<i>Scarus taeniopterus</i>	22.52	53.63	195.06	226.70	217.58	244.17
<i>Scarus vetula</i>	629.05	523.50	1110.98	2071.12	1740.03	2296.53
<i>Sparisoma aurofrenatum</i>	36.35	66.12	87.49	100.83	123.84	150.16
<i>Sparisoma chrysopteron</i>	0.00	0.00	73.98	251.11	73.98	251.11
<i>Sparisoma rubripinne</i>	0.00	0.00	60.45	205.18	60.45	205.18
<i>Sparisoma viride</i>	21.81	74.01	893.49	1429.43	915.30	1427.38
Scarus	705.24	454.05	1306.04	1293.69	2011.27	1579.42
Sparisoma	58.16	50.77	1115.42	821.43	1173.58	825.45
Barcadera Scarids	763.40	324.24	2421.45	1043.55	3184.85	1215.84

Appendix C. Biomass of initial and terminal phase Scarids in Bonaire, March 2009

Oil Slick Leap Scarids	Initial /100 m2	Initial SD	Terminal /100 m2	Terminal SD	Total /100 m2	Total SD
<i>Scarus iserti</i>	92.85	150.75	41.83	95.43	134.69	202.21
<i>Scarus taeniopterus</i>	71.43	128.61	183.30	186.12	254.73	306.91
<i>Scarus vetula</i>	595.26	503.19	1137.04	905.91	1732.30	1276.25
<i>Sparisoma aurofrenatum</i>	35.77	60.25	115.82	266.09	151.59	278.23
<i>Sparisoma chrysopteron</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sparisoma rubripinne</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sparisoma viride</i>	437.23	264.28	1236.76	1027.56	1673.98	1184.53
Scarus	759.54	420.76	1362.17	786.48	2121.71	1153.20
Sparisoma	473.00	259.46	1352.58	811.07	1825.57	1036.61
Oil Slick Leap Scarids	1232.54	344.26	2714.75	796.41	3947.29	1088.30
Forest Scarids						
<i>Scarus iserti</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Scarus taeniopterus</i>	189.87	261.40	468.93	441.33	658.80	548.16
<i>Scarus vetula</i>	617.27	223.52	984.56	1362.29	1601.84	1488.77
<i>Sparisoma aurofrenatum</i>	29.39	69.92	318.87	284.05	348.27	256.28
<i>Sparisoma chrysopteron</i>	0.00		0.00	0.00	0.00	0.00
<i>Sparisoma rubripinne</i>	27.60	93.66	0.00	0.00	27.60	93.66
<i>Sparisoma viride</i>	215.65	363.31	308.89	520.90	524.54	746.95
Scarus	807.14	368.97	1453.49	931.15	2260.64	1189.68
Sparisoma	272.64	209.45	627.77	340.76	900.40	463.77
Forest Scarids	1079.78	310.08	2081.26	683.05	3161.04	901.87
Bonaire Scarids						
<i>Scarus iserti</i>	106.03	175.04	174.79	278.95	280.83	334.42
<i>Scarus taeniopterus</i>	142.87	168.93	275.00	324.32	417.87	338.79
<i>Scarus vetula</i>	472.07	493.96	924.95	1266.82	1397.02	1506.99
<i>Sparisoma aurofrenatum</i>	65.79	110.13	211.84	354.71	277.63	386.41
<i>Sparisoma chrysopteron</i>	12.28	38.58	35.10	100.72	47.39	133.15
<i>Sparisoma rubripinne</i>	10.95	37.18	63.99	217.19	74.94	226.96
<i>Sparisoma viride</i>	332.78	382.40	649.16	843.27	981.94	993.38
Scarus	720.98	395.83	1374.74	902.02	2095.71	1119.90
Sparisoma	421.81	260.63	983.91	602.81	1486.61	747.54
Bonaire Scarids	1142.78	346.95	2334.82	766.50	3477.61	968.75

Appendix D. Average biomass and density of predatory reef fish, Bonaire 2009.

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Bachelor's Beach - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	292.1	293.4	1.0	0.0	49.0	16.1
<i>Bodianus rufus</i>	84.9	0.0	0.1	0.0	36.0	0.0
<i>Bothus lunatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx rubber</i>	1342.2	564.6	1.4	0.0	42.2	9.4
<i>Epinephelus cruentatus</i>	339.3	120.6	1.9	0.0	22.6	5.2
<i>Epinephelus fulvus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon carbonarium</i>	61.6	0.0	0.1	0.0	28.0	0.0
<i>Haemulon chrysargyreum</i>	1462.4	21.1	10.0	0.0	16.8	1.0
<i>Haemulon flavolineatum</i>	353.1	60.7	2.5	0.0	19.4	3.0
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	188.3	0.0	0.3	0.0	36.0	0.0
<i>Hypoplectrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus apodus</i>	288.6	165.7	1.5	0.0	21.8	6.4
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	380.2	74.5	3.3	0.0	18.9	4.1
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	168.8	405.0	0.4	0.0	30.0	13.1
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	4.1	3.5	0.3	0.0	10.5	0.7
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	74.2	38.1	0.3	0.0	33.0	1.4
Aulostomidae	292.1	293.4	1.0	0.0	49.0	16.1
Carangidae	1342.2	564.6	1.4	0.0	21.1	4.7
Haemulidae	2065.3	81.8	12.9	0.0	16.7	0.7
Labridae	84.9	0.0	0.1	0.0	36.0	0.0
Lutjanidae	837.6	645.1	5.1	0.0	11.8	3.9
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	343.3	124.1	2.1	0.0	4.1	0.7
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	74.2	38.1	0.3	0.0	33.0	1.4
All Predators	5039.8	269.1	22.9	0.0	21.8	10.1

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Barcadera - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	58.3	0.0	0.1	0.0	36.0	0.0
<i>Aulostomus maculatus</i>	89.5	155.6	0.4	0.0	47.3	12.2
<i>Bodianus rufus</i>	152.6	307.4	0.6	0.0	22.9	10.3
<i>Bothus lunatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx ruber</i>	722.5	585.4	0.7	0.0	43.1	10.4
<i>Epinephelus cruentatus</i>	184.1	155.2	1.1	0.0	21.3	5.9
<i>Epinephelus fulvus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon carbonarium</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon chrysargyreum</i>	1965.8	51.5	14.2	0.0	16.1	2.9
<i>Haemulon flavolineatum</i>	360.6	69.5	2.4	0.0	19.5	3.9
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	235.2	886.7	0.3	0.0	36.5	10.4
<i>Hypoplectrus sp</i>	20.3	51.9	0.3	0.0	16.8	3.8
<i>Lutjanus apodus</i>	459.4	721.9	0.6	0.0	34.4	12.3
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	1008.3	0.0	0.1	0.0	100.0	0.0
<i>Lutjanus mahogoni</i>	398.6	105.1	1.6	0.0	25.4	4.8
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	37.9	159.5	0.1	0.0	28.0	5.7
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	1.7	0.0	0.1	0.0	10.0	0.0
<i>Sphyræna barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	77.1	415.0	0.1	0.0	41.0	9.9
Aulostomidae	89.5	155.6	0.4	0.0	47.3	12.2
Carangidae	722.5	585.4	0.7	0.0	21.5	5.2
Haemulidae	2619.8	1007.7	16.9	0.0	18.0	2.9
Labridae	152.6	307.4	0.6	0.0	22.9	10.3
Lutjanidae	1904.2	986.5	2.3	0.0	31.3	3.8
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	185.8	155.2	1.3	0.0	3.9	0.7
Sphyrænidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	77.1	415.0	0.1	0.0	41.0	9.9
All Predators	5771.8	884.6	22.5	0.0	20.1	9.7

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Calabas - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	90.8	103.4	0.4	0.0	46.3	7.5
<i>Bodianus rufus</i>	134.2	220.9	0.4	0.0	25.3	9.3
<i>Bothus lunatus</i>	7.2	0.0	0.1	0.0	20.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx ruber</i>	568.6	555.9	0.7	0.0	38.9	11.0
<i>Epinephelus cruentatus</i>	394.1	123.6	2.3	0.0	21.7	6.0
<i>Epinephelus fulvus</i>	29.0	288.4	0.1	0.0	21.0	12.7
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon carbonarium</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon chrysargyreum</i>	352.2	20.5	2.1	0.0	17.8	1.0
<i>Haemulon flavolineatum</i>	387.0	57.6	2.9	0.0	18.8	3.2
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	390.6	216.4	0.6	0.0	34.7	3.9
<i>Hypoplectrus sp</i>	5.3	7.8	0.3	0.0	10.4	1.7
<i>Lutjanus apodus</i>	691.3	283.7	1.8	0.0	27.9	7.8
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	205.7	119.2	1.4	0.0	20.3	5.5
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	335.8	192.4	3.5	0.0	15.7	7.1
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	109.8	166.4	0.3	0.0	34.2	5.7
Aulostomidae	90.8	103.4	0.4	0.0	46.3	7.5
Carangidae	568.6	555.9	0.7	0.0	19.5	5.5
Haemulidae	1129.9	294.5	5.6	0.0	11.9	1.3
Labridae	134.2	220.9	0.4	0.0	25.3	9.3
Lutjanidae	1232.8	595.2	6.6	0.0	10.6	3.4
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	423.1	412.1	2.4	0.0	5.3	2.3
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	109.8	166.4	0.3	0.0	34.2	5.7
All Predators	3701.6	258.6	16.9	0.0	21.9	9.4

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Forest - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	124.5	107.2	1.0	0.0	42.1	11.1
<i>Bodianus rufus</i>	175.7	391.5	0.4	0.0	29.0	10.7
<i>Bothus lunatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx ruber</i>	934.5	938.8	0.9	0.0	40.9	15.4
<i>Epinephelus cruentatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus fulvus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon carbonarium</i>	250.0	148.8	1.3	0.0	22.9	6.3
<i>Haemulon chrysargyreum</i>	894.6	16.7	5.2	0.0	18.2	0.8
<i>Haemulon flavolineatum</i>	89.8	55.4	0.5	0.0	21.5	2.6
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	30.0	0.0
<i>Haemulon sciurus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hypoplectrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus apodus</i>	1104.2	355.0	1.7	0.0	34.4	5.6
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	113.3	113.5	0.5	0.0	24.5	4.1
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	113.1	183.6	0.1	0.0	42.0	2.8
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	77.3	64.1	0.1	0.0	37.0	1.4
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	2.4	0.0	0.1	0.0	11.0	0.0
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	124.5	0.0	1.0	0.0	42.1	11.1
Carangidae	934.5	0.0	0.9	0.0	20.4	7.7
Haemulidae	1234.4	0.0	6.9	0.0	15.4	1.6
Labridae	175.7	0.0	0.4	0.0	29.0	10.7
Lutjanidae	1294.7	0.0	2.3	0.0	16.0	1.9
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	115.5	0.0	0.3	0.0	6.6	0.4
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	4234.3	396.9	12.6	0.0	26.1	10.8

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Front Porch - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	202.8	196.2	0.9	0.0	44.9	15.3
<i>Bodianus rufus</i>	270.9	356.2	0.6	0.0	28.2	10.2
<i>Bothus lunatus</i>	54.2	450.5	0.1	0.0	28.0	11.3
<i>Caranx latus</i>	563.3	539.5	0.8	0.0	33.1	7.5
<i>Caranx rubber</i>	245.7	644.2	0.3	0.0	36.4	15.6
<i>Epinephelus cruentatus</i>	448.0	117.9	1.6	0.0	26.5	3.7
<i>Epinephelus fulvus</i>	128.7	142.1	0.3	0.0	31.5	3.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon carbonarium</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon chrysargyreum</i>	503.7	0.0	1.9	0.0	22.0	0.0
<i>Haemulon flavolineatum</i>	316.7	37.8	1.6	0.0	22.7	1.7
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	249.8	258.4	0.3	0.0	36.4	3.8
<i>Hypoplectrus sp</i>	1.2	0.0	0.1	0.0	11.0	0.0
<i>Lutjanus apodus</i>	906.1	301.5	1.6	0.0	32.9	5.9
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	975.1	88.5	3.5	0.0	26.7	3.3
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	486.8	236.9	2.8	0.0	19.6	9.5
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	2.6	0.0	0.2	0.0	10.0	0.0
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	72.5	64.1	0.2	0.0	36.0	2.0
Aulostomidae	202.8	0.0	0.9	0.0	44.9	15.3
Carangidae	809.0	0.0	1.1	0.0	34.7	11.5
Haemulidae	1070.2	0.0	3.8	0.0	13.5	0.9
Labridae	270.9	0.0	0.6	0.0	28.2	10.2
Lutjanidae	2367.9	0.0	7.8	0.0	13.2	3.1
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	579.2	0.0	2.1	0.0	8.5	0.8
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	72.5	0.0	0.2	0.0	36.0	2.0
All Predators	5428.0	279.5	16.7	0.0	26.8	9.4

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Karpata - 10 m (Sample size = 8)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	44.5	108.1	0.4	0.0	36.7	11.5
<i>Bodianus rufus</i>	256.8	438.0	0.4	0.0	35.0	7.5
<i>Bothus lunatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx ruber</i>	351.0	1296.3	0.3	0.0	47.0	18.4
<i>Epinephelus cruentatus</i>	881.4	208.0	2.5	0.0	27.9	6.4
<i>Epinephelus fulvus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	430.9	554.1	0.4	0.0	43.3	5.8
<i>Haemulon carbonarium</i>	51.6	109.3	0.3	0.0	23.0	4.2
<i>Haemulon chrysargyreum</i>	608.0	18.0	4.3	0.0	16.6	0.9
<i>Haemulon flavolineatum</i>	105.8	59.2	0.5	0.0	23.0	2.6
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hypoplectrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus apodus</i>	527.6	571.6	0.6	0.0	37.2	7.4
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	585.1	722.4	0.9	0.0	35.4	11.1
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	0.0	0.0	0.0	0.0	0.0	0.0
Aulostomidae	44.5	108.1	0.4	0.0	36.7	11.5
Carangidae	351.0	1296.3	0.3	0.0	23.5	9.2
Haemulidae	765.4	186.4	5.0	0.0	10.4	1.3
Labridae	256.8	438.0	0.4	0.0	35.0	7.5
Lutjanidae	1112.7	1294.0	1.5	0.0	12.1	3.1
Muraenidae	430.9	554.1	0.4	0.0	43.3	5.8
Serranidae	881.4	208.0	2.5	0.0	3.5	0.8
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	0.0	0.0	0.0	0.0	0.0	0.0
All Predators	3842.7	443.1	10.4	0.0	25.7	10.7

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Oil Slick - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	25.2	41.9	0.3	0.0	33.0	6.8
<i>Bodianus rufus</i>	115.4	242.3	0.4	0.0	25.3	9.3
<i>Bothus lunatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx ruber</i>	127.2	439.0	0.3	0.0	32.0	11.5
<i>Epinephelus cruentatus</i>	202.2	113.6	0.9	0.0	24.3	4.3
<i>Epinephelus fulvus</i>	33.1	0.0	0.1	0.0	32.0	0.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon carbonarium</i>	83.8	141.6	0.2	0.0	30.0	3.5
<i>Haemulon chrysargyreum</i>	1261.1	18.3	6.1	0.0	19.7	0.8
<i>Haemulon flavolineatum</i>	376.2	65.5	2.9	0.0	18.5	3.9
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	381.5	147.6	0.5	0.0	36.0	2.6
<i>Hypoplectrus sp</i>	3.6	12.6	0.2	0.0	10.7	2.5
<i>Lutjanus apodus</i>	98.3	258.1	0.3	0.0	26.2	6.7
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	117.6	84.0	0.8	0.0	20.6	3.9
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	89.2	351.0	0.3	0.0	28.0	9.9
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	5.9	3.9	0.3	0.0	11.0	0.7
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	86.4	213.2	0.2	0.0	37.7	5.7
Aulostomidae	25.2	0.0	0.3	0.0	33.0	6.8
Carangidae	127.2	0.0	0.3	0.0	16.0	5.8
Haemulidae	2102.7	0.0	9.7	0.0	17.4	1.8
Labridae	115.4	0.0	0.4	0.0	25.3	9.3
Lutjanidae	305.1	0.0	1.4	0.0	12.5	3.4
Muraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Serranidae	241.2	0.0	1.3	0.0	8.4	0.6
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	86.4	0.0	0.2	0.0	37.7	5.7
All Predators	3006.8	172.0	13.7	0.0	21.5	6.4

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Eighteenth Palm - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	142.8	361.3	0.2	0.0	33.3	5.0
<i>Aulostomus maculatus</i>	75.5	107.9	0.7	0.0	35.1	10.7
<i>Bodianus rufus</i>	63.6	159.2	0.4	0.0	18.1	9.3
<i>Bothus lunatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx rubber</i>	1332.5	494.6	1.7	0.0	37.9	11.6
<i>Epinephelus cruentatus</i>	101.6	120.7	1.3	0.0	16.1	6.1
<i>Epinephelus fulvus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus guttatus</i>	6.4	0.0	0.1	0.0	20.0	0.0
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	51.8	0.0	0.1	0.0	40.0	0.0
<i>Haemulon carbonarium</i>	77.0	173.7	0.1	0.0	30.0	2.8
<i>Haemulon chrysargyreum</i>	16.4	0.0	0.1	0.0	16.0	0.0
<i>Haemulon flavolineatum</i>	341.9	94.3	2.1	0.0	20.1	5.1
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	28.0	0.0
<i>Haemulon sciurus</i>	238.8	69.4	0.4	0.0	32.3	1.4
<i>Hypoplectrus sp</i>	3.9	0.0	0.1	0.0	16.0	0.0
<i>Lutjanus apodus</i>	238.5	171.1	0.8	0.0	26.2	7.2
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	429.3	471.5	0.2	0.0	52.0	3.5
<i>Lutjanus mahogoni</i>	20.3	28.0	0.3	0.0	17.0	2.0
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	185.4	429.9	0.7	0.0	21.5	13.2
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	25.2	29.4	0.1	0.0	29.0	1.4
Aulostomidae	75.5	0.0	0.7	0.0	35.1	10.7
Carangidae	1332.5	0.0	1.7	0.0	18.9	5.8
Haemulidae	816.8	0.0	2.9	0.0	26.6	2.4
Labridae	63.6	0.0	0.4	0.0	18.1	9.3
Lutjanidae	873.4	0.0	1.9	0.0	19.4	4.3
Muraenidae	51.8	0.0	0.1	0.0	40.0	0.0
Serranidae	108.0	0.0	1.3	0.0	4.5	0.8
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	25.2	0.0	0.1	0.0	29.0	1.4
All Predators	3374.5	465.8	9.3	0.0	26.2	12.0

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Reef Scientifico - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Aulostomus maculatus</i>	190.9	85.3	1.5	0.0	38.3	8.3
<i>Bodianus rufus</i>	1.5	0.0	0.1	0.0	12.0	0.0
<i>Bothus lunatus</i>	21.1	0.0	0.1	0.0	28.0	0.0
<i>Caranx latus</i>	1246.5	0.0	3.2	0.0	28.0	0.0
<i>Caranx rubber</i>	459.8	434.8	0.8	0.0	34.0	8.9
<i>Epinephelus cruentatus</i>	491.2	197.4	1.9	0.0	25.1	5.6
<i>Epinephelus fulvus</i>	4.1	0.0	0.1	0.0	16.0	0.0
<i>Epinephelus guttatus</i>	19.8	79.9	0.1	0.0	23.0	4.2
<i>Epinephelus adscensionis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gymnothorax sp.</i>	468.3	2768.1	0.1	0.0	60.0	14.1
<i>Haemulon carbonarium</i>	212.4	0.0	0.7	0.0	24.0	0.0
<i>Haemulon chrysargyreum</i>	85.7	41.6	0.4	0.0	20.7	1.6
<i>Haemulon flavolineatum</i>	404.1	47.6	1.8	0.0	23.5	2.0
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	246.0	326.2	0.5	0.0	29.5	8.0
<i>Hypoplectrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus apodus</i>	440.5	442.0	0.9	0.0	30.3	8.2
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus mahogoni</i>	614.7	165.1	3.1	0.0	23.2	3.7
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	239.9	313.0	1.0	0.0	21.9	11.1
<i>Scorpaena plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Serranus tigrinus</i>	1.6	4.9	0.2	0.0	8.3	1.5
<i>Sphyraena barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	20.2	0.0	0.1	0.0	34.0	0.0
Aulostomidae	190.9	0.0	1.5	0.0	38.3	8.3
Carangidae	1706.3	0.0	4.0	0.0	31.0	4.5
Haemulidae	948.2	0.0	3.4	0.0	16.3	1.9
Labridae	1.5	0.0	0.1	0.0	12.0	0.0
Lutjanidae	1295.1	0.0	5.0	0.0	12.6	3.8
Muraenidae	468.3	0.0	0.1	0.0	60.0	14.1
Serranidae	516.7	0.0	2.3	0.0	9.1	1.4
Sphyraenidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	20.2	0.0	0.1	0.0	34.0	0.0
All Predators	5168.2	415.3	16.5	0.0	26.8	8.1

	Biomass (g per 100 m2)		Density (# per 100 m2)		Fork Length (cm)	
Windsock - 10 m (Sample size = 16)	Mean	SD	Mean	SD	Mean	SD
<i>Anisotremus surinamensis</i>	31.4	0.0	0.1	0.0	30.0	0.0
<i>Aulostomus maculatus</i>	129.4	153.1	0.7	0.0	42.2	13.7
<i>Bodianus rufus</i>	155.9	363.9	0.4	0.0	28.2	9.6
<i>Bothus lunatus</i>	32.3	0.0	0.1	0.0	32.0	0.0
<i>Caranx latus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Caranx ruber</i>	47.4	47.4	0.1	0.0	31.0	1.4
<i>Epinephelus cruentatus</i>	692.5	172.1	3.8	0.0	21.8	6.7
<i>Epinephelus fulvus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus guttatus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epinephelus adscensionis</i>	40.3	0.0	0.1	0.0	36.0	0.0
<i>Gymnothorax sp.</i>	19.2	0.0	0.1	0.0	30.0	0.0
<i>Haemulon carbonarium</i>	41.2	150.4	0.1	0.0	27.0	4.2
<i>Haemulon chrysargyreum</i>	1338.2	22.8	9.5	0.0	16.5	1.1
<i>Haemulon flavolineatum</i>	331.6	53.7	1.9	0.0	21.0	2.8
<i>Haemulon plumieri</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Haemulon sciurus</i>	1401.7	200.6	3.5	0.0	27.9	6.3
<i>Hypoplectrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus apodus</i>	345.4	266.0	0.7	0.0	31.1	6.7
<i>Lutjanus cyanopterus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lutjanus griseus</i>	345.9	0.0	0.1	0.0	70.0	0.0
<i>Lutjanus mahogoni</i>	148.3	108.9	1.5	0.0	17.0	5.4
<i>Lutjanus synagris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca bonaci</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mycteroperca venenosa</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ocyurus chrysurus</i>	138.0	177.6	1.1	0.0	17.8	7.5
<i>Scorpaena plumieri</i>	107.8	115.0	0.1	0.0	33.0	1.4
<i>Serranus tigrinus</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sphyræna barracuda</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Synodus intermedius</i>	40.5	0.0	0.1	0.0	34.0	0.0
Aulostomidae	129.4	0.0	0.7	0.0	42.2	13.7
Carangidae	47.4	0.0	0.1	0.0	15.5	0.7
Haemulidae	3144.1	0.0	15.1	0.0	20.4	2.4
Labridae	155.9	0.0	0.4	0.0	28.2	9.6
Lutjanidae	977.6	0.0	3.4	0.0	22.6	3.2
Muraenidae	19.2	0.0	0.1	0.0	30.0	0.0
Serranidae	732.7	0.0	3.8	0.0	7.2	0.8
Sphyrænidae	0.0	0.0	0.0	0.0	0.0	0.0
Synodontidae	40.5	0.0	0.1	0.0	34.0	0.0
All Predators	5386.9	326.7	23.9	0.0	21.4	8.3

