Status and Trends of Bonaire’s Coral Reefs 2017:
The first clear evidence of coral reef resilience in the Caribbean

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Status and Trends of Bonaire’s Reefs in 2017: Clear signs of resilience

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Executive Summary

Status and Trends of Bonaire’s Coral Reefs:
The First Clear Evidence of Coral Reef Resilience in the Caribbean

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Background and Our Approach:

The “resilience” of coral reef ecosystems has been an important goal of managers and policy makers for decades. At its most basic level, resilience means that if coral reefs suffer damage fromsay a hurricane or bleaching mortality event, they will recover to their previous state. Remarkably, this has never been documented for any coral reef ecosystem in the Caribbean.

In a highly cited scientific study entitled: “Disturbance and recovery of coral assemblages” (Connell 1997) all existing data on trends of coral reefs world-wide were reviewed but no examples of coral reefs recovering from disturbance in the Caribbean were found (Fig. 1).

![Percent of coral reefs recovering from disturbance](image)

Fig. 1. The percent of coral reefs documented to have recovered from a mortality event. Data from Connell 1997.
Several important studies have documented the decline of coral reef ecosystems in the Caribbean (Gardiner et al. 2003, Jackson et al. 2014) and in the tropical Pacific (Bruno and Selig 2007). The global decline of coral reefs was the impetus for very high impact scientific papers with titles such as “Confronting the coral reef crisis” (Bellwood et al. 2004) and “Rising to the challenge of sustaining coral reef resilience” (Hughes et al. 2010) or specifically asking the shocking question: “Are U.S. coral reefs on the slippery slope to slime?” (Pandolfi et al. 2005). These alarming titles and the associated press coverage caught the attention of managers and policy makers but to date there has been little progress operationalizing coral reef management for resilience. Nevertheless, some studies gave clear advice to managers such as, “Capturing the cornerstones of coral reef resilience, linking theory to practice” (Nyström et al 2008). In that paper, the authors proposed that research identify:

“…empirical indicators of the cornerstones of coral reef resilience. These indicators include functional group approaches” … “identifying ‘good’ and ‘bad’ colonizers of space, measurements of spatial heterogeneity, and estimates of potential space availability against grazing capacity. The essence of these operational indicators of resilience is to use them as predictive tools to recognize vulnerability before disturbance occurs that may lead to abrupt phase shifts [of coral loss and seaweed increase]. Moving toward operationalizing resilience theory is imperative to the successful management of coral reefs in an increasingly disturbed and human-dominated environment.”

The Nyström et al. 2008 quote describes precisely the approach we have taken since our reef monitoring began in Bonaire in 2003. In 2005, the Bonaire National Marine Park asked for advice on developing a monitoring program, to which we advocated three points: 1) keep monitoring data simple, 2) focus on known drivers and indicators of reef health and 3) monitor trends among those drivers.

Although coral reefs are complex ecosystems, relatively few “drivers” control much of their structure and how they function. “Drivers” are key processes that control critically important aspects of coral reefs. Several processes can interact with one another (Fig. 2). For example seaweed (also called “macroalgae”) are known to poison corals (Rasher and Hay 2010) and reduce or halt the settlement and survival of juvenile corals (Arnold et al. 2010, Steneck et al. 2014). It has also been shown that herbivorous fishes are capable of reducing or eliminating macroalgae from coral reefs (Lewis 1986, Williams and Polunin 2001). Thus herbivores such as parrotfish enable the recruitment of reef corals, reduce toxic seaweed and facilitate the growth of complex coral habitats into which juvenile reef fish recruit (Caselle and Warner 1996). These drivers and their interactions have been viewed as integral to a complex system of feedbacks that maintain healthy coral reefs (Fig. 2: Mumby and Steneck 2008); they are the “cornerstones” advocated by Nystrom et al. (2008).
Fig. 2. Conceptual model illustrating the reinforcing feedback processes driving a reef toward a healthy and resilient state dominated by corals with high structural complexity (from Mumby and Steneck 2008). The numbers in circles represent the chapters in this report containing information for each relevant node in this model.

Evaluating key drivers of coral reef health and resilience identified in Fig. 2 is complicated because all components interact. Therefore, it is difficult or impossible to define a specific level as being particularly healthy or unhealthy for any given coral reef. Instead, our monitoring protocol measures components to determine changes through time. This is because there is a consensus on trends that constitute healthy trajectories in reef condition. For example, trends of increasing live coral cover or decreasing macroalgal abundance are both moving towards improved conditions (Fig. 3). This allows us to create a very simple means of reporting condition and monitoring trends in key drivers. Importantly, this approach was developed explicitly in the 2005 Bonaire report and has been applied semiannually ever since. All semiannual Bonaire Reports
beginning in 2003 are available via STINAPA’s website (http://stinapabonaire.org/nature/coral-reefs-adjacent-waters/).

**Coral Reef Monitoring Priorities**

<table>
<thead>
<tr>
<th>Positive Trends</th>
<th>Negative Trends</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coral Cover</td>
<td></td>
</tr>
<tr>
<td>Macroalgae</td>
<td></td>
</tr>
<tr>
<td><strong>Herbivory</strong></td>
<td></td>
</tr>
<tr>
<td>Large Parrotfish</td>
<td></td>
</tr>
<tr>
<td>Large Carnivorous Fish</td>
<td>(Groupers, Snappers &amp; Barracuda)</td>
</tr>
<tr>
<td>Coral Recruitment</td>
<td>(density of corals &lt; 40 mm diam)</td>
</tr>
</tbody>
</table>

Fig. 3. Key drivers of reef health and resilience, which are the focus for monitoring Bonaire’s reefs (from Bonaire Report 2005). The underlined variables are prime drivers. Carnivorous fish were included as a measure of fishing pressure and to evaluate the efficacy of the fish protected areas (Fig. 4).

**Managing for coral reef resilience in Bonaire National Marine Park**

First, it is important to acknowledge there are several unique biophysical and social factors that play a role in the health of Bonaire reefs. The island is sufficiently far south that hurricane frequency is very low compared to elsewhere in the Caribbean. It is a relatively dry island with very little agriculture, generally low runoff and no rivers that can carry harmful sediment, nutrients and chemicals to coral reefs. In 1971, the island banned the use of spearfishing and there was traditionally very little use of fish traps that are so common throughout the Caribbean. We know of no other coral reef system in the Caribbean with those restrictions but those two factors alone protect herbivorous parrotfish that are easy to shoot with spears and readily enter fish traps. The consequences of these factors are that Bonaire’s coral reefs have relatively intact habitat architecture and an abundance of herbivorous parrotfish that keep seaweed cropped short (Steneck, personal observation, 1990, Kramer 2003).
With the quality of Bonaire’s reefs attracting divers from around the globe, a diver fee was instated to fund a non-governmental organization (STINAPA Bonaire) that manages the Bonaire National Marine Park (BNMP) (Solofa, Chapter 10). Without this NGO, the management of Bonaire’s reefs may have been impossible.

We began monitoring reef sites in Bonaire in 2003. The six initial sites (Fig. 4) were designated by Ms. Kalli DeMeyer who was the first Manager of the Bonaire National Marine Park (BNMP). In 2008 enforcement of the Fish Protected Areas (FPAs) began so in 2009, Mr. Ramón de León, the then Manager of BNMP suggested the addition of three sites to balance sampling around the FPAs. In 2010 one additional site (free of divers) was added making the total of 11 monitored sites (Fig. 4).

Stratification of sampling design and repeated sampling at fixed locations is necessary for precision and statistical power. Accordingly, we have repeatedly visited the same sites (adding sites when FPA’s were established), at 10 m depths, employing identical methods for the past 14 years (Fig. 4). These sites are physically similar in terms of wave action and sediment effects so they can be combined to assess long-term trends.

**Bonaire’s monitored and protected sites**

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Treatment</th>
<th>2003</th>
<th>2005</th>
<th>2007</th>
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<th>2011</th>
<th>2013</th>
<th>2015</th>
<th>2017</th>
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<td>✓</td>
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<tr>
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<td>FPA</td>
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<td></td>
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<td></td>
</tr>
<tr>
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</tbody>
</table>

**Table:**

- **Number of sites:** 6 6 6 9 11 11 11 11
- **FPA’s established:**

Fig. 4. The location, management treatment (Fish Protection Area (FPA) or control), and years of study for Bonaire’s monitored sites, 2003 to 2017.
Coral reef ecosystems are created by, and require, live coral for their structure and function. Bonaire’s reefs remain among the healthiest in the Caribbean in that corals occupy more space than any other group (specifically seaweed: Fig. 5; Steneck, Chapter 1). In contrast, most formerly coral-dominated reefs are now seaweed-dominated reefs throughout the Caribbean. Nevertheless, static measures of coral or algal cover are not as telling as are the trends.

![Graph showing trends in coral and seaweed cover in Bonaire's reefs](image)

**Fig. 5.** Comparison and trends in live coral and seaweed (macroalgae) from over 35,000 studies throughout the Caribbean (Jackson et al. 2014) and Bonaire (Steneck Chapter 1).

**Trends and trajectories for Bonaire’s Coral Reefs**

At all 11 monitored sites, coral cover was high (greater than 45%) and algal cover was extremely low from 1999 until the coral bleaching event of 2010, when about 10% of the coral died and seaweed abundance increased sharply (Fig. 6 A,B; Steneck, Chapter 1). For those two indicators of coral reef health, the negative impact of the bleaching event
was easy to document. However, how the ecosystem responded after the bleaching disturbance was extremely important. Coral cover continued to decline following the bleaching event hitting a low in 2013 but then coral started increasing – slowly at first but it accelerated in 2017 (Fig. 6a; Steneck, Chapter 1). We observed some of the heavily impacted coral species recovering from the bleaching event. Fortunately, the 2016-2017 bleaching event killed very little coral (Kowalsky, Chapter 9). Juvenile coral densities also increased steadily after 2013 to a record high in 2017 (Fig. 6c).

![Bar chart showing trends in coral, seaweed, and juvenile coral densities.](image)

Fig. 6. Trends in coral, seaweed, and juvenile coral densities. Recent trends since 2011 (post-2010 bleaching) illustrate how Bonaire’s coral reef ecosystem has responded since the bleaching event. Data for 2017 are in Steneck chapter 1 for coral and seaweed and in Rossin and de León Chapter 5. Vertical lines on bars show variance as standard error.

The trend of steadily declining seaweed abundance following the 2010 phase shift is unusual for most Caribbean coral reefs but it suggests strongly that Bonaire’s coral reefs are resilient and all monitored “key drivers” (Fig. 3) have trended towards a positive state (Figs. 6B, 7).

Negative effects of seaweed on coral reefs does not necessarily relate to their percent cover. A low-canopy that is no more than 5 mm above the reef surface has much lower negative impacts on reef corals than does a thick carpet (high canopy) of seaweed. Many
researchers now use the algal volume (e.g. Mumby et al, 2013) which is determined by multiplying the percent cover times canopy height. This “algal index” scales with seaweed biomass (see Steneck et al. 2014). The spike in macroalgae recorded in 2011 was less than an algal index of 300 (Fig. 6B) but given that the Caribbean average ranges between 700 and 900, Bonaire’s seaweed was modest in 2011 and it has been trending in a better (i.e. lower) direction (Fig. 6B).

The decline in harmful seaweed likely resulted from the steady increase in herbivory (Fig. 7A). There was less seaweed on reef sites in Bonaire that had more abundant parrotfish (see Fig. 10 in Steneck Chapter 1). However, as coral cover increases (Fig. 6A), it concentrates parrotfish grazing on the remaining reef (Williams et al. 2001). Also, Bonaire’s coral reefs are more complex in their habitat architecture than most coral reefs in the Caribbean (see Fountain, Chapter 6). The “rugosity” or spatial complexity created by the corals corresponds with parrotfish abundance (Fountain, Chapter 6) so interactions and feedback between and among grazers (Lieberman, Chapter 8) and corals (e.g. Fig. 2) may contribute significantly to the resilience of Bonaire’s coral reefs.

Fig. 7. Trends in parrotfish, Diadema and carnivorous fishes. Red line indicates coral bleaching event of 2010. 2017 data for parrotfish are in Boenish and Wilson (Chapter 2), Diadema in Hartill (Chapter 3) and carnivorous fish in Boenish and Richie (Chapter 4).
Herbivory in Bonaire is primarily accomplished by grazing parrotfish and surgeonfish (the latter being much more important in shallower depths than our 10 m monitoring stations). Territorial damselfishes can inhibit other, mostly smaller, herbivorous fishes (Martin, Chapter 7) but overall their impact is modest. The long-spined sea urchin *Diadema antillarum* was an important herbivore in the past (Hughes 1994) and remains important in some small shallow areas in the Caribbean today (Idjadi et al. 2010). However, population densities of this sea urchin must exceed one per square meter to function as an herbivore that removes seaweed. Population densities of *Diadema* in Bonaire have consistently remained well below those functional levels (i.e. < 0.02 urchins/m²; Hartill, Chapter 3; Fig. 7B). Because we find small (mostly juvenile) sea urchins during each monitoring session (see Hartill, Chapter 3), and we know adult urchins do persist in a few shallow areas, we suspect that predators rather than recurrent disease or pollution on the reefs have been keeping *Diadema* populations at their persistently low levels.

Carnivorous fish species including groupers, snappers, jacks, barracuda and grunts are highly desirable for both commercial and recreational fishing and are the primary target for most fishers in Bonaire (Nenadovic 2007). Historically, fish traps had not been used on Bonaire’s coral reefs until relatively recently. Significantly, in spear fishing was banned in 1971. When fish traps began being used over the past decade STINAPA became concerned and proposed legislation in 2010 designed to phase them out. As a result of these practices, carnivorous reef fish were only harvestable by hook and line fishing. This approach may be working since all groups of carnivorous fishes have varied without trend since 2011 and abundances overall have increased in 2017 (Fig. 7C).

We do not mean to imply there is no fishing pressure on Bonaire’s reefs. To estimate the impacts fishing may have on predatory fishes we compared the biomass of all fished (“control”) sites with Fish Protected Areas (FPAs). FPA reefs have higher biomass of carnivorous fish species (Fig. 8). In contrast, there was no significant difference between FPA and control sites for parrotfishes or other non-targeted species (Boenish and Wilson, Chapter 2). These results suggest fishing pressure does exist Bonaire’s coral reefs and likely results in the virtual absence of large groupers (Boenish and Richie Chapter 4).

![Carnivore biomass in Fish Protection Area (FPA) and all other sites from Boenish and Richie (Chapter 4; see Fig. 4). Variance as in Fig. 6.](image)
Recent trends among the strongest drivers of reef health (i.e. Fig. 2) such as increases in coral (juvenile and adult) and decreases in parrotfish and seaweed abundances, are all “positive trends” (Fig. 9). However, the recovery took considerably longer than expected given the documented high rates of herbivory and low abundance of seaweed prior to the 2010 bleaching event.

Fig. 9. Summary showing positive trends in all four key drivers of coral health since 2010. Significant positive trends are signified with blue rectangles (summary data in Figs. 6, 7).

Studies suggested that Caribbean coral reefs may be particularly vulnerable to seaweed colonization because seaweed growth rates are greater than on Pacific reefs (Roff and Mumby 2012). The fragility of herbivore control of seaweed was evident from the 2010 event. Several studies have suggested there are threshold values for coral, seaweed and
herbivores that if not maintained, can lead to a rapid shift to an alternative state that is relatively coral-free (MacNeil et al. 2015, Nystrom et al. 2008, Steneck et al. 2014). So far, at least, it appears Bonaire’s reefs remained on the positive side of these thresholds, enabling them to be resilient in the face of disturbances, even if recovery time may be slow.

Feedback interactions illustrated in the conceptual model (Fig. 2; Mumby and Steneck 2008) were strong between the structural complexity of Bonaire’s reefs and the population density of parrotfishes (Fig. 10). Abundant structure-producing corals such as *Orbicella* spp. (Steneck, Chapter 1), likely create Bonaire’s structurally complex coral reefs (Fig. 10A; Fountain, Chapter 6). This may improve recruitment of juvenile parrotfishes (Fig. 10B; Boenish and Wilson, Chapter 2) resulting in a higher parrotfish abundance driving down macroalgae (Fig. 10C, Boenish and Wilson, Chapter 2; Steneck, Chapter 1). At lower levels of seaweed abundance, higher rates of coral recruitment were recorded (Fig. 10D, Rossin and de León, Chapter 5). Presumably with time, coral recruits grow and create more complex reefs further concentrating grazing (Figs. 2, 10A).

Fig. 10. Complex interactions between A) coral and structural complexity, B) structural complexity and parrotfish abundance, C) parrotfish abundance and macroalgae, and D) macroalgae (seaweed) abundance and juvenile corals. Chapters where studies can be found are included in each graph.
Overall, Bonaire’s monitored coral reefs have relatively abundant fish that contribute to healthy reinforcing of ecological feedbacks (Figs. 2, 9, 10) that maintain resilience in recovery against disturbances such as the coral bleaching event in 2010 (Fig. 6). Although Bonaire’s carnivorous reef fish biomass varied without trend since that event, the increases in herbivore populations and other key drivers of resilience were not compromised. In fact, overall fish biomass falls close to that expected for fully protected and fully functional coral reefs (MacNeil et al. 2015).

If there is one lesson we’ve learned about the management of coral reefs it is that they are fragile ecosystems that maintain a delicate balance. It would be a mistake to take the current healthy state of Bonaire’s coral reefs for granted and assume management can be relaxed. As coastal development increases it becomes more important than ever to keep all impacts to a minimum. Only with continued vigilance will it be possible for Bonaire to keep its clear signs of resilience functioning into the future.

**Literature Cited**

Arnold, S., Mumby, P. Steneck, R. S. 2010 Running the gauntlet to coral recruitment through a sequence of local multiscale processes. Marine Ecology Progress Series. DOI 10.3354/meps08724.


Chapter 1: Patterns and trends in abundance of corals and seaweeds at Bonaire’s monitored coral reefs

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1University of Maine, School of Marine Sciences

Abstract

Surveys on the distribution and abundance of stony coral, seaweed (called “macroalgae”) and crustose coralline algae conducted at the 11 monitored sites (total of 44 transects, 10m each) determined overall abundance of coral is high (47.3 % ±1.7 SE) and macroalgae is low (6.02% ± 0.98 SE). The 2010 bleaching event caused a abrupt 10% decline in coral cover resulting in a sharp increase in macroalgae. However, subsequent years showed steady recovery and in this report we document that coral abundance, macroalgae, and crustose coralline algae all are at or near prebleaching levels. Taxa-level abundances have not changed and dominant corals in rank order remain two species of Orbicella (mountainous star coral), Madracis, Montastraea and Undaria (formerly Agaricia). The four northern-most sites have significantly greater abundance of macroalgae. That pattern could be due to those sites having greater exposure to waves than other monitored sites.

Introduction

Stony corals define coral reef ecosystems. While most coral reefs in the Caribbean are now seaweed reefs (i.e. macroalgal reefs), Bonaire is an exception. It has maintained live coral cover close to what had existed in the Caribbean in the 1970s (Gardner et al. 2003). While regional declines in coral abundance are well accepted, it remains unclear why so many coral reefs have been unable to recover. Some have pointed to the role of algae in poisoning corals (Rasher and Hay 2010) and reducing coral recruitment (Arnold et al. 2010) as precluding coral recovery. Others have wondered if reefs have shifted to macroalgae (Bruno et al. 2009) and whether herbivory drives algal abundance patterns (Suchley et al. 2016). Some of these disagreements relate to the sampling design and how the reefs and their algae have been quantified. Without careful sampling stratification and commensurable survey methods, these questions cannot be resolved.

In 1999-2000, the first standardized, species-specific, high-resolution assessment of Caribbean coral reefs was developed as the Atlantic and Gulf Reef Rapid Assessment or “AGRRA” protocol and initial assessments were conducted throughout the region, including 20 reef sites in Bonaire. Those surveys determined that Bonaire had among the highest coral cover and lowest seaweed abundance in the Caribbean in 1999 (summarized in Kramer 2003). Building from this baseline in 2003, a team from the University of Maine began long-term monitoring of Bonaire’s coral reefs. All surveys were conducted at fixed depths (10 m) on specific monitored reefs selected by STINAPA. I alone have monitored the reef corals and algae during the first two weeks of March every other year since 2003. During these monitoring trips, we consistently recorded high abundance of
coral and low abundance of macroalgae through the 2009 monitoring period (Bonaire Report 2009). Then, in 2010 Bonaire suffered a bleaching event that killed 10% of coral and triggered a significant increase in macroalgae (Bonaire Reports 2011, 2013, 2015).

Coral reefs of the Caribbean rarely, if ever, recover from serious disturbances such as coral bleaching or disease (Connell 1997). Some have argued this problem results from feedbacks in which herbivore loss contributes to increased seaweed which further kills adult corals inhibiting recruitment of juvenile corals (Mumby and Steneck 2008, Rasher and Hay 2010, Steneck et al. 2014). It remains unclear how Bonaire’s reefs, which exceed most Caribbean averages in terms of coral cover and herbivory, would respond to this external shock such as the 2010 bleaching event.

This report is the next in the series of standardized surveys all conducted at identical sites and on permanent transects quantifying patterns in the distribution, abundance and species composition of stony coral, macroalgae and crustose coralline algae at monitored sites along Bonaire’s coral reefs. With this study, we continue to build the data (both electronic and hard copy in the appendix of this report) on the trajectory of the structure and functioning of these coral reef ecosystems and specifically the reef’s capacity to recover from the 2010 bleaching event.

**Methods**

The distribution and abundance of major reef-occupying groups such as stony coral, macroalgae and crustose coralline algae (abbreviated “CCA”) were quantified along replicate 10m line transects (methods of Benayahu and Loya 1977 and commensurable with the AGRRA protocol, Kramer 2003) at 10m depth at each of our 11 study sites (listed in Fig. 2). Specifically, for each 10m transect, all benthic organisms occupying hard substrate under the tape were measured. This included each coral species, gorgonians, sponges, and algae. Algae were subdivided into ecological “functional groups” (see Steneck and Dethier 1994) such as crustose coralline, articulated coralline, foliaceous macroalgae (or simply “macroalgae”), and non-coraline crusts (e.g. peyssonelids). The macroalga *Lobophora* was also singled out because of its particularly threatening encrusting growth form that can negatively affect small and juvenile corals. Because reefs are often divided by sand channels and voids, all data were corrected to reflect percent cover of hard substrates. I focused this chapter on the most abundant and diagnostic groups of corals, macroalgae and crustose coralline algae.

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

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

Results

Species patterns

*Orbicella annularis*, *O. faveolata* (Mountainous star corals), *Madracis auretenra*, *Montastrea cavernosa* and *Undaria agaricites* are the top five most abundant corals comprising 75% of the coral cover on monitored reefs (Fig. 1). Of these, the *Orbicella* contribute most to the reefs habitat architecture (see Fountain, Chapter 6).

**Dominant Corals at 10 m**

<table>
<thead>
<tr>
<th>Species</th>
<th>% live coral</th>
</tr>
</thead>
<tbody>
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<tr>
<td><em>Orbicella faveolata</em></td>
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<td><em>Madracis auretenra</em></td>
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<tr>
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<tr>
<td><em>Undaria agaricites</em></td>
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<tr>
<td><em>Millepora alcicornis</em></td>
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<tr>
<td><em>Colpophyllia natans</em></td>
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<tr>
<td><em>Porites asteroides</em></td>
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<tr>
<td><em>Siderastrea siderea</em></td>
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<tr>
<td><em>Meandrina meandrites</em></td>
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<tr>
<td><em>Orbicella franksi</em></td>
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<td><em>Madracis pheroensis</em></td>
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<td><em>Millepora complanata</em></td>
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<td><em>Eusmilia fastigata</em></td>
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<td><em>Madracis decactus</em></td>
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<td><em>Undaria humilis</em></td>
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<td><em>Undaria lamarkii</em></td>
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<tr>
<td><em>Diploria labirintheformis</em></td>
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<tr>
<td><em>Porites porites</em></td>
<td></td>
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<tr>
<td><em>Pseudodiploria strigosa</em></td>
<td></td>
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<tr>
<td><em>Leptoseris natans</em></td>
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Fig. 1. Abundance of coral species at the 11 monitored sites. Error bars reflect ± one standard error of the mean (SE).

Patterns among monitored sites

Live coral was relatively abundant (i.e., 47% of hard substrate was occupied by live coral; Fig. 2), with only modest variations among sites. Nevertheless, some sites such as Forest on Klein Bonaire and Karpata had higher than average coral cover while other sites such as Calabas and Barcadera had lower than average coral cover (Fig. 2).
Macroalgal abundance is low compared to most coral reefs in the Caribbean. However, among study sites, the four northernmost sites from Barcadera to the No-dive reserve were consistently above average in algal percent cover, canopy heights and overall algal volume (also known as the algal index; Fig 3A-C, respectively). Several recent studies simply use the algal index or algal volume to illustrate algal abundance (e.g., Mumby et al. 2013, Webster et al. 2015). *Lobophora* is an alga of particular concern because it can functionally encrust some reef substrates and in so doing, cover small and newly settled corals (Arnold et al. 2010). Lobophora was absent from most monitored reefs but it increased in abundance among the northernmost sites (Fig. 4). Another site with higher than average algal abundance is Calabas (Fig. 3).
Fig. 3 Macroalgal abundance expressed in terms of A) percent cover, B) canopy height (mm) and C) an algal index or algal volume which is % cover X canopy height. Variance and island wide averages expressed as in Fig. 2.

Fig. 4. *Lobophora* abundance with variance and island wide averages expressed as in Fig. 2.
Algal turfs are a diverse combination of filamentous algae and cyanobacteria. This “epilithic algal matrix” is nutritious and is a favored food of grazing parrotfish (Clements et al. 2016). Algal turfs colonize all hard substrates very rapidly and invariably are the first group to colonize dead coral. Because this assemblage occupies all available hard substrate, quantifying abundance as purely a function of the area it covers is not very telling.

The height of algal canopies is independent of percent cover and thus is a good way to monitor the effective rates of herbivory. This is necessary because the accumulation of algae is both a function of rates of algal growth and rates of algal removal by herbivores. This metric can be usefully applied to diminutive filamentous turf algae which grows remarkably rapidly. Thus, the average canopy height at any location integrates the rates of algal growth (increasing the canopy height) and the rates of herbivore cropping (reducing canopy heights). Therefore, herbivory is best measured as bite rates per unit area, and as such turf canopy heights become a good indicator of grazing rates.

Turf algae impedes coral settlement, traps sediment and kills other organisms when its canopy height reaches or exceeds 4 mm. The average turf canopy heights on the monitored reefs was less than 2 mm (Fig. 5). Two sites with higher than average turf canopies were Windsock and Barcadera. Nevertheless neither site reached an average canopy height thought to be damaging to the health of the reef.

![Turf Canopy heights](image)

Fig. 5. Turf canopy heights with variance and island wide averages expressed as in Fig. 2.
Crustose coralline algae occupies considerable area on some coral reefs but because they grow slowly and other turf and macroalgae can grow on them, they can disappear from coral reefs where herbivory low or almost absent (Steneck 1997). Coralline cover on monitored coral reefs averaged about 7% on Bonaire’s monitored reefs (Fig. 6). The highest abundance was in the No Dive Reserve and the lowest were at Calabas and Reef Scientifico.

![Crustose Coralline Algae](image)

**Fig. 6.** Abundance of crustose coralline algae with variance and island wide averages expressed as in Fig. 2.

*Patterns among monitored years*

The best way to monitor the “health” of coral reefs is to track changes over time (see Executive Summary). This has been done for the most important drives of coral reef health, coral, macroalgae and CCA abundances.

Temporal trends since 1999 reveal several important changes. Coral cover had remained well above 40% cover from 1999 through 2009. Then coral bleaching in November of 2010 resulted in a 10% loss of coral cover, which has since recovered slightly (Fig. 7). Coral cover was lowest in 2013 but showed a slight recovery at first but then a strong
increase in 2017 (Fig. 7). I observed *Colpophyllia* colonies that had suffered considerably in the 2010 bleaching event, but there is clear evidence that they are recovering now (many formerly damaged colonies have grown together as they heal from the bleaching event).

Fig. 7. Trends in coral abundance 1999 to 2017 with error bars as in Fig. 1.

Macroalgae had been increasing slowly through 2009, with a sharp increase following the 2010 bleaching event (Fig. 8). However, every subsequent monitoring period has shown declines in algal abundance. As of 2017, the monitored reefs have macroalgal abundance close to what existed prior to the 2010 bleaching event.
Crustose coralline algae had declined for a decade to its low abundance in 2009 (Fig. 9). However it increased following the bleaching event and has remained relatively constant since.
Discussion:

While the consequences of Bonaire’s 2010 bleaching event were initially uncertain, found that the relatively stable and high coral cover (more than twide Caribbean average Jackson et al. 2014), prepared Bonaire well for full recovery from the bleaching disturbance. This, along with the increase in CCA the decline in macroalgae (Figs. 8, 9) and increase in juvenile corals (Rossin Chapter 5) suggests that Bonaire’s reefs are resilient.

This is unusual for the Caribbean where reefs have rarely shown any evidence of recovering from disturbances (Connell 1997). Key to the recovery may be in maintaining low algal biomass. This is particularly difficult in the Caribbean because algal colonization rates and growth are greater in the Caribbean than in other reef systems (Roff and Mumby 2012). The critical impacts of herbivorous fish was shown in an experiment in which large parrotfish were restricted from grazing in small areas that shifted to macroalgae dominance and reduced coral recruitment (Steneck et al. 2014). Other studies have demonstrated toxic effects of macroalgae on reef-building corals (Rasher and Hay 2010). Therefore the steady decline in macroalgal abundance (Fig. 8) is necessary for the structure and healthy functioning of coral reef ecosystems.

Drivers of algal abundance

Numerous studies have explored which factors most affect the abundance of harmful macroalgal (seaweed). Above we pointed out a trend of increasing algal abundance at the northern most sites. It is possible this may be due to higher water motion there from swells that wrap around the northern tip of Bonaire. I could find no physical oceanographic studies examining flow fields around Bonaire but there are numerous “Google Earth” images that allowed me to look for coastal waves breaking on shore from a constant altitude of 600 m. Waves were only detected at the northern sites.

The other likely driver would be herbivory. To investigate if patterns of parrotfish (scarid) abundance were consistent with patterns of algal abundance, averages for both variables per site were plotted. The resulting inverse relationship (Fig. 10) is consistent with the pattern of herbivore control.
Fig. 10. The relationship between macroalgal abundance and parrotfish densities. Each point represents one monitored site.

Other chapters explore the distribution, abundance and grazing rates of herbivorous fishes (see Boenish and Wilson, Chapter 2, and Liebermann, Chapter 8). However, the degree to which herbivory meets or exceeds the rates of algal production is the critically important dynamic in determining algal abundance. Given that, it is evident that herbivore impacts outweigh the island wide gradient of production.

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

**Literature Cited**


Chapter 2. Status and trends of herbivores in Bonaire’s monitored coral reefs

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Abstract

Herbivorous fish are key contributors to the resilience of functioning coral reef ecosystems in the face of anthropogenic and non-anthropogenic disturbances. Despite Bonaire’s proactive management efforts, herbivores declined from 2003-2011, and remained near stasis through 2015. This year, for the first year since monitoring began in 2001, significant increases in both herbivore density and biomass were observed, suggesting strong signs of recovery of Bonaire’s reefs following an acute coral bleaching event in 2010. Of the herbivorous feeding groups present, scarids (parrotfish) dominated both in density and biomass and comprised the bulk of the recovery. Site to site variation was high, though all sites monitored consecutively since 2011 (fish protected area and control) had significant increases in density following the recent herbivore equipoise. Overall, scarid density increased 105% and biomass increased 36% since 2015, suggesting strong recruitment has occurred in recent years. Our findings are not consistent with the 2015 herbivore report suggestions that herbivore stasis may have been due to carrying capacity limitations. Scarid density is currently approaching 2003 levels, justifying speculation that herbivores may still be on a positive trajectory following recent disturbance events, with further room for recovery.

Introduction

Caribbean coral reefs have experienced pervasive well-documented shifts from coral-dominated to algal-dominated ecosystems in recent decades (Mumby et al. 2007, Jackson et al. 2014). A key driver of these widespread phase shifts has been a regional decline in coral reef herbivores (Mumby & Steneck 2008). In coral-dominated ecosystems, herbivorous fish and/or urchins graze down algae, facilitating growth and recruitment of competing juvenile corals. However, when grazing levels are too low to match algal growth, algae physically overgrow adult and juvenile corals, chemically inhibit coral growth and recruitment, and develop chemical defenses against consumers, locking the system into an algal-dominated state (Rasher & Hay 2010, Arnold et al. 2010, Steneck et al. 2014). Without living coral, biotic and abiotic erosion causes reefs to lose their structure and provide fewer complex habitats for recruiting organisms including herbivorous fish and urchins (Connell & Jones 2006, Alvarez-Filip et al. 2009). This loss of structure acts as a reinforcing feedback, further inhibiting recovery of functional herbivory (Mumby & Steneck 2008).

In order to safeguard against algal phase shifts, recommendations have been made to manage for “surplus herbivory” (Mumby et al. 2007, Mumby & Steneck 2008) as well as herbivore diversity (Burkepile & Hay 2008, Adam et al. 2015). Herbivores increase the
resilience of reef systems to weather events, climate shifts, and disease outbreaks by suppressing algal growth on damaged coral and enabling coral recovery (Mumby et al. 2007, Roff & Mumby 2012). However, resilience in the face of these stressors requires a buffer of herbivory capacity beyond levels typically required to maintain coral dominance. Resilience also requires diversity of herbivores to ensure “complementarity” of functional roles even if a subset of species become threatened or extirpated.

Lack of sufficient herbivory has been to a large extent responsible for the large-scale algal phase shifts that have occurred on Caribbean reefs in recent decades. The mass mortality of *Diadema antillarum* urchins in the 1980’s greatly reduced herbivory levels and left only herbivorous fish such as scarids (parrotfish), acanthurids (tangs and surgeonfish) and yellowtail damselfish as key algal-denuding grazers (Mumby 2006). A concurrent outbreak of white band disease on acroporid corals (Lentz et al. 2011) increased space for algal colonization and thus increased need for algal suppression from herbivores. Simultaneously, increasing fishing pressure on herbivorous fish drove herbivory levels below the threshold required to maintain coral-dominance, resulting in widespread shifts to an algal dominated state (Jackson et al. 2014).

Due in part to proactive management, Bonaire is one of the few exceptions to today’s algal-dominated Caribbean reefs. Over the past few decades it has maintained significantly higher live coral cover and lower algal abundance than other Caribbean reefs (Jackson et al. 2014). While Bonaire was not exempt from the *Diadema antillarum* mortality event, several management initiatives have helped maintain high herbivorous fish biomasses, thus maintenance of functional herbivory. Fishing size regulations were first instated in 1961, and a subsequent (and unprecedented) ban on all spearfishing was put in place in 1971. While general fishing pressure in the following decades was low compared to elsewhere in the region (Nenadovic, Chapter 8, Bonaire Report 2007), De Stichting Nationale Parken (STINAPA) and Bonaire’s Marine National Park instated two no-take “Fish Protection Areas” (FPAs) in 2008, and a formal ban on parrotfish harvest along with the phasing out of fish traps in 2010 (Arnold, Chapter 3, Bonaire Report 2011).

Since the inception of this monitoring program in 2003, Bonaire’s herbivorous fish populations have been quantified to better understand the health and dynamics of Bonaire’s reefs, aid local management decisions, and offer regional comparisons. This study examines herbivorous fish populations at eleven monitoring sites in 2017 in conjunction with historical trends. For 2017, we found increases in both herbivore density and biomass, suggesting Bonaire’s reefs are still recovering from the particularly strong bleaching event of 2010.

**Methods**

We quantified herbivorous fishes with visual surveys at 11 reef sites in Bonaire, a Dutch Caribbean island in the Leeward Antilles, in March of 2017 (Table 1). All monitoring sites were located on the west and leeward coast of Bonaire, with one site, Forest, located on Klein Bonaire, a small island less than one kilometer off Bonaire’s west coast. Five
sites have been biannually surveyed since 2003 and an additional six since 2011. The 11 monitoring sites include four denoted as fish protection areas (FPAs), where SCUBA diving is allowed but fishing is not. One site, No Dive Reserve, allows hook and line fishing but disallows recreational SCUBA activities. Compliance with fishing regulations is thought to be relatively high, with an overall low magnitude of hook and line fishing on the island.

Table 1. North-South orientation of sites including fish protection (FPA) status and diving access over survey years. “X” denotes an affirmation, “-” denotes absence, and * suggests survey data were incompatible with other years.

<table>
<thead>
<tr>
<th>Monitoring Site (North to South)</th>
<th>Management status</th>
<th>Year Surveyed</th>
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<tbody>
<tr>
<td></td>
<td>FPA</td>
<td>Diving</td>
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<tr>
<td>No-Dive Reserve</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Karpata</td>
<td>-</td>
<td>x</td>
</tr>
<tr>
<td>Oil Slick</td>
<td>-</td>
<td>x</td>
</tr>
<tr>
<td>Barcadera</td>
<td>-</td>
<td>x</td>
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<tr>
<td>Reef Scientifico</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Forest (Klein Bonaire)</td>
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<td>x</td>
</tr>
<tr>
<td>Front Porch</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Calabas</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Eighteenth Palm</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Windsock</td>
<td>-</td>
<td>x</td>
</tr>
<tr>
<td>Bachelor</td>
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The focal species of these surveys were denuding herbivorous fish pertaining to the scarid (family Labridae, parrotfish only) and acanthurid (family Acanthuridae, tangs and surgeonfish) groups, as well as yellowtail damselfish (*Microspathodon chrysurus*) (see Appendix A for complete species list). We conducted 30 m x 4 m (120 m²) belt transects at 10 m depth, consistent with past reports. We recorded count and total length (to the nearest centimeter) of herbivores and carnivores (for carnivore fish analysis, see Boenish and Ritchie, Chapter 4). Additionally, we recorded life history phases (juvenile, initial, terminal) for all scarid species. Sample size ranged from eight (Front Porch) to 13 transects (Windsock, Eighteenth Palm, Forest, and Barcadera). Individual transects were completed over approximately 10 minutes. Visual calibration was done with pre-marked PVC pipe to ensure consistency between surveyors. We conducted all surveys in daylight hours at approximately 9:00 or 12:00. Due to logistical limitations, Eighteenth Palm was surveyed at approximately 14:30.

**Data Analysis**

To maintain consistency with past Bonaire reports, length-weight conversions for herbivorous fish were taken from Bohnsack and Harper (1988), with modifications made by Peter Mumby (Appendix A). We calculated biomasses using species-specific allometric parameters (Equation 1):
where weight $W$ in grams is estimated by a function of length $L$ (mm) and the empirically-based growth parameters $a$ and $b$. We aggregated data by species and standardized to 100 m$^2$ for analysis. Computations were done exclusively in R (R Core Team 2017).

**Results**

*2017 Patterns by Site*

Total herbivorous fish biomass differed significantly between sites, with Calabas and Front Porch falling above Bonaire’s 2017 average and Bachelor, Reef Scientifico, and Karpata falling below (Fig. 1). Investigating site-level differences among scarids and acanthurids shows that scarids dominate at most sites, apart from Eighteenth Palm and No-Dive Reserve which have high but variable acanthurid biomasses driven by large schools of primarily blue tang (*Acanthurus coeruleus*) that swam through a subset of transects (Fig. 2).

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Fig. 1. Biomass of all algal-removing fishes by site, 2017. Dashed line indicates across-site average for 2017. Error bars indicate ± standard error by site (arranged north (left) to south).
Fig. 2. Scarid and acanthurid biomass by site, 2017. Error bars as in Fig. 1. Scarids made up the majority of total herbivore biomass, though Eighteenth Palm and No-Dive Reserve had high acanthurid contributions due to schooling blue tangs that passed through a subset of transects. The high standard error of acanthurid biomass in these sites reflects the variability among transects.

With regards to scarid biomass on Bonaire reefs, our results suggest there is considerable inter-site variation. Calabas and Front Porch had the highest scarid biomasses, while Bachelor, Eighteenth Palm, Reef Scientifico, and Karpata fell below the Bonaire average (Fig. 3a).

We found striking differences in scarid size composition between sites, and resultantly scarid density often showed different patterns than biomass (Fig. 3b). For example, Forest, which had a scarid biomass just above the 2017 Bonaire average, had a scarid density nearly two-fold higher than average. Similarly, Karpata had the second highest scarid density despite being one of the lowest sites in terms of scarid biomass. Conversely, Calabas had Bonaire’s highest scarid biomass but lowest density. Expectedly, trends in scarid weight distributions corresponded with these biomass and density patterns (Fig. 3c). Calabas had the largest fish on average, while Forest and Karpata had the smallest.
Fig. 3. Scarid biomass, density and individual weight by site in 2017. a) 2017 Scarid biomass plot arranged by site (North (left) to south). b) Scarid density plots by site. Dashed line indicates across-site average for 2017. Error bars as in Fig. 1. c) Individual Scarid weight distributions. Boxes represent inter-quartile range with bars at median values.

Long-term trends

Scarid biomasses showed steady declines from 2003 to 2009, relative stability from 2009 to 2015, and a significant increase from 2015 to 2017 (Figs. 4a, 5, Wilcoxon test, p<0.05). Scarid densities showed similar historical trends and an even larger increase between 2015 and 2017 (Figs. 4b, 6, Wilcoxon test, p<0.001). Every site monitored consecutively
since 2011 showed a 2017 increase in density, collectively amounting to an overall 105% increase over the 2015 survey. While the 2017 scarid biomass remains below the maximum observed in 2003, 2017 scarid densities are approaching 2003 levels.

Fig. 4. Average scarid biomass (a) and density (b) across monitoring sites from 2003 through 2017. Error bars as in Fig. 1. Note lack of scarid density data from 2007 to 2009. Both biomass and density declined from 2003 levels, with relative stability between 2009 and 2015 and increases between 2015 and 2017. Scarid biomass increased by 34% from 2015 to 2017, while density increased by 105%, nearly reaching 2005 levels.
Fig. 5. Average scarid biomass, 2003-2011. Error bars as in Fig. 1. The Bonaire average scarid biomass increased significantly from 2015 to 2017. Front Porch showed the largest site-level increase between 2015 and 2017, with Calabas also showing a notable 2015-2017 increase.

Fig. 6. Average scarid density, 2003-2011. Error bars as in Fig. 1. Bonaire average scarid density increased sharply from relatively stable levels in 2011-2015 to current levels in 2017.

Biomass and density proportions by species show that the scarid group is almost entirely comprised of three main species: stoplight parrotfish, queen parrotfish, and princess parrotfish (Sparisoma viride, Scarus vetula and Scarus taeniopterus, respectively) with notable contributions from redband parrotfish (Sparisoma aurofrenatum) (Fig. 7). Stoplight parrotfish biomass decreased from 2011 to 2013, with a corresponding increase in the biomass of queen parrotfish, though proportions have remained relatively constant between 2013 and 2017. Proportional distributions of scarid densities show expected patterns of species dominance, with the majority of density made up of princess and stoplight parrotfish and significant contributions from queen and redband parrotfish. Examining density changes by scarid phase shows increases from 2015 to 2017 across all phases (Fig. 8).
Fig. 7. Scarid biomass and density proportions by species, 2011-2017. Both biomass and density are dominated by stoplight, queen, princess and redband parrotfishes (*Sparisoma viride*, *Scarus vetula*, *Scarus taeniopterus* and *Sparisoma aurofrenatum*, respectively).

Fig. 8. Scarid density by phase, 2011-2017. Error bars as in Fig. 1. While densities of all three phases remained relatively stable from 2011-2015, all three phases increased from 2015 to 2017.
Effects of management status on herbivorous fish populations

Fish Protection Area status had no significant effect on herbivorous fish biomass (Fig. 9, one-way Anova, F=1.004,6, p<0.5). The 2015-2017 increase in herbivorous fish biomass occurred in both FPA and control sites, but was only significant for the control (Wilcoxon test, p<0.01, p>0.05). There was no statistically significant difference between biomass in the control sites and FPAs for 2017 (Wilcoxon test, p>0.05).

![Graph of herbivorous fish biomass by functional group in Fish Protection Areas (dark) and control sites (light) from 2011 – 2017. Error bars represent ± standard error. Management status had no significant effect on herbivore biomass (one-way Anova, F=1.004, 6, p>0.05).](image)

**Discussion**

2017 Patterns by site

Our surveys found differences in herbivorous fish populations among monitoring sites in terms of biomass, density, and average fish size, but come with some caveats. The abrupt increase in scarid densities and decrease in average scarid size found at Forest and Karpata suggest recent recruitment events, which might affect some sites more than others. Forest’s unique position at Klein Bonaire might expose it to different currents that facilitate scarid recruitment. However, we acknowledge site-specific differences in biomass and density could be connected to a range of factors, including algal abundances, reef structural complexity and predatory fish abundances (see Steneck, Chapter 1;
Fountain, Chapter 6; and Boenish and Richie, Chapter 4). Water quality and land use changes unfortunately were not documented in this report and although they might also contribute to site-level differences in herbivore populations, we note that some groups such as parrotfish increased at sites with existing or increasing coastal development (e.g. Calabas and Front Porch) and decline in undeveloped areas (e.g. Karpata). It is also important to acknowledge that our sampling frequency allows for only one temporal snapshot of each site every two years. To compensate for lack of survey frequency, we employed an experimental design that leans heavily on the variation among multiple sites. This work underscores the importance of continued monitoring of multiple sites to gain a more holistic understanding of larger trends on Bonaire’s reefs.

**Long-term trends**

Prior to this year’s report, stagnant scard trends raised concerns for the outlook of Bonaire’s reefs. Scared biomass and density declined steadily from the start of monitoring in 2003 through 2011. Populations remained relatively stable from 2011 to 2015, following the 2010 bleaching event and corresponding spike in macroalgal abundance (see Steneck, Chapter 1), as well as the 2010 ban on scard harvest and gradual cessation of fish trap use. In understanding why herbivorous fish and specifically scard populations had not recovered to historical levels, the 2015 report suggested that herbivores may have reached their carrying capacity on Bonaire reefs and/or that settling recruits may be limited by healthy populations of reef carnivores (Arnold, Chapter 2, Bonaire Report 2015). As we have seen considerable increases in biomass for both herbivores and carnivores (See Boenish and Ritchie, Chapter 4), we suggest that neither may be the case. Our evidence suggests that herbivores may still be on a positive recovery trajectory following recent strong recruitment.

Evidence for recent recruitment is further supported by the measured decrease in average scard length from 2015 to 2017 and a greater increase in density (105%) than biomass (36%). Ratios of dominant scard species remained fairly consistent over the course of these increases, suggesting that all dominant species are continuing to recruit (Fig. 7). We found that density increases occurred in all phases but most strikingly in the initial phase (Fig. 9). Juveniles in all sites made up a very small portion of biomass (<2%), but a moderate proportion (21%) of density. At most sites, the initial phase biomass proportion was ~30% ± 10%, while in Calabas and Front Porch, it was ~50%. There was a weak decreasing trend in average scard length from southern to northern sites (p=0.0013, df=69) (Fig. 10). Although this could be explained by a variety of factors, it does suggest that the recent strong scard recruitment was not spatially uniform across monitoring sites.
Fig. 10. Scarid length by latitude, 2017. Transect means of scarid length (cm) decrease significantly from south to north (p<0.005, \( r^2 =0.139 \)).

Effects of FPAs on herbivorous fish

The above general trends were seen inside and outside of Bonaire’s FPAs. As harvest of herbivorous fish prior to the establishment of FPAs in 2008 was thought to be relatively low and scarid harvest has been banned across all sites since 2010, it is intuitive that we did not find significant effects of FPAs on herbivorous fish. If FPAs effectively increase predator populations in coming years, we may see a converse effect due to predation limitations of herbivore recruits.

Implications for management and future outlooks

Following the bleaching event in 2010, there was a dramatic increase in macroalgae and turf canopy height (see Steneck, Chapter 1). As the reef has recovered, macroalgal abundance has declined. We speculate the years with more abundant macroalgae may have provided more food resources for herbivores, scarids particularly, that may have supported the recent increase in density. As algae is now re-approaching pre-bleaching levels, it is uncertain how strong of a factor competition and food limitation may play in scarid population dynamics. Pre-bleaching (2003) herbivore biomass was near 6kg/100m\(^2\), compared to the current levels of ~4.2 kg, suggesting there may still be room for further recovery. We observed quite extensive inter- and intra-species herbivore competition, which may result in compensatory responses to growth rates and grazing. Predominantly, herbivores were deterred by scarids and various species of damselfish (Family: Pomacentridae, Genera: Stegastes and Microspathodon). Given the reported high density and increases in damselfish abundance, it is unclear how close scarids are today to carrying capacity. If ecosystem structure remains intact following the recent disturbances and scarid dynamics mirror the resilience seen in other aspects of the reef, we may anticipate further increases in biomass. Because scarids are particularly known
for high levels of intra and inter-specific competition, full recovery will to a large extent hinge upon population size structure, territory structure, and food availability.

It remains an open question whether “surplus herbivory” described by Mumby and Steneck (2008) is attainable, but the recovery observed suggests reef resilience found nowhere else in the Caribbean. As noted in Mumby et al. 2007, herbivory levels required to maintain coral dominance are often close to the maximum levels observed, in which case feasible herbivory buffers might be quite narrow. If Bonaire’s declines in scarid biomass and densities from 2003 to 2015 were due to trophic limitations, a sizeable herbivory buffer may be unattainable. However, while herbivory levels were not sufficient to prevent the algal spike that followed the 2010 bleaching event, they have been sufficient in steadily reducing algal abundance in the years that followed. Seven years after the bleaching event, coral cover has returned to pre-bleaching levels and algal levels have been significantly reduced, indicating the phase shift to algal-dominance was reversed. The high scarid recruitment suggested from this year’s surveys is promising for the capacity to prevent and reverse future phase shifts in the face of unpredictable stressors.

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Chapter 3: Spatial and temporal patterns of the abundance and distributions of sea urchins Diadema and Echinometra on Bonaire’s coral reefs

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Abstract

Sea urchins are important benthic invertebrates that can have a profound effect on algal abundances in many marine ecosystems. The two most abundant urchins in Bonaire are the long-spined sea urchin Diadema antillarum, and the common urchin Echinometra viridis. I studied spatial and temporal trends in distribution and abundance of both urchin species on Bonaire’s coral reefs at the eleven monitored sites. The average densities of D. antillarum and E. viridis were 0.018 m$^{-2}$ (±SE 0.003) and 1.05 m$^{-2}$ (±SE 0.05), respectfully. Although densities have decreased slightly for both species since 2015, Diadema showed no net trend since monitoring began whereas Echinometra abundance increased following the 2010 bleaching event coincident with the post-bleaching increase in macroalgae. Diadema densities have remained below functional levels (>1m$^{-2}$) since surveying began in 2003. To explore predator effects, I compared urchin densities in Fish Protection Areas (FPA) and control sites. Diadema abundance increased among sites having more predators. However, most Diadema were immature and thus low food value for predators. The opposite was true for E. viridis. Its population declined at sites with more urchin predators. Importantly, E. viridis is reproductive at a much smaller size so most of the urchins recorded could have had gonads and thus may be much higher food value than Diadema. Nevertheless, the low densities of small Diadema recorded every year since 2003, indicate that they are failing to survive to large sizes. This pattern is consistent with the idea that Bonaire’s reefs either have too many urchin predators and/or not enough predator free refugia for Diadema in which to grow to adult size. Since both species have about the same size-frequency distribution in Bonaire despite Diadema typically growing to much larger sizes as adults than Echinometra, the presence of high food value gonads in the latter may explain why only the latter species showed evidence of predator effects.

Introduction

Sea urchins can play a critical role in controlling macroalgal growth in many different marine ecosystems. In the Caribbean, Diadema antillarum (long-spined urchin) has historically been an important herbivore in reef ecosystems (Carpenter 1981), effectively controlling macroalgal biomass and increasing the abundance of juvenile corals (Edmunds & Carpenter 2001). In contrast, Echinometra viridis (common urchin) is a crevice-dwelling urchin that is also common on Caribbean coral reefs (Steneck 2013) but feeds on drift algae and does not reduce algal biomass. In fact, its abundance correlates positively with algal biomass (McClanahan 1999).

In January of 1983, and over the course of the following 13 months, D. antillarum populations across the Caribbean suffered >93% mortality due to a waterborne pathogen
that originated in Panama (Lessios et al. 1984; Lessios 1988). The sudden removal of this important herbivore lead to phase shifts towards macroalgaedominated reefs, mostly on more heavily fished reefs (Hughes 1994). Bonaire’s reefs appear to have been able to resist similar phase shifts; this is likely due to high abundances of herbivorous reef fish that were released from interspecific competition following the die-off (Hay & Taylor 1985). Since then, *D. antillarum* populations have not returned to functional densities on many Caribbean coral reefs (Lessios 1995; Beck et al. 2014).

In this study, I surveyed the abundance and size distribution of four species of urchin present on Bonaire’s coral reefs. In an effort to determine if there were any temporal or spatial patterns in urchin population density, I compared my results to those from previous years and among study sites, particularly fish protection areas (FPAs) versus control sites. Lastly, I examined the two most abundant sea urchins, *D. antillarum* and *E. viridis* relative to urchin predatory fishes, reef rugosity and algal biomass.

**Methods**

I surveyed the abundance of the sea urchins *Diadema antillarum*, *Echinometra viridis*, *Eucidaris tribuloides* and *Lytechinus williamsi* via SCUBA at eleven sites along the leeward shore of Bonaire as a part of a long-term study of the health of their coral reefs (See Fig 4 in the Executive Summary). I surveyed four to eleven 20m² transects at each site. Each transect was placed parallel to shore at approximately 10m depths, where hard substrates were dominant. Each urchin along the 10 x 2m transect was recorded as well as its test diameter, which was noted to the nearest millimeter. I approximated the test diameters of the urchins that were completely nestled into crevices, as it was not possible to measure using a ruler.

For the purpose of this study, I focused on the urchins *D. antillarum* and *E. viridis* because the other species observed were rare and do not play a significant role as herbivores (Furman & Heck 2009). I made comparisons of the densities of *D. antillarum* and *E. viridis* at Fish Protected Areas (FPAs) and at the control sites in order to test for the potential effects of fish predators. I investigated size-frequency distributions for both species in order to determine if there were any density dependent size trends. I compared this year’s overall average density with those from previous years to investigate the trajectory of *D. antillarum* recovery.

In order to determine if there was a relationship between the presence of urchin predators and urchin density at each site, I calculated an Urchin Predator Index (UPI). An extensive study of the diets of 212 reef fish species described numerous urchin predators (Randall, 1965), fifteen of which correlated with species surveyed by Wilson and Boenish (Chapter 2). In Randall’s study the percent echinoid stomach content by volume was determined for each species, I multiplied this number by the biomass of the corresponding species surveyed in each transect at the Bonaire study sites. I calculated the sums of the products for each transect, and then I averaged these to find the UPI for each survey site.
I explored whether the rugosity of the reef (i.e., “spatial heterogeneity”) had an impact on urchin density. For this, I plotted urchin density as a function of spatial heterogeneity index at each site (see Fountain, Chapter 6). Lastly, in order to determine if urchins were food limited, I compared the macroalgal index computed by Steneck (Chapter 1) to the abundance of urchins at each site.

**Results**

Urchins were present at all survey sites, but *D. antillarum* was absent from Oil Slick and Karpata. Urchin densities at the FPAs were higher than at the control sites. The average *D. antillarum* density inside the FPAs was 0.027 m$^{-2}$ (±SE 0.002) and the average density for the control sites was 0.013 m$^{-2}$ (±SE 0.004) (Fig 1). *E. viridis* was found at all survey sites, with higher densities outside of the FPAs. *E. viridis* density inside the FPAs was 0.08 m$^{-2}$ (±SE 0.028) and the average density for the control sites was 0.28 m$^{-2}$ (±SE 0.067) (Fig 2). The average density of *D. antillarum* on Bonaire’s coral reefs was 0.018 m$^{-2}$ (±SE 0.0097). The overall average density of *E. viridis* was 1.05 m$^{-2}$ (±SE 0.0525, Appendix 1).

![Fig. 1. Average densities of *D. antillarum* at Fish Protected Area sites (left) and control sites (right). Column bars indicate ±SE for site density and lines represent the island-wide average density and average ±SE.](image-url)
The vast majority of *D. antillarum* were under 50mm in size (Fig 3a.). However, two larger individuals (80mm) were recorded (Fig 3a). The size frequency for *E. viridis* had a similar size-frequency distribution with test diameter between 20mm and 40mm (Fig 3b). Importantly, while the size distribution for *E. viridis* is typical for the species, Diadema recorded were significantly smaller than than recorded when they were abundant (Carpenter 1981). The overall urchin densities for 2017 were lower than the previous survey year for both species (Fig. 4).
Fig. 4. Densities of *D. antillarum* and *E. viridis* at surveyed sites over time. Error bars as in Fig. 1.

Fig. 5. Urchin density (No./m²) as a function of Urchin Predator Index (biomass of urchin predators per site multiplied by historical proportion of echinoid stomach volume, Randall 1965). Each data point represents a different survey site (Barcadera was omitted, see Methods and Appendix 2 for in-depth UPI calculations).

The UPI shows an increase in densities of *D. antillarum* where predator biomass is high (Fig. 5a). The UPI for *E. viridis* showed a lower density of urchins where predators where high (Fig. 5b). Barcadera had an abnormally high UPI due to a number of large fish, specifically black margate and porcupinefish, (*Anisotremus surinamensis*, and *Diodon hystrix*, respectively). Therefore this site was omitted from Fig. 5 (see Appendix 2 for complete summary of UPI and urchin densities).
Fig. 6. Urchin density (No./m²) as a function of spatial heterogeneity (m/m) for *D. antillarum* (left) and *E. viridis* (right), each point represents a different site (see Fountain, Chapter 6 for Spatial Index computation).

Fig. 7. Urchin abundance (No./20m²) as a function of macroalgal index for each site (see Steneck, Chapter 1 for Algal Index computation).

The population density of *D. antillarum* declined as a function of spatial heterogeneity, whereas *E. viridis* density increased (Fig 6). Importantly, whereas *D. antillarum* varied inversely with algal abundance, *E. viridis* varied positively (Fig 7).

**Discussion**

Sea urchin population densities in Bonaire remain low for both *Diadema antillarum* (Fig. 1) and *Echinometra viridis* (Fig. 2). Both species have declined since the previous survey (Fig. 4) but *D. antillarum* remain well below the reported 1 m⁻² density at which they have been documented to control algae on coral reefs (Mumby et al. 2006).
*D. antillarum* appears to have higher densities in FPAs, whereas *E. viridis* had higher densities at the control sites. Harborne et al. (2009) found that urchins were absent in areas protected from fishing (similar to FPAs), but this was not supported in this study for *D. antillarum*. Similarly, *D. antillarum* densities corresponded positively with UPI, (Fig 5). This is contrary to conventional wisdom what has been reported in the literature (Brown-Saracino et al. 2007; Harborne et al. 2009). The urchin predators described by Randall (1965) were not exclusively feeding on either of these species and therefore have sustained themselves even with extremely low *D. antillarum* densities, perhaps shifting their preference and preying more often on *E. viridis*. However, it is possible that the predators are optimal foragers and seek adult urchins packed with nutritious gonads. Whereas only a small fraction of the *D. antillarum* were large enough to reproduce, the majority of *E. viridis* were. Therefore the high food value of urchin gonads, could result in urchin predators targeting *E. viridis* rather than *D. antillarum*. Also it is possible, despite the trend in Fig. 5a, that these predators are inhibiting the return of *D. antillarum* to pre-mortality population density by preying on urchins as they outgrow the small shelter spaces that they currently occupy (Lessios 1988).

*D. antillarum* seek small crevices to hide in during the day (Carpenter 1984). Adults are gregarious and used to be found in large aggregations, where their proximity to each other provided refuge (Randall 1964). The size frequency distribution shows a decline in individuals with a 30mm test diameter or larger (Fig. 3). All small Diadema recorded were in shelters or crevices. Only one of the large (80mm) individuals was not protected by shelter. This lack of larger individuals could be due to a scarcity of medium and large sized shelters on Bonaire’s reefs. At low population densities where food is not limiting, *D. antillarum* grow rapidly, to sizes exceeding 100mm (Carpenter 1981; Hughes 1994). They can shrink their tests when population densities become high and food is limited, in order to conserve energy for reproduction (Levitan 1988). Yet this density-dependent size regulation occurs when *D. antillarum* densities exceed 10 m⁻² (Carpenter 1981; Levitan 1988), which is certainly not the case on Bonaire.

In comparing urchin densities to spatial heterogeneity of the reefs, we found that as reef complexity increased, densities of *E. viridis* increased as well (Fig. 6). The opposite relationship was true for *D. antillarum*, which could be due to the sizes of the crevices available for refuge. The majority of urchins were found within *Montastraea annularis* crevices, which are perfectly sized for the more compact and robust *E. viridis*. Around the same time that the *D. antillarum* die-off occurred, two important shallow reef-building coral species, *Acropora cervicornis* and *A. palmata*, suffered mass mortality due to white-band disease (Aronson and Percht 2001). Perhaps the refuges provided by the present framework of Bonaire’s reefs are not as ideal for larger *D. antillarum* as those provided by the acroporids. It is important to note that acroporids were most abundant in shallow reefs, from 1 to 5m depths (Aronson and Percht 2001), and that *D. antillarum*, although it has been recorded at depths of 400m, was also most abundant at those depths (Randall et al. 1964). Our surveys were conducted at 10 m.

McClanahan (1999) found that *E. viridis* was positively correlated with algal biomass, which is in agreement with what we found when comparing urchin abundance and algal
index for each site (Fig. 7). This highlights that E. viridis is more of an ecosystem passenger not an ecosystem driver as is the case with D. antillarum.

In conclusion, it seems that there are multiple factors limiting the return of D. antillarum to pre-mortality densities, including the lack of shelter from predators for intermediate-sized urchins and subsequent predation pressure. Bonaire’s reefs, although spatially complex, appear to not have the appropriate shelter space to allow D. antillarum to grow up and out of the size easily eaten by predators. Although we did not find a negative relationship between predators and D. antillarum densities, the documented presence of juvenile urchins for over a decade suggests something is killing them before they reach adult size, so predation pressure cannot be ruled out as a contributor to the low densities.

**Literature Cited**


Randall, J.E. (1965) Food Habits of Reef Fishes of the West Indies.
Chapter 4: Status and trends of carnivorous fish on the reefs of Bonaire
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Abstract

We quantified the population density, biomass and size distributions of carnivorous fish at 11 monitored reef sites along Bonaire’s leeward coast. We specifically compared Fish Protected Areas (FPAs) and open-access control sites to determine the effects of fishing pressure in Bonaire. We assessed trends in carnivore populations over the course of this monitoring program (2003-2017) as well as between 2015 and 2017 to better understand long-term patterns and current trajectories. Minimal differences in carnivore populations between FPAs and control sites suggest generally low fishing pressure in Bonaire. While Bonaire’s average carnivorous fish density showed no change from 2015 to 2017, there was a notable increase in biomass. Carnivorous fish populations show fluctuating trends since the onset of monitoring in 2003, but recent increases in biomass are an encouraging sign of Bonaire’s proactive reef management.

Introduction

The world’s coral reef ecosystems have declined in recent decades (Selig et al. 2010). This is particularly noticeable among Caribbean coral reefs (Gardner et al. 2003). Often fishing pressure is cited as a driving factor of reef declines (Bellwood et al. 2004). Carnivorous reef fish are usually among the first groups to be overfished and depleted on coral reefs due in part to their feeding habits and their suitability for consumption (Sala et al. 2001). However, Bonaire stands as an exception because it has some of the strongest fisheries management regulations in the Caribbean.

Legislation restricting spearfishing and fish traps in 1971 and 2010, respectively, has limited commercial and recreational fishing in Bonaire to a small hook-and-line fishery. Bonaire furthered their commitment to conservation of their reef ecosystems with the implementation of two no-take reserves called Fish Protection Areas (FPAs) in 2008. Such reserves have been found in other regions to increase the average trophic level of fish inside, as well as in the surrounding area (McClanahan et al. 2008). These effects have been shown to be enhanced when coupled with island-wide gear restrictions (McClanahan et al. 2008).

A central goal of this chapter is to evaluate the effects of Bonaire’s reef management on carnivorous fish populations. The long time-series of data is critical in assessing the efficacy of FPA-type management (Barrett et al. 2007). Previous studies have concluded that no-take reserves (such as Bonaire’s FPAs) shift reef fish communities to higher trophic levels by increasing carnivore abundance, particularly of large carnivores (McClanahan et al. 2008, Barrett et al. 2007). Carnivores are most vulnerable to fishing pressure, making them good indicators for the influence of management on the condition of the coral reef ecosystem.
The effects of carnivorous fishes on their environment can be difficult to quantify, with some studies finding that they lend stability to reef ecosystems (e.g. McManus et al. 2000), and others arguing they have little influence on lower trophic levels (e.g. Casey et al. 2017). Many suggest that top down forcing on reefs is diffuse and weak (Mumby et al. 2006).

In this chapter, we quantify patterns in the distribution, abundance, species composition and body size of carnivorous fishes at the 11 monitored sites in Bonaire. We investigate differences in abundance and biomass within and outside FPAs to test for the effects of fishing pressure, both on the total carnivore populations as well as on different groups of targeted fish. In addition to assessing inter-site differences, we also investigate long-term (2003-2007) trends in carnivore populations. The results of this research present an important example for other Caribbean systems attempting to gain ecosystem stability through proactive management.

Methods

Carnivorous fishes were quantified with visual surveys at 11 leeward reef sites on Bonaire and Klein Bonaire, Caribbean Netherlands, during the first two weeks of March, 2017 (Table 1, Appendix 4). Five of the 11 sites have been biannually surveyed since 2003 and six since 2009. The long timescale collection of data is critical in assessing the efficacy of FPA type management (Barrett et al. 2007) and is an essential part of the ongoing Before-After-Control Impact (BACI) study design (see Chapter 6a, 2011 Bonaire Report). Four sites fall within the boundaries of two Fish Protection Areas (FPAs), where SCUBA diving is allowed, but fishing is not. The FPAs were instated in 2008 motivated by scientific evidence suggesting predatory fish contribute significantly to reef resilience. One site (No-Dive Reserve) allows fishing but disallows recreational SCUBA activities (Table 1). Compliance of the fishing regulations is relatively high (Ramon de León, personal communication), with an overall low magnitude of hook-and-line fishing on the island.

Table 1. North-South orientation of sites including fish protection areas (FPA) and diving access over survey years. “X” denotes an affirmation, “-” denotes absence, and * denotes survey data were incompatible with other years.

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Visual surveys were conducted by two divers completing 30 m x 4 m (120 m²) belt transects at 10 m depth (methods modified from AGRRA protocol). Sample size ranged from 8 (Front Porch) to 13 transects (Windsock, 18th Palm, Forest, and Barcadera). A reel with 30 m of line spooled out from a diver swimming in along a 10 m depth contour. Fish size (total fork length) was estimated to the nearest centimeter for all herbivores and carnivores encountered on each transect. For the purpose of these analyses, we used only data on grunts, snappers, and groupers, (families Haemulidae, Lutjanidae, and Serranidae, respectively; see Appendix 5 for complete species list). Individual transects were completed over approximately 10 minutes. Visual calibration was done with pre-marked PVC pipe to ensure consistency between surveyors. Surveys were all carried out in daylight hours, approximately at 9:00 or 12:00. Due to logistical limitations, 18th Palm was surveyed at approximately 14:30.

Data Analysis

To ensure consistency with historic analysis, we calculated biomass for each species using species-specific allometric parameters obtained from previous survey years (Camacho, Chapter 4, Bonaire Report 2015; Appendix 6 of this report). When individual species parameters were unavailable, we used a congeneric species from Fishbase.org. We calculated biomass via the length-weight conversion equation (Equation 1):

\[ W = a \times L^b \]  

(1)

where weight, W in grams is given by multiplying growth parameter \( a \) by fork length, \( L \) (cm) to the power of \( b \). We aggregated data by species and family, and standardized to units per 100 m² for analysis (Appendix 4). Computations were done exclusively in R (R Core Team 2017).

Results

Density Trends

The population density of carnivorous fish ranged from about 20 to 50 individuals per 100 m² (Figs. 1 and 2). Calabas, Front Porch, and Bachelor showed the highest overall levels of carnivore density. The lowest level of carnivore density was found at Forest and Reef Scientifico. The most abundant carnivore species were French, smallmouth, and blue-striped grunts.
Fig. 1. Short-term changes in predatory fish density (number/100 m²) by site, 2015-2017. Error bars represent ± standard error.

Fig. 2. Overall predatory fish density (number/100 m²), aggregated by year, 2015-2017. Error bars as in Fig. 1.
The three most dominant carnivore families were the grunts (Haemulidae), snappers (Lutjanidae), and groupers (Serranidae). Of the three most common species observed in the survey, all three were from the grunt family. From examination of these three families, survey sites seem to fall in one of three general density patterns (Fig. 3). With the notable exception of Front Porch, which had high densities of all three families (>5 per 100 m$^2$), five sites either had relatively low or even densities between the families (<5 per 100 m$^2$), and five had low densities of snappers and groupers, with high levels of grunts. The distinction was not dependent on the management strategy or relative location (e.g. north-south) of the site.

![Density (#/100 m$^2$) of Dominant Predator Families by Site (2017)](image)

Fig. 3. Predatory fish density (number/100 m$^2$), by major family and site in 2017. Error bars as in Fig. 1.

Interestingly, length-frequency of all three families was much more consistent than density (Fig. 4). In all sites, snappers on average were larger than the other two dominant families. Calabas and No Dive had the largest average size of snappers, while Windsock has the smallest. Grunts were generally between 16-22 cm by site, with no notable outliers. Groupers, which were mostly composed of graysbys, where the smallest of the three major carnivore families, with only a 14-21 cm average length by site. This is ironic because species such as black, tiger and goliath groupers were historically among the largest carnivores on Bonaire’s reefs.

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Only six of the 11 sites increased in overall density from 2015 to 2017 (Fig. 1). The largest percentage decrease by site was found at Reef Scientifico (-50.7%), while the largest increase was found at Calabas (+104.6%). As was noted in the 2015 report, Bonaire’s FPA sites have higher predator density than controls (Camacho, Chapter 4, Bonaire Report 2015). This pattern was again confirmed for 2017 though the difference was not significant (Fig. 5, Wilcox test, p=0.1576). We found marginal, statistically non-significant increases in both control and FPA site average density from 2015 to 2017 (Fig. 5, Wilcox test, p_{control}>0.05, p_{FPA}>0.05). Overall, there was a modest (10.3%), though non-significant increase in carnivore density from 2015-2017 (Fig. 2, Wilcoxon test, p>0.05).
Biomass Trends

As with carnivore density, there was considerable site-to-site variation in biomass (Fig. 6). We found the most abundant carnivores by biomass were the French grunt, black margate, and schoolmaster snapper. Predator biomass at Calabas was approximately three-fold higher than most other sites (14.2 kg/100 m²). Average biomass was 5.5 kg/100 m² among all sites. FPAs had an average biomass of 7.7 kg/100 m², while control sites (excluding No Dive) sites had average biomass of only 4.1 kg/100 m² (Fig. 7). The majority of difference between FPA and Control sites is explained by the inclusion of Calabas. Without Calabas, FPA sites averaged 4.2 kg/100m², only 0.1 kg/100 m² more than controls and were not statistically different (one-tailed Wilcoxon test, p>0.05).
Fig. 6. Short-term changes in predatory fish biomass (g/100 m$^2$) by site, 2015-2017. Error bars as in Fig. 1.

Fig. 7. Mean Site biomass (kg/100 m$^2$) comparison for predatory fish, 2015-2017. Error bars as in Fig. 1. There was no significant difference between FPAs or controls from 2015-17 (Wilcoxon test, $p_{FPA} > 0.05$, $p_{control} > 0.05$).
Site-wise biomass of the three most abundant carnivore families showed large variation. Forest, Reef Scientifico, Karpata, and No Dive showed higher snapper biomass as compared to grunts and groupers (Fig. 8). In the remaining sites, grunts showed similar biomass to snappers. Furthermore, groupers never had the highest biomass at a site and their biomass never exceeded 0.7 kg/100 m² whereas in some sites grunts and snapper biomass approached 2 kg/100 m². Calabas had the highest biomass for snapper and grouper and among the highest for grunts. Karpata, in contrast, showed the lowest grunt and grouper biomasses with the second lowest snapper biomass.

![Mean Site Biomass of Dominant Predator Families (2017)](image)

Fig. 8. Mean site biomass (kg/100m²) of dominant families in 2017. Error bars as in Fig. 1.

Compared to the 2015 survey, three out of 11 sites showed a decrease in biomass (Fig. 6). Of the remaining 8 sites, increases ranged considerably, but were generally large (>50%). The site with the largest increase in biomass was Calabas (+337.5%), followed by its southern neighbor, 18th Palm (+91.9%). In 2015 Karpata had moderate biomass, but suffered the largest loss in 2017 (-53.3%). No Dive (no dive control) had similar biomass levels to the other sites in 2017. Although almost all sites showed population increases, FPA biomass increased substantially more, 96% vs. 36%, respectively, but due to high inter-site variation, neither increase was significant at α=0.05 (Fig. 7, Wilcox test, p_{fpa}>0.05, p_{control}>0.05). Overall predator biomass did increase across all sites from 2015 to 2017 (Wilcox test, p<0.05), amounting to a total gain of 58% from the 2015 survey.

**Discussion**

Overall, we found a modest and insignificant increase in population densities of carnivorous fishes (Fig. 1) but a sharp increase in biomass (Fig. 6) between the 2015 and 2017 surveys. Grunts had the greatest biomass and highest density though specific sites
exhibited variation in species and family composition (Figs. 3, 8). Given the significant increase in predatory fish biomass, the 2017 monitoring survey provides cause for optimism regarding the recovery potential of predatory fishes on the reefs of Bonaire following management action.

After relaxation of fishing pressure, biomass typically increases before population density (Barrett et al. 2006). In our analyses, Bonaire’s carnivore density did not show as clear an increase as biomass, although in the majority of sites there appeared to be either an increase or no change (Fig. 1). If biomass, and by proxy reproductive capacity, continues to increase as the current population of predators age, positive recruitment effects (e.g. increased density) could occur. However, the time lag for these changes may be long (MacNeil et al. 2015).

The FPA sites showed no statistically significant difference in density from the control sites and did not differ significantly from the corresponding 2015 numbers (Fig. 5). These findings are consistent with the overall low fishing pressure in Bonaire before and after the implementation of FPAs. We suggest that the modest difference between FPAs and fished reefs indicates relatively low fishing pressures on Bonaire’s reefs. The island-wide increase in predatory fishes may also be the result of improvements to the larger ecosystem (see Executive Summary). Bonaire’s efforts to restrict reef-harming activities and to enhance coral health through the protection of herbivorous fish would benefit carnivorous fish across sites. The recent trend of increasing or steady carnivore biomass in all sites suggests that current management strategies may be effective or possibly that fishing pressure is declining among younger people in Bonaire. If carnivorous fish populations and that densities are increasing then it is possible that further increases may
come as reproductive capacity builds. However, the fluctuation in biomass recorded over time from 2003-2017 (Fig 9) cautions against trying to predict future trajectories.

**Literature Cited:**


Chapter 5: Juvenile corals: patterns in time and space

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Abstract

We quantified the distribution, abundance and species composition of juvenile corals and their relationship with algae at 11 monitored reef sites in Bonaire. Identical data collection methods used since 2003 were employed to determine trends over time. The most abundant juvenile corals were Undaria agaricites and Porites asteroides. Overall, the density of juvenile corals varied relatively little among sites (averaging 27.2 juvenile corals per meter square ± 1.5 SE). The highest densities of juvenile corals were found at monitored sites of Windsock, Reef Scientifico, Calabas, and the No-Dive Reserve. Juvenile coral densities declined from 2003 to 2009, and were then exposed to a coral bleaching event in 2010 that triggered a sharp rise in macroalgal abundance known to inhibit coral recruitment. Since 2013, juvenile coral abundances have increased steadily as macroalgae has declined. Overall, the increase in coral recruitment is a promising trend suggesting that Bonaire’s coral reefs are resilient.

Introduction

In the 1980s coral reefs throughout the Caribbean collapsed with the disease-induced mortality of large branching Acropora species and the resulting reduction in habitat architecture (Gardner et al 2003, Alvarez-Filip et al 2009, Lirman and Schopmeyer 2016). A simultaneous die-off of the urchin Diadema antillarum, a key herbivore, stimulated a sharp increase in macroalgae that outcompetes juvenile corals for settlement space throughout most Caribbean coral reefs (Hughes 1994, Kramer 2003, Box and Mumby 2007).

Corals are known to compete with algae (Tanner 1995, Edmunds and Carpenter 2001, Lirman 2001, Kuffner et al. 2006). Macroalgae in high abundances can shade, poison or smother juvenile corals (Box and Mumby 2007, Rasher et al. 2011). Adult coral colonies that interact with high abundances of macroalgae can have reduced growth rates and fecundity, as well as an increase in tissue mortality (Potts 1977, Lewis 1986, Hughes 1989, Coyer et al. 1993, Tanner 1995, Lirman 2001). However, Bonaire’s reefs have traditionally had exceptionally low levels of algae compared to the rest of the Caribbean (Kramer 2003), suggesting good prospects for coral recruitment (e.g. Arnold et al. 2010).

The purpose of our study was to determine juvenile coral abundance and density at Bonaire’s 11 monitoring sites and to test for potential relationships with macroalgae or filamentous turf algae. These data were compared among years and among sites with unconstrained fishing pressure and the no-take reserves or Fish Protected Areas (FPA). This study is intended to inform managers of the reef conditions where “baby” corals thrive.
Materials and Methods

We evaluated 11 sites on the leeward side of Bonaire (Caribbean Netherlands, Southern Caribbean) via SCUBA from 5 to 9 March 2017. All reefs were analyzed at 10 m depth to remain consistent with previous reports. Four 10-meter transects were laid out parallel to shore at each site. Along each transect, five quadrats that were 25 cm by 25 cm were randomly placed on either side of the transects at 0 m, 2.5 m, 5 m, 7.5 m, and 10 m. Two divers surveyed on opposite sides of the transect to ensure no double-counting. Quadrat sampling was stratified for hard substrates where juvenile corals can recruit. Accordingly, if live coral, gorgonian or sponges occupied more than 25% of the substrate, the quadrat was moved. Percent cover of corallines, gorgonians/sponges, hard corals, macroalgae and turf algae were visually estimated within each quadrat. Average canopy height was determined for both macroalgae and turf algae to calculate the algal index per quadrat (Steneck and Dethier 1994). Juvenile corals (corals less than 40 millimeters in maximum diameter) were identified to the species level and counted within each quadrat (Bak and Engel 1979).

Data were analyzed to determine average juvenile density at each of the 11 sites. We then analyzed to test for trends between control and FPA sites and across years of the study. We also determined the relationship between number of juveniles per quadrat with macroalgae and turf algae indices. Statistical significance was determined using a z-test to compare between means with known deviation.

Results

Undaria agarites (previously Agaricia agaricites), Porites asteroides and Orbicella annularis were the most abundant juvenile corals (Fig. 1). The mean density of the three most abundant corals was significantly different from the mean of the other species’ densities (p-value<0.05, z-value=1.96). It is likely that O. annularis juveniles are remnants of adults that suffered mortality rather than individuals that recruited as larvae (Hughes and Tanner 2000).
Fig. 1. Juvenile density versus species of coral. Error bars indicate ± one standard error. *Orcicella annularis* juveniles are most likely remnants of old, large colonies that are now regrowing rather than new recruits to the reef.

The highest density was $36.44 \pm 5.61$ juveniles/m$^2$ at Windsock (Fig. 2). The lowest juvenile density was $21.1 \pm 5.92$ juveniles/m$^2$ at Barcadera (Fig. 2). There was no statistical difference between control and FPA sites (p-value 0.713 and z-value 1.96).

Fig. 2. Juvenile coral density versus site. Sites are listed from south to north. Error bars as in Fig. 1.

Macroalgalae have continued to decline since 2011 (as measured with a macroalgal index which is a proxy for algal biomass; Steneck, Chapter 1). The lowest macroalgal index was $6.78 \pm 2.35$ at Windsock (Fig. 3). Algal abundance increased among northern sites
with the highest having an index of 208.25 ± 45.44 at Oil Slick (Fig. 3). There was statistical significance between control and FPA sites (p-value<0.001 and z-value=1.96).

![Graph showing macroalgal index versus reef site](Image)

Fig. 3. Macroalgal index versus reef site, shown from the south to the north. Error bars as in Fig. 1.

The maximum density of juvenile corals was limited by macroalgae (Fig. 4). The same was found for juvenile abundance and filamentous turf algae (Fig. 5). Both declined with a macroalgal index of greater than 300.

![Graph showing juvenile abundance per quadrat versus macroalgal index](Image)

Fig. 4. Juvenile abundance per quadrat versus macroalgal index. Macroalgal index is percent cover of macroalgae per quadrat multiplied by average canopy height of the same quadrat.
Fig. 5. Juvenile abundance versus turf algal index. Turf algal index is percent cover of turf algae per quadrat multiplied by average canopy height of the same quadrat.

The island-wide juvenile densities declined to low points in 2009 and 2013 but they have increased since to a record high in 2017 of 27.23 ± 1.63 juveniles/m² (Fig. 6).

Fig. 6. Population density of juvenile corals 2003 - 2017. There is no data available from 2007. Error bars as in Fig. 1.
Discussion

The abundance of *Undaria agaricites*, and *Porites asteroides* juveniles reflects the shift from branching elkhorn and staghorn coral (*Acropora*) species to less structurally complex mound or platy species (Pandolfi and Jackson 2003, Alvarez-Filip et al 2009). This shift has the potential to decrease recruitment by fishes due to a decreased rugosity or complexity (McCormick 1994, Beukers and Jones 1998). Importantly, today’s dominant coral, *Orbicella annularis*, provides only modest structural complexity as an adult.

Note that juvenile *O. annularis* were most likely a remnant after mortality of an adult colony rather than a new recruit resulting from larval settlement (Hughes and Tanner 2000). Numerous studies of coral settlement in the Caribbean failed to ever record *Orbicella* recruitment (e.g. Ritson-Williams et al 2009, Arnold et al. 2010, Arnold and Steneck 2011, Steneck et al. 2014). Overall, the increase in juveniles is promising for the continuation of reef habitat in Bonaire, and a potential for reef growth and increased complexity and over time.

The highest densities of juvenile corals occurred at sites with the lowest macroalgal indeces (e.g. Windsock). The inverse relationship between juvenile corals and macroalgal abundances that we quantified (Fig. 4) is consistent with experiments showing algal inhibition on juvenile coral settlement (Box and Mumby 2007, Arnold et al. 2010). This also conforms to larger geographic trends throughout the Caribbean showing Bonaire to have among the lowest algal abundance Caribbean (Kramer 2003) and thus the highest recruitment potential for reef corals.

Juvenile coral densities on Bonaire’s reefs were on average the highest recorded since monitoring began in 2003 (Fig. 6). There has been a steady increase in juvenile coral densities since 2013 suggesting a true recovery of the reefs since the 2010 bleaching event.

Literature Cited


Chapter 6: Architectural complexity of Bonaire’s reefs and implications for reef health

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Abstract

Habitat architecture of coral reefs is an integral component affecting both its biodiversity and ecological processes. Measuring the rugosity, or the structural complexity, of Bonaire’s reefs improves our understanding of the relationship between habitat architecture and important associated organisms. I found strong positive relationships between reef rugosity and the abundance of parrotfish, the decline in macroalgae, and increases in both coral and calcareous coralline algae. By comparing habitat complexity at the 11 monitored reefs between 2015 and 2017, I concluded that the reefs in Bonaire remain significantly more complex than the greater Caribbean average. Measuring rugosity as part of this larger reef monitoring effort helps us understand drivers of coral growth and reef complexity. Bonaire’s coral reef habitat architecture varies among monitored sites in ways that cultivate key ecological interactions such as parrotfish grazing on macroalgae and the overall impact this may have on the condition of reef corals.

Introduction

In 1983 Bradbury and Reichelt compared the architectural complexities of coral reefs to that of the human lung, another living surface with high fractal dimension. They go on to state that coral reefs, as living surfaces, grow in the attempt to maximize their likelihood of contact with the water flow around them (Bradbury and Reichelt 1983). Clearly, reef corals are “ecosystem engineers” (sensu Jones et al. 1994), since as corals grow they change the habitat architecture and environment used by other organisms for shelter and altering water flow (Lacharite and Metaxas 2013). These complexities, one of the distinguishing features of coral reefs, provide ecosystem services that increase their capacity to support biodiverse communities (Alvarez-Filip et al. 2009; Alvarez-Filip et al. 2011). These communities in turn add functional resilience to reef ecosystems, but when sufficiently disturbed can result in the degradation of reef architectural complexity.

Habitat degradation has been tracked since 1969 in the Caribbean and has been attributed to multiple events synergistically flattening these reefs (Alvarez-Filip et al 2009). These events include large scale die-offs of elkhorn (Acropora palmate) and staghorn (Acropora cervicornis) corals due to white band disease in the late 1970s, the Diadema antillarum die off in 1983-4 (Williams et al 2001), fishing pressures on large herbivorous fish and the compounding effects of the 1998 El Niño event and episodic hurricane damage (Alvarez-Filip et al. 2009; Steneck et al. 2014). These regional scale disturbances have led to the homogenization of Caribbean reef complexity resulting from a shift in dominance from towering Acropora and Orbicella reefs to more stress-resistant and less complex, “weedier”, coral species such as Porites astreoides (Alvarez-Filip et al.
These effects have resulted in a phase shift to algal dominated reefs throughout the Caribbean (Roff and Mumby 2012). As coral cover declined so too did grazing surface area and habitat architecture (Williams et al 2001). Therefore, it is important to study relationships between reef habitat architecture, benthic composition and herbivory to gain insights into resilience of today’s coral reef ecosystems.

The goal of this study was to measure habitat architecture, quantified as a spatial index (meters of reef surface under linear meter transect), at the 11 long term monitoring sites in Bonaire to determine relationships between this metric and the abundance of key drivers of reef health (e.g. herbivory, macroalgae, coralline algae and coral abundance – all from other studies in this report). I also compared my 2017 results to those measurements in Bonaire in 2015, and to those of other coral reef ecosystems throughout the Caribbean.

Methods

To measure the architectural complexity of the 11 study sites in Bonaire and to be able to draw comparisons between those baseline data collected in 2015, the same methods were employed from the 2015 report. Methods evolved from previous work that showed a correlation between fish species diversity and topographic complexity (Risk 1972). This approach developed into a metric called the “Spatial Index” (sensu Rogers et al. 1982) as a way of evaluating rugosity, or spatial heterogeneity. For this, the length of reef surface under a 10 m line marked at meter intervals was used to calculate the spatial index (measured as meter of reef surface under a linear meter). This method was used by Alvarez-Filip et al. (2009), and provides a means of consistent measurement useful for data comparison across locations (Fig.1). A spatial index measurement of higher values indicates a more architecturally complex section of reef and index values equal to one indicate a flat surface.

Fig. 1. Methodology for surveying the rugosity of the reefs in Bonaire, noting differentiation of recorded measurements (Wilson, Chapter 6, Bonaire Report 2015).

To calculate the spatial index at each site, I utilized multiple 10 m transect lines along the 10 m depth contour of the reef. Each 10 m transect was partitioned into 1 m sections that
were surveyed for the benthic composition of topographic highs, side length, and bottom length. Measurements along each meter were then added together and used to calculate the spatial index per meter along each 10 m transect. In the end the resulting culmination of each transect were added together and divided by the number of meters surveyed to create an average spatial index per study site. These average spatial indices were then used to compare the study sites and determine the spectrum of complexity of the reefs in Bonaire.

Results

The average spatial index for Bonaire in 2017 was 1.87 m/m. This is consistent with 2015 that had an average of 1.85 m/m (Figs. 2, 3). Collectively these data show that the complexity of reefs in Bonaire remain significantly above the average of the rest of the reefs in the Caribbean, which had a grand mean of 1.2 (m/m) reported in 2008 by Alvarez-Filip et al. (2009).

Fig. 2. Spatial heterogeneity data collected in 2017, represented as spatial index. Horizontal dashed lines indicating the average spatial index across all study sites, 1.87 and horizontal dotted line indicating the region wide Caribbean average, 1.2.

Fig. 3. Spatial heterogeneity data collected in 2015, represented as spatial index. Error bars and Bonaire and Caribbean averages as in Fig. 1.
Overall, the spatial indices from 2017 and 2015 averaged about the same although there were slight differences among sites between years. Slight variation among spatial indices measured at each site were most likely due to difference in exact surveying location and technique between 2015 and 2017. In 2015 Front Porch was measured to have to lowest spatial index, falling below the Caribbean average, but in 2017 I found Front Porch to have a spatial index comparable to the Bonaire average. This variation is important to consider when recognizing that the complexities of a reef may change markedly within meters and illustrates the inherent variability in coral reef ecosystems and why larger sample sizes will generally yield results with lower variance and better statistical power.

The variability among sites was measured additionally by quantifying the frequency distribution of side heights (i.e. height of live and dead coral heads, annotated in Fig. 1). Sites varied considerably in their habitat architecture. Specifically note that the greatest spatial index difference existed between Oilslick and the No-Dive Reserve (Fig. 4). The vertical height, spacing and density of branches likely dictates the suitability of habitat architecture for many reef-dwelling organisms. Side height frequency differences for all sites is presented in Fig. 7.

![Frequency distribution of side height (cm) at sites that contrast in habitat architecture. Oil Slick had the lowest spatial index and smallest mode and smallest side height. No Dive Reserve had the highest spatial index, a larger mode and larger maximum side height. Forest had the largest mode and largest maximum side measured but almost no small height relief (i.e. 10 – 20 cm high corals were rare).](image-url)
Habitat architecture drives many ecological processes such as both coral cover and crustose coralline algae (CCA) abundance, which both scale with habitat architecture (Fig. 5). Additionally, benthic composition, quantified by percent cover, were compared to the spatial indices of each site to further tease apart drivers of reef complexity (Fig. 5.). Spatial index values positively correlated most significantly with sites that contained higher percentages of the benthos covered by coral (Fig. 5A). Increases in spatial index also positively correlated with increases in crustose coralline algae, although the statistical strength of this relationship was marginal (Fig. 5B). Percent macroalgae cover and algal index values (percent cover multiplied by canopy height, see Steneck, Chapter 1) when compared to spatial index values by site showed a negatively correlated relationship (Fig. 5C and D). Correlations between macroalgal percent cover and algal index values were evaluated in the absence of the No-Dive Reserve study location which showed a disproportionally abundant amount of macroalgae. This is important to note and could be driven by increased exposure to waves wrapping around Bonaire’s northern tip, but it was removed from analysis as an outlier. The relationship between macroalgal cover showed no statistically significant relationship when compared to spatial index, however the relationship between algal index and spatial index did show a marginally significant negative relationship. Although marginal, the importance in recognizing these subtle trends warrants additional investigation.

Fig. 5. Benthic trends observed with increasing reef complexity: A) Coral % Cover, showing a statistical significant relationship at p<0.05 B) Crustose Coralline Algae (CCA) % Cover, marginally significant at
p<0.1 C) Algae % Cover, showing no statistical relationship, p>0.1 D) Algal Index, showing a marginally significant relationship at p<0.1. Algae % Cover and Algal Index comparisons were done without inclusion of the No-Dive Reserve site. This point was an outlier and potentially related to wave wrap around effect, resulting in removal.

A

B

Fig. 6. Relationships between two different measurements of contour and parrotfish (scarid) density. A) Correlation between parrotfish density and mean side height significant at the level of P<0.001. B) Contrasted with the correlation between parrotfish density and spatial index showing no statistical significance, p>0.1.

Parrotfish abundance scales with habitat architecture (Fig. 6). In fact, the strongest association is with mean side height (Fig. 6a; Table 1). While this association is clear and was reported previously (Wilson, Chapter 6, 2015 Bonaire Report), exactly what drives this association is uncertain.

Table 1. Data collected in 2017 used in the correlation analysis. Data shown in a South to North orientation based on study site.

<table>
<thead>
<tr>
<th>Study Site, 2017</th>
<th>Spatial Index (m/m)</th>
<th>Mean Side Height (cm)</th>
<th>Scarid Density (inv. 100m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bachelor</td>
<td>1.82</td>
<td>38.60</td>
<td>16.42</td>
</tr>
<tr>
<td>Windsock</td>
<td>1.91</td>
<td>40.20</td>
<td>14.70</td>
</tr>
<tr>
<td>18th Palm</td>
<td>1.77</td>
<td>40.69</td>
<td>17.02</td>
</tr>
<tr>
<td>Calabas</td>
<td>1.75</td>
<td>33.38</td>
<td>12.33</td>
</tr>
<tr>
<td>Front Porch</td>
<td>1.90</td>
<td>47.61</td>
<td>18.33</td>
</tr>
<tr>
<td>Forest</td>
<td>2.02</td>
<td>68.95</td>
<td>36.78</td>
</tr>
<tr>
<td>Reef Scientifico</td>
<td>1.81</td>
<td>41.10</td>
<td>14.40</td>
</tr>
<tr>
<td>Barcadera</td>
<td>1.71</td>
<td>48.90</td>
<td>17.02</td>
</tr>
<tr>
<td>Oil Slick</td>
<td>1.68</td>
<td>37.80</td>
<td>17.14</td>
</tr>
<tr>
<td>Karpata</td>
<td>1.97</td>
<td>51.01</td>
<td>26.66</td>
</tr>
<tr>
<td>No-Dive Reserve</td>
<td>2.23</td>
<td>52.20</td>
<td>18.88</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>1.87</strong></td>
<td><strong>45.49</strong></td>
<td><strong>19.07</strong></td>
</tr>
</tbody>
</table>
Fig. 7. Frequency diagrams from each site showing differences in side height distribution, measured in cm. Additionally, a linear regression plotting the relationship between mean side height (MSH) and spatial index (SI), of each site, showing statistical significance at $p<0.05$.

**Discussion**

Clearly Bonaire’s coral reefs are more structurally complex than most coral reefs in the Caribbean. Among the interesting correlates related to the rugosity of coral reefs is the association with herbivorous parrotfishes. How they use the differences in the shapes and spaces at each location (Figs. 4, 7) has yet to be fully studied. We know grazing is concentrated on topographic high spots (Lieberman, Chapter 8), but we do not know if scarid recruitment or protection from predators are enhanced by specific habitat architecture.

Parrotfish movement within the habitat may be a limiting factor in their grazing effectiveness. This habitat limitation may mark an overlapping transition in habitat space filled by smaller herbivores. This idea speaks to the fractal compartmentalization of reefs, scaling habitat space with the space taken up by their associates, defining manageable size dependent niche space of herbivores.
Recent studies have been looking at this topic on the “Microtopographic” scale showing that these microscale refuges affect the dynamics between grazing herbivorous fish and benthic organisms (Brandl and Bellwood 2016).

Parrotfish Deterrents (PDs; Steneck et al. 2014) comprised of a ring of stainless steel posts separated by four centimeters were effective at preventing large parrotfish (> 30 cm) from grazing within the ring. Clearly that scale excludes large but not small scarids. However, excluding only large parrotfish was sufficient to trigger an algal phase shift. So an increase in rugosity and vertical height on coral reefs facilitates scarids and their grazing but at very high density structures with small spaces, the reef becomes inhibitory to those herbivores. Once such areas of high reef complexity become overgrown by algae they far exceed the capacity for local herbivore management resulting in a potential algal dominated phase shift, an idea supported by Williams et al. (2001) and Steneck et al. (2014).

In concordance, algal index values showed a decreasing trend with increases in reef complexity, suggesting that both the complexity of the habitat and availability of grazable substrate may be two important independent drivers of algal abundance. The importance of how accessible grazable substrate scales with herbivore size and habitat complexity constitutes an area for future investigation.

With Caribbean-wide trends in reef homogenization, flattening and shifts towards more stress resistant, “weedier” coral species, resultant decreases in architectural complexity have been observed. This shift has also been seen in conjunction with algal dominated phase shifts, alternative stable states mediated by herbivory. My data suggest that habitat complexity measured as a spatial index and vertical side heights provides insights on how coral reefs create refugia and space for parrotfish and other fish. As such this can affect not only the recruitment and survival of parrotfish but secondarily improve conditions for recruiting and juvenile reef corals (e.g. Rossin and de León, Chapter 5). Ultimately, the rugosity of coral reefs may be a driver of resilience for these beleaguered ecosystems.

**Literature Cited**


Brandl, S. J. and D. R. Bellwood, 2016. Microtopographic refuges shape consumer-


Chapter 7: Damselfish: Patterns of Distribution and Abundance in Relation to Coral Reef Health in Bonaire

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Abstract

The aggressive behavior of territorial damselfish reduces the grazing rates and positive impacts of herbivorous reef fishes such as parrotfish on coral reefs. I quantified the distribution and abundance of territorial three-spot and longfin damselfishes, planktivorous bicolor damselfish, and herbivorous yellowtail damselfish at a depth of 10 m at 11 monitored coral reef sites on the leeward side of Bonaire and of Klein Bonaire. Of the damselfish I recorded, bicolors were the most abundant, while yellowtails were the least abundant. Overall, adult three-spot damselfish population increased at seven sites, whereas longfin population declined at six. Longfin populations declined successively from Barcadera to the northern-most site at the No Dive Reserve. Geographically, southern damselfish populations have increased from Bachelor’s Beach to Reef Scientifico since 2013, whereas northern sites have fluctuated without a discernable trend.

Introduction

Although small in size, damselfish are one of the most functionally important groups of fish on coral reefs. In Bonaire at the monitored sites, four common species are distributed among three functional groups. The first group includes the territorial three-spot damselfish (*Stegastes planifrons*) and longfin damselfish (*S. diencaeus*). These species are the most abundant around 10 m, but are present from 1 m – 30 m (Allen 1991).

Yellowtail damselfish (*Microspathodon chrysurus*) comprise the second functional group. They are only moderately territorial, but because they are larger fish and repeatedly graze in the same locations, algal abundance remains low when their population density is high (Vermeij et al. 2015). The third functional group includes bicolor damselfish (*S. partitus*). Bicolors are non-aggressive planktivores.

Three-spot and longfin damselfish act as biological cages by actively chasing away other herbivorous fishes. Their territorial activity results in a net increase in algal turf abundance (Hixon 1997) and diversity (Brawley and Adey 1977). Algal turf growth within damselfish territories impedes coral recruitment and settlement (Arnold et al. 2010), and can increase rates of adult coral mortality (Vermeij et al. 2015).

Common damselfish predators include tiger groupers, graysbys, and rock hinds (Serranidae), schoolmaster, yellowtail and mahogany snappers (Lutjanidae), bar jacks (Carangidae), and spotted scorpionfish (Scorpaenidae) (Randall 1967).
To determine the potential impact of damselfishes on coral reefs, I recorded patterns of population density, age class, species composition, and abundance at the 11 biannually monitored reefs in Bonaire. By comparing data from 2017 to previous years, we can determine how damselfish populations are changing and consider the implications this has on Bonaire’s reefs.

Methods

Damselfish species of the family Pomacentridae at the monitored coral reefs of Bonaire include three-spot, longfin, bicolor, and yellowtail damselfishes. I recorded population densities, age class, and size (fork-length) at the 11 monitored sites via 10 m x 2 m (i.e. 20 m²) belt transects on the fringing reefs around Bonaire and Klein Bonaire from March 5th-9th, 2017. Eight transects were conducted at Bachelor’s Beach, Eighteenth Palm, Forest, Front Porch, Reef Scientifico, Oil Slick, Karpata, and at the No Dive Reserve. Seven transects were conducted at Windsock, and six were conducted at Calabas and Barcadera. Four 10 m transect tapes were placed at specific monitored locations at 10 m depth parallel to the shoreline, and additional tapes were placed as necessary. Species and body lengths of all damselfish within one meter to the right and to the left of the transect line were recorded. To visually calibrate fish sizes, a 15 cm PVC tube with 5 cm marks was used for reference.

Data from the 2011, 2013, and 2015 Bonaire Reports were used during analyses to compare trends in damselfish population density and abundance over time. Damselfish predator trends were accessed from Boenish and Richie (Chapter 4).

Results

Damselfishes are abundant on Bonaire’s coral reefs with average densities between 100 – 200/m². Bicolor damselfish were the most abundant species (Fig. 1), while yellowtail damselfish were the least abundant. Bicolor and yellowtail population densities (# individuals per 100m²) are inversely related; as bicolor density increases from southern to northern sites, yellowtail density decreases along the same geographic gradient (Fig. 1). Longfin and three-spot population densities are intermediate between bicolor and yellowtail. Longfin and three-spot population densities are similarly inversely related; as longfin population density decreases toward the north, three-spot density increases along the same geographic gradient (Fig. 1).
Fig. 1. Population densities of bicolor, three-spot, longfin and yellowtail damselfishes at monitored sites ranging from south (left) to north (right).

The two strongly territorial damselfish (three-spot and longfin damselfishes) had similar adult population densities, but varied considerably among sites (Figs. 2 and 3). Adult three-spot population density is greater than juvenile population density at all sites except for Barcadera (Fig. 2). Adult longfin population density is greater than juvenile population density at all sites (Fig. 3).

Fig. 2. Adult and juvenile three-spot damselfish population densities. Error bars represent ± one standard error.
Fig. 3. Adult and juvenile longfin damselfish population densities. Error bars as in Fig. 2.

The population densities of the two territorial damselfish were inversely correlated (Fig. 4), potentially because they share the same niche, and could therefore be strong competitors.
Fig. 4. Inverse relationship between adult three-spot and longfin damselfishes (each point represents a study site).

Adult three-spot population density increased from 2013 to 2017 at all sites except Forest, Barcadera, and the No Dive Reserve (Fig. 5). Due to its small sample-size, 2015 data has been omitted from the analysis in figures 5 – 8. Adult three-spot populations remain constant from 2013 to 2017 at Karpata. Adults were absent from Front Porch in 2013 (Fig. 5). Juvenile three-spot populations increased from 2013 to 2017 at all sites except Windsock and Forest. Juvenile populations at Reef Scientifico remained constant from 2013 to 2017. Juveniles were absent from Calabas in 2013 (Fig. 6).

Adult longfin populations decreased from 2013 to 2017 at all sites except Calabas, Front Porch, Barcadera, and the No Dive Reserve (Fig. 7). Juvenile longfin populations have increased from 2013 to 2017 at Eighteenth Palm, Reef Scientifico, and Oil Slick, but have decreased at Windsock, Front Porch and Barcadera. Juvenile longfins were absent from Karpata and the No Dive Reserve in 2013 and 2017. Juvenile longfins were absent from Bachelor’s Beach in 2013 and from Calabas in 2017 (Fig. 8).

Fig. 5. Adult three-spot population densities measured in 2013 and in 2017. Error bars as in Fig. 2.
Fig. 6. Juvenile three-spot population densities measured in 2013 and in 2017. Error bars as in Fig. 2.

Fig. 7. Adult longfin population densities measured in 2013 and in 2017. Error bars as in Fig. 2.
Fig. 8. Juvenile longfin population densities measured in 2013 and in 2017. Error bars as in Fig. 2.

Total damselfish population densities show considerable variability but a general upward trend since 2011, the year all 11 sites were monitored for the first time. Nevertheless, some sites such as Barcadera have had consistently high population densities (Fig. 9). The 2011 average population density was 21.3 individuals/100m²; in 2013 the average was 37.8; in 2015 the average was 21.0; and in 2017 the average was 39.2.

Fig. 9. Combined adult three-spot and longfin damselfish population densities from south (left) to north (right), 2011-2017. Error bars as in Fig. 2.
Adult and juvenile three-spot population densities suggest a slight increasing trend as a function of total predator (Serranidae, Lutjanidae, Carangidae, and Scorpidae) biomass increases (Fig. 10), however, this is not a significant regression. Adult and juvenile longfin population densities show a decreasing trend as total predator biomass increases (Fig. 11).

Fig. 10. Total three-spot damselfish population density (# individuals/100m$^2$) as a function of total predator biomass (kg/100m$^2$). No significant trend exists between combined predator biomass and adult and juvenile three-spot damselfish population densities.

Discussion

Damselfish population densities in 2017 have surpassed previously high 2013 densities at most sites (Fig. 9). Damselfish populations can be controlled by predators via top-down mechanisms (Hixon and Beets 1993); the most common predators are tiger groupers, graysbys, rock hinds, schoolmaster snappers, yellowtail snappers, mahogony snappers, bar jacks, and spotted scorpionfish. Since 2008, after the establishment of Fish Protection Areas (FPAs) around Bonaire, predatory fish biomass has increased (Boenish and Richie, Chapter 4). Interestingly, three-spot damselfish show the greatest population density increases in the four monitored sites within the FPAs. This is contrary to what we would expect if damselfish were controlled by predatory fishes, and if the FPAs actually caused predatory fish abundance to increase. However, to date the FPA’s trend only slightly higher than control fished reefs (Richie and Boenish Chapter 4).

There is no clear trend between combined damselfish predator biomass and three-spot and longfin damselfish population density (Figs. 10, 11). Three-spot and longfin damsels, although less abundant than bicolor, are two of the most functionally important fishes;
their territorial behaviour limits herbivory from other fishes creating a “garden” with abundant and high canopy filamentous algae but due to this a reduced cover of coral (Vermeji et al. 2015). Three-spot and longfin damselfishes exclude herbivores from their territory. Algal abundance increases because three-spots and longfins are “non-denuding” herbivores (Steneck 1988). Turf algae usually is cropped to 2 mm canopy height, but inside three-spot and longfin territories it can have canopies up to 4 mm. This small difference of 2 mm in canopy height has been shown to be significant enough to reduce coral recruitment by 75% (Arnold et al. 2010). There is a clear link between herbivory (i.e., bite rates) and the canopy height of algal turfs (see Lieberman, Chapter 8). Continually rising ocean temperatures coupled with increasing ocean acidification suggests that coral bleaching events will continue to test coral reef resilience. Transient bleaching events, where corals can potentially recover, might end in more frequent terminal bleaching events with subsequent reef devastation.

Three-spot adults are more abundant than juveniles (Fig. 2). Juvenile three-spot population densities have increased at most sites from 2013 to 2017 (Fig. 6), indicating high recruitment rate and low adult mortality. Longfin adults are more abundant than juveniles (Fig. 7, 8), but longfins have a smaller population density than three-spots (Fig. 1). Juvenile longfin population densities have decreased at most sites (Fig. 8), suggesting possibly lower juvenile recruitment rates than three-spot damselfish. Predators may be preying equally on three-spot and longfin juveniles, but because three-spots have a higher recruitment rate and greater population density, the effects of predation are less profound (Figs. 10, 11), and more juveniles survive to the adult stage (Figs. 5, 7) and propagate.

Three-spot and longfin damselfish are ecologically equivalent species in that they are about the same size, eat the same algal food, live in similar habitats and are equally aggressive. Curiously, their population densities are inversely correlated (Fig. 4) which would be consistent with the two species being under strong pressure of interspecific competition. It is possible that three-spot damselfish have larger populations than longfins (Figs. 5, 8) because they use the available habitat space more efficiently. It is also possible that stochastic processes drive the abundance of these damselfish as was found to happen in the Great Barrier Reef. There, Sale (1974) found that the damselfish species most abundant among a diversity of congeners was the one that happened to have its larval fish arriving to the reef just at the right time to recruit. This chance recruitment driven demography is referred to as the “Lottery Hypothesis” (Sale 1978).

Bonaire’s reefs continue to thrive in the face of adversity. Although damselfish population densities have increased from 2011 to 2017, coral recruitment has also increased, and reef rugosity has remained constant (Rossin and de Leon, Chapter 5; Fountain, Chapter 6). While a large portion of the Caribbean has faced macroalgal dominance and shifted into an alternative stable state, the fringing reefs on the western coast of Bonaire persist. Herbivory is sufficient to keep algal abundance low. This may be driven by large parrotfish which remain abundant on Bonaire reefs because there is no spearfishing or trap fishing on the monitored reefs. Large parrotfish are known to have greater capacity to remove algae from reefs fostering coral recruitment (Steneck et al. 2014). However, large parrotfish are also least negatively affected by damselfishes
(Lieberman, Chapter 8) and thus the “biological cage” effect of damselfish territoriality is negated.

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Chapter 8: Spatial and temporal trends in herbivorous fish grazing rates on Bonaire’s coral reefs

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Abstract

Herbivory is a critical process on coral reefs that promotes coral growth and reproduction by reducing competition from algae. I quantified grazing rates of herbivorous reef fish at 11 long-term monitoring sites on Bonaire’s leeward shore. Specifically, I quantified bite rates of parrotfish, surgeonfish, and damselfish (Scaridae, Acanthuridae, and Pomacentridae, respectively) at both Fish Protected Areas (FPAs) and fished sites (controls). Due to the significance of parrotfish as reef herbivores, I also investigated relationships between parrotfish population demographics (i.e. biomass, density, life phases, size, and species) and herbivory rates. I compared the relationships between parrotfish herbivory rates and benthic and fish community structure for the 2017 survey sites as well as with Bonaire-wide trends in herbivory rates since 2003. After the 2010 coral bleaching event, the macroalgal spike was matched with a sharp increase in parrotfish grazing rates. Parrotfish grazing rates paralleled declining macroalgal trends from 2011-2015, but increased from 2015 to 2017 while macroalgae continued to decline to pre-bleaching levels. This relationship between algal abundance and grazing rates suggests herbivores have played a central role in the resilience of Bonaire’s reefs.

Introduction

Coral reefs are ecologically biodiverse ecosystems that also provide many valuable resources for adjacent coastal human populations. However, natural processes (such as disease and storms) and human exploitation of reefs can lead to the degradation of these ecosystems. In recent decades, an overall decline in Caribbean reef health has been characterized by the proliferation of macroalgae and reduction of coral recruits. This widespread shift has resulted from multiple interacting disturbances such as the die-off of Diadema antillarum (Caribbean long-spined urchins) in 1983 (Williams & Polunin 2001, Harborne et al. 2009), the Acroporid coral die-off (Roff & Mumby 2012), and several coral bleaching events including a significant event in 2010. Bonaire has not been exempt from these disturbances but remains an anomaly in the Caribbean with high coral cover and low algal abundances compared to regional averages.

Macroalgae compete with coral for space and light, and, when left unchecked, can degrade the structure and functioning of reefs (Hay 1997). Macroalgae grow rapidly, smother coral recruits, and some can produce secondary metabolites that poison corals that contact them (Rasher & Hay 2010). Algae can negatively impact coral fecundity, growth, and survivorship, as well as increase localized tissue mortality where algae contact coral tissues (Lirman 2001). Herbivory is a key driver of resilience on coral reefs as it controls algal growth and proliferation (Diaz-Pulido and McCook 2003, Hay 1997).
and allows corals to compete (Rasher et al. 2011). Herbivorous fishes feed on a variety of algae including macroalgae, turf, encrusting and endolithic algae (Steneck 1988, Williams & Polunin 2001), although some herbivores such as damselfish (pomacentrids) and surgeonfish (acanthurids) have only a modest functional capacity to eat tough, leathery or corticated macrophytes (Steneck 1988; Knowlton 1992).

Though most Caribbean reefs have experienced a phase shift to algal dominated systems, Bonaire has avoided this change thus far. In 1971, Bonaire’s government banned spearfishing, and in 2010 the harvest of parrotfish was banned; these fisheries policy changes have allowed fish populations to flourish. Assessing herbivory trends may provide some insight into how Bonaire has resisted shifting from a coral-dominated to an algal-dominated reef.

I studied herbivory by quantifying bite rates at 11 different survey sites in Bonaire, six of which have been surveyed since 2003 as an ongoing reef monitoring initiative with STINAPA. I compared herbivory rates across sites and assessed relationships with herbivore functional groups, scarid demography, and site management designations (Fish Protected Areas vs. fished controls). Additionally, I evaluated long-term trends in grazing rates in Bonaire.

Methods

Study sites and experimental design

In March of 2017, I collected fish bite rate data at 11 monitoring sites on the leeward shore of Bonaire, Dutch Caribbean. The sites surveyed were part of an ongoing monitoring initiative by STINAPA. Six sites were surveyed since 2003 (from south to north: Windsock, 18th Palm, Forest on Klein Bonaire, Reef Scientifico, Barcadera, and Karpata). In 2008, the Bonaire government and STINAPA created four Fish Protected Areas (FPAs) (18th Palm, Calabas, Front Porch and Reef Scientifico). STINAPA added four monitoring sites in 2009 (from south to north: Bachelor’s Beach, Calabas, Front Porch and Oil Slick) to investigate the potential benefits of FPAs. In 2011, one more monitoring site was added to assess the coral recovery following the 2010 bleaching event (No-dive reserve). There are four monitoring sites positioned within FPAs (18th Palm, Calabas, Front Porch and Reef Scientifico). There are seven monitoring sites at non-FPA sites serving as controls (Bachelor’s Beach, Windsock, Forest on Klein Bonaire, Oil Slick, Barcadera, Karpata and the No-dive reserve).

At each location, I quantified fish grazing within 1 m² quadrats placed at topographic highs at approximately 8-10 m depths with more than 50% algal cover during five-minute intervals. Quadrats were measured with a 1 m tape and then removed before the observation period to prevent grazing bias. In each quadrat, I estimated of the percent cover of stony corals, crustose coralline algae, turf algae, and Dictyota and measured the canopy height of turfs and macroalgae. I also quantified the topographical relief of each quadrat.
During the observation periods, I recorded the number of bites on topographical highs (see Chandler and Rasher, Chapter 7, 2015 Bonaire Report) and other surfaces and recorded the species of fish, life phase (juvenile, initial, and terminal, when applicable), and fork length for all surgeonfish, parrotfish and territorial damselfishes (families Acanthuridae, Scaridae, and Pomacentridae, respectively). Before the observation period, I calibrated my eye with a measured PVC pipe to facilitate size estimations of fish. The estimated fish size classes were small (< 13 cm), medium (13 – 20 cm), large (21 – 30 cm), and extra-large (> 30 cm).

**Data analysis**

I calculated average bite rates at each monitoring site grouped by both herbivore functional group (excavator/scaper = parrotfish; denuder = surgeonfish and yellowtail damselfish; non-denuder = territorial damselfish; *sensu* Steneck 1988) and management status (FPA vs. fished control). I compared my 2017 data with previous monitoring years to determine trends over time.

Since parrotfish have a significant impact on the benthic structure on reefs, I also analyzed scarid rates for each site as a function of life phase, species identification, and size class. I plotted scarid bites as a function of the macroalgal index (product of canopy height and macroalgal cover, used as a biomass proxy), coral cover, and scarid biomass and density across sites and survey years to determine the patterns of herbivory with these parameters.

**Results**

*FPA effects and spatial variability*

Overall, control sites were grazed almost twice as much as than FPA sites by all functional groups except for denuders (surgeonfish and yellowtail damselfish; Fig. 1). Denuders grazed the least out of all the functional groups, and their grazing rates were the most variable among study sites. Average bite rates for non-denuders (territorial damselfish) differed the least between FPA and control sites, though damselfish grazed about 25% more in control sites than FPA sites.
Fig. 1. Average bite rates (bites per m² per 5 minutes) of A) non-denuders (territorial damselfish), B) denuders (surgeonfish + yellowtail damselfish), and C) excavators/scrapers (parrotfish) at 11 long-term monitoring sites. Sites are arranged in south to north orientation within each management designation (FPA or control). N= 5-7 replicate observations for each location. Error bars indicate ± one standard error.

Medium, large, and extra-large parrotfish exhibited higher bite rates in the control sites than in the FPA sites (Fig. 2). Small parrotfish (<10 cm) grazing rates were similar between control and FPA sites. Grazing in control sites was dominated by princess, red band, and stoplight parrotfish, while grazing in FPA sites was dominated by princess, queen, and stoplight parrotfish (Fig. 3). In the control sites, terminal phase parrotfish had higher grazing rates than all other life stages of grazers observed (Fig. 4). In the FPA sites, juvenile fish had the highest grazing rates, followed by terminal parrotfish. Overall, grazing rates were higher in the control sites for all life phases of fish except for juveniles.
Fig. 2. Scarid bite rates (average bites per m² per 5 min) by size class across A) individual FPA and control sites individually, and B) FPA and control averages. The estimation fish size classes were: small (< 13 cm), medium (13 – 20 cm), large (21 – 30 cm), and extra-large (>30 cm).

Fig. 3. Average scarid bite rates (bites per m² per 5 min) by species across A) individual FPA and control sites and B) FPA and control site averages.
Fig. 4. Average scarid bite rates (bites per m² per 5 min) by life phase in A) individual FPA and control sites and B) FPA and control site averages.

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

There were no significant trends between site grazing rates and scarid density or biomass (Figs. 5A, B). However, the highest grazing rate observed was at the lowest scarid density, and one of the highest site grazing rate averages was at a relatively low scarid density (Fig. 5A),

![Graph showing scarid herbivory rates](image)

Fig. 5. Average scarid bite rate (bites per m² per 5 min) as a function of A) scarid density and B) scarid biomass. Density and biomass data from Boenish and Wilson, (Chapter 2). The equation of the linear regression line in A is $y = -0.1606x + 12.968$, and $R^2 = 0.0599$. Error bars as in Fig. 1.
Increased turf canopy heights were associated with decreased scarid grazing rates and increased territorial damselfish grazing rates (Figs. 6A, B). Turf grazing rates on other topographic surfaces were variable and increased with increasing canopy heights for both scarids and territorial damselfish, though the associations were weak (Figs. 6C, D).

Fig. 6. Relationship between herbivore bite rates (bites per m² per 5 min) and turf algae canopy height (mm) by A) scarid bites on topographical highs, B) damselfish bites on topographical highs, C) scarid bites on other surfaces, and D) damselfish bites on other surfaces for all 11 sites in Bonaire. The linear regression equation and R² values are y = -0.0668x + 2.7102, R² = 0.1851; y = 0.0196x + 2.3613, R² = 0.0459; y = 0.1816x + 1.7085, R² = 0.2095; and y = 0.0839x + 2.2688, R² = 0.0644 for panels A, B, C, and D, respectively.

Overall, as scarid bite rates increased macroalgal abundance declined slightly (Fig. 7A). Scarid herbivory rates generally increased with increasing stony coral, gorgonian, and sponge cover, likely due to the concentrating effect these have on algal patches (Fig. 7B).
Fig. 7. A) macroalgal index (biomass proxy) as a function of scarid bite rates (average bites per m² per 5 minutes) and. No discernable relationship was found. B) Average scarid bite rates across categories of coral, gorgonian, and sponge cover. Error bars as in Fig. 1.

The bite rates of territorial damselfish can be used as a measure of their aggressive territorial influence. Scarid bite rates decreased precipitously with increasing territorial damselfish bite rates (Fig. 8A). Acanthurid bite rates also declined with increased damselfish bite rates, though this trend was less pronounced (Fig. 9B). The effects of damselfish territoriality on scarids of different size classes showed no clear trends, indicating that damselfish can be effective in deterring scarids of varying sizes (Fig. 8C).

Fig. 8. Effects of territorial damselfish aggression (detected by their bite rates) on bite rates (bites per m² per 5 min) of A) scarids, B) acanthurids, and C) scarids plotted by size class.

Scarid bite rates on topographic highs varied among sites but were higher for sites with higher rugosity indexes (a measure of habitat complexity that is calculated as the number of meters of reef surface per linear meter; see Fountain, Chapter 6). Scarids preferentially grazed on topographical highs compared to other orientations on grazable surfaces (Fig. 9).
Fig. 9. Bonaire-wide average scarid bite rates on different topographical orientations. Error bars as in Fig. 1.

**Bonaire-wide temporal trends: scarid herbivory rates and community dynamics**

Parrotfish grazing rates showed declining trends from 2003-2009, leading up to the 2010 bleaching event (Fig 10A). After the 2010 bleaching event, grazing rates spiked but have since declined to pre-bleaching event levels. The 2015 bite rates were the lowest recorded since 2003, but as of 2017 they have recovered to almost exactly the levels recorded in 2009.

Declining herbivory rates from 2003-2009 tracked decreases in scarid biomass (Boenish and Wilson, Chapter 2), but scarid biomass remained relatively stable after that period while grazing rates spiked, declined and recovered from 2011-2017 (Fig. 10B). Correlations between grazing rates and scarid density show a similar trend in which they show initial correlations but become uncoupled after 2007 (Fig. 10C). Note that the greatest departure between grazing rates and scarid demographics (both biomass and density) was in 2011 immediately following the bleaching event and resultant live coral cover decline and macroalgae spike (Steneck, Chapter 1; Figs. 10D, E). The variations in herbivory rates since the 2010 bleaching event suggests that scarids responded slowly but effectively to this disturbance.
Fig. 10. Average scarid grazing rates (bits per m² per 5 min) on six sites monitored from 2003-2017 plotted A) alone, B) with scarid biomass, C) with scarid density, D) with coral abundance, and E) with macroalgal index. Averages (±SE) were calculated for the six sites surveyed since 2003. Bite rates are plotted as solid circles with solid lines, and other data are plotted with dashed lines. The vertical line indicates the 2010 bleaching event.

Discussion

Parrotfish are the dominant grazer on Bonaire’s reefs (Figs. 2 – 4). Surgeonfish (acanthurid) grazing rates were much lower and only recorded at FPA sites. Their absence from control sites was surprising, but is likely a result of their tendency to feed in bursts of large school foraging activities. My sample size was likely insufficient to account for the inherent variability in these acanthurid feeding patterns. Additionally, acanthurid abundance is greater at depths shallower than 10 m, which potentially increased variability in whether or not they passed through my monitoring stations.

The reduction of high value turf algal resources may intensify competition for food. Intraspecific competitive aggression within parrotfish species is known to reduce their grazing as they fight one another (Mumby and Wabnitz 2002). While not statistically significant, my data suggest bite rates decline with increasing scarid density (Fig. 5A). This trend is opposite what would be expected if there were no competitive interactions among these herbivores.

Parrotfish grazing pressure was greatest on topographic high points (Fig. 9) possibly because these surfaces are dominated by palatable turf algae while tougher, less palatable macroalgae tends to occupy topographic side and low surfaces. Among high spots with high rates of parrotfish grazing, turf canopy heights were measurably reduced (Fig. 6).
Topography affected not only parrotfish grazing trends but also those of territorial damselfish. Damselfish aggression (reflected in their bite rates) has been shown to be greatest on topographically complex substrates (Snekser et al. 2009). Similar to parrotfish preferences, my data reflect increased damselfish territoriality on topographic reef highs (Figs. 6B, D). There, where damselfish were most aggressive, they most suppressed grazing parrotfishes (Fig. 8A).

Herbivory rates measured at the monitored reef sites since 2003 reflect the dynamics of changes evident in Bonaire’s coral reefs. From 2003 to 2009, grazing rate declines paralleled declines in parrotfish population densities and biomass (Fig. 10B, C). During this time coral cover was high and macroalgal abundance was low (Fig. 10D, E). Most reef surfaces were covered by fine filamentous algal turfs that are preferred food for all of Bonaire’s parrotfishes. The 2010 bleaching event triggered a spike in macroalgae and decline in coral cover (Steneck, Chapter 1; Figs. 10D, E) and a spike in grazing rates on topographic highs, while scarid density and biomass remained stable (Boenish and Wilson, Chapter 2; Figs. 10B, C). It is possible that the sharp increase in macroalgae - which was most abundant on side and low surfaces – concentrated grazing on topographic highs that remained turf-covered and that intensified grazing on these surfaces kept algal abundance low there during the phase shift. Grazing rates on less palatable macroalgae across the reef generally declined after the bleaching event (see McMahan, Chapter 4, 2011 Bonaire Report). Increased grazing on turfs and slow but persistent grazing on macroalgae likely plaid a key role in enabling Bonaire’s recovery from the bleaching event.

Low macroalgal abundance, high coral cover, and relatively abundant herbivore populations characterize Bonaire’s reefs in 2017. This suggests that Bonaire’s reefs remain resilient following the 2010 bleaching event and have defied a phase shift to an alternative stable state of macroalgae-dominated reefs. The recent increase in scarids could reflect a functional response (sensu Holling 1965) of the herbivorous fish populations to expanded turf algal resources and thus illustrate resilience among key herbivores in this ecosystem.

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Chapter 9: Impacts of the 2015-2016 El Niño on coral bleaching in Bonaire

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Abstract

In 2015-2016, an El Niño event led to several localized coral bleaching events around the world. This study assesses the effects of this El Niño event on coral health at 11 long-term monitoring sites in Bonaire via the Atlantic Gulf Rapid Reef Assessment (AGRRA) protocol. Both Fish Protected Areas (n=4) and fished sites (n=7) were surveyed to determine if bleaching, paleness or mortality relate to fishing pressure on coral reefs. Overall, there was an average of 1.4% bleached tissue and 0.67% paling, suggesting that the 2015-2016 bleaching event that devastated vast areas of the Indopacific was a minor event for Bonaire’s reefs. Specifically, the event resulted in “transient bleaching” and most corals are expected to recover fully. Likely due to relatively low fishing pressure across Bonaire’s reefs, I found no difference in bleaching between fished and unfished reefs.

Introduction

Coral bleaching is one of the factors contributing to the decline of coral reefs throughout the tropics. As the oceans warm, the thermal tolerance of corals and their symbiotic algae are exceeded (Hoegh-Guldberg 1999). When this happens, coral expel their symbiotic algae necessary for their nutrition. Severe bleaching, brought on by higher than average water temperatures or longer periods of time, can cause corals to die (Brandt 2009). This makes coral reefs one of most vulnerable ecosystems to changes in climate or weather patterns (Hoegh-Guldberg 1999).

Often, severe bleaching events take place when there is an El Niño event. El Niño is a climate cycle that occurs when warm water in the western Pacific Ocean moves east towards the South American coast. This event impacts climate variability at a global, inter-annual time scale and can lead to sustained above-average ocean temperatures in various regions of the world (Hughes et al. 2017, Ampou et al. 2017). In 1998, a worldwide coral bleaching event occurred (Aronson et al. 2000). Since then there have been several localized bleaching events (e.g., 2005 in the Caribbean; Eakin et al. 2010). Bonaire has historically been spared from most coral bleaching, however, in the fall of 2010 it suffered a massive bleaching event that killed over 10% of the corals (Jekielek 2011). The 2015-2016 El Niño event created several hotspots that resulted in massive coral mortality throughout the Indopacific including the Great Barrier Reef (Hughes et al. 2017), however it spared most of the Caribbean and especially the southern Caribbean including Bonaire. My research sought to determine if the recent El Niño resulted in lethal bleaching as had happened in 2010.

After the 2015-2015 El Niño event, concerned NOAA scientists issued a declaration that 2016 may be the third major global coral bleaching event on record following the 1983
and 1998 events. There were observations of bleaching in Bonaire (Ramon DeLeon personal communication) but to date there has been no systematic study quantifying levels of bleaching and bleaching-induced mortality in Bonaire from the 2015–2016 bleaching event.

Materials and Methods

To quantify bleaching, I employed a sampling technique adapted from the Atlantic Guld Rapid Reef Assessment (AGRRA) protocol (http://www.agrra.org/coral-reef-monitoring/coral-indicator/), which incorporates a measure of coral bleaching. By using a standard protocol, I am able to ensure my data is comparable to other studies employing these techniques. At each of Bonaire’s 11 monitoring sites, I quantified coral condition along four permanent 10 m transects (see Steneck, Chapter 1) plus between one and five more additional transects within the site area.

I made two modifications to the AGRRA protocol. The first was that rather than running a belt-transect for each 10 meter transect laid at each site, I deployed a line intercept transect. With this method, the transect would be laid on the site the same way as described in the AGRRA protocol by looping the two ends on dead coral. However, I did not count all corals in a half meter wide belt as the protocol called for but rather only quantified coral condition (bleaching level and any mortality) that were directly in line with my transect. The reasoning behind this modification in the protocol was that the scientific value resulting from the detailed analysis is too low and compromises the sample size (i.e. number of transects I can complete per site). For the same reason, I did not measure the length, width and height of each of the coral colonies. Each coral that was sampled on the transect was evaluated and identified as either healthy, partially bleached (but still alive, considered “transient bleaching”), pale or fully bleached. I estimated the percent affected.

Results

There were a total of 18 species surveyed across all eleven monitored sites. The most abundant species was *Orcicella annularis* with 293 colonies and *Agaricia agaricites* with 185 colonies. The least abundant were *Siderastrea siderea* and *Favia fragum* with three and two colonies respectively (Fig. 1).

Overall, there was an average of 0.12% new mortality, 13.4% old mortality, 1.4% bleached tissue and 0.67% pale tissue. Across sites, the average old mortality (excluding the standing dead corals) ranged from 8.5–29.5%. Bleaching levels varied considerably among coral taxa (Fig. 2). *Montastrea cavernosa* showed the highest incidence of bleaching with only 3.5% bleached tissue. Many species showed absolutely no evidence of bleaching including *P. porites*, *Favia fragum* and *Orcicella faveolata* (Fig. 2).

Two species, *Orcicella annularis* and *Porites porites*, had higher incidences of paling than all other species combined. The majority of species had no pale tissue and were recorded as being “healthy” (Fig. 3).
Fig. 1. Number of colonies of each species identified on transects in Bonaire in March, 2017.

Fig. 2. Averages of percent of bleached tissue seen in each species in Bonaire, March 2017.

Fig. 3. Averages of pale tissue seen in coral species in Bonaire, March 2017.
Control sites showed an average 1.8% new mortality while Fish Protection Areas (FPAs) had an average 0.4% new mortality. There was no clear difference between fished and FPA sites.

The highest amount of paling was seen in Windsock and the No Dive Reserve and the least amount of bleaching was seen in Calabas and Front Porch (Fig. 4). Paled tissue in the control sites averaged 1.0% while in the FPA sites only 0.5%. In the FPA, paling was highest in the Northernmost sites and lowest in the southernmost sites. Forest, a site on Klein Bonaire, showed the highest levels of paling at 2.9% (Fig. 5).

Discussion

Clearly, this was a minor bleaching event in Bonaire and nothing like what was documented in 2010. Four months after a bleaching event I quantified a small percentage of corals that were pale and/or bleached and seemed to be recovering from the event and a low percent of “new” mortality. The area of tissue that is paled indicates that the reefs
may be in a state of recovery or prolonged stress which can have long-term effects such as reproduction (Hughes et al. 2017).

Different species with morphologies had different susceptibilities to coral bleaching and paling. Larger, more dome-shaped species such as *O. annularis*, *O. faveolata*, *Montastrea cavernosa* and *O. franksi* all showed significant amount of new mortality where as species that are smaller like *Porites porites* or individual colonies such as *E. fasniga* did not show as much or any bleaching-related mortality (Fig. 2). I had expected to see higher rates of new mortality in Colpophyllia natans due to its domal nature and past observations (e.g. Brandt 2009) but perhaps there was less because so much was already lost in the 2010 bleaching event (Jekielek 2011). These species are important members of the coral community because they are the remaining reef-building species after Caribbean-wide declines in Acroporiids, and because they are generally resistant to disturbances (Jekielek 2011). The trends I saw in this survey agree with the results from Brandt 2009 in that larger colonies experience more bleaching than smaller colonies.

NOAA satellite images of the Caribbean show temporal hotspots around the Florida Keys (where bleaching was observed), but less significant temperature increases in the southern Caribbean including Bonaire. In fact, earlier predictions of the 2016 El Niño event indicated the Caribbean would be spared from bleaching, which appears to have been the case (https://coralreefwatch.noaa.gov).

Although information suggests that the coral’s tolerance of thermal stress and capacity for acclimatization has already been exceeded, the coral reefs in Bonaire seem to be recovering nicely from the small, yet detectable bleaching event of 2015-2016 (Hoegh-Guldberd 1999).

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Chapter 10: History and Status of Management and Governance of Bonaire National Marine Park

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Abstract

The coral reefs surrounding the island of Bonaire are among the healthiest found in the Caribbean, attracting myriad tourists and providing an important source of revenue for the island. I examined the current management and governance structure relating to the Bonaire National Marine Park, looking at governance across multiple management scales that allow Bonaire to chart its unique course in the management of its coral reefs. Management of the Bonaire National Parks Foundation (BNMP) has been the mandate of Stichting Nationale Parken Bonaire (STINAPA) a non-governmental, not-for-profit organization since the Marine Park’s establishment. The role played by STINAPA is facilitated by a Management Agreement between STINAPA and the Bonaire local government, effectively charging the NGO with maintaining the health of Bonaire’s reefs and, through that, the revenue stream generated from tourism relating to those reefs. A key and pioneering feature in Bonaire’s management structure is the implementation of a “diver fee” on all those who dive on Bonaire’s coral reefs. Revenues generated from those fees make up the majority of funding that STINAPA is given to carry out its role. The innovative approaches that have been implemented in the management of the Marine Park have been successful for the Marine Park, for STINAPA, and for the Bonaire Island Government. However, there are challenges that come with implementing governance of natural resource systems, such as clarity of roles and responsibilities amongst stakeholders of the BNMP; institutional arrangements, policies and legislation across different governance levels; communication and awareness between stakeholders; and, financing.

Introduction

Bonaire was annexed together with the Caribbean islands of Aruba, Curaçao, Saba, St. Eustatius and St. Maarten to become part of the Kingdom of the Netherlands in 1954, collectively referred to as the Dutch Antilles. On 10 October, 2010, following a referendum on the status of each of the islands in relation to the Kingdom of the Netherlands, Bonaire, St. Eustatius and Saba became ‘special municipalities’ of the Kingdom of the Netherlands and are now collectively known as the Caribbean Netherlands. Aruba, Curaçao and St. Maarten obtained autonomous status. All six islands combined are referred to as the Dutch Caribbean. The capital city of Bonaire is Kralendijk, and the island has an estimated local population of ~19,000 people.

The Bonaire National Marine Park (BNMP) was established in 1979 to control the perceived threat of diving and the dive industry to the health and wellbeing of the island’s reefs (STINAPA 2006). The Marine Park surrounds Bonaire, including the island of Klein Bonaire. The Marine Park area that includes 2,700 hectares of coral reef, seagrass and mangrove ecosystems that are home to over 50 species of stony coral and more than 350 species of reef fish. The boundaries of the Marine Park begin at the high-water mark and extend seaward to roughly 200ft, or the 60 m depth contour, and the fringing coral
reefs are among the healthiest in the Caribbean (Kramer 2003). The BNMP is world famous for instituting in 1992 what was one of the first dive destinations to introduce admission fees for scuba divers. Importantly, the revenue generated from diver fees are given to the managing agency of the Marine Park – a non-governmental organisation – rather than being incorporated into Bonaire government coffers. This greatly increases the efficiency and linkages between management needs of the Marine Park resulting from increasing tourism, and the funds necessary to address those needs.

Management of the BNMP has been the mandate of Stichting Nationale Parken Bonaire (Bonaire National Parks Foundation, STINAPA), a non-governmental not-for-profit organization since the Marine Park’s establishment in 1979. Through a Management Agreement with the Bonaire Island Government (Openbaar Lichaam Bonaire, OLB),
STINAPA manages the island’s two national parks – the Bonaire National Marine Park and the Washington Slagbaai National Park (Fig. 1). STINAPA’s activities are centred around three objectives:

1. To protect, preserve and rehabilitate Bonaire lands and waters;
2. To protect and preserve flora and fauna on and around Bonaire; and,
3. To provide education about Bonaire’s nature and environment.

(STINAPA 1998)

STINAPA is headed by a Director who oversees the functions of four operational sections – Administration, the Bonaire National Marine Park, the Washington Slagbaai National Park, Nature/Wildlife, and Education/Communications. The Director also liaises between the operational sections and the STINAPA Board, which provides oversight on the functions and activities of the organisation. The STINAPA board consists of nine members, representing stakeholder sectors of the BNMP – the OLB; Tourism Cooperation Bonaire (TCB); Bonaire Hotel and Tourism Association (BONHATA); the Dive industry; Bonaire fishers/farmers; and two independent members.

The management arrangement between the OLB and STINAPA has led to STINAPA and the BNMP being portrayed as an example of a successful public-private partnership in nature management and conservation in the Caribbean region. STINAPA’s working relationships with both the local government and private sector (primarily the tourism industry) is seen as a strong innovative approach to advocating for and securing the interests of nature conservation. It has led to development of legislation on nature management, including the setting up of diver fees, which has assisted in organizing structural funding for outreach and education, and has also opened doors to funding of marine and terrestrial research activities on the island.

STINAPA executes its management role relating to the Bonaire National Marine Park in collaboration with a number of partners and similarly-oriented organisations and agencies which operate at a variety of levels, and with varying objectives and capacities. The complexities of management of the Bonaire National Marine Park are compounded by issues that are common in most natural resource systems governance processes – coordination within and between stakeholder organisations/agencies; division of roles and responsibilities along lines of jurisdiction and different governance levels; challenges relating to budgetary and resource constraints etc. The objective of this report was to explore the management arrangements and flows relating to the BNMP.

**Methods**

*Review of relevant policies, legislation and documents*

I conducted an initial search and request for information pertaining to policies – both local, and regional – that are associated with management of the BNMP. This also entailed collection of relevant legislation that are applicable in the management of the Marine Park. In particular, I evaluated policies that stem from commitments made under international and regional (i.e., Dutch Caribbean) treaties and agreements to determine the various actors/agencies that would logically play a role in the implementation of those policies and legislation, as well as how the those actors/agencies would be expected to work with other actors/agencies in the management of the BNMP. In this aspect, the
levels of the various roles that were identified from review of the policies and legislation spanned local, national, regional, and international.

*Semi-structured interviews*

Based on information gleaned from the various documents and information found online, confirmatory, I scheduled semi-structured interviews with identified stakeholders in the BNMP management process. The purpose of the interviews was to verify concepts and information that had been gleaned from available documents, policies, and legislation relating to management of the BNMP. I explored arrangements and interactions between those organisations/agencies involved in the management process with representatives of those organisations/agencies with a view to identify challenges and opportunities that are faced by stakeholders and managers of the Marine Park.

**Results & Discussion**

I conducted a total of four interviews on-site in Bonaire following a review of relevant documents, policies and legislation relating to the management of the Bonaire National Marine Park (many of which are listed in the ‘Literature Cited’ section of this report). I conducted semi-structured interviews with a representative of the Rijksdienst Caribisch Nederland (RCN), and with a representative from the office of the Directorate of Spatial Planning and Development (DRO) of the Bonaire local governing body. I conducted two additional interviews with the current BNMP Manager and with a former BNMP Manager. Supplementary information relating to the local Bonaire governing body and functions were obtained from the body’s website ([http://bonairegov.com/nl](http://bonairegov.com/nl)) and translated to English using the Google Translate web service ([http://translate.google.com](http://translate.google.com)). Information obtained and verified are discussed below, applying broad categories of natural resource systems governance to the Bonaire National Marine Park situation.

*Policies and Legislation relating to management of the BNMP*

There are several policies and pieces of legislation that are applicable to resources in the Bonaire National Marine Park. As can be seen in Appendix 1, these range from international policy instruments, to regional policies that apply to the Caribbean Netherlands islands, to policies and legislation that are specific to Bonaire, and to the BNMP. A review of the policies and legislation documents show no apparent conflict between the various instruments of governance, when related to management of the Marine Park. In fact, the linkages between commitments made under international agreements, such as the Convention of Biological Diversity, can be seen to be reflected at the regional level (Nature Policy Plan CN) and, from there, tailored to local situations in the Bonaire National Policy Plan and associated Nature Management Ordinance resolutions.
Institutional arrangements relating to management of the BNMP

Fig. 2 illustrates three governance levels of policies and legislation that pertain to management of the Marine Park, and the relevant agencies/organisations that are involved in the implementation or execution of those governance instruments.

Following the referendum of 2010, the Dutch government allocated management tasks to what is known in the Caribbean Netherlands as “Rijksdienst Caribisch Nederland” (RCN, which roughly translates to ‘National Department for the Dutch Caribbean’). The RCN works together with local authorities and organizations to improve the situation on the islands and, in the case of the BNMP, represents the functions of two government ministries of the Netherlands - the Ministry of Infrastructure and Environment (IenM)) and the Ministry of Economic Affairs (EZ). The IenM is responsible for management of waters around the Dutch Caribbean, while the EZ plays an advisory role for IenM in
relation to permitting on the islands. In Bonaire, the IenM is embodied by an on-site representative, while the EZ is represented by a liaison. Through the RCN, the Dutch government's role is to monitor good governance of national and local laws and policies as they are implemented on the islands of the Caribbean Netherlands (van Voskuiljen 2016).

Providing support to nature conservation initiatives on the three Caribbean Netherlands (in addition to the autonomous Dutch Caribbean islands) is the Dutch Caribbean Nature Alliance (DCNA). This non-profit organisation was created to protect the natural environment and to promote sustainable management of natural resources on the six Dutch Caribbean islands, with its Mission being to help and assist the protected area management organisations and other nature conservation organisations within the Dutch Caribbean. The DCNA was contracted to drive the development of the Nature Policy Plan CN, provided support in development of the Bonaire National Policy Plan 1999-2009, and continues to provide support to STINAPA in the execution of its mandated functions in the management of the BNMP (and the Washington Slagbaai National Park). At the local governance level, the Bonaire Public Body (Openbaar Lichaam Bonaire, OLB), which provides financial support to STINAPA in the form of annual subsidies, is directly involved in governance of the BNMP through the office of the Directorate of Spatial Planning and Development (DRO). The OLB, through the DRO, also plays a role in enforcement support and processing of permits. However, as per the conditions of the management agreement between the OLB and STINAPA, day-to-day management and enforcement of rules and regulations pertaining to the Bonaire National Marine Park is left to STINAPA.

STINAPA executes its management mandate through the BNMP Manager, the Chief Biologist, a team of BNMP Rangers, and Communications and Outreach personnel. Together with relevant partners, STINAPA plans and implements activities relating to monitoring and maintenance of the Marine Park. STINAPA BNMP Rangers, those who have completed specialised training, also have some powers of enforcement as ‘buitengewoon agent van politie’ (BAVPol, which roughly translates to ‘extraordinary police’).

While the previous section outlined the logical flow of developing governance instruments (from international agreements down to local policies and legislation), insertion of the implementing agencies into the picture raises the question of potential coordination challenges in the execution of their respective functions and mandates.

**Challenges relating to management of the BNMP**

**Budget**

Activities toward management of the Bonaire National Marine Park are made possible primarily from revenues earned from Diver fees, which are currently set at USD$25 per diver. In 2008, diver fees constituted ~93% of the income of the BNMP, raising an estimated USD 1,039,597 in revenue for the Marine Park (STINAPA 2009). In 2015, the calculated operational budget for management of BNMP was roughly USD 56,000, not including personnel costs (STINAPA 2015). There is concern that revenue earned from
diver fees, together with subsidies from the OLB is not sufficient to maintain normal operational activities, whilst expanding other areas of STINAPA’s management responsibilities such as communication and outreach. In a study of Bonaire tourist divers’ willingness to pay (WTP) for access to the Marine Park, Uyarra et al. (2010) found that fewer than half of the tourists polled were prepared to pay a higher access fee, and that the majority were satisfied with the Marine Park’s conditions given the fees they were paying. Given that the article was produced before the 2010 referendum, it may be worth revisiting tourists’ perceptions on WTP, as interviewees have indicated a surge in visitor numbers in the years following the referendum. An added significance of the 2010 referendum is the growing number of Dutch moving to live on Bonaire, leading to a more permanent increase in the island’s population. There remains to be seen when how or when this increase in population will stabilise, however, and if reaching or exceeding diver capacity in Bonaire as highlighted by Cesar et al. (2003) in Egypt will impact on the health of Bonaire’s reefs and, therefore, on tourism for the island.

_Institutional arrangement issues_

Roles played by the various stakeholder organisations and agencies involved in management of the BNMP have been outlined in the previous section, and allude to complex relationships between the different stakeholders. An interesting insight that arose from the semi-structured interviews was an added layer of reporting that has been put in place since the referendum of 2010. While processing of permits was previously carried out locally within the OLB, an unfilled vacancy within the relevant department has meant that completion of the permitting process must be done from the Netherlands. This has led to a backlog of permit requests awaiting approval from the Netherlands government that is affecting the effectiveness of the management process on Bonaire. Fig. 3, taken from Cooper (2011), shows the changes in roles and responsibilities across the different governance levels pre- and post-2010 in relation to biodiversity conservation and management in Bonaire. The table demonstrates shifts in a number of decision-making roles that were previously carried out within the Dutch Antilles/Dutch Caribbean, to the Netherlands Government, thus speaking to the concerns raised by interviewees.
There appears to be a renewed need for clarity of roles and responsibilities relating to the BNMP management process. For example, in relation to enforcement, STINAPA BNMP Rangers have limited capacities to enforce Marine Park rules and regulations if they have completed the specialised BAVPol training. Local Bonaire law enforcement have full powers of enforcement but are not necessarily executing the role in the BNMP, which is largely left to STINAPA Rangers and staff. Interestingly, this is also reflected in Fig. 3 where BNMP rules and regulations that fall within local policies and legislation are not specifically allocated as the responsibility of any one of the identified stakeholders.

**Outreach & Awareness**

As with many other nature conservation and management initiatives, the BNMP management process is faced with the on-going challenge of developing and resourcing its communications, outreach and awareness campaigns. Given the budget constraints that STINAPA is faced with in meeting its operational cost requirements, expanding its
communications and education programmes – which are critical to build awareness and a sense of ownership of the local community – is a major challenge. While funding resources were recently made available to furnish educational programmes relating to the work of STINAPA and the importance of the national parks, further resources are needed to continue building awareness and garner more support for the work of nature conservation in Bonaire.

The Bonaire National Marine Park is an important source of revenue for the island of Bonaire. The innovative approaches that have been implemented in the management of the Marine Park have been successful for the Marine Park, for STINAPA, and for the Bonaire local governing body. However, there are complexities and challenges that come with implementing governance of natural resource systems and the BNMP, despite its relative successes, is not immune to these. Add to that changes to the institutional arrangements within Bonaire’s relationship to the Netherlands governance (changes which will take some time to be fully incorporated into the management process), and the responsibility of managing national parks with limited capacity, authority and resourcing becomes a daunting undertaking. The important role that the BNMP plays, both as an area of successful management of biodiversity conservation in the Caribbean region, and as a source of revenue for the island of Bonaire, requires that managers and stakeholders of the Marine Park continue to find ways and means to maintain and improve the management system.

**Literature Cited**


