PAPER

Progression of the Coral-Algal Phase Shift in the Caribbean: A Case Study in Bonaire, Dutch Caribbean

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ABSTRACT

Coral reefs around the globe are subject to environmental and anthropogenic stressors that are causing habitat degradation and a decline in reef resilience. Past studies of Caribbean reefs document a decrease in coral cover with a simultaneous increase in algal cover after significant stress, disturbance, or coral mortality. The long-term shift from coral-dominated reefs to algae-dominated reefs is known as a coral-algal phase shift. This study assessed the progression of a coral-algal phase shift at a fringing reef around Bonaire, Dutch Caribbean, by comparing current coral and algal benthic cover to historical data, from 1997 to 2008, at a site nearby. Research was conducted over a 5-w period from September to October 2012. Twenty 10-m transects were filmed and analyzed through Coral Point Count with Excel extensions software to determine percent live coral and algal cover. Mean coral cover at the study site was 14.3%, and algal cover was 72.4%. In comparison to historical data, a significant increase in the algae-coral ratio indicated a progression of a coral-algal phase shift in Bonaire. This study contributes to the scientific knowledge of coral-algal phase shifts in the Bonaire reef ecosystem and the broader scientific reef conservation.

Keywords: phase shift, coral reef, algae, resilience, reef conservation

Introduction

Recent assessments of coral reef health place one third of the world's coral species at risk for extinction, indicating an immediate need for increased conservation efforts (Huang, 2012). Some reefs are expected to be in irreversible decline within the next 10 years (Titlyanov & Titlyanova, 2008). Global climate change and local anthropogenic stressors have been identified as primary causes for coral reef degradation and are targets of research to assess anthropogenic impacts (Aronson & Precht, 2006; Crabbe, 2010; Fung et al., 2011; Muthukrishnan & Fong, 2014). The first scientific observation of a coral-algal phase shift (Figure 1), which is defined as a transition from coral to algal dominance, was in a 25-year study in the Caribbean by Antonius and Ballesteros (1998). It is evident that coral-algal phase shifts occur as environmental conditions on reefs cross thresholds for optimal coral growth and make reversal to a coral-dominated state unlikely (Fung et al., 2011).

Case studies in the Caribbean including the U.S. Virgin Islands (Rogers & Miller, 2006), Jamaica (Crabbe, 2010; Goreau, 1992; River & Edmund, 2001), Bonaire (Bak et al., 2005; Bries et al., 2004), Curacao (Bak et al., 2005; Bries et al., 2004), and other locations have documented declines in coral reef health by measuring the percentage of benthic substrate occupied by live coral versus algae over time. As an example, strong hurricanes have caused the degradation of reefs in Jamaica, which has led to live coral cover of less than 5% and an algal cover of more than 90% (Goreau, 1992; River & Edmunds, 2001). In some cases, allelopathic algae species have been shown to produce feedback suppression of coral resilience, preventing recovery of coral colonies after a disturbance while promoting stability of algal beds (Rasher & Hay, 2010). Increased presence of algal species can affect coral communities on the microbial level with these chemical defenses, eventually affecting overall reef health in ways that are difficult to predict (Morrow et al., 2012).

Even in well-studied marine ecosystems, it is difficult to determine the baseline condition of coral and algal balance due to a lack of knowledge of historical reef states (Bruno et al., 2014). A rapid increase of algal benthic cover can affect the reef system in multiple ways. Algae recruit on dead substrate and compete with coral colonies

FIGURE 1

Example of a coral-algal phase shift from a coral-dominated reef (left) and an algae-dominated reef (right) in the Dutch Caribbean (photo credit: Dutch Caribbean Nature Alliance, 2013).

for space (Aronson & Precht, 2006), where an overabundance of algae inhibits coral recruitment (Titlyanov & Titlyanova, 2008). Furthermore, algal contact may also serve as a trigger for onset of coral disease (Nugues et al., 2004).

Similar to other populated tropical islands, marine environments on Bonaire experience anthropogenic pressures (Debrot et al., 2013; Govers et al., 2014; Slijkerman et al., 2013). The ecosystems on Bonaire are subject to pressure from coastal populations including litter contamination (Debrot et al., 2013), release of coastal waste products and sewage (Govers et al., 2014; Slijkerman et al., 2013), and physical damage from high recreational diver traffic (Lamb et al., 2014). The release of waste products and coastal runoff contributes to eutrophication of tropical water, which has detrimental affects on the stability of coral reef systems and also decreases resilience in other marine ecosystems (Govers et al., 2014; Slijkerman et al., 2013; Stokes et al., 2010; Thurber et al., 2014). Overfishing of herbivorous reef fish also affects coral communities because these species play an important role in depressing algal abundance on coral reefs (Edwards et al., 2014; Loh & Pawlik, 2014; McManus et al., 2000). Additionally, a rise of storm frequency and intensity, increased ocean temperatures, and increasing ocean acidity are factors in increasing reef vulnerability to damage and stress, often resulting in coral mortality (Bries et al., 2004).

On Bonaire, reefs serve as an important economic resource and biological habitat. Increased stressors that affect the marine environment have resulted in a degradation of reefs around the island in the last 30 years (Stokes et al., 2010). A study completed by Stokes and colleagues (2010) gave a comprehensive view on the state of coral-algal phase shifts at multiple sites in 2008. This study reported that, at the sites surveyed, live coral cover was half the recorded values in 1982, while algal cover increased between 2- and 20-fold. The researchers described an algae-dominated reef as one that has an algae-coral benthic cover ratio of higher than 1:1.

Small-scale rate of change assessments of benthic composition are useful for studying phase shifts and have ecological implications (McManus & Polsenberg, 2004). This described study is a small-scale survey on the island of Bonaire in which video transects and laboratory video analyses were used to determine the percent of coral and algal cover as well as disease presence. By studying coral and algal cover percentages, conclusions can be drawn on current reef health, degradation over time, and resilience (Stokes et al., 2010). This principle served as the base for this study. Verification of study hypotheses provides evidence of and reason to evaluate human impacts on near-shore reefs at Bonaire and to increase conservation efforts. It is hypothesized that the algae-coral ratio on Yellow Sub reef will be greater than 1:1 and will be higher than ratios observed in 2008. It is also expected that several coral diseases and coral bleaching will be frequently observed on the study site.

Materials and Methods

Study Site

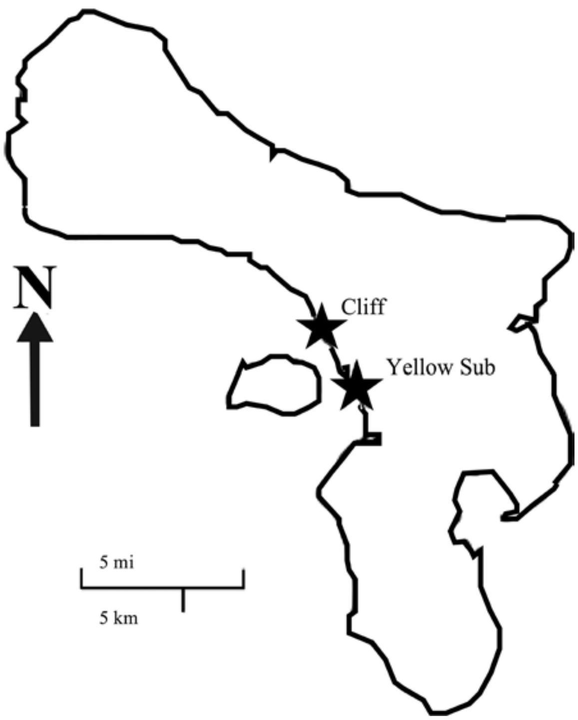
The study site is located in the southern Caribbean Sea on the island of Bonaire, Dutch Caribbean. Benthic cover and coral disease transect surveys were conducted at a study site, commonly known as Yellow Sub reef (12°09′36.47″N 68°16′55.16″W), at Kralendijk, on the leeward side of Bonaire. The historical data according to Stokes and colleagues (2010) were collected at the Cliff study site (68°17′26.62″W 12°10′26.44″N) 1,812 m north of Yellow Sub reef (Figure 2). The Yellow Sub study reef is located within close proximity to the capital city of Kralendijk and is subject to island pollution and runoff, boat travel, and diver traffic. No previous data have been collected at this site in concern to a coral-algal phase shift.

Field Research

At the Yellow Sub reef study site, underwater video transects were used

FIGURE 2

Map of Bonaire, Dutch Caribbean. Black stars mark Cliff (68°17′26.62″W 12°10′26.44″N) and Yellow Sub (12°09′36.47″N 68°16′55.16″W) study sites.



to survey benthic cover. Twenty total transects were recorded, with five replications at each depth of 6, 9, 12, and 15 m. Adjacent transects at each depth range were separated by a distance of 1–2 m. Transects were 1 m in width and 10 m in length. Using Ocean Images housing with aiming rod and Sony Handycam camcorder, transects were filmed at a height of 0.5 m on the east side of the transect tape.

Laboratory Research

Coral and Algae Cover

Video data from each transect were uploaded onto computers using the Picture Motion Browser (PMB) v5.2 PC software. Start and end times were recorded for each. Using the Microsoft Excel random number generator, 15 time points were selected as still frames. The PMB video-trimming function was used to save 15 still frames from video. Frames did not overlap.

Still frames were opened in Coral Point Count with Excel extensions (CPCe) v4.0 Windows software. Fifteen randomized points were assigned on each still frame. Each point was scored using preselected categories: coral, gorgonian, sponge, macroalgae, coralline algae, overgrowing organism, sand/rubble/pavement, other organism, and tape/wand/shadow. Corals were identified to species level. Species surveyed in this study include *Orbicellaa annularis* (OANN), *Undaria agaricites* (UAGA), *Orbicella faveolata faveolata* (OFAV), *Porites astreodies* (PAST), and *Meandrina meandrites* (MMEA) coral species codes identified by Atlantic and Gulf Rapid Reef Assessment Coral Codes v5.5 (2013). Macroalgae category includes turf algae along with other macroalgae identified to the genus level. The CPCe program calculated total coral percent cover, coral species percent cover, and macroalgae percent cover. Mean coral and algal percent cover was determined for the study site, for each area, and for each depth. Algae-coral ratio was calculated by dividing the mean algae percent cover by the mean coral percent cover for each transect and averaged over the entire study site.

Coral Disease

Original transects uploaded to PMB were analyzed for disease separately from percent cover. The entire length of transects was surveyed to record presence of coral disease. For each transect, diseases were identified and quantitatively totaled based on the absence or presence of infection in each coral species. Additionally, diseases recorded were totaled across depths, areas, and species affected.

Data Analysis

The Mann-Whitney *U* test was used to determine the significance of differences, if any, in coral and algae mean percent cover between each depth in this study. Differences in coral disease presence between depths and between species were qualitatively inferred through differences in calculated averages.

The Mann-Whitney *U* test was also used to compare historical data sets to the current study results for both percent coral cover and algae-coral ratio. Coral cover and the algae-coral ratio in this study were compared with data collected in 1997 and 2008 as described by Stokes and colleagues (2010) at the Cliff study site.

Cliff and Yellow Sub reef communities are similar in depth distribution and diver traffic. After consultation with CIEE researchers familiar with Bonaire reef ecology, the study sites were considered sufficiently similar in this study to allow for comparisons.

Comparisons were made by choosing historical depth data points closest to those used in this study. The 1997 data set did not include benthic cover estimates at 15 m.

Results

Mean Percent Coral Cover

Mean percent coral cover at the Yellow Sub study site was 14.25% ± 7.20%. The percent coral cover across depths increased with 4.76% ± 4.98% at 6 m, 12.65% ± 7.11% at 9 m, 19.05% ± 2.60% at 12 m, and 20.56% ± 7.93% at 15 m (Figure 3). A Mann-Whitney *U* test determined that percent coral cover was significantly higher at 12 m than at 6 m ($p < 0.01$) and at 15 m than at 6 m ($p < 0.05$). No significant differences were found in percent coral cover at 9 m.

Coral Cover by Species

Analyses of the benthic cover of OANN, UAGA, OFAV, PAST, and MMEA yielded comparable data with percent cover greater than 0.20%. Other species observed were *Diploria spp., Siderastrea siderea,* and *Millepora spp.* that comprised less than 0.20% mean cover.

The most dominant benthic cover species was OANN (4.98% ± 3.94%), followed by UAGA (4.49% ± 4.19%), OFAV (1.94% ± 2.84%), PAST (0.64% ± 1.10%), and MMEA (0.45% ± 0.77%) (Figure 4).

Distribution of species by depth revealed that OANN and PAST cover was highest at 12 m (8.66% ± 4.19% and 1.21% ± 1.75%, respectively) and lowest at 6 m (2.14% ± 2.77% and 0.00% ± 0.00%, respectively) (Figure 5). UAGA and OFAV cover was highest at 15 m (9.17% ± 4.40% and 3.47% ± 5.36%, respectively) and lowest at 6 m (0.43% ± 0.43% and 1.02% ± 1.09%, respectively). MMEA cover was highest at 9 m (0.81% ± 1.13%) and lowest at 15 m (0.26% ± 0.40%).

In regard to species composition, a Mann-Whitney *U* test indicated that OANN and UAGA had significantly higher mean coral cover than MMEA ($p < 0.01$), PAST ($p < 0.01$), and OFAV ($p < 0.05$). Mean percent cover of OFAV was significantly higher than MMEA cover ($p < 0.01$) and PAST ($p < 0.05$). There was no significant difference in mean cover between OANN and UAGA, MMEA, or PAST ($p > 0.05$).

Mean Percent Algae Cover

Total mean algae percent cover was 72.37% ± 11.63%. The mean algae cover was 87.91% ± 12.40% at 6 m, 74.60% ± 8.29% at 9 m, 62.73% ± 11.00% at 12 m, and 64.23% ± 9.31% at 15 m (Figure 6). Algae cover was significantly higher at 12 m as compared with percent cover at 6 m (Mann-Whitney *U* test, $p < 0.01$).

Coral Disease

Ultimately, total disease found on the reef was 2.40 ± 0.55, while, in comparison, disease per species was 2.00 ± 0.71. Yellow band disease was found on PAST, OANN, and OFAV; white plague was found on OFAV and UAGA; and dark spot disease was found only on OFAV. Additionally, coral bleaching was observed in MMEA, OANN, UAGA, and PAST. No significant difference was found between disease occurrence across depths or species.

Yellow Sub Site Algae-Coral Ratio

The mean ratio of algae to coral cover was 5.07 ± 1.21. The algae-coral ratio across depths was highest in relative comparisons at 6 m and lowest at 15 m (Figure 7). Algal-coral percent cover ratio across depths was as

FIGURE 3

Mean percent coral benthic cover for five sample areas as a function of depth (meters). Black line depicts total mean percent coral cover. Data collected from Coral Point Count analysis of 20 video transects at Yellow Sub reef study site on Bonaire, Dutch Caribbean.

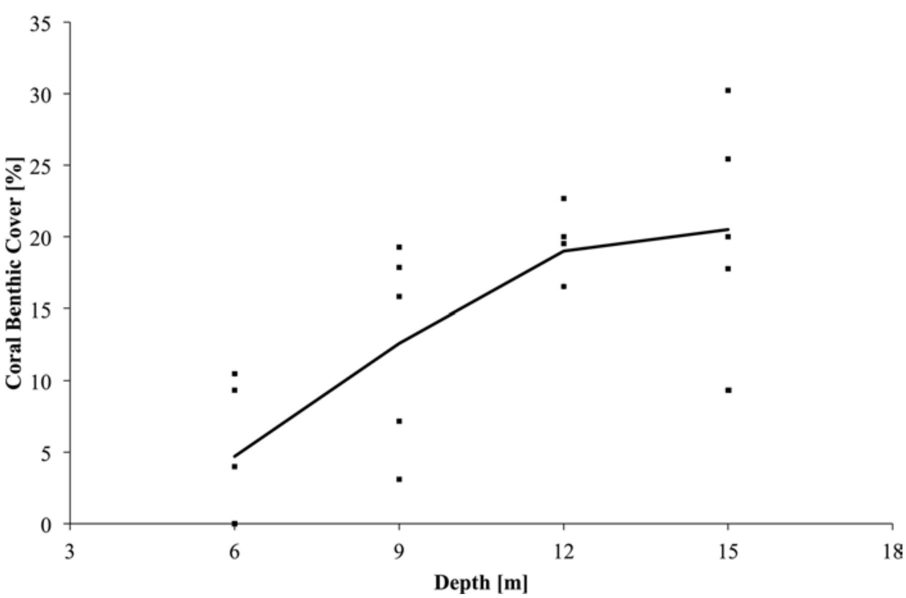


FIGURE 4

Total mean percent benthic cover of coral species. Error bars represent standard deviation. Coral species codes according to AGRRA protocol v5.5 (2013). Data collected from Coral Point Count analysis of 20 video transects at Yellow Sub reef study site on Bonaire, Dutch Caribbean.

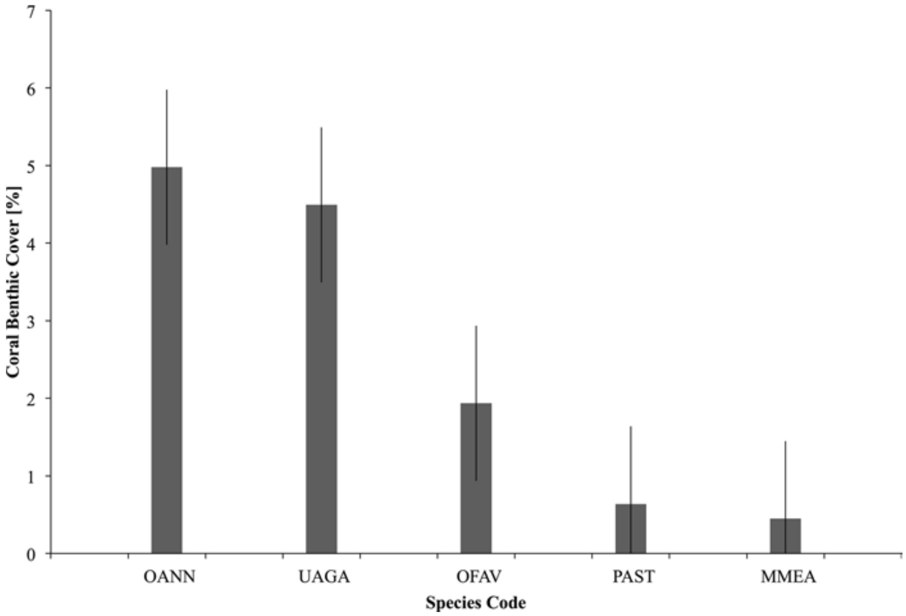
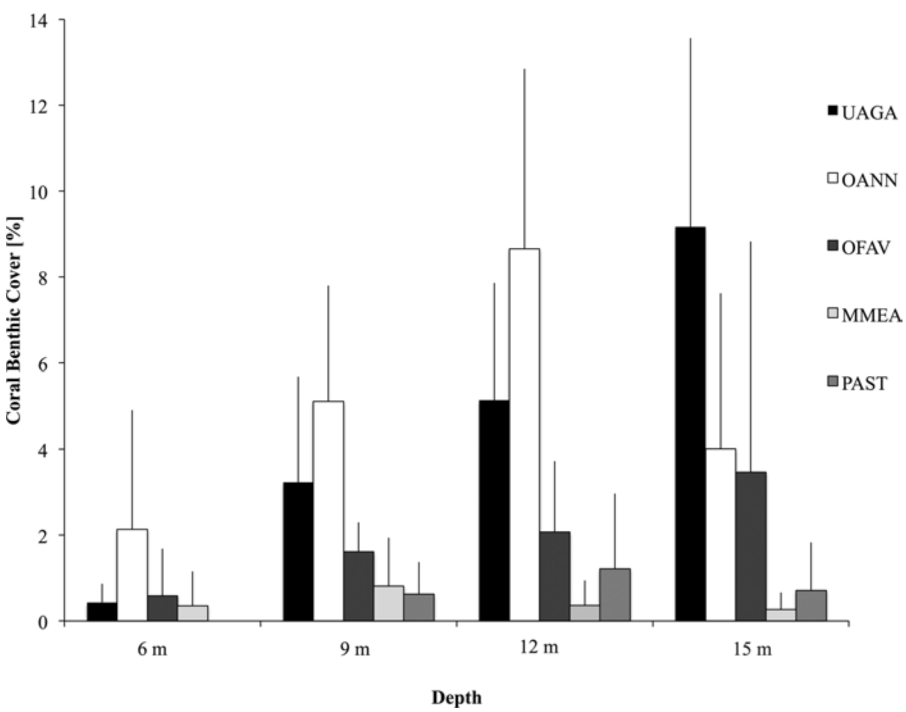


FIGURE 5

Mean percent benthic cover by coral species as a function of depth (meters). Species codes according to AGRRA protocol v5.5 (2013). Data collected from Coral Point Count analysis of 20 video transects at Yellow Sub reef study site on Bonaire, Dutch Caribbean.



follows: 6 (18.70), 9 (5.92), 12 (3.30), and 15 (3.13) m.

Comparison to Historical Data

Coral cover and algae-coral ratio were compared to available historical data as described in Stokes et al. (2010). Coral cover at Cliff in 1997 was 6 m (32.00%), 9 m (30.30%), and 12 m (29.30%), while in 2008, it was 6 m (5.86%), 9 m (26.6%), 12 m (28.00%), and 15 m (30.10%). Overall average coral cover at Cliff in 1997 was 30.53% ± 1.37%, which was higher than 2008 Cliff cover of 22.64% ± 11.28%. Both these means were higher than the 2012 Yellow Sub cover of 14.25% ± 7.20%. No significance was found between these historical coral cover data and the data collected during this study. Yet, the mean algae-coral ratio in 2008 at Cliff (2.38 ± 0.54) was significantly lower than that at Yellow Sub in 2012 (5.07 ± 1.21) (Mann-Whitney *U* test, $p < 0.05$). This ratio was lowest in 1997 and highest in 2012 (Figure 8). The mean algae-coral ratios in 1997 at Cliff were 6 m (3.40), 9 m (1.00), and 12 m (0.70) with an overall mean of 1.7 ± 1.48, while in 2008, it was 6 m (1.80), 9 m (3.10), 12 m (2.20), and 15 m (2.40) with an overall mean of 2.38 ± 0.54 (Figure 8).

Discussion

Progression of Coral-Algal Phase Shift

The mean percent coral cover recorded in this study (~14%) is lower than historical mean coral cover on Bonaire, which was reported as ~48% from 1999 to 2009 according to Steneck and colleagues (2011). This indicates a possible decline in resilience and habitat degradation at Yellow Sub reef study site. In 2008,

FIGURE 6

Mean percent algae benthic cover as a function of depth (meters). Black line depicts total mean percent cover. Data collected from Coral Point Count analysis of 20 video transects at Yellow Sub reef study site on Bonaire, Dutch Caribbean.

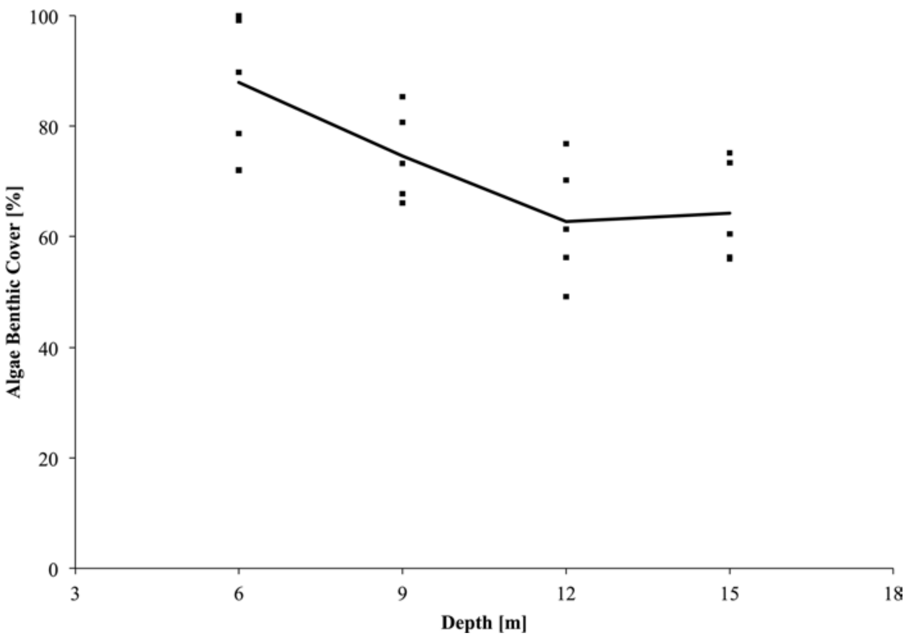
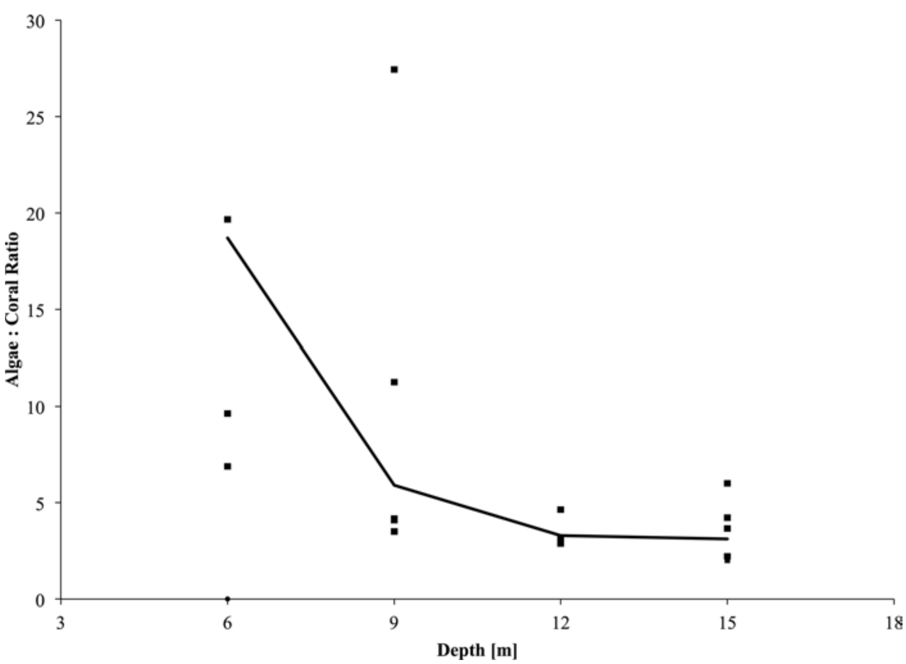


FIGURE 7

Mean algae-coral ratio as a function of depth (meters). Black line depicts total mean algae-coral ratio. Data collected from Coral Point Count analysis of 20 video transects at Yellow Sub reef study site on Bonaire, Dutch Caribbean.

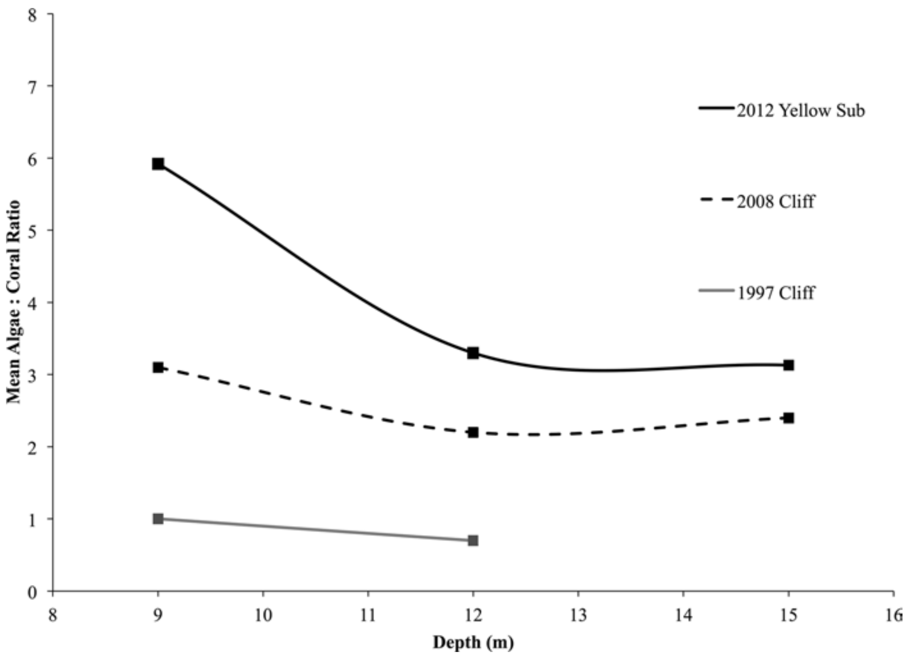


the study by Stokes and colleagues (2010) shows an average percent coral cover of 23%–38% on the leeward shore of the island. In 2011, estimates of island coral cover were ~38% (Steneck et al., 2011). Oppositely, the mean percent algae cover at the Yellow Sub study site (~72%) was higher than values observed in previous studies on Bonaire (Figure 7). In 2008, the algae cover ranged from 10% to 65% with an average of ~40% (Stokes et al., 2010), and 3 years later, in 2011, the average algae cover was ~50% (Steneck et al., 2011). This inverse relationship supports documentation of a coral-algal phase shift and indicates that coral-algal competition exists for space (Aronson & Precht, 2006). The high algae-coral ratio and presence of disease indicate that Yellow Sub reef may be experiencing habitat degradation due to external stresses. A continued increase in algal dominance on these reefs decreases the likelihood of recovery to a coral-dominated ecosystem (Fung et al., 2011).

In studies described in the last 5 years, coral cover is consistently low at shallow depths (Steneck et al., 2011; Stokes et al., 2010). Before these studies, shallow coral cover was shown to be higher, in the range of 26%–32%, and primarily composed of *Acropora spp.* (Stokes et al., 2010). In this study, OANN and UAGA were the most abundant coral species and occupied a high percentage of cover at deeper depths. After the disturbance of Hurricane Omar in 2008, mortality in *Acropora spp.* increased, and the species cover declined. As fragile *Acropora spp.* declined, other coral species were able to recruit to the benthic substrate, allowing coral with previously lower presence to become the new dominant species (Stokes et al., 2010). A return to

FIGURE 8

Mean algae-coral ratio of 2012 Yellow Sub (black line), 2008 Cliff (black dashed line), and 1997 Cliff (gray line) surveys on Bonaire, Dutch Caribbean, as a function of depth (meters). Data for 2012 survey collected from Coral Point Count analysis of 20 video transects at Yellow Sub reef. Historical data obtained from Stokes et al. (2010).



Acropora spp.–dominated systems may be prevented because larval recruitment is compromised with increasing ocean acidification, eutrophication, and water temperature (Albright et al., 2010). The loss of *Acropora spp.* and resulting loss of reef complexity and habitat are likely to have consequences for reef organisms, ecosystem functioning, and reef biodiversity (Nanami et al., 2013; Alvarez-Filip et al., 2009).

The algae-coral ratio at Yellow Sub study site of 5.07 exceeds the algal dominance threshold of 1.00 (Figure 8), as previously defined (Stokes et al. 2010). This increased ratio of the leeward study sites on Bonaire is significant and indicates a possible progression of a coral-algal phase shift over a relatively short period of 4 years. The shift to algal dominance in reefs has a direct effect on resilience and the ability of the ecosystem to revert to a coral-dominated state (Fung et al., 2011). The degradation of reef habitat affects fish stocks and coastal resilience and results in a decrease of biodiversity (Crabbe, 2010; Muthukrishnan & Fong, 2014; Stokes et al., 2010).

Presence of Disease

In this study, yellow band disease, dark spot disease, white plague, and coral bleaching were all observed. These diseases were also recorded in previous studies (Steneck et al., 2011; Stokes et al., 2010). Disease presence indicates deterioration of coral health and possibly has connections to the increase in algal cover as algal contact has been documented to trigger onset of disease (Nugues et al., 2004). Runoff from the urban center of Kralendijk may also decrease coral fitness and allow opportunistic pathogens to manifest (Steneck et al., 2011; Thurber et al., 2014). Furthermore, nonpoint sources of physiological stress on corals such as rising sea temperature may have a similar effect by increasing susceptibility to disease and infection along with suppressed ability to recover from disease or other stresses (Thurber et al., 2014). Extreme stress on coral organisms in tropical environments often presents as bleaching, a process that also leaves organisms vulnerable to disease and decreased survival or reproduction rates (Aronson & Precht, 2006).

Conclusions

This study presents results that indicate the leeward Bonaire study site at Yellow Sub is experiencing a coral-algal phase shift and benthic cover is currently dominated by algae. Deterioration of reef health at the study site could imply that other sites on Bonaire are experiencing a similar shift. The long-term trend of deterioration in the Bonaire reef system is reflected by the short-term changes observed in the current and previous studies.

Bonaire reefs are a major component of the island economy. A decrease in biodiversity would affect the diving, fishing, and tourist industries. Therefore, conservation efforts and mitigation need to increase in order to reduce anthropogenic stress on island reefs including pollution, sewage treatment, and overexploitation of reef fish. Physical stressors like increasing acidity, increases of ocean temperature, and increased storm intensity due to climate change also contribute to global reef degradation, leading to reef communities to change in ways that are difficult to predict and prevent. It is of upmost importance to reduce anthropogenic impacts on coral reefs at local, regional, and global scales.

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