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ORIGINAL PAPER

The effect of recreational SCUBA divers on the structural complexity and benthic assemblage of a Caribbean coral reef

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Abstract The effect of recreational SCUBA diving on coral reefs is likely secondary to many of the commonly cited stressors that threaten the long-term survival of coral reefs, such as rising temperatures. However, recreational SCUBA diving has had documented effects on various benthic organisms. Most research on the effect of SCUBA divers has focused on broken and abraded benthic organisms or the rate at which divers contact the benthos. We tested for differences in the structural complexity and benthic assemblage between pairs of heavily and lightly trafficked dive sites in Bonaire, a popular Carribbean diving destination. There was roughly 10 % less structural complexity in areas of heavy traffic. This is alarming given that the structural complexity of shallow reefs in Bonaire is substantially lower than in the 1970s. Different functional groups of benthic organisms were affected differentially by diving traffic. For instance, massive corals such as *Orbicella annularis* were 31 % less abundant at heavy than light diver traffic areas, while gorgonians and sponges had similar abundances at heavy and light diver traffic areas. Our results match those of previous studies on the resistance and resilience of tropical benthic reef organisms to physical disturbances that suggest that stony corals are more prone to physical damage than gorgonians and sponges. We provide a number of possible management strategies that could reduce the effects of recreational SCUBA divers on Bonaire

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and elsewhere, including education/intervention by dive guides and concentration of diving traffic away from areas of stony coral abundance.

Keywords Ecotourism · Bonaire · Physical disturbance · Structural complexity · Management

Introduction

Over the past few decades, a number of local, regional, and global stressors have led to declines in the abundance and diversity of coral reefs (Hughes et al. 2003; Pandolfi et al. 2003). While many corals are resistant and resilient to some acute physical disturbances, the combination of multiple chronic anthropogenic stressors has resulted in widespread coral decline and phase-shifts from coral to algae-dominated systems (Hughes et al. 2010). In many locations, progress is being made towards protecting coral reef ecosystems by creating marine parks and reserves that shift the focus of local economies from unsustainable overfishing to tourism and other no-take activities. Ecotourism, including SCUBA diving, is on the rise worldwide including in the Caribbean where almost US$16 billion and close to 4 % of total employment was accounted for by ecotourism in 2012 (Wilson et al. 2014). Despite the economic benefits of tourism, excess diving activity can ultimately have a detrimental effect on coral reefs (Hawkins et al. 1999).

Much of the research on diver impacts has documented the presence of greater amounts of fragmented, abraded, or dislodged stony coral individuals in heavily dove areas (Hawkins and Roberts 1992; Chadwick-Furrnan 1995; Zakai and Chadwick-Furman 2002). In some instances, a decline in coral health without a reduction in coral cover or abundance has been documented where intensive diving occurs (Lamb et al. 2014). However, limited research has examined whether intensive diving has a differential effect on different groups of benthic organisms (although see Chadwick-Furrnan 1995; Hawkins et al. 1999), and no research to our knowledge has examined the effect of intensive diving on the structural complexity of reefs.

Bonaire, a volcanic island in the southern Caribbean (Fig. 1), is one of the top diving destinations in the world (TCB 2011). Bonaire is attractive to tourist SCUBA divers because it is fringed with corals of relatively high abundance compared to the rest of the Caribbean region (Jackson et al. 2014). In 1991, nearly 17,000 SCUBA divers visited Bonaire's reefs (Dixon et al. 1993), but this number has more than doubled to 36,444 divers in 2014 (P. Bertuol, pers. comm.). The effect of diving traffic on Bonaire's reefs has not been extensively examined since the early 1990s (Dixon et al. 1993; Hawkins et al. 1999). These previous studies concluded that massive corals (e.g. *Orbicella annularis*) were affected by divers while weedy, branching, and leafy corals (e.g. *Undaria agaricites*) were largely spared of the negative effect of recreational diving (Dixon et al. 1993; Hawkins et al. 1999). The most recent study on Bonaire looked exclusively at diver impacts around cryptic species (frogfishes and seahorses) and found only small-scale damage (Uyarra and Côté 2007).

In light of the large increase in divers over the past few decades on the relatively healthy coral reefs surrounding Bonaire, this study addresses whether prolonged intensive diving has affected the structural complexity and benthic assemblage on Bonaire's reefs. We examined the structural complexity and the abundance of different functional groups of

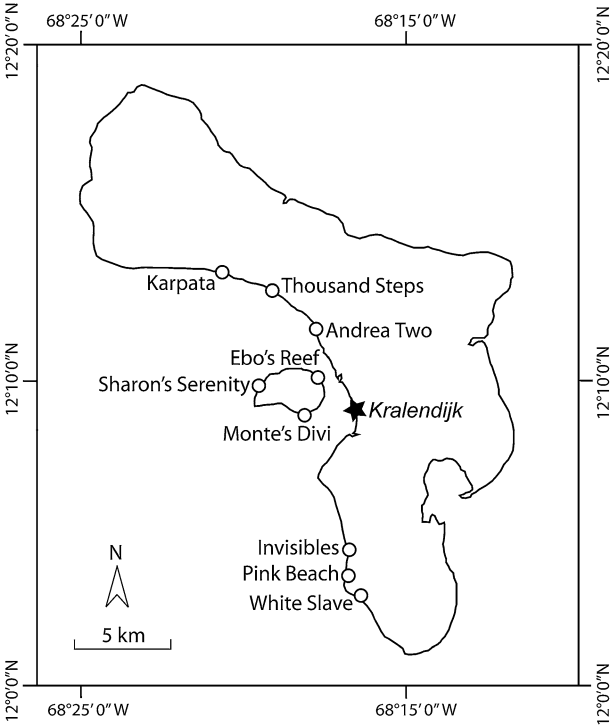

Fig. 1 Sites sampled to examine the effects of recreational SCUBA divers: Karpata (12°13′08.2″N, 68°21′09.1″W), Thousand Steps (12°12′36.8″N, 68°19′20.6″W), Andrea Two (12°11′29.8″, 68°17′55.2″), Ebo's Reef (12°09.940′N, 68°17.800′W), Shannon's Serenity (12°09′17.9″N, 68°19′44.5″W), Monte's Divi (12°08′43.3″N, 68°18′17.0″W), Invisibles (12°04′40.0″N, 68°16′48.6″), Pink Beach (12°03′51.5″N, 68°16′53.4), White Slave (12°03.456′N, 68°16.846′W). Kralendijk is the capital city of Bonaire around which the main population is centered

benthic organisms (massive stony corals, branching stony corals, gorgonians, sponges, etc.) at paired heavily and lightly trafficked dive sites. We predicted that with a historical abundance of divers in Bonaire, diver-induced damage would go beyond broken fragments and abrasions and would include a loss of structural complexity and a shift in the benthic assemblage from species more prone to physical damage, such as stony corals (Meesters et al. 1997), to organisms more resistant and resilient to physical damage, such as sponges (Wulff 2006).

Materials and methods

Site description

A typical reef in Bonaire consists of a sand, rubble, or a hard pan shelf ~5 m depth extending 50–150 m from the shore and a reef slope of ~45°. Our study focused on the shallow reef slope, which is dominated by scleractinian corals particularly the leafy corals

U. agaricites, and massive corals including *O. annularis* and *Porites astreoides*. Gorgonians and sponges are also prevalent on the upper shelf and slope.

Recreational divers typically use the western leeward shore of Bonaire and Klein Bonaire. Most of the sites on the western shore of Bonaire, including those in this study, are accessible by both shore and boat divers, while the Klein Bonaire sites are only accessible by boat. The eastern shore of Bonaire was omitted from this study as it is rarely accessed by recreational divers because of fast currents and large swell. Dive sites are conspicuously marked with yellow rocks on the shoreline and/or yellow dive buoys which are almost always used as entry points for dives.

Sampling scheme

There are 86 marked dive sites along the western shore of Bonaire and around Klein Bonaire. Of these, we chose nine sites with the goal of sampling an assortment of sites with different characteristics while maintaining criteria described below (Fig. 1). We sampled two locations at each of site: the yellow rock/buoy entry (hereafter as heavy traffic) and 200 m away from the entry (hereafter as light traffic). Recreational divers typically remain within 200 m of an entry point (Hawkins et al. 1999; Tratalos and Austin 2001) and we rarely observe divers entering the water away from marked sites. Thus, chosen sites had to be greater than 400 m from the nearest site(s) in one or both directions. For sites that were greater than 400 m from the nearest sites in both directions, a coin was flipped to determine the direction in which the reef was sampled 200 m away from the entry. This criteria eliminated the possibility of sampling the middle section of the western shore of Bonaire between the sites Invisibles and Andrea Two (Fig. 1).

At heavy and light diver traffic areas, three parallel 10-m transects were laid 2 m apart. Starting just below the reef crest, transects were laid between 10 and 17.5 m deep. The depths of the transects at heavy and light diver traffic locations were not statistically different (heavy diver traffic mean $\pm$ SEM: 12.50 ± 0.38 m; light diver traffic: 12.47 ± 0.30 m; Paired t test: $t = 0.113$, $df = 8$, p value $= 0.913$).

Rugosity

For each 10-m transect, rugosity (most commonly used term for structural complexity on coral reefs) was measured using the method of Risk (1972). A weighted chain with 170-mm links was fitted to the contour of the reef for the entire length of each 10-m transect and rugosity was defined as the ratio of the chain length spanning the 10-m transect to the linear distance (10 m). Essentially, the metric characterizes how much the surface of the reef drops and ascends. A number of different metrics have been described for estimating rugosity on coral reefs (McCormick 1994), but we used the chain-and-tape method (Risk 1972) because it performs well at characterizing different forms of complexity and is the most commonly used metric (McCormick 1994).

For each location, the rugosity of all three transects was averaged. Prior to the analysis, Shapiro–Wilk normality tests and a Bartlett test were used to examine whether data were normally distributed and whether there was equal variance between heavy and light diver traffic locations. We found that the data violated the normality assumption, but an exponential transformation normalized the data for both heavy diver traffic ($W = 0.890$, p value $= 0.200$) and light diver traffic locations ($W = 0.876$, p value $= 0.141$) and maintained homogeneity of variance (Bartlett's K-squared $= 1.285$, $df = 1$, p value = 0.257). Transformed data were analyzed using a paired t test, in which locations (heavy and light diver traffic) within each site were paired.

Benthic assemblage analysis

For each 10-m transect, the benthic assemblage was estimated using a video transect. A Sony® HDR-SR5 camcorder and Ocean Images™ housing was used to film a belt ~50 cm wide along each transect. All video transects were recorded on the side of the transect furthest from shore. Non-overlapping frames of the entire length of the transect were obtained using Sony® Picture Motion Browser© v5.2. For each location, 15 m^2 of benthic assemblage was sampled (three 10 * 0.5-m^2 belts). Benthic assemblage was estimated using Coral Point Count with Excel Extensions© (CPCe) v4.1 (Kohler and Gill 2006). The software randomly assigned 10 points on each frame and the identity of the abiotic or biotic substratum under each point was assessed by the user using categories roughly based on the Atlantic Gulf Rapid Reef Assessment© (Table 1).

These data were analyzed in three different ways. First, we plotted the data using Non-Metric Multidimensional Scaling (NMDS) to visualize if certain substrata tended to be associated with heavy versus light diver traffic areas. Using the "vegan" package of R (version 2.15.1), we ran an NMDS using several random starts to come up with a stable solution (Oksanen et al. 2012). We used a square root transformation and Wisconsin double standardization both of which reduced stress (0.136) and resulted in a stable solution with two dimensions (Oksanen et al. 2012). Plots were created using Sigmaplot©10 (Systat Software, Inc.).

Next we used the R package "ICSNP" (Nordhausen et al. 2012), to run a Hotelling's T2 (multivariate analog of the paired t test) to examine differences in the whole benthic assemblage between paired heavy and light diver traffic locations. Prior to this, we examined the data for multivariate normality using Shapiro–Wilk test and QQ plots with

Table 1 Categories of biotic and abiotic substrates used to estimate abundance in CPCe

Category	Included species/description
Pavement	Hard non-living structure that is withstanding to water movement up to the scale of a hurricane
Rubble	Hard non-living structure that is likely to be moved by non-hurricane typical water movement
Sand	Sediment with a diameter roughly less than 5 mm
Branching coral	*Acropora palmata, Acropora cervicornis, Porites porites, Madracis auretenra, Dendrogyra* spp., *Millepora alcicornis*
Flower coral	*Eusmilia fastigata*
Leaf coral	*Undaria agaricites, Millepora complanata, Mycetophyllia* sp.
Massive coral	*Orbicella faveolata, Orbicella annularis, Montastraea cavernosa, Siderastrea sidera, Porites asteroides*
Meandroid coral	*Colpophyllia natans, Diploria labyrinthiformis, Diploria strigosa, Meandrina meandrites*
Gorgonian	Sea Whips, Sea Fans, Sea Rods
Sponge	Tube Sponges, Barrel Sponges, Rope Sponges
Encrusting	*Trididemnum solidum, Briareum asbestinum, Cliona* spp.

Mahalanobis' distance. Both methods indicated that untransformed data were not normally distributed and common transformations did not normalize the data. Thus, when we ran the Hotelling's T2 test we used a Chi square approximation to calculate a p value (Nordhausen et al. 2012).

Lastly, post hoc paired t tests were used to examine whether each substratum (Table 1) differed in abundance (percent cover) at heavy and light diver traffic locations. Some substrata were log10 transformed to meet the assumptions of a t test (normal data, homogeneity of variance). One substratum (massive coral) could not be made to meet assumptions even with the standard set of transformations and was thus analyzed with a wilcoxon-signed rank test. For each of these comparisons, we calculated effect size (Cohen's d) and corrected p values for multiple testing using the Benjamini and Hochberg (1995) method for controlling the false discovery rate.

Results

Heavy diver traffic locations had a 9.8 % reduction in rugosity compared to light diver traffic locations (Mean ± SEM: 1.96 ± 0.07 vs. 2.17 ± 0.08; $t = -3.138$, $df = 8$, p value = 0.014; Fig. 2). The sites White Slave, Andrea Two, and Invisibles had the largest difference in rugosity between the light and heavy diver traffic locations (0.52, 0.42, and 0.39, respectively; Fig. 2). All three of those sites are on Bonaire, where there is more diver traffic than Klein Bonaire.

Heavy and light diver traffic locations separated primarily along axis 1 of the NMDS (Fig. 3a). For all sites with the exception of Karpata, the heavy diver traffic locations were mostly associated with sponges, gorgonians, sand, and rubble while light diver traffic locations were mostly associated with pavement, massive coral, meandroid coral, flower coral, leaf coral, encrusting invertebrates, and branching coral (Fig. 3b). The benthic assemblage was significantly different between heavy and light diver traffic locations (Hotelling's T2 = 44.941, df = 11, p value <0.001; Fig. 4). However, not all substrata

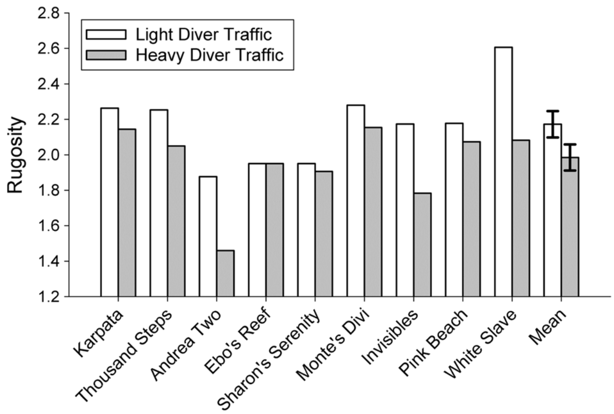

Fig. 2 Rugosity at the nine sampled sites both in light diver traffic and heavy diver traffic locations. Sites are ordered from left to right going from North to South. The last two columns are means of the nine sites and the *error bars* represent SEM. The *star* denotes a significant difference between groups (paired t test, $p < 0.05$)

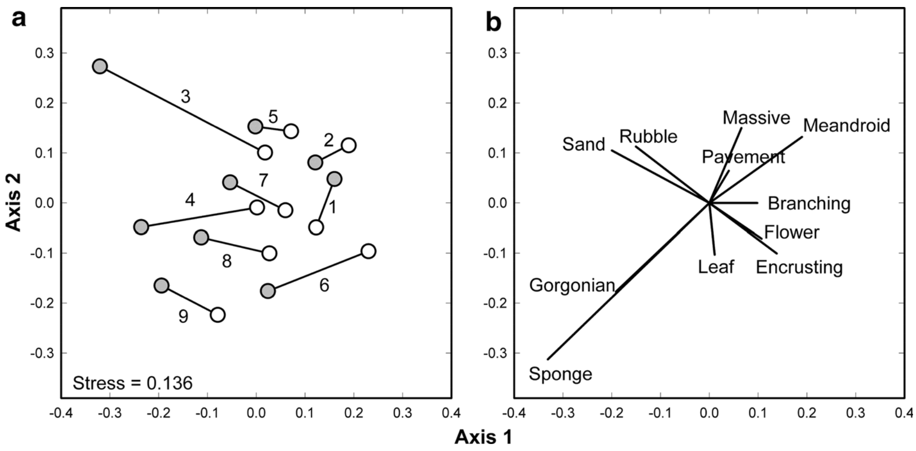

Fig. 3 **a** Non-metric Multidimensional Scaling ordination of sites in benthic assemblage space. *Shaded grey circles* represent heavy diver traffic sites and *open circles* represent light diver traffic sites. Pairs of locations within sites are connected with solid lines. Sites are numbered in order going from North to South: *1* Karpata, *2* Thousand Steps, *3* Andrea Two, *4* Ebo's Reef, *5* Sharon's Serenity, *6* Monte's Divi, *7* Invisibles, *8* Pink Beach, *9* White Slave. Distances between points (*sites*) approximate dissimilarity between the benthic communities at those sites. **b** *Solid lines* represent direction (angle) and strength (length) of correlations between the axes and types of substratum

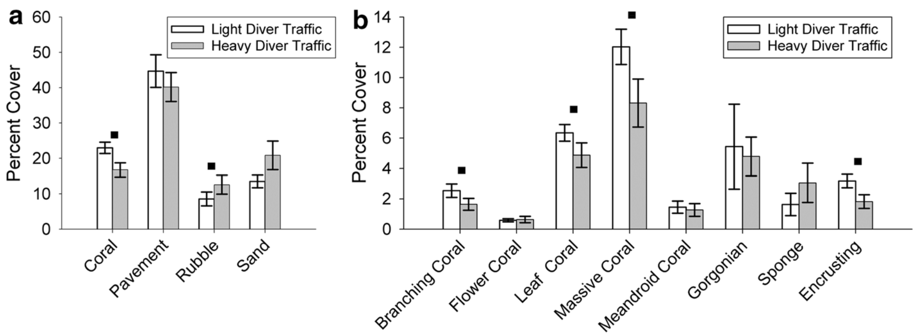

Fig. 4 Mean percent cover of **a** major biotic and abiotic substrata, and **b** all biotic substrata types at light and heavy diver traffic areas. Note the difference in y-axis scales. *Squares* above substrata denote a marginally significant difference in percent cover between light and heavy diver traffic locations. *Error bars* represent SEM

had different abundances between heavy and light diver traffic areas. Corals (all sub-groups), rubble, branching coral, leaf coral, massive coral, and encrusting invertebrates all had statistically significant differences in abundance between heavy and light diver traffic areas and marginally significant differences when accounting for the false discovery rate (Table 2; Fig. 4). Corals (all sub-groups) were 27.1 % less abundant at heavy diver than light diver traffic locations, branching coral was 35.5 % less abundant, leaf coral 23.2 % less abundant, massive coral 30.9 % less abundant, and encrusting invertebrates 42.6 % less abundant at heavy diver traffic than light diver traffic locations. Rubble was 31.8 % more abundant at heavy diver traffic than light diver traffic locations.

Table 2 Post-hoc comparisons of abiotic and biotic substrata between heavy and light diver traffic locations

Substratum	Effect size (Cohen's d)	Transformation	t	p value	Corrected p value
Coral (all subgroups)	1.315	None	−3.944	**0.004**	**0.051**
Pavement	0.439	None	−1.316	0.225	0.300
Rubble	0.948	None	2.843	**0.022**	**0.063**
Sand	0.639	Log10(X + 1)	1.917	0.091	0.157
Branching	0.945	None	2.834	**0.022**	**0.063**
Flower	0.015	Log10(X + 1)	−0.044	0.966	0.966
Leaf	0.906	None	−2.717	**0.026**	**0.063**
Massive	0.901	None	5*	**0.039**	**0.078**
Meandroid	0.352	Log10(X + 1)	−1.055	0.322	0.387
Gorgonian	0.246	Log10(X + 1)	0.737	0.482	0.526
Sponge	0.587	Log10(X + 1)	1.762	0.116	0.174
Encrusting	0.929	None	−2.788	**0.024**	**0.063**

Bolded values are marginally significant

p values were corrected using the Benjamini and Hochberg method for controling the false discovery rate

* Result of Wilcoxon–signed rank test

Discussion

Bonaire's benthic communities differed between heavy and light diving traffic areas both in structural complexity and in benthic assemblage. There was lower rugosity at heavy diver traffic than light diver traffic areas. To our knowledge, this is the first time that diving impact has been shown to directly reduce structural complexity of coral reefs, although previous studies have demonstrated that an increase in diving traffic reduces survivorship of upright organisms (e.g. Coma et al. 2004), which certainly reduces structural complexity. The average rugosity of all sites in this study was 2.06, which is greater than the Caribbean-wide average of 1.2 (Alvarez-Filip et al. 2009), but lower than values from Bonaire's shallow reefs in the late 1970s, which were as high as 3.62 (Luckhurst and Luckhurst 1978). Given that structural complexity is important to ecologically important mobile organisms that inhabit reefs (Gratwicke and Speight 2005) it is concerning that there has already been a large loss of structural complexity on Bonaire's shallow reefs and that diving traffic reduced rugosity by an additional 9.8 %.

Diving traffic had an effect on the abundance of some benthic substrata but not on others. Similar to the results of two previous studies on the effect of diving in Bonaire, we found that divers are having an effect on massive corals (Dixon et al. 1993; Hawkins et al. 1999). We also found lower abundances of branching and leafy corals at heavy diver traffic locations, whereas Dixon et al. (1993) and Hawkins et al. (1999) found that branching corals were more abundant in diving areas than no-diving reserves on Bonaire. They concluded that diving impact favored branching and leafy species by giving these "weedy" species a competitive advantage over massive corals. In addition, they found that gorgonians were more abundant at heavy diver traffic areas than light diver traffic areas. We found that while gorgonians and sponges were correlated with heavy diver traffic locations in our multivariate analysis, there was no significant difference in their abundances between heavy and light diving traffic sites.

There are a couple explanations for why our results differ from those of Dixon et al. (1993) and Hawkins et al. (1999). First, surveys of Dixon et al. (1993) were conducted in 1991 and Hawkins et al. (1999) in 1994. Since that time the number of SCUBA divers in Bonaire has more than doubled from 17,000 in 1991 (Dixon et al. 1993) to 36,444 divers in 2014 (Bertoul, pers. comm.). Thus, benthic organisms such as branching stony corals and gorgonians that once benefited from the disturbance caused by divers (possibly due to reduced competition with stony corals), may now be negatively affected by the greater amounts of diver traffic. Second, other global and local anthropogenic stressors have had increasing impacts on Bonaire's reefs. The population of Bonaire has risen from $\sim$ 10,000 in 1991 to 15,666 in 2011 (Daantje-Cecilia and van der Linden 2012), and consequently nutrient pollution has increased in Bonaire (Wieggers 2007). Moreover, Bonaire's reefs were damaged by Hurricane Lenny in 1999, Omar in 2008, and a moderate bleaching event in 2010. The importance of synergistic effects of multiple stressors on marine systems is becoming increasingly apparent (Nyström et al. 2000) and the physical disturbance caused by divers may act synergistically with these other stressors.

Resistance and resilience of benthic organisms to diving disturbance

Given the variety of morphologies of different benthic invertebrates, it is no surprise that different groups are more resistant and/or resilient to dislodgement, fragmentation, or abrasion caused by divers and other physical disturbances. We found no effect of diving traffic on sponges and gorgonians, both of which are flexible and thus likely to be unaffected by abrasion and breaking but are prone to dislodgement (Yoshioka and Yoshioka 1991; Lin and Dai 1996). Even when these groups are abraded, they often have a relatively fast recovery. For example, one of the faster regenerating stony corals (*Acropora palmata*), regenerates 1 cm^2 lesions in roughly 25 days (Meesters et al. 1992), while the slowest regeneration rate from similar sized lesions of three Caribbean gorgonians under various environmental conditions was 10.6 days (Wahle 1983). Larger-scale disturbances such as hurricanes dislodge and fragment upright sponges and gorgonians (Woodley et al. 1981; Ostrander et al. 2000), but our data imply that it is relatively uncommon for divers to dislodge these organisms (although see Coma et al. 2004). Therefore, that we found no effect of diver traffic on gorgonians and sponges is probably best explained by the high resistance and resilience of these organisms to the types and scale of damage caused by divers.

In contrast with sponges and gorgonians, we found significantly lower abundances of branching, leafy, and massive corals at heavy compared to light diver traffic locations. Despite the different morphologies and growth rates of different stony corals, the effect of diving on the percent cover of each of these stony coral groups was similar (i.e. the effect sizes were approximately equivalent with the exception of flower corals). This result is possibly because the stony coral groups that are less resistant to physical disturbance are also able to recover more quickly (i.e. are more resilient) and vice versa. For example, branching and leafy stony corals have little resistance to breakage and fragmentation by physical disturbance of divers and are often cited as the benthic organism most commonly broken by divers (Hawkins and Roberts 1992; Chadwick-Furrnan 1995; Rouphael and Inglis 2002). However, many branching and leafy corals recover more quickly following abrasion than massive corals (Meesters et al. 1992; Hall 1997). Moreover, in many branching corals such as acroporids, fragmentation is a form of asexual reproduction and survivorship following fragmentation can be relatively high (Smith and Hughes 1999). Massive and meandroid stony corals are less likely to be dislodged or fragmented compared to branching and leafy corals, but can still be abraded by the fins and equipment of SCUBA divers (Zakai and Chadwick-Furman 2002), and our data suggests that this may affect their survivorship. Growth form is just one of many variables that may affect the resistance and resilience of stony corals to physical damage. For example, the type, extent, and location of damage itself also affect how quickly corals regenerate and recover from physical disturbance (Bak et al. 1977; Hall 1997).

Physical damage to stony corals caused by divers may also increase their susceptibility to disease, and therefore reduce their resilience to physical damage (Hawkins et al. 1999). For example, experimentally fragmented *Acropora cervicornis* and *A. palmata* are more likely to be infected and killed by disease than unfragmented corals in control plots (Bak and Criens 1981) and the Caribbean-wide disappearance of acroporids can largely be attributed to white pox and white band disease (Bythell et al. 2004). Heavily dove sites in Thailand have a higher prevalence of physically damaged, overgrown, necrotic, and diseased corals than infrequently dove sites, and corals that are physically damaged are four times more susceptible to skeletal eroding band disease than corals not physically damaged (Lamb et al. 2014). Thus, it may not be enough for a coral to regenerate damaged tissue following contact by a diver if local disease prevalence is high. Indeed, disease prevalence of some massive stony corals in Bonaire has been historically high with 91 % of *Orbicella faveolata* and *O. annularis* infected with yellow band disease and 53 % of *Siderastrea siderea* infected with dark spots disease between 1997 and 1998 (Cervino et al. 2001).

It is clear from our findings and those of others that stony corals are much less resistant and resilient to physical damage (by divers or otherwise) than are gorgonians or sponges. Stony corals provide the structural framework for reefs and thus management actions to prevent the effect of recreational SCUBA divers on stony corals are needed.

Potential management strategies

Compared with other anthropogenic local and global stressors affecting coral reefs (overfishing, nutrient pollution, development, rising temperatures, ocean acidification), the effects of recreational SCUBA diving are probably easier to control. Bonaire already has several rules in place to reduce the effect of SCUBA divers (Thodé and Gonzalez 2010). Anchoring is forbidden by vessels over four meters and only allowed by fishers that use “stone anchors.” A system of moorings is present for dive operators and other vessels to use. Divers visiting Bonaire must participate in an introduction to the Bonaire National Marine Park and an orientation dive, both of which are conducted by the host dive company of the visitor. These measures seem to have a positive effect on the behavior of divers in Bonaire, who intentionally or accidentally contact the benthos a mean of 7.5 contacts * h^{-1} (Bertuol and Oliveira 2008) compared with other locations: between 62.6 and 242.4 contacts * h^{-1} in Australia (Harriott et al. 1997), between 21.6 and 247.2 contacts * h^{-1} in the Mediterranean Sea (Di Franco et al. 2009; Luna et al. 2009), between 15 and 33 contacts * h^{-1} in the Red Sea (Zakai and Chadwick-Furman 2002), and 18 contacts * h^{-1} in the Florida Keys (Krieger and Chadwick 2013). Even with relatively few mean contacts per diver, the sheer number of divers may be to blame for the effects on Bonairean reefs that we documented. Clearly, measures to further reduce the number of contacts would benefit Bonaire’s reefs.

Offering divers sufficient marine education may reduce the frequency of contacts by divers. Pre-dive briefings are one of the most effective educational tools for introducing divers to conservation and ecological awareness. Pre-dive briefings focused on environmental awareness, diver impacts, and conservation concepts significantly decreases the amount of contact divers have with the benthos (Medio et al. 1997; Townsend 2000; Camp and Fraser 2012; Krieger and Chadwick 2013), in some cases by as much as 70 % (Medio et al. 1997; Townsend 2000). Briefings that give divers knowledge about coral reef ecology (Meyer 2002) and methods for minimizing their impacts while diving are most effective (Belknap 2008). Because Bonaire already has in place a mandatory introduction and orientation dive, we suggest this education stresses the ecological and economic importance of the reefs, the fragility of the system, the evidence of diver impacts in Bonaire, and the ways personal impacts can be reduced. Beyond information gained from dive briefings, Meyer (2002) found that divers with a stronger understanding of coral reef ecology had lower contact rates with the benthos. Thus, affiliation with a coral reef conservation program (ex. NOAA Blue Star, Reef Environmental Education Foundation, PADI Aware, Coral Restoration Foundation) could provide effective information dissemination via educational pamphlets, updated online information on coral conservation, and coral identification cards (Krieger and Chadwick 2013). Affiliation promotes a conservation-focused education and benefits the dive shop as an attractive marketing tool (Camp and Fraser 2012).

While education is an effective method for increasing dive awareness, additional efforts in the form of direct intervention can help reduce the level of diver impact. A significant proportion of the physical damage caused by SCUBA divers occurs during unintentional contact of the benthos while focusing on weight placement, gear malfunctions, and buoyancy issues. In these circumstances, the presence of a dive guide can reduce the likelihood of a diver contacting the benthos. Interventions by dive guides reduce the number of contacts by 20 to 80 % (Barker and Roberts 2004; Krieger and Chadwick 2013). Divers are also more likely to directly contact the reef during the first 10 min of any dive, during night dives, and when using cameras (Harriott et al. 1997; Rouphael 1997; Barker and Roberts 2004; Bertuol and Oliveira 2008). Thus, the first 10 min of each dive should involve more monitoring/intervention by guides and be spent in areas with minimal stony coral cover and special attention should be paid to camera users and divers at night.

An effort to concentrate divers in areas away from high stony coral abundance might help reduce their impact, considering that we found that stony corals are prone to the effects of SCUBA divers while gorgonians and sponges were relatively resistant or resilient. Economic incentives to dive in those areas (ex. cheaper marine park admission tags to those that only dive those sites) could reduce the amount of diving in sites with a large abundance of stony corals that are prone to diver impacts.

Bonaire has often been referred to as a "diver's paradise" and is regarded as one of the healthiest coral reef ecosystems in the Caribbean (Jackson et al. 2014). However, Bonaire's reefs have seen a major decrease in both structural complexity (Luckhurst and Luckhurst 1978) and coral cover (Bak et al. 2005) in the last few decades along with major outbreaks of coral disease (Cervino et al. 2001). Our data implies that this degradation may be partly due to the increasing influx of recreational divers in Bonaire, and studies from elsewhere imply the effect of SCUBA divers is not unique to Bonaire. The economy of many tropical locations is dependent on healthy reefs. Thus, it is clear that more efforts are needed to reduce the effect of recreational SCUBA divers to help promote the long-term ecological and economic sustainability of coral reef communities.

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