Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles

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ABSTRACT.—Coral reefs throughout the Caribbean have suffered the effects of human activities, including overfishing, nutrient pollution, and global climate change. Yet despite systematic deterioration of reef health, there still exists appreciable variability of reef conditions across Caribbean sites. The mid-depth (20 m) fringing reefs of Bonaire and Curaçao, in the leeward Netherlands Antilles, remain healthier than reefs on many other Caribbean islands, supporting relatively high fish biomass and high coral cover. Approximately one half of the fish biomass is composed of planktivorous species, with the balance comprised of herbivorous and carnivorous species. Only a small fraction (<7%) of the fish biomass is composed of apex predators, predominantly due to the essential absence of sharks from these reefs. Coral cover across these islands averages 26.6%, with fleshy macroalgae and turf algae covering most of the remaining benthos. Coral cover was not correlated with the biomass of any fish groups, failing to provide a clear link between fish activities (e.g., herbivory) and the health and persistence of corals. However, there was a strong, positive correlation between macroalgal cover and herbivorous fish biomass. This result is in contrast to previously published reports and may identify a disparity between correlational studies conducted within islands (or nearby islands) versus studies comparing results from across islands. These data provide insights into the structure of reef communities in the southern Caribbean Sea.

KEYWORDS.—reef fish, algae, coral, trophic structure

INTRODUCTION

Coral reef community structure has changed significantly from historical baselines in most regions (Friedlander and DeMartini 2002; Hughes et al. 2003; Pandolfi et al. 2003, 2005), though the systematic degradation of reef habitats is particularly apparent in the Caribbean (Hughes 1994; Jackson 1997; Gardner et al. 2003; Pandolfi and Jackson 2006). Caribbean reefs have suffered from a suite of human impacts, including overfishing, pollution, and climate change, resulting in dramatic restructuring of the communities. Perhaps most notable is the reduction of fish standing stocks, especially among large predatory fishes (Jackson 1997; Jackson et al.

2001; Pandolfi et al. 2003), and the shift from coral- to algal-dominated benthos (Hughes 1994; Gardner et al. 2003).

In a recent survey of four northern Caribbean regions, Newman et al. (2006) described coral reef community structure along sites of high to low fish biomass (from almost 600 to 15 g m^{-2}). Sites with highest fish biomass were largely within borders of marine protected areas, suggesting that human exploitation is a principal factor reducing fish biomass. Additionally, a negative correlation was noted between the biomass of herbivorous fish and fleshy algae (Newman et al. 2006), which is consistent with a model of top-down control of fleshy algae by herbivores across this large gradient of fish biomass (Williams and Polunin 2001). These data and other related studies (Dulvy et al. 2002; Friedlander and DeMartini 2002) demonstrate that observational approaches of describing reef com-

munity structure can provide snapshot assessments of reef health and trophic interactions, especially in the context of the growing suite of data that allow large-scale spatial comparisons.

Here we present descriptions of the community structure of two southern Caribbean islands, Bonaire and Curaçao in the Netherlands Antilles. These islands lie outside of the path of most hurricanes and support extensive reef development (van Duyl 1985). Additionally, the islands are subject to particularly strong flows of the Caribbean Current due to their situation in the southern Caribbean (Gordon 1967; Frantantoni 2001). Historically, this region appears to have suffered time-delayed coral mortality relative to most other Caribbean sites (Gardner et al. 2003), with more significant coral declines in the 1990s relative to the 1980s. As such, the islands provide a unique opportunity to describe reef structure in an oceanographically and historically distinct region as compared to the northern Caribbean sites investigated by Newman et al. (2006). Finally, because of the economic importance of tourism on these islands, especially diving tourism, providing an ecological baseline of current reef condition is critical for monitoring reef health in the future.

MATERIALS AND METHODS

Study sites

Fieldwork was conducted on the fringing reefs of the two leeward islands of the Netherlands Antilles, Bonaire (12°N, 68°W) and Curaçao (12°N, 69°W). The reefs of the southwestern shores typically begin with an approximately 50 m wide terrace, dominated by small corals scattered throughout the sand and coral rubble. The terrace ends at a drop-off beginning at 7-12 m depth, with a seaward slope varying from 45° to vertical (Bak 1975). The windward, northeast shores are similar, though the shallow terrace often extends over 150 m seaward with extensive algal cover (Bak 1975). The dominant trade winds are from the east, producing consistently high wave activity

on the NE and typically calm conditions along the southwestern shores (van Duyl 1985).

We selected 11 sites in total, 6 on Bonaire and 5 on Curaçao (Fig. 1), and specifically chose sites far from one another in order to minimize the potential effects of spatial autocorrelation within islands. One site on each island was located on the windward northeastern coast, with the remaining sites located on the leeward southwestern coast. All surveys were conducted between 18-23
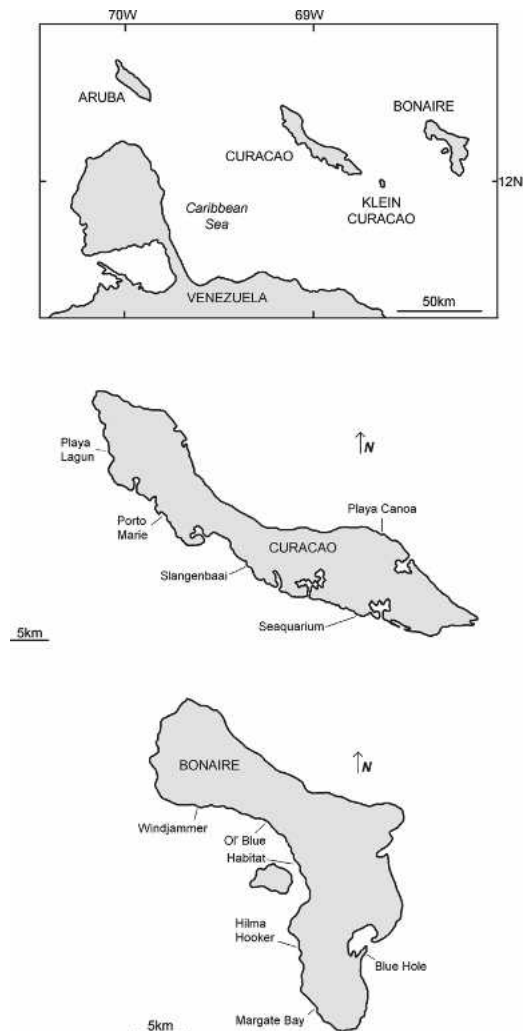

FIG. 1. Study locations in the leeward Netherlands Antilles. All study sites are on the leeward sides of the islands, except for one north coast site on each Bonaire (Blue Hole) and Curaçao (Playa Canoa).

m depth, within the sloping fore reef habitat.

Fish censuses and biomass estimation

At each location, 6 quadrats (5 m × 2 m) were sampled (except for Playa Lagún, with only 5 quadrats) to characterize the diurnal fish assemblage, resulting in 65 total sampled quadrats. Quadrat sites were selected haphazardly along the 20 m isobath at least 25 m from one another. All diurnal fish found in the quadrat (including benthic associates and mid-waters fishes in the water column) were counted using two techniques based on species activity patterns. Site-attached fishes were censused exhaustively during a 12 min sampling interval. Two divers independently recorded the species identity and total length of all site-attached fish present. Mobile species were counted three times throughout the same 12 min sampling interval, with counts taken each 6 min, i.e., at minutes 0, 6, and 12. Prior to the counts, the two divers left the quadrat for one minute, then each diver recorded an instantaneous scan sample of all fish in the water above the quadrat. Divers returned to the quadrat for the two intervening 5 min episodes to count the site-attached fish, as described above. In each scan sample, individual fast-moving fish were counted, recording species identity and length. Aggregated, midwater planktivores shoaling above the reef surface, predominately *Chromis multilineata* and *Clepticus parrae*, were counted noting only species identity and abundance. Because of high densities of these midwater planktivores in the water column, individual length estimates could not be recorded efficiently. Instead, the lengths of these two species were set to the values of 6 and 18cm, respectively, based on mean lengths of the adults (S. A. Sandin, *unpublished data*).

Due to the difficulty of precisely estimating densities of shoaling species, we found that replicated density estimations of these shoaling species in a smaller area yielded more precise data than single density estimation in a larger area (S. A. Sandin and E. M. Sampayo, *unpublished data*). Repeating estimation of highly mobile individuals three times within the same quadrat is analogous to conducting a scan sample of this group across an area three times as large at one point in time (Altmann 1974). To account for replicated effort of the scan sampling, each mobile fish recorded was weighted to 1/3 the value of a site-attached individual (Altmann 1974; see below).

The accuracy and precision of fish census data were maintained through testing and replication. The lengths of fish were estimated to the nearest centimeter by sight and by corroboration with measurement of nearby landmarks as needed. Accuracy of length estimates was maintained with periodic tests for the divers *in situ*. The same two divers (SAS and EMS) collected all census data. After each sampling interval the divers compared species lists to confirm census accuracy, making immediate corrections as necessary. Because the two divers collected data at the same time in each quadrat, the quadrat-specific means of the two divers' size-specific abundance estimates were used in the analyses below.

Total lengths of fish were converted into biomass density estimates based on published weight-length relations (available online at http://www.fishbase.org; Froese and Pauly 2005). The simple allometric function $M = \alpha L^{\beta}$ was used, where M is the mass of the fish (in grams), L represents fish standard length (in centimeters), and α and β are species-specific constants (Table 1). For species lacking specific allometric constants, parameters from a closely related, similarly shaped species were used. Final quadrat biomass estimates were calculated as the sum of all site-attached fish plus one third of the biomass of each fish counted in each of the three mobile fish counts. The mobile fish biomass estimates thus were averaged across the three replicate scan samples.

For more detailed analyses, fish were organized into trophic groups based on primary diet composition. Species were classified into four major groups: herbivores, planktivores, carnivores, and apex predators (Table 1). Trophic classifications were based on information from Bohnsack et al.

TABLE 1. Mass-length scaling parameters (α and β) for surveyed fish species. Mass, m, is approximated by the function $m = \alpha L^{\beta}$, where L is fish length. Italicized parameters indicate values dervied from studies of congeners with similar body shape. Species are organized by trophic groups, with major trophic classifications (predominantly used in the text) in capital letters and sub-classification in lower case.

Species	α	β	Species	α	β
HERBIVORES			CARNIVORES		
Acanthurus bahianus	0.024	2.98	Micro-invertivores		
Acanthurus chirugus	0.023	3.00	*Abudefduf saxatilis*	0.023	3.14
Acanthurus coeruleus	0.031	3.00	*Amblycirrhitus pinos*	0.003	3.43
Canthigaster rostrata	0.073	2.50	*Coryphopterus lipernes*	0.035	2.68
Coryphopterus glaucofraenum	0.035	2.68	*Gobiosoma spp*	0.008	3.14
Microspathodon chrysurus	0.024	3.08	*Halichoeres maculipinna*	0.003	3.69
Ophioblennius atlanticus	0.033	2.39	*Hypoplectrus chlorurus*	0.009	3.04
Scarus iserti	0.017	3.02	*Hypoplectrus nigricans*	0.009	3.04
Scarus taeniopterus	0.018	3.00	*Hypoplectrus puella*	0.009	3.04
Scarus vetula	0.018	3.00	*Hypoplectrus unicolor*	0.011	3.18
Sparisoma atomarium	0.012	3.03	*Liopropoma rubre*	0.015	3.05
Sparisoma aurofrenatum	0.021	3.00	*Mulloidichthys martinicus*	0.016	3.00
Sparisoma chrysopterum	0.014	3.10	*Serranus tigrinus*	0.015	3.05
Sparisoma rubripinne	0.016	3.06	Macro-invertivores		
Sparisoma viride	0.037	2.91	*Bodianus pulchellus*	0.015	3.05
Stegastes planifrons	0.038	2.86	*Bodianus rufus*	0.015	3.05
PLANKTIVORES			*Diodon holocantus*	0.022	3.00
Chromis cyanea	0.019	3.24	*Equetus punctatus*	0.009	3.20
Chromis insolata	0.019	3.24	*Haemulon flavolineatum*	0.021	3.00
Chromis multilineata	0.019	3.24	*Haemulon sciurus*	0.025	2.96
Clepticus parrae	0.018	3.00	*Halichoeres garnoti*	0.005	3.38
Clinidae sp	0.035	2.68	Piscivores		
Coryphopterus hyalinus	0.035	2.68	*Aulostomus maculatus*	0.004	2.87
Gramma loreto	0.015	3.05	*Caranx ruber*	0.008	3.19
Inermia vittata	0.007	2.94	*Cephalopholis cruentata*	0.012	3.08
Melichthys niger	0.006	3.55	*Cephalopholis fulva*	0.022	2.93
Paranthias furcifer	0.014	3.04	*Lutjanus apodus*	0.017	3.01
Stegastes partitus	0.018	3.15	*Lutjanus mahogoni*	0.429	2.72
Thalassoma bifasciatum	0.011	2.92	*Ocyrus chrysurus*	0.031	2.79
CARNIVORES			*Scorpaena plumieri*	0.024	2.95
Browsers			APEX PREDATORS		
Cantherhines pullus	0.068	2.56	*Gymnothorax miliaris*	0.001	2.57
Centropyge argi	0.131	2.26	*Gymnothorax moringa*	0.001	3.16
Chaetodon aculeatus	0.022	3.14	*Lutjanus jocu*	0.031	2.86
Chaetodon capistratus	0.047	2.86	*Muraenidae spp*	0.001	2.57
Chaetodon striatus	0.022	3.14	*Mycteroperca tirgris*	0.015	3.11
Holacanthus ciliaris	0.043	2.86			
Holacanthus tricolor	0.034	2.90			
Lactophrys bicaudalis	0.029	3.00			
Lactophrys polygonia	0.018	3.00			
Lactophyrs triqueter	0.031	3.00			
Pomacanthus paru	0.020	3.13			

(1999), with more coarse groupings following the scheme of Newman et al. (2006).

Benthic characterization

Benthic composition was estimated using digital photographs of ten 2 m² quadrats randomly positioned along a 100 m transect at each site. The transect line was laid haphazardly along the 20 m isobath and random numbers were generated to define the position of each quadrat along the transect. The benthic cover was recorded at each of 100 points overlaid on

each photograph and classified into one of five groups: (1) macroalgae, including primarily species of *Dictyota*, *Lobophora*, and *Halimeda*; (2) algal turf, identified as rock area principally covered by filamentous algae; (3) stony corals, including scleractinian and milleporid corals; (4) sand; and (5) other, principally including gorgonians and sponges. Additionally, the density of the sea urchin, *Diadema antillarum*, was recorded in a 2 m wide swath along the 100 m transect.

Statistical analyses

A principal component analysis (PCA) was conducted using site-specific estimates of four fish and five benthic functional groups. Fish biomass data were natural logarithmically transformed (ln[x+1]) and benthic cover data were arcsine square-root transformed. All transformed data were standardized to equal mean (0) and standard deviation (1). Linear regression analysis was used to test for relationships between cover of algal functional groups (individually for turf algae and macroalgae) and biomass of herbivores. All analyses were performed using the program R (R Development Core Team 2005).

RESULTS

The biomass of the fish assemblage ranged from 49-189 g m^{-2} across sites on Bonaire and Curaçao (134.5 ± 12.2 g m^{-2} [grand mean ± SE]; Fig. 2A). Approximately 50% of the mean biomass was composed of planktivores (78.6 ± 11.7 g m^{-2}), while apex predators composed less than 7% of the total biomass (9.8 ± 4.6 g m^{-2}; Fig. 2A). Few large predators were observed, and notably, no sharks were counted in quantitative surveys (Table 1) or in over 80,000 2-second remote videographic segments evenly spread across 723h of real time on the reef (Sandin and Pacala 2005).

The reef benthos ranged widely in coral cover from 9-44% (26.6 ± 3.4% [mean ± SE]) across sites (Fig. 2B). Species of *Montastraea*, *Madracis*, and *Porites* were the most common members of the coral assemblage. Turf algae were the most common benthic type
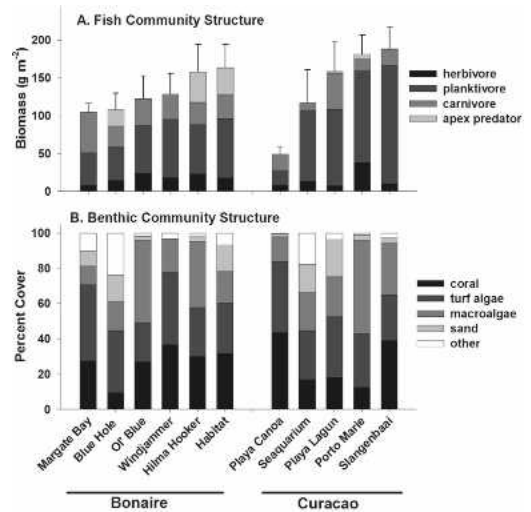

FIG. 2. (A & B) Community composition of sites across Bonaire and Curaçao. A) Biomass density of the diurnal fish assemblage, separated by four trophic categories. Error bars indicate standard errors of total fish biomass. B) Mean percent cover of each benthic functional group across sites. The figures are organized with the six sites on Bonaire on the left and the five sites on Curaçao on the right. Note that these data include one windward site per island, i.e., Blue Hole and Playa Canoa.

(32.5 ± 2.0%), and macroalgae were similarly abundant (26.1 ± 4.2%). Turf algal cover ranged from 22.3-43.2%, while macroalgal coverage was more variable with almost double the range of turf (10.5-52.8%; Fig. 2B). The density of the herbivorous sea urchin *Diadema antillarum* was low, not exceeding 0.1 individuals m^{-2} at any site.

The PCA revealed that over 60% of the variability in the nine fish and benthic functional groups was described with only two dimensions (Fig. 3). The vector loadings of the PCA suggest that the variability of coral cover and apex predator biomass are predominantly orthogonal to variability of turf cover and carnivorous fish biomass and to macroalgal cover and herbivorous fish biomass (Fig. 3). Models of trophic cascades on coral reefs predict that as predators become more abundant, herbivore populations become reduced resulting in increases of algal cover and commensurate reductions of coral cover (Mumby et al. 2006). Similar to the empirical conclusions of Mumby and colleagues (2006), we found little evidence
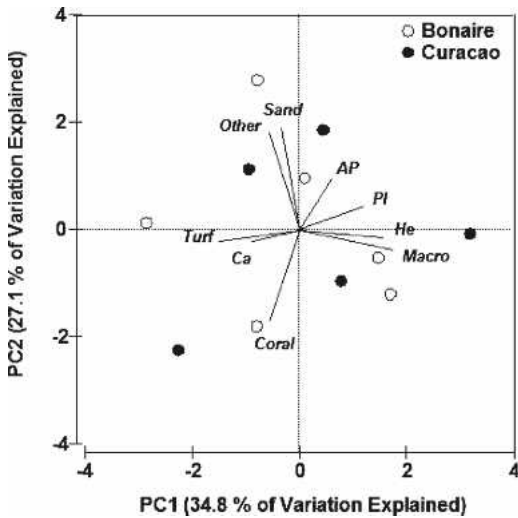
FIG. 3. Principal component analysis for transformed and standardized fish biomass and benthic cover data. Fish biomass data were natural logarithmically transformed (ln(x+1)) and benthic cover data were arcsine, square-root transformed. Variable loadings along the first two axes are presented as labeled vectors (fish labels: AP = apex predators, Ca = carnivores, Pl = planktivores, He = herbivores; benthic labels [in all lower case] are self-explanatory).

of such linear trophic cascades involving apex predators and corals. However, carnivorous fish (over 65% by biomass of carnivorous fish counted contain small fish in their reported diets; Randall 1967) were loaded in the opposite direction to herbivorous fish and in the same direction as turf algae (Fig. 3). Despite the opposite loading directions of turf and herbivorous fish biomass in the PCA, independent regression analysis failed to reveal a statistically significant negative correlation between these variables ($F_{1,9} = 1.9$, p > 0.20, $R^2 = 0.08$). In contrast, macroalgal cover was positively correlated with herbivorous fish biomass ($F_{1,9} = 20.6$, p < 0.002, $R^2 = 0.70$).

DISCUSSION

The fringing reef community of Bonaire and Curaçao supports high fish biomass relative to many other Caribbean sites. Newman et al. (2006) found that only 7 of 27 sites at 15 m depth exceeded the mean biomass reported here for Bonaire and

Curaçao (135g m^{-2}), with the majority of these fish-heavy sites within well-managed marine protected areas. Although there is fishing pressure on both islands, gear types are limited predominantly to illegal gill netting and legal hook-and-line fishing. Bonaire and Curaçao are uncommon in the Caribbean in maintaining legal limitations against spearfishing (though enforcement is not absolute; Hoetjes, et al. 2002). Consequently, this limited exploitation may result in the relatively high total biomass observed (Fig. 2A). However, it should be stressed that these fish assemblages are not pristine, as evidenced by the functional extirpation of sharks from the islands (Jackson et al. 2001). Instead, the piscivore assemblage is dominated by relatively small-bodied predators, including serranids (especially epinephelines) and some lutjanids.

Our data suggest that the fish biomass of Bonaire and Curaçao is distributed across functional groups in a manner distinct from those of northern Caribbean sites. Notably, planktivores composed almost one half of the total fish biomass on each island relative to the less than 10% composition in the northern sites surveyed by Newman et al. (2006). The discrepancy is likely due to differences in reef geomorphology of sites selected. While the majority of surveys conducted by Newman et al. (2006) were conducted on reef terraces (M. J. H. Newman, personal communication), our censuses were conducted along fairly steep (20-50° slope relative to horizontal) fringing reefs. Shoaling planktivores tend to aggregate disproportionately along reef edges, such as these steep fringing reefs common to the 20 m isobath of Bonaire and Curaçao, and not in areas of relatively horizontal reef terraces (Hobson 1991). Regardless of the cause, the large biomass subsidy from planktivores deserves closer inspection to determine the potential importance of oceanographic conditions in determining planktivore biomass and the degree of trophic coupling linking these midwater fishes with the benthic community.

Similar to the fish assemblage, coral cover on Bonaire and Curaçao was high relative to present conditions at other Ca-

ribbean sites (Gardner et al. 2003). With a mean of over 25% coral cover (Fig. 2B), these islands appear to have not suffered as much coral loss as the average Caribbean reef which currently displays only 10% coral cover (Gardner et al. 2003). This current quantification of coral cover in the leeward Antilles is consistent with comparable studies from other habitats and sites surveyed on these islands in the past (Bak and Nieuwland 1995; Bak et al. 2005). Of particular note, Bak et al. (2005) have found that this level of coral cover has been relatively stable, with slight, if any, decreases in the past decade. However, present estimates of coral cover remain well below the reports of over 40% coral cover in the 10-20 m depth range at the beginning of their sampling in the early 1970s (Bak et al. 2005).

The only significant correlation noted between the benthic and fish assemblages was a positive relationship between herbivorous fish biomass and macroalgal cover. These results are in contrast to comparable results from across the Caribbean (McClanahan et al. 2001; Williams and Polunin 2001; Newman et al. 2006) revealing a negative relationship between these functional groups. Potentially competitive herbivores, particularly the sea urchin *Diadema antillarum*, are equally rare on Bonaire and Curaçao as at the sites sampled by these other studies. One potential explanation for the disparity is the differing spatial scale of the studies, with our work conducted within one region (i.e., two adjacent islands in the leeward Netherlands Antilles) and the other work conducted across distant regions (i.e., disjunct islands of the Caribbean). Closer inspection of the correlations presented by Williams and Polunin (2001) reveals only weak evidence of a within-region negative relationship between the sites, with the majority of the correlation driven by an among-region trend. Reconciliation of these distinct patterns requires more detailed consideration of both the roles of bottom-up (e.g., nutrient fertilization) and top-down (e.g., herbivory) effects on macroalgal dynamics and the spatial scales at which each type of effect is manifested.

Through the description of reef community structure it is possible to provide snapshot assessments of reef health, offering baseline data against which to judge the efficacy of conservation and management efforts. Importantly, however, insights into the health of reefs also provide direct insights into the economic potential of reefs for local industry, especially tourism. In a study of dive tourism in the Caribbean, Green and Donnelly (2003) concluded that tourist dollars are disproportionately spent in or near to marine protected areas. This conclusion is not unexpected, as dive tourists aesthetically value similar characteristics as reef managers aim to protect, namely structural complexity, high activity (i.e., fish movements), and biodiversity (Dinsdale and Fenton 2006). Given that Bonaire and Curaçao support reefs that are 'healthy' relative to many other Caribbean sites (e.g., high fish biomass and high coral cover), dive tourists should be expected to continue to value these reefs and support local dive industries. The protection and maintenance of reef health in Bonaire and Curaçao is a laudable goal both economically and for the conservation of the few, yet rapidly diminishing, windows of reef health in the Caribbean.

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