Declining Importance of Herbivores in Structuring a Heavily Impacted Urban Coral Reef near Cartagena Bay, Colombia

Andrew Shantz (✉ ashantz@fsu.edu)

Florida State University   https://orcid.org/0000-0001-5641-8914

Tomás López-Londoño

Penn State: The Pennsylvania State University

Kelly Gomez-Campo

Penn State: The Pennsylvania State University

Roberto Iglesias-Prieto

Penn State: The Pennsylvania State University

Mateo López-Victoria

Pontificia Universidad Javeriana - Cali

Mónica Medina

Penn State: The Pennsylvania State University

Research Article

Abstract

Coral reefs are beginning to experience conditions unlike any in recent history. Understanding ecosystem function on future reefs will require reassessing ecological processes under novel environmental regimes. For many coastal reefs, severely degraded water quality will be a hallmark of these novel regimes. While herbivory has traditionally been considered essential for maintaining coral dominance recent evidence from urban reefs suggests this pattern may be changing. Here, we reexamined the importance of herbivory on a shallow, turbid reef exposed to extensive coastal development. We found that although herbivore biomass, size-structure, and grazing rates were significantly reduced relative to a nearby protected reef, coral cover on this shallow urban reef remained > 45%. In contrast, coral cover at the nearby protected site was roughly 50% lower. Differences in coral cover between the sites were due to greater cover of two groups of corals at the urban site: depth-generalist *Orbicella* spp. (*O. faveolate* and *O. annularis*), and weedy species *Agaricia* spp. Both groups are tolerant of low light levels but susceptible to coral bleaching. Our results suggest that diminished top-down pressure did not promote algal dominance. Instead, turbidity-induced reductions in available light drove community structure, leading to dominance of coral and algae species able to acclimate to low-light. Our study demonstrates how environmental context can alter the importance of critical processes on coral reefs and highlights the need to reexamine traditional paradigms in reef ecology to understand ecosystem function on future reefs.

Introduction

A paradigm in coral reef ecology is that reefs thrive in oligotrophic, clear waters. Under these conditions, nutrient recycling between corals and their endosymbionts allows corals to prosper while low nutrients limit the productivity of macroalgal competitors (Odum and Odum 1955; Muscatine and Porter 1977). In turn, limited macroalgal productivity facilitates top-down control of algae, helping herbivores maintain reefs in coral dominated states (*e.g.* Odum and Odum 1955; Littler and Littler 1984; Burkepile and Hay 2006). In this regard, low nutrients and high rates of herbivory are traditional cornerstones of resilient, coral dominated reefs (Bellwood et al. 2004).

However, humans are degrading these pillars of reef resilience. Development increases sediment, nutrients, and other pollutants in coastal runoff, thereby reducing light reaching the benthos, smothering corals, and facilitating algal growth and coral diseases (Fabricius 2005; Smith et al. 2010; Vega Thurber et al. 2014). Similarly, reductions in herbivory from overfishing and disease allow algal proliferation and can drive transitions from coral to algae dominated reefs (Bellwood et al. 2004; Jackson et al. 2014). Thus, after disturbances occur poor water quality and reduced herbivory are often considered the greatest impediments to coral recovery (Houk et al. 2010), and recommendations for preserving reefs into the future usually begin with reducing these local stressors until greenhouse-gas emissions are addressed (Bellwood et al. 2004; Baskett et al. 2010; Jackson et al. 2014).

Despite the paradigm that reefs require clear water and abundant herbivores, numerous reefs exist in conditions typically considered inhospitable to corals. For example, nearshore turbid-zones traditionally

seen as marginal or unsuitable for corals are proving to hide seemingly resilient communities with remarkably high levels of coral cover (Morgan et al. 2017). One example of such a reef is Varadero, a recently described reef at the mouth of Cartagena Bay with remarkably high coral cover (López-Victoria et al. 2015; Pizarro et al. 2017). Reefs like Varadero that persist in these unusual environments challenge our conventional views of coral ecosystems and provide opportunities to study the ubiquity of processes that dictate reef ecosystem function. Here, we compare herbivory and the benthic composition of a heavily impacted coastal reef with a nearby protected reef to explore the importance of herbivory under severe coastal pollution. Given the contrasting environments, we predicted that the extreme pollution at Varadero would spur macroalgal growth and necessitate a robust herbivore community larger than the protected community at Rosario to maintain coral cover and prevent algal overgrowth.

Materials & Methods

Varadero is an urban reef at the mouth of Cartagena Bay, Colombia with a long history of human impacts (López-Victoria et al. 2015; Pizarro et al. 2017). Located between the Magdalena and Sinú Rivers, Cartagena was founded in 1533 and has grown into the largest port in Colombia and a major metropolitan area with over one million residents. In the late 1920's the Colombian government began a series of development projects to dredge and widen the Dique Canal, a partially blocked 16th century Spanish canal connecting Cartagena Bay to the Magdalena river (Vega et al. 2013). The Magdalena drains ~ 25% of the Colombian interior and is the largest sediment input into the Caribbean and as the Canal was reopened, seagrass in the area declined by > 90% and the hard bottom of Cartagena Bay was covered by terrigenous mud (Restrepo et al. 2016). Today, the Canal carries industrial waste, sewage, and ~ 5,900,000 t•sediment•yr^{-1} to the coast to mix with the polluted waste water from Cartagena (Restrepo et al. 2006), with Varadero sitting at the edge of this polluted sediment plume (10°18'10"N, 75°34'55"W; Fig. 1a). Compounding this pollution, rapid development, and industrialization in Cartagena, combined with poor wastewater management further expose Varadero to high levels of coliforms, nutrients, metals, from the city's wastewater drainage (Tosic et al. 2019). In contrast, the Rosario Islands (hereafter Rosario) are just over 20 km southwest of Cartagena Bay. Buffered by distance from the Canal del Dique, Rosario sits in the 1,200km^2 Corales del Rosario y San Bernardo National Park (10°11'4"N, 75°44'34"W), which has been protected since 1977.

To examine differences in the herbivore communities, in November of 2017 we swam fifteen, 50x2m transects (5•day^{-1} for 3 days) between 4-10m depth at each site. Along each transect, a diver recorded the species and size of herbivorous fishes and photographed 0.25m^2 sections of the benthos every 2m along five of the transects. To calculate benthic cover, we superimposed a 100-point grid over each photo and identified the organism or substrate below each point to the lowest taxonomic level possible (typically genus). Groups with challenging taxonomy that could not be identified in photos (e.g., CCA, filamentous turf) were binned into functional groups based on Steneck (1988). For corals, we also recorded whether bleaching or symptoms of disease were present.

To estimate herbivory rates, at each site we filmed ten, 1x1m haphazardly selected sections of the benthos using GoPro HD cameras. Temporary, 1 m^2 square plots were marked out with red nylon string held down with dive weights in each corner and markings every 20 cm along the string to help calculate the size of fishes entering the plots. Three-to-four cameras were deployed between 09:00 and 14:00 over three days at each site and left undisturbed to film. After 100 minutes, cameras were retrieved by divers and 90 minutes of video were scored, excluding the initial and final 5 minutes, to record the species, length, and number of bites taken by all herbivorous fishes feeding in the plots.

Statistical Analyses

We used published length-weight relationships (Bohnsack and Harper 1988) to calculate the biomass of every herbivorous fish recorded in our transects and grazing videos. We tested for differences in the log-transformed biomass of parrotfishes and surgeonfishes between Varadero and Rosario via a mixed-effects model that included site and fish family as interacting factors and a random effect for date. We tested for differences in parrotfish and surgeonfish size-distributions between sites using one-sided Mann-Whitney U-tests. Differences in grazing rates for each family were assessed using mixed-effects models that included site as a fixed factor and date as a random effect. Because parrotfish bite size and the amount of algae and substrate consumed increases with fish size (Adam et al. 2018), bites by different sized fishes are not equivalent. Therefore, to account for differences in the size of fishes feeding we multiplied the number of bites taken by each fish by the fish's biomass to calculate a biomass-corrected grazing rate, which we analyzed in an identical manner to the standard grazing rates (Holbrook et al 2016; Shantz et al. 2020).

We tested whether the benthic communities at Rosario and Varadero differed via PERMANOVA based on Bray-Curtis distances with 9,999 permutations. We analyzed differences between sites in total macroalgae cover and the five most abundant algae groups, as well as total coral cover and the most common coral families using ANOVA that included site and group/coral family as interacting factors. For these analyses, algal cover was log transformed and coral cover square root transformed to meet assumptions of parametric statistics. Finally, we used ANOVA to test for differences in coral bleaching and disease prevalence between the sites. All results are reported as means ± 1 SD.

Results

Herbivore biomass on Varadero was significantly less than on Rosario (^{2}(1) = 21.57, p < 0.001). Although herbivore diversity was similar between the two sites (Table 1), parrotfish biomass at Varadero was only 278 ± 115 g·100m^{-2}, extremely low for the Caribbean (Shantz et al. 2020) and significantly lower than nearby Rosario (Tukey's HSD: p = 0.008; Fig. 1b). Furthermore, the size distribution of parrotfish on Varadero was skewed towards smaller individuals than Rosario (W = 49,162, p < 0.001; Fig. 1c). Surgeonfish biomass (Tukey's HSD: p = 0.86) and size distribution (W = 733, p = 0.53) did not differ between sites.

Table 1
Species of herbivorous fishes observed by divers along transects at Rosario and Varadero. * Denotes species only observed at Rosario while   indicate species only observed at Varadero.

Rosario	Varadero
Acanthurus coeruleus	Acanthurus chirurgus
Acanthurus tractus	Acanthurus coeruleus
Scarus iseri	Acanthurus tractus
Scarus taeiopterus	Scarus iseri
Scarus vetula*	Scarus taeiopterus
Sparisoma aurofrenatum	Sparisoma aurofrenatum
Sparisoma chrysopterum*	Sparisoma viride
Sparisoma viride	

Parrotfish bite rates were similar between Varadero and Rosario but after correcting for size, parrotfish biomass-corrected grazing rates were over 2x higher at Rosario (^{2}(1) = 7.252; p = 0.008; Fig. 2). Only 3 observations of surgeonfish grazing on Varadero were recorded, making statistical comparisons impossible.

Despite the limited herbivorous fish community at Varadero, total coral cover was 47.8 ± 4.5%, over 2x higher than Rosario ($F_{(6,56)}$ = 8.97, p < 0.001; Fig. 3a). Corals from the family Merulinidae, particularly O. faveolata, occupied 18 ± 9% of the benthos at Varadero but just 1.4 ± 1% at Rosario (Tukey's HSD: p < 0.001). Likewise, the cover of Agaricidae, predominantly A. tenuifolia and A. agaricites, was 17.6 ± 3.5% at Varadero versus 6.3 ± 1.1% at Rosario (Tukey's HSD: p = 0.001). Surprisingly, total macroalgal cover was similar at both sites but differences in the algal composition, specifically the more homogenous community dominated by Halimeda spp. at Varadero, suggesting that the communities were structured through different pathways ($F_{5,48}$ = 7.99, p < 0.001; Fig. 3b). The percent cover of CCA and finely cropped turf algae (< 5mm), which are indicators of top-down pressure (Littler and Littler 1984), were significantly higher at Rosario than Varadero (Tukey's HSD: p = 0.028 & p < 0.001 respectively). In contrast, Halimeda spp. occupied on average 2x more space on Varadero than Rosario (Tukey's HSD: p < 0.001). Cumulatively, the benthic communities differed substantially between sites (PERMANOVA; p = 0.008), with Varadero associated with high coral cover and Halimeda and Rosario dominated by closely cropped turf algae and CCA (Fig. 3c).

Bleaching prevalence was over 5x higher at Rosario than Varadero ($F_{1,8}$ = 75.99, p < 0.001; Fig. 4). In contrast, disease prevalence tended to be greater at Varadero, however the high variability in disease incidence meant this pattern was not statistically significant (Fig. 4)

Discussion

Herbivory is one of the strongest drivers of coral reef community structure (Burkepile and Hay 2006; Holbrook et al. 2016). Reductions in herbivory, often driven by overfishing, are a common cause of coral decline, loss of resilience, and phase-shifts to algae dominated states (Bellwood et al. 2004; Rasher et al. 2012; Holbrook et al. 2016). We found that herbivorous fish biomass and grazing potential were significantly lower at Varadero than nearby Rosario. In turn, Varadero had significantly higher cover of *Halimeda* spp., whereas the benthic community at Rosario was dominated by closely cropped turf and CCA, groups typically associated with more resilient, coral dominated reefs (Fig. 3b). Yet, despite the limited herbivore community, high sedimentation, and greater *Halimeda* abundance at Varadero, an extensive coral community persists between 1–12 m (Pizzarro et al. 2017; this manuscript). Total coral cover was over 2x higher at Varadero than Rosario (Fig. 3a) and among the highest levels reported in the Caribbean (Jackson et al. 2014). Thus, our results suggest herbivorous fishes played a minimal role in maintaining coral cover on Varadero.

Relatively few studies to date have examined herbivory on highly turbid reefs. Those that have, report limited herbivore communities and very low rates of herbivory (e.g. Cheal et al. 2013; Guest et al. 2016; Bauman et al. 2017). This limited herbivory can likely be ascribed to the greater attenuation of light which, when studied across depth gradients, reduces algal productivity (Tebbett and Bellwood 2021). In turn, this lower productivity may in turn support fewer grazers and lead to concurrent declines in the biomass, diversity, and grazing rates of herbivorous fishes (Brokovich et al. 2010; Cooper et al. 2019). For instance, algal productivity on the Great Barrier Reef was ~ 3–5x lower and herbivore biomass ~ 2–7x lower at 15 m than at 3 m (Russ 2003). On Varadero, the annual average daily integrated irradiance at 3.5 m between 2016–2017, when our study took place, was roughly equivalent to light levels nearly 10 m deeper on Rosario (López-Londoño et al. 2021). Thus, reductions in light due to turbidity at Varadero likely limited algal productivity and reduced the need for strong top-down control.

Because our study only involved a single sampling period it is unclear if the patterns we observed hold year-round. Herbivory is typically stronger during warmer periods and relaxes during cooler seasons (Lefèvre and Bellwood 2010). However, water temperatures are similar at both Rosario and Varadero throughout the year, with slightly cooler conditions at Rosario (López-Londoño et al. 2021). Thus, any temperature-driven fluctuations in grazing rates should be the same at both sites and not influence our overall patterns. Similarly, while seasonal upwelling influences algal cover on some Colombian reefs (Diaz-Pulido and Ferreira 2002) both Rosario and Varadero are south of the major Colombian upwelling zone in Guajira (Gomez Gaspar and Acero 2020). Accordingly, while a more in-depth evaluation of the seasonal dynamics at both sites would be valuable, we do not anticipate that it would change the overall patterns in herbivory or coral cover recorded here.

The turbid conditions at Varadero also appear responsible for maintaining the coral community. Turbidity can limit harmful interactions between high temperatures and irradiance that promote coral bleaching (Cacciapaglia and van Woesik 2016). Furthermore, turbid systems often have greater amounts of

suspended particulate matter that some corals species can consume to maintain a positive energy balance, survive bleaching, and reestablish symbiosis (Anthony and Fabricius 2000; Grottoli et al. 2006; Tremblay et al. 2016). As a result, turbid reefs are garnering attention as potential refuges from thermal stress. Our study occurred at the end of a 3-year global coral bleaching event (Eakin et al. 2019). The dramatically higher bleaching frequency we recorded at Rosario (nearly one-in-ten corals still bleached) versus Varadero (fewer than one-in-fifty) suggests that protection from bleaching had substantial impacts on preserving Varadero's coral community. Interestingly, in the early 2000's Rodríguez-Ramírez et al. (2010) reported coral cover was dominated by *Agaricia* spp. and *Orbicella* spp. were abundant. However, both these coral groups are sensitive to bleaching and during our surveys *Agaricia* spp. accounted for only 6% of benthic cover, and *Oribcella* spp. <1.5% (Fig. 4). Accordingly, as climate change has caused increasingly frequent bleaching events, the unique abiotic conditions at Varadero that help corals survive bleaching appear to be more important for community structure than the absence of strong top-down pressure.

Yet the turbid outflow and pollution from the Dique canal also appears to make Varadero's existence precarious. Nutrient enrichment promotes coral diseases (Vega Thurber et al. 2014) and coral microbial communities at Varadero display increased microbial diversity that is indicative of stress (Roitman et al. 2020). Further, the average disease prevalence on Varadero, while highly variable, was > 2x greater than Rosario (Fig. 4) and at depths below 10 m the reef is dominated by coral rubble and the skeletons of dead *Orbicella* and *Agaricia* spp. (Pizarro et al. 2017; López-Londoño et al. 2021). This coral mortality at depth was absent at Rosario and suggests light limitation has killed corals in the deeper zones of Varadero (> 12 m), and that further declines in water clarity could endanger shallower corals. Therefore, Varadero appears to be narrowly situated where the Dique canal's sediment plume helps shallow corals persist under low herbivory levels, but the pollution and light limitation still threaten the reef by promoting disease and truncating the depth range where corals can survive.

Many reefs have experienced substantial declines in coral cover due to increasing pollution and coastal development but in the past decade numerous reports of robust coral communities in turbid systems have surfaced (reviewed by Zweifler et al. 2021). Results from our study and other investigations of turbid reefs suggest that rates of herbivory are low and the importance of herbivores in maintaining coral dominance on these reefs is reduced (Cheal et al. 2013; Guest et al. 2016b; Bauman et al. 2017). However, the safe operating space for these turbid reefs may also be reduced. Corals that survive in these environments must be resilient to sedimentation and either capable of tolerating low light or proficient in heterotrophic feeding. Such species typically constitute only a small portion of reef communities and as a result, expanding urbanization is likely to lead to the loss of diversity and structural complexity on most coastal reefs (Heery et al. 2018). Further, while herbivory does not appear to be essential for maintaining coral cover, the low rates of herbivory on turbid reefs could retard recovery when corals die in these turbid environments (Heery et al. 2018). Thus, while our study suggests that high rates of herbivory are not essential for maintaining coral cover on turbid coral reefs, their impacts on the resilience of these ecosystems warrants further attention. Likewise, as anthropogenic impacts on the planet increase, studying reefs in suboptimal conditions like Varadero will continue to provide insight into how future

reefs will function and helps us understand processes that are important for maintaining reefs in human-dominated habitats.

Declarations

Conflicts/Competing interests: The authors have no financial or proprietary interests in any material discussed in this article.

Data availability: Data and code for this manuscript will be made available upon publication at the authors personal website (aashantz.weebly.com), and github page.

Author Contributions: AAS designed the study; AAS, TLL and KGC performed the field work and data collection; AAS performed the analyses and wrote the manuscript; all authors contributed to manuscript revisions.

Ethics: The research was conducted under the permit No. 0546 from 2014 issued by "Autoridad Nacional de Licencias Ambientales ANLA". No human subjects were used in this study. As this study was strictly observational, no IACUC approval was required.

Consent to Publish: The authors affirm that this is their original work and neither the article nor portions of it have been previously published elsewhere. This manuscript in not under consideration for publication in another journal. All authors consent to the publication of the manuscript in Urban Ecosystems, should the article be accepted by the Editor-in-chief upon completion of the refereeing process.

References

1. Adam TC, Duran A, Fuchs CE, Roycroft MV, Rojas MC, Ruttenberg BI, Burkepile DE (2018) Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. Mar Ecol Prog Ser 597:207–220
2. Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Biol Ecol 252:221–253
3. Baskett ML, Nisbet RM, Kappel CV, Mumby PJ, Gaines SD (2010) Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison. Glob Change Biol 16:1229–1246
4. Bauman AG, Hoey AS, Dunshea G, Feary DA, Low J, Todd PA (2017) Macroalgal browsing on a heavily degraded, urbanized equatorial reef system. Sci Rep 7:8352

5. Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

6. Bohnsack JA, Harper DE (1988) Length-weight relationships of selected marine reef fishes from the southeastern United States and Caribbean. In: Comerce UDo (ed) 1–35

7. Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M (2010) Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. Mar Ecol Prog Ser 399:69–80

8. Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. Ecology 87:3128–3139

9. Cacciapaglia C, van Woesik R (2016) Climate-change refugia: shading reef corals by turbidity. Glob Change Biol 22:1145–1154

10. Cheal AJ, Emslie M, MacNeil MA, Miller I, Sweatman H (2013) Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. Ecol Appl 23:174–188

11. Cooper AM, MacDonald C, Roberts TE, Bridge TCL (2019) Variability in the functional composition of coral reef fish communities on submerged and emergent reefs in the central Great Barrier Reef, Australia. PLOS ONE 14:e0216785

12. Diaz-Pulido G, Garzón-Ferreira J (2002) Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. Bot Mar 45:284–292

13. Eakin CM, Sweatman HPA, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545

14. Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar Pollut Bull 50:125–146

15. Gomez Gaspar A, Acero AP (2020) Comparison of the upwellings of the Colombia Guajira and eastern Venezuela. Boletín de Investigaciones Marinas y Costeras 2020:131–172

16. Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

17. Guest JR, Verges. A, Bauman AG, Campbell AH, Chou LM, Feary D, Low JK, Marzinelli EM, Tun K, Steinberg PD (2016) Examining the relationship between fish herbivore biomass, coral and macroalgal cover on Singapore's heavily disturbed reefs. PeerJ Preprints 4:e1907v2

18. Heery EC, Hoeksema BW, Browne NK, Reimer JD, Ang PO, Huang D, Friess DA, Chou LM, Loke LHL, Saksena-Taylor P, Alsagoff N, Yeemin T, Sutthacheep M, Vo ST, Bos AR, Gumanao GS, Syed Hussein MA, Waheed Z, Lane DJW, Johan O, Kunzmann A, Jompa J, Suharsono, Taira D, Bauman AG, Todd PA (2018) Urban coral reefs: Degradation and resilience of hard coral assemblages in coastal cities of East and Southeast Asia. Mar Pollut Bull 135:654–681

19. Holbrook SJ, Schmitt RJ, Adam TC, Brooks AJ (2016) Coral Reef Resilience, Tipping Points and the Strength of Herbivory. Sci Rep 6:35817

20. Houk P, Musburger C, Wiles P (2010) Water Quality and Herbivory Interactively Drive Coral-Reef Recovery Patterns in American Samoa. PLOS ONE 5:e13913

21. Jackson JBC, Donovan MK, Cramer KL, Lam W (2014) Status and trends of Caribbean coral reefs: 1970–2012. In: Jackson JBC, Donovan MK, Cramer KL, W. L (eds). Global Coral Reef Monitoring Network, IUCN, Gland

22. Lefèvre CD, Bellwood DR (2010) Seasonality and dynamics in coral reef macroalgae: variation in condition and susceptibility to herbivory. Mar Biol 157:955–965

23. Littler MM, Littler DS (1984) Models of tropical reef biogenesis: The contribution of algae. Progress in Phycological Research 3:323–364

24. López-Londoño T, Galindo-Martínez CT, Gómez-Campo K, González-Guerrero LA, Roitman S, Pollock FJ, Pizarro V, López-Victoria M, Medina M, Iglesias-Prieto R (2021) Physiological and ecological consequences of the water optical properties degradation on reef corals. Coral Reefs 40:1243–1256

25. López-Victoria M, Rodriguez-Moreno M, Zapata FA (2015) A paradoxical reef from Varadero, Cartagena Bay, Colombia. Coral Reefs 34:231

26. Morgan KM, Perry CT, Johnson JA, Smithers SG (2017) Nearshore Turbid-Zone Corals Exhibit High Bleaching Tolerance on the Great Barrier Reef Following the 2016 Ocean Warming Event. Frontiers in Marine Science 4:224

27. Muscatine L, Porter JW (1977) Reef Corals: Mutualistic Symbioses Adapted to Nutrient-Poor Environments. Bioscience 27:454–460

28. Odum HT, Odum EP (1955) Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll. Ecol Monogr 25:291–320

29. Pizarro V, Rodríguez SC, López-Victoria M, Zapata FA, Zea S, Galindo-Martínez CT, Iglesias-Prieto R, Pollock J, Medina M (2017) Unraveling the structure and composition of Varadero Reef, an improbable and imperiled coral reef in the Colombian Caribbean. PeerJ 5:e4119–e4119

30. Rasher DB, Engel S, Bonito V, Fraser GJ, Montoya JP, Hay ME (2012) Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. Oecologia 169:187–198

31. Restrepo JC, Escobar J, Otero L, Franco D, Pierini J, Correa I (2016) Factors Influencing the Distribution and Characteristics of Surface Sediment in the Bay of Cartagena, Colombia. Journal of Coastal Research:135–148

32. Restrepo JD, Zapata P, Díaz JM, Garzón-Ferreira J, García CB (2006) Fluvial fluxes into the Caribbean Sea and their impact on coastal ecosystems: The Magdalena River, Colombia. Global Planet Change 50:33–49

33. Rodríguez-Ramírez A, Reyes-Nivia MC, Navas-Camacho SZ, Garzón-Ferreira R, Bejarano J, Herrón S, Orozco P C (2010) Recent dynamics and condition of coral reefs in the Colombian Caribbean. Revista de Biologi Tropical 58:107–131

34. Roitman S, López-Londoño T, Joseph Pollock F, Ritchie KB, Galindo-Martínez CT, Gómez-Campo K, González-Guerrero LA, Pizarro V, López-Victoria M, Iglesias-Prieto R, Medina M (2020) Surviving

marginalized reefs: assessing the implications of the microbiome on coral physiology and survivorship. Coral Reefs 39:795–807

35. Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral Reefs 22:63–67

36. Shantz AA, Ladd MC, Burkepile DE (2020) Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. Ecol Monogr 90:e01403

37. Smith JE, Hunter CL, Smith CM (2010) The effects of top–down versus bottom–up control on benthic coral reef community structure. Oecologia 163:497–507

38. Steneck R (1988) Herbivory on coral reefs: A synthesis. Proeedings of the 6th International Coral Reef Symposium 1:37–49

39. Tebbett SB, Bellwood DR (2021) Algal turf productivity on coral reefs: A meta-analysis. Marine Environmental Research 168:105311

40. Tosic M, Restrepo JD, Lonin S, Izquierdo A, Martins F (2019) Water and sediment quality in Cartagena Bay, Colombia: Seasonal variability and potential impacts of pollution. Estuarine, Coastal and Shelf Science 216: 187–203

41. Tremblay P, Gori A, Maguer JF, Hoogenboom M, Ferrier-Pagès C (2016) Heterotrophy promotes the re-establishment of photosynthate translocation in a symbiotic coral after heat stress. Scientific reports 6:38112–38112

42. Vega L, Ordoñez JI, Pinilla G (2013) Towards a systemic assessment of environmental impact (SAEI) regarding alternative hydrosedimentological management practice in the Canal del Dique, Colombia. Ing E Investig 33:41–48

43. Vega Thurber RL, Burkepile DE, Fuchs C, Shantz AA, McMinds R, Zaneveld JR (2014) Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. Glob Change Biol 20:544–554

44. Zweifler A, O'Leary M, Morgan K, Browne NK (2021) Turbid Coral Reefs: Past, Present and Future—A Review. Diversity 13
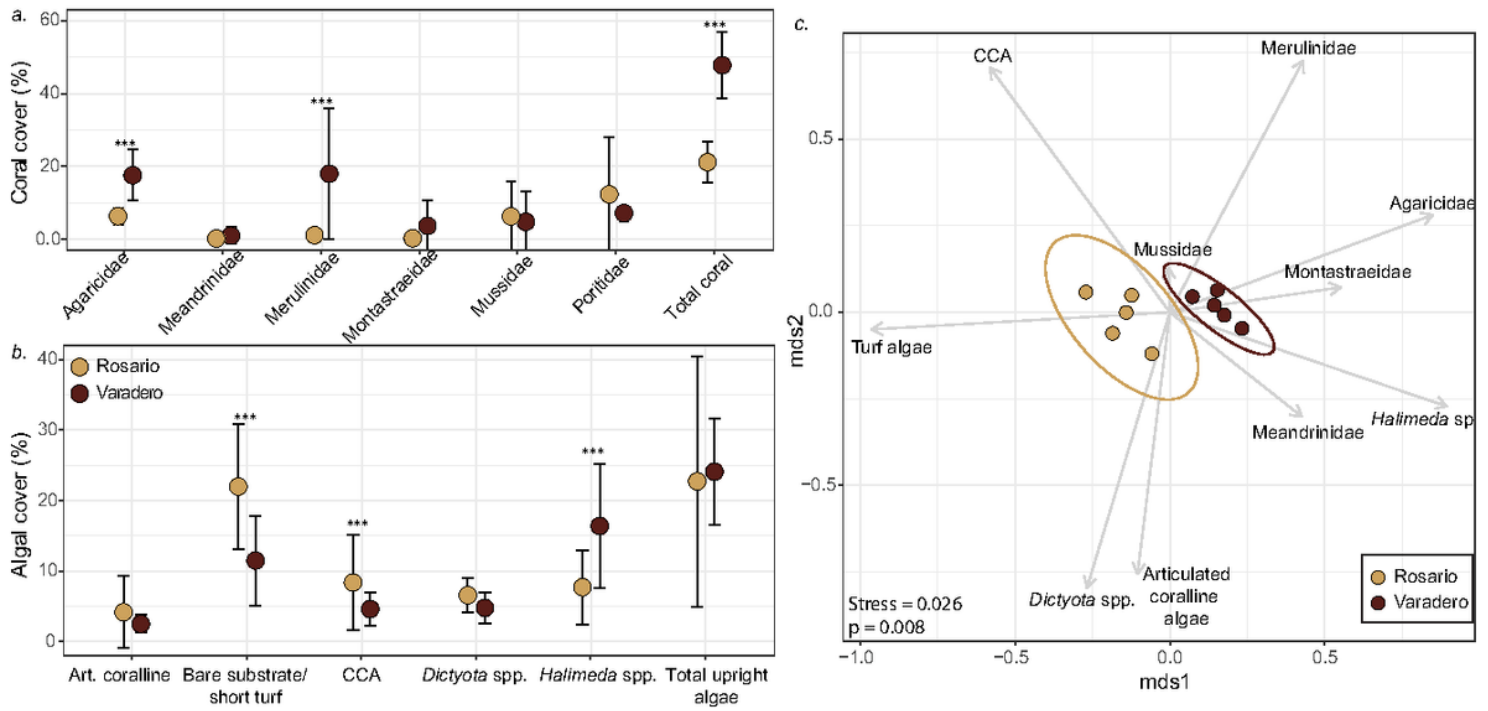
Figures
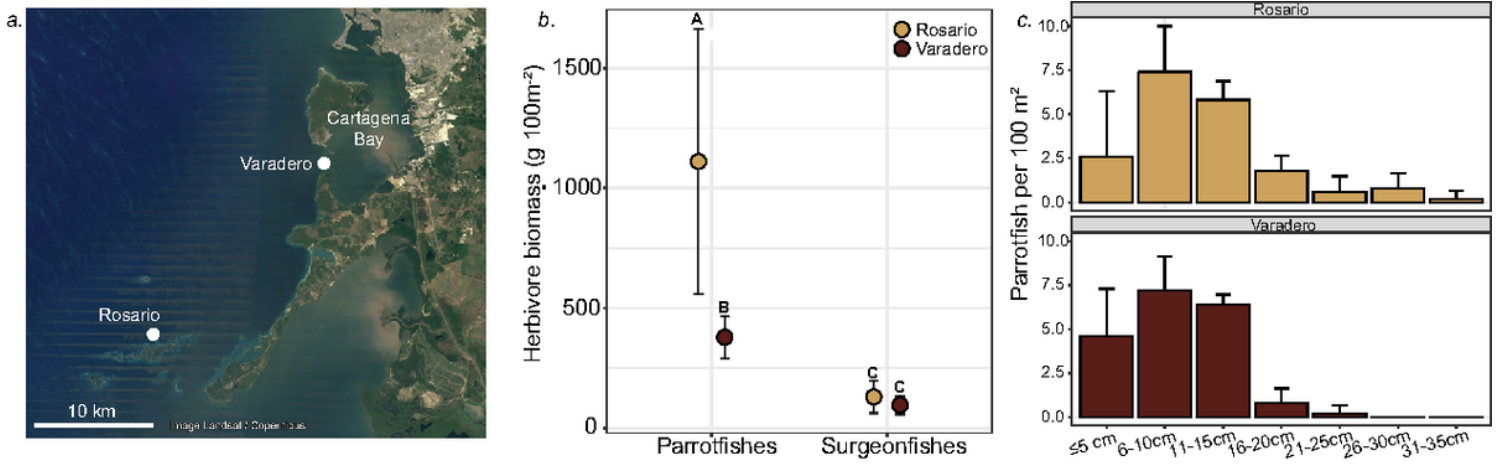
Figure 1

(*a*) Satellite image of the study location. (*b*) Parrotfish and surgeonfish biomass at Rosario and Varadero. Letters indicate significant differences based on Tukey's HSD. (*c*) Histograms showing the size structure of parrotfish populations at Rosario and Varadero.
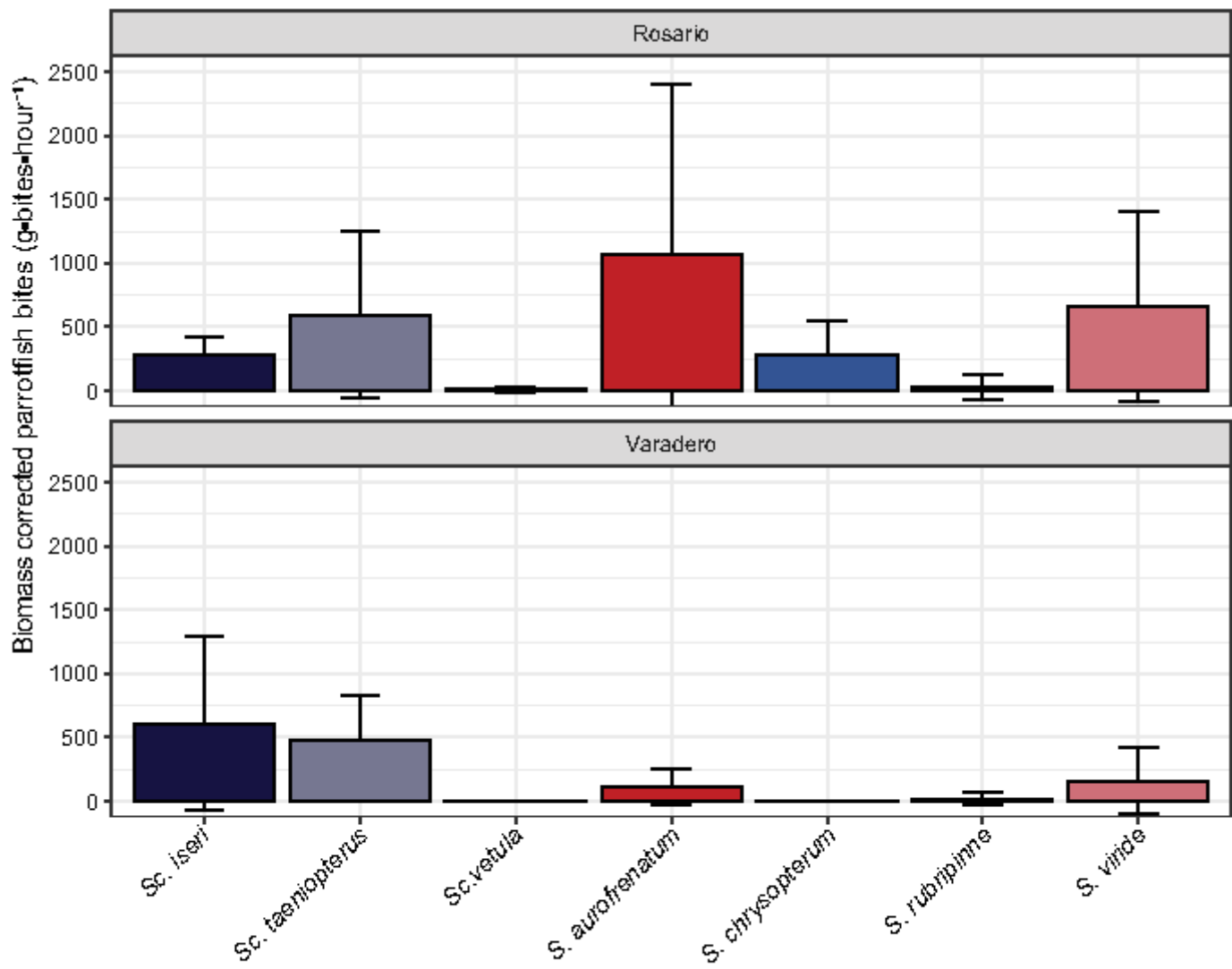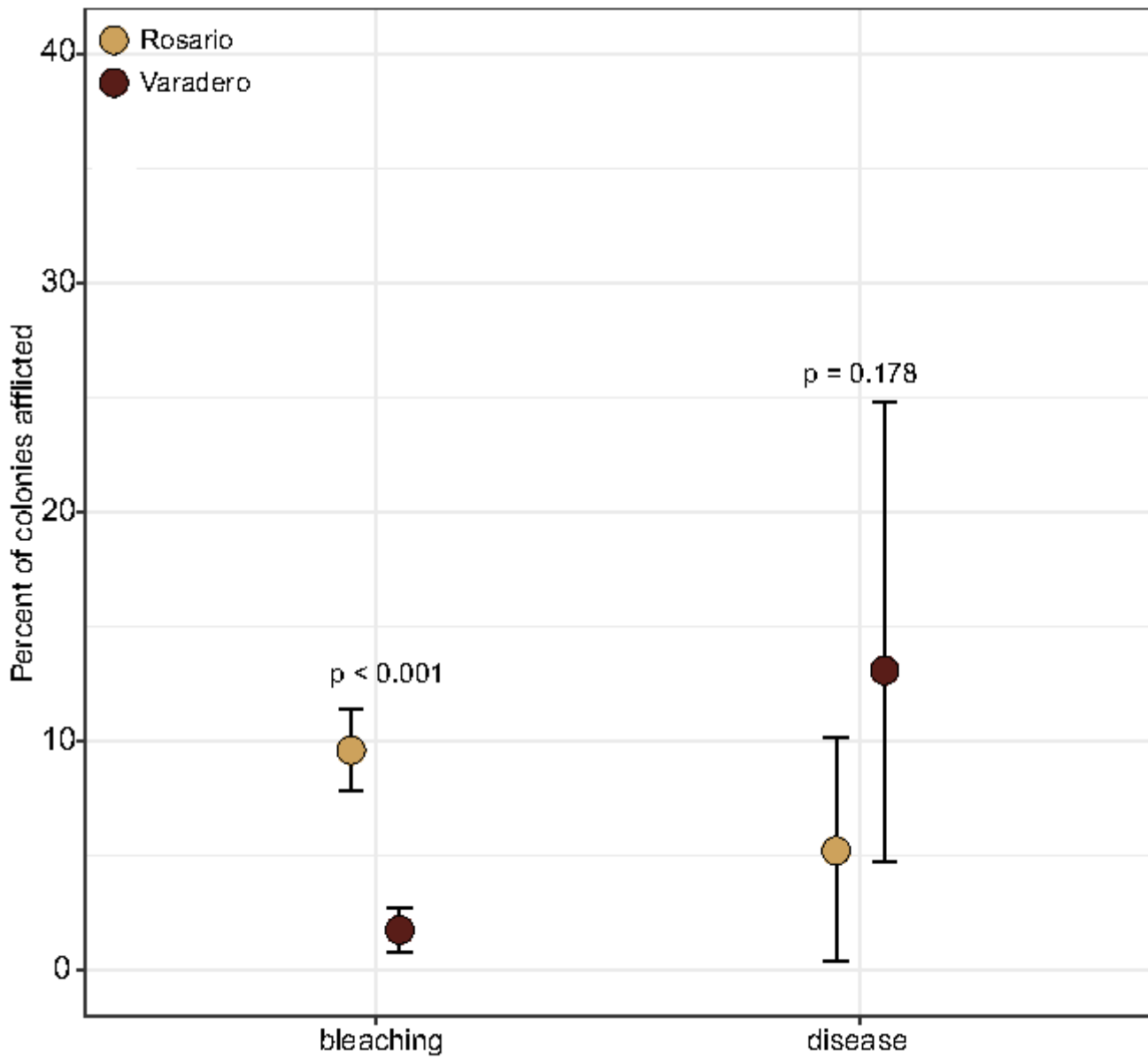
Figure 2

Biomass-corrected bites per hour taken by parrotfishes recorded feeding at Rosario and Varadero.

Figure 3

Percent cover of the 5 most common algal groups (*a*) and coral families (*b*) calculated from photoquadrats at Roasario and Varadero. Asterisks denote within group differences based on Tukey's HSD. (*c*) nMDS plot showing the benthic communities at Rosario and Varadero with P-value based on PERMANOVA. Arrows indicate the loading vectors for different benthic groups.

Figure 4

Prevalence of bleached (*a*) and diseased (*b*) corals in photoquadrats at Rosario and Varadero. P-values are from one-way ANOVA.