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Alain Duran
Florida International University, adura023@fiu.edu

A. A. Shantz
University of California, Santa Barbara

D. E. Burkepile
University of California, Santa Barbara

Ligia Collado-Vides
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University and Universidad Nacional Autonoma de Mexico,, colladol@fiu.edu

W. M. Ferrer
University of Havana

See next page for additional authors

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Authors

Alain Duran, A. A. Shantz, D. E. Burkepile, Ligia Collado-Vides, W. M. Ferrer, Laura Palma, A. Ramos, and S. P. Gozalez-Diaz

research paper

Fishing, pollution, climate change, and the long-term decline of coral reefs off Havana, Cuba

[1] Florida International University, 11200 S.W. 8th St., Miami, Florida 33199.

[2] Department of Ecology, Evolution, & Marine Biology, University of California, Santa Barbara, Santa Barbara, California 93106.

[3] Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California 93106.

[4] Florida International University, Southeast Environmental Research Center 11200 S.W. 8th St., Miami, Florida 33199.

[5] Center for Marine Research, University of Havana, 16th St, No. 114, between 1st and 3rd Ave, Miramar, Havana.

* Corresponding author email: <adura023@fiu.edu>.

A Duran [1] *
AA Shantz [2]
DE Burkepile [2, 3]
L Collado-Vides [1, 4]
VM Ferrer [5]
L Palma [1]
A Ramos [5]
SP Gonzalez-Díaz [5]

ABSTRACT.—Understanding temporal and spatial variation of coral reef communities allows us to analyze the relative effects of local stressors, such as fishing and eutrophication, and global stressors, such as ocean warming. To test for spatial and temporal changes in coral reef communities, we combined recent benthic and fish surveys from 2016 with long-term data, dating back to the late 1990s, from four zones located at different distances from Central Havana, Cuba's largest population center. These changes may indicate the shifting importance of local vs global stressors affecting reef communities. Regardless of the distance from Havana, we found that coral cover was uniformly low (approximately 10%), whereas macroalgal abundance was often high (approximately 65%). Similarly, fish biomass was low across zones, particularly for herbivorous fishes (approximately 12 g m^{-2}) that are critical ecological drivers of reef structure and coral resilience. Analyses of longer-term trends revealed that coral cover near Havana has been below about 10% since at least 1995, potentially because of local stressors. In contrast, reefs farther from Havana maintained relatively high coral cover (approximately 30%) until the early 2000s, but declined more recently to approximately 15%, putting them near the Caribbean-wide average. These distinct spatial and temporal trajectories of reef communities may be the result of the expansion of local stressors away from Havana as the human population increased, or as fishers ventured farther away to exploit new resources. Alternatively, the more recent decline of reefs farther from population centers may have resulted from increasingly frequent global stressors, such as bleaching events and hurricanes.

The impact of global and local stressors, including climate change, ocean acidi-fication, overfishing, and coastal pollution growth, have caused a dramatic decline in coral reefs world-wide (De'ath et al. 2012, Roff and Mumby 2012, Fabricius et al. 2014). Some studies suggest that global stressors (e.g., climate change) exert the strongest control over coral reef health (e.g., Spalding and Brown 2015, Bruno and Valdivia 2016, Hughes et al. 2017), while others emphasize that human activities at a local scale might be the determinant factor of coral reef resilience (e.g., Jackson et al. 2014, Cinner et al. 2016). It is likely that both global and local stressors act con-currently with additive or synergistic effects (Harborne et al. 2017). For instance, localized nutrient enrichment can interact with regional thermal stress events to increase the susceptibility of corals to diseases and bleaching (Vega Thurber et al. 2014). Consequently, the interaction of multiple stressors may determine the func-tion of coral reefs (Ban et al. 2014), and thus explain site-specific variation in the condition of coral reefs.

The frequency and intensity of coral bleaching driven by thermal stress events, one of the most prevalent global and regional stressors, have increased dramatically since the 1980s (Hoegh-Guldberg 1999). Accordingly, the number of coral reefs affected by bleaching events tripled between 1985 and 2012 (Heron et al. 2016), contributing to the accelerating loss of coral cover world-wide (Roff and Mumby 2012). For example, the Caribbean Sea has been warming by roughly 0.29 °C per decade (Chollett et al. 2012), causing multiple severe bleaching events (Oxenford et al. 2008, Jackson et al. 2014). The conspicuous loss of coral throughout the Caribbean region (approximate-ly 50% since 1970s) has been largely attributed to coral diseases, bleaching events, storms, and the subsequent failure of corals to recover (Aronson and Precht 2006, Bruno and Valdivia 2016). Losses are often particularly pronounced in areas where overfishing has reduced herbivory and macroalgae are abundant (Jackson et al. 2014). Today's Caribbean coral reefs are the result of current and past impacts of global, regional, and local stressors. Yet disentangling the primary drivers of reef decline is challenging because of the paucity of long-term data and the many potential factors that can influence reef health.

The Cuban mainland is the largest island in the Caribbean region and exhibits significant variation of coastal geomorphology (e.g., wide and shallow shelf with patch reefs to narrow shelf with a series of terrace reefs) bordered by coral reefs with varying levels of human impact (Claro et al. 2001, Pina-Amargos et al. 2014). The less impacted reefs are typically fully protected and distant from major cities (e.g., Gardens of the Queen), whereas others, such as the reefs in northwestern Cuba near Havana, are heavily impacted by anthropogenic activities (Gonzalez-Diaz et al. 2003, Gonzalez-Sanson et al. 2009, Pina-Amargos et al. 2014). Yet temporal analyses of the trajectory of Cuban coral reefs are surprisingly rare (but see Jackson et al. 2014).

The northern reefs off Havana (from Cabañas to Bacunayagua, see Fig. 1) exhibit spatial variation in fish and benthic community structure in relation to local anthro-pogenic drivers (Herrera and Alcolado 1983, Gonzalez-Diaz et al. 2003, Gonzalez-Sanson et al. 2009). In 2012, the City of Havana had a population of more than two million individuals, with 20,019 and 40,984.2 ind km^{-2} in Habana Vieja and Centro Habana, respectively, the two closest municipalities to Havana Bay (Cuban Office of Statistics 2016). In addition to heavy artisanal fishing pressure, Havana's reefs are also exposed to pollutants that include heavy metals, fertilizers, and other inorganic and organic compounds released into the coastal area through two main sources,

Figure 1. Study sites within each zone located at different distances from Havana, Cuba: Zone 0 (Havana) indicated by the circle, Zone 1, the closest to the city includes three study sites (Calle 16, Calle 30, and Santa Fe), Zone 2 includes sites at intermediate distances (21–35 km; Baracoa and Calderas) and Zone 3 the farthest away from the city with two sites (Henequen west and Bacuanayagua east). Similar shapes indicate sites within same zone while shape fill is unique for each site across all figures.

Havana Bay (Armenteros et al. 2009) and the Almendares River (Graham et al. 2011), as well as other less conspicuous sources such as street drainage and smaller rivers. As a result, the coral reefs in northwest Cuba have suffered from long-term impacts of localized anthropogenic activities, such as overfishing and pollution that likely decrease in impact with increasing distance from the city (Herrera and Alcolado 1983, Gonzalez-Diaz et al. 2003, Gonzalez-Sanson et al. 2009).

This gradient of anthropogenic effects, along with the availability of long-term data of coral and algal abundance from published and unpublished reports, allowed us to analyze the spatial and temporal changes in benthic and fish communities in northwest Cuba as potential indicators of the shifting importance of local vs global drivers of reef communities. Specifically, we aimed to answer the following questions: (1) How does the reef benthic community and fish community change with increasing distance from Havana?; and (2) How has the benthic community changed through time across this distance gradient? To address these questions, we assessed nutrient availability, reef structural complexity, and benthic and fish community composition of coral reefs at increasing distances from Havana in 2016. We also compiled existing data on benthic communities to look for temporal changes in coral and macroalgal abundance within the region, as well as examine the frequency of coral bleaching events and hurricanes. We anticipated that the historically high fishing pressure and poor water quality near Havana have led to a gradient in declining reef condition (e.g., lower coral cover, higher algal abundance, and lower fish biomass) with proximity to the city. At more distant sites, we expected to see a gradual decline in coral cover and rise in macroalgae over time as local stressors expanded from the human population center and global stressors, such as coral bleaching events, became more prevalent.

Methods

Study Site.—The northwest coast of Cuba is a narrow shelf characterized by a flat submarine terrace that drops smoothly to an edge (8–10 m) approximately 150–300 m from the shoreline. From the terrace edge, the shelf drops vertically to a deeper terrace (>12 m) followed by spur and groove formations with distinct levels

of development. Our study region included seven reef sites located at the terrace edge distributed along a 120 km stretch of the Havana shelf (from Bacunayagua to Cabañas following the old administration division, or division of provinces). Each reef was located at different distances from Havana, with the center of Havana Bay used as the reference point for the city (henceforth "Zone 0"; see Fig. 1). Zone 0 is characterized by the highest human density in the country (>20,000 ind km^{-2}) and proximity to two major pollutant sources (Havana Bay and Rio Almendares) that release large amounts of organic matter, hydrocarbons, and heavy metals (Armenteros et al. 2009, Graham et al. 2011). Pollutants discharged to the ocean by Havana Bay and Rio Almendares are carried to the west and east by ocean currents (Alcolado and Herrera 1987, Aguilar et al. 2004), creating a gradient of pollution in both directions.

We surveyed a total of seven sites varying in distance both east and west from Havana. Previous studies in the region have identified zones that experience distinct effects of local stressors on communities of fish, corals, and other invertebrates (Alcolado and Herrera 1987, Aguilar and Gonzalez-Sanson 2007, Alcolado-Prieto et al. 2012). Therefore, we classified our study sites by these previously defined zones to assess whether these patterns in anthropogenic impacts have changed. Our sites and zones were defined as follows. Zone 1 covered the area from Miramar to Santa Fe (approximately 7–20 km west from Havana Bay) where we included three study sites (Fig. 1; Calle 16, Calle 30, and Santa Fe). Zone 2 extended approximately 21–35 km from Havana Bay and included two sites, Calderas toward the east and Baracoa toward the west (Fig. 1). Zone 3 was located the farthest from Havana Bay (>35 km) and included two sites, Henequen to the west and Bacunayagua to the east (Fig. 1).

Analysis of Present-day Nutrient Content, Rugosity, and Benthic and Fish Community Composition.—Present-day status of these reefs (except those located in Zone 0) was studied in situ between May 17 and 31, 2016. Zone 0 was not sampled due to previously reported high levels of harmful toxins and the need for a special permit to access sites close to the entry of Havana Bay (Armenteros et al. 2009). Nutrient availability at each site was estimated from nutrient content in the tissue of *Sargassum hystrix* J.Agardh, a common brown macroalga that was present at all study sites. Because macroalgae are frequently used as a proxy for nutrient availability (e.g., Diaz-Pulido and McCook 2005, Reef et al. 2012), we collected four samples (10–15 g) of *S. hystrix* from each site. Samples were immediately transported on ice and kept frozen in the lab until processed. After cleaning off epiphytes, we dried the samples at 65 °C for 72 hrs, ground them to a fine powder and sent them to the Analytical Lab of the Marine Science Institute, University of California, Santa Barbara, to obtain levels of δN^{15} and percent of nitrogen content (dry weight, DW). δN^{15} is particularly useful to distinguish anthropogenic nitrogen sources (Heaton 1986, Swart et al. 2013).

To assess structural complexity of the reef, we laid out four, 50-m transects running parallel to the reef ledge at each site. Along each transect, a 5-m chain was laid out every 10 m, ensuring that the chain followed the contours of the reef (Risk 1972). We calculated a rugosity index as the ratio between the actual length of the chain (5 m) divided by the measured linear length. Higher values of the rugosity index indicate greater reef complexity.

Benthic communities were assessed using the point intercept technique within a 50 × 50-cm gridded plot (25 points per plot). Plots were laid out every 5 m along the

same transects described above for a total of 40 plots per site. Specimens found at each point were visually identified to the lowest possible taxonomic level to obtain a percent cover value per plot. We also quantified percent cover of turf algae, which is an assemblage of short (<1 cm) filamentous species (e.g., *Polysiphonia* spp., *Ceramiun* spp.). We surveyed the density of juvenile corals (<4 cm in diameter) within a 25 × 25-cm subsection of each plot. Finally, we quantified the number of sea urchins [*Echinometra* spp. and *Diadema antillarum* (Philippi, 1845)] in 1-m wide swaths along each of our 50-m transects.

Fish communities were characterized and quantified via visual surveys along 12 (30 × 2 m) belt transects at each site. Transects were haphazardly placed to run parallel to the reef ledge and separated by at least 5 m. On each transect, we identified each fish encountered and estimated its size (total length) to the nearest cm. This information was used to calculate density and biomass per species using published weight-length relationships (Bohnsack and Harper 1988). We further classified fishes as herbivores, invertivores, and piscivores following Sierra et al. (2001).

Analysis of Temporal Changes of Benthic Community Structure.—We compiled data on reefs in this area from published and gray literature, including graduate student theses and technical reports (see Online Supplemental Material) to analyze temporal trends in coral and algal abundance. We collated benthic data from 85 sites within the previously defined zones (0, 1, 2, and 3) sampled between 1995 and 2015. From the 85 sites, we found 46 sites that had information regarding algal cover and 78 sites that included coral cover. From these studies, we used the average cover of macroalgae and coral at each site as a single data point to assess temporal changes within each zone.

Statistical Analysis.—We tested for differences across zones in algal tissue nutrient content, reef rugosity, percent cover of benthic groups, juvenile coral density, sea urchin density, and fish biomass using analysis of variance (ANOVA) with site nested within zone. When response variables differed among zones, we used the Tukey's honest significant different test (Tukey's HSD) as post-hoc analysis to determine which zones were different. Within each zone, we analyzed temporal changes in macroalgal and coral cover using linear mixed effect models (lme) that included sites as random factors to test for changes in cover through time. Data are presented as means plus standard errors and all analyses were carried out using the following packages in R v3.2.2 (R Core Team 2012): doBy (Soren 2016) and nlme (Pinheiro et al. 2017) for ANOVA, and linear and mixed effect models, respectively.

Results

Analysis of Present-day Nutrient Content, Rugosity, and Benthic and Fish Community Composition.—Current δN^{15} levels in *Sargassum hystrix* J.Agardh tissue ranged from 1.8‰ to 6.2‰, and decreased with distance from Havana. Zone 1, closest to Havana, exhibited values twice as high as those recorded at sites in Zones 2 and 3 (Fig. 2A) (ANOVA: $F_{2,21} = 102.46$, $P < 0.001$). Similarly, nitrogen content in *S. hystrix* was the highest in Zone 1, while Zone 2 had the lowest values with Zone 3 being intermediate in nitrogen content (Fig. 2B) (ANOVA: $F_{2,21} = 25.09$, $P < 0.001$). Reef structural complexity, estimated as the rugosity index, averaged 1.24 (SE
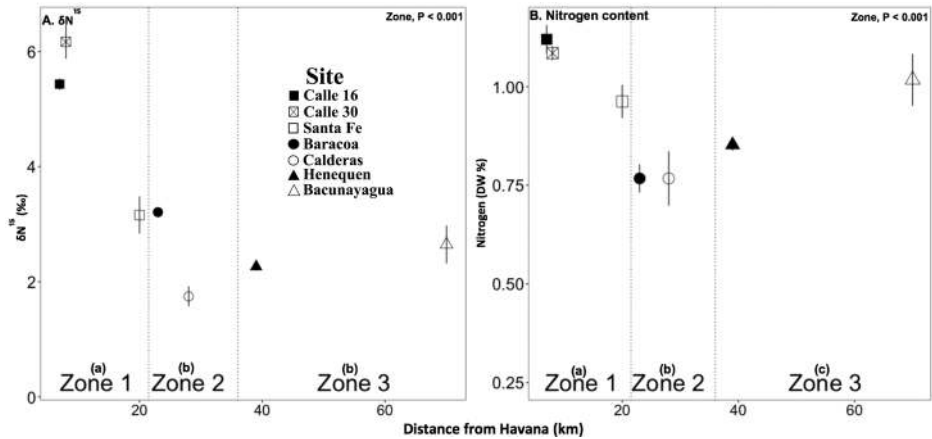
Figure 2. Delta N[15] (A) and nitrogen concentration (B) in *Sargassum* tissue samples by sites within each zone. Data are mean ± SE. Probability values comes from analysis of variance among zones with bolded results distinguishing statistically significant values ($P < 0.05$). Letters along the bottom indicate differences between zones based on Tukey's honest significant difference test. Error bars of Delta N[15] of Baracoa and Henequen are difficult to see because of small values.

0.1) with no differences among zones (see Online Supplemental Material) (ANOVA: $F_{2, 122} = 1.09$, $P = 0.338$).

Benthic communities were dominated by algae (>60% cover of all algal groups) across all zones (Fig. 3A) (ANOVA: $F_{2, 21} = 0.98$, $P = 0.393$). Zone 2 was dominated by cyanobacteria and turf, which covered >20% of the benthos, particularly at the Calderas site (Fig. 3B, C) (ANOVA: Cyanobacteria, $F_{2, 21} = 4.46$, $P = 0.024$; Turf, $F_{2, 21} = 11.19$, $P < 0.001$). *Dictyota* spp. and *Lobophora variegata* (J. V. Lamour.) Womersley ex Oliveira were up to twice as abundant in Zones 1 and 3 compared to Zone 2 (Fig. 3D, E) (ANOVA: *Dictyota*, $F_{2, 21} = 5.38$, $P = 0.014$; *L. variegata*, $F_{2, 21} = 8.19$, $P = 0.002$). *Sargassum* spp. were most abundant in Zone 1 (23.5%, SE 1.2%) compared to Zones 2 and 3 (Fig. 3F) (ANOVA: $F_{2, 21} = 27.84$, $P < 0.001$). *Amphiroa* spp. (2.48%, SE 0.40%), *Jania* spp. (2.78%, SE 0.50%), and *Halimeda* spp. (3.98%, SE 0.42%) covered approximately 9% of the benthos combined, but only *Amphiroa* spp. showed differences among zones (Fig. 3G–I).

Across all sites, the percent cover of coral averaged 9.7% (SE 0.8%) with Zone 2 having the lowest coral cover of approximately 5% (Fig. 4A) (ANOVA: $F_{2, 21} = 13.77$, $P < 0.001$). *Siderastrea* was the dominant coral genus region-wide, and cover was highest in Zone 1, covering 7.6% (SE 1.1%) of the benthos (ANOVA: $F_{2, 21} = 6.76$, $P = 0.005$). *Porites*, *Orbicella,* and *Agaricia* had the next highest percent cover with *Porites* having the highest cover in Zone 1 (ANOVA: *Porites,* $F_{2, 21} = 10.39$, $P < 0.001$; *Orbicella*, $F_{2, 21} = 3.62$, $P = 0.067$; *Agaricia*, $F_{2, 21} = 0.90$, $P = 0.422$).

Total density of juvenile corals averaged 20.9 (SE 1.8) juveniles m^{-2} in Zone 1 and decreased with distance from Havana. Bacunayagua, the farthest site from the city, had the lowest juvenile coral density, with just 5.6 (SE 2.0) juveniles m^{-2} (Fig.4B) (ANOVA: $F_{2, 21} = 4.49$, $P = 0.024$). Approximately 50% [8.1 (SE 1.2) juveniles m^{-2}] of the juvenile corals region-wide belonged to the genus *Porites,* which were most abundant in Zone 1 with 11.5 (SE 1.9) juveniles m^{-2} (ANOVA: $F_{2, 21} = 7.18$, $P = 0.004$). In contrast, *Siderastrea* averaged 2.7 (SE 0.5) juveniles m^{-2} region-wide with Zone 3 [4.8 (SE 1.5) juveniles m^{-2}] having twice as many juveniles as Zone 1 [2.05 (SE 0.30)
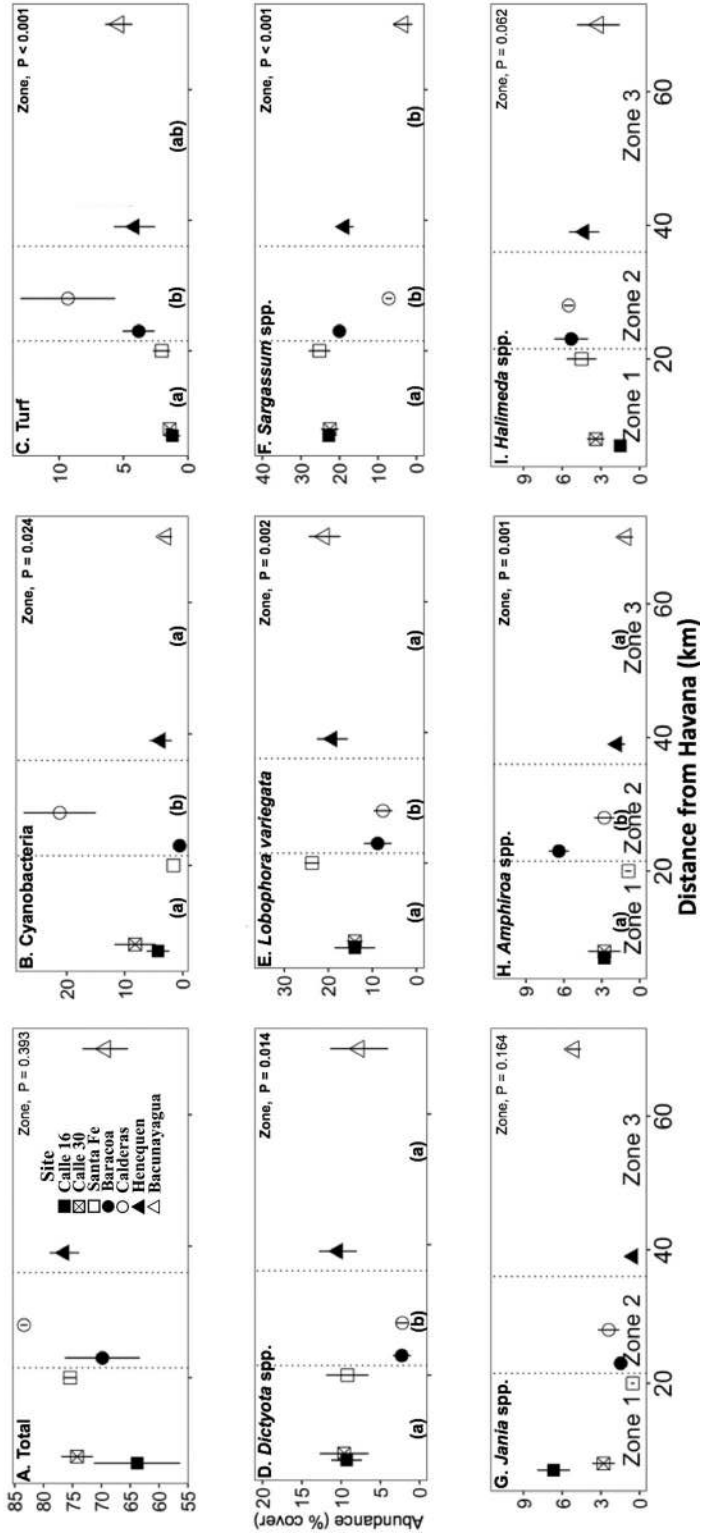
Figure 3. Average abundance of total and common algal taxa by site within each zone: (A) total algal (all species of algae), (B) Cyanobacteria, (C) Turf, (D) *Dictyota* spp., (E) *Lobophora variegata*, (F) *Sargassum* spp., (G) *Jania* spp., (H) *Amphiroa* spp. and (I) *Halimeda* spp. Data are mean ± SE. Probability values comes from analysis of variance with bold font indicating statistically significant values ($P < 0.05$). Letters along the bottom indicate differences among zones based on Tukey's honest significant difference test.

Figure 4. Total abundance of corals (A) and density of juveniles (<4 cm diameter) (B) by site within each zone. Data are mean ± SE. Probability values comes from analysis of variance with bold font indicating statistically significant values ($P < 0.05$). Letters along the bottom indicate differences among zones based on Tukey's honest significant difference test.
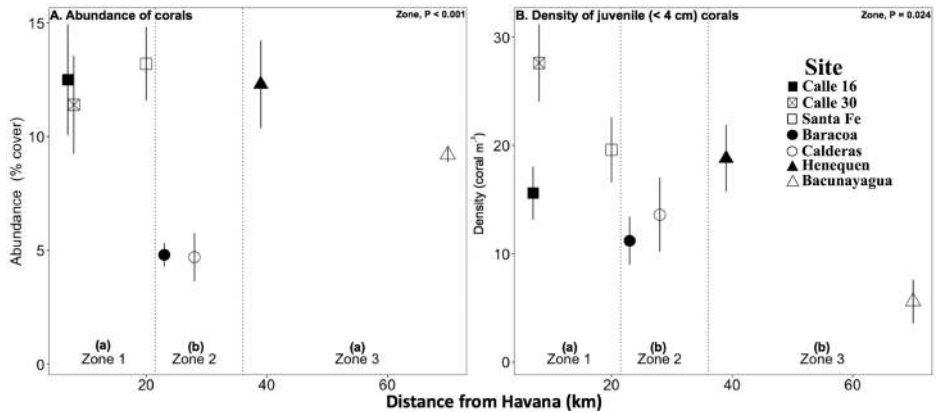
juveniles m^{-2}] (ANOVA: $F_{2, 21} = 0.91$, $P = 0.419$). *Agaricia*, the coral genus with the second highest density of juveniles in the region [4.3 (SE 0.8) juveniles m^{-2}], showed no variation among zones (ANOVA: $F_{2, 21} = 0.43$, $P = 0.657$).

The total fish biomass averaged 26.1 (SE 5.0) g m^{-2} across all zones (Fig. 5A) (ANOVA: $F_{2, 77} = 1.23$, $P = 0.299$). Herbivorous fishes (parrotfishes and surgeonfishes) were approximately 50% of the total fish biomass [11.9 (SE 1.3) g m^{-2}] with no change in biomass relative to zone (Fig. 5A) (ANOVA: $F_{2, 77} = 1.08$, $P = 0.344$). Similarly, the biomass of invertivores (e.g., family Labridae) averaged 7.9 (SE 0.9) g m^{-2} and did not differ across zones (Fig. 5B) (ANOVA: invertivores, $F_{2, 77} = 1.59$, $P = 0.211$). In contrast, the biomass of piscivores (e.g., families Serranidae and Sphyraenidae) was the highest in Zone 3 with 13.3 (SE 4.4) g m^{-2} (Fig. 5C) (ANOVA: piscivores, $F_{2, 77} = 4.41$, $P = 0.015$). In addition to low herbivorous fish biomass region-wide, we recorded low densities (0.02 ind m^{-2}) of the herbivorous sea urchins *Echinometra* spp. and *D. antillarum*, with Zone 3 having the highest density with 0.24 ind m^{-2} (Fig.5D) (ANOVA: $F_{2, 21} = 6.89$, $P = 0.005$).

Analysis of Temporal Changes of Benthic Community Structure.— Macroalgal abundance in northwest Cuba showed both temporal and spatial variation between 2000 and 2016 (lme: Year:Zone, $\chi^2_1 = 14.05$, $R^2 = 0.24$, $P < 0.001$). Zone 0 (Havana) exhibited a reduction in algal cover from approximately 85% in 2008 to approximately 40% in 2012 (Fig. 6A) (lme: Year, $\chi^2_1 = 7.70$, $R^2 = 0.46$, $P = 0.006$). However, since survey data only goes back to 2008, it is difficult to ascertain if this is indicative of anomalously high algal cover in 2008 or a true, long-term trend in declining algal cover. Zone 1 averaged 55% and Zone 2 45% macroalgae cover, without significant changes through time (Fig. 6B, C) (lme: Year, Zone 1, $\chi^2_1 = 2.70$, $R^2 = 0.16$, $P = 0.101$; Zone 2, $\chi^2_1 = 0.03$, $R^2 = 0.01$, $P = 0.856$). In contrast, Zone 3 displayed a three-fold increase in macroalgae from approximately 23% in 2000 to 67% in 2016 (Fig. 6D) (lme: Year, $\chi^2_1 = 11.09$, $R^2 = 0.60$, $P < 0.001$).

Coral cover also showed zone specific variations through time (Fig. 6E–H) (lme: Zone:Year, $\chi^2_1 = 5.86$, $R^2 = 0.52$, $P = 0.015$). Both Zone 0 and Zone 1 were characterized by low coral cover [3.8% (SE 0.8%) and 9.8% (SE 0.6%), respectively] with little
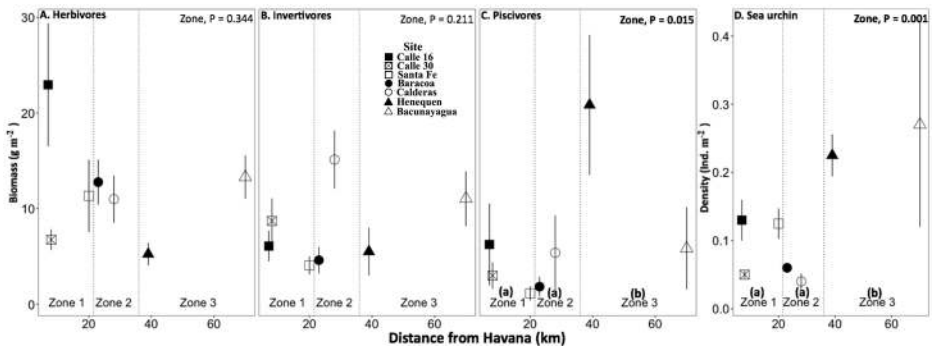
Figure 5. Biomass of fishes by trophic group by site within each zone: (A) herbivores (e.g., parrotfish and surgeonfish); (B) invertivores (e.g., grunts and wrasses); and (C) piscivores (e.g., groupers, snappers and barracudas). Data are mean ± SE. Probability values comes from analysis of variance with bold font indicating statistically significant values ($P < 0.05$). Letters along the bottom indicate differences among zones based on Tukey's honest significant difference test.

change since 1997 (Fig 6.E, F) (lme: Year, Zone 0, $\chi^2_1 = 2.63$, $R^2 = 0.24$, $P = 0.105$; Zone 1, $\chi^2_1 = 0.04$, $R^2 = 0.01$, $P = 0.843$). In contrast, coral cover in Zone 2 and Zone 3 declined by >50% over the same time period (Fig. 6G,H) (lme: Zone 2, $\chi^2_1 = 5.07$, $R^2 = 0.21$, $P = 0.024$; Zone 3, $\chi^2_1 = 5.73$, $R^2 = 0.39$, $P = 0.017$).

Discussion

We found that coral reefs near Havana are in poor condition, even at significant distances from the city. Nitrogen content (Nitrogen DW% and δN^{15}) in algal tissue increased with proximity to Havana (Zone 0), suggesting both an increase in N availability and increasing contribution of anthropogenic N sources to reefs. At all zones, fish biomass was low and the benthic communities were dominated by macroalgae (>60% cover) with low coral cover. In contrast, the highest densities of juvenile corals were at sites closest to Havana. Our analyses of long-term benthic trends revealed that coral cover has remained low and macroalgal cover high on the reefs nearest to
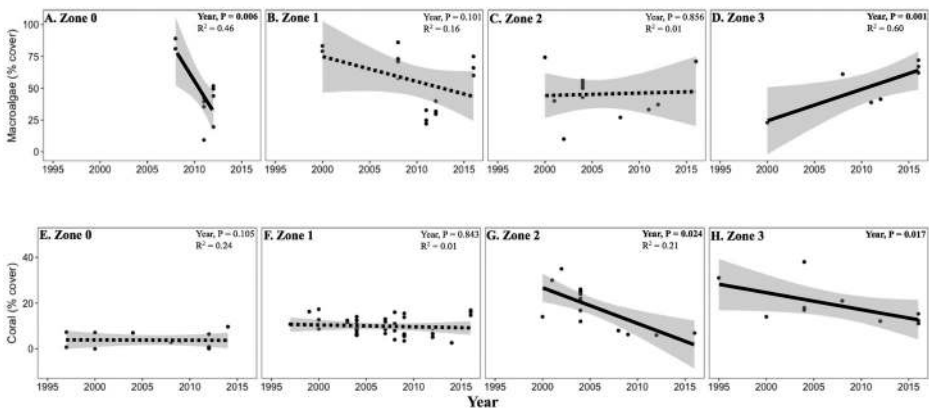

Figure 6. Macroalgal (A–D) and coral cover (E–H) by zone over time. Points represent average percent cover from individual sites taken from the literature and authors' unpublished data. Probability values indicates results of linear mixed effect model. Solid lines indicate significant relationships, while dashed lines indicate non-significant relationships.

Havana since the 1990s. Yet, at sites farthest from Havana, coral cover has declined by approximately 50% and macroalgae increased by >100% during the same time period.

Havana is home to more than two million people concentrated in approximately 730 km^2 (Cuban Office of Statistics 2016). The metropolitan area includes several rivers, such as Almendares and Quibu, which carry high levels of pollutants that are delivered to coastal areas (Armenteros et al. 2009, Graham et al. 2011). One would expect to find higher δN^{15} (an indicator of human waste N sources) and nitrogen content in algal tissue samples from areas adjacent to the city. While this was the case, we also found high nitrogen content at the farthest site from Havana (Bacunayagua, Zone 3), suggesting site-specific N delivery unrelated to population density. Based on low δN^{15} values, nutrients could be coming from sources other than human waste, such as fertilizers from agricultural runoff. Along the north coast of Havana there are many small rivers, some of which are close to our study sites (e.g., Rio Jaimanitas, Rio El Mosquito, Rio Jaruco) that could be significant sources of nutrients. Unfortunately, information regarding the water quality and drainage from these rivers is scarce. High levels of nutrient availability can promote algal abundance on coral reefs (Lapointe 1997, Littler et al. 2010), which may partially explain the increase in macroalgae since the early 2000s at sites distant from Havana. In addition, these distant sites suffered a reduction of coral cover over the past decade, leaving more suitable space to be colonized by macroalgae.

Low levels of herbivory have likely contributed to the ubiquitously high cover of macroalgae. Herbivorous fish biomass averaged slightly <12 g m^{-2} across the region, compared to approximately 30 g m^{-2} on unfished Caribbean reefs (Edwards et al. 2014). During our surveys, we did not record any herbivores >20 cm total length, suggesting fishing pressure is high across all three zones. In contrast, Gonzalez-Sanson et al. (2009) reported that in 2004 there were differences in fish communities between Zones 1, 2, and 3, with average fish size declining and shifts in species composition occurring at sites closer to Havana Bay. The presence of zone-specific fish communities just a decade ago suggests a fairly recent expansion of fishing pressure across the region. Moreover, herbivorous urchin abundance was low at all of our sites (Fig. 5D). Consequently, algal communities were dominated by palatable species such as *Sargassum* spp. and red articulated calcareous algae (e.g., *Jania* spp. and *Amphiroa* spp.) that are often preferentially consumed by herbivorous fishes (Burkepile and Hay 2008, Adam et al. 2015). It is likely that the low biomass of herbivorous fishes and sea urchins resulted in reduced herbivore control over macroalgae across all of the zones. Similar results have been reported in other overfished Caribbean reefs after the massive sea urchin (*D. antillarum*) die-offs in the early 1980s (Jackson et al. 2014).

Surprisingly, despite the elevated cover of macroalgae, we found that the abundance of juvenile corals in our study region (21 juveniles m^{-2}) was high when compared to other regions, such as the Florida Keys (approximately 7 juveniles m^{-2}, Moulding 2005, Burkepile et al. 2013) and Curaçao (7 juveniles m^{-2}, Vermeij et al. 2011). The high abundance of macroalgae might not be inhibiting recruitment, as is often observed (Vermeij et al. 2009), but it could be limiting the growth of juvenile corals via competition. Unexpectedly, Zone 1, which was predicted to be the most heavily impacted, contained the highest density of juvenile corals. The greater number of juveniles in Zone 1 may be due to the high prevalence of brooding species in this region (see Online Supplemental Material), which have short planktonic durations and

low dispersal distances that promote larval retention (Ritson-Williams et al. 2009). Interestingly, brooding species are often associated with unstable or degraded habitats (Szmant 1986), perhaps reflecting a longer history of human impacts in Zone 1. Additionally, other biophysical drivers, such as larval supply, oceanic currents, and temperature regimes likely contribute to the observed distribution of juvenile corals (Ritson-Williams et al. 2009, Green and Edmunds 2011). In the future, reefs in these zones may provide an interesting setting to study propagule supply and the population genetics of the coral community.

Although there is very little information on current or historical fishing pressure in the region, parrotfishes have been targeted by local fishers since at least the 1970s, when large individuals of midnight parrotfish (*Scarus coelestinus* Valenciennes, 1840) and rainbow parrotfish (*Scarus guacamaia* Cuvier, 1829) were still present (Aguilar and Gonzalez-Sanson 2007). However, the dense low-income population in and around Havana combined with easy access to the reefs facilitated by the narrow shelf has created a large artisanal fishery (AD, pers obs), and we frequently encountered spear fishers during our surveys, even at sites >40 km from Havana. It is likely that the high artisanal fishing pressure has not only increased near Havana, but also has expanded farther away as fish have become less abundant and human population increases. This high fishing pressure could explain the low fish biomass region-wide.

The current coral cover at our study sites (10%) is lower than the current Caribbean-wide average (16%) reported by Jackson et al. (2014). However, the decline in coral cover in the region appears to have happened in at least two different time periods that may be associated with distinct types of stressors. Closer to Havana (Zones 0 and 1), the coral cover was already low in the 1990s (<10%), whereas reefs farther from the city (Zones 2 and 3) still maintained >30% coral cover. Prior to the 1990s, Havana Bay was considered one of the 10 most polluted bays on Earth, containing high concentrations of lead, zinc, selenium, and mercury along with heavy loads of organic sediment (Armenteros et al. 2009, Díaz-Asencio et al. 2011). Exposure to high sedimentation and high concentrations of nutrients and heavy metals can negatively affect growth, photosynthesis, fertilization, larval survival, and the microbiome of corals (Gilmour 1999, Jessen et al. 2013, Tout et al. 2015), resulting in reduced coral abundance in polluted areas (De'ath and Fabricius 2010). Prior to the 1990s, reduction of coral cover close to Havana may have been related to high levels of pollution released onto the reefs from Havana Bay.

In contrast, coral cover in the two zones more distant from Havana (Zones 2 and 3) remained high (25%–30%) into the early 2000s, but suffered an approximate 50% reduction in the last 15 yrs. Declining coral cover at these more distant sites may indicate the expansion of local stressors, increasing impacts of global stressors, or a combination of both. It is possible that the effects of local stressors that were concentrated around Havana before the 2000s have expanded outward as a result of economic pressure in a growing metropolitan population. The nitrogen content in algae showed high values in areas farther from the city, suggesting region-wide increases in nutrient concentrations. Similarly, fish biomass is now low region-wide, suggesting that fishing pressure has expanded since the initial classification of the reef zones around Havana. According to the Cuban Office of Statistics (2016), the population of Havana has increased from 1,954,413 in 1980 to 2,200,000 individuals between 1995 and 2000, with a recent (2014) count of 2,121,871 individuals. A rapidly increasing population in the late 1990s might have increased the impact of local stressors.

Over the past 15 yrs, there have also been increases in global stressors in the region. During at least five summers between 2003 and 2015, corals in Havana reefs experienced large-scale bleaching events (51%–75% corals bleached), with 2009 being the worst with >75% of corals bleached (see Online Supplemental Material; Alcolado 2006, Alcolado and Iglesias 2010). In the Caribbean region, similar thermal stress events have led to widespread coral mortality, particularly in areas with high coral cover (Oxenford et al. 2008, Eakin et al. 2010, Alemu and Clement 2014). The frequency of coral bleaching events has increased since the first event was described in 1980; the first documented world-wide bleaching event occurred in 1998 (Hoegh-Guldberg 1999). Coral reefs located in Caribbean regions, including south Florida, The Bahamas, and Cuba, have suffered an average of 7 thermal stress events between 1985 to 2012 (Heron et al. 2016). It is likely that the recent increase in frequency and severity of bleaching events has contributed to coral loss in those sites farther from the Havana. Coral cover in Zone 0 and Zone 1 was already low before 2000; however, it is possible that bleaching had less of an impact on the remaining corals. Consistent with this idea, *Siderastrea* and *Porites* were both very abundant closer to Havana, and these taxa tend to be some of the most resistant species to bleaching (Okazaki et al. 2017). In contrast, *Orbicella* and *Agaricia* showed higher cover away from the city, although they were low in overall cover (see Online Supplemental Material). These taxa are more susceptible to bleaching than *Siderastrea* and *Porites* (Fournie et al. 2012, Okazaki et al. 2017), and may have declined the most during recent coral losses at sites distant from Havana.

Hurricanes can also cause substantial losses of coral cover (Gardner et al 2005). The occurrence of five hurricanes in 2005, two of which were Category 5, presumably had strong impacts on these reefs. Unfortunately, we did not find information directly related to these hurricanes. But, given the narrow reef shelf around Cuba, it is likely that their effects were widespread across multiple sites in the region. For instance, Hurricane Wilma (in 2005) occurred >80 km from Havana, and Jones et al. (2008) described damage to gorgonians, sponges, and corals as deep as 15 m on Havana's coral reefs. Corals in areas near Havana (Zone 0 and 1) have not been affected directly by hurricanes for >50 yrs; this relative calm could make them more vulnerable to major storms as it has been proposed that the larger the lapse between hurricanes, the slower the recovery (Mumby et al. 2011). In contrast, at least two hurricanes affected Zones 2 and 3 at western sites (Hurricane Charley in 2004) and eastern sites (Hurricane Dennis in 2005). It is possible that these hurricanes facilitated the downward trajectory of corals in sites farther from Havana.

Understanding the drivers of coral reef decline is critical for management and conservation strategies (Keller et al. 2009). The current status of reefs around Havana is likely the result of combined global and local stressors that have both reduced coral cover and limited their ability to recover. The coral reefs near Havana have experienced different spatial and temporal trajectories of coral decline and a rise in macroalgae in the last 20 yrs. The temporal decline in coral abundance can be likely attributed to both global stressors (e.g., bleaching events followed by increase of diseases) and local stressors, such as high nutrient levels and overfishing. Yet, the failure of corals to recover is probably influenced by local impacts to these reefs, particularly overfishing, which has led to very low herbivorous fish biomass and a rise in macroalgae. Our results suggest that despite the wide-spread decline, coral recruitment is still occurring and there is a robust population of juvenile corals, even at sites near

Havana. Decreasing nutrient influx and implementing artisanal fishery regulations may help reduce macroalgae and provide these reefs with an opportunity to recover after stress events such as bleaching. Ultimately, however, global-scale efforts are required to decelerate the current rate of carbon emissions that drive climate change, the major driver of future coral mortality.

Acknowledgments

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