

Improving estimates of coral reef construction and erosion with in situ measurements

Ilsa B. Kuffner ^{1*}, Lauren T. Toth ¹, J. Harold Hudson,² William B. Goodwin,³
Anastasios Stathakopoulos,¹ Lucy A. Bartlett,⁴ Elizabeth M. Whitcher⁵

¹U.S. Geological Survey, St. Petersburg Coastal and Marine Science Center, St. Petersburg, Florida

²Reef Tech, Inc., Miami, Florida

³NOAA Florida Keys National Marine Sanctuary, Key Largo, Florida

⁴Contracted by Cherokee Nation Technologies to U.S. Geological Survey, St. Petersburg Coastal and Marine Science Center, St. Petersburg, Florida

⁵Florida Institute of Technology, Melbourne, Florida

Abstract

The decline in living coral since the 1970s has conspicuously slowed reef construction on a global scale, but the related process of reef erosion is less visible and not often quantified. Here, we present new data on the constructional and deconstructional sides of the carbonate-budget equation in the Florida Keys, U.S.A. We documented *Orbicella* spp. calcification rates at four offshore reefs and quantified decadal-scale rates of *Orbicella*-reef erosion at a mid-shore patch reef. Using *Orbicella* coral heads fitted with permanent markers in 1998, we measured reef-elevation loss at 28 stations over 17.3 yr to estimate a mean erosion rate of $-5.5 (\pm 3.2, \text{SD}) \text{ mm yr}^{-1}$. This loss equates to an erosion rate of $-8.2 (\pm 4.8, \text{SD}) \text{ kg m}^{-2} \text{ yr}^{-1}$ on dead *Orbicella* colonies, or $-6.6 \text{ kg m}^{-2} \text{ yr}^{-1}$ when adjusted reef-wide. Calculating net carbonate production using a census-based approach on the same patch reef in 2017, we estimated a reef-wide bioerosion rate of $-1.9 (\pm 2.0, \text{SD}) \text{ kg m}^{-2} \text{ yr}^{-1}$, and a net carbonate production rate of $0.5 (\pm 0.3, \text{SD}) \text{ kg m}^{-2} \text{ yr}^{-1}$. Substituting the erosion rate we estimated with the markers would suggest that net carbonate production at this patch reef was lower and negative, $-4.2 \text{ kg m}^{-2} \text{ yr}^{-1}$. This divergence could be a function of high erosion rates measured on the tops of *Orbicella* colonies, which may be preferentially targeted by parrotfish. Nonetheless, our study suggests the need for new field data to improve estimates of reef-structure persistence as coral reefs continue to degrade.

Coral reefs provide economically valuable ecosystem services, foremost shoreline protection, and food production (fisheries), to coastal communities on a globally relevant scale (Costanza et al. 1997, 2014). Reduction in the quality and estimated value of this essential, natural capital has resulted (Costanza et al. 2014; Beck et al. 2018) from repeated high-temperature anomalies (Veron et al. 2009; Eakin et al. 2010), coastal development (Halpern et al. 2008), and overextraction of resources (Cinner et al. 2016). The loss of reef elevation resulting from coral-reef degradation is a contributor to coastal community vulnerability in the tropics (Yates et al. 2017; Storlazzi et al. 2018). The physical, three-dimensional structure of coral reefs in the western Atlantic is heavily reliant on a handful of reef-building species, principally *Acropora palmata* and *Orbicella* spp. (Kuffner and Toth 2016), and unfortunately, these corals are particularly vulnerable to climate change and

disease (Aronson and Precht 2001; Miller et al. 2009). Following coral mortality, the reef structure is left exposed to the physical and biological agents of reef erosion (Perry et al. 2014).

Carbonate budgets provide a method to estimate the balance of constructional (i.e., calcification) and deconstructional (i.e., erosion) processes that determine whether a reef builds or dwindles away (Stearn et al. 1977; Scoffin et al. 1980; Hubbard et al. 1990; Perry et al. 2012); however, the calcification rates used in present-day budgets are necessarily based on literature that is, in many cases, decades old, and researchers must rely on data from congeners for species for which data do not exist. Additionally, evidence indicates that calcification rates may have slowed in recent years (De'ath et al. 2009; Cantin et al. 2010), heightening the need for new data. Calcification rates reported in the past were largely estimated by multiplying annual linear extension rates, measured by examining X-rays or (more currently) computerized tomography (CT) scans of coral cores and slabs taken to reveal annual growth bands (Knutson et al. 1972), by the bulk density of coral specimens measured in various ways (Manzello et al. 2015). While simple in concept, the bulk density of coral skeletons is difficult to measure and can be plastic in response to growth

*Correspondence: ikuffner@usgs.gov

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

environment (Smith et al. 2007; Kuffner et al. 2017). One approach to circumvent the uncertainty associated with density is to directly measure calcification rate (Jokiel et al. 1978). While most often applied in the laboratory, the technique can also be used for field-grown specimens by temporarily transporting the corals to land to use a balance (Morrison et al. 2013). Since 2009, we have used this approach to measure calcification rates on the outer-reef tract of the Florida Keys (Kuffner et al. 2013).

As the abundance of living corals continues to decline, the relative importance of erosive processes is increasing on reefs around the world (Perry et al. 2013; Kuffner and Toth 2016; Toth et al. 2018). Given that ocean acidification will facilitate bioerosion (Wisshak et al. 2012; Fang et al. 2013; Enochs et al. 2016) and carbonate dissolution (Eyre et al. 2018) in the future, baseline knowledge about the rates of reef erosion is critical to predicting the persistence of reef structures. Although numerous laboratory and short-term field studies have recently evaluated the agents and processes of reef bioerosion (e.g., Fang et al. 2013; Enochs et al. 2015; Silbiger and Donahue 2015), bioerosion is a long-term process (Glynn 1997), which requires decadal-scale studies to observe adequately. Data directly quantifying reef erosion rates, in volume or linear depth, are rare (however, see Hudson 1977; Bruggemann et al. 1996; Roff et al. 2015). Most assessments of reef erosion have used a census approach, wherein counts of bioeroding taxa are combined with published data on estimated rates of bioerosion to ascribe a rate of bioerosion for a given reef (Perry et al. 2012). Direct, field-based measurements of reef erosion rates are critical to validating the census approach and to provide baseline, real-world data on the rate of reef-structure loss.

Here, we document spatial and temporal variability in coral calcification rates using a field experiment in which calcification rates of 50 *Orbicella* spp. colonies were measured biannually from 2013 to 2015. To estimate long-term rates of bioerosion, we also completed an experiment performed on an *Orbicella*-dominated mid-shelf patch reef started in 1998 wherein 28 dead colonies were fitted with permanent, stainless-steel, and cement markers. We quantified the change in elevation of those corals 17 yr later, in 2015. For a comparison with these erosion measurements, we also performed benthic and fish species surveys at the same reef in 2017 to evaluate the carbonate budget using the census-based approach (Perry et al. 2012). Improving estimates of the constructional and deconstructional processes through empirical measurements is paramount to gaining confidence in carbonate budgets that are used to predict reef futures in a time of accelerating climate change and sea-level rise (Perry et al. 2018).

Methods

The Florida Keys Reef Tract (FKRT) is a bank-barrier reef system stretching 350 km along the Florida Straits (Stephenson and Stephenson 1950). The offshore reefs are found approximately 10 km off the coast of the island chain of the Florida Keys, with numerous patch reefs lining the seaward and landward edges of Hawk Channel that spans the length of the reef tract seaward of

the islands (Lidz et al. 2006). Our study sites (Fig. 1) for the calcification-assessment network were located at Pulaski Shoal Light (PLS, 24.69355°N 82.77280°W) in Dry Tortugas National Park, Mote Marine Aquarium's Looe Key coral nursery (LOO, 24.56275°N 81.40013°W), Sombrero Reef (SMK, 24.62687°N 81.10893°W), and Crocker Reef (CRK, 24.90908°N 80.52665°W) in the Florida Keys National Marine Sanctuary (FKNMS), and Fowey Rocks (FWY, 25.59047°N 80.09560°W) in Biscayne National Park. The long-term reef erosion experiment and the carbonate-budget census took place at Hen and Chickens Reef Sanctuary Preservation Area (24.93424°N, 80.54950°W) in the FKNMS, a mid-shelf patch reef at the seaward edge of Hawk Channel.

Calcification measurements

In 2009, a calcification monitoring network was established at sites along the FKRT at offshore reefs from Miami to the Dry Tortugas (Kuffner et al. 2013). For this study, *Orbicella* spp. fragments-of-opportunity were obtained from the FKNMS Truman Pier Annex mitigation project. On 13 March 2013, 50 colonies of approximately 60 cm² planar surface area were collected from holding baskets attached to the underside of the NOAA Discovery Center docks in Key West, FL. We epoxied the corals to PVC disks fitted with stainless-steel bolts, photographed and weighed them using the buoyant-weight method (Jokiel et al. 1978), and held them under the docks until randomly selected groups of 10 corals were deployed to the experimental sites on 15 May 2013 (PLS), 12 June 2013 (CRK, LOO), or 13 June 2013 (SMK, FWY). Underwater temperature data were recorded every 15 min with two HOBO[®] Water Temp Pro v2 temperature loggers (Onset[®], Pocasset, MA, U.S.A.) deployed at each offshore-reef site (Kuffner 2019). The corals were deployed to pre-existing calcification monitoring stations (concrete blocks) with removable fasteners (Morrison et al. 2013) allowing their removal every 6 months to be weighed using the buoyant-weight method (Jokiel et al. 1978) and photographed, and then returned to the blocks. Calcification rates were normalized to the planar, two-dimensional footprint of the colony, equivalent to a tree's "dripline" or crown area (Uzoh and Ritchie 1996), at the beginning of the study. Planar-area footprint was measured by tracing the colony on a digital photographic image calibrated with a ruler, placed in the horizontal plane where the colony had the greatest diameter, using iSolution Capture[®] version 3.1 image analysis software (IMT i-Solution, Vancouver, BC, Canada). Only corals that gained mass during all weighing intervals were used to estimate calcification rates.

Reef erosion measurements

As part of a decades-long research program on coral growth and reef erosion at Hen and Chickens Reef (Fig. 1), on 24–26 June 1998, 12 coral colonies that had likely bleached and died from high-temperature stress were fitted with 1.9-cm-diameter (3/4-in.), 61-cm-long (24-in.) 316-stainless-steel rods that were prestamped with identification numbers. Single rods were placed into the top surface of each colony using a hydraulically driven, surface-

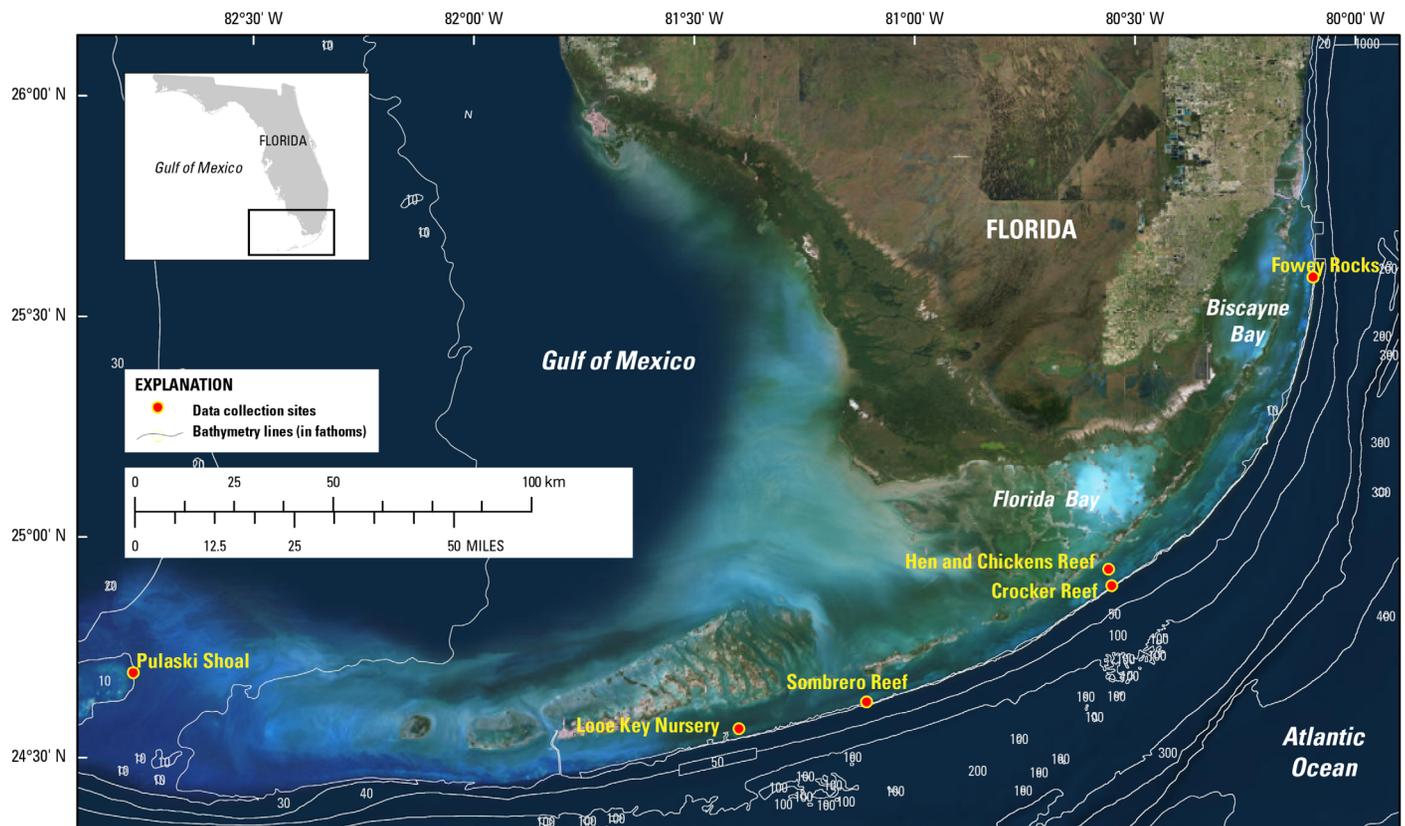


Fig. 1. Map showing locations of the six study sites along the FKRT. Base map is from World Imagery—Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGDA, USGS, AES, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

powered drill to make a 46-cm-deep (18-in.) hole in each coral, and the rods were inserted into the holes with quick-set epoxy filled flush to the colony surface and approximately 15 cm of the rod protruding out of the colony. Exact measurements of the rod height projecting from each coral were recorded and the rods were photographed (images available in Kuffner et al. 2019) at the time of installation (Fig. 2A). In addition, as part of an earlier study on coral-growth rates, 10-cm-diameter (4-in.) cores were collected in August 1995 from 24 *Orbicella* colonies that had died of unknown causes. Three years later, the empty bore holes were relocated, and on 8–10 July 1998, the holes were filled with type II Portland cement and fitted with a stainless-steel 10-cm-diameter, 10-cm-tall cylinder assembly that was capped with a numbered plate to make coral “monuments” (Fig. 2C). The holes were filled with cement up to the top of each cylinder, which protruded from the dead colony by approximately 5–8 cm. Once installed, each monument was photographed (images available in Kuffner et al. 2019) and measured relative to the colony’s surface 10 cm from the monument at the four cardinal compass points with a specially designed measuring device. The device fit snugly over the cylinder to support a hacksaw blade placed on its side. Once in place, strips of rigid, white-PVC plastic were marked with a pencil through a hole at the end of the saw blade to denote the height down to the reef surface, 10 cm away from the base of the monument in each cardinal direction.

Over 17 yr later, on 12–13 October 2015, all 12 rods and 16 monuments were relocated, cleaned of epibionts to reveal the identification numbers, photographed (images available in Kuffner et al. 2019), and measured. A hacksaw blade, fitted with a plastic triangle to hold the blade out 10 cm from the edge of the rod or monument, was used to mark PVC strips to measure the height down to the reef surface in each cardinal direction. We used this same technique for the monuments, rather than using the special device described above (it was too time consuming to remove all the biofouling from the sides of the cylinder so that the device would fit), and then later subtracted the height of the device recorded in 1998 to obtain the original height of the monument. The erosion rate at each marker was calculated by subtracting the means, from 1998 to 2015, of the four heights measured 10 cm away from the base of the marker.

For a separate, weight-based estimation of erosion rates, we used the 18 corals from the calcification monitoring network that did not meet the criteria for inclusion in the growth analyses (i.e., lost mass during at least one time interval). If a coral lost mass during two or more time-intervals, the rates for all such intervals were averaged.

Carbonate budgets

We developed carbonate budgets for Hen and Chickens Reef using a modified version of the ReefBudget protocol outlined in

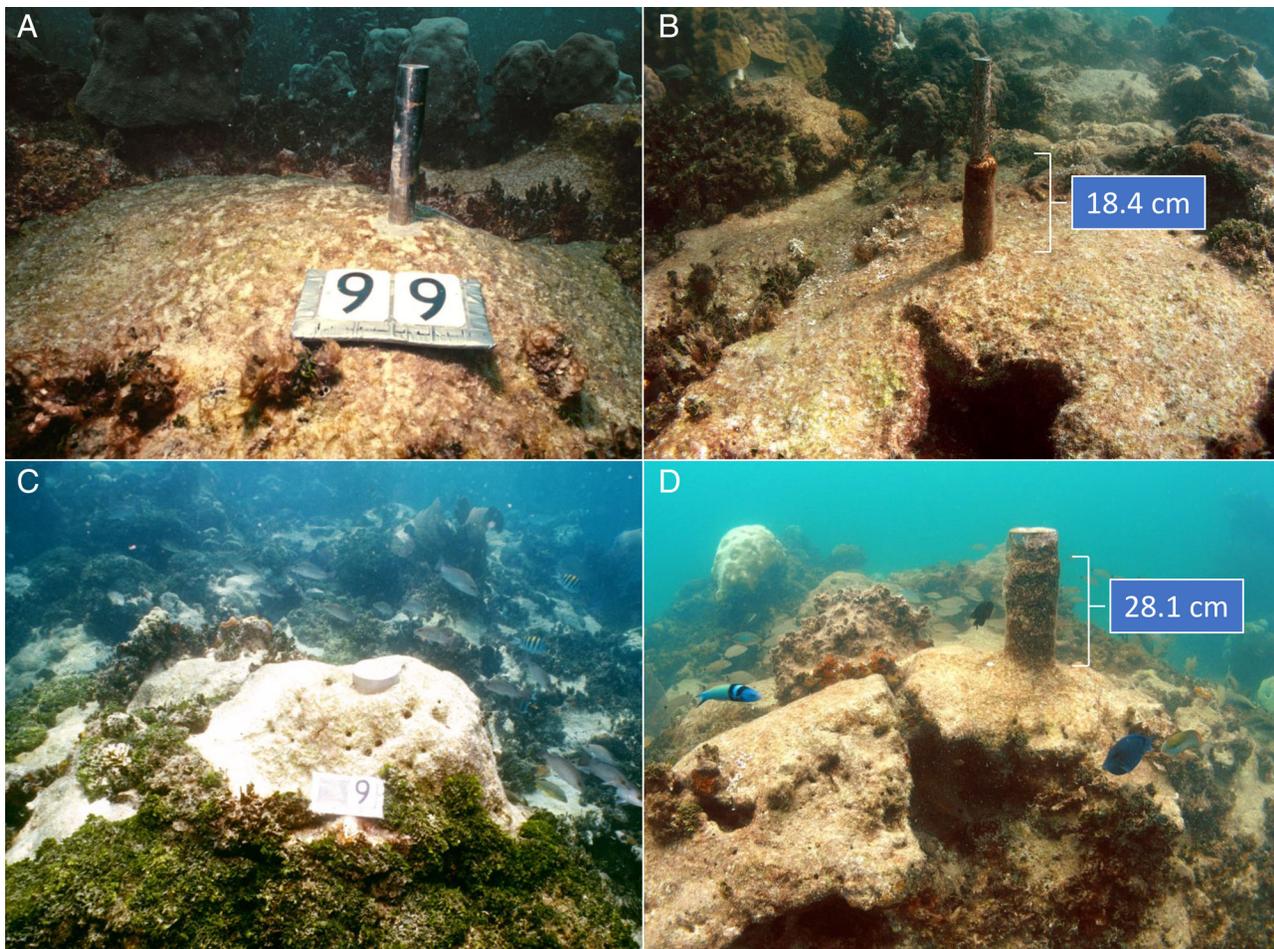


Fig. 2. Photographs from Hen and Chickens Reef, Islamorada, FL, in summer 1998 of stainless-steel marker number “99B” (A) and cement monument number “9” (C) aside photographs of the same markers 17 yr later in October 2015 (B, D). The amount of reef erosion can be easily visualized because the markers were secured with epoxy or cement, which is still intact, whereas the reef around it has eroded away. The blue boxes contain the measured reef elevation lost for each marker pictured. For scale in the left-hand photographs, the stainless-steel rod in (A) is 4 cm diameter, and the cement marker in (B) is 10 cm diameter. See Kuffner et al. (2019) for time-series photographs of all 28 erosion markers.

Perry et al. (2012), summarized in Whitcher (2017). From 07 May 2017 to 09 May 2017, we collected ecological data along six, 10×1 m benthic transects and six belt transects to quantify fish abundance, within three sites at Hen and Chickens Reef (SW, NE, and middle [MD]). Along each 10×1 m benthic transect, we collected photographic transects of the benthos to determine the coverage of hard corals and crustose coralline algae. The percent coverage of all coral species and other benthic constituents was determined by point-count analysis (25 points per image) in the online program CoralNet[®] (<https://coralnet.ucsd.edu/>). Abundance of the bioeroding urchins *Echinometra lucunter*, *Echinometra viridis*, *Diadema antillarum*, and *Eucidaris tribuloides* within 20-mm bins of test sizes and the approximate area in cm^2 covered by the bioeroding sponges *Cliona aprica*, *C. caribbaea*, *C. tenuis*, *C. varians*, *C. delitrix*, and *Siponodictyon coralliphagum* were quantified along the same 10×1 m transects. A diver slowly swam the belt transects to count initial and terminal phase parrotfish (*Scarus vetula*, *Sc. taeniopterus*, *Sc. iseri*, other *Scarus* spp., *Sparisoma viride*,

Sp. aurofrenatum, *Sp. rubripinne*, *Sp. chrysopterus*, and other *Sparisoma* spp.) across five size classes as assigned based on fish fork length (5–14, 14–24, 24–34, 34–44, and > 45 cm). The fish transects were generally 30×4 m; however, some transects were shortened to ensure the surveys were only conducted on reef habitat, and some transects were narrowed because of low water clarity during some surveys.

We estimated gross carbonate production at Hen and Chickens Reef by multiplying the proportional coverage of calcifying taxa (hard corals and crustose coralline algae) by taxon-specific calcification rates and a rugosity correction (based on Bozec et al. 2015 and modified by Whitcher 2017) and summing the gross calcification of each taxon. We used calcification rates reported locally at Florida Keys reefs for crustose coralline algae: $0.047 \text{ g cm}^{-2} \text{ yr}^{-1}$ (Kuffner et al. 2013), *S. siderea*: $0.99 \text{ g cm}^{-2} \text{ yr}^{-1}$ (Kuffner et al. 2013), and *Orbicella* spp.: $0.55 \text{ g cm}^{-2} \text{ yr}^{-1}$ (this study), and for all others used Perry et al.’s (2012) default numbers. We adjusted the calcification rates with a growth-form

correction factor following Guest et al. (2018) because we did not measure reef rugosity. Net carbonate production was determined by subtracting estimated rates of bioerosion from gross carbonate production. We first estimated bioerosion using the census-based approach outlined by Perry et al. (2012), wherein published bioerosion rates for bioeroding urchins, parrotfish, and sponges were combined with our field-based estimates of the abundances of those organisms to estimate bioerosion. We estimated the contribution of microbioerosion by multiplying the rate suggested by Perry et al. (2012) of $0.27 \text{ kg m}^{-2} \text{ yr}^{-1}$ by the proportion of available (i.e., not occupied by living coral or sand) substratum. We compared the net carbonate production determined using the census-based approach to that estimated using direct measurements of bioerosion from the bioerosion experiment at Hen and Chickens Reef and measured rates of *Orbicella* bioerosion from the calcification-assessment network.

Statistical analyses

Statistical analyses were performed using the software package Statistix[®] 10.0 (Analytical Software, Tallahassee, FL, U.S.A.) and RStudio. Assumptions for the various tests applied were assessed by examining residuals for normality and sphericity, and if the assumptions were not met, the data were transformed, or a non-parametric test was substituted. The predeployment calcification rates of colonies deployed to each site were compared to ensure that there were not pre-existing differences in growth with one-way ANOVA. Calcification rates during the 2-yr deployment were tested for site and time-interval effects using two-way, repeated-measures ANOVA. Post hoc comparisons by site were made using Tukey's Honestly Significant Difference (HSD) test. To test for seasonal effects on calcification, which was deemed appropriate (i.e., no two-way interaction), a linear contrast of winter vs. summer intervals was performed using Student's *t*-test based upon the a priori hypothesis that calcification would vary with season. The underwater temperature data were analyzed by site using a one-way Kruskal-Wallis test because the assumptions of parametric ANOVA were not met (residuals not normally distributed and unequal variance among ANOVA cells). To test for a difference in monitoring method (cement vs. stainless-steel rod markers) on reef-erosion measurements, we conducted a two-sample Student's *t*-test. ANOVAs were used to test for significant differences in erosion rates estimated with the reference markers and the census-based estimates of gross carbonate production and erosion among sites at Hen and Chickens Reef. The raw data were published and are available in Kuffner et al. (2019).

Results

Mean calcification rates of the 50 *Orbicella* spp. corals during the predeployment period, while the corals were under the dock in Key West harbor, were not statistically different among future-site assignments (one-way ANOVA, $F_{4,45} = 0.88$, $p = 0.48$), and averaged $2.0 \pm 0.6 \text{ mg cm}^{-2} \text{ d}^{-1}$ ($\pm 1 \text{ SD}$). After deployment to the five sites, 28 of the corals sustained growth for the duration of

the study, 21 lost mass during one or more weighing interval, died, or lost more than 50% live-tissue area, and one colony was physically lost. Partial mortality was the norm in this study and, on average, colonies lost $21\% \pm 37\%$ of their live tissue, but only four colonies died, defined as the absence of any live tissue. Percent loss of tissue was not statically different among sites (one-way Kruskal-Wallis test, $H_{3,35} = 6.1$, $p = 0.10$). Of the 10 corals that were placed at the Looe Key coral nursery, 6 grew (mean calcification $1.7 \pm 0.7 \text{ mg cm}^{-2} \text{ d}^{-1}$), 3 lost mass, and 1 lost > 50% tissue. The Looe Key corals were injured by predatory snails or a white-syndrome disease early in the study and were removed from the experiment after the first year.

For the 22 corals placed at the offshore reefs (i.e., not including Looe Key) that grew during all time intervals, mean calcification rate was statistically different among time intervals but not among sites (Fig. 3; two-way repeated-measures ANOVA on rank-transformed data, time effect: $F_{3,54} = 3.4$, $p = 0.026$, site effect: $F_{3,54} = 2.1$, $p = 0.14$, two-way interaction: $F_{9,54} = 2.0$, $p = 0.058$). The overall, average offshore rate of calcification was $1.5 \pm 1.3 \text{ mg cm}^{-2} \text{ d}^{-1}$, or $0.55 \text{ g cm}^{-2} \text{ yr}^{-1}$ ($5.5 \text{ kg m}^{-2} \text{ yr}^{-1}$). Tukey HSD all-pairwise comparisons test groupings ($\alpha = 0.05$) revealed that the second time-interval (winter 2014) had slower calcification rates than during the third time-interval (summer 2014), but there was no significant seasonality observed (a priori contrast of summers vs. winters, Scheffe's test: $F_{3,54} = 1.65$, $p = 0.19$).

Underwater temperature was significantly different among sites during the 2-yr study (Fig. 3, one-way Kruskal-Wallis test,

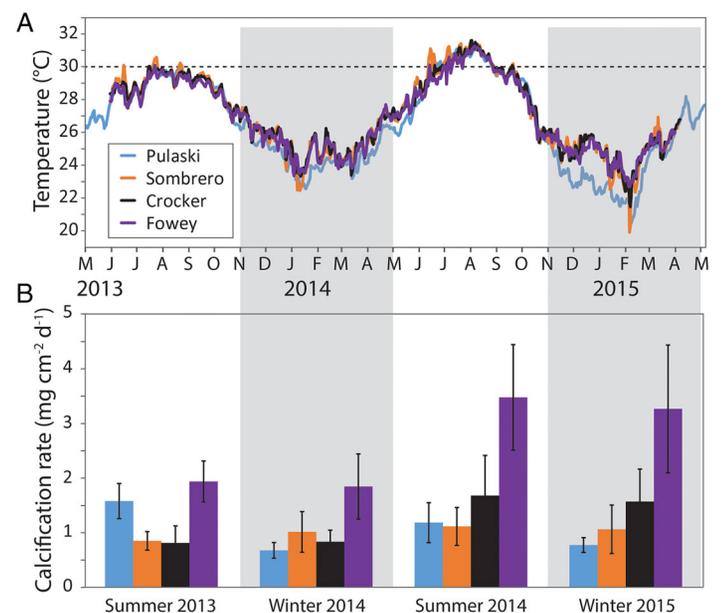


Fig. 3. Graphs showing daily mean underwater temperature (**A**) and mean (\pm SE) calcification rate of 22 *Orbicella* spp. colonies (**B**) at four sites: Pulaski ($n = 6$ corals), Sombrero Key ($n = 6$), Crocker ($n = 4$), and Fowey ($n = 6$), from May 2013 to May 2015. The horizontal dashed line at 30°C in (**A**) denotes a generalized stress threshold for corals. The alternating white and gray shading marks the four weighing intervals (two summers, two winters) during which change in buoyant mass was measured to calculate calcification rate.

$H_{3,18} = 23.7$, $p < 0.0001$). Water temperatures were elevated above seasonal climatology throughout the region because of El Niño conditions during late summer of 2014 (Manzello et al. 2018), but overall, temperatures were cooler in the Dry Tortugas (PLS, 26.5°C) compared with the other three sites (SMK = 27.1°C, CRK = 27.1°C, and FWY = 27.0°C; $H_{3,2747} = 23.7$, $p < 0.0001$, Dunn's all-pairwise groupings: PLS > SMK = CRK = FWY).

The long-term erosion study at Hen and Chickens Reef revealed that all 28 markers showed loss of reef elevation except for one (Table 1; Fig. 2), with a mean loss of 9.4 ± 5.6 cm over the 17.3-yr period, which translates to a mean erosion rate of 5.5 ± 3.2 mm yr⁻¹. See Kuffner et al. (2019) for time-series photographs of all 28 erosion markers. There was no statistical difference in reef-erosion measurements between the stainless-steel rod and cement monument marker-types (two-sample

Student's *t*-test: $t = 0.65$, $df = 26$, $p = 0.52$), or among the three reef sites ($F_{2,25} = 0.3$, $p = 0.75$). Based on the mean density of *Orbicella* spp. reported by Perry et al. (2012) of 1.5 g cm⁻³, this equates to an average erosion rate of -8.2 ± 4.8 kg m⁻² yr⁻¹ for the large, dead *Orbicella* spp. coral colonies at Hen and Chickens Reef. To estimate reef-wide erosion rates at this site, we scaled the point-based erosion rates by the average proportion of erodible substratum, that is, all substrata excluding living coral and sediment (cf. Perry et al. 2012) on the reef measured during our 2017 surveys: $80.9\% \pm 10.6\%$, which results in an estimated reef-wide erosion rate of -6.6 kg m⁻² yr⁻¹ (95% confidence interval = -8.5 to -4.9 kg m⁻² yr⁻¹). The fact that *Orbicella* spp. corals historically accounted for ~80% of the coral assemblage at Hen and Chickens Reef (Hudson et al. 1976), suggests that rates of *Orbicella* erosion should provide a

Table 1. Reference markers installed in June/July 1998 at Hen and Chickens Reef, Islamorada, Florida, U.S.A. for measuring reef erosion. Marker identification (ID) refers to the identifying characters welded or stamped on top of the stainless-steel marker. For marker type, M = cement monument and R = stainless-steel rod. Site abbreviations are SW, southwest; MD, middle; and NE, northeast. Reef eroded is the difference between the measurement made during marker installment in summer 1998 and 17 yr later in October 2015.

Marker ID	Marker type	Site	Latitude	Longitude	Water depth (m)	Reef eroded (cm)	Erosion rate (mm yr ⁻¹)
2	M	SW	24.93375	-80.55129	3.4	9.2	5.3
3	M	SW	24.93375	-80.55135	3.0	5.7	3.3
4	M	SW	24.93369	-80.55129	3.4	12.0	6.9
5	M	SW	24.93349	-80.55097	3.7	6.5	3.8
6	M	SW	24.93363	-80.55121	3.7	6.2	3.6
7	M	SW	24.93356	-80.55118	3.7	8.1	4.7
8	M	SW	24.93362	-80.55106	2.7	8.1	4.7
9	M	SW	24.93350	-80.55102	2.7	28.1	16.3
10	M	MD	24.93404	-80.54948	3.0	15.8	9.2
16	M	MD	24.93421	-80.54948	3.4	12.0	7.0
19	M	MD	24.93473	-80.54873	2.7	13.2	7.7
20	M	MD	24.93468	-80.54874	3.7	-1.1	-0.6
21	M	MD	24.93459	-80.54869	3.7	11.7	6.8
22	M	MD	24.93460	-80.54868	3.7	12.4	7.2
23	M	MD	24.93441	-80.54944	3.0	8.4	4.9
24	M	MD	24.93434	-80.54965	3.7	4.0	2.3
89B	R	NE	24.93729	-80.54765	3.0	11.5	6.6
90B	R	NE	24.93731	-80.54772	4.0	7.8	4.5
91B	R	NE	24.93743	-80.54775	3.7	7.9	4.6
92B	R	NE	24.93731	-80.54779	3.7	3.9	2.3
93B	R	MD	24.93465	-80.54917	3.7	14.0	8.0
94B	R	MD	24.93468	-80.54929	4.0	9.2	5.3
95B	R	MD	24.93460	-80.54917	3.7	5.5	3.2
96B	R	NE	24.93741	-80.54780	3.7	9.2	5.3
97B	R	NE	24.93745	-80.54785	3.4	1.2	0.7
98B	R	NE	24.93747	-80.54784	3.7	8.5	4.9
99B	R	NE	24.93727	-80.54776	3.0	18.4	10.6
100B	R	NE	24.93722	-80.54771	4.0	7.0	4.1
Mean					3.4	9.4	5.5
SD					0.4	5.6	3.2

reasonable approximation of substratum erosion at this site. For the 18 individual corals in the calcification-assessment study that lost mass during one or more weighing intervals, the net erosion rates were highly variable, ranging from -2.1 to -0.03 $\text{mg cm}^{-2} \text{d}^{-1}$ and averaged -0.51 ± 0.54 $\text{mg cm}^{-2} \text{d}^{-1}$ or -1.9 $\text{kg m}^{-2} \text{yr}^{-1}$.

Our surveys in 2017 revealed that the average percent cover of living coral on Hen and Chickens Reef was $15.0\% \pm 8.0\%$, with *Orbicella* spp. at $6.2\% \pm 6.0\%$, *Siderastrea siderea* at $3.9\% \pm 3.8\%$, and *Colpophyllia natans* at $2.4\% \pm 3.6\%$, together accounting for nearly all corals observed on our transects. Crustose coralline algae made up $1.9\% \pm 2.3\%$ of the reef on average and $38.7\% \pm 10.1\%$ was composed of bare substratum with algal turfs. Gross carbonate production at Hen and Chickens Reef was estimated to be 2.4 ± 1.3 $\text{kg m}^{-2} \text{yr}^{-1}$ on average and did not vary significantly among sites (Fig. 4, ANOVA: $F_{2,15} = 0.79$, $p = 0.47$). Estimated rates of bioerosion by parrotfish, sponges, microbioeroders, or the total of those groups were also similar among sites (Fig. 4, ANOVAs: $F_{2,15} = 0.54$, $p = 0.59$;

$F_{2,15} = 0.34$, $p = 0.72$; $F_{2,15} = 0.19$, $p = 0.83$; $F_{2,15} = 0.10$, $p = 0.91$, respectively). The abundance of adult parrotfishes in our surveys averaged 10.0 ± 21.4 individuals per 100 m^2 and the estimated rate of parrotfish bioerosion was -1.6 ± 2.0 $\text{kg m}^{-2} \text{yr}^{-1}$ reef-wide. *Cliona varians* and *C. delitrix* were the most abundant endolithic sponges on Hen and Chickens Reef and on average sponge bioerosion contributed -0.1 ± 0.1 $\text{kg m}^{-2} \text{yr}^{-1}$ to the total carbonate budget. We did not observe bioeroding urchins on any of the transects. We estimated based on Perry et al. (2012) that the contribution of microbioerosion was -0.2 ± 0.03 $\text{kg m}^{-2} \text{yr}^{-1}$ on average. In total, the census-based approach estimated an average, total bioerosion rate of -1.9 ± 2.0 $\text{kg m}^{-2} \text{yr}^{-1}$, which suggests that net carbonate production at Hen and Chickens Reef is 0.5 ± 0.3 (SD based on $n = 3$ sites) $\text{kg m}^{-2} \text{yr}^{-1}$. Substituting the rate of bioerosion estimated from the small, eroding corals in the calcification experiment (-1.9 $\text{kg m}^{-2} \text{yr}^{-1}$), the estimated net production was the same: 0.5 $\text{kg m}^{-2} \text{yr}^{-1}$; however, using the long-term erosion rate estimated from the linear loss of reef at Hen and Chickens (corrected for the proportion of substratum available for bioerosion, -6.6 $\text{kg m}^{-2} \text{yr}^{-1}$) suggests that net carbonate production was much lower and negative, -4.2 $\text{kg m}^{-2} \text{yr}^{-1}$.

Discussion

Considering the value of reefs in shoreline protection (Beck et al. 2018), understanding the balance between the growth and destruction of coral reefs is a major research priority (Perry et al. 2018), particularly through the lens of continuing sea-level rise (Storlazzi et al. 2018). Florida's subtropical reefs may present a canary in a coal mine scenario because reef building throughout the reef tract ceased ~ 3000 yr ago (Toth et al. 2018) and loss of reef elevation has already been documented over the last century (Yates et al. 2017). Our study presents evidence that even *Orbicella*-dominated patch reefs that were thought to be reef refugia based on populations of corals being acclimated to dynamic temperature regimes (Vega-Rodriguez et al. 2015) may be measurably eroding, as evidenced by direct, long-term observations.

Direct measurement of weight-based calcification rates is rare outside of the laboratory. Our experiment using this approach in the field revealed that *Orbicella* spp. colonies growing at four sites on Florida's offshore reef had a mean calcification rate of 0.55 $\text{g cm}^{-2} \text{yr}^{-1}$. This value is about half the production rate typically used for this species in carbonate budgets, representing means of calculated values from the published literature (e.g., 1.05 $\text{g cm}^{-2} \text{yr}^{-1}$ in Guest et al. 2018), though our colonies at Fowey Rocks calcified at rates close to those during the two final time intervals (Fig. 3, 0.95 $\text{g cm}^{-2} \text{yr}^{-1}$). Manzello et al. (2018) reported recent calcification rates (calculated from CT-scan estimates of linear extension and skeletal density) at a Florida Keys patch reef as high as 1.3 $\text{g cm}^{-2} \text{yr}^{-1}$, whereas values were lower at an offshore Keys reef, at 0.97 $\text{g cm}^{-2} \text{yr}^{-1}$ (Manzello et al. 2015). Ideally, and as recognized by Perry et al. (2015), locally and recently collected data on taxon-specific growth parameters should be used whenever possible to accurately predict net-carbonate production.

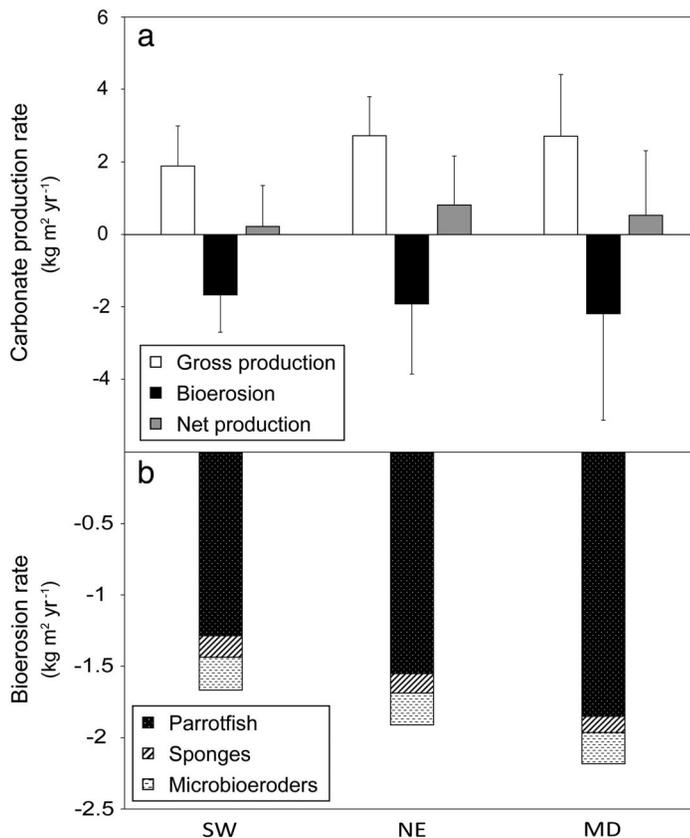


Fig. 4. Graphs of census-based estimates of carbonate production at southwest (SW), northeast (NE), and middle (MD) survey sites at Hen and Chickens Reef; **(A)** provides a comparison of the estimates of gross production (white), bioerosion (black), and net production (gray) at the three sites. Uncertainties in gross production and bioerosion are presented as error bars (+1 SD); because fish surveys were not conducted across the same transects as the other census surveys, the net production uncertainty is presented as the root-mean-square error of the SDs in site-level gross production and bioerosion. In **(B)**, the average contribution of parrotfish, sponges, and microbioeroders to total bioerosion is shown.

Our study and Manzello et al.'s (2018) revealed that underwater temperatures were elevated well above average during the summer of 2014, with more than 2 months above the Caribbean wide coral-bleaching threshold of 30.4°C, and several weeks spent above 31°C (Fig. 3). It is possible that the low calcification rates we observed in our small colonies do not accurately reflect rates that are still achievable by healthy, large colonies today, but they are becoming rare. Also, the colonies we used were acclimated to a harbor environment and could have experienced irradiance stress after being moved to optically clear water on the reef crest. The average tissue loss of 21% indicates that stress was a factor, but whether this was reflective of what was happening at the time to wild colonies at the respective sites is unknown. *Orbicella faveolata* is remarkably resistant to complete mortality (Edmunds 2015), as recently demonstrated in the Florida Keys during repetitive bleaching events in 2014 and 2015 (Gintert et al. 2018); however, percent coverage of *Orbicella* spp. across the Florida reef tract has declined significantly since 1998, most likely because of partial mortality (Toth et al. 2014).

With our long-term, permanent markers, we measured a linear erosion rate of -5.5 ± 3.2 mm yr⁻¹ of large, dead *Orbicella* colonies present at a mid-shore patch reef in the Upper Florida Keys. A recent, reefscape-scale analysis of seafloor-elevation change estimated the vertical erosion rate for 36 km² of coral habitat in the Upper Florida Keys at -2.9 mm yr⁻¹ (Yates et al. 2017). These rates, arrived at using very dissimilar approaches, are surprisingly similar. An early study, also conducted at Hen and Chickens Reef, estimated erosion of *Orbicella* spp. colonies using X-rays to measure the disappearance of annual growth bands and found an average loss of -6.7 mm yr⁻¹ (Hudson 1977). On a windward reef in Belize, Roff et al. (2015) measured a much slower loss of -0.7 mm yr⁻¹ from *Orbicella annularis* colonies that were killed by El Niño bleaching in 1998. While differences in the abundance of eroding taxa would be a primary hypothesis accounting for the difference, possible heterogeneity in the density of reef substrata should be not be discounted. Roff et al.'s (2015) reef in Belize is a windward-facing, fringing reef, so the dead colonies were likely fortified by secondary cementation and colonization of crustose coralline algae in the high-energy wave environment (Adey and Burke 1976; Adey 1998), thereby hardening the dead corals and making them more resistant to bioerosion (Bruggemann et al. 1996) than those found in low-energy environments. This idea will remain merely speculation, however, until there are empirical measurements of reef erosion rates, bioeroder abundance, and reef-framework density across gradients in wave exposure to assess the vulnerability of reefs to erosion.

The convergence of evidence suggesting that reef framework is losing elevation in relation to sea level and eroding away faster than it is being produced (Yates et al. 2017; Perry et al. 2018) is alarming. The mechanisms driving the erosion that we measured, both as a loss in mass from the small colonies, and loss in linear height in the large colonies at Hen and Chickens Reef, are likely a combination of external removal of the skeletal surface by excavating, herbivorous fish and internal weakening and

removal by cryptic, infesting sponges and microbes. Indeed, at Hen and Chickens Reef, our census-based estimates suggested that parrotfish were responsible for more than 80% of the total bioerosion at present. However, Hudson (1977) implicated six species of bioeroding sponges as the main agents of erosion, with parrotfish and the urchin *D. antillarum* (still abundant during the time of the study in the mid-1970s) taking a secondary roll. We noted abundant sponge galleries in the slabs we prepared from our small colonies for another study, supporting the conclusion that bioeroding sponges are a significant source of bioerosion on the Florida reef tract as others have noted (Hudson 1977; Enochs et al. 2015); however, our census-based estimates of erosion suggest that sponges only accounted for ~7% of bioerosion on Hen and Chickens Reef.

Our deployed-coral method of assessing net carbonate production is similar to the method of deploying experimental substrates (usually blocks cut from dead, massive coral colonies) to measure bioerosion rates (Tribollet and Golubic 2005). One could conclude from our reference-marker results that the substrate-deployment method might not be very scalable over longer time periods or larger spatial scales, but the divergence just highlights the need to reconcile these differences with future experiments. When paired with image analyses wherein the bioeroding agents can be identified, the substrate method will continue to be useful for partitioning the microbioerosion, macrobioerosion, and external (grazing) terms in the budget equations (Tribollet and Golubic 2005). While the census method separately and by species accounts for external erosion by grazers and internal macroerosion by sponges, a single value for microbioerosion is applied uniformly to all non-sand substratum, but there are known to be cross-shelf patterns in this process and interactions among the three erosion categories (Tribollet and Golubic 2005). The weight-based substrate-deployment approach, by design, lumps together all three types of erosion to arrive at a net erosion (or production) rate for the deployed block of carbonate. Thus, it is indeed complicated but instructive to compare the data resulting from these different approaches. Regardless, as infaunal erosion rates will increase from ocean acidification (Wisshak et al. 2012; Crook et al. 2013; Enochs et al. 2015) and coastal eutrophication (Chen et al. 2013), and passive, chemical erosion of carbonate material will increase with ocean acidification (Eyre et al. 2018), the physical structure of reefs is increasingly at risk.

More direct measurements of calcification, erosion, and linear loss in reef height (e.g., this study and Roff et al. 2015) could help reduce the uncertainty in carbonate budgets. Our study suggests that the census method could be underestimating erosion rates in some reef settings. Hen and Chickens Reef appears to be eroding at rates up to three times faster than rates we determined using the census-based carbonate-budget approach. It is possible that our long-term measurement of *Orbicella* bioerosion rates do not apply across the reefscape because parrotfish prefer grazing on the topographic highs of dead, low skeletal-density corals, such as *Orbicella* and *Colpophyllia*, infested with endolithic algae (Bruggemann et al. 1996). However, most of Hen and Chickens Reef was built by

Orbicella (80% of massive corals according to Hudson et al. 1976), suggesting that the majority of erodible substratum is also *Orbicella* spp., so our study likely provides a reasonable estimate of bioerosion at least as it pertains to decreases in reef elevation. Getting the erosion terms correct in carbonate budgeting will not be easy, as it has been shown that bioerosion rates by fishes vary not just with species (Bellwood and Choat 1990), but also with reef zone and substratum density (Bruggemann et al. 1996). Additionally, grazing rates by fishes can vary with season, reef type, food supply, and schooling behavior (Polunin and Klumpp 1992; Ferreira 1998; Paddock et al. 2006). The amount of reef carbonate removed per species per bite is based on few observational studies (Scoffin et al. 1980, Bruggemann et al. 1996, and reviewed in Glynn and Manzello 2015), so this could also be a large source of uncertainty in carbonate budgets. Adding this uncertainty to variation in reef density, which influences how much purchase an excavating herbivore gets with each bite (Bruggemann et al. 1996), could easily lead census-based net carbonate budgets to be off by an order of magnitude. Some reefs are more heavily cemented than others (Macintyre and Marshall 1988; Stathakopoulos and Riegl 2015), and are therefore denser and less easily eroded by excavating herbivores (Bruggemann et al. 1996). The high rates of erosion we observed at Hen and Chickens Reef could be, in part, due to the lagoon setting of this patch reef, as inshore reefs are typically characterized by low levels of reef cementation (Marshall 1985), higher rates of skeletal bioerosion (Sammarco and Risk 1990), and higher levels of reef porosity (Hein and Risk 1975).

While there are differing views on the effectiveness of managing parrotfish abundance to promote reef resilience in the western Atlantic region (Adam et al. 2015; Bozec et al. 2016; Steneck et al. 2018; Bruno et al. 2019), our results highlight the importance of balancing any ecological benefits of herbivore management against the potential cost of increased bioerosion. What is clear is that more direct measurements are badly needed to empirically improve our prediction of the erosional side of the carbonate-budget equation. The installation of reference markers over a range of reef types (e.g., inshore patch reefs, offshore barrier reefs, etc.), on different species of coral, and along bioeroder-abundance gradients could be a great step toward reducing uncertainty in reef-carbonate budgeting. Our understanding of reef persistence depends upon extending our observations under the reef surface for clues as to its structural integrity under continued ocean acidification and warming (Toth et al. 2018).

As coral populations continue to decline around the world, live-coral planting (Lirman and Schopmeyer 2016), as well as more interventionist strategies (van Oppen et al. 2017), are gaining recognition as important components of restoration activities to restore ecosystem services (Suding et al. 2015). However, these efforts can only be a stop-gap solution as ocean-warming mitigation efforts get underway. Until then, reef-restoration techniques that successfully increase coral populations serve several purposes. First is the obvious increase in carbonate production by live corals that are actively calcifying (Perry et al. 2013, 2015), but second, live corals also form a protective veneer on reef framework, making it

unavailable to excavating herbivores (Bruggemann et al. 1996; Kuffner and Toth 2016). Third, live corals provide topographical complexity, which increases the frictional coefficient of a reef, thereby increasing the amount of wave energy absorbed (Ferrario et al. 2014). Because low recruitment of juvenile corals is a driving force behind lack of reef recovery in the western Atlantic (Hughes and Connell 1999), particularly for the major reef-building corals *Orbicella* spp. (Edmunds 2002), *A. palmata* (Williams et al. 2008), and other broadcast-spawning species (Tougas and Porter 2002), populations of reef-building corals are unlikely to increase without intervention measures. Fortunately, the focus of reef restoration efforts is shifting from restoring populations of the weedy, branching *Acropora cervicornis* to mixed-species, ecologically minded restoration (Shaver and Silliman 2017), with increased attention to processes like herbivory and predator-prey interactions (Lirman and Schopmeyer 2016), coral recruitment (Montoya-Maya et al. 2016), and facilitating sexual recombination to increase genetic diversity (Baums 2008). A new approach is taking shape wherein the focus is restoring whole-reef ecosystems capable of self-rejuvenation (Suding et al. 2015) under continuing climate change (Webster et al. 2017), because restoration will only succeed in the long term if organisms are able to adapt to the changing conditions.

Data availability statement

Data from the study are publicly available at <https://doi.org/10.5066/P92NVINW> and <https://doi.org/10.5066/F71C1TZK>.

References

- Adam, T. C., D. E. Burkepile, B. I. Ruttenberg, and M. J. Paddock. 2015. Herbivory and the resilience of Caribbean coral reefs: Knowledge gaps and implications for management. *Mar. Ecol. Prog. Ser.* **520**: 1–20. doi:10.3354/meps11170
- Adey, W. H. 1998. Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *J. Phycol.* **34**: 393–406. doi:10.1046/j.1529-8817.1998.340393.x
- Adey, W. H., and R. B. Burke. 1976. Holocene bioherms (algal ridges and bank-barrier reefs) of the eastern Caribbean. *Geol. Soc. Am. Bull.* **87**: 95–109. doi:10.1130/0016-7606(1976)87<95:HBARAB>2.0.CO;2
- Aronson, R. B., and W. F. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* **460**: 25–38. doi:10.1023/A:1013103928980
- Baums, I. B. 2008. A restoration genetics guide for coral reef conservation. *Mol. Ecol.* **17**: 2796–2811. doi:10.1111/j.1365-294X.2008.03787.x
- Beck, M. W., I. J. Losada, P. Menéndez, B. G. Reguero, P. Díaz-Simal, and F. Fernández. 2018. The global flood protection savings provided by coral reefs. *Nat. Commun.* **9**: 2186. doi:10.1038/s41467-018-04568-z
- Bellwood, D. R., and J. H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): The ecological

- implications. *Environ. Biol. Fishes* **28**: 189–214. doi:[10.1007/BF00751035](https://doi.org/10.1007/BF00751035)
- Bozec, Y.-M., L. Alvarez-Filip, and P. J. Mumby. 2015. The dynamics of architectural complexity on coral reefs under climate change. *Glob. Chang. Biol.* **21**: 223–235. doi:[10.1111/gcb.12698](https://doi.org/10.1111/gcb.12698)
- Bozec, Y.-M., S. O'Farrell, J. H. Bruggemann, B. E. Luckhurst, and P. J. Mumby. 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proc. Natl. Acad. Sci. USA* **113**: 4536–4541. doi:[10.1073/pnas.1601529113](https://doi.org/10.1073/pnas.1601529113)
- Bruggemann, J. H., A. M. van Kessel, J. M. van Rooij, and A. M. Breeman. 1996. Bioerosion and sediment ingestion by the caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Mar. Ecol. Prog. Ser.* **134**: 59–71. doi:[10.3354/meps134059](https://doi.org/10.3354/meps134059)
- Bruno, J. F., I. M. Côté, and L. T. Toth. 2019. Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Ann. Rev. Mar. Sci.* **11**: 307–334. doi:[10.1146/annurev-marine-010318-095300](https://doi.org/10.1146/annurev-marine-010318-095300)
- Cantin, N. E., A. L. Cohen, K. B. Karnauskas, A. M. Tarrant, and D. C. McCorkle. 2010. Ocean warming slows coral growth in the central Red Sea. *Science* **329**: 322–325. doi:[10.1126/science.1190182](https://doi.org/10.1126/science.1190182)
- Chen, T., S. Li, and K. Yu. 2013. Macrobioerosion in *Porites* corals in subtropical northern South China Sea: A limiting factor for high-latitude reef framework development. *Coral Reefs* **32**: 101–108. doi:[10.1007/s00338-012-0946-4](https://doi.org/10.1007/s00338-012-0946-4)
- Cinner, J. E., and others. 2016. Bright spots among the world's coral reefs. *Nature* **535**: 416–419. doi:[10.1038/nature18607](https://doi.org/10.1038/nature18607)
- Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S. J. Anderson, I. Kubiszewski, S. Farber, and R. K. Turner. 2014. Changes in the global value of ecosystem services. *Glob. Environ. Chang.* **26**: 152–158. doi:[10.1016/j.gloenvcha.2014.04.002](https://doi.org/10.1016/j.gloenvcha.2014.04.002)
- Costanza, R., and others. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**: 253–260. doi:[10.1038/387253a0](https://doi.org/10.1038/387253a0)
- Crook, E. D., A. L. Cohen, M. Rebolledo-Vieyra, L. Hernandez, and A. Paytan. 2013. Reduced calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification. *Proc. Natl. Acad. Sci. USA* **110**: 11044–11049. doi:[10.1073/pnas.1301589110](https://doi.org/10.1073/pnas.1301589110)
- De'ath, G., J. M. Lough, and K. E. Fabricius. 2009. Declining coral calcification on the Great Barrier Reef. *Science* **323**: 116–119. doi:[10.1126/science.1165283](https://doi.org/10.1126/science.1165283)
- Eakin, C. M., and others. 2010. Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS One* **5**: e13969. doi:[10.1371/journal.pone.0013969](https://doi.org/10.1371/journal.pone.0013969)
- Edmunds, P. J. 2002. Long-term dynamics of coral reefs in St. John, US Virgin Islands. *Coral Reefs* **21**: 357–367. doi:[10.1007/s00338-002-0258-1](https://doi.org/10.1007/s00338-002-0258-1)
- Edmunds, P. J. 2015. A quarter-century demographic analysis of the Caribbean coral, *Orbicella annularis*, and projections of population size over the next century. *Limnol. Oceanogr.* **60**: 840–855. doi:[10.1002/lno.10075](https://doi.org/10.1002/lno.10075)
- Enochs, I. C., D. P. Manzello, R. D. Carlton, D. M. Graham, R. Ruzicka, and M. A. Colella. 2015. Ocean acidification enhances the bioerosion of a common coral reef sponge: Implications for the persistence of the Florida Reef Tract. *Bull. Mar. Sci.* **91**: 271–290. doi:[10.5343/bms.2014.1045](https://doi.org/10.5343/bms.2014.1045)
- Enochs, I. C., D. P. Manzello, G. Kolodziej, S. Noonan, L. Valentino, and K. E. Fabricius. 2016. Enhanced macroboring and depressed calcification drive net dissolution at high-CO₂ coral reefs. *Proc. R. Soc. Lond. B Biol. Sci.* **283**: 20161742. doi:[10.1098/rspb.2016.1742](https://doi.org/10.1098/rspb.2016.1742)
- Eyre, B. D., T. Cyronak, P. Drupp, E. H. De Carlo, J. P. Sachs, and A. J. Andersson. 2018. Coral reefs will transition to net dissolving before end of century. *Science* **359**: 908–911. doi:[10.1126/science.aao1118](https://doi.org/10.1126/science.aao1118)
- Fang, J. K. H., M. A. Mello-Athayde, C. H. L. Schönberg, D. I. Kline, O. Hoegh-Guldberg, and S. Dove. 2013. Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Glob. Chang. Biol.* **19**: 3581–3591. doi:[10.1111/gcb.12334](https://doi.org/10.1111/gcb.12334)
- Ferrario, F., M. W. Beck, C. D. Storlazzi, F. Micheli, C. C. Shepard, and L. Airoidi. 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat. Commun.* **5**: 3794. doi:[10.1038/ncomms4794](https://doi.org/10.1038/ncomms4794)
- Ferreira, C. E. L. 1998. Seasonal grazing rates and food processing by tropical herbivorous fishes. *J. Fish Biol.* **53**: 222–235. doi:[10.1111/j.1095-8649.1998.tb01029.x](https://doi.org/10.1111/j.1095-8649.1998.tb01029.x)
- Gintert, B. E., D. P. Manzello, I. C. Enoch, G. Kolodziej, R. Carlton, A. C. R. Gleason, and N. Gracias. 2018. Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: A nugget of hope, aberrance, or last man standing? *Coral Reefs* **37**: 533–547. doi:[10.1007/s00338-018-1678-x](https://doi.org/10.1007/s00338-018-1678-x)
- Glynn, P. W. 1997. Bioerosion and coral reef growth: A dynamic balance, p. 69–98. *In* C. Birkeland [ed.], *Life and death of coral reefs*. Chapman & Hall.
- Glynn, P. W., and D. P. Manzello. 2015. Bioerosion and coral reef growth: A dynamic balance, p. 67–97. *In* C. Birkeland [ed.], *Coral reefs in the Anthropocene*. Springer.
- Guest, J. R., and others. 2018. A framework for identifying and characterising coral-reef “oases” against a backdrop of degradation. *J. Appl. Ecol.* **55**: 2865–2875. doi:[10.1111/1365-2664.13179](https://doi.org/10.1111/1365-2664.13179)
- Halpern, B. S., and others. 2008. A global map of human impact on marine ecosystems. *Science* **319**: 948–952. doi:[10.1126/science.1149345](https://doi.org/10.1126/science.1149345)
- Hein, F. J., and M. J. Risk. 1975. Bioerosion of coral heads: Inner patch reefs, Florida reef tract. *Bull. Mar. Sci.* **25**: 133–138.
- Hubbard, D. K., A. I. Miller, and D. Scaturro. 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): Applications to the nature of reef systems in the fossil record. *J. Sediment. Petrol.* **60**: 335–360.
- Hudson, J. H. 1977. Long-term bioerosion rates on a Florida reef: A new method, p. 491–497. *In* Proceedings of the 3rd International Coral Reef Symposium. May 1977, Miami, Florida, U.S.A.
- Hudson, J. H., E. A. Shinn, R. B. Halley, and B. Lidz. 1976. Sclerochronology: A tool for interpreting past environments.

- Geology **4**: 361–364. doi:[10.1130/0091-7613\(1976\)4<361:SATFIP>2.0.CO;2](https://doi.org/10.1130/0091-7613(1976)4<361:SATFIP>2.0.CO;2)
- Hughes, T. P., and J. H. Connell. 1999. Multiple stressors on coral reefs: A long-term perspective. *Limnol. Oceanogr.* **44**: 932–940. doi:[10.4319/lo.1999.44.3_part_2.0932](https://doi.org/10.4319/lo.1999.44.3_part_2.0932)
- Jokiel, P. L., J. E. Maragos, and L. Franzisket. 1978. Coral growth: Buoyant weight technique, p. 529–541. *In* D. R. Stoddart and R. E. Johannes [eds.], *Coral reefs: Research methods*. UNESCO.
- Knutson, D. W., R. W. Buddemeier, and S. V. Smith. 1972. Coral chronometers: Seasonal growth bands in reef corals. *Science* **177**: 270–272. doi:[10.1126/science.177.4045.270](https://doi.org/10.1126/science.177.4045.270)
- Kuffner, I. B. 2019. Underwater temperature on off-shore coral reefs of the Florida Keys, U.S.A. (ver. 4.0, March 2019): U.S. Geological Survey data release. [accessed on 2019 March 13]. Available from <https://doi.org/10.5066/F71C1TZK>.
- Kuffner, I. B., T. D. Hickey, and J. M. Morrison. 2013. Calcification rates of the massive coral *Siderastrea siderea* and crustose coralline algae along the Florida Keys (USA) outer-reef tract. *Coral Reefs* **32**: 987–997. doi:[10.1007/s00338-013-1047-8](https://doi.org/10.1007/s00338-013-1047-8)
- Kuffner, I. B., and L. T. Toth. 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conserv. Biol.* **30**: 706–715. doi:[10.1111/cobi.12725](https://doi.org/10.1111/cobi.12725)
- Kuffner, I. B., E. Bartels, A. Stathakopoulos, I. C. Enochs, G. Kolodziej, L. T. Toth, and D. P. Manzello. 2017. Plasticity in skeletal characteristics of nursery-raised staghorn coral, *Acropora cervicornis*. *Coral Reefs* **36**: 679–684. doi:[10.1007/s00338-017-1560-2](https://doi.org/10.1007/s00338-017-1560-2)
- Kuffner, I. B., L. T. Toth, J. H. Hudson, W. B. Goodwin, A. Stathakopoulos, L. A. Bartlett, and E. M. Witcher. 2019. Experimental data on construction and erosion of *Orbicella* coral reefs in the Florida Keys, U.S.A. USGS data release. [accessed on 2019 April 15]. Available from <https://doi.org/10.5066/P92NVINW>.
- Lidz, B. H., C. D. Reich, R. L. Peterson, and E. A. Shinn. 2006. New maps, new information: Coral reefs of the Florida Keys. *J. Coast. Res.* **22**: 260–282. doi:[10.2112/05A-0023.1](https://doi.org/10.2112/05A-0023.1)
- Lirman, D., and S. Schopmeyer. 2016. Ecological solutions to reef degradation: Optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ* **4**: e2597. doi:[10.7717/peerj.2597](https://doi.org/10.7717/peerj.2597)
- Macintyre, I. G., and J. F. Marshall. 1988. Submarine lithification in coral reefs: Some facts and misconceptions, p. 263–272. *In* Proceedings of the 6th International Coral Reef Symposium. V. 1. James Cook University, 8–12 August 1988, Townsville, Australia.
- Manzello, D. P., I. C. Enochs, G. Kolodziej, and R. Carlton. 2015. Recent decade of growth and calcification of *Orbicella faveolata* in the Florida Keys: An inshore-offshore comparison. *Mar. Ecol. Prog. Ser.* **521**: 81–89. doi:[10.3354/meps11085](https://doi.org/10.3354/meps11085)
- Manzello, D. P., I. C. Enochs, G. Kolodziej, R. Carlton, and L. Valentino. 2018. Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. *Mar. Biol.* **165**: 99.
- Marshall, J. F. 1985. Cross-shelf and facies related variations in submarine cementation in the central great barrier reef, p. 221–226. *In* Proceedings of the 5th International Coral Reef Symposium, 27 May to 1 June 1985, Tahiti.
- Miller, J., E. Muller, C. Rogers, R. Waara, A. Atkinson, K. Whelan, M. Patterson, and B. Witcher. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* **28**: 925–937. doi:[10.1007/s00338-009-0531-7](https://doi.org/10.1007/s00338-009-0531-7)
- Montoya-Maya, P. H., K. P. Smit, A. J. Burt, and S. Frias-Torres. 2016. Large-scale coral reef restoration could assist natural recovery in Seychelles, Indian Ocean. *Nat. Conserv.* **16**: 1–17. doi:[10.3897/natureconservation.16.8604](https://doi.org/10.3897/natureconservation.16.8604)
- Morrison, J. M., I. B. Kuffner, and T. D. Hickey. 2013. Methods for monitoring corals and crustose coralline algae to quantify in-situ calcification rates, p. 11. U.S. Geological Survey Open-File Report 2013-1159. [accessed on 2013 July 30]. Available from <http://pubs.usgs.gov/of/2013/1159/>.
- Paddack, M. J., R. K. Cowen, and S. Sponaugle. 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* **25**: 461–472. doi:[10.1007/s00338-006-0112-y](https://doi.org/10.1007/s00338-006-0112-y)
- Perry, C. T., E. N. Edinger, P. S. Kench, G. N. Murphy, S. G. Smithers, R. S. Steneck, and P. J. Mumby. 2012. Estimating rates of biologically driven coral reef framework production and erosion: A new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* **31**: 853–868. doi:[10.1007/s00338-012-0901-4](https://doi.org/10.1007/s00338-012-0901-4)
- Perry, C. T., G. N. Murphy, P. S. Kench, S. G. Smithers, E. N. Edinger, R. S. Steneck, and P. J. Mumby. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat. Commun.* **4**: 1402. doi:[10.1038/ncomms2409](https://doi.org/10.1038/ncomms2409)
- Perry, C. T., G. N. Murphy, P. S. Kench, E. N. Edinger, S. G. Smithers, R. S. Steneck, and P. J. Mumby. 2014. Changing dynamics of Caribbean reef carbonate budgets: Emergence of reef bioeroders as critical controls on present and future reef growth potential. *Proc. R. Soc. Lond. B Biol. Sci.* **281**: 2014–2018. doi:[10.1098/rspb.2014.2018](https://doi.org/10.1098/rspb.2014.2018)
- Perry, C. T., R. S. Steneck, G. N. Murphy, P. S. Kench, E. N. Edinger, S. G. Smithers, and P. J. Mumby. 2015. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Glob. Chang. Biol.* **21**: 1153–1164. doi:[10.1111/gcb.12792](https://doi.org/10.1111/gcb.12792)
- Perry, C. T., and others. 2018. Loss of coral reef growth capacity to track future increases in sea level. *Nature* **558**: 396–400. doi:[10.1038/s41586-018-0194-z](https://doi.org/10.1038/s41586-018-0194-z)
- Polunin, N. V. C., and D. W. Klumpp. 1992. Algal food supply and grazer demand in a very productive coral-reef zone. *J. Exp. Mar. Biol. Ecol.* **164**: 1–15. doi:[10.1016/0022-0981\(92\)90132-T](https://doi.org/10.1016/0022-0981(92)90132-T)
- Roff, G., J.-X. Zhao, and P. J. Mumby. 2015. Decadal-scale rates of reef erosion following El Niño-related mass coral mortality. *Glob. Chang. Biol.* **21**: 4415–4424. doi:[10.1111/gcb.13006](https://doi.org/10.1111/gcb.13006)
- Sammarco, P. W., and M. J. Risk. 1990. Large-scale patterns in internal bioerosion of *Porites*: Cross continental shelf trends on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **59**: 145–156. doi:[10.3354/meps059145](https://doi.org/10.3354/meps059145)
- Scoffin, T. P., C. W. Stearn, D. Boucher, P. Frydl, C. Hawkins, I. G. Hunter, and J. K. MacGeachy. 1980. Calcium carbonate budget

- of a fringing reef on the west coast of Barbados: Part II - erosion, sediments and internal structure. *Bull. Mar. Sci.* **30**: 475–508.
- Shaver, E. C., and B. R. Silliman. 2017. Time to cash in on positive interactions for coral restoration. *PeerJ* **5**: e3499. doi:[10.7717/peerj.3499](https://doi.org/10.7717/peerj.3499)
- Silbiger, N. J., and M. J. Donahue. 2015. Secondary calcification and dissolution respond differently to future ocean conditions. *Biogeosciences* **12**: 567–578. doi:[10.5194/bg-12-567-2015](https://doi.org/10.5194/bg-12-567-2015)
- Smith, L. W., D. Barshis, and C. Birkeland. 2007. Phenotypic plasticity for skeletal growth, density and calcification of *Porites lobata* in response to habitat type. *Coral Reefs* **26**: 559–567. doi:[10.1007/s00338-007-0216-z](https://doi.org/10.1007/s00338-007-0216-z)
- Sthakopoulos, A., and B. M. Riegl. 2015. Accretion history of mid-Holocene coral reefs from the Southeast Florida continental reef tract, USA. *Coral Reefs* **34**: 173–187. doi:[10.1007/s00338-014-1233-3](https://doi.org/10.1007/s00338-014-1233-3)
- Stearn, C. W., T. P. Scoffin, and W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados part I - zonation and productivity. *Bull. Mar. Sci.* **27**: 479–510.
- Steneck, R. S., P. J. Mumby, C. MacDonald, D. B. Rasher, and G. Stoyle. 2018. Attenuating effects of ecosystem management on coral reefs. *Sci. Adv.* **4**: eaao5493. doi:[10.1126/sciadv.aao5493](https://doi.org/10.1126/sciadv.aao5493)
- Stephenson, T. A., and A. Stephenson. 1950. Life between tide-marks in North America: The Florida Keys. *J. Ecol.* **38**: 354–402. doi:[10.2307/2256451](https://doi.org/10.2307/2256451)
- Storlazzi, C. D., and others. 2018. Most atolls will be uninhabitable by the mid-21st century because of sea-level rise exacerbating wave-driven flooding. *Sci. Adv.* **4**: eaap9741. doi:[10.1126/sciadv.aap9741](https://doi.org/10.1126/sciadv.aap9741)
- Suding, K., and others. 2015. Committing to ecological restoration. *Science* **348**: 638–640. doi:[10.1126/science.aaa4216](https://doi.org/10.1126/science.aaa4216)
- Toth, L. T., R. van Woesik, T. J. T. Murdoch, S. R. Smith, J. C. Ogden, W. F. Precht, and R. B. Aronson. 2014. Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. *Coral Reefs* **33**: 565–577. doi:[10.1007/s00338-014-1158-x](https://doi.org/10.1007/s00338-014-1158-x)
- Toth, L. T., I. B. Kuffner, A. Sthakopoulos, and E. A. Shinn. 2018. A 3000-year lag between the geological and ecological collapse of Florida's coral reefs. *Glob. Chang. Biol.* **24**: 5471–5483. doi:[10.1111/gcb.14389](https://doi.org/10.1111/gcb.14389)
- Tougas, J. I., and J. W. Porter. 2002. Differential coral recruitment patterns in the Florida Keys, p. 789–811. *In* J. W. Porter and K. G. Porter [eds.], *The Florida Everglades, Florida Bay, and coral reefs of the Florida Keys - an ecosystem sourcebook*. CRC Press.
- Tribollet, A., and S. Golubic. 2005. Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs* **24**: 422–434. doi:[10.1007/s00338-005-0003-7](https://doi.org/10.1007/s00338-005-0003-7)
- Uzoh, F. C. C., and M. W. Ritchie. 1996. Crown area equations for 13 species of trees and shrubs in northern California and southwestern Oregon, p. 13. Research paper PSW-RP-227-Web. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. [accessed on 2018 March 13]. Available from https://www.fs.fed.us/psw/publications/documents/psw_rp227/psw_rp227.pdf.
- van Oppen, M. J. H., and others. 2017. Shifting paradigms in restoration of the world's coral reefs. *Glob. Chang. Biol.* **23**: 3437–3448. doi:[10.1111/gcb.13647](https://doi.org/10.1111/gcb.13647)
- Vega-Rodriguez, M., and others. 2015. Influence of water-temperature variability on stony coral diversity in Florida Keys patch reefs. *Mar. Ecol. Prog. Ser.* **528**: 173–186. doi:[10.3354/meps11268](https://doi.org/10.3354/meps11268)
- Veron, J. E. N., and others. 2009. The coral reef crisis: The critical importance of <350 ppm CO₂. *Mar. Pollut. Bull.* **58**: 1428–1436. doi:[10.1016/j.marpolbul.2009.09.009](https://doi.org/10.1016/j.marpolbul.2009.09.009)
- Webster, M. S., M. A. Colton, E. S. Darling, J. Armstrong, M. L. Pinsky, N. Knowlton, and D. E. Schindler. 2017. Who should pick the winners of climate change? *Trends Ecol. Evol.* **32**: 167–173. doi:[10.1016/j.tree.2016.12.007](https://doi.org/10.1016/j.tree.2016.12.007)
- Whitcher, E. M. 2017. Reef-building threatened by ecosystem decline: A case study from Buck Island, U.S. Virgin Islands. Masters thesis. Florida Institute of Technology.
- Williams, D. E., M. W. Miller, and K. L. Kramer. 2008. Recruitment failure in Florida Keys *Acropora palmata*, a threatened Caribbean coral. *Coral Reefs* **27**: 697–705. doi:[10.1007/s00338-008-0386-3](https://doi.org/10.1007/s00338-008-0386-3)
- Wisshak, M., C. H. L. Schonberg, A. Form, and A. Freiwald. 2012. Ocean acidification accelerates reef bioerosion. *PLoS One* **7**: e45124. doi:[10.1371/journal.pone.0045124](https://doi.org/10.1371/journal.pone.0045124)
- Yates, K. K., D. G. Zawada, N. A. Smiley, and G. Tiling-Range. 2017. Divergence of seafloor elevation and sea level rise in coral reef ecosystems. *Biogeosciences* **14**: 1739–1772. doi:[10.5194/bg-14-1739-2017](https://doi.org/10.5194/bg-14-1739-2017)

Acknowledgments

We thank A. Rosenberg and International SeaKeepers Society for in-kind contribution of the vessel from which we conducted the reef-erosion surveys. For field and laboratory help, we thank J. Morrison, C. Reich, B. Reynolds, K. Jackson, and R. Fidler. We also thank M. Colella of the Florida Fish and Wildlife Conservation Commission and two anonymous reviewers for their highly constructive suggestions that improved the manuscript. The study was conducted under scientific permits from the Florida Keys National Marine Sanctuary (FKNMS-2013-024-A2 and FKNMS-2016-085-A1) and the National Park Service (BISC-2013-SCI-0011, BISC-2014-SCI-0020, BISC-2015-SCI-0003, DRTO-2013-SCI-0008, and DRTO-2015-SCI-0010), and coral samples are curated under NPS accession numbers BISC-228 and DRTO-274. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was funded by the U.S. Geological Survey (USGS) Coastal-Marine Hazards and Resources Program of the Hazards Mission Area.

Conflict of Interest

None declared.

Submitted 14 September 2018

Revised 21 February 2019

Accepted 03 April 2019

Associate editor: Bradley Eyre