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NATURAL HISTORY NOTE

Global Conservation Potential in Coral Reef Halos: Consistency over Space, Time, and Ecosystems Worldwide

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ABSTRACT: Halos around coral reefs are landscape-scale patterns arising from multispecies interactions that collectively structure reefscapes over many thousands of square kilometers. First described in the 1960s, halos are known from a handful of locations and continue to captivate scientists. What remains unknown is how globally widespread, persistent, and dynamic halos are. We examined satellite imagery of reefs globally, coupled with in situ field observations, to show that halos are a globally ubiquitous, persistent, yet dynamic ecological phenomenon spanning vastly different systems. We further document the previously undescribed presence of halos outside the tropics surrounding seagrass "reefs" and highlight the temporal scales over which coral reef halos change, merge, and persist. Specifically, we show that halos can change in size over relatively short temporal scales of months, despite persisting over decades. In doing so, we document patterns suggesting that additional biophysical mechanisms than previously assumed may shape halos. Understanding the full suite of mechanisms governing halo formation and maintenance may enable us to use them as proxies for species interactions. Given the global extent of halos, their role in affecting sedimentary carbon storage, and their relationship with marine reserve existence and maturity, they may ultimately serve as globally relevant indicators of coral reef ecosystem functioning and health.

Keywords: coral reef, grazing halo, reef halo, herbivory, predation risk, remote sensing.

Introduction

Coral reef halos, often known as grazing halos or sand halos, are a striking example of regular pattern formation in nature. In reef halos, the seabed at the coral reef–seagrass/algae interface shows a clearly visible band of bare substrate immediately surrounding spatially isolated coral patch reefs (i.e., reef structures that are separated from one another by expanses of sandy bottom habitat) or along continuous reef edges. Halo bands are generally meters to tens of meters wide around these reef patches, which themselves are generally tens of meters in diameter and can range from near-perfect circles to various amoeba-like shapes. Patch reefs (and their surrounding halos) are generally situated within larger, "whole-reef" ecosystems that include reef slopes, crests, flats, and the lagoonal areas in which patch reefs are generally found. Reef halos were first reported in the 1960s and 1970s in the Caribbean Sea (Randall 1965; Ogden et al. 1973) but were rarely discussed in the literature in subsequent decades (table S1; but see Tribble 1981; Hay 1984; Shulman 1985; Macintyre et al. 1987). Reef halos have long been attributed to fish and invertebrate herbivory (Ogden et al. 1973; Valentine et al. 2007), which is spatially constrained by predators (Randall 1965; DiFiore et al. 2019), and substantial evidence supports this notion. Specifically, predators create predation risk throughout the reef system, both near and far from individual coral patch reefs around which halos form (Madin et al. 2019*b*). These patch reefs offer refugia from predation risk by providing shelter for their prey (Almany 2004*a*, 2004*b*), many of whom are smaller herbivorous fishes and invertebrates. As a result, herbivorous prey tend to spend more time in the immediate vicinity of their patch reef refugia, with the cumulative foraging intensity of the reef's many herbivores mirroring their spatial distribution (Madin et al. 2010)—ultimately resulting in the absence of benthic algae surrounding the patch reef. However, other mechanisms have also been hypothesized to lead to halo formation, including nutrient toxicity (Alevizon 2002), sediment deposition (Garrett et al. 1971), local water

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movement due to eddies (Steiner and Willette 2014), and incidental (Glynn 1985) or spatially constrained (Alevizon 2002; Steiner and Willette 2014) bioturbation. Of these proposed additional mechanisms, only spatially constrained bioturbation has been demonstrated empirically to contribute to halo formation or maintenance (Madin et al. 2019*b*). In this context, bioturbation refers to the physical disturbance of marine sediments and the primary producers (e.g., benthic algae) that live atop the sediments caused by living organisms. Large fishes, such as emperors and sweetlips, have been shown to engage in bioturbation as they root through surface sediments in search of infaunal invertebrate food, in turn disrupting benthic algae and expanding the halo boundary (Madin et al. 2019*b*).

Likely because of the large spatial scales (i.e., hundreds to tens of thousands of square meters) over which individual halos occur, no experimental manipulations have unequivocally tested the full suite of mechanisms leading to halo formation. Consequently, it remains unknown whether additional mechanisms may contribute to halo formation or maintenance. Even observational studies have proven difficult over more than a hyperlocal scale (i.e., one to a few individual patch reefs/halos, with patch reefs generally ranging from a few to hundreds of meters in diameter). However, the recent availability of very high resolution (VHR; 0.3–1 m pixel^{-1}) satellite imagery and low-cost drones (<5 cm pixel^{-1}) now makes possible larger-scale studies, over scales of tens to thousands of square kilometers whose upper bound is limited only by imagery availability, thus allowing comparisons even between different regions across the globe. Despite these technical advances, this ecological knowledge gap limits our ability to fully unlock any clues that halos may provide regarding species interactions or general reef ecosystem health, although evidence from field studies suggests that such clues likely exist.

Reef halos are of interest in part because they have been observed to be associated with marine reserves designed to protect harvested species (e.g., predators, herbivores; DiFiore et al. 2019; Madin et al. 2019*a*) and can affect sedimentary carbon storage (Atwood et al. 2018), thereby offering promise as a diagnostic tool for reef ecosystem structure and functioning. Specifically, Madin et al. (2019*a*) explored halo prevalence and size among the network of fished and unfished reefs within Australia's Great Barrier Reef Marine Park, where predatory fishes are targeted by fishing but herbivores are generally not fisheries' targets. They found that while halos occurred in both fished and unfished areas, no-take marine reserves that did not allow fishing and that had existed long enough for previously fished predator populations to recover to a detectable level had a significantly higher prevalence of halos. Furthermore, the likelihood of halo occurrence increased with reserve age, suggesting that halo prevalence may be indicative of the recovery of previously fished populations. Unlike the Great Barrier Reef, herbivores are often targeted by fishers on many Caribbean reefs, in addition to predators. DiFiore et al. (2019) surveyed reef halos within two Caribbean no-take reserves and found that within the halos, the more predators that were present, the less herbivores grazed overall. They also found that herbivore density and the area of the interior patch reef around which halos were formed were, unsurprisingly, strongly correlated and that these two factors collectively explained much of the variation in halo width. The findings of Madin et al. (2019*a*) and DiFiore et al. (2019) together indicate that halo presence is a potential indicator of predator (and possibly herbivore) recovery from fishing and that halo size is likely indicative of herbivore recovery. Atwood et al. (2018) further demonstrated that halos can affect sedimentary carbon storage. Specifically, they determined that the spatial gradient in risk imposed by predators on their herbivorous prey, where risk is lowest near patch reef edges and increases with distance from these reefs, was responsible for the higher levels of grazing immediately surrounding the patch reefs that formed the halos, subsequently leading to reduced carbon storage within the halo zone. While the halos themselves are depleted of sedimentary carbon, the predation risk that creates the halos largely prevents grazing of benthic algae beyond the halos' edges, in effect concentrating the grazing into a small zone (the halo) and allowing benthic algae to flourish—and generate sedimentary carbon storage—everywhere else. This finding, which mirrors findings from other ecosystem types (Wilmers et al. 2012; Atwood et al. 2014; Schmitz et al. 2014), has implications for reef ecosystem functioning in that it documents a potentially unexpected (but measurable) role played by predator-prey interactions in governing marine carbon sequestration. In effect, predation risk safeguards sedimentary carbon sequestration via halos, providing yet another reason to protect predator populations on coral reefs.

To date, the documented spatial and temporal scale of reef halos has been limited. Although halos are known to occur throughout specific regions, such as the Caribbean's West Indies (Randall 1965), publications focusing on halos have been limited to the local scale, that is, from a single whole-reef tract, island, or archipelago (table S1). Collectively, these studies describe halos in just six countries, with all but those from Australia occurring in the Caribbean (table S1). The longest period between documentation of halos around the same patch reefs is 8 years (Andréfouët et al. 2001), and these authors conclude on the basis of initial and final time points that the halos were spatially stable throughout the intervening period. Unknown is how long reef halos can persist, whether they are static over time, what biophysical factors may influence their persistence and size, and how common they are worldwide.

Here, we use VHR satellite imagery to provide descriptive observations, at a global scale, of the presence of halos that allow us to make novel inferences about the broader ecological processes both shaping and resulting from halos. Specifically, we (1) subsample the global tropics and partial subtropics to estimate halo occurrence worldwide, (2) conduct qualitative in situ surveys of two locations, (3) use quantitative time series of satellite-derived data from a subset of locations to reveal halos' spatial and temporal dynamics, and (4) utilize historical imagery from four locations to qualitatively understand the long-term persistence capacity of halos. Our results should lend insight into whether mechanisms other than those previously proposed to lead to halo formation may exist and into their utility as a potential global-scale ecosystem indicator to aid in coral reef conservation and management.

Methods

Global Spatial Comparison

To examine the prevalence of halos globally, we subsampled the global tropics using a stratified latitudinal survey of the satellite image mosaic within Google Earth Pro. Specifically, we used lines of latitude every 1° from 29°N to 29°S as line intercept transects. A total of 59 latitudinal transects across 66 countries were surveyed. If a latitudinal transect intersected a reef (i.e., a kilometer-scale reef consisting of multiple types of subreefs, of which spatially isolated patch reefs are one), we created a 1-km buffer on either side of the transect along the length of the transect overlapping with the reef. Within this buffer, we measured the total whole-reef area intercepted by the transect (with the whole-reef boundaries defined as visually apparent differences in pixel color separating shallow reef substrate from deeper water) and approximated the percentage of the total whole reef that was area covered by halo "fields" (i.e., areas of substrate that were covered with repeated, adjacent, relatively evenly distributed halos surrounding patch reefs; see the appendix for details). This estimate therefore included both the area of the halos and individual reefs themselves as well as the space between adjacent halos. Although Randall (1965) included in his definition of a halo the halolike borders that commonly occur along the edges of continuous, spatially connected reefs, we focused solely on halos surrounding spatially isolated patch reefs. We did so because when identifying halos from satellite imagery in the absence of ground truthing (as we did for the vast majority of locations in this study), there are many possible causes of differently colored substrate along continuous reef boundaries, and we could not be sure such patterns were necessarily halos. Based on these values, the proportion of surveyed reef area that is covered in halo fields (P) is calculated as

$$P = \frac{\sum_{i=1}^{n} h_i}{\sum_{i=1}^{n} r_i}, \tag{1}$$

where r_i is the area of reef i that was surveyed for halo presence and extent, h_i is the area of reef i that contained halos, and n is the total number of reefs surveyed. Based on the assumption that our latitudinally stratified survey is representative of coral reefs globally, we calculate the estimated area of coral reefs globally that is covered by halo fields (A) as

$$A = P \cdot T, \tag{2}$$

where T is the established total areal extent of coral reefs globally, or 284,300 km^2 (Spalding et al. 2001).

In addition to our stratified latitudinal survey, we also conducted a targeted survey of no-take reserves to increase our sample size of unfished reefs, which constituted only a small portion of the stratified latitudinal survey. To do so, we located all no-take reserves within the same 0–29° latitudinal range. For each reserve, the virtual belt transect was centered on the latitudinal centroid of each no-take reserve shapefile (to the nearest hundredth degree), and the area 0.5 km above and below the latitudinal centroid was surveyed. All other methods were as described for the stratified latitudinal survey.

In addition to the latitudinal surveys, we also conducted a targeted search using Google Earth Pro for halos in a small number of subtropical locations in the Mediterranean Sea, where another type of regular pattern formation has been documented (Ruiz-Reynés et al. 2017). We initially did not expect to find halos in this area; rather, we were looking for evidence within satellite imagery of the widespread "fairy circles" described within a bay of Mallorca Island, Spain, by Ruiz-Reynés et al. (2017) when we came across what appeared to be halolike patterns. We then conducted a more extensive imagery search for apparent halos surrounding each of Spain's other large islands of the Balearic archipelago.

Qualitative In Situ Surveys

We ground truthed two locations containing apparent halos from satellite imagery: Heron Island on Australia's Great Barrier Reef and the patch reefs adjacent to Key West in the United States's Florida Reef Tract. Previous studies had confirmed the existence of halos at Heron Island (Madin et al. 2011; Atwood et al. 2018; Ollivier et al. 2018). One study had previously documented halos in another part of the Florida Reef Tract using aerial photography and

IKONOS satellite imagery (Andréfouët et al. 2001) but had not conducted any ground truthing. To validate halos observed from satellite imagery in this study and qualitatively document the resident primary producer, herbivore, and predator species assemblages within the halos, two locations were surveyed. Twenty-two halos occurring within the lagoon of Heron Island, Queensland, Australia (23°27′7.23″S, 151°56′52.44″E), were photographed in May 2013 (Madin et al. 2019*b*). Two halos within the channel between the offshore reef crest and Key West, Florida, United States (24°29′50.67″N, 81°42′49.16″W), were photographed in June 2015 along a haphazardly placed transect radiating outward from each interior reef, through the halo, and into the surrounding seagrass meadow.

Time Series Comparisons

Quantitative Comparisons of Satellite Imagery. To determine whether and how halos change in size over time, we measured halo presence and size from time series of satellite images. Four geographically dispersed locations were chosen from among those with multiple high-quality images available at different time points using the archival access to imagery within Google Earth Pro (table S2). Our criteria for inclusion of locations were that multiple halos were present in their imagery and at least four clear, <1-m spatial resolution images taken of the location at different times were available. Because of the limited available imagery, we were not able to specify particular time intervals or choose particular imagery years; instead, we selected the maximum number of images that met the above criteria and used those in our analysis. The locations with suitable imagery we used were Heron Reef (28 km^2), Australia; just outside Biscayne Bay (~1,100 mi^2), United States; near Momi Bay (~50 km^2), Fiji; and near Merizo (~10 km^2), Guam. For each location, as many isolated patch reefs were enumerated at each location as possible and then randomly subsampled. The same patch reefs and, when present, their halos were manually digitized in each available satellite image. All patch reefs and their halos were outlined within Google Earth Pro (locations in the United States [Biscayne Bay and Guam] and Fiji) or after import to QGIS 2.14.8-Essen (Heron Reef; QGIS Development Team 2021). Using QGIS, the areas of the polygons surrounding the reefs and halos were subsequently calculated. Halo width was calculated by subtracting the radius of a circle with the same area as the reef from the radius of a circle with the area enclosed by the outer edge of the halo. Reef radii are assumed (and were observed; see the appendix) to not change appreciably in shape between time points and have been shown to not change in satellite imagery pixel color appreciably over timescales of at least 8 years (Andréfouët et al. 2001); therefore, ratio changes over time are indicative of changes in halo width while accounting for differences in satellite imagery among time points.

Some degree of temporal dependency among halo widths over time can be expected. We searched for evidence of temporal dependency among halo widths using the data from Guam, where the images were by far the most frequent and thus the most likely to show dependency. We used two approaches: calculation of a semivariogram and examination of the residuals of a model predicting halo width using an intercept and random effects for image ID (which incorporates image date) and patch reef. Details of both methods can be found in the appendix. Because of the uncertainty of temporal dependency even among the most frequent images in our data set (i.e., those from Guam), we concluded that such dependency could safely be neglected when interpreting our results.

Qualitative Comparisons of Historical Aerial and Modern Imagery. To determine whether and for how long the earliest documented halos have persisted over time, we visually examined historical aerial (airplane-derived) imagery from the 1960s and 1970s of patch reefs and halos from three Caribbean locations found in Randall (1965; Lameshur Bay, St. John, US Virgin Islands [USVI], collected in April 1961, and New Providence Island, Bahamas, collected in June 1962) and Ogden et al. (1973; Knight Bay, St. Croix, USVI, collected in January 1973). For the USVI sites, the exact locations of the reefs and halos were known or could be discerned from landmarks, whereas the Bahamas site consisted of a single reef and halo whose exact location could not be determined. We then visually compared modern historical imagery of the exact (USVI) or nearby (Bahamas) reefs to determine whether a visually apparent halo still existed at each location.

To determine whether and how halos change in shape over time, we visually examined the sequence of historical satellite imagery available in Google Earth Pro for the exceptionally distinct apparent halos found in Ras Muhammad National Park, Egypt. We then visually compared the same section of reefs and halos over multiple time points. We present a sequence of four of the clearest images, showing the most visually apparent changes in halos size, for two distinct sections of reefs and halos within this location.

Results

Global Spatial Comparison

Coral reef halos are far more geographically widespread than previously reported (table S3), and we show that they are found throughout the global tropics. We find that halos occur in all tropical ocean basins (other than the

South Atlantic; fig. 1*A*), across which high levels of species dissimilarity exist (fig. 1*B*). We estimate that the total coral reef area globally that contains halo fields is approximately 24,500 km^2 (eq. [2]). This estimate is based on our finding that of the 804 km^2 of coral reef area sampled by our standardized belt transect method applied to satellite imagery, ~9% (or 69 km^2) contained measurable halo fields (eq. [1]). Considering only locations containing the requisite patch reef habitat, this number rises to 18% (eq. [1]). These findings demonstrate that while the percentage of reefs and reef area covered by halos is small, the total area over which halos occur globally is substantial. Our survey further shows that halos are pan–tropically distributed (fig. 2), occurring in all ocean basins other than the South Atlantic.

Additionally, we provide evidence (fig. 3) from a haphazard satellite imagery survey of a handful of subtropical locations that an analogous halolike vegetation pattern can also be seen in nonreef marine systems beyond the tropics. Specifically, we show that such patterns appear to exist at the seagrass-algae boundary in Mediterranean ecosystems, well outside the latitudinal bounds of coral reef ecosystems.

Qualitative In Situ Surveys

As predicted by inspection of satellite imagery, we visually confirmed that halos exist in both locations and that these locations contain vastly different species assemblages. Indeed, near complete species turnover is known to exist between these two locations, as illustrated with a small subset of species in figure 1*B*.

Time Series Comparisons

Quantitative Comparisons of Satellite Imagery. We found that individual halos can change significantly in size (i.e., width) over relatively long (year-to-year) timescales, as shown in the nonoverlapping 95% confidence bounds among some halos at the same location within the time series shown in figure 4*B*. We also observed changes in halo size over shorter (month-to-month) timescales, but these differences were not statistically significant (fig. 4*B*). Given the limited frequency of available satellite imagery, particularly over shorter timescales, we are unable to determine with certainty the shortest possible interval between significant changes in halo width.

Qualitative Comparisons of Historical Aerial and Modern Satellite Imagery. By using historical aerial and satellite imagery, we also found that halos can be found in the same places repeatedly over at least a half century (the earliest data available). Specifically, some halos originally described from multiple locations in the Caribbean (Randall 1965; Ogden et al. 1973) in the 1960s and early 1970s are still visible today (fig. 4*A*).

At one location, Egypt's Ras Mohammed National Park, we found previously undescribed transient "corridors" between adjacent halos (fig. 5)—that is, apparently bare, sandy areas connecting adjacent halos. Specifically, on observation dates when halos were of intermediate width relative to other dates, an apparently vegetation-free linear path formed between pairs of adjacent halos. Based on the visual similarity with the halos themselves, we assume that the observed corridors are correspondingly vegetation-free. We observed similar simultaneous expansion and contraction of halos at other locations in our study (e.g., fig. 1*A*, subpanels *A* and *D*). Specifically, halos in a given location were observed to be larger, on average, on some dates and smaller, on average, on other dates.

Discussion

Our survey combining historical aerial imagery and recent satellite imagery reveals that coral reef halos are a globally ubiquitous seascape pattern that is far more persistent over time and consistent across geography than previously understood, yet dynamic over year-to-year temporal scales and local spatial scales. Halos therefore provide a novel example of regular pattern formation in ecosystems (Rietkerk and van de Koppel 2008) occurring over landscape scales spanning widely different reef ecosystems and species assemblages. The temporally and spatially dynamic nature of the phenomenon, including the occurrence of newly described corridors between halos (fig. 5), provides evidence that additional biophysical factors than previously assumed, or perhaps extensions of known mechanisms, may play a role in the formation and maintenance of halos. This finding should be considered when interpreting what halos might mean in terms of reef ecosystem health. In addition, given the role of reef halos in affecting sedimentary carbon storage (Atwood et al. 2018), we can infer from our findings of their widespread global distribution that they are visual indicators of how predation risk affects carbon storage occurring on a scale far larger than previously appreciated. Importantly, in conjunction with previous studies of halos as indicators of aspects of reef ecosystem health (Bilodeau 2019; DiFiore et al. 2019; Madin et al. 2019*a*), our finding of their globally widespread distribution (fig. 2) substantiates the notion that halos could potentially be used as the basis for a pantropical conservation assessment tool (Madin et al. 2011). With the knowledge we now have that halos are likely indicators of healthy, carbon-sequestering ecosystems, this could take the form of identifying conservation target locations. As we develop a more complete understanding of the full suite of mechanisms underlying

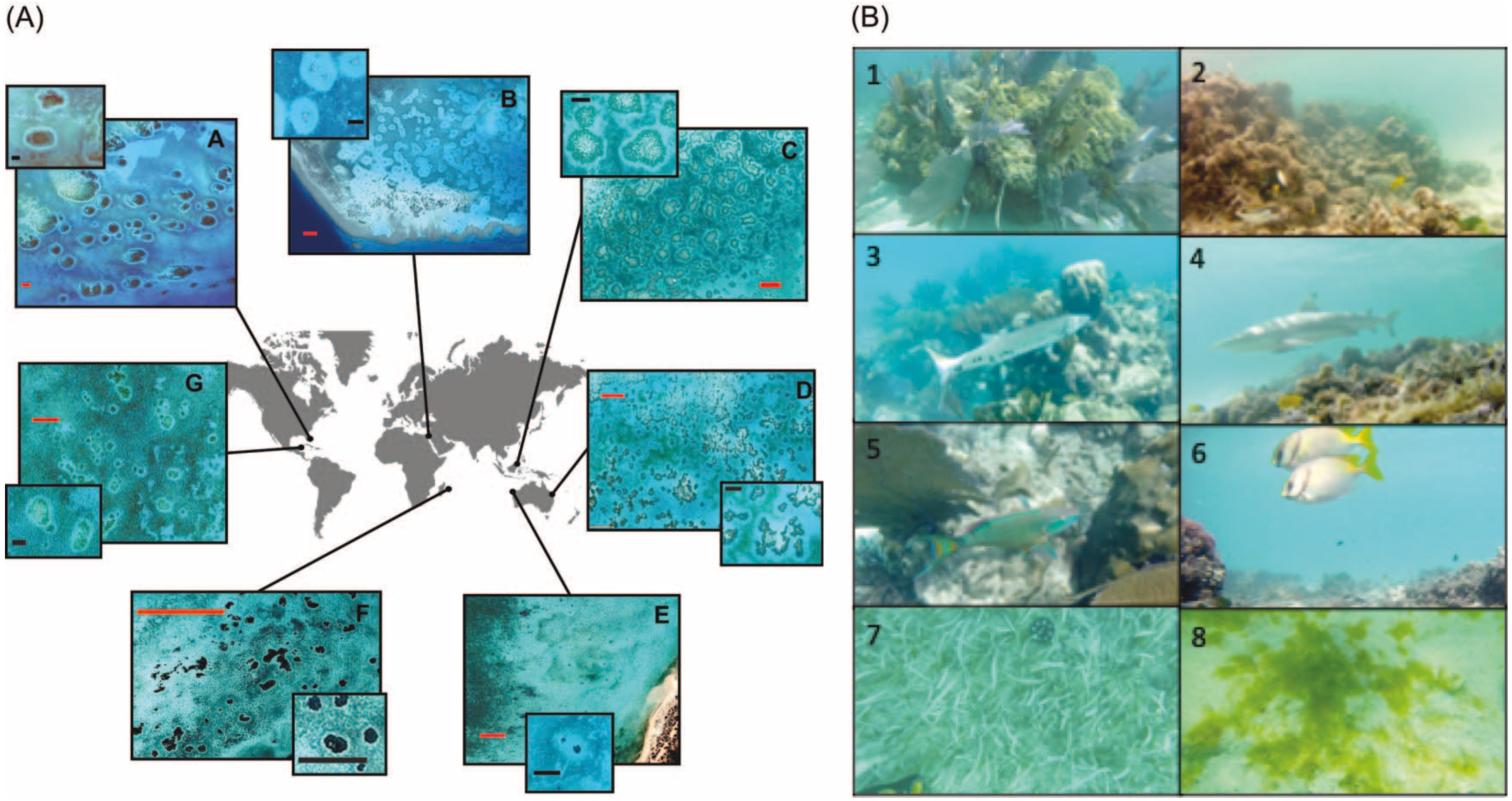

Figure 1: *A*, Grazing halos are found worldwide. Selected example locations are the Florida Keys, United States (subpanel *A*); Red Sea, Egypt (subpanel *B*); Borneo, Malaysia (subpanel *C*); Great Barrier Reef, Australia (subpanel *D*); Ningaloo Reef, Australia (subpanel *E*); Mauritius, Republic of Mauritius (subpanel *F*); and Mesoamerican Barrier Reef, Belize (subpanel *G*). These locations represent a small subset of the hundreds of locations within at least 29 countries where apparent halos have been observed from satellite imagery and are based on a nonexhaustive search. Scale bars within images are 100 m (red) and 30 m (black). Colors were autoscaled to improve image exposure and contrast. All images were taken from Google Earth Pro. Image copyrights: Google, DigitalGlobe (satellites WorldView-1 [resolution, 46 cm], WorldView-2 [50 cm], WorldView-3 [30 cm], WorldView-4 [31 cm], GeoEye-1 [41 cm], QuickBird [60 cm]), and/or CNES (Centre National d'Etudes Spatiales)/Astrium (satellites SPOT 6 and 7 [1.5 m] and/or Pléiades 1A and 1B [0.5 m]). *B*, Examples of ecological components observed during ground-truthing surveys. Examples are from Biscayne Bay, United States (*left column*; corresponding to subpanel *A* within panel *A*) and Heron Island, Australia (*right column*; corresponding to subpanel *D* within panel *A*). Images show examples of reef structure (1, 2), predators (3, 4), herbivores (5, 6), and primary producers (7, 8) found within each reef system.

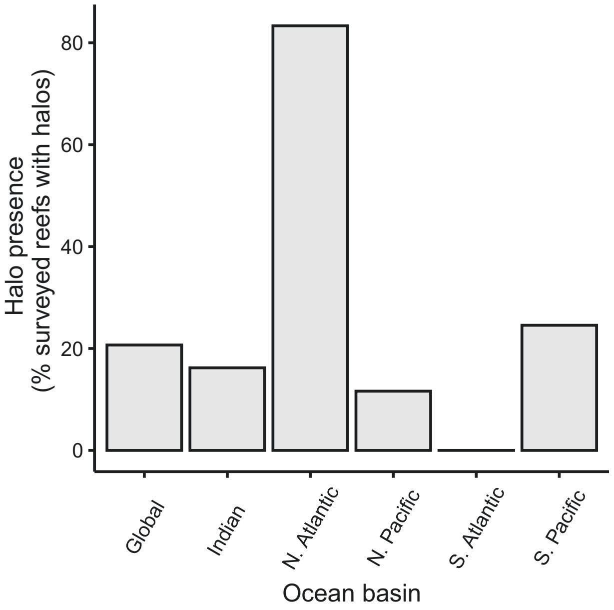

Figure 2: Global reef halo presence, derived from a latitudinally stratified survey of very high resolution satellite imagery spanning coral reefs globally. The bar plot represents the global average of halo presence among the five ocean basins containing coral reefs as well as each basin's average. Halo presence is defined as the percentage of surveyed reefs containing halo fields after accounting for locations where imagery characteristics (e.g., low image spatial resolution, cloud cover) and/or environmental factors (e.g., lack of suitable patch reef habitat, depth more than ~5 m) prevented reefs and halos from being clearly identified. Further details can be found in the methods section and in the appendix.

halos, we may ultimately be able to use satellite imagery of halos to monitor and/or assess the health of specific ecosystems, allowing comparisons over both space and time. These tools may be particularly useful for reefs within the North Atlantic, given its relatively high (>80%) prevalence of halos. This region encompassed multiple transects within the very large Grand Bahama Bank (GBB), which has abundant halos; thus, this region's halo prevalence was likely driven in large part by the GBB's unusually high halo density. Why this shallow shelf area has such extensive halo fields remains unknown.

Our finding that reef halos occur throughout the global tropics, as well as possibly also within subtropical nonreef systems, leads us to infer that the same emergent pattern can occur despite near-complete species turnover (figs. 1, 3). Additionally, our tentative finding that the same apparent pattern both exists in a novel ecosystem type (i.e., seagrass reefs vs. coral reefs; fig. 3) and is not limited to the tropics (halos' currently known domain) leads us to infer that two organisms (coral and seagrass) with ostensibly different functional roles may nonetheless play functionally similar roles in this context. Specifically, this finding suggests that seagrass reefs serve as oases of physical shelter in otherwise macroalgae-dominated seascapes, likely playing a similar functional role to corals in terms of habitat provisioning for foraging fishes. Evidence for this functional role exists (Smith et al. 2011) but is not conclusive (Horinouchi 2007). Likewise, although much remains unknown about the nature of these apparent halos, it seems plausible that similar risk-induced spatial constraints on herbivorous fish and/or invertebrate foraging may exist, thereby concentrating foraging close to the shelter of the dense seagrass beds. In this study, we did not search for halos outside the tropics/subtopics other than in this particular Mediterranean region, nor did we search among different benthic habitat types (e.g., rocky reef). Determining how prevalent halos are in such places warrants further study.

Our global satellite imagery survey suggests that just under 10% of the world's suitable coral reef habitat contains reef halos (eq. [1]), highlighting their potential as globally relevant conservation monitoring tools. This translates into an area larger than the country of Belize being covered by halos—and therefore potentially also having altered carbon storage potential. This estimate is conservative, however, because we know from inspecting satellite imagery as part of this study and from numerous field expeditions to Heron Island, Australia, that halos can disappear and reappear over time at the same location. Our field surveys at Heron Island suggest that when halos "disappear" from satellite imagery, it is due to the temporary thinning or disappearance of the algal meadows that form the backdrop for halos rather than the breakdown of the mechanisms causing the halos themselves. The intermittent algal meadow disappearance at this location appears to be associated with strong wind events that mechanically dislodge the algae from the sediment rather than changes in foraging behaviors of herbivores. The latter conclusion results from camera trap surveys conducted when background algae was low enough that it was not likely visible in satellite imagery, yet herbivore foraging patterns were in line with what would be expected to generate halos (Madin et al. 2019*b*). The present study's global survey results thus allow us to infer that sedimentary carbon storage capacity on reefs is likely altered by the presence of halos on a scale not previously recognized and that the disappearance and reappearance of halos does not undermine this conclusion. The halos themselves have reduced sedimentary carbon storage, but the surrounding areas' carbon stocks are "protected" by predation risk and other factors that create halos. The long-term persistence in these carbon-protecting mechanisms—despite shorter-term fluctuations in halos' visual presence—suggests that the presence of halos can be used as a diagnostic tool for identifying where sedimentary carbon stores are likely elevated. Rietkirk et al. (2008) note that regular pattern

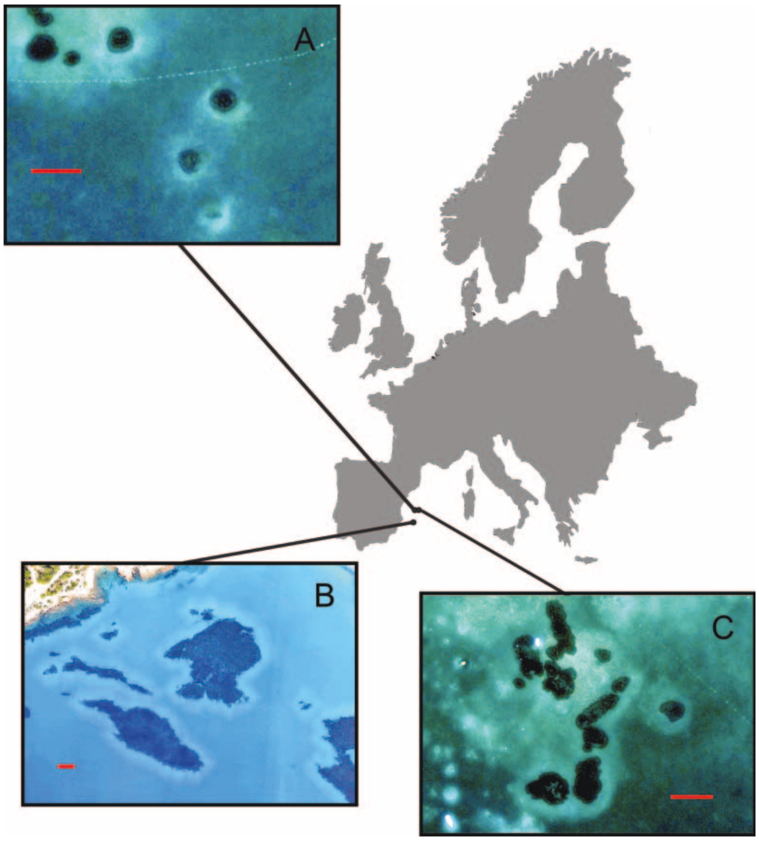

Figure 3: Apparent halos surrounding seagrass "reefs" within algal beds in the Balearic Islands off the coast of Spain. *A*, *C*, Pollença Bay, Mallorca Island; *B*, near Playa des Codolar, Ibiza Island. Dark patches that are loosely contoured by lighter halolike bands are likely comprised primarily of the seagrass species *Cymodocea nodosa* and *Posidonia oceanica* (Ruiz-Reynés et al. 2017). These reefs and halos appear to be situated within meadows of benthic algal assemblages that likely include *Caulerpa prolifera* (on muddy substrate), photophilic algal stands dominated by *Cystoseira* spp. or *Padina pavonica* (on rocks and dead *Posidonia* rhizomes), *Ruppia cirrhosa* (at very sheltered sites), and various coralline algal species (Ribera et al. 1997). Red scale bars are 30 m. Image dates and coordinates are February 4, 2016, at 39°54′28.15″N, 3° 5′50.95″E (*A*); October 28, 2015, at 38°52′0.60″N, 1°20′38.40″E (*B*); and February 4, 2016, at 39°54′15.65″N, 3° 6′22.95″E (*C*). Note the small bright spots on the left-hand side of *C*, which are likely the result of boat mooring/anchor damage to algal meadows (e.g., boat moored atop the bottommost bright spot). Images copyright 2021 Maxar and Google.

formation can have emergent effects on ecosystem functioning; halos are a clear example of this, given their effects on long-term carbon storage. One limitation of our analysis is that the Google Earth Pro image mosaic is a compilation of various types of VHR image sensors (i.e., <1-m pixel size). As a result, pixel resolution is not consistent and varies across locations and dates, slightly impacting halo detectability. Future studies can overcome this by acquiring VHR imagery from the same sensor covering reefs globally. Such imagery does not exist at present at regular (or even very frequent) time intervals for the vast majority of the world because this type of imagery is generally collected on a per-request basis. Particularly for more remote reefs that are far from major cities, little coverage currently exists. However, imagery of lower spatial resolution (i.e., ~3–5-m pixel size) is now collected daily for all of the world's land and nearshore areas, potentially allowing for more regular, albeit noisy, analyses of halo presence and size going back in time to approximately 2018. It is also worth noting that halos may be underidentified in regions with less satellite imagery coverage, more cloud cover, and/or greater average wind speeds (the latter of which leads to surface ripples and sun reflectance, making benthic features difficult or impossible to distinguish).

We find that halos can persist (i.e., occur regularly, even if not continuously) for at least 50 years (fig. 4*A*) yet can be highly dynamic over both space and time where they occur. For example, halos that change significantly in scale over year-to-year timescales (e.g., fig. 4*B*; Australia's Heron Reef) can nonetheless persist over at least a decade (e.g.,

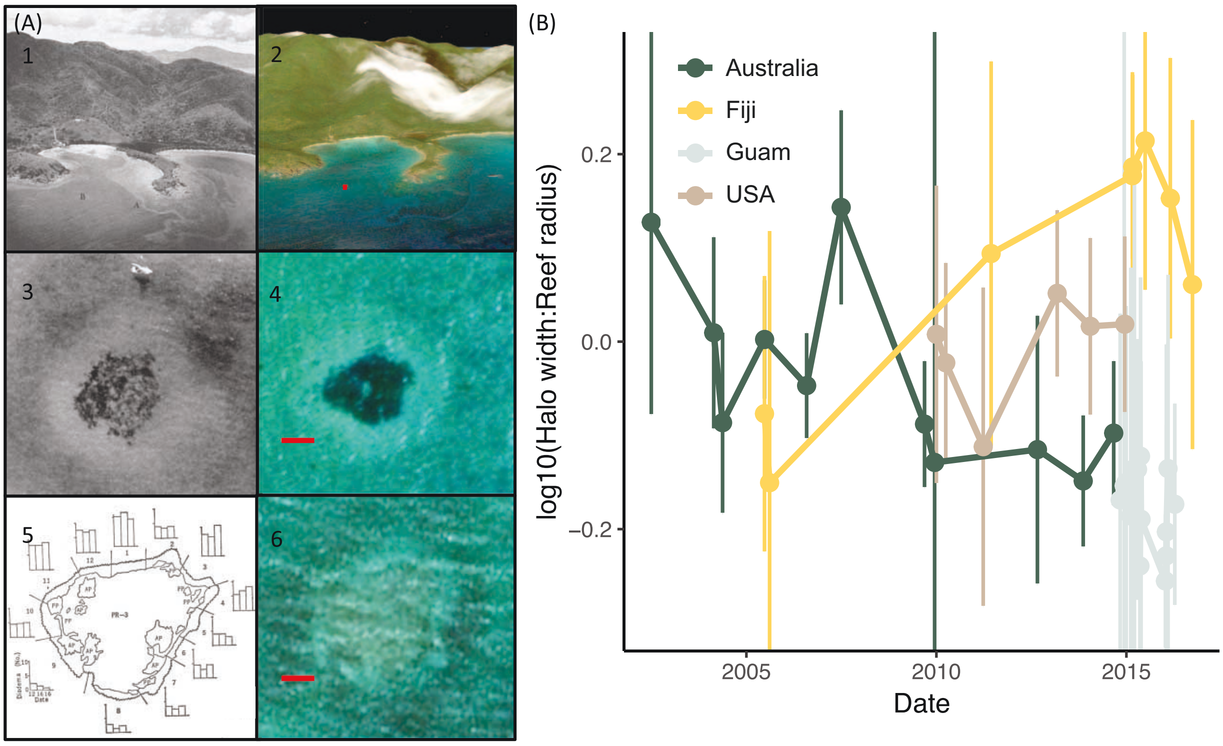

Figure 4: *A*, Long-term temporal persistence of halos on three Caribbean islands. Halos can be seen in images as a pale border along or a ring around reef edges. Reefs are darker underwater areas immediately adjacent to and extending underwater from the peninsula shown in subpanels 1 and 2, the black interior shapes at the center of subpanels 3 and 4, the hand-drawn interior shape in subpanel 5, and the pale brown interior shape in subpanel 6. Locations are as follows: Lameshur Bay, St. John, US Virgin Islands (USVI), April 1961 (1) and February 2017 (2); New Providence Island, Bahamas, June 1962 (3) and November 2019 (4); and Knight Bay, St. Croix, USVI, January 1973 (5) and July 2019 (6). Red scale bars are 10 m. Tiny bar plots in subpanel 5 are the maximum number of *Diadema* urchins per linear meter of perimeter (*y*-axis) in each of 12 reef sectors over three time points (*x*-axis). Note that because exact geographic coordinates were not provided in Randall (1965), the reefs and halos shown in subpanels 3 and 4 are distinct from one another but are assumed to be from within the same cluster of reefs and halos immediately east of New Providence Island. Images in subpanels 1 and 3 are from Randall (1965), reprinted with permission from John Wiley and Sons. The image in subpanel 5 is from Ogden et al. (1973), reprinted with permission from the American Association for the Advancement of Science. Images in subpanels 2 and 4 are copyright Google and Maxar, and the image in subpanel 6 is copyright Google and CNES (Centre National d'Etudes Spatiales)/Airbus. *B*, Cross-site comparison of halo persistence and average size over time. Data are time series of transformed ratios of mean halo width to mean reef radius (with 95% confidence intervals) at a subset of locations where halos are found globally. The US time series (labeled "USA") corresponds to subpanel *A* within figure 1*A* and the left-hand column in figure 1*B*; the Australia time series corresponds to subpanel *D* within figure 1*A* and the right-hand column in figure 1*B*. Data points represent dates where freely available, cloud-free, high-resolution satellite imagery was available and are therefore not necessarily reflective of temporal end points of halo existence or minimum temporal scales of changes in width. An expanded view of the Guam time series can be found in the appendix (fig. A1).

Madin et al. [2011] demonstrate that halos existing today were evident at least ~10 years prior). Collectively, these data show that halos can change fairly dramatically over shorter timescales but that they also remain comparatively stable over longer periods. Understanding the nature of these temporal fluctuations is important for interpreting halos' persistence and size in the context of ecosystem monitoring. Importantly, this finding suggests that data from multiple time points may be necessary to avoid drawing erroneous conclusions based on halo presence or size. Additionally, these findings are relevant to the broader ecological questions of how and why landscapes are patterned and the degree to which cross-scale interactions shape landscape patterns. Changes in patch shape of regularly patterned ecosystems have been cited as likely early-warning signals of large-scale ecosystem degradation (Rietkerk et al. 2004; Kéfi et al. 2014). Further research coupling time series of halo occurrence and scale with established indicators of ecosystem health may reveal whether this prediction holds true for the systems in which halos occur.

In the specific context of coral reef landscape ecology, figure 4*B* demonstrates that because of their variability over monthly to yearly timescales that cannot be easily explained by large-scale changes in predator, herbivore, or bioturbator

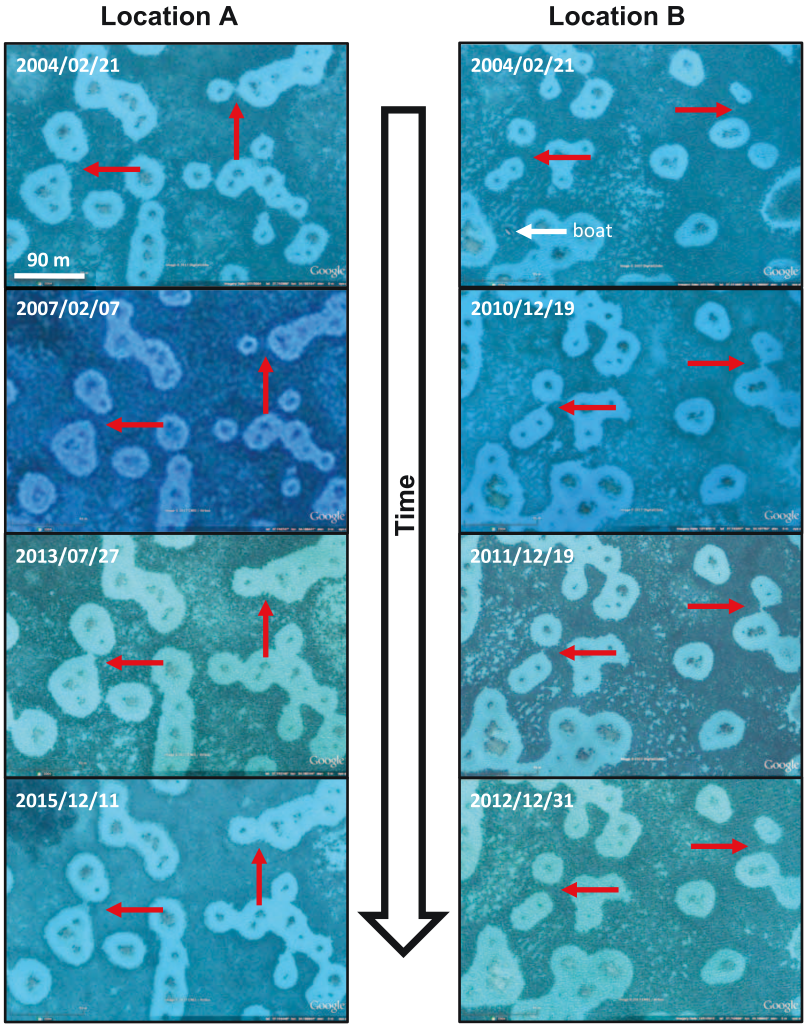

Figure 5: Visual depiction of the dynamic nature of halo widths and shapes over timescales of years. Two sequential images of halos (one sequence per column) within Ras Muhammad National Park, Egypt, show how halos are persistent over many years but can widen or narrow, leading to merging and separating of halos around neighboring patch reefs. Red arrows compared between images indicate formation and disappearance of corridors apparently devoid of primary producers between adjacent halos. These corridors may be newly formed corridors, remnants of corridors, or remnants of previously merged halos. These corridors indicate that some process is leading to bare substrate that is not radially symmetrical and therefore not simply a geometric consequence of merging/separating halos. Slight within-column variations in reef locations are due to image processing rather than movement of reefs. Image dates in white text are in the format YYYY/MM/DD. Locations A and B refer to areas within the same reef tract separated by <3 km. Images copyright 2017 CNES (Centre National d'Etudes Spatiales)/Astrium, DigitalGlobe, and Google.

population size or behavior, previously unknown biophysical factors may shape halos. This result further suggests that these factors are likely operating similarly over long timescales in biogeographically disparate coral reef systems. It remains unknown what these novel mechanisms (or extensions of known mechanisms) may be, but the spatial and temporal scales over which they appear to operate suggest that they may be environmental correlates (such as temperature, nutrient availability, or other factors) that can affect primary producer or consumer growth and/or physiology. We show that 60 years is the lower bound of potential halo persistence, yet the upper bound remains unknown because of the lack of accessible, pre-1960s aerial imagery. The known mechanisms behind halo formation and maintenance include spatially constrained herbivory and bioturbation as direct mechanisms, with the indirect mechanism of predation risk as the constraining factor supported by available empirical and theoretical evidence (Atwood et al. 2018; DiFiore et al. 2019; Madin et al. 2019*a*, 2019*b*). Other mechanisms of halo formation have also been hypothesized. However, there is no a priori expectation that any of the known or hypothesized mechanisms acting independently or in concert would lead to the spatially synchronous bidirectional changes in halo size over relatively short timescales (months to years) that we describe (fig. 4*B*). By demonstrating these previously unknown fluctuations in halo size over time, our results provide circumstantial evidence that mechanisms other than those previously identified or hypothesized may be at work. Therefore, although this study does not provide evidence as to what these other mechanisms may be, knowing that other mechanisms may be driving halo formation is important when trying to interpret the clues that halos provide about reef ecosystem health. Specifically, these spatial and temporal dynamics suggest that comparisons over time to yield insight into reef health will require additional knowledge of other, as-yet unidentified biophysical factors in order to enable accurate interpretation.

In addition to the dynamics described above, our results show that periods of halo expansion and contraction can co-occur with the appearance and disappearance of previously undescribed corridors between adjacent halos (fig. 5). These corridors consist of apparently bare substrate extending from halos that is not radially symmetrical, as halos generally are, and therefore the corridors are not simply a geometric consequence of merging/separating halos. These corridors lead us to infer that yet another mechanism is contributing to the creation of these patterns. One possible explanation for this pattern is that the spatial constraint (i.e., the "inhibitor" in Turing's [1952] model) on herbivory and/or bioturbation (i.e., Turing's "activator") that creates the bare substrate within halos is violated via a behavioral response due to a perceived difference in the risk-reward trade-off (Lima and Dill 1990; Brown and Kotler 2004). We are not aware of other spatially isolated regular landscape patterns (e.g., fairy circles; Tarnita et al. 2017; Meyer et al. 2021) in which adjacent patterns merge in this way, limiting mechanistic comparisons. However, exploration of whether corridors occur in terrestrial or other marine systems should lend insight into the mechanisms behind these respective patterns.

Conclusions

Coral reef halos are a long-recognized phenomenon from a handful of locations (table S1), and recent advances in remote imaging technologies now allow ecologists to use a collective "macroscope" (Dornelas et al. 2019) to quantify their global scale. Reef halos have garnered significant interest in recent years because halos, as a highly visible "footprint" of small-scale interactions among multiple trophic groups, hold promise as an inexpensive diagnostic tool for an ecosystem facing a global crisis: coral reefs (Hughes et al. 2017). As Rietkirk and van de Koppel (2008) point out, what we can discern, in terms of loss or gain of resilience or resistance, from a change in regular patterns in nature remains unknown—and is deserving of exploration. Reef halos show promise as such a tool, given the correlation between their prevalence and coral reefs' protection from fishing (Madin et al. 2019*a*). However, key to harnessing halos as a reef assessment tool is unravelling the mystery of exactly what they can tell us. The first step in this process is recognizing the full suite of mechanisms that dictate their prevalence and size. Our results reveal that additional mechanisms than previously recognized are likely at play, suggesting that further inquiry into these mechanisms will bring us one step closer to using these striking features to help diagnose the health status of coral reef ecosystems worldwide.

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Statement of Authorship

E.M.P.M. was responsible for conceptualization, funding acquisition, methods development/experimental design, data collection, data analysis, data validation, data visualization, supervision, and writing—original draft. A.S. was responsible for methods development/experimental design, data collection, data validation, and writing—original draft. K.P. was responsible for data collection, data analysis, data validation, data visualization, and writing—review and editing. C.M.R. was responsible for data collection, data validation, data visualization, and writing—review and editing.

Data and Code Availability

All data and code used in this study are available for download on Zenodo (https://doi.org/10.5281/zenodo.6426257; Madin 2022).

APPENDIX

Global Spatial Comparison

Survey Structure. To assess the prevalence of grazing halos globally, we performed a virtual belt transect survey using Google Earth Pro. We subsampled the globe using latitudinal transects, which serve as proxy line intercept transects, defined as every 1° of latitude from 29°N to 29°S.

Measuring Reef Characteristics. We first set an arbitrary starting point of the equator and the prime meridian. The starting point served as a reference to know when the observer completed a full revolution around the globe before moving on to the next latitudinal transect line. Moving from west to east, we scanned the entire latitudinal line and recorded any reef that intercepts the given latitudinal transect. Once a reef was intercepted, a yellow "pin" was dropped on the current latitude transect line at approximately the horizontal midpoint along the reef/transect intercept. We then created a rectangular polygon extending for the length of the intercept and 0.5 km above and below the latitude line overlaying the reef. This polygon served as our "belt transect," or survey area, within which we created a second polygon to delineate the extent of the reef area within the rectangular polygon belt transect.

If grazing halos were found on the reef and were within the rectangular belt transect, we created a third polygon to measure the area of reef that contained halos. Some belt transects contained multiple noncontiguous reef and/or halo areas. In these cases, we created separate polygons for each and summed the individual reef and/or halo areas, respectively. Some locations had multiple imagery dates available, and halo visibility can vary over time within a single location. To ensure consistency in our data set, for locations with more than one imagery date, we first reviewed each reef image date that was available. We then selected the date that had the largest total halo field area and outlined that image date's halo fields.

Classifying Halo Visibility. After visually scanning the entirety each of entire focal (i.e., intercepted) reef for grazing halos, we assigned it one of the following codes to describe the imagery and location's suitability for halo detection: HP = halos are present (and visible enough to outline); TF = too faint (i.e., there are patch reefs and possibly halos, but halos are too faint to reliably outline); NH = no halos (but image is clear and the required patch reef habitat exists); NP = no patch reefs (and therefore no halos, since patch reefs are a prerequisite for halo formation under this study's definition); BR = bad resolution (of satellite imagery; i.e., imagery is too pixelated or otherwise not clear enough to detect halo presence and/or patch reefs); CC = cloud cover (i.e., reef is not visible because of cloud cover in satellite image); DR = deep reef (i.e., reef is known to exist in this location but is not visible; it appears as dark blue because of imagery "masking"); SR = surface reflectance (i.e., reef is not visible because of sun glint in satellite image).

Focal reefs were coded as CC (cloud cover) or SR (surface reflectance) if more than a small portion (e.g., 15%) of the focal reef within our belt transect was fit within these categories. This ensured that only reefs where most or all of the patch reefs (and halos) occurring within the reef would be visible and accounted for, if present. In the vast majority of cases, transects were either fully covered by these characteristics or were completely free of them (i.e., rarely were our transects partially covered by either). Because most locations had multiple time points from which to choose the clearest image, these categories were rarely used (once each).

Identifying Reef Attributes. For every reef location intercepted in this survey, we recorded key corresponding attributes. Each surveyed reef was categorized by the country and ocean basin in which it occurred. For each reef intercept, we recorded its respective country of origin. For ocean basins, we split the Pacific and Atlantic Oceans into the Northern and Southern Hemispheres. Each reef intercept was classified into one of the following ocean basins: North Pacific, South Pacific, North Atlantic, South Atlantic, and Indian. To minimize the number of ocean basin categories, we classified reefs found on the equator as falling within the Southern Hemisphere portion of their respective ocean basin. For the equatorial transect, six reefs were classified as South Pacific and one was classified as South Atlantic. All other equatorial reef intercepts were found in the Indian Ocean, which is not subdivided by hemisphere.

Time Series Comparison: Quantitative Comparisons of Satellite Imagery

Data Extraction. Images from Heron Island, Australia, were obtained from DigitalGlobe through an exclusive academic data-sharing agreement. The hypothesis that halos vary synchronously across a given area was formed after viewing images from Heron Island, Biscayne Bay, and other locations not studied further. Additional sites were therefore needed to serve as an independent data set. Additional locations were selected that had halos in the default image displayed by Google Earth for which at least six good-quality images over time were available in Google Earth and which were geographically dispersed. The locations chosen were Biscayne Bay, United States; near Momi Bay, Fiji; and Merizo, Guam. Image dates are given in table S3. The Fiji location was selected because satellite images of it were available at eight times spread over 11 years. The Guam location was selected because of the large number of images closely spaced in time.

To sample the patch reefs, we first enumerated 100 and 67 isolated patch reefs, respectively, at Biscayne Bay and near Momi Bay that were visible in a single image with good quality. Patch reefs within the regions bounded by the longitudes and latitudes given in table S3 were chosen on the basis of the criteria of being far enough from others that adjacent halos were not merged, not touching the edge of the image, and being approximately circular in shape. We then randomly selected patch reefs and examined each in all images until a minimum of 70 halos were outlined at Biscayne Bay and 110 halos were outlined near Momi Bay. A single annotator manually outlined 81 halos from 17 reefs at six time points (Biscayne Bay) and 118 halos from 25 reefs at eight time points (Fiji). As we were interested in halo size rather than halo presence, if the reef or halo was not clearly visible, if the reef was surrounded by no or a partial halo, or if the outer edge of the halo was too difficult to identify and outline, the halo was marked as missing data for that reef in that image. Some reefs and their halos at Fiji were outlined twice to estimate reliability.

The images at Guam were of primary interest because of their close spacing in time. Because relatively few reefs had halos in these images and our interest was in halo size rather than presence, only four reefs at Guam were selected and outlined, for a total of 52 halos at 15 time points. The small sample size at this location was thus the result of having relatively few halos and even fewer that could be reliably observed/outlined among time points. Because of this small sample size, we needed to minimize the signal-to-noise ratio in our measurements. These reefs and their halos were therefore outlined by the same annotator twice on different days to reduce annotation noise; the repeated measurements of the radii of the reefs and halos were averaged.

Preliminary review of the Heron lagoon satellite images indicated that some areas of the lagoon appeared to have visible benthic algae more often than others. As algae is a prerequisite for halo visibility, we focused our sampling on these areas. To sample the patch reefs, reefs were enumerated in an image with good resolution and many halos (December 15, 2009). Reefs were chosen within the algae-prone areas according to the same criteria as at the other locations. The list of reefs was randomized and halos were outlined with the constraint that no more than 12 reefs were selected in each subarea of the lagoon; this led to a total of 172 halos outlined around 51 reefs at 11 time points.

Measurement variation due to differences in image quality was examined by plotting the patch reef radii and the halo radii at Guam, where the images were taken so frequently that little real change in patch reef size is expected. There was no appreciable difference in the quality of imagery available at Guam versus other locations. The reef radii were considerably more consistent than the halo radii, leading us to conclude that noise deriving from image quality variation is smaller than the true variation in halo widths.

Halo widths at each reef were compared nonparametrically for visual data exploration by plotting their widths at each patch reef in all pairs of images.

Data Analyses. To test for temporal dependency among halo widths over time, we first used a semivariogram. The data consisted of one-dimensional coordinates, reflecting the number of days since the earliest image, and the estimated random effect for image from a linear model predicting halo width using only an intercept and random effects for image and for reef. The default parameters for the function variogram in the R package gstat were used, and the sample variogram estimate for each bin was calculated on the basis of between one and seven pairs of images. The median number of days between pairs of images was 21 (minimum, 1; maximum, 234). The resulting semivariogram showed no pattern, neither an increase in variance as the shortest intervals increased nor any indication of a sill at longer intervals, and is therefore not presented. This may be a result of the small number of pairs of images in each semivariogram bin or may indicate that the period over which there is dependency is shorter than can be seen well with these data.

The second approach we used to search for evidence of temporal dependency among halo widths was to examine the residuals of a model predicting halo width using an intercept and random effects for image ID (which includes image date) and patch reef. With only 15 points in time, it is difficult to be sure whether there is time dependency among the residuals, but it cannot be ruled out at very short time intervals of approximately a week or less.

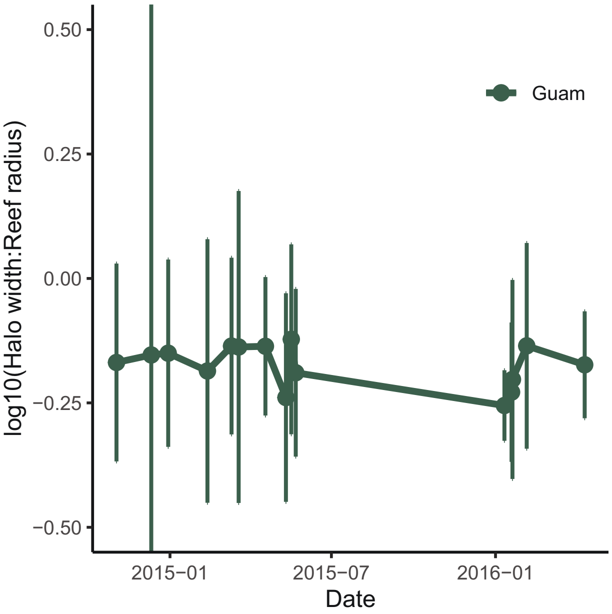

Figure A1: Expanded view of halo persistence and average size over time at the Guam study location. Data are time series of transformed ratios of mean halo width to mean reef radius (with 95% confidence intervals) for reefs near Merizo, Guam. Data points represent dates where freely available, cloud-free, high-resolution satellite imagery was available and are therefore not necessarily reflective of temporal end points of halo existence or minimum temporal scales of changes in width.

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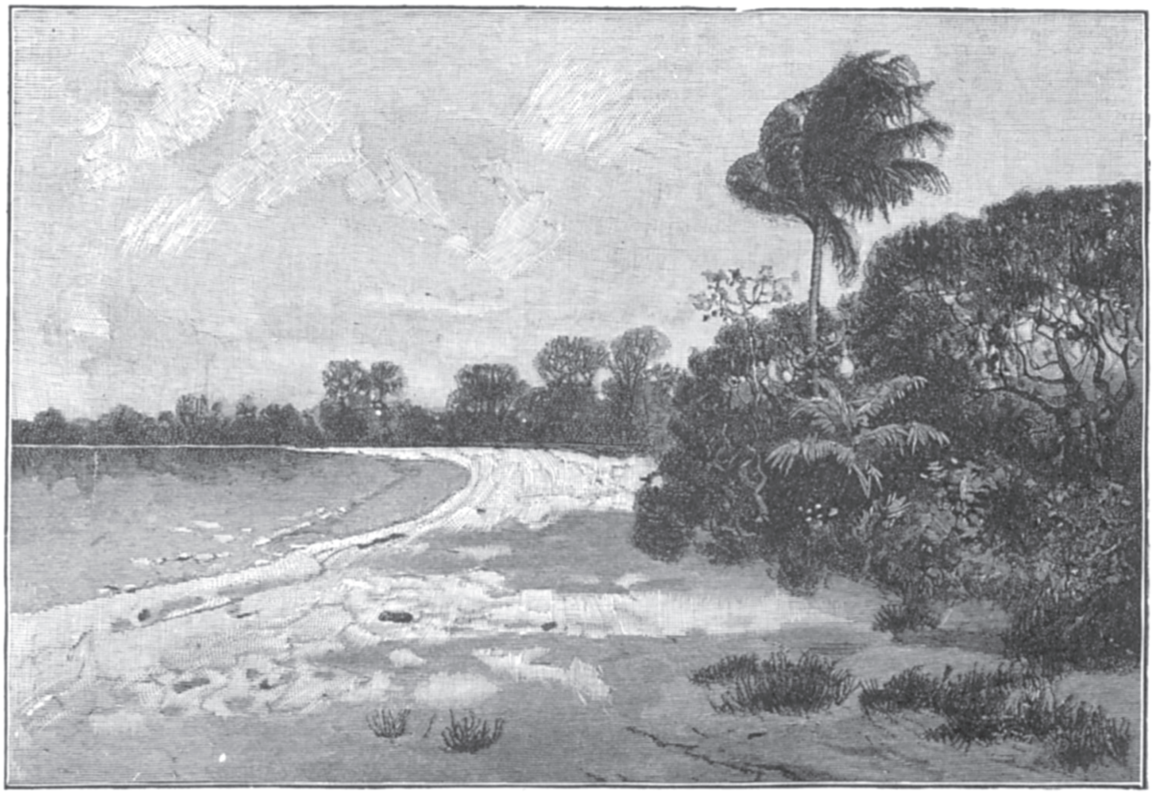

"Caroline island is a genuine atoll, of the type described by Darwin and Dana; [the figure] will convey an idea of the scenery of a Pacific atoll." From the review of *Memoirs of the National Academy of Sciences* (*The American Naturalist*, 1885, 19:780–781).