REVIEW ARTICLE

Benthic pattern formation in shallow tropical reefscapes: does grazing explain grazing halos?

Stephanie M. Bilodeau · Craig A. Layman · Miles R. Silman

Abstract

Context Species interactions generating consistent landscape or seascape patterns are important to ecosystem health and function. One widely-documented pattern in shallow, tropical reefscapes is sand "halos" that separate coral patches from surrounding vegetation. Multiple hypotheses for this pattern have been proposed, but individual explanations are rarely integrated to reflect the complexity of systems where halos occur.

Objectives To evaluate and synthesize multiple hypotheses of halo formation and maintenance into a single model, connect the halo pattern with similar terrestrial phenomena, and identify targets to guide future research and conservation.

Methods We reviewed halo accounts from over fifty years in the scientific literature and combined them with related research on marine nutrients, bioturbation, analogous terrestrial processes, and new field measurements to create a conceptual model of halo formation and maintenance.

Results Though halos are widely attributed to herbivory, grazing alone cannot explain patterns at all locations. Nutrients have large effects on tropical reefscapes but remain understudied for halos. Coupling nutrients and grazing explains a variety of observed halo patterns. Fish and invertebrate bioturbators also appear important. We combine these factors to explain pattern variability and present a framework for more comprehensive halo research.

Conclusions Explanations for halos to date have been overly simplistic. Halos are common patterns with complex underlying causes, including foraging behavior and nutrient cycling. Not all halo-like patterns may be created or maintained by the same mechanism(s). Our integrated model provides a more complete understanding of factors contributing to these patterns, a framework for ecological interpretations, and a guide for conservation.

Keywords Bioturbation · Grazing · Halos · Nutrients · Seascape · Food webs

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Ecological patterns and processes

In ecosystems, simple patterns can often be the result of complex underlying mechanisms, including species interactions and the intersection of biotic and abiotic processes (e.g., Cramer and Barger 2013; Juergens 2013). Regular pattern formation occurs in a variety of different ecosystems and can be driven by scale-dependent feedbacks (Rietkerk and van de Koppel 2008). An important feature of pattern formation in natural communities is that multiple species are typically involved in different ways, often acting in concert with abiotic features of the environment. A number of these naturally-occurring patterns in different systems resemble symmetrical circles, rings, or "halos" (Randall 1965; Bartholomew 1970; Tschinkel 2012) while others may be perceived as ribbons, splotches, or labyrinthine maze-like patterns (Lejeune and Tlidi 1999; Rietkerk and van de Koppel 2008; Liu et al. 2014).

It can be tempting, when a new spatial pattern is first identified, to oversimplify and attribute its occurrence to a single factor, such as a dominant local species or limiting abiotic resource. This tendency can be seen in multiple conflicting explanations for the spatial pattern of rings in the Namib Desert, termed "fairy circles," which have variously been attributed to ants (Picker et al. 2012), termites (Juergens 2013), plant competition (Cramer and Barger 2013), and geological seepage (Naudé et al. 2011). Another such example is the bare zone of minimal vegetation found between shrub and grassland communities in California, which was initially assumed to result from plant allelopathy (Muller et al. 1964). Bartholomew (1970) showed that these bare zones can instead be maintained by the grazing and seed foraging activities of a community of herbivores, including mice, rabbits, and birds, which feed on the edges of the grasslands and rely on the shrubs for protection. In a follow-up experiment, Halligan (1973) found that both herbivores and allelopathy play a role in this pattern, as do differences in soil moisture, which may result from changes in the plant communities driven by allelopathy and herbivory. Patch reef halos, which we focus on here, are a shallow marine reefscape pattern reminiscent of the bare zones described by Muller et al. (1964) and also have been attributed to single explanations, such as local hydrodynamics (Mitchell-Tapping 1975; Steiner and Willette 2014) or herbivory (Randall 1965; Ogden et al. 1973; Hay 1984; Madin et al. 2011).

The ability of certain species to modify their surrounding environment through processes like selective seed predation, bioturbation, and redistribution of water or nutrients creates positive feedbacks that can lead to the formation and persistence of long-term, stable landscape patterns (Rietkerk and van de Koppel 2008). Peterson (1984) highlighted ecosystem-structuring feedbacks in an early exploration of alternative stable states theory, which featured multiple marine and terrestrial examples. These include marine sediment manipulation by active bioturbators like worms and burrowing shrimp, but also by seagrasses and other immobile organisms that alter flow and sediment deposition by their presence in the water column. Peterson (1984) also described multiple terrestrial tree species that can alter fire regimes with the buildup of needles they drop, reducing the ability of less fire-resistant competitors to grow. Such ecosystem feedbacks may create mosaics of different habitat types (e.g., forest and savanna; Staver et al. 2011) across a broad geographic area or maintain smaller features like nutrient hotspots (e.g., termite mounds; Davies et al. 2016) in certain regions.

With growing access to high-resolution satellite imagery, spatial patterns have garnered increased attention in terrestrial landscapes and shallow marine seascapes around the world (Fig. 1; see Rietkerk and van de Koppel 2008 for additional examples across various ecosystems). Such self-organizing patterns occur at a variety of scales, from individual patches of vegetation that form rings in water-stressed environments (Sheffer et al. 2011) to larger phenomena like the landscape patterns of African termite mounds (Pringle et al. 2010) and fairy circles (Tschinkel 2012). In these cases, the pattern has been linked explicitly to one or more underlying biological processes that involve limited resources in the environment. For example, the uniform spacing of termite mounds increases the abundance, biomass, and reproductive output of secondary and tertiary consumers in the local ecosystem, and the mounds are productivity hotspots, highlighting the importance of pattern-producing species and processes to overall ecosystem health and functioning (Pringle et al. 2010). Coral reefs likewise serve as centers of productivity, where marine animals congregate for food and shelter, producing nutrients that fertilize the reefs and
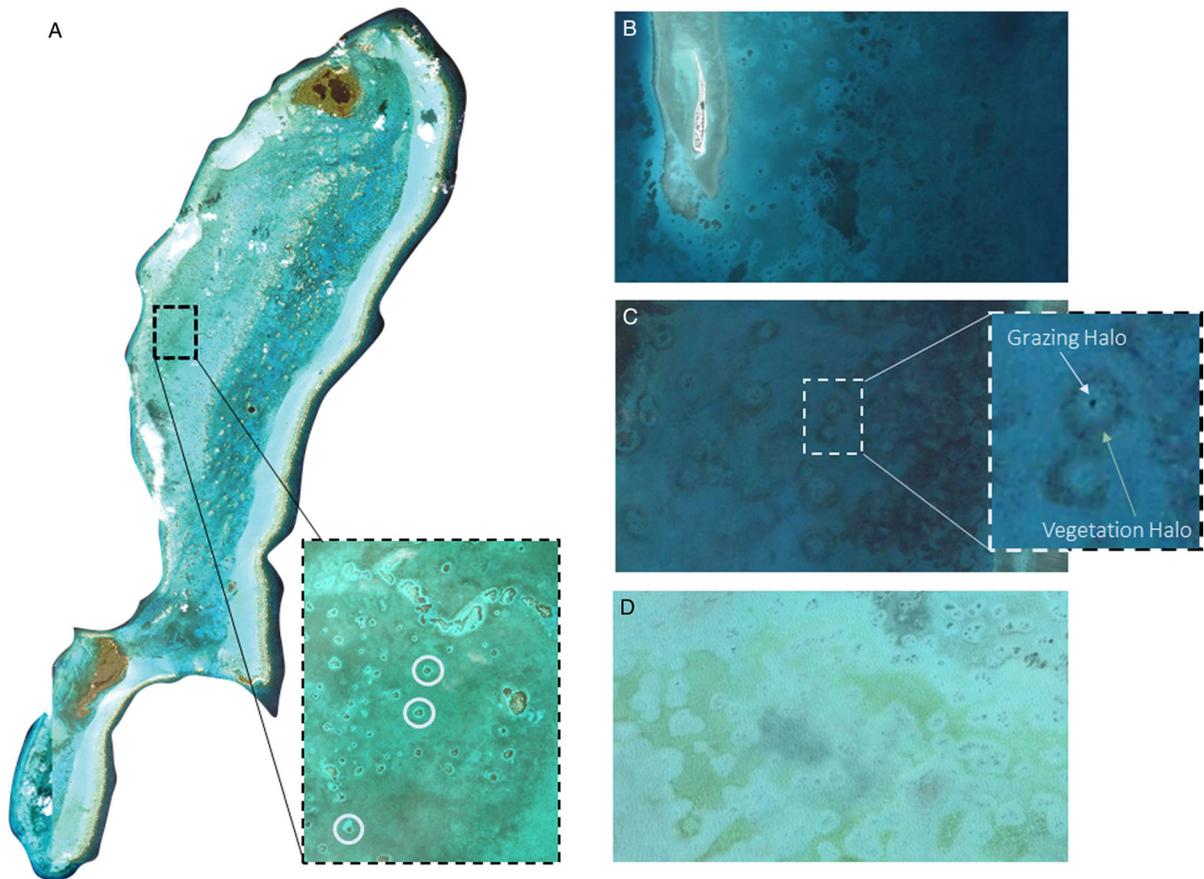
Fig. 1 Examples of "grazing halos," a common benthic pattern worldwide. **a** Lighthouse Reef Atoll, Belize (©DigitalGlobe), with an enlarged view of halos in the lagoon (circled in the inset). **b–d** Examples of halos in the Red Sea (**b**), Fiji (**c**), and Australia (**d**), all ©Google Earth. Patch reefs in Fiji (**c**) display both a traditional "grazing halo" of bare sand immediately adjacent to each patch and an outer vegetation halo or band between the grazing halo and surrounding benthic cover

surrounding benthos (Hatcher et al. 1990; Layman et al. 2013; Allgeier et al. 2017a, b). It seems likely that the barren halos which form around coral patches are the product of a complex system of interactions akin to those responsible for visually analogous terrestrial patterns.

Marine systems exhibit patterning driven by similar biotic and abiotic processes to terrestrial landscapes, including the interactions of grazing herbivores, primary producers, and nutrient flows across a heterogeneous seascape (e.g., Burkepile and Hay 2006; Allgeier et al. 2013; Adam et al. 2020; Oakley-Cogan et al. 2020), but our understanding of how these processes interact to create and maintain such patterns is still limited in coral reef and reef-adjacent ecosystems. As new technologies expand our ability to study seascapes at a variety of scales and

depths, there has been an increased appreciation in the field of landscape ecology for the analogous and interconnected patterns and processes in terrestrial and marine realms (Pittman et al. 2018). Shallow, near-shore seascapes, especially tropical reefscapes, feature many diverse and easily-observable patterns at the intersection of distinct benthic cover types. Some of these patterns, like the scattered patch reefs found in lagoon environments around the world, are reminis-cent of terrestrial phenomena like the evenly-spaced distribution of termite mounds (Pringle et al. 2010) or fairy circles (Tschinkel 2012). Using a well-docu-mented and widespread example from the marine ecology literature—patch reefs and the bare sand halos that surround them—we examine the existing hypotheses for pattern formation. When possible, we draw on analogous examples from well-studied

terrestrial ecosystems. We elucidate a complex interplay of factors behind this marine spatial pattern and suggest future avenues of research to disentangle them.

Halos as a benthic pattern

One of the best documented benthic patterns seen in coral reef and seagrass ecosystems is bare sand "halos" around individual coral patches that separate corals from seagrass or algal beds. Sometimes called "grazing halos," they are often described in marine ecology literature as heavily-grazed or otherwise bare sandy areas immediately surrounding small coral heads in a patch reef ecosystem (e.g., Ogden et al. 1973; Bilodeau 2019; DiFiore et al. 2019; Madin et al. 2019b). Halos circle potentially hundreds of thousands of coral patches in reefscapes all over the world. Casual inspection of coral reefscapes using high-resolution satellite imagery (e.g., Madin et al. 2011; DiFiore et al. 2019; see Fig. 1), also reveals halo-like buffers of sand along the edges of larger contiguous reef patches and on the lagoon-side of reef walls in multiple locations (e.g., Belize, the U.S. Virgin Islands). The halo provides an open area with little cover compared to the shelter provided by a reef and seagrass beds. Randall described these patterns in 1965, and the halo phenomenon has experienced a recent resurgence of interest in the past decade. Recently, aerial and satellite imagery has provided photos of similar patterns in the Red Sea (Madin et al. 2016), off the coast of Australia (Madin et al. 2011), and in patch reefs off the coast of Belize, including Lighthouse Reef Atoll (Bilodeau 2019).

These halos typically occur in shallow, tropical systems where coral patch reefs are interspersed with beds of seagrass and/or macroalgae. The functional value of the interplay between seagrass beds and reefs is widely recognized in tropical and temperate marine systems (Harborne et al. 2006; Swadling et al. 2019). Many species of fish and other animals move between seagrass and coral or rocky reef environments, occupying one or both habitats at different life stages (e.g., Harborne et al. 2006; Unsworth et al. 2008). The borders of adjacent seagrass, bare sand, and reef structures represent the intersection of distinct habitat types, home to a variety of organisms, and halos incorporate all of these. This benthic mosaic in which

halos occur can vary widely by location. For example, Lighthouse Reef Atoll, Belize (a case study relied on in this paper), is a representative Caribbean lagoon environment where patch reefs are largely surrounded by dense seagrass meadows, whereas patch reefs on the Bahama Banks sit on sand flats dominated by sparse macroalgae, with increased seagrass growth in the nutrient-rich areas adjacent to the reef (Alevizon 2002). Local variations in benthic cover can lead to different halo varieties and features in different locations, but all halos share the core feature of reduced vegetation growth surrounding an underwater structure.

Descriptions of halos in the literature are varied. Reefs at Heron Island, Australia, feature 6–14 m halos in an algae-dominated environment (Madin et al. 2011, 2019b), whereas halos in the U.S. Virgin Islands, apparently the result of grazing by *Diadema antillarum* urchins, range from 2 to 10 m in width (Ogden et al. 1973). Halos described by Alevizon (2002) in The Bahamas are only 1–2 m of bare sand, with an additional 4–5 m of algal-dominated growth before the vegetation transitions to seagrass. Halos at Ningaloo Reef in Australia were reported to extend > 90 m from the patch and were surrounded by large brown macroalgae that did not grow within the halo area (Downie et al. 2013). Even within a single geographic location, halos can show wide individual variation, appearing in a variety of bottom cover types and to varying extents. Halos measured at Lighthouse Reef in 2018 were found in both algae- and seagrass-dominated areas, some with vegetation inside the halo and some with nearly bare sand, and ranged from 5 to 15 m + in width (Bilodeau 2019). Most halos appear similar when viewed from the surface of the water or in high resolution aerial and satellite imagery, suggesting that they represent a general, recurring pattern.

Halos present an opportunity to examine interactions of reef-dwelling organisms at multiple spatial scales, from benthic primary producers to macrograzers and invertivores, to the predators that prey on them. Such patterns may serve as important diagnostic tools when monitoring and evaluating ecosystems for conservation and management. The potential of halos to indicate changes in carbon sequestration within seagrass and macroalgae beds (Atwood et al. 2018) and changes in fishing pressure (Madin et al. 2010a, b; DiFiore et al. 2019; Madin et al. 2019a, 2019b) makes them a particularly salient study target. Overfishing of

top predators, large herbivores, or bioturbators can alter mesopredator and herbivore communities. Reductions in herbivory allow for rapid colonization of macroalgae (Mumby et al. 2006) that, in turn, can cause difficult-to-reverse phase shifts in previously coral-dominated systems (Schmitt et al. 2019). Reduction of predation risk due to overfishing of top predators may also alter risk-driven foraging behaviors that structure the benthos (Valentine et al. 2007; Madin et al. 2010a, b). In this way, alterations to the halo pattern may be indicative of changes in community composition at different trophic levels that affect not only reefs themselves but also the surrounding mosaic of benthic vegetation.

Halos may originate and/or persist through a combination of abiotic and biotic interactions in the complex ecosystems where they occur (Fig. 2). However, the majority of halo studies to date focus on single explanations for halo formation or maintenance at different locations, even though multiple of these processes may reasonably occur together, with complementary effects. Potential explanations for the halo phenomenon include both physical and biological mechanisms and fall generally into four categories: (1) grazing by herbivorous fish or other animals, potentially controlled through predation risk; (2) increased nutrients adjacent to the reef; (3) abiotic effects, including wave action, shading, and sediment variation; and (4) bioturbation and sediment processing by sand-dwelling organisms.

Current explanations for halo formation

Herbivores

The most common recent explanation is that halos are produced and maintained by concentrated grazing
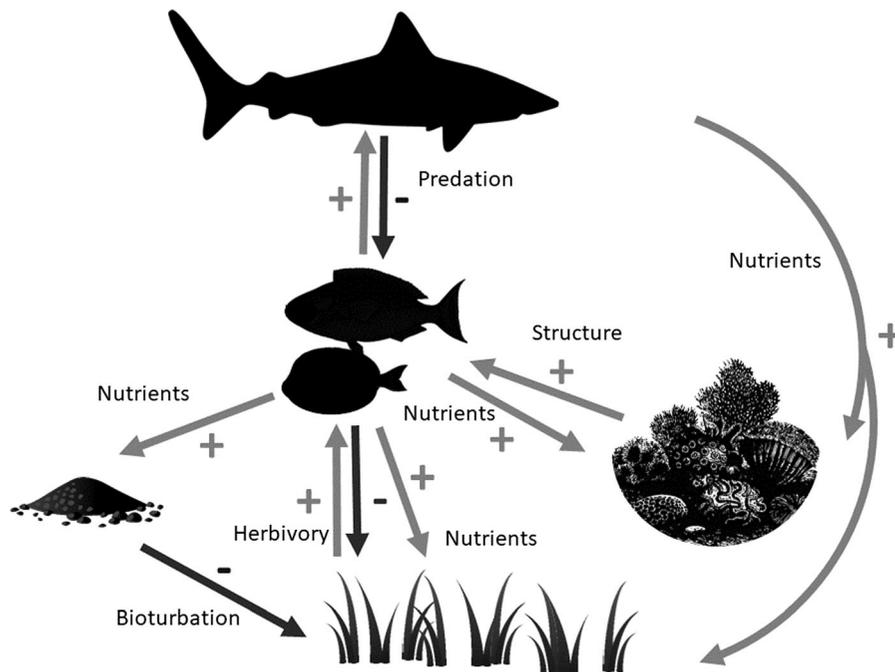

Fig. 2 A web of potential positive and negative interactions and effects of coral-seagrass community members. Dark arrows with plus (+) signs indicate positive interactions or effects in the direction of the arrow. Lighter arrows with minus (−) signs indicate negative interactions or effects. Predatory and herbivorous fish and invertebrates aggregate on reefs and similar structures and provide nutrients to the reef, which also positively affect reef-adjacent vegetation and sand-dwelling organisms (represented here by a mound of disturbed sediment). Predators

control not only the abundance of herbivores, but also their distribution and foraging behavior through indirect fear effects. The intensified activities of herbivores and bioturbators close to the reef reduce the growth of vegetation and decline with distance, as do the nutrients these animals produce. We acknowledge that this diagram simplifies interactions in complex food webs, but it provides a framework for hypothesis-testing regarding mechanisms generating halo patterns

close to a reef or similar underwater structure (e.g., Randall 1965; Ogden et al. 1973; Hay 1984; Madin et al. 2011; Atwood et al. 2018). This creates a halo-like pattern of heavily-grazed vegetation immediately surrounding the reef, with a clear demarcation past which reduced herbivory permits denser algae or seagrass to persist. Einbinder et al. (2006) observed a similar pattern of more intense grazing immediately adjacent to artificial reefs, with a halo of 10–20 m, indicating that the presence of coral itself is not necessary to create a halo. Multiple grazing assays at different locations have indicated that herbivory is strongest immediately adjacent to reefs and decreases with distance (Randall 1965; Ogden et al. 1973; Hay 1984; Madin et al. 2011; Bilodeau 2019; DiFiore et al. 2019). The presence of reef-based herbivores on and around a patch could create this halo pattern of grazing through simple geometry if the majority of herbivores are central-place foragers. If herbivores congregate on reefs, whether for shelter or other purposes, there will always be more grazers in the small radius next to the reef than at any given point farther from it. This pattern is supported by published observations of fish distributions around artificial reefs in The Bahamas (Layman et al. 2013).

Predation risk is a commonly-cited explanation for the reef-centered foraging of herbivores that could create or maintain halo patterns (e.g., Randall 1965; Hay 1984; Madin et al. 2011; Atwood et al. 2018; DiFiore et al. 2019). In this landscape of fear (also referred to as a "seascape of fear," see Atwood et al. 2018), reef-dwelling herbivores use the patch reefs for protection and are unwilling to graze past a threshold distance from the reef for fear of predators. Randall (1965) ascribed the formation of the halos he first observed to herbivorous fish, which he described as "tied to the reefs for shelter." Armitage and Fourqurean (2006) offer evidence that fish are incentivized to venture beyond the halo area when more appealing food options make such a trade-off advantageous (e.g., Brown and Kotler 2004), suggesting that foraging farther from the structure of the reef is normally too costly. While few early studies explicitly tested the role of predation in the halo pattern (Madin et al. 2010a, b), DiFiore et al. (2019) showed that higher predator density was correlated with lower grazing intensity at sites in Belize and Florida, although predator density did not affect how far herbivores

grazed from the reef edge, which is a key prediction of the landscape of fear hypothesis.

Three recent studies (DiFiore et al. 2019; Madin et al. 2019a, b) found that herbivore density and patch size, not predator density or protected reef status, predict the foraging distance of herbivores from the reef and the width of the halo, which suggests that competition for resources may be stronger in larger patch communities that support more herbivores but have comparatively smaller area-to-perimeter ratios, and this increased competition may push herbivores to make riskier foraging decisions that alter the vegetative cover. However, the relationship between patch size and halo width described by Madin et al. (2019a, b) on the Great Barrier Reef and by DiFiore et al. (2019) in the Caribbean does not appear consistent at other locations throughout the worldwide tropics (K. Precoda, cited in Madin et al. 2019b), so the ubiquity of this pattern remains unclear. There are likely many, yet unquantified relationships between patch size, shape, perimeter, and herbivore community structure that influence halo characteristics.

Halos appear in different regions with different primary producers, grazers, and predators, demonstrating that this pattern is not tied to a specific organism or a common suite of species (e.g., Randall 1965; Ogden et al. 1973; Madin et al. 2011). In marine grazing systems with diverse herbivore communities, species with different escape speeds subject to predation risk would be expected to graze at different maximum distances from the reef (termed flight initiation distance, or FID; Cooper and Blumstein 2015) owing to their varying capacities to retreat quickly in the case of a predator (Atwood et al. 2018). Slow central place foragers like sea urchins might also be limited in the total distance they can travel. Variation in mobility and/or FID between species could create a gradient edge to the halo where the surrounding vegetation gradually increases in density with distance from the reef in response to decreased grazing pressure, rather than transitioning suddenly from bare halo to dense seagrass or macroalgae at a set distance. Bartholomew (1970) posited that a similar gradient seen in his terrestrial "halos" could also be caused by decreasing grazing activity near the edge of the bare region. This gradient edge effect is a feature found at some patch reefs (Alevizon 2002; Bilodeau 2019). In locations where the gradient is visible underwater, it may not be obvious in satellite imagery,

making the edge of the halo appear more abrupt at larger scales (e.g., Bilodeau 2019). In heavily-fished ecosystems with reduced herbivore diversity, the gradient halo edge might not occur. Ogden et al. (1973) observed a transition zone of cropped plants near the outer edge of urchin-grazed halos that could result from observed variation in the foraging distances of individual urchins (i.e., diversity within a single population), but schooling fish that forage together might show less individual variation than urchins. Herbivore site fidelity likely plays an important role in the way that diverse marine grazer communities partition resources spatially or temporally, but little detail is known about the ranges and movements of herbivorous fish (Welsh and Bellwood 2014). This highlights the need for more long-term underwater observations of herbivore behaviors and movement patterns (e.g., Bilodeau et al. 2021).

The complexity of herbivore movement and behavioral interactions in multi-species grazing systems suggests that predation risk is just one of several contributing factors in the formation of halos. Certain halos in The Bahamas are found around patch reefs with few or no herbivores (Alevizon 2002), indicating that whatever role herbivory may play for halos, it is not their only cause. Though grazing has been the most studied, below we highlight three additional factors that may also contribute, in varying degrees, to the formation or maintenance of the halo pattern.

Nutrients

One dramatic effect of fish aggregation on reefs is nutrient hotspots that form as the result of fish excretion and egestion (Allgeier et al. 2017b). Fish-derived nutrients play an important role in structuring marine vegetation through their effects on productivity and community composition, and gradients formed due to fish aggregations could be expected to produce symmetrical patterns. Fish have been shown to increase nutrient availability adjacent to the structures around which they aggregate, which may increase primary productivity and growth of adjacent seagrass and benthic microalgae (Allgeier et al. 2013; Layman et al. 2013). Fish-derived nutrients may, therefore, be strongly tied to the movement and other behaviors of reef herbivores, including the grazing hypotheses outlined above.

Cromsigt and Olff (2008) describe how terrestrial grazing lawns in southern Africa form because of local disturbances like megaherbivore wallows or middens, which attract the grazing pressure necessary to form patches of intensely-grazed, highly productive, and nutritious plant growth. The process is aided by the increased nutrients from megaherbivore waste, and a similar herbivore-aggregating effect is seen with the nutrient hotspots formed by termite mounds (Davies et al. 2016). It is easy to imagine an equivalent marine scenario with the seascape "disturbances" represented by coral patches, where the presence of a patch reef (or similar large underwater object) attracts fish and other grazers, which aggregate for foraging, shelter, and social reasons, leading to an increase in grazing pressure on seagrass immediately adjacent to the reef, as well as an increase in nutrients due to the increased fish biomass (Allgeier et al. 2017b).

The role of nutrients in structuring reef-adjacent vegetation must be considered in the context of not only nutrients' effect on productivity, but also modified competitive interactions among producers and producer–consumer interactions. In the absence of other factors, increased nutrients should increase seagrass density and productivity near reefs, the inverse of the pattern observed with halos (Madin et al. 2011). Indeed, Alevizon (2002) documented the increased growth of macroalgae and seagrass in a large band surrounding one artificial reef structure and several natural patch reefs in The Bahamas, although the center of each ring was still dominated by a bare sand halo immediately adjacent to the reef. This suggests that heightened nutrients around reef patches promote greater vegetative growth in the general vicinity of the reef but somehow have the opposite effect immediately adjacent to the structure or are counterbalanced by some other halo-forming process. One potential explanation is that the highest levels of nutrient availability might increase epibiont growth, alter competitive hierarchies among producers, and counterintuitively decrease seagrass productivity (Alevizon 2002). A nutrient-driven increase in epibionts could both decrease the growth of reef-adjacent vegetation and increase herbivore consumption of those same marine plants. Epibionts are the preferred food of many grazers (Campbell et al. 2017), and heavier epibiont loads have been linked to increased seagrass consumption in Belize (Goss et al. 2018). Thus, increased nutrient loads could increase seagrass

or algal cover or decrease it, depending on the local herbivores' response to vegetation abundance and quality and the relative rates of productivity changes and herbivore offtake.

Nutrients may also play a role in structuring halos by increasing the nutrient content of reef-adjacent seagrass, thereby increasing its consumption by grazers (Campbell et al. 2017), especially those species for which seagrass is not a normally a significant portion of their diet. Many primarily algae-grazing herbivorous fish consume varied percentages of seagrass in the Caribbean (as based on Randall's stomach content analysis; 1967), but few common Caribbean fish species sampled by Randall showed substantial seagrass consumption. Some of the seagrass removed from halos in seagrass-dominated environments may be ingested incidentally by fish grazing on associated algae or epibionts or displaced by sand-foraging invertivores. However, herbivorous fish in the Caribbean did consume turtle grass (*Thalassia testudinum*) when presented with it in a food preference test (Ogden 1976), even when the grass was cleaned of epibionts (Hay et al. 1983). Furthermore, reef fish observed by Randall (1967) to have relatively little seagrass in their stomachs were found to consume *T. testudinum* quite rapidly when presented with it inside of halos in Belize, with remnant vegetation showing heavy browsing, as evidenced by bite marks (Bilodeau, 2019). Reef-adjacent seagrass may, therefore, be more appealing as a food source than seagrass in general, even for primarily algae-consuming fish, due to both its increased nutrient content and its proximity to the predator-safe shelter of the reef. High nitrogen and phosphorus (N and P) output from fish assemblages has been linked to increased N and P content in seagrass (Allgeier et al. 2013), and in tropical seagrass ecosystems, high seagrass nutrient levels can increase herbivory (Campbell et al. 2017). Terrestrial termite mounds in African savanna systems play an analogous role by serving as nutrient hotspots that are preferentially grazed by herbivores (Davies et al. 2016), which in turn alter the vegetative composition of the mounds relative to the surrounding savanna (Okullo and Moe 2012). Like the plants on termite mounds, reef-adjacent seagrass or algae might be preferentially grazed relative to the surrounding vegetation because of high nutrient content, making nutrients an important missing piece of traditional grazing hypotheses.

Reef-based nutrients may spread across the halo area to adjacent seagrass or macroalgal beds through the water column or via the activities of sediment-dwelling animals (e.g., Uthicke 2001), as well as sediment bacteria and microalgae that grow even in "bare" halo areas. Rhizophytic algae and marine diazotrophs can be important facilitators of seagrass and macroalgae growth by concentrating nutrients in the sediment (Williams 1990; Hamisi et al. 2009) and might help to make reef-based nutrients available to seagrass or macroalgae beyond the halo by forming a biotic "bridge," even in high-flow systems where water-borne nutrients are quickly dispersed (Larned 1998) or oligotrophic systems where water column uptake is rapid. Atwood et al. (2018) did not find a significant relationship between N content in sediments and algal canopy height, but N and P content of seagrasses has been shown to decline with distance from reefs in The Bahamas, even beyond the width of halos reported for that area (Alevizon 2002; Layman et al. 2013). Roaming predators and forays into the surrounding seagrass by reef-based animals, like nocturnal invertivores, could also contribute to nutrient deposition in the surrounding seagrass, even though the majority of halo foragers do not venture that far.

Abiotic factors

Many large-scale patterns across reefscapes are created in full or in part by physical processes, including spur-and-groove formations (wave action; Stoddart 1962; Shinn 1963), sand lobes (sedimentation; Field and Roy 1984), and depth limits of vegetation and corals (light attenuation; Kahng et al. 2019). Although Randall (1965) initially considered halos a likely result of local currents or small-scale hydrodynamics, he abandoned this explanation after observing that the halo pattern occurs at sites with a variety of depths and differing amounts of wave action. Mitchell-Tapping (1975) conducted a series of experiments in the U.S. Virgin Islands, concluding that halos there were primarily the result of wave action. More recently, Steiner and Willette (2014) have attributed shallow water halos in nearby Dominica to erosion by local eddies, in combination with various biotic effects. Most halo studies have largely discounted abiotic effects, such as water movement, shading, and variation in sediment size, in favor of species interaction-

based explanations (e.g., Randall 1965; Madin et al. 2011, 2019b), although not all such studies test abiotic hypotheses. Both shading and variation in hydrodynamics would be expected to produce oblong or asymmetrical halos, consistently following the pattern of the sun or flow of the water, which has not been observed in past studies (Randall 1965; Madin et al. 2011). The latter is especially unlikely in shallow lagoon environments with minimal current and reduced waves.

Randall (1965) and Madin et al. (2011) address the hypothesis that variations in sand grain size or coarseness might affect the formation of these halos by noting that there is no observable difference between sand grains close to the reef and at the edge of the halo. Garrett et al. (1971) did observe differences in sediment composition forming a halo pattern around patch reefs in Bermuda, but acknowledge that a similar study (Hoskin 1963) found variations in sediment size to be more correlated with depth. Ollivier et al. (2018) also found differences in sediment particle size with distance from the reef. Although observations at Lighthouse Reef, Belize (Bilodeau 2019) have revealed some variation in texture between halo sediment and surrounding seagrass sediment, this is highly variable among locations and not statistically significant (Bilodeau 2019). This variability likely has more to do with the presence of seagrass inducing the accumulation of finer sediments and organic matter than the inverse. This conclusion is also supported by Atwood et al. (2018) and could explain the pattern seen by Ollivier et al. (2018) and others. Marine vegetation and/or benthic invertebrate distributions might alter seafloor sediments as easily as being controlled by them.

Bioturbation and sediment processing

Bioturbation is ubiquitous in seagrass and sand reefscapes (Scoffin 1992; Cabaço et al. 2008) and is caused by a variety of mobile and sedentary organisms. Sand-processors (e.g., lugworm *Arenicola* spp., thalassinidean shrimp, holothurians) can have large effects on primary productivity, sediment turnover, and potentially seawater chemistry (Suchanek 1983; Uthicke 1999; Schneider et al. 2013; Wolfe and Byrne 2017). Glynn (1985; Panama), Alevizon (2002; The Bahamas), and Allgeier and Layman (unpublished data; West Andros, The Bahamas) suggest that halos

in Panama and The Bahamas may be generated by the physical movement of reef animals (e.g., schooling fish, spiny lobster, burrowing organisms) repeatedly disturbing the sediment by a reef. Madin et al. (2019b) also highlight the potential role of bioturbation by sand-foraging fish (e.g., Haemulidae, Lethrinidae) in extending or maintaining the halo edge beyond the zone of heightened reef-adjacent herbivory observed in halos near Heron Island, Australia. The same predation risk driving a landscape of fear for herbivores could affect the foraging behavior of mobile bioturbators (Madin et al. 2019b) and other functional groups of reef-based organisms, although radiating, reef-centered foraging behavior is not the only movement pattern that might generate halos.

The consistent movement of large numbers of fish around an isolated structural unit could create biologically-driven hydrodynamics (or direct physical sediment disturbance) that would have more symmetrical results than abiotic currents or waves. Huge fish aggregations occur around artificial reefs on West Andros, The Bahamas (Layman, *personal observation*), one of the least-fished places in the entire Wider Caribbean region (Layman et al. 2011). In over two decades of conducting fish surveys in shallow coastal systems of the Caribbean, one author (CAL) has not observed adult fish densities approaching those around the artificial structures on West Andros. Hundreds, even thousands, of adult fish aggregate around reefs made of just 84 standard-sized cinder blocks. Regardless of the actual number of fish, halos are present around these reefs, even though the fish community is devoid of herbivores (reefs constructed in 2014 and surveys conducted 2014–2016; Allgeier and Layman, *unpublished data*). Physical activity of fish contributes to—and perhaps is the primary driver of—halo formation in this system.

While the attention of halo researchers has largely focused on mobile vertebrates (e.g., rays, certain fish), tropical reefscapes harbor a high diversity and high biomass of more sedentary organisms (e.g., lugworms, shrimp, sea cucumbers) that greatly alter the benthos. Even halos that were not originally generated by sediment-processing organisms could still be maintained by their presence, as the sandy span between the reef and seagrass also serves as habitat for a variety of burrowing animals, including lugworms (*Arenicola marina*), gobies (Gobiidae), and shrimp. High densities of sand-processing organisms, e.g., ghost shrimp

(*Callianassa* spp.) have been shown to have dramatic negative effects on seagrass growth (Suchanek 1983). In a pilot study of 24 patch reefs at Lighthouse Reef, the number of sand-processing lugworm or shrimp mounds was significantly higher in the halo areas adjacent to patches than in the surrounding seagrass, although there was also significant site-to-site variability across the whole atoll (Bilodeau 2019). Given their potentially large negative effects on seagrass productivity (Suchanek 1983), and their effects on modifying substrate (Uthicke 1999; Wolfe and Byrne 2017), bioturbators could, in turn, affect algal colonization and seagrass succession and prevent the establishment of "climax" species like *T. testudinum*. The constant sediment disturbance from the builders of terrestrial termite mounds similarly promotes the growth of pioneer plants while preventing competitively superior species from establishing (Okullo and Moe 2012). Reef-adjacent areas with strong bioturbation could experience altered benthic vegetation even in the absence of significant herbivory, or the two processes might work together to structure the halo plant community (or lack thereof), as well as sand infauna and microbial communities. Disturbed sediments from mobile bioturbators might result in similar patterns of diminishing vegetation close to the reef as patch-centered grazing, including features like a gradient rather than an abrupt halo edge (e.g., the "algal transition zone" in Madin et al. 2019b).

An integrated conceptual model of halo formation and maintenance

Halos likely have multiple, potentially complex underlying causes such that not all halo-like patterns may be created or maintained by the same mechanism(s). The evidence presented above shows that individual explanations for halos to date are not universally applicable. Creation and subsequent maintenance of halos also may be distinct processes with distinct causes. While processes like grazing and bioturbation could create new halos, which form relatively quickly around underwater structures (e.g., Alevizon 2002), these same processes might also maintain halos created through an entirely different mechanism by suppressing the regrowth of vegetation. It is possible that changing ecosystem conditions may allow for the maintenance of existing halos but not the

creation of new ones, or that new halos may be formed but then quickly lost again if the mechanism for their maintenance and long-term stability changes. An integrated conceptual model incorporating grazing pressure, fish movement and behavior, bioturbation, primary production, and nutrient distributions best explains the halo phenomenon. These primarily biotic interactions (Fig. 2) contribute to overlapping gradients (Fig. 3) capable of maintaining, and possibly generating, the general halo pattern and some of the specific features documented at certain locations. There could be many variations of this model based on site-specific factors like grazer community composition or benthic productivity, but the model provides a generalized framework for depicting and testing potential processes generating halos and related reefscape patterns.

Heightened nutrients and grazing pressure with proximity to the reef, both driven by a gradient of increasing fish density, combine to create concentric zones where either primary productivity or grazing pressure dominates in terms of plant growth and standing biomass. Mobile, bioturbating, reef-based fish likely follow a similar distribution pattern to that of halo-bound grazers, with varied net effects on vegetation. These gradients of nutrients and grazing or bioturbation not only interact to create the cleared halo region but may also result in heavily-grazed yet persistent vegetation immediately adjacent to the reef (Bilodeau 2019) and/or a dense outer ring of vegetation between the halo and surrounding benthic cover, which is not necessarily of the same density or vegetative composition, as observed by Alevizon (2002) in The Bahamas (e.g., Fig. 3b). When nutrients are high enough, relative to grazing, to promote seagrass or algal growth, vegetation can persist even if it is subject to high grazing pressure. When grazing pressure exceeds the enhancement from fish-derived nutrient fertilization, a halo forms but vegetation eventually is found again as grazing pressure drops off with distance from the reef. This results in a ring of nutrient-supported benthic vegetation outside the lighter-colored grazing halo. In areas with [a] background reefscapes where vegetation otherwise dominates, the outer ring may not be visible. Both of the patterns predicted by this gradient interaction were seen at Lighthouse Reef Atoll (Bilodeau 2019), and both are visible in satellite imagery from multiple locations worldwide (see examples of the vegetative

Fig. 3 Hypothesized interaction between gradients of decreasing nutrients and grazing with distance from the reef. There could be many variations of this model based on site-specific factors, but this provides a generalized framework for depicting potential processes generating seascape patterns. **a** An uneven decline of these gradients (nutrients are shown in dark red, grazing pressure in blue) creates bands of vegetation, cleared sand, and further vegetative growth with increasing distance from the reef. **b** Bands are shown with a top-down view of the patch reef (fish density shown in purple). Enhanced sediment processing by sand- or reef-dwelling organisms within the sand halo may also serve as a reinforcing process to inhibit vegetative regrowth. Beyond the outer ring (a vegetative halo), bottom cover (labeled as "surrounding benthos") may be sand, seagrass, algae, or some combination of the three. The visibility of this outer ring at any given site depends on its visual contrast with the surrounding benthic cover. Inset image of patch reef halos in The Bahamas showing both inner and outer bands of vegetative growth (©Google Earth)
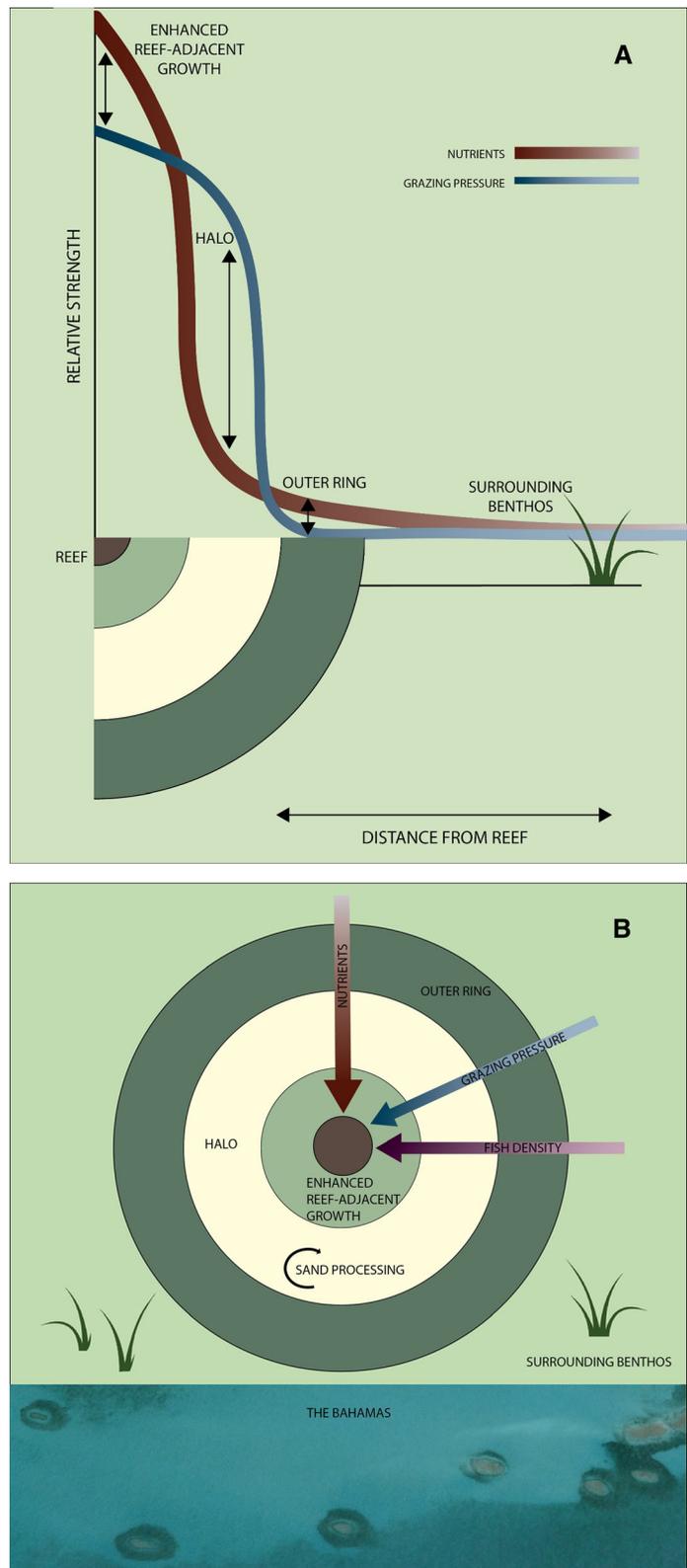
outer halo from Fiji in Fig. 1c and both inner and outer vegetative bands in The Bahamas in Fig. 3b).

Inhibition of vegetative growth in the halo may be reinforced by a positive feedback loop where seagrass, once removed, cannot easily recolonize due to a combination of disturbed sediment and the immediate removal through herbivory of any early successional vegetation that attempts to reestablish. The limited vegetation in the halo likely increases grazing pressure on anything that does manage to grow, and the cleared sand may also create habitat for bioturbators like burrowing shrimp that further disturb the sediment and reduce the ability of seagrass or macroalgae to recolonize. However, plants with sufficient growth to withstand the heavy herbivory may persist in the zone of highest nutrients adjacent to the reef and avoid entering the positive feedback loop, as may those sufficiently far from the reef to escape the majority of reef-based grazers. This integrated model provides a guide for future research linking benthic pattern to process, especially in the context of natural- and anthropogenic-based changes to coral reefs and shallow tropical environments.

The biotic interactions described in this model likely act in concert with abiotic features of the environment, including small-scale hydrodynamics or differences in sediment. Certain features of the halo, including the inner and outer rings of vegetation described by our conceptual model, are difficult to explain without biotic factors, but that does not mean that past studies supporting differences in sediment (Garrett et al. 1971) or wave action (Mitchell-Tapping 1975; Steiner and Willette 2014) at certain locations do not also have merit. These abiotic processes could either form initial halo patterns that are then further reinforced through biotic interactions or could themselves help to enforce and strengthen the different zones in existing biotic halos. Seemingly abiotic effects like small-scale currents and variations in sediment composition can also result from biotic processes, like the movement of schooling fish or activities of sediment-dwelling organisms, making biotic and abiotic features of the halo difficult to disentangle.

Implications and future directions

Despite strong evidence for heightened herbivory within halos around the world, exceptions suggest that grazer response to predation risk is not the singular, or even necessary, cause of the pattern. Investigations thus far into the halo phenomenon have paid relatively little attention to the potential roles of sediment-disturbing organisms and heightened nutrient levels due to fish aggregation, even though these are ubiquitous phenomena in shallow marine environments with strong effects (e.g., Suchanek 1983; Allgeier et al. 2013; Madin et al. 2019b). The ability of sediment-foraging fish or invertebrate bioturbators to impede the growth of reef-adjacent vegetation has recently received increased attention (e.g., Madin et al. 2019b), especially in cases where grazing alone does not explain an observed pattern (DiFiore et al. 2019). The ability of bioturbators to complement or fully usurp the role traditionally assigned to grazers merits further research.

Given the obvious interactions among nutrients, plant growth, and grazing pressure, as well as the documented ability of fish-derived nutrients to alter benthic cover (Allgeier et al. 2013; Layman et al. 2013), nutrient differences within the halo area are also a particularly promising avenue for future inquiry. The role of nutrients in our conceptual model is based on observed patterns from separate studies, most of which were not designed to address the halo pattern directly. Combined measurements of herbivore and/or bioturbator activity, nutrients, and plant growth will be necessary to verify the hypothesized relationships presented here, particularly regarding the way these gradients overlap to create distinct zones around the reef, only one of which is the traditional sand halo.

When reef communities are altered by overfishing, knowledge of not only fish abundance but also fish biomass (proportional to nutrient output and producer offtake) and trophic level will be central to understanding observed responses of the benthic environment (Allgeier et al. 2016). For example, fishing concentrated on predators could relax the landscape of fear and expand halos, whereas harvest concentrated on herbivores and/or bioturbators could cause a rapid fading or complete disappearance of halos (Bilodeau 2019), intensified by the remaining nutrient inputs of omnivorous and carnivorous fish sheltering on patch reefs (for an example of this herbivore/carnivore ratio

and grazing-nutrient dynamic on reefs, see Burkepile et al. 2013). Given the redundancy of consumers at different trophic levels, halos could show resilience in the face of harvesting, up to a point where the last grazers or bioturbators are removed. Evidence of this can be seen in the urchin-caused halos of Jamaica described by Ogden (1976), which persisted even though grazing fish had been effectively removed from the ecosystem (enduring because of large populations of herbivorous urchins). Reefs in the western Caribbean with healthy fish populations maintain halos in the absence of most grazing urchins, which appear to be less important consumers than herbivorous fish (Hay 1984), but these halo patterns may visually fade when harvests deplete grazing fish populations (Bilodeau 2019).

Because of their temporal stability, halos may be important as a monitoring tool, offering an early visual indication of changes in community structure or ecosystem processes (as suggested by Madin et al. 2011). At Lighthouse Reef, halos remain largely consistent year-to-year, although changing benthic vegetation may cause halos to become visibly more or less distinct in certain regions of the atoll during a given season (Bilodeau and Silman, *personal observation*). Older marine reserves with more prevalent halos also suggest that these features may accumulate over time in healthy ecosystems (Madin et al. 2019a). However, a deeper understanding of the halo pattern and its cause(s) will be necessary to interpret what visual changes to halos might mean. In the wake of recurrent and increasingly common bleaching events worldwide (Hughes et al. 2018), we may see dramatic changes in previously stable benthic patterns across affected regions, including potential fading or dissolution of the halos, as local ecosystems adjust to the reduction in live coral cover (and associated structure), increases in algae, and potential decreases in local herbivore species or other changes to fish community structure (Pratchett et al. 2011). Similar changes may also be expected in degraded reef systems subject to overfishing or other forms of habitat destruction. In addition to serving as indicators of marine community stability, changing benthic seascapes can also have important implications for carbon sequestration, as seagrass and algal beds are valuable carbon sinks, and the behavior of halo-dwelling and foraging organisms helps to shape the way that carbon is stored (Atwood et al. 2018).

While marine protected areas might be expected to have more stable, healthy, and diverse reef communities (e.g., Fraschetti et al. 2013; Bonaldo et al. 2017) that would support halos, this is not always the case (e.g., Valentine et al. 2007). Madin et al. (2019a) found that halo patterns are more prevalent in established (≥ 8 years old) marine reserves on the Great Barrier Reef, compared to nearby reefs subject to fishing. Halos within the Half Moon Caye protected area in Belize are also visibly more distinct underwater and experience higher grazing pressure than nearby unprotected halos (Bilodeau 2019). However, the effect of protected area status on halos does not appear so clear at all locations (e.g., Dunn 2008). These discrepancies could be the result of differences in the halo pattern and underlying processes between locations or an indication that certain protected areas are not well-designed or well-managed (Edgar 2011; Edgar et al. 2014). Though increasingly rare, less-altered sites such as those alluded to on West Andros, The Bahamas, may therefore play an important role as comparative natural "controls" that have experienced little direct human impact. Identification of halo presence and specific halo features (size, shape, benthic composition) in heavily-fished and comparatively untouched areas, whether officially protected or not, will be important to determine whether or not halos have utility as indicators of fishing pressure and other anthropogenic effects.

Greater appreciation for the interaction between multiple biotic, and likely abiotic, processes for linked coral and seagrass ecosystems will lead to a deeper and more complete understanding of the formation and persistence of halos, allowing us to better employ them as diagnostic tools in conservation ecology. Aquatic and terrestrial grazing systems include multiple analogous patterns of community structure and function, which suggests that future comparisons between the two could be fruitful, especially in identifying key processes responsible for recurrent spatial phenomena like halos and fairy circles. Persistent landscape or seascape features created through the interaction of multiple species and their abiotic environment are a sign of healthy, complex ecosystems at work. It is important to appreciate all the factors that contribute to these patterns' formation and maintenance and avoid the temptation to oversimplify. Rather than attributing these features to a single cause that may fail to explain subtle aspects, we must

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent All authors consent to the submission and publication of this manuscript.

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