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RESEARCH

Halos of herbivory, feeding-preference, and predation risk on contemporary Belizean reefs

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Abstract Biotic interactions in marine ecosystems can create visible patterns on the benthos. An archetypal example of such a pattern is the conspicuous 'halos' (i.e., areas largely cleared of macrophytes) that surround many tropical reefs. While early ecological studies identified the role of herbivores and the predators that feed on them in the formation of halos on Caribbean reefs, recent evidence has highlighted the context-dependent nature of these biotic interactions. Widespread ecosystem changes and associated alterations in food webs suggest potential changes in the context for Caribbean reefs since those early studies. However, the extent to which different herbivores and predators contribute to halo formation and/or maintenance on contemporary Caribbean reefs remains unclear. We quantified herbivory on five macrophyte species across adjacent reef, halo, and seagrass zones, in a manner that allowed us to partially partition herbivory between sea urchins and fishes. Furthermore, we directly tethered the urchin *Diadema antillarum* on reefs and in halos to quantify predation risk for this key herbivore. The removal of macrophyte assays was high on coral reefs and in halos when compared to seagrass beds, with macrophyte selection by herbivores conserved across zones. Fishes, rather than urchins, were the major herbivores in halos. Moreover, we documented higher predation on urchins in halos compared to reefs, revealing that predation may still shape diurnal urchin distribution in exposed habitats. Despite substantial ecological changes on Caribbean reefs since early studies, halo formation/maintenance by selective fish feeding activity is an enduring feature in the functioning of contemporary Belizean seascapes.

Keywords Coral reefs · Ecosystem function · Fear effects · Predation · Seagrass · Sea urchins

Introduction

Consumers are renowned for their capacity to structure benthic dynamics through top-down effects in marine ecosystems (Hughes et al. 2007; Steneck et al. 2013; Ling et al. 2015). In shallow tropical seascapes, the conspicuous 'halos' (i.e., areas largely cleared of seagrass and algae) that surround patch reefs may be one of the clearest manifestations of such top-down effects (Randall 1965; Valentine et al. 2007; Madin et al. 2019b; cf. Bilodeau et al. 2021). Indeed, these halos can be found in tropical seascapes around the world and can be so extensive that they are visible from space on satellite imagery (Madin et al. 2011, 2022; DiFiore et al. 2019). Given the distinctiveness of reef halos, it is unsurprising that they piqued the interest of pioneering marine ecologists as they strove to decipher the possible

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organisms and ecological processes responsible for forming these fascinating benthic patterns (Randall 1965; Ogden et al. 1973).

Recently, there has been renewed interest in the study of halos in contemporary tropical seascapes. This research has largely focused on the distribution of halos (Madin et al. 2019a, 2022) and potential mechanisms underpinning their formation/maintenance (Downie et al. 2013; Madin et al. 2019b; Bilodeau et al. 2021), especially with respect to the 'landscape of fear' hypothesis (i.e., the role of predators in shaping halo formation via non-consumptive effects) (Madin et al. 2011; Atwood et al. 2018; DiFiore et al. 2019). Increasingly, this research is revealing that the mechanisms underpinning halo formation and the organisms involved can be far more complex and context dependent than initially thought (Bilodeau et al. 2021; Madin et al. 2022). For example, beyond herbivory and other biotic factors, a range of abiotic factors such as small-scale hydrodynamics and differences in sediment composition can play a role in halo formation and/or maintenance (reviewed in Bilodeau et al. 2021). Nevertheless, herbivory is still often viewed as a key ecosystem process underpinning the formation and maintenance of halos (Downie et al. 2013; DiFiore et al. 2019; Madin et al. 2019b; Bilodeau et al. 2021). Continuing to disentangle the nuances of how herbivory manifests in halos and the key taxa involved remains critical in deciphering how halos are formed and maintained under different contexts.

Many of the pioneering insights about herbivory on coral reefs (e.g., Ogden 1976; Morrison 1988; Steneck 1988), especially in respect to halo formation and maintenance (e.g., Randall 1965; Ogden et al. 1973; Tribble 1981; Hay 1984), were derived from studies in the Caribbean. However, contemporary Caribbean reefs now exist in a markedly different ecological context from those of the recent past. This means the insights gleaned from early studies often need to be reevaluated to ensure they are still applicable under contemporary conditions (as suggested in Bellwood et al. 2019). For example, while early studies in the Caribbean revealed that herbivory on assayed macrophyte material was generally high in halos (e.g., Randall 1965; Ogden et al. 1973; Tribble 1981; Hay 1984), the mechanistic basis that led to this pattern of herbivory in exposed halos around coral reefs may have changed. This is because patterns of herbivory can be underpinned by a trade-off between the need for herbivores to access nutritional resources and the need to minimize predation risk (Gil et al. 2017; DiFiore et al. 2019), with the factors shaping this trade-off changing dramatically in the Caribbean since early studies. Specifically, from the early 1980s until today, coral cover has collapsed across the Caribbean, with coral cover now a fraction of what it once was (Gardner et al. 2003; Schutte et al. 2010). This collapse in coral cover has been associated with concomitant increases in macroalgae and/or turf cover on reefs (Jackson et al. 2014; Alves et al. 2022; Tebbett et al. 2023a), thereby potentially increasing the availability of nutritional resources to herbivores on reefs (depending on the palatability of the macroalgae involved). This means that the extent to which different herbivores need to venture into 'riskier' halo habitats to access nutritional resources may have also changed.

In addition to the composition of the reef benthos, the abundance and composition of the herbivore community has changed fundamentally in the Caribbean since early studies. In this respect, fishes were initially identified as the agents of herbivory that underpinned the formation and maintenance of reef halos, especially in Saint John, US Virgin Islands (Randall 1965). Subsequent studies also highlighted the importance of fishes over sea urchins in plant removal from halos, despite sea urchin densities often being high on the reef (Tribble 1981; Hay 1984). Yet, in Saint Croix, US Virgin Islands, where herbivorous fishes were uncommon due to overfishing, urchins were found to be the key drivers of halo formation and maintenance (Ogden et al. 1973). In this latter case, the urchin *Diadema antillarum* made regular migrations out over the sand at night where they were documented to feed heavily on seagrass (Ogden et al. 1973). Given the capacity for *D. antillarum* to overgraze algae and competitively exclude other herbivores when at high densities (Hughes et al. 1987; Carpenter 1990a; Robertson 1991), reductions in on-reef algal resources via urchin grazing may have been a factor encouraging fishes or urchins, depending on the reef in question, to access nutritional resources more extensively in adjacent seagrass beds. However, these early studies were all conducted before the mass *D. antillarum* mortality event that occurred in the Caribbean during the 1980s (Lessios et al. 1984). Critically, this event profoundly changed herbivory dynamics in the Caribbean, especially with respect to the relative abundance of urchins and fishes, as well as the extent of competition between herbivores on Caribbean reefs (Hughes et al. 1987; Carpenter 1990a; Robertson 1991). As a result, due to the current low density of *D. antillarum* on Caribbean reefs, it is likely they play a reduced role in herbivory, and due to the alleviation of urchin grazing pressure and subsequent reductions in competition between herbivores on reefs, there may also be limited need for herbivores to access off-reef nutritional resources on contemporary Caribbean reefs.

Beyond resource availability and competition, herbivory patterns around contemporary Caribbean reefs, and the relative roles of fishes versus urchins therein, may also be shaped by selective feeding and direct predation pressure. Patterns of herbivory can ultimately be shaped by selective feeding as not all macrophytes are equal and different herbivores will selectively feed on different macrophytes to varying extents (Littler et al. 1983; Mendes et al. 2015; Ritter et al. 2021; Spiers and Frazer 2023). Yet most early and contemporary studies on herbivory in halos have relied on assays composed of a single macrophyte (commonly a single seagrass species such as *Thalassia testudinum*) (e.g., Hay 1984; Valentine et al. 2007; Madin et al. 2011; Downie et al. 2013), which means the extent that patterns of herbivory are shaped by macrophyte selection, and if this selection is conserved across habitat zones, remains unclear (but see Gil et al. 2017). Moreover, while studies have linked patterns of herbivory by fishes in halos to fear-effects (e.g., Madin et al. 2011; Atwood et al. 2018; DiFiore et al. 2019), the potential for direct consumptive effects to shape herbivory patterns has received less attention (but see Sweatman and Robertson 1994). This is particularly true in the case of urchins which, given their less mobile nature, may be increasingly susceptible to direct predation in halos, with predation on urchins generally higher in open habitats compared to habitats with shelter (Heck and Valentine 1995; McClanahan 1999). Indeed, past observations of nocturnal feeding patterns in *D. antillarum* were assumed to be indicative of an anti-predator response to diurnally active predators (Ogden et al. 1973). However, while *D. antillarum* represented an abundant nutritional resource for urchin predators on past reefs, since the mass *D. antillarum* die-off the abundance of *D. antillarum* has remained consistently low for several decades (Lessios 2016), with a dietary shift in a key predator reported (Reinthal et al. 1984). As such, it is unclear whether putative urchin predators still target *D. antillarum* when they are available, and consequently, if this direct predation may constrain the feeding activities of *D. antillarum* around contemporary Caribbean reefs.

Of all the locations quantified across the Caribbean in past studies, the reefs of Carrie Bow Cay, Belize, have received a disproportionate share of the research. Indeed, many pioneering insights into herbivory, including in halos, were established on these reefs (e.g., Hay 1981; Littler et al. 1983; Lewis and Wainwright 1985; Lewis 1986). Like the broader Caribbean, the reefs of Carrie Bow Cay have also experienced marked reductions in coral cover and concomitant increases in algal cover (Jackson et al. 2014). As such, these reefs represent a versatile location in which to explore contemporary herbivory dynamics in relation to halo formation/maintenance. The aim of this study, therefore, was to explore the contribution of fishes and urchins to removal of seagrass and macroalgae across contemporary reefs, adjacent halos, and seagrass beds at Carrie Bow Cay, Belize. Specifically, we deployed 24-h herbivory assays (following Ritter et al. 2021), testing five macrophyte species in vertical (i.e., water-column assays accessible to fishes) and horizontal (i.e., benthic assays accessible to both fishes and urchins) orientations across three habitat zones: coral reefs, adjacent halos, and seagrass beds. The deployment of these assays allowed us to evaluate the consistency of selection of different macrophytes across the three habitat zones, while also allowing us to partially partition the potential contributions of fishes and fishes plus urchins to macrophyte removal. We also tethered the urchin *D. antillarum* within coral reefs and halos to quantify relative contemporary predation pressure on this habitat-modifying urchin species and explore if this relative predation risk differs between halos and coral reefs.

Methods

Study site and ecological surveys

This study was conducted in the shallow tropical seascape surrounding Carrie Bow Cay, Belize, from September to October 2018 (Fig. 1). Three feeding assay sites were established in 3 to 6 m of water, all with coral reef patches, surrounding halos, and adjacent seagrass beds (i.e., the three habitat zones of interest). To provide an overview of the ecological characteristics of the three habitat zones of interest, ecological surveys following the Reef Life Survey methods were conducted (Edgar et al. 2020). All surveys were conducted at the same or nearby sites (due to logistical constraints), to those where feeding assays were performed.

To characterize the benthic and consumer communities, the ecological surveys consisted of three components: (a) census of non-cryptic reef fishes, (b) census of benthic invertebrates and cryptic fishes, and (c) photoquadrats to determine benthic cover. Non-cryptic reef fishes were counted in two adjacent blocks (50 × 5 m), with two blocks surveyed in each zone, at each of three sites. For all fishes, the species identity, abundance, and size to the nearest size class (2.5, 5, 7.5, 10, 12.5, 15, 20, 25, 30, 35, 40 and 50 cm total length, and in 12.5 cm bins above 50 cm) were recorded. Following the reef fish census, all mobile macroinvertebrates > 2.5 cm as well as cryptic fishes were recorded in two adjacent blocks (50 × 1 m) along the same transect. Finally, 20 benthic photoquadrats (0.3 × 0.3 m) were photographed every 2.5 m along the transect. The percentage cover of benthic components was then calculated under 5 points per photoquadrat (100 points per transect), using Squidle+ (Friedman 2022). In a haphazard subset of 10 photoquadrats from each zone, at each site, the photographs were also processed to examine *Thalassia* blade density. To do this, all living *Thalassia* blades present in the photoquadrat were counted. In addition, we recorded if there was evidence of any fish herbivory or urchin herbivory on the blades, based on different bite mark patterns that are left by these taxa on *Thalassia* blades (Hay et al. 1983) (Fig. S1).

Herbivory assays

To examine the relative intensity of herbivory in each of the zones encapsulating diel differences in foraging by predominantly diurnal fishes and nocturnal urchins, a series of 24-h

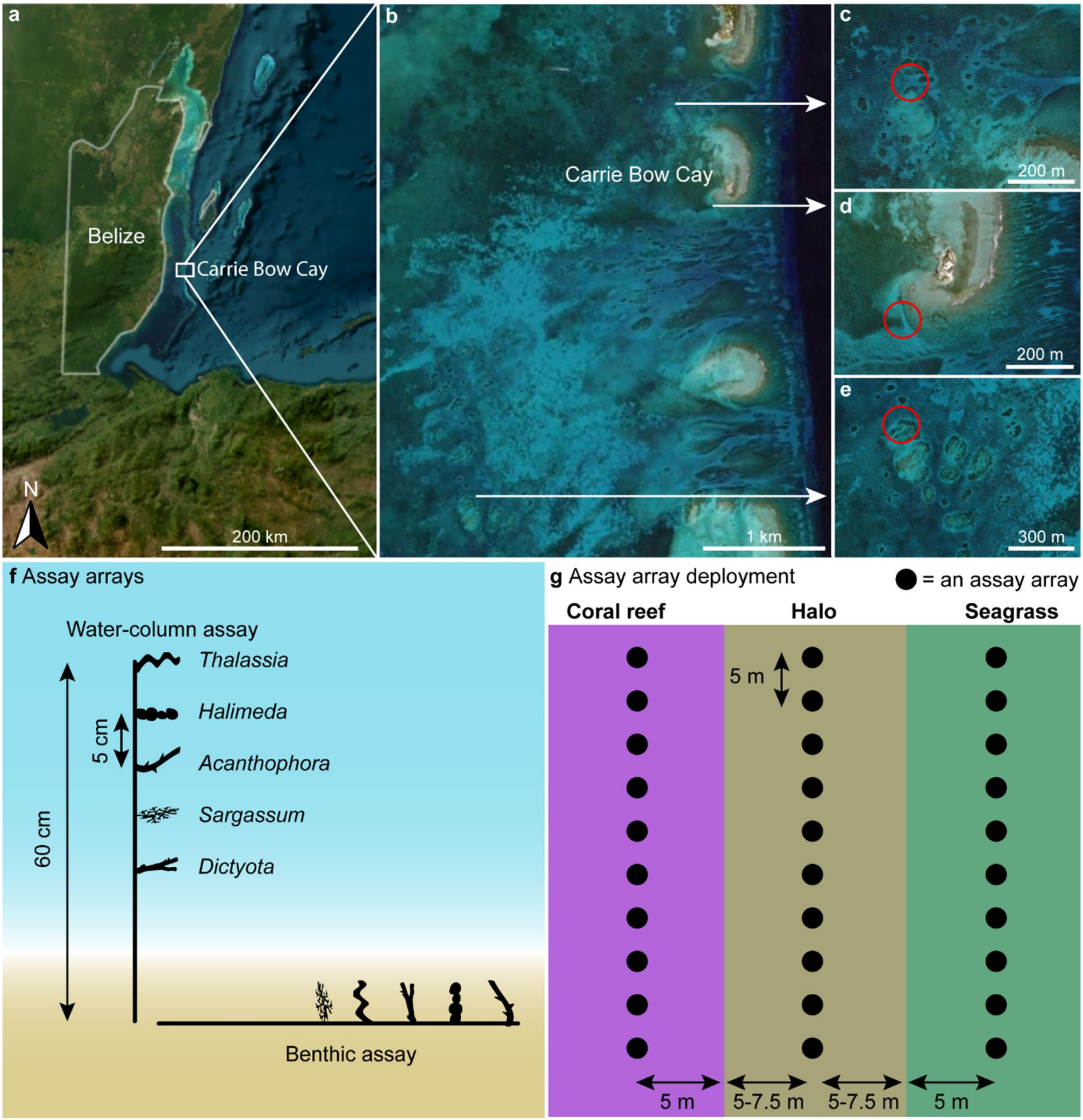

Fig. 1 **a** Location of Carrie Bow Cay relative to Belize, **b** Carrie Bow Cay showing the general location of the three study sites, **c–e** the three study sites showing the halo formations at each site that were quantified (red circles). Images were sourced from Esri *World Imagery* (sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community) via the *leaflet* (Cheng et al. 2024) package in R (R Core Team 2024). **f** Schematic diagram showing an assay array composed of a water-column and benthic assay, with the five different macrophytes haphazardly arranged on each assay. **g** Schematic diagram showing how the ten assay arrays in each zone, at each of the sites, were arranged

macrophyte assays were conducted. In all cases an ‘assay array’ consisted of two treatments a) ‘benthic’ treatments that were laid flat on the seafloor, and b) ‘water-column’ treatments that were set perpendicular to the seafloor, with algal pieces being suspended a minimum of ~ 30 cm from the benthos (Fig. 1f). Each of the treatments included five macrophyte pieces, composed of one piece each of (a) turtlegrass (*Thalassia testudinum*), (b) *Acanthophora* sp., (c) *Dictyota* sp., (d) a highly calcified *Halimeda* sp., and (e) *Sargassum* sp. (following Ritter et al. 2021). All macrophyte pieces on the arrays measured ~ 7 × 2 cm. As benthic treatments were laid on the seafloor, they were accessible to both fishes and urchins, while water-column treatments were only accessible to fishes over the duration of the assay period (following methods of Ling et al. 2018). Assays were secured to either 60 cm high garden stakes or 60 cm lengths of rope, which were weighted on one or both ends for vertical and horizontal treatments, respectively. In the case of stakes, macrophyte pieces were zip-tied to 5 cm long nylon fishing line loops tied to the garden stakes. In the case of weighted ropes, macrophyte pieces were attached by forcing open the rope braid and sliding the macrophyte piece between the tri-braided nylon rope. Assay pieces for both vertical and horizontal treatments were attached 5 cm apart over a 20 cm section starting at 40 cm along each stake/rope. This spacing ensured that vertical assays had a minimum separation of ~ 30 cm above the benthos to ensure urchins could not access assays. Prior to deployment, relative herbivory rates on ropes versus stakes in the same orientation were compared across the five macrophyte species, and no differences were detected (see the supporting information Text S1). Across deployments, the order of macrophyte species was haphazard on assay arrays.

A total of 90 assay arrays were deployed (30 at each site, with 10 in each zone at each site). As each assay array was composed of 10 macrophyte pieces, a total of 900 macrophyte pieces were deployed in this study (note that the final number of macrophyte pieces considered in analyses was 892 as eight macrophyte pieces became dislodged during deployment). In each zone, replicate assay arrays were deployed parallel with the edge of the specific zone, with ~5 m separating replicate assay arrays (Fig. 1g). For coral reefs and seagrass beds, assays were deployed in the habitat zone ~5 m away from the edge of the habitat (i.e., where it bordered the halo). In the halos, assays were deployed in the middle of the halo, approximately equidistant between the edges of the coral reef and seagrass bed (with the total width of the halos being ~ 10–15 m in all cases) (Fig. 1g). All assay arrays were deployed for 24 h, and on collection the following day, evidence of removal of every macrophyte piece was noted in situ as a binomial response of either removed ('1'; including partial removal) or not removed ('0'). The threshold for evidence of removal was set at 25% of the macrophyte missing, i.e., at least one quarter or ~2 cm of the 7 cm long piece. In addition, the total amount of the assay removed (to the nearest 25%) was recorded.

Urchin predation assays

Urchin tethering assays were conducted to examine relative predation rates on urchins in coral reefs and in open halo habitats. Tethering urchins enabled relative predation rates to be determined across the habitat zones by ensuring individual live urchins, or broken test remains, could be tracked over 24 h. Ten *D. antillarum* (test size diameter 30–65 mm) at each site, in each habitat (reefs or halos in this case), were tethered following the methods of Ling and Johnson (2012). Specifically, in the field laboratory, two small holes (~ 1 mm in diameter) were drilled through the urchin's test using a hypodermic needle, a 150-mm length of monofilament line was threaded back through the holes via the needle, and a swivel-clip was threaded over the monofilament line before the line ends were crimped together with a leader sleeve. Tethered urchins were held in aquaria for 24 h before being deployed to control against any immediate mortalities resulting from the surgical tethering process. Healthy tethered urchins were then deployed by individually clipping them to the base of a 60 cm high garden stake secured into the benthos. Urchin assays were deployed in the same arrangement at each site as for herbivory assays (i.e., on coral reefs ~ 5 m away from the reef edge, and in halos approximately equidistant between the reef edge and seagrass edge) with ~ 5 m separating replicate urchin assays in each zone at each site. Urchin assays were not deployed in seagrass beds due to limits of holding aquaria and logistical constraints of collection, handling, tethering, and deploying *D. antillarum.* In the coral reef habitat, the tethers enabled individual urchins to partially access any locally available shelter within a 150 mm radius of the stake, whereas there was no shelter/vertical relief available in the halo habitat. Following a 24 h assay deployment period, any consumption of individual urchin assays was recorded in situ as a binomial response of either consumed ('1') or unconsumed ('0').

Statistical analyses

We initially examined differences among coral reef, halo, and seagrass habitat zones based on the ecological survey data collected. We focused on the benthic cover as a percent of major benthic categories (hard coral, soft corals/gorgonians, macroalgae, turf, sand, Thalassia, 'other' [e.g., sponges, hydrocorals]), the abundance of urchins (four species were recorded), and the biomass of three key trophic groups of fishes (i.e., roving nominal herbivores, urchin-predators [urchinivores], and carnivores [see Table S1 for details of which fish species were considered in each trophic group]). Biomass of fishes was calculated based on their visually estimated length (following diver calibration against centimeter marks along the transect line), and published length–weight regression parameters sourced from FishBase (Froese and Pauly 2024). The average cover/abundance/biomass of each key ecological component at each site, in each zone, was then used to generate a Bray–Curtis dissimilarity matrix. Prior to generating the Bray–Curtis matrix, the dataset was range-standardized to place each of the ecological components on an equivalent scale, thereby accounting for the fact that different units of measurement had been used (i.e., cover, abundance, biomass). The Bray–Curtis matrix was then visualized in multivariate space using a non-metric multidimensional scaling (nMDS) ordination, with the size of individual points for each site scaled based on their cover of *Thalassia*. A permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations was used to test for differences in the composition of ecological characteristics among zones and sites. Homogeneity of dispersions were also checked among zones and sites using permutational analysis of multivariate dispersions, which suggested dispersions were homogenous among zones but not sites. To provide further contextual information about the structure of each habitat zone, the density of *Thalassia* blades in each zone and the relative number of blades with evidence of fish/urchin bites were explored graphically (due to the high number of zeros and complete absence of *Thalassia* blades in some cases).

To examine differences in herbivory among habitat zones and macrophyte species, we used a generalized linear mixed effects model (GLMM). Given the binary nature of the data (i.e., removed or not removed) the model was based on a binomial distribution with a logit-link function. We initially fitted the GLMM with a three-way interaction between the categorical fixed effects of habitat zone, treatment (benthic or water-column), and macrophyte species. In addition, we also fitted other candidate models based on simplified fixed effects structures. We compared models using the corrected Akaike Information Criterion and used the model with the lowest AICc for subsequent inferences (Table S2). In addition, assay replicate identity, nested within site, was included as a random effect to account for the lack of spatial independence. Due to an issue with near-complete separation in the model fit (caused by nil herbivory on one of the macrophytes), we fitted the model with weakly informative priors (based on a normal distribution with a mean of zero and standard deviation of three) to regularize the near-complete separation (based on the 'priors' argument in the *glmmTMB* package [Brooks et al. 2017]). Model fit and assumptions were examined using plots and tests based on simulated residuals (namely QQ plot, residual versus predicted plot, and dispersion test), which were satisfactory based on visual inspection and test statistics in all cases. We also conducted post-hoc pairwise comparisons, based on a Tukey's correction, to examine within factor-level differences. While > 96% of assays were either untouched or completely removed, therefore making these data well-suited to analysis using a binomial response, we also ran an analysis based on the percent of each assay removed as the response variable to ensure our inferences were robust. In this case, the model was based on a beta-binomial distribution, with all other model fitting and checking procedures following those outlined above.

To examine the likelihood of tethered urchins being consumed, we also used a GLMM based on a binomial distribution and logit-link function. In this case, habitat zone was treated as a categorical fixed effect, while site was treated as a random effect. Model fit and assumptions were examined as above and were again satisfactory. All data handling, plotting, and analyses were performed in R (R Core Team 2024; version 4.2.2), using the *tidyverse* (Wickham et al. 2019), *glmmTMB* (Brooks et al. 2017), *vegan* (Oksanen et al. 2019), *DHARMa* (Hartig 2020), and *emmeans* (Lenth 2020) packages.

Results

Ecological context

The contemporary coral reefs at the study sites supported low hard coral cover (13.2 ± 3.6%; mean ± SE), relatively high macroalgae (17.0 ± 16.0%) and turf cover (45.5 ± 16.9%), low *D. antillarum* abundance (0.3 ± 0.3 individuals 50 m^{-2}), and a relatively abundant herbivorous fish community (abundance = 78.5 ± 15.1 individuals 250 m^{-2}; biomass = 1.6 ± 0.5 kg 250 m^{-2}) (Figs S2–S4). Across the three habitat zones at these study sites, the biological communities were clearly different (Fig. 2a). The PERMANOVA identified differences among habitat zones ($F_{2,3} = 7.045$, $p < 0.01$), but not among sites ($F_{3,3} = 0.969$, $p = 0.516$). The nMDS ordination revealed that coral reef patches were typified by a range of benthic components (e.g., hard and soft corals, turf, and macroalgae), reef-dwelling urchins (*D. antillarum*, and *Echinometra viridis*), as well as high biomass of urchinivorous, and to a lesser extent, roving herbivorous, fishes (Figs. 2a, S2–S4). In contrast, the sandy halos were typified by high biomass of carnivorous fishes, while seagrass beds were typified by high *Thalassia* cover and the urchin *Tripneustes ventricosus* (Fig. 2a). These patterns corresponded with counts of individual *Thalassia* blades, with the mean (± SE) density of blades increasing from coral reefs (0.8 ± 0.7 blades 900 cm^{-2}) to halos (31.2 ± 2.4 blades 900 cm^{-2}) and seagrass beds (62.7 ± 3.0 blades 900 cm^{-2}) (Fig. 2b). Evidence of fish bites on *Thalassia* blades followed an inverse pattern to that of *Thalassia* blade density, with relatively high levels documented on coral reefs and in halos (Figs. 2c, 3a). Urchin bites were universally low across zones, with less than 2.5% of *Thalassia* blades showing evidence of urchin bites on average (Fig. 2d).

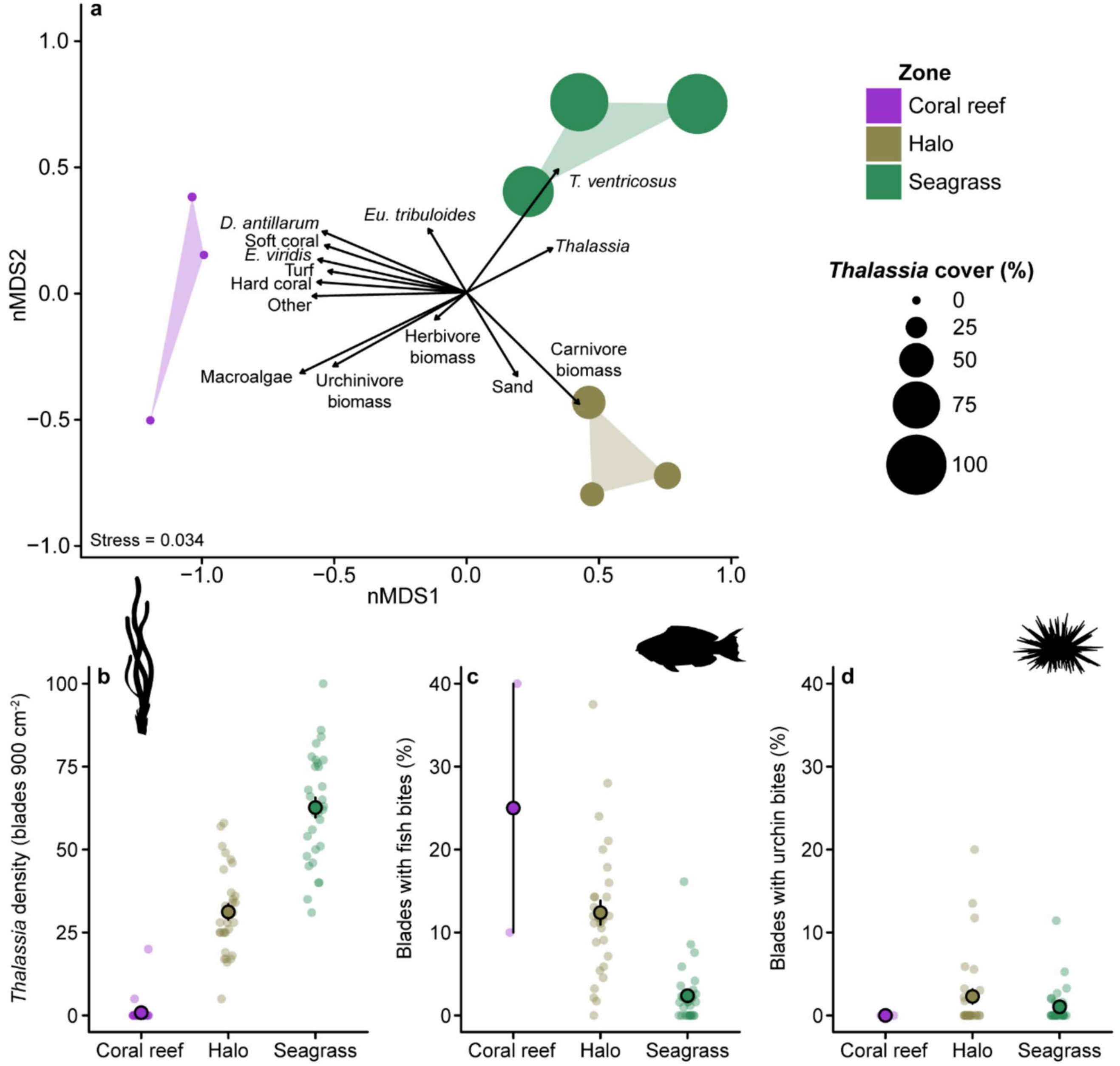

Fig. 2 **a** Multivariate non-metric multidimensional scaling (nMDS) ordination of community survey data showing the ecological characteristics of each studied habitat zone at Carrie Bow Cay, Belize. Survey data were based on the proportional cover of benthic categories, the biomass of key functional groups of fishes, and the abundance of different urchin species (*D.* = *Diadema*, *E.* = *Echinometra*, *Eu.* = *Eucidaris*, *T.* = *Tripneustes*) (also see Figs S2–S4). Circles represent sites, and their radii are scaled by the cover of the seagrass *Thalassia*, the focal benthic cover in this case. **b** The density of *Thalassia* blades recorded in photoquadrats in each zone, and the percent of blades with evidence of **c** fish bites, or **d** urchin bites, in quadrats where *Thalassia* was present. In **b–d** the large colored points denote the mean, the solid line ranges the standard error, while the smaller semi-transparent colored circles are the raw data

Herbivory assays

Three clear general patterns emerged from the herbivory assay data. Firstly, macrophytes differed markedly in their likelihood of being removed (Figs. 3, 4; Table S3). *Acanthophora* was more likely to be removed than all other macrophytes (GLMM, $p < 0.001$ in all cases; Table S4), *Dictyota* and *Thalassia* were equally likely to be removed (GLMM, $p = 0.9997$, Table S4) and both were more likely to be removed than *Sargassum* and *Halimeda* (GLMM, $p < 0.01$ in all cases; Table S4). *Sargassum* was more likely to be removed than *Halimeda* (GLMM, $p < 0.001$; Table S4), with no evidence of any *Halimeda* removal across all assays (Fig. 4c). Notably, the ordering of this removal likelihood

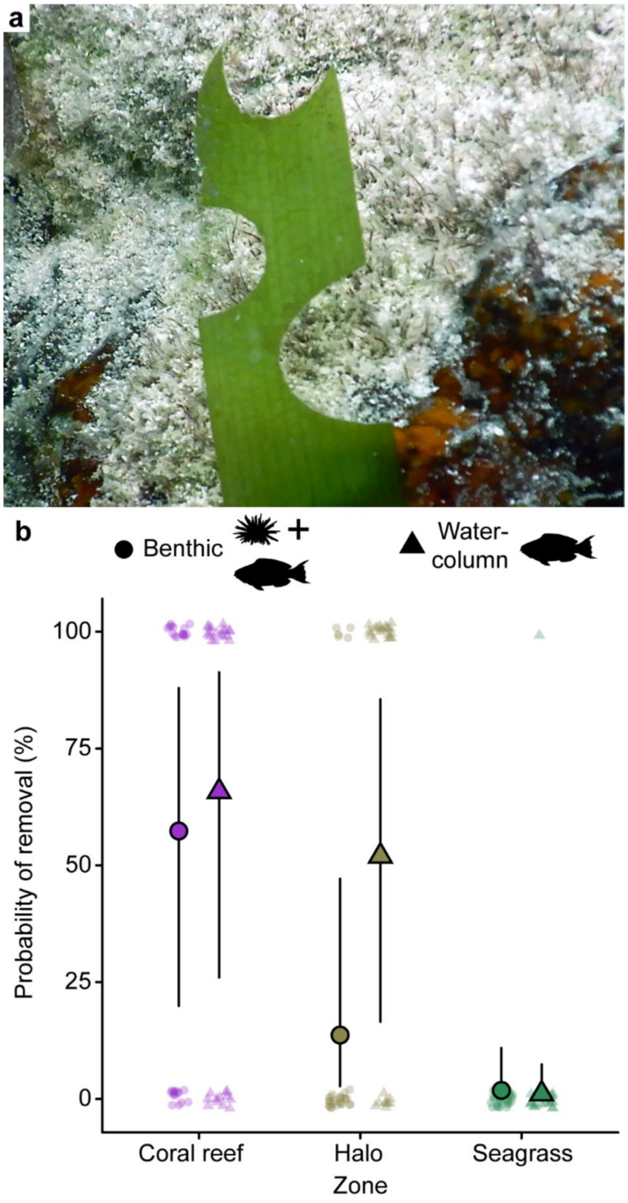

Fig. 3 **a** Photograph showing herbivorous fish bite marks on the seagrass *Thalassia testudinum* (photograph SB Tebbett—note photograph was taken in the Florida Keys, not the study location). **b** The probability of benthic (circles—accessible to both herbivorous fishes and urchins) and water-column (triangles—only accessible to herbivorous fishes) assays of *Thalassia testudinum* being removed to some extent across three habitat zones at Carrie Bow Cay, Belize. The larger circles/triangles and line ranges show the predicted mean and 95% confidence intervals from a generalized linear mixed effects model, while the smaller semi-transparent circles and triangles are the raw data, which have been jittered for clarity, hence why they are not at exactly 0 or 100 ($n = 30$ for each zone and treatment). For results of analyses based on percent of each assay removed refer to Fig. S5

(i.e., *Acanthophora* > *Thalassia*/*Dictyota* > *Sargassum* > *Halimeda*) was consistent across orientations and habitat zones, as the AICc suggested the interactions between macrophyte type and orientation/zone were not influential (Table S2). Moreover, consideration of algal assay removal as a continuous response rather than a binary response did not change any of the inferences or patterns described (Figs S5, S6; Table S3, S4).

Secondly, the likelihood of assays being removed clearly differed among zones (Figs. 3, 4; Table S3), being highest on coral reefs, followed by halos, and then seagrass beds (GLMM, $p < 0.001$ in all cases; Table S4). Benthic assays on coral reefs were 6.2-fold more likely to be removed compared to those in halos on average, while benthic assays in halos were 8.1-fold more likely to be removed than assays in seagrass beds. Water-column assays were removed at similar likelihood in coral reefs versus halos (GLMM, $p = 0.163$; Table S4), but were 107.4-fold and 72.6-fold more likely to be removed in coral reefs and halos relative to seagrass beds, respectively (GLMM, $p < 0.001$ in both cases, Table S4). Consideration of algal assay removal as a continuous response revealed the same patterns (Figs S5, S6), apart from a higher percent of vertical assay material removed in coral reefs versus halos (GLMM, $p = 0.005$; Table S4).

Finally, the likelihood of macrophyte assays being removed differed between orientations in different zones (Figs. 3, 4; Table S3). There were no differences in the likelihood of macrophytes being removed from water-column versus benthic assays on coral reefs or in seagrass beds (GLMM, $p = 0.251$ and $p = 0.431$, respectively; Table S4). In halos, however, macrophytes on water-column assays were more likely to be removed than on benthic assays (GLMM, $p < 0.001$; Table S4). These results were consistent when algal assay removal was considered as a continuous response (Figs S5, S6), apart from a slightly higher percent removal of macrophyte material from water-column assays compared to benthic assays on coral reefs (GLMM, $p = 0.038$; Table S4).

Urchin assays

Tethered *D. antillarum* were readily consumed on both coral reefs and in halos (Fig. 5). However, the GLMM revealed that urchins were more likely to be consumed in open halo habitat compared to coral reefs where shelter was available ($p = 0.043$; Table S5). Specifically, the model revealed that the mean ± SE likelihood of urchins being consumed in halos (87.1 ± 6.6%) was 1.4-fold higher than on coral reefs (63.7 ± 10.0%) (Fig. 5).

Discussion

The halos that occur around patch reefs in tropical seascapes are a clear manifestation of how biotic interactions can shape benthic dynamics and habitat structure (Valentine et al. 2007; Madin et al. 2019b). While these interactions can be

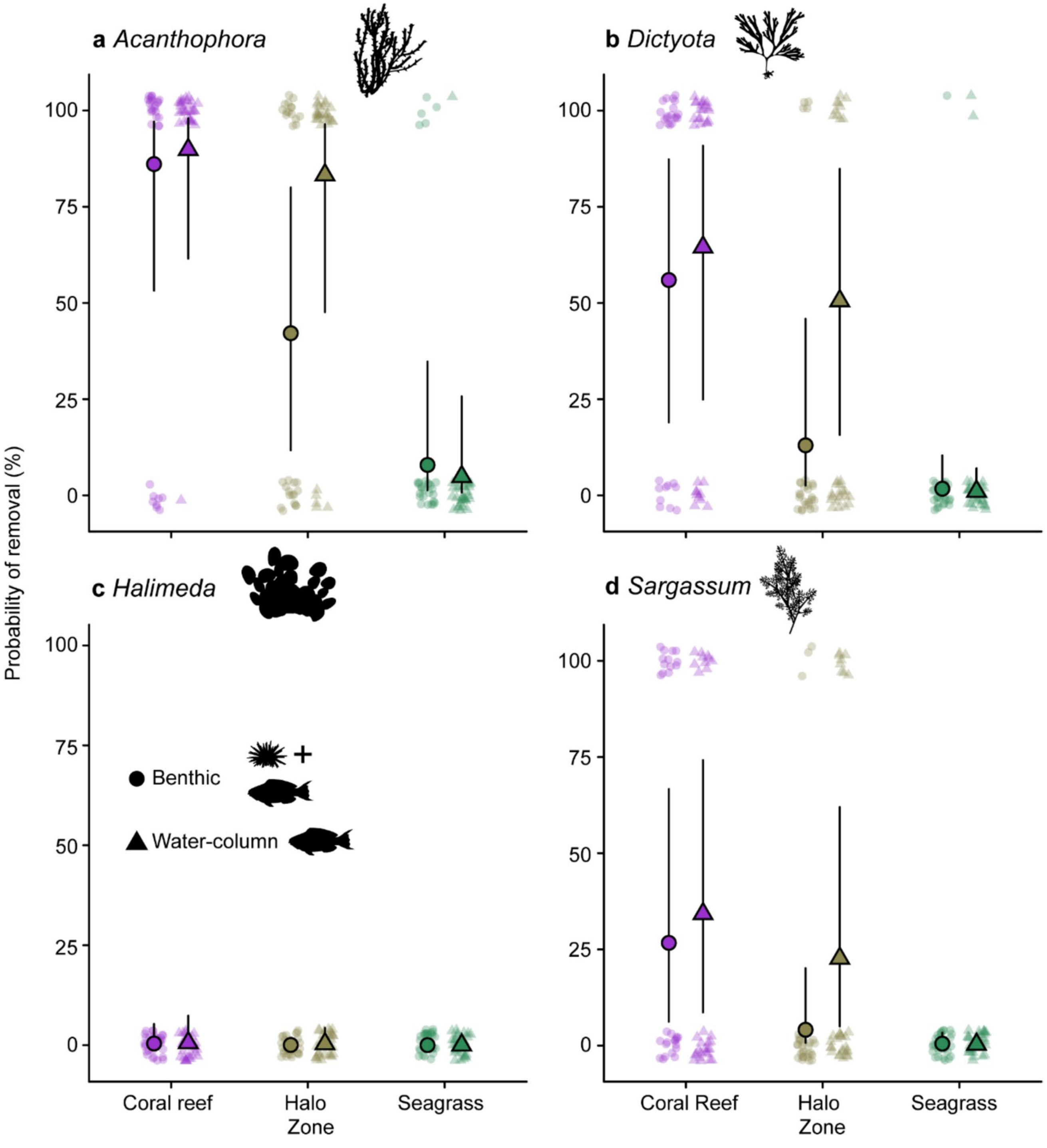

Fig. 4 The probability of benthic (circles—accessible to both herbivorous fishes and urchins) and water-column (triangles—only accessible to herbivorous fishes) assays of the macroalgae **a** *Acanthophora*, **b** *Dictyota*, **c** *Halimeda*, and **d** *Sargassum* being removed to some extent across three habitat zones at Carrie Bow Cay, Belize. The larger circles/triangles and line ranges show the predicted mean and 95% confidence intervals from a generalized linear mixed effects model, while smaller semi-transparent circles and triangles are raw data, which have been jittered for clarity, hence why they are not at exactly 0 or 100 ($n = 27$–30 for each zone, species, and treatment). For results of analyses based on percent of each assay consumed refer to Fig. S6

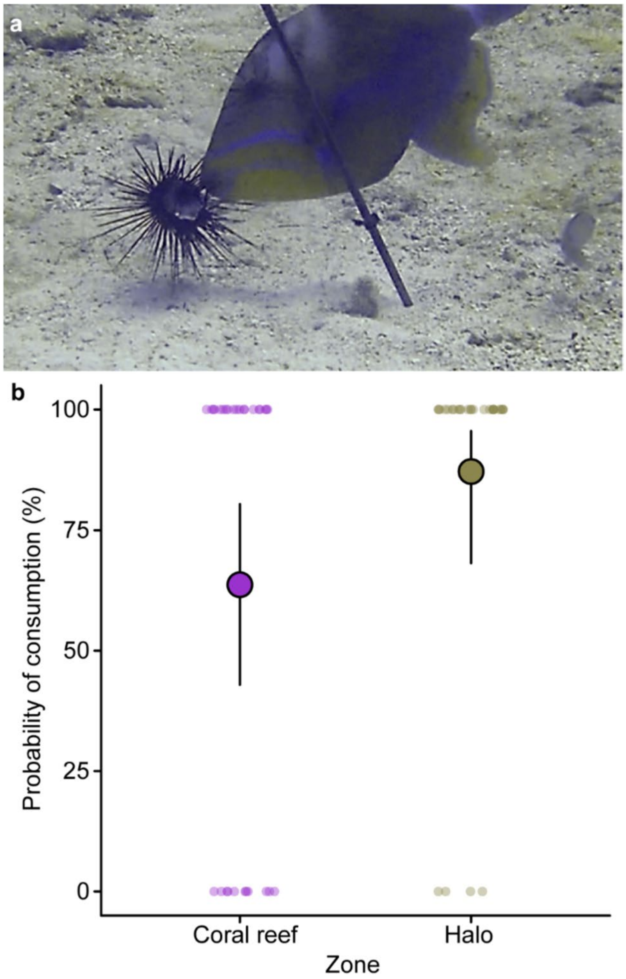

Fig. 5 **a** A triggerfish (*Balistes vetula*) consuming a tethered urchin (photograph SD Ling). **b** The probability of tethered urchins being consumed in coral reef versus halo zones at Carrie Bow Cay, Belize. The larger circles and line ranges show the predicted mean and 95% confidence intervals from a generalized linear mixed effects model, while the smaller semi-transparent circles are raw data ($n = 30$ per zone)

context dependent (Gil et al. 2017; Bilodeau et al. 2021), the removal of seagrasses by herbivores can play a crucial role in halo formation and/or maintenance (Randall 1965; Ogden et al. 1973; Madin et al. 2011; DiFiore et al. 2019). Indeed, the results of our study on contemporary reefs at Carrie Bow Cay align with past studies across the Caribbean (e.g., Randall 1965; Tribble 1981), emphasizing the role of spatially constrained herbivory in structuring halo formation and maintenance (Fig. 6). Despite the ecological context of Caribbean reefs changing fundamentally since early studies, the patterns of removal of macrophytes from coral reefs and adjacent halos by herbivores appear to have transcended these changes. Moreover, our study extends on previous results by highlighting that the selective removal of different macrophytes is conserved across the different habitat zones. This underscores that herbivores are selective feeders and are willing to venture into halos to target select macrophytes. However, selective feeding in halos, at least at the distance from the reef edge that we tested, is largely the result of fish-based herbivory, as benthic assays in halos were rarely removed. Indeed, grazing by *D. antillarum* in open areas around the study reefs is likely constrained by their low overall density and high rates of predation, with *D. antillarum* still clearly targeted by urchinivorous fishes when available and exposed in halos (Fig. 6). Despite limited contributions from *D. antillarum*, the process of herbivory in halos (as visible from space [Madin et al. 2011; DiFiore et al. 2019]) remains functionally intact for Belizean reefs, with the same directional trend as in early studies across the Caribbean (i.e., highest on reefs and halos and lowest in seagrass beds [Randall 1965; Ogden et al. 1973]).

The ecological conditions we documented on contemporary Belizean reefs, that is low coral cover, high algal cover, and low *D. antillarum* abundance, are reflective of many contemporary reefs across the Caribbean and represent a fundamentally different condition to Caribbean reefs before the 1980s (Gardner et al. 2003; Jackson et al. 2014; Lessios 2016). For example, *D. antillarum* densities of 0.7–4.3 individuals m^{-2} were reported from reef habitats at Carrie Bow Cay in 1982 (Lewis and Wainwright 1985), while in our study densities ranged from 0 to 0.02 m^{-2} on reef habitat. Contemporary low *D. antillarum* densities suggest this species may no longer exert the same feeding pressure that it once did on and around Caribbean reefs (e.g., Hughes et al. 1987; Carpenter 1990b). Indeed, while *D. antillarum* were historically reported to produce grazing halos under some contexts in the Caribbean (Ogden et al. 1973) we found no evidence that *D. antillarum* played a major role in macrophyte removal from halos at our study sites. This was evidenced by the limited macrophyte removal on benthic assays (accessible to urchins and fishes) compared to water column assays (accessible only to fishes) in halos. This finding is further supported by the fact that urchin bite marks on naturally occurring *Thalassia* blades were limited across the three habitat zones relative to fish bite marks; urchin bites within seagrass beds were likely from *Eucidaris tribuloides* and *Tripneustes ventricosus* based on relative abundance of these species (see Figs. 2a, S4). We were, however, missing direct observations of nocturnal activity and urchin densities, with diurnal observations potentially producing a biased perspective of the contributions of invertebrates (Jones et al. 2025).

The low densities of *D. antillarum* on contemporary Caribbean reefs also mean that any predation pressure on this species will be concentrated on the few individuals that remain, thereby having a larger potential impact on structuring the spatial distribution and grazing impact of this species. Our data suggest that despite *D. antillarum* densities

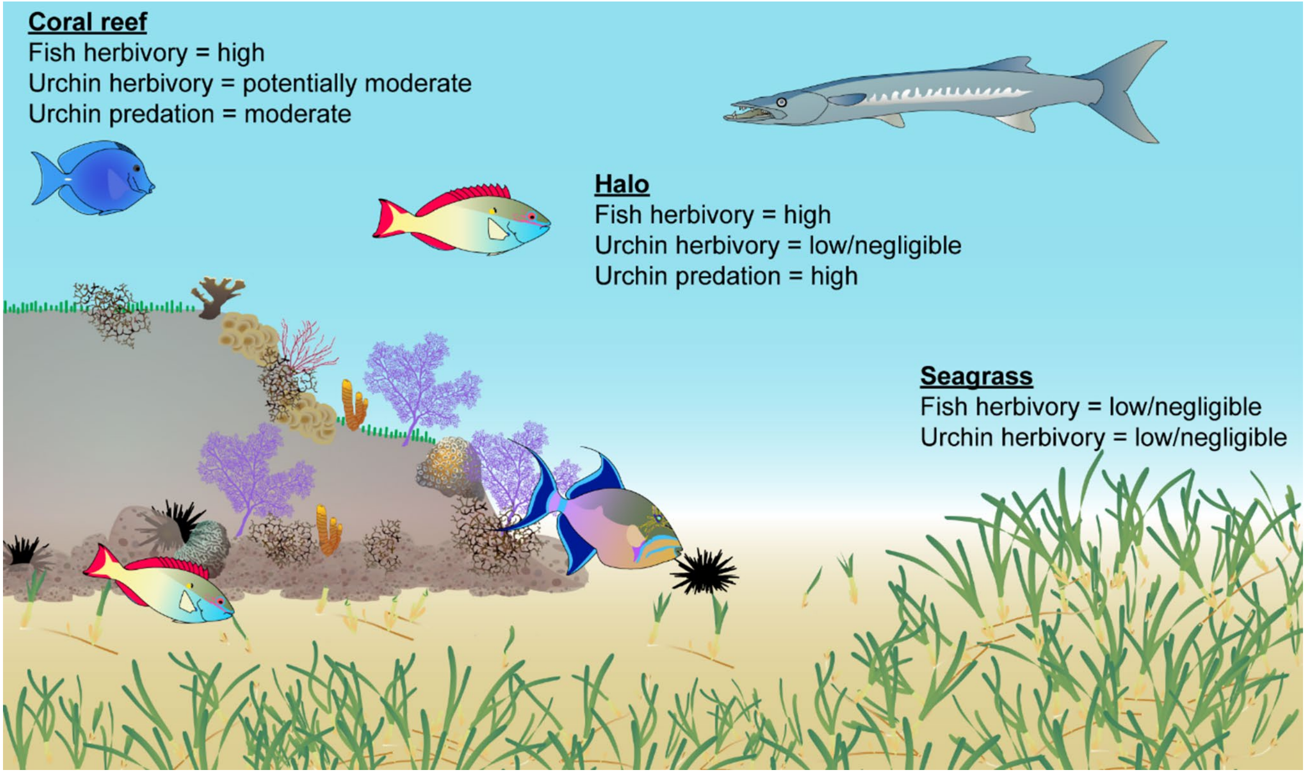

Fig. 6 Conceptual diagram highlighting how the distribution of key organisms and processes varies in each of the three habitat zones at Carrie Bow Cay, Belize. The presence and placement of the herbivorous parrotfish and surgeonfish represent higher herbivorous fish biomass and macrophyte removal on coral reefs and in adjacent halos. The placement of the triggerfish and sea urchin in the halo denote higher levels of predation on tethered urchins in exposed halo habitats relative to coral reefs. The placement of the barracuda represents higher biomass of carnivorous fishes observed in halo habitats

remaining low across the Caribbean for several decades (Lessios 2016), and therefore likely only making a small contribution to the diet of urchinivorous fishes (Reinthal et al. 1984), *D. antillarum* still experiences substantial predation pressure when available. Indeed, 87.1% of *D. antillarum* tethered in halos were consumed, with this predation directly attributed to at least the triggerfish *Balistes vetula* and the sparid *Calamus calamus*, which were observed feeding on tethered urchins during our study (pers obs SDL) and are known urchin predators (Randall 1967; McClanahan 1999). Compared to another study based on tethering *D. antillarum* without shelter in the Florida Keys (in which ~ 10% of urchins were consumed after 24 h) (Delgado and Sharp 2021) our levels were relatively high. Moreover, our results align with studies that show tethered urchins in exposed areas (such as halos) are at higher risk of predation compared to areas with shelter (Heck and Valentine 1995; McClanahan 1999; Delgado and Sharp 2021).

Beyond the lack of shelter, *D. antillarum* are likely to be particularly prone to predation in the sandy halo zone on contemporary reefs. This is because the tube feet of urchins are unlikely to adhere to sand as efficiently as on hard substrata, disabling their ability to resist inversion and attacks to the less defended oral surface (Laur et al. 1986; Levitan and Genovese 1989; Ling and Johnson 2012). Within the contemporary low-density regime, aggregations of *D. antillarum* with interlocking spines as a predatory defense on open reefs (as was noted historically), and/or potentially within halos themselves (e.g., Randall et al. 1964; Pearse and Arch 1969; Rodríguez-Barreras et al. 2018), are also unlikely to occur and were not observed during daytime only sampling in the current study. Given the concentrated predation rates on *D. antillarum* by mobile urchinivorous fishes that will feed over sandy halos (Randall 1967) and the lack of antipredator aggregation mechanisms available to *D. antillarum* on contemporary reefs, direct predation pressure, at least during diurnal periods, therefore appears to be a mechanism that may spatially limit *D. antillarum* grazing to patch reef habitats.

While predation pressure appears to have also historically shaped the grazing behavior of *D. antillarum*, constraining feeding in halos to nocturnal periods (at least at Saint Croix [Ogden et al. 1973]), the need for *D. antillarum* to venture into halos in search of food may also no longer be apparent on contemporary reefs. Historically, high feeding pressure and densities may have driven *D. antillarum* to spillover off the reef into halos in search of food to meet their nutritional demands. In contrast, on contemporary reefs, the few remaining *D. antillarum* may meet their nutritional demands from algae found on the reef. This inference is supported by well-documented increases in algal cover and biomass on Caribbean reefs following the mass mortality of *D. antillarum* (e.g., De Ruyter Van Steveninck and Bak 1986; Liddell and Ohlhorst 1986; Carpenter 1990b), and that *D. antillarum* historically avoided re-grazing the same reef areas on successive nights (Carpenter 1984). Moreover, increases in herbivorous fish populations following the mass mortality or experimental removal of *D. antillarum* suggest that high *D. antillarum* densities reduced nutritional resources to such an extent that it suppressed abundances of herbivorous fishes (Hay and Taylor 1985; Carpenter 1990a; Robertson 1991).

Based on the lack of competition with *D. antillarum*, and the higher overall algal cover on contemporary coral reefs, it could be assumed that there is now also less motivation for herbivorous fishes to access nutritional resources in halos away from the cover of coral reefs. However, this was clearly not the case in our study, with herbivorous fishes selectively removing macrophytes from water column assays in halos at a similar probability to those on coral reefs. The likelihood of different macrophyte species being removed aligns with previous studies conducted in the Caribbean, including at Carrie Bow Cay, which have revealed that herbivores will readily remove *Acanthophora* as well as *Dictyota* and *Thalassia*, while *Sargassum* and *Halimeda* are often removed less frequently (Littler et al. 1983; Paul and Hay 1986; Tebbett et al. 2020; Ritter et al. 2021; Spiers and Frazer 2023). Despite the strength of this selective feeding, the fact that assays of even highly palatable taxa such as *Acanthophora* were rarely removed in seagrass beds suggest that herbivorous fish foraging is spatially constrained near to reef structure (also see Downie et al. 2013; Gil et al. 2017). While the overall sizes of herbivorous fish foraging areas are shaped by factors such as reef size, nutritional resource availability, and competition (Carlson et al. 2017; DiFiore et al. 2019), within these constraints, selection of specific macrophytes clearly shapes how herbivory is delivered over tropical reefscapes.

Consideration of selective removal of macrophytes by herbivorous fishes could hold the key, at least in part, to understanding why fishes still readily remove macrophytes from surrounding halos despite increases in algal cover on reefs and reduced competition with *D. antillarum*. While macroalgal cover has increased on Caribbean reefs since the 1980s (Schutte et al. 2010; Jackson et al. 2014; Tebbett et al. 2023a), in many cases, including at our study sites at Carrie Bow Cay (Fig. S2), macroalgae are still not the dominant benthic cover, with benthic cover often typified by high cover of short (~ < 2 cm) turfs (i.e., the epilithic algal matrix) (de Pablo et al. 2021; Tebbett et al. 2023b). Although turfs represent a highly productive nutritional resource for many herbivorous fishes and urchins (Steneck 1988; Humphries et al. 2020), browsing herbivorous fishes, especially some sparisomatine parrotfishes in the Caribbean, generally feed preferentially on upright macrophytes (including seagrass) instead of turfs (McAfee and Morgan 1996; Ritter et al. 2021; Burkepile et al. 2022; Spiers and Frazer 2023), potentially targeting highly nutritious cyanobacteria and other microbial photoautotrophs epiphytic on the macrophytes (Clements et al. 2017). Therefore, despite high algal cover on contemporary Caribbean reefs, the cover of the specific macrophytes and associated microbial communities on reefs that certain fishes selectively feed on may still not be high enough to meet their nutritional needs. As such, the need for fishes to feed on surrounding seagrass in halos may represent a persistent feature of Caribbean tropical seascape functioning that is decoupled from the contemporary benthic configuration of reefs.

It should be highlighted that one of the hypotheses put forward to explain why herbivorous fish grazing is spatially circumscribed near reefs is that seagrass closer to the reef structure may have higher nutritional quality (reviewed in Bilodeau et al. 2021). However, beyond the seagrass itself, it may be that the quantity and quality of epiphytic microbial photoautotrophs on seagrass at different distances to the reef holds the key, as these appear to be the nutritional resources that sparisomatine parrotfishes specifically target (Clements et al. 2017). Indeed, there is evidence that epiphyte cover on seagrass can be higher closer to reef structure (Alevizon 2002), with higher nutrient concentrations closer to patch reefs due to fish aggregations (Layman et al. 2013; Shantz et al. 2015) potentially underpinning these patterns in epiphyte cover (Bilodeau et al. 2021). Future studies based on the selection of macrophytes with and without epiphytic microbial photoautotrophs in grazing halos at different distances from the reef could help further tease apart the mechanisms involved in selective herbivorous fish foraging in grazing halos.

In addition to the quality of nutritional resources, fear effects and predation risk have been put forward as a key mechanism that drives spatially circumscribed feeding by herbivorous fishes near reefs (Madin et al. 2011; DiFiore et al. 2019). In our case, large piscivores, including *Sphyraena barracuda,* were recorded in fish censuses (Fig. S3) and were observed swimming along the reef-halo habitat interface (pers obs SDL). Herbivorous fishes, particularly the parrotfish *Sparisoma aurofrenatum* and the surgeonfish *Acanthurus coeruleus*, were also observed quickly darting off the reef to feed on macrophytes on water-column assays in halos before darting back to the reef for shelter (pers obs SDL). From the perspective of fear effects, these observations and selective removal of macrophytes from water-column assays rather than benthic assays in halos could suggest fishes avoided benthic assays to maintain a greater degree of vision and remain more vigilant in higher-risk habitats. However, a more parsimonious interpretation of these data could be that water-column assays were more visually apparent and/or more accessible, enticing mobile fishes off the reef to feed selectively on specific macrophytes. The strength of this latter conclusion is supported by recent studies which suggest fear effects in herbivorous fishes may be less pronounced than commonly assumed, especially when shelter is available (Tebbett et al. 2024). The relative strength of top-down versus bottom-up factors in shaping herbivorous fish feeding, especially in the context of halos, remains an area of ongoing research, with the relative strength of these two forces likely to be highly context dependent (Gil et al. 2017).

While our experimental design could tease apart the selective removal of macrophytes from halos, and the relative role of fishes versus urchins therein, several potential caveats should be highlighted. While a lack of benthic assay removal, such as in halos, is evidence of limited urchin grazing, fishes are more mobile than urchins and will feed over larger reef areas (Sandin and McNamara 2012). This means that the relative roles of urchins versus fishes in macrophyte removal in halos could change if assays were placed at different distances from the reef edge. Therefore, as our assays were set in halos at a single distance from the reef (~ 5 to 7.5 m), and this was moderately far from the reef edge, we can only conclude that urchins make limited contributions to macrophyte removal in halos at this distance from the reef. Moreover, in cases where both water-column assays and benthic assays are removed (e.g., on reefs in our case) the potential role of urchins cannot be discounted as we cannot ascribe benthic assay removal to either fishes or urchins. Secondly, the binomial approach to scoring assay removal is relatively coarse. However, the inferences between this binomial approach and a more continuous approach were largely consistent. Moreover, even if we had specifically measured algal mass before and after deployment, this would not have resulted in any additional insights. This is because the data would have been essentially the same (i.e., > 96% of values at either 0 or 100%) after calculating the percent of mass lost (as is common practice with assay data to standardize it [e.g., Hoey and Bellwood 2010; Tebbett et al. 2020]). Finally, while urchin tethering can give an indication of relative predation risk (Boada et al. 2015; Rhoades et al. 2024), tethering likely inflated predation intensity, as urchin mobility was restricted and tethered urchins were presented in exposed areas for 24 h. Although urchins may be injured during tethering, potentially inflating predation further, we minimized this effect by holding urchins in aquaria for 24 h after the surgical procedure. We also employed a minimally invasive tethering procedure that has been shown to result in low (< 5%) mortality in diadematid urchins with urchin survival of > 100 days on the reef in cases when predation pressure was low (Ling and Johnson 2012).

Overall, our study highlights that the role fishes play in the removal of algae and seagrass from the area around coral reefs, which creates and maintains the halos that have fascinated many marine ecologists, persists on contemporary reefs at Carrie Bow Cay. However, we also highlight the limited contemporary role of *D. antillarum* in determining this ecosystem pattern, with a clear indication that predation risk can constrain urchin distribution to the shelter of patch reefs. In this respect, our study emphasizes the ongoing need to reevaluate our understanding of how reefs, and tropical seascapes more generally, may have functioned in the past, present and into the future, given the potential for change in key ecosystem components. In many cases, the reefs that were studied in the past are unlikely to function in the same way today, either because of fundamental changes to the communities of organisms that inhabit them (e.g., mass mortality of *D. antillarum* and the loss of large fishes) and/or through the increasing intensity of anthropogenic stressors that are now reshaping these ecosystems (Jackson et al. 2001; Bellwood et al. 2019; Williams et al. 2019). In our case, despite changing reef benthic composition and potential changes in the relative contributions of herbivores through time, the persistence of halos in tropical seascapes highlights the remarkable resilience of the ecological links between predators–prey–primary producers and the potential ecological trade-offs between access to shelter and the need to feed (cf. Madin et al. 2022). Given the persistent nature of halos in tropical seascapes to date, any major shift in the structure of these benthic patterns in the future would likely indicate major upheaval of the ecological processes and interactions operating across these ecosystems.

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Authors contribution KDC, VJP, SJ, JED, ASH, GJE, and SDL conceived and designed the study; KDC, VJP, SJ, MDJ, and SDL performed the field work; GASA and SDL compiled the data; SBT analyzed the data, produced the figures, and wrote the original manuscript; all authors reviewed the manuscript.

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Data availability Data are provided within the supplementary information files.

Declarations

Competing interests Sterling B. Tebbett is a topic editor at Coral Reefs and Valerie J. Paul is an editorial board member at Coral Reefs.

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