

Grazing halos on coral reefs: predation risk, herbivore density, and habitat size influence grazing patterns that are visible from space

Bartholomew P. DiFiore^{1,2,3,*}, Simon A. Queenborough², Elizabeth M. P. Madin^{4,5}, Valerie J. Paul³, Mary Beth Decker⁶, Adrian C. Stier¹

¹Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106, USA

²Yale School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511, USA

³Smithsonian Marine Station at Fort Pierce, Fort Pierce, Florida 34949, USA

⁴Hawai'i Institute of Marine Biology, University of Hawai'i, Kane'ohe, Hawai'i 96744, USA

⁵Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

⁶Department of Ecology and Evolution, Yale University, New Haven, Connecticut 06511, USA

ABSTRACT: The behavior of organisms at local scales can have dramatic effects on the distribution of habitat and ecosystem processes at large spatial scales. Grazing halos—barren areas of sand surrounding coral reefs—are readily visible in remotely sensed imagery, and are formed by herbivores preferentially grazing close to the safety of the reef. Grazing halo size can vary by more than an order of magnitude, yet we lack an understanding of what underlies this variation. Changes in grazing intensity and the distance herbivores travel may be influenced by predation risk, resource availability, and structural attributes of the reef. Here, we tested how predator density, herbivore density, and patch reef area are correlated with halo size and grazing patterns by linking satellite imagery with mensurative experiments on patch reefs in the Caribbean. Chronic predation risk suppressed the overall foraging intensity of herbivorous fishes; a doubling in predator density led to a 29% decrease in grazing. Variation in herbivore density, which was tightly correlated with patch reef area, was linked to the distance herbivores foraged from the reef. Furthermore, herbivore density and/or reef area was the best predictor of halo width at field sites, and reef area explained a significant proportion of the variation in halo size across the landscape. Our results contribute to a growing body of research suggesting that halos may function as footprints of ecological processes, such as herbivory, that can be quantified using remote sensing, and offer a potential avenue to improve monitoring of coral reef management.

KEY WORDS: Predator-prey interaction · Foraging ecology · Herbivory · Predation risk · Remote sensing · Seagrass · Landscape ecology

— Resale or republication not permitted without written consent of the publisher —

1. INTRODUCTION

Certain patterns in ecological systems are most conspicuous from a distance. For example, aerial surveys and satellite imagery reveal the banding of mussel beds, the regular spacing of saltmarsh sedges, and the overdispersed pattern of ‘fairy circles’—regularly spaced barren patches found in the Namibian desert (van Rooyen et al. 2004, Rietkerk

& van de Koppel 2008). Such widespread variation in patterns of primary and secondary producers can have key consequences for ecosystem productivity and resilience (Pringle et al. 2010, Bonachela et al. 2015, Tarnita et al. 2017). Therefore, it is crucial to understand what mechanisms underlie these patterns.

Grazing halos, i.e. heavily foraged areas of seagrass or algae adjacent to coral patch reefs, are con-

*Corresponding author: bdifiore@ucsb.edu

© Inter-Research 2019 · www.int-res.com

spurious patterns in coral reef landscapes that are readily visible in satellite images (Fig. 1b,c). While halos are found throughout tropical oceans in the Atlantic, Pacific, and Indian Oceans (E. Madin unpubl. data), their size can vary tremendously between reefs. For example, in the Florida Keys, USA, grazing halo width (i.e. the distance from patch reef edge to halo boundary) can vary from 1–70 m (Fig. 1d). Herbivorous fishes or sea urchins drive halo formation by grazing more intensively on algae and seagrass near the edge of their natal reef (Randall 1965, Ogden et al. 1973). Thus, variation in the intensity of grazing and the distance herbivores travel from a given reef likely explain variation in halo size. However, we do not understand what ecological processes cause such widespread variation in herbivore grazing pressure.

Foraging theory offers insight into the potential mechanisms driving variation in grazing patterns across space and thereby grazing halo width. Central-place foraging theory predicts that predation

risk, the energetic cost of movement, and resource availability influence when, where, and how much herbivores eat (Brown & Kotler 2004). Herbivores are expected to graze heavily near a central shelter where predation risk and travel costs are low, and graze less intensely further from a shelter where predation risk and travel costs are higher (for a review, see Covich 1976). However, herbivores must balance risk with reward. The distance (or amount of time) herbivores are willing to forage away from a shelter is not only expected to change with predation risk (Sih 1980, Werner et al. 1983), but also with resource availability, which can vary as a function of herbivore density (Hughes et al. 1994, Grand & Dill 1999) and resource quality (Brown 1992).

Empirical evidence from marine systems supports the idea that grazing halo size is driven by herbivores balancing the risks and rewards of foraging. Marine herbivores reduce foraging in areas of high predation risk (Heithaus et al. 2012, Madin et al. 2016), and non-consumptive effects between species may alter

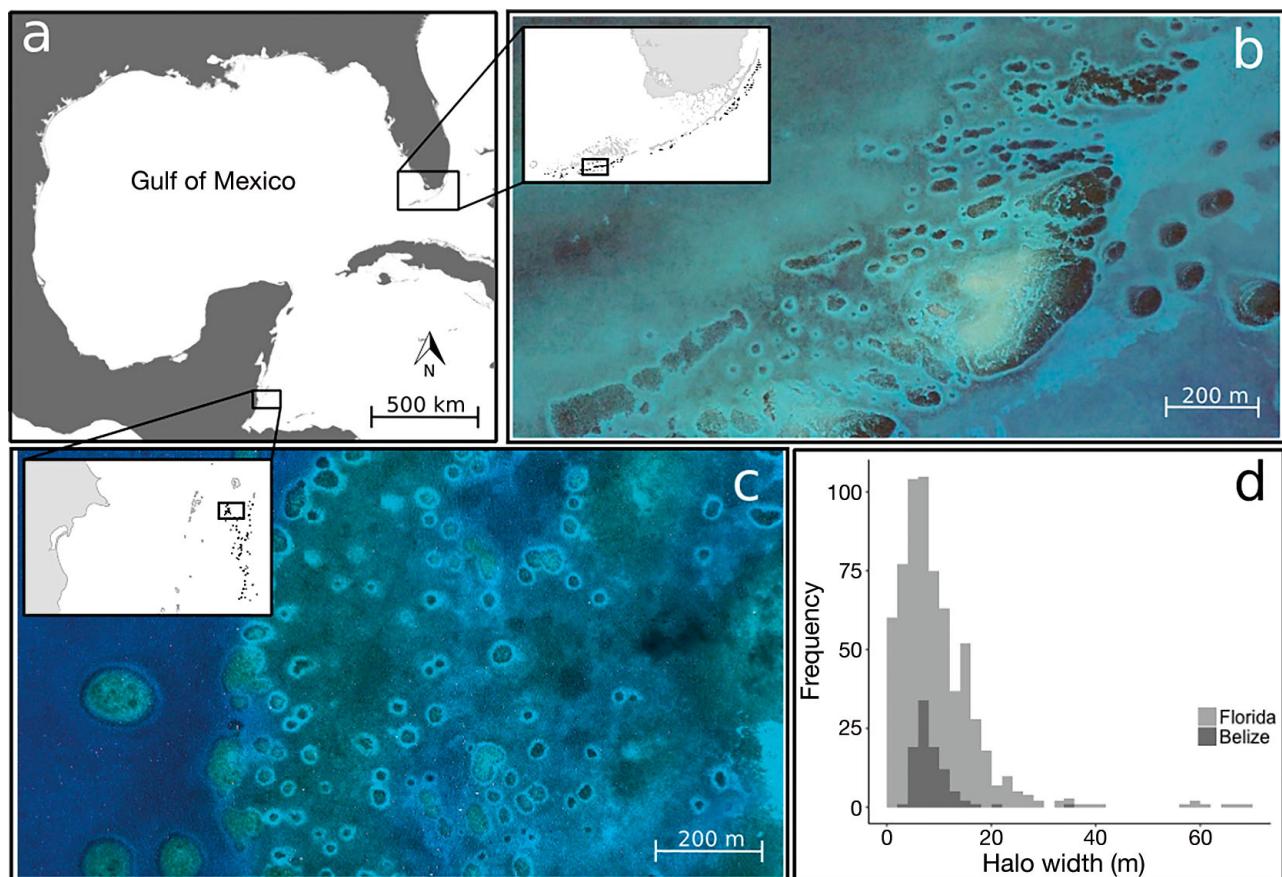


Fig. 1. (a) Overview of study regions in the wider Caribbean. High-resolution satellite images of grazing halos—light areas of sand formed by the intense foraging of herbivores—surrounding mosaics of patch reefs in (b) Florida, USA (© Google Earth) and (c) Belize (© 2016 DigitalGlobe Foundation). Black points in inset maps are digitized grazing halos (Florida, $n = 662$ reefs; Belize, $n = 95$ reefs). (d) Variation in grazing halo width, i.e. the mean distance from the reef edge to the halo boundary

the distribution of resources at the landscape scale (Matassa & Trussell 2011). On coral reefs, predatory fish reduce herbivore excursion distances (Madin et al. 2010a), the amount that herbivores consume (Rizzari et al. 2014, Catano et al. 2016), and the spatial distribution of foraging (Rasher et al. 2017). However, herbivores will venture into riskier habitats in order to forage in patches with greater resource availability (Gil et al. 2017) or to alleviate competition and increase per capita consumption (Grand & Dill 1999, White & Warner 2007). For example, parrotfish species on coral reefs will increase foraging range in areas with higher conspecific densities, despite greater predation risk (Nash et al. 2012, Davis et al. 2017). Furthermore, refuge size, quality, and configuration can influence herbivore density, movement patterns, and foraging decisions (Anderson 2001, Overholtzer-McLeod 2004, Shima et al. 2008, Harborne et al. 2012). Thus, variation in grazing behavior, and therefore grazing halo size, is likely controlled by a combination of predation risk and resource availability.

Previous studies of grazing halos have found unequivocal evidence that grazing decreases with distance from the patch reef, and have hypothesized that when predation risk is high, herbivores forage more intensively and closer to the reef, resulting in narrower grazing halos (Randall 1965, Ogden et al. 1973, Madin et al. 2011, Downie et al. 2013, Atwood et al. 2018). However, these studies have not explicitly tested whether predation risk alters *in situ* grazing patterns in order to drive variation in halo size (see Madin et al. 2019a for an exception), nor explored whether these grazing patterns are correlated to the heterogeneous landscape of resource availability that exists naturally in coral reef ecosystems. Here, we used a combination of remote sensing and mensurative experiments to ask: What causes variation in grazing halo size in Caribbean coral reef ecosystems? Specifically, we conducted a satellite analysis of patch reefs in the Florida Keys and Belize to determine how grazing halo size varies across the landscape ($n = 757$ patch reefs). We then explored how grazing patterns changed across natural gradients of predator density, herbivore density, and refuge size for a subset of patch reefs ($n = 13$). We hypothesized that herbivores would forage further from the reef and more frequently when predation risk is low and competition for resources is high. Our results demonstrate that predators do in fact suppress grazing in the halo zone. However, herbivore abundance, which is tightly linked to patch reef size, rather than predator abundance, is the better predictor of halo width and the spatial distribution of grazing.

2. MATERIALS AND METHODS

2.1. Study site and species

We explored variation in grazing patterns and grazing halo width across natural gradients of patch reef size, herbivore density, and predator density at 2 reef systems: the Florida Keys National Marine Sanctuary (FKNMS), USA (24.6°N , 81.4°W), and the South Water Caye Marine Reserve (SWCMR), Belize (16.8°N , 88.1°W) (Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m627p071_supp.pdf). Both the FKNMS and the SWCMR are multi-use marine reserves that encompass extensive areas of mangrove, seagrass, back reef, and fore reef habitats. Patch reefs in both locations varied from low-relief rubble aggregates to highly complex reefs composed of branching and massive corals. Algae, gorgonian corals, and seagrass (*Thalassia testudinum* Banks ex König; Hydrocharitaceae) dominated the substrate surrounding patch reefs in Florida, while patch reefs in Belize were mainly surrounded by *T. testudinum*.

2.2. Quantifying variation in grazing halos

To quantify variation in grazing halos, we estimated halo and patch reef geometries at 757 patch reefs using high spatial resolution ($>2.5\text{ m}$) satellite images provided by the Digital Globe Foundation (Belize) or available through Google Earth (version 7.1.5) (Florida). Specifically, a single observer digitized the patch reef edge and the halo boundary to generate polygon shapefiles for each individual reef and its respective halo. We visually estimated the halo boundary as the point of greatest transition in substrate reflectance surrounding the reef. We calculated patch reef area and mean halo width, the average nearest neighbor distance between dense clouds of points located along the halo and reef polygons, using ArcGIS[®] (version 10.4, ESRI 2017) and QGIS (version 2.18.13, QGIS Development Team 2017) software. See Text S1.1 for further details.

2.3. Quantifying grazing and fish communities at the local scale

We selected 13 patch reefs from our landscape analysis to test for differences in grazing patterns and halo width as a function of herbivore and predator densities using a mensurative experimental approach that exploited gradients in predator and herbivore

densities across different patch reefs. While our experimental goal was not to test for differences in protection status, we sampled patch reefs inside no-take marine protected areas and at nearby fished locations (Table S1) in order to ensure variation in predator and herbivore abundances between sites. No-take marine protected areas have been shown to alter the density, composition, and size structure of marine fishes compared with unprotected reference sites (Lester et al. 2009), and previous work in the greater Caribbean region has shown changes in grazing patterns and fish communities inside and outside of no-take marine protected areas (Mumby et al. 2006, Valentine et al. 2008). All research was conducted in summer 2016 using freediving equipment.

We assessed the distance that herbivorous fish grazed away from the reef edge using standardized seagrass (*T. testudinum*) assays (Hay 1984, Valentine et al. 2008). Each assay consisted of 2 seagrass blades clipped to weighted clothespins spaced ~30 cm apart, which were photographed prior to deployment. We deployed assays every 2 m along 20 m transects ($n = 3$), which extended outwards perpendicular to the patch reef edge at haphazard intervals around the reef with a minimum separation distance of 20 m. The assays were collected and photographed after 24 h (Belize) or 72 h (Florida). We calculated the proportion of seagrass consumed by comparing assay area before and after deployment using ImageJ software (Schneider et al. 2012; version 1.39) and divided by the duration of the deployment (proportion consumed d^{-1}). To directly compare grazing patterns between locations, we needed to account for the difference in deployment time between regions and the fact that $\sim 1 \text{ cm}^2$ of each grazing assay was hidden in the clothespin. Therefore, we normalized the proportion of each assay that was grazed in the range [0, 1] within regions by subtracting the minimum from each point and dividing by the range. To verify the relationship between satellite imagery and field data, we compared satellite reflectance, resource density, and grazing intensity along transects extending from the edge of 4 patch reefs (Text S1.2).

At each patch reef, we conducted 3–5 belt-transect fish surveys positioned along random compass headings extending through the center of the reef. For each survey, we recorded the identity and approximate size of all fish within a 5 m band centered on a 50 m transect line. We classified fish as either piscivores (hereafter predators), herbivores, or other according to the established literature (Randall 1967, Bohnsack et al. 1999, Valentine et al. 2008) (Table S2). Fish were classified as predators if there was

dietary evidence that they consumed fish prey (particularly herbivorous species like parrotfish and surgeonfish) and are considered common predators in the greater Caribbean region (Catano et al. 2017). We calculated the density of herbivores and predators as the mean number of encounters per transect at a particular patch divided by the transect area. We chose to focus our analysis on the effect of all herbivorous fish species rather than only Scarinae species, the dominant grazers in coral reef systems (Adam et al. 2015), because we were interested in how total herbivore density influenced grazing patterns. Considering the importance of Scarinae as grazers, however, we included an analysis of how Scarinae density alone influenced foraging (Fig. S3). Previous work on grazing halos has suggested that urchins, rather than herbivorous fish, are primarily responsible for halo formation (Ogden et al. 1973). However, preliminary analysis of urchin density at our field sites revealed consistently low urchin densities. Therefore, we excluded urchins from our analyses (see Text S1.3 for further details).

Our experimental design makes specific assumptions about how herbivores forage near patch reefs. Specifically, we assumed that herbivorous fish are central-place foragers that use the patch reef as shelter, and do not reside in interstitial spaces between reefs. We feel that this is a reasonable assumption, because sand gaps between reefs are known to inhibit the movement of herbivores (Turgeon et al. 2010), and the territory sizes of common Scarinae spp. are typically smaller than the sizes of the patch reefs where we conducted field work (Mumby & Wabnitz 2002). Very few herbivore species strictly inhabit seagrass plains, except *Sparisoma radians*, which is known to display this behavior. However, *S. radians* was not seen in this study. In assuming that herbivores are central-place foragers, we are also assuming that they make short foraging excursions away from the reef edge before returning to the safety of the reef structure. Therefore, we assume that our assays, which were arranged linearly with distance from the reef edge, are independent and approximate the foraging behavior of herbivores grazing in one dimension away from the reef (e.g. Madin et al. 2010b).

2.4. Data analysis

To understand the relationships among our local predictor variables (predator density, herbivore density, and patch reef area), we created bivariate plots and calculated Pearson's product moment correlation

coefficients. Preliminary analysis revealed that patch reef area was highly correlated with herbivore density ($r = 0.82$, $p < 0.001$). To address this collinearity, we used PCA to create a new variable, PCA 1, which accounted for 89% of the variation between patch reef area and herbivore density (Graham 2003).

To test what factors were linked to the spatial distribution of grazing at the local, patch-reef scale, we constructed a statistical model that examined grazing as a function of predator density, herbivore density/patch reef area (PCA 1), and distance from the reef edge (hereafter distance). We modeled grazing as 2 biologically relevant processes: grazing incidence (i.e. the binomial probability that an assay was grazed) and grazing intensity (i.e. the normalized proportional amount of the assay that was consumed, given that grazing occurred). We therefore used a 2-part hurdle model, which separates the data into 2 components: (1) a process that models the probability of a binomial occurrence (grazing incidence), and (2) a process that models the predicted amount of the response given its presence using a truncated distribution (grazing intensity) (Zuur et al. 2009) (see Text S2 for details).

Considering that our primary interest was in understanding how distance, predator abundance, and herbivore density/reef area influenced grazing while accounting for variation between regions, sites, and transects, we included region, site (i.e. patch reef), and transect as nested random effects. Models were fit using the 'glmmTMB' package (Brooks et al. 2017) in R version 3.4.2 (R Development Core Team 2017), which uses maximum likelihood estimation and the Laplace approximation to integrate over random effects. To model grazing incidence, we constructed a generalized linear mixed effects (GLME) model with a binomial distribution and logit link. To model grazing intensity, we used a linear mixed effects (LME) model with a beta distribution and logit link. We tested for main effects and all interactions between distance, predator abundance, and PCA 1 on both response variables, grazing incidence, and grazing intensity. Specifically, we included a 3-way interaction (predator abundance \times distance \times PCA 1) to determine if the effect of predation risk on grazing was contingent on the relationship between distance from the reef edge and herbivore abundance/reef area. To ask if variation in chronic predation risk (e.g. predator density) or herbivore density/reef size (PCA 1) changed the spatial distribution of grazing, we included interaction terms for distance \times predator abundance and distance \times PCA 1. We also allowed for a predator abundance \times PCA 1 interaction in

order to determine if the relationship between grazing and predation risk was mediated by herbivore density. A significant interaction between distance and either of the other predictor variables indicates that the impacts of predator abundance or PCA 1 on grazing are context-dependent (i.e. depend on the distance from the reef where the herbivores are foraging). Significant main effects reveal a mean change in grazing incidence or intensity due to the predictor.

We selected final models for grazing intensity and grazing incidence by dropping non-significant interactions ($\alpha > 0.1$). For reporting and visualization purposes, we calculated overall predicted grazing as the product of the probability of grazing incidence and intensity. To assess model fit, we visually inspected for heteroscedasticity and normality of residuals. A predictor variable was deemed significant ($\alpha < 0.05$) via Wald's tests, and confirmed using chi-square likelihood ratio tests. To validate our assumption that patch reefs were spatially independent, we visually assessed spatial correlograms and calculated Moran's I , a measure of spatial autocorrelation, for each of our predictor variables. We found no evidence for spatial autocorrelation in PCA 1 or predator density between nearby patch reefs.

To link local-scale drivers with landscape patterns, we explored relationships between predator density, herbivore density, and patch reef area using both local observations and regional patterns of variation in grazing halos. Specifically, in our local dataset we tested for relationships between halo width and predator density, PCA 1, and location using multiple linear regression. To ask how changes in patch reef area resulted in shifts in grazing halo width in our satellite data set of 757 patch reefs, we regressed patch area as a function of halo width and included an interaction with location to test for a difference in the relationship between Florida ($n = 662$) and Belize ($n = 95$). Spatial semivariogram plots of the model residuals revealed significant spatial autocorrelation in the regional data set. To account for this autocorrelation, we used a generalized least squares (GLS) regression approach that included a spatial correlation structure within each region (Pinheiro & Bates 2000) fit with the 'nlme' package (Pinheiro et al. 2018). We fit multiple correlation structures and selected an exponential correlation structure as the most parsimonious model by comparing Akaike's information criterion (AIC) and examining residual semivariogram plots. Considering that the area of a circle scales exponentially with its radius, the relationship should be linear in log-log space. Therefore, we \log_{10} -transformed both patch area and halo width to linearize the relationship.

3. RESULTS

Across 757 patch reefs, in 2 locations in the broader Caribbean region, grazing halo width varied from <1.0 to 69.7 m (9.58 ± 8.4 m, mean \pm SE unless otherwise stated; Fig. 1d). At local field sites, grazing halos ranged from 4–36 m wide on reefs that varied in size by more than a factor of 10. Local surveys of fish communities revealed differences in herbivore and predator densities between patch reefs. Herbivore density ranged from 0.059 to 0.440 ind. m^{-2} and predominantly consisted of parrotfishes (Scarinae) and damselfishes (Pomacentridae), while predator density ranged from 0.000 to 0.070 ind. m^{-2} , and predominantly consisted of snappers (Lutjanidae). The rank order of abundance of individual species differed between Florida and Belize, but we found no evidence for systematic differences in herbivore density or predator density between locations (ANOVA, location \times trophic level: $F_{1,90} = 1.19$, $p = 0.27$). While grazing patterns varied between individual patch reefs, grazing consistently declined with distance from the reef edge (Fig. S4) despite increasing resource density farther from the reef ($r^2 = 0.71$, $p < 0.001$, $n = 4$ patch reefs; Figs. S5 & S6). Of the grazing assays, 47% showed evidence of grazing, and herbivores grazed $27 \pm 37\%$ ($n = 612$) of each assay. On average, $80.4 \pm 23\%$ of the total grazing that occurred at reefs occurred inside the halo boundary.

Herbivory assays suggested that grazing patterns were correlated with components of the fish community and reef size. Across our study sites, higher predator density was correlated with a significant reduction in grazing intensity ($\beta_{\text{intensity}} = -0.45 \pm 0.1$, $p = 0.002$). When predator density doubled, grazing declined by 29% overall (Fig. 2a). However, how far herbivores grazed from the reef edge was not influenced by predator density (distance \times predator abundance interaction: $\beta_{\text{incidence}} = 0.28 \pm 0.2$, $p = 0.07$; $\beta_{\text{intensity}} = -0.07 \pm$

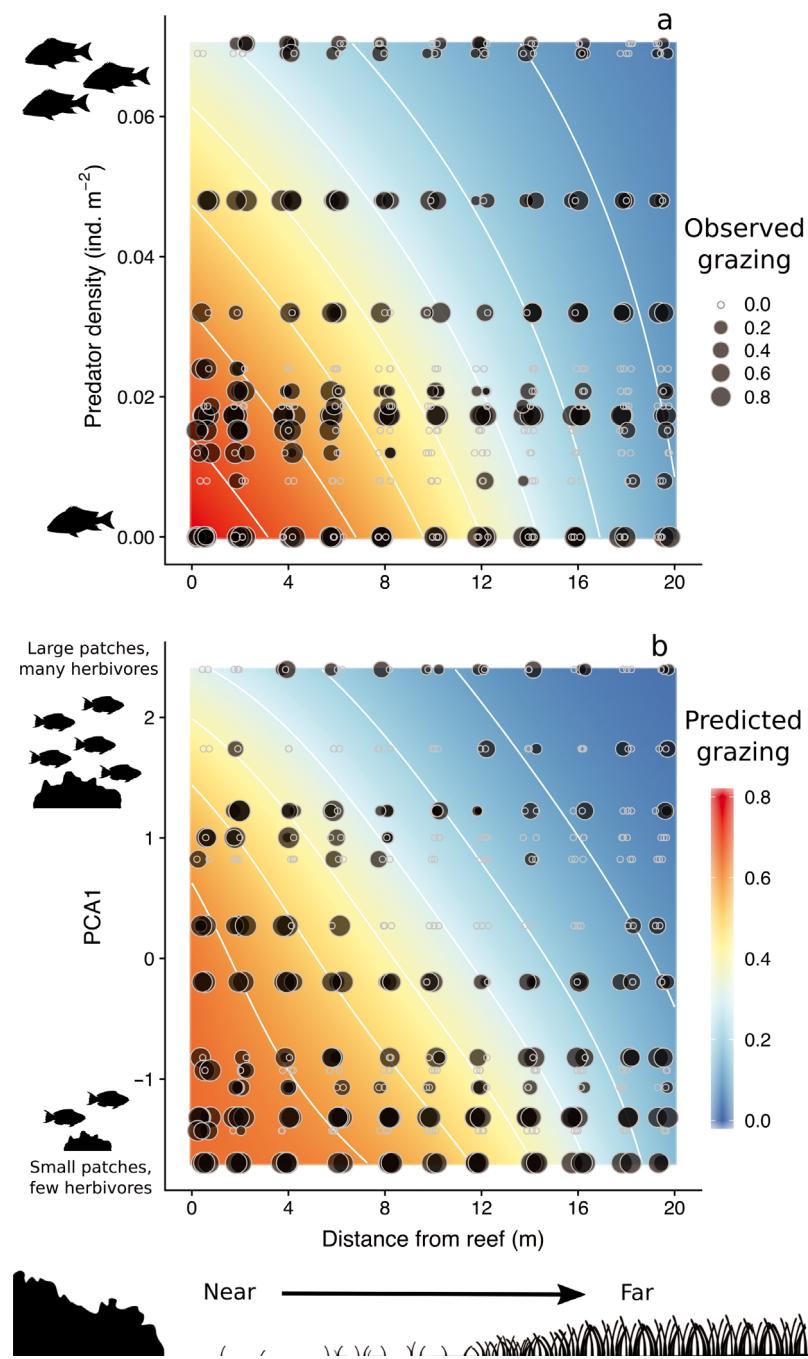


Fig. 2. Relationship between grazing, distance from the reef edge, and (a) predator density or (b) PCA1, which is the first principal component of variation between herbivore density and patch reef area at 13 patch reefs in the broader Caribbean region. Color represents predicted grazing incidence multiplied by grazing intensity, and circles represent observed proportion grazed. Contours are spaced at 0.1 unit intervals. Predators suppressed grazing intensity ($\beta_{\text{intensity}} = -0.45 \pm 0.1$, $p = 0.001$), but did not alter the spatial distribution of either grazing incidence or intensity (distance from the reef \times predator density: $\beta_{\text{incidence}} = 0.28 \pm 0.2$, $p = 0.07$; $\beta_{\text{intensity}} = -0.07 \pm 0.1$, $p = 0.44$). PCA 1 predicted the distance herbivores foraged from the reef edge (distance \times PCA 1: $\beta_{\text{incidence}} = 0.48 \pm 0.18$, $p = 0.007$; $\beta_{\text{intensity}} = -0.31 \pm 0.1$, $p = 0.005$). Results are based on a mixed effects hurdle model (see Section 2.4 for details)

0.1, $p = 0.4$). Rather, changes in patch reef size and herbivore density altered the relationship between grazing and the distance that herbivores foraged from the reef edge (Fig. 2b). Grazing at larger patch reefs with higher herbivore densities (high values of PCA 1) was concentrated closer to the reef edge than at smaller reefs with fewer herbivores (distance \times PCA 1 interaction: $\beta_{\text{incidence}} = 0.48 \pm 0.2$, $p = 0.007$; $\beta_{\text{intensity}} = -0.31 \pm 0.1$, $p = 0.001$; Fig. 3).

This result contradicts the patterns we observed in grazing halo width at both local and regional scales. While the results of our grazing assays suggest that grazing halos would be most narrow on large patch reefs with many herbivores, we found that smaller patch reefs with fewer herbivores had significantly narrower halos than larger patch reefs with many herbivores (PCA 1 was positively correlated with halo width; $R^2 = 0.40$, $p < 0.001$; Fig. 4a), and the slope of the relationship did not differ significantly between locations (PCA 1 \times location, $p = 0.08$). This pattern was consistent at the landscape scale; across 757 patch reefs, halo width was positively correlated with patch reef area (Fig. 4b; $p < 0.001$), and there was no

evidence of differences between locations. Given that predators reduced grazing on our assays in this experiment and the clear evidence of predation risk on grazing in the literature, we expected predators to be a strong predictor of halo size. However, there was no detectable relationship between predator abundance and halo width ($p = 0.45$).

4. DISCUSSION

Species interactions can have dramatic effects on the distribution of biogenic habitat and ecosystem processes at large spatial scales (Atwood et al. 2015, Schmitz et al. 2017, Tarnita et al. 2017). Our study attempted to link herbivore behavior at local scales with pattern formation in coral reef landscapes across 10s–100s of km². An abundance of evidence indicates that consumers reduce foraging intensity farther from refuge habitats (Brown & Kotler 2004), and that grazing declines with distance from coral patch reef edges (Valentine et al. 2007, Downie et al. 2013, Gil et al. 2017). Our results confirm this general

pattern, and build upon previous findings by exploring the potential factors that cause grazing to decline with distance from coral patch reefs. Specifically, we show that, at the patch reef scale, predation risk reduced the overall amount of grazing that occurred. Predation risk did not, however, influence the spatial distribution of grazing or grazing halo width. The distance herbivores foraged from the reef edge and halo width were correlated with the density of herbivores on the reef, which was tightly linked to patch reef size. While the connection between herbivore density, foraging behavior, and halo width remains ambiguous, the results of our landscape analysis corroborate our local mensurative experiment. Larger patch reefs with more herbivores tended to have wider halos, and patch reef size was strongly correlated with halo width across the broader Caribbean region. Together our results offer novel insights into how herbivore density, refuge size, and predation risk interact to influence the spatial distribution of foraging and vegetation patterns visible from space.

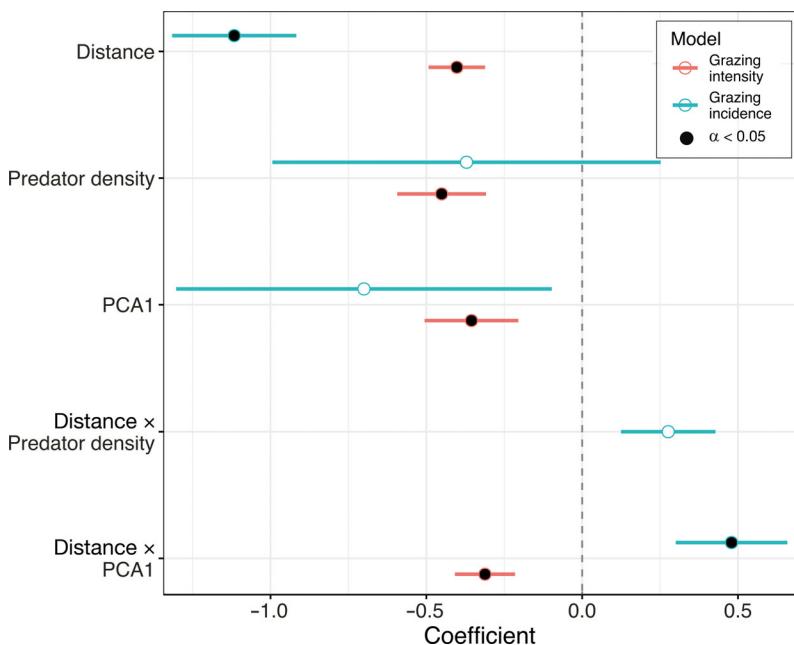


Fig. 3. Coefficient estimates (mean \pm SE) depicting main effects and interactions of distance from the reef edge, predator density, and PCA 1, or the first principal component of variation between herbivore density and patch reef area, on the probability that herbivores grazed (grazing incidence) and the grazing intensity. Grazing was quantified using standardized *Thalassia testudinum* assays deployed along transects extending from the patch reef edge across the halo zone. Results are based on a mixed effects hurdle model (see Section 2.4 for details). Filled coefficient estimates were significant ($\alpha < 0.05$), and all predictor variables were scaled in order to compare effect sizes. Main effects are included for reference only despite significant higher-order interactions

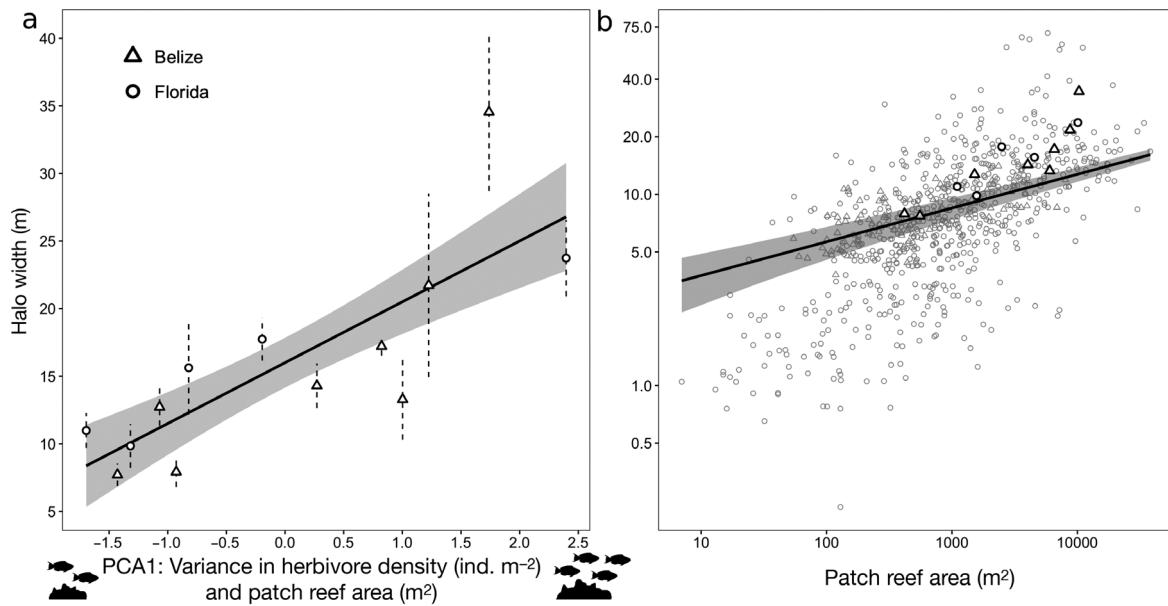


Fig. 4. (a) Linear relationship between grazing halo width and variation in herbivore density and/or patch reef size (PCA 1). Dashed vertical error bars represent \pm SE around mean estimates of halo boundaries at each patch reef by 4 independent observers. Larger patch reefs with more herbivores tended to have wider halos than smaller patch reefs with fewer herbivores ($R^2 = 0.40$, $p < 0.001$). Solid line represents the ordinary least squares linear regression estimate; shaded area represents \pm SE of the regression estimate. (b) Log₁₀-log₁₀ relationship between patch area and halo width at 757 patch reefs showing a similar pattern, with larger patch reefs having wider halos ($p < 0.001$). **Bold** symbols are patch reefs where fieldwork was conducted ($n = 13$), while gray symbols are patch reefs analyzed using satellite imagery. Solid line represents model prediction of a generalized least squares regression that includes a correlation structure to account for spatial autocorrelation; shaded region represents \pm SE of the regression estimate

Predation risk has been proposed as the primary indirect mechanism behind variation in grazing halo size (Madin et al. 2011) and decreased grazing pressure farther from coral patch reefs (Randall 1965, Ogden et al. 1973), because of the extensive evidence that predators alter herbivore behavior (e.g. Lima & Dill 1990, Schmitz et al. 2004), and decrease foraging pressure away from the safety of refuges (Brown & Kotler 2004). When presented with model predators, an experimental proxy for acute predation risk, coral reef herbivores remain closer to refuges and decrease bite rates (Rizzari et al. 2014, Catano et al. 2016). Coral reef herbivores also reduce foraging excursions in areas with greater predator abundance, a result attributed to higher chronic predation risk (Madin et al. 2010a). Furthermore, movements of large predators on coral reefs can be shaped by landscape configuration, and herbivores modify when and where they forage in order to reduce encounters with predators (Rasher et al. 2017). Consistent with previous work, we found that predators indeed reduced the overall amount of grazing that occurred. However, despite the abundance of empirical and theoretical support that predators limited the distance herbivores forage, we found no evidence that

predator density—a proxy of predation risk— influenced how far herbivores grazed from the reef edge. Instead, variation between herbivore density and patch reef area (PCA 1) predicted the spatial distribution of grazing (Fig. 2b).

The results of our field assays reveal that grazing pressure on small reefs with fewer herbivores was more diffuse than at large reefs where grazing was concentrated along the reef edge (Fig. 2b). This result would suggest that grazing halo width should be widest on the smallest reefs. However, we found the exact opposite. At both our local field sites and across the landscape, grazing halo width scaled with patch reef size (Fig. 4). We propose 3 alternative explanations for this discrepancy. (1) Halo formation and maintenance are processes that occur over the temporal scale of the resource's life-history strategy (~ months to years). Therefore, our short-term (24–72 h) feeding assays may not have been conducted at long enough temporal scales to adequately capture spatial variation in the process of herbivory. (2) While foraging by herbivores has been widely assumed to be the primary mechanism of halo formation, other functional groups may play a role. Recent research conducted in Australia suggests that invertivorous

fish, which forage by bioturbating substrate and disturbing benthic algae, may create wider halos than is predicted by the distribution of herbivores alone (Madin et al. 2019a). The mismatch between our assay results and large-scale patterns could therefore be explained if larger reefs support greater populations of bioturbators. (3) Large roving piscivores, like reef sharks, are notoriously challenging to sample (McCauley et al. 2012), often foraging in shallow water only at night, or avoiding interactions with divers. Our sampling design, which was focused on monitoring reef-associated predators (e.g. barracuda, groupers, and snappers), may have underestimated chronic predator risk, and unobserved relationships between reef size and predator abundance could explain the mismatch between the grazing assay results and patterns in halo width. Future research into the drivers of grazing halo formation should focus on experimental manipulations in order to fully parse the mechanistic link between higher herbivore densities, larger reefs, and wider grazing halos.

While the root mechanism linking the observed *in situ* grazing patterns with halo size remains unclear, our results provide compelling evidence that grazing halo size scales with habitat area. Across hundreds of patch reefs in a broad biogeographic region, larger patch reefs were surrounded by wider halos (Fig. 4b). This is consistent with a recent analysis of halo width conducted in the Great Barrier Reef, Australia, which found similar positive scaling of halo width with reef area (Madin et al. 2019b). The strong relationship between habitat size and halo width suggests that some biological component of larger reefs drives increased grazing halo size. Indeed, we found that herbivore abundance was positively correlated with patch reef area, which is consistent with previous work on abundance-area scaling in coral reefs (Harborne et al. 2012). One plausible explanation for the observed relationship between grazing halo width and reef size is competition for resources between herbivores. When per capita resource availability near larger refuges decreases due to higher herbivore density, consumers are willing to assume greater risk and forage further in order to meet energetic needs (Grand & Dill 1999, White & Warner 2007). Indeed, previous work suggests that exploitative competition for resources rather than predation risk drove the spatial foraging patterns of parrotfish on coral reefs (Nash et al. 2012, Davis et al. 2017). An alternative explanation for the observed relationship between grazing halo width and reef area may be geometric scaling. Larger reefs tend to support higher densities of herbivores. As a reef's area increases, its area:

perimeter ratio also increases. Consequently, higher densities of herbivores must forage in functionally less perimeter space, resulting in wider halos (Madin et al. 2019b).

Linking large-scale patterns with local processes is central to understanding how ecosystems function (Levin 1992). In this study, we provide evidence linking local interactions between predators, herbivores, and resources, with widespread variation in grazing halo size, a landscape-scale pattern. While previous studies have assumed that the indirect mechanism behind halo formation is predation risk, our results suggest that predation risk alone is not enough to alter grazing patterns and produce a halo. Rather, where herbivores graze is largely dependent on the number of herbivores on a patch reef, which is linked to reef size. Grazing halo width is therefore likely driven by complex interactions between predation risk, herbivore density, and resource availability. While our results raise questions regarding the mechanisms that link grazing patterns and halo width, they contribute to a growing understanding of the underlying factors driving grazing halo formation (Madin et al. 2019a,b). As we continue to build this understanding, grazing halos have the potential to emerge as indicators of key ecological processes, such as herbivory, that are critical for the resilience of coral reef and seagrass ecosystems.

Developing cost-effective, remote observation techniques to monitor ecosystem processes is essential to improving management of coral reef ecosystems (e.g. to quantify coral bleaching; Levy et al. 2018), and grazing halos may offer opportunities to monitor reef function at large scales in remote areas. For example, grazing halos could be used as indicators of declining herbivore populations due to targeted fisheries, or increasing herbivore populations following the implementation of no-take marine reserves (*sensu* Madin et al. 2011). Recent research has also shown that the species interactions that drive grazing halo formation alter the spatial distribution of sediment organic carbon stocks (Atwood et al. 2018). Thus, grazing halos could also be used to remotely monitor shifts in critical carbon sinks. Merging field experiments with remote sensing observations in order to advance technological methods of monitoring ecosystem processes is essential to improve the management of coral reef ecosystems in the Anthropocene.

Data availability and code. All data and code used to analyze data can be found at: <https://github.com/bartdifiore/GrazingHalos.git>

Acknowledgements. We thank 3 anonymous reviewers, the Stier and Queenborough labs, and the Ucross High Plains Stewardship Initiative working group for constructive feedback on the manuscript. Special thanks to A. Looby, L. DiFiore, T. Petronzio, T. Hodges, and S. Thomas-Train for field assistance, and to O. Schmitz, J. Campbell, and L. Comita for informative conversation and ideas. We thank D. Burkepile for reviewing a previous version of this manuscript. This research was supported by an NSF GRFP grant, the Yale Tropical Resources Institute, the Link Foundation, the Yale School of Forestry and Environmental Studies, and the Digital Globe Foundation. All research in the USA was conducted under NOAA permit number FKNMS-2016-069. We thank the Belize Fisheries Department for permits to work in Belize. This is contribution 1027 of the Smithsonian's Caribbean Coral Reef Ecosystems (CCRE) Program and #1120 of the Smithsonian Marine Station.

LITERATURE CITED

- Adam TC, Burkepile DE, Ruttenberg BI, Paddock MJ (2015) Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar Ecol Prog Ser* 520:1–20
- Anderson TW (2001) Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82: 245–257
- Atwood TB, Connolly RM, Ritchie EG, Lovelock CE and others (2015) Predators help protect carbon stocks in blue carbon ecosystems. *Nat Clim Chang* 5:1038–1045
- Atwood TB, Madin EMP, Harborne AR, Hammill E and others (2018) Predators shape sedimentary organic carbon storage in a coral reef ecosystem. *Front Ecol Evol* 6:110
- Bohsack JA, McClellan DB, Harper DE, Davenport GS and others (1999) Baseline data for evaluating reef fish populations in the Florida Keys, 1979–1998. US Department of commerce, NOAA, NMFS, SEFSC, Miami, FL
- Bonachela JA, Pringle RM, Sheffer E, Coverdale TC and others (2015) Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science* 347:651–655
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400
- Brown JS (1992) Patch use under predation risk. I. Models and predictions. *Ann Zool Fenn* 29:301–309
- Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 7:999–1014
- Catano LB, Rojas MC, Malossi RJ, Peters JR, Heithaus MR, Fourqurean JW, Burkepile DE (2016) Reefscape of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. *J Anim Ecol* 85:146–156
- Catano LB, Barton MB, Boswell KM, Burkepile DE (2017) Predator identity and time of day interact to shape the risk-reward trade-off for herbivorous coral reef fishes. *Oecologia* 183:763–773
- Covich AP (1976) Analyzing shapes of foraging areas: some ecological and economic theories. *Annu Rev Ecol Syst* 7: 235–257
- Davis K, Carlson PM, Bradley D, Warner RR, Caselle JE (2017) Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish. *Oecologia* 184:139–149
- Downie RA, Babcock RC, Thomson DP, Vanderklift MA (2013) Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs. *Mar Ecol Prog Ser* 482:217–225
- ESRI (2017) ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, CA
- Gil MA, Zill J, Ponciano JM (2017) Context-dependent landscape of fear: algal density elicits risky herbivory in a coral reef. *Ecology* 98:534–544
- Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815
- Grand TC, Dill LM (1999) The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? *Anim Behav* 58: 443–451
- Harborne AR, Mumby PJ, Ferrari R (2012) The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environ Biol Fishes* 94:431–442
- Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? *Ecology* 65:446–454
- Heithaus MR, Wirsing AJ, Dill LM (2012) The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Mar Freshw Res* 63:1039–1050
- Hughes JJ, Ward D, Perrin MR (1994) Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology* 75:1397–1405
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J and others (2009) Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384:33–46
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73: 1943–1967
- Levy J, Hunter C, Lukaczyk T, Franklin EC (2018) Assessing the spatial distribution of coral bleaching using small unmanned aerial systems. *Coral Reefs* 37:373–387
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Madin EMP, Gaines SD, Warner RR (2010a) Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology* 91:3563–3571
- Madin EMP, Gaines SD, Madin JS, Warner RR (2010b) Fishing indirectly structures macroalgal assemblages by altering herbivore behavior. *Am Nat* 176:785–801
- Madin EMP, Madin JS, Booth DJ (2011) Landscape of fear visible from space. *Sci Rep* 1:14
- Madin EMP, Dill LM, Ridlon AD, Heithaus MR, Warner RR (2016) Human activities change marine ecosystems by altering predation risk. *Glob Change Biol* 22:44–60
- Madin EMP, Precoda K, Harborne AR, Atwood TB, Roelfsema CM, Luiz OJ (2019a) Multi-trophic species interactions shape seascape-scale coral reef vegetation patterns. *Front Ecol Evol* 7:102
- Madin EMP, Harborne AR, Harmer AMT, Luiz OJ, Atwood TB, Sullivan BJ, Madin JS (2019b) Marine reserves shape seascapes on scales visible from space. *Proc R Soc B* 286: 20190053
- Matassa CM, Trussell GC (2011) Landscape of fear influences the relative importance of consumptive and non-consumptive predator effects. *Ecology* 92:2258–2266
- McCauley DJ, McLean KA, Bauer J, Young HS, Micheli F (2012) Evaluating the performance of methods for esti-

- mating the abundance of rapidly declining coastal shark populations. *Ecol Appl* 22:385–392
- 👉 Mumby PJ, Wabnitz CCC (2002) Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environ Biol Fishes* 15: 265–279
- 👉 Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV and others (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- 👉 Nash KL, Graham NAJ, Januchowski-Hartley FA, Bellwood DR (2012) Influence of habitat condition and competition on foraging behaviour of parrotfishes. *Mar Ecol Prog Ser* 457:113–124
- 👉 Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182:715–717
- 👉 Overholtzer-McLeod KL (2004) Variance in reef spatial structure masks density dependence in coral-reef fish populations on natural versus artificial reefs. *Mar Ecol Prog Ser* 276:269–280
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer-Verlag, New York, NY
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018) nlme: Linear and nonlinear mixed effects models. R package version 3.1-137. <https://CRAN.R-project.org/package=nlme>
- 👉 Pringle RM, Doak DF, Brody AK, Jocqué R, Palmer TM (2010) Spatial pattern enhances ecosystem functioning in an African savanna. *PLOS Biol* 8:e1000377
- QGIS Development Team (2017) QGIS geographic information system. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- 👉 Randall JE (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46: 255–260
- Randall JE (1967) Food habits of reef fishes of the West Indies. Institute of Marine Sciences, University of Miami, Coral Gables, FL
- 👉 Rasher DB, Hoey AS, Hay ME (2017) Cascading predator effects in a Fijian coral reef ecosystem. *Sci Rep* 7:15684
- 👉 Rietkerk M, van de Koppel J (2008) Regular pattern formation in real ecosystems. *Trends Ecol Evol* 23:169–175
- 👉 Rizzari JR, Frisch AJ, Hoey AS, McCormick MI (2014) Not worth the risk: apex predators suppress herbivory on coral reefs. *Oikos* 123:829–836
- 👉 Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett* 7:153–163
- 👉 Schmitz OJ, Miller JRB, Trainor AM, Abrahms B (2017) Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. *Ecology* 98:2281–2292
- 👉 Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9: 671–675
- 👉 Shima JS, Osenberg CW, St. Mary CM (2008) Quantifying site quality in a heterogeneous landscape: recruitment of a reef fish. *Ecology* 89:86–94
- 👉 Sih A (1980) Optimal behavior: Can foragers balance two conflicting demands? *Science* 210:1041–1043
- 👉 Tarnita CE, Bonachela JA, Sheffer E, Guyton JA, Coverdale TC, Long RA, Pringle RM (2017) A theoretical foundation for multi-scale regular vegetation patterns. *Nature* 541: 398–401
- 👉 Turgeon K, Robillard A, Gregoire J, Duclos V, Kramer DL (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecology* 91:3332–3342
- 👉 Valentine JF, Heck KL Jr, Blackmon D, Goecker ME and others (2007) Food web interactions along seagrass–coral reef boundaries: effects of piscivore reductions on cross-habitat energy exchange. *Mar Ecol Prog Ser* 333:37–50
- 👉 Valentine JF, Heck KL Jr, Blackmon D, Goecker ME and others (2008) Exploited species impacts on trophic linkages along reef–seagrass interfaces in the Florida Keys. *Ecol Appl* 18:1501–1515
- 👉 van Rooyen MW, Theron GK, van Rooyen N, Jankowitz WJ, Matthews WS (2004) Mysterious circles in the Namib Desert: review of hypotheses on their origin. *J Arid Environ* 57:467–485
- 👉 Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548
- 👉 White JW, Warner RR (2007) Behavioral and energetic costs of group membership in a coral reef fish. *Oecologia* 154: 423–433
- Zuur AF, Leno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer-Verlag, New York, NY

Editorial responsibility: Peter Edmunds,
Northridge, California, USA

Submitted: February 18, 2019; *Accepted:* July 12, 2019
Proofs received from author(s): September 10, 2019