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Context-dependent landscape of fear: algal density elicits risky herbivory in a coral reef

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Abstract. Foraging theory posits that isolation from refuge habitat within a landscape increases perceived predation risk and, thus, suppresses the foraging behavior of prey species. However, these effects may depend fundamentally on resource availability, which could affect prey boldness and can change considerably through bottom-up processes. We conducted a field survey and experiment in a coral reef to test the effects of isolation from refuge habitat (i.e., reef structure) on herbivory by reef fishes and whether these effects depend on resource density. By fitting continuous-time, pure death Markov processes to our data, we found that at both the local and landscape scale distance from refuge habitat reduced herbivory in attractive resource patches of palatable benthic algae. However, our field experiment revealed that higher initial resource densities weakened negative effects of distance from refuge habitat on herbivory. Furthermore, we observed higher bite rates and greater total lengths of herbivorous fishes with greater distance from refuge habitat—responses consistent with higher perceived predation risk. Our results suggest that while the loss or fragmentation of refuge habitat reduces consumer control of resources, greater resource densities can partially counteract this effect by altering landscapes of fear of consumer species. Our findings emphasize the importance of considering the spatial context of species interactions that structure communities.

Key words: behavioral tradeoff; benthic algae; foraging theory; maximum likelihood; pure death Markov processes; spatial ecology; top-down vs. bottom-up processes.

Introduction

Some habitat provides refugia that protect animals from predators; thus, the availability (i.e., proximity, abundance) of refuge habitat can affect how an animal forages across space by shaping its "landscape of fear" (Laundre et al. 2001). Foraging theory predicts that animals should harvest fewer resources in habitat patches that are more exposed to predators, including habitat patches more isolated from refuge habitat (Brown 1988, 1999). Indeed, empirical studies across terrestrial and aquatic systems have shown that prey forage less in patches that are more distant from refuge habitat (Brown and Kotler 2004). In addition, foraging theory predicts that animals should forage more in habitat patches with higher resource densities (Fretwell and Lucas 1970, Charnov 1976), a pattern that has also been supported empirically (e.g., Dreisig 1995, Katz et al. 2013). However, whether the relationship between resource harvest rate and predation risk depends on resource availability remains largely untested (but see O'Dowd and Hay [1980] on seed harvest by rodents), while the magnitude and frequency of shifts in resource availability rise across ecosystems.

While the abundance of primary producers can rise abruptly in response to top-down, consumer-mediated processes (e.g., predation or fear thereof), it can similarly rise in response to bottom-up processes, such as enrichment with nutrients (Vitousek et al. 1997, Elser et al. 2007, Fabricius 2011) or other limiting factors (Polis et al. 1997), competitive release (McCook et al. 2001), or increased recruitment (e.g., changing winds/currents increasing larval supply; Bellgrove et al. 2004, Elmhirst et al. 2009). Predation risk may interact with resource density to influence spatial patterns of herbivory and, thus, influence the ability of herbivores to control resource populations. Three qualitative outcomes are possible: (1) herbivores could under-exploit increases in resource density in riskier habitat patches (i.e., those more exposed to predators); (2) increases in resource density may entice herbivores to overcome fear of predation in exposed habitat patches; or (3) higher resource densities may stimulate uniform increases in consumption across levels of risk, homogenizing increases in resources across spatially heterogeneous landscapes (Appendix S1: Fig. S1).

Coral reefs are characterized by spatially heterogeneous landscapes, in which habitat dominated by reef structures are intermixed, in various spatial configurations, with open sand flat habitat. While ambush predators, like groupers, snappers, and eels, can be more abundant or more lethal within reef habitat, these mesopredators typically pose a greater threat to juvenile fishes and a lesser

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threat to adult fishes, which are more vulnerable to larger, transient predators, like sharks, barracudas, and jacks, which chase down their prey (Almany 2004). In systems where they still dominate, blacktip reef sharks have been shown to preferentially forage along reef edges and within adjacent sand flat habitat (Papastamatiou et al. 2009). Thus, for roving herbivorous reef fishes that are dominant herbivores in most reef systems, reef habitat provides critical refuge from predators (Bellwood et al. 2004, Madin et al. 2010*a*, *b*). However, this means that algae growing on or near reef habitat are typically most competed for, causing fish to forage in adjacent sand flat habitats that can accumulate algae (Fong and Paul 2011, Madin et al. 2011) but provide little to no refuge from predators. Distance from refuge habitat can suppress community-wide herbivory rates even when herbivores are highly mobile (Madin et al. 2011), presumably because the further into sand flat habitat a forager ventures, the more time it will spend in this riskier habitat and, thus, the greater its integrated risk of predation over time. However, higher densities of algae may counteract effects of landscapes of fear on herbivory, though this relationship remains untested in coastal marine systems.

We quantified and modeled, using a stochastic process, how herbivory changed due to isolation from refuge habitat (coral reef) and resource density (algae) in a coral reef. We took two approaches to test our hypotheses that isolation from refuge weakens herbivory across spatial scales and interacts with algal density. First, we quantified herbivory of outplanted patches of a palatable macroalga as a function of various distances from reef habitat in a spatially heterogeneous landscape. Next, we conducted a field experiment that quantified harvest rates of multiple algal species across five levels of isolation from refuge habitat and two initial densities of algae (representative of bottom-up stimulation). We also quantified the traits of herbivores that visited our experimental patches.

Methods

Study location

This study took place in the backreef off of the north shore of the island of Mo'orea, French Polynesia (17°28′59″ S, 149°50′2″ W), a system in which blacktip reef sharks are dominant predators, palatable algae readily accumulate in sand flat habitat, and nutrient enrichment drives demonstrable increases in algal density (Appendix S1). We conducted the survey of herbivory and the field experiment in the Austral winters (June and July) of 2011 and 2012, respectively.

We used Google Earth imagery and field surveys to select 30 locations that differed in their level of isolation from reef structural habitat (herbivory survey) and three locations characterized by a distinct interface between habitat dominated by dense (contiguous) coral reef and relatively structure-free sand flat habitat (field experiment). For our survey, we compared herbivory rates across a spatially heterogeneous backreef location, covering an area of approximately 2,100 m^2 (Fig. 1a). While sites were different at the landscape scale, they were consistent at the patch scale, each consisting of a mostly dead *Porites* spp. coral colony (the locally dominant taxon) of similar size and depth (1.4–2.1 m). We marked each site with a handheld GPS device, which we also used to ground truth our study map. We quantified isolation at each site using various predictor variables, including distance from contiguous reef habitat, as well as the composition of surrounding habitat (Appendix S1).

Landscape-scale survey

For our survey, we assessed herbivory rates across study sites by measuring consumption of the macroalga *Acanthophora spicifera*, collected from nearby inshore reef locations. We chose this species because it is palatable and attractive to a wide range of herbivorous fishes, particularly those of the family Acanthuridae that dominate at our study locations (Poray and Carpenter 2014, Brooks 2016), and thus its consumption provides a measure of the relative potential for herbivores to control algae (Littler and Littler 2007, Loffler et al. 2015). We cut these algae into unbranched strands of similar color, thickness, and morphology. We used clothespins to secure the strands upright by their bases, with 5.0 cm of each algal thallus available to herbivores. We tied six of these clothespins to each of three nylon strings that we deployed atop each site (18 algal strands per site, using site as our level of replication), anchored on either end using nails buried under coral rubble. At each of the 30 sites, covering a continuous range of isolation from refuge habitat, we conducted a single herbivory assay, and we initiated these assays at three sites per day over days of similar weather conditions, taking care to select sites over a range of refuge habitat isolation for a given day. After 6, 24, 30, and 48 h, we re-measured each algal strand to the nearest mm to quantify losses (which we assumed were entirely due to herbivory).

Field experiment

For our experiment, at each of our three study locations, we created two parallel linear arrays, separated by at least 30 m, and each running perpendicular to the reef-sand boundary. Each array consisted of five sites, each at a different distance from structural refuge habitat: inside the reef habitat (2 m in from the reef edge), and 5, 10, 20, and 30 m away from the reef edge (i.e., in the sand flat habitat). We chose these distances based on observations in our system and in other systems (e.g., Madin et al. 2011) that sand flats within approximately 5–10 m are often picked clean of algae, forming "grazing halos." We placed a small cinderblock (l × w × h = 25 × 20 × 11 cm), to be used for herbivory trials, at each site 2 weeks prior to our study, to allow fishes to acclimate to the new objects, which resemble small dead coral colonies or piles

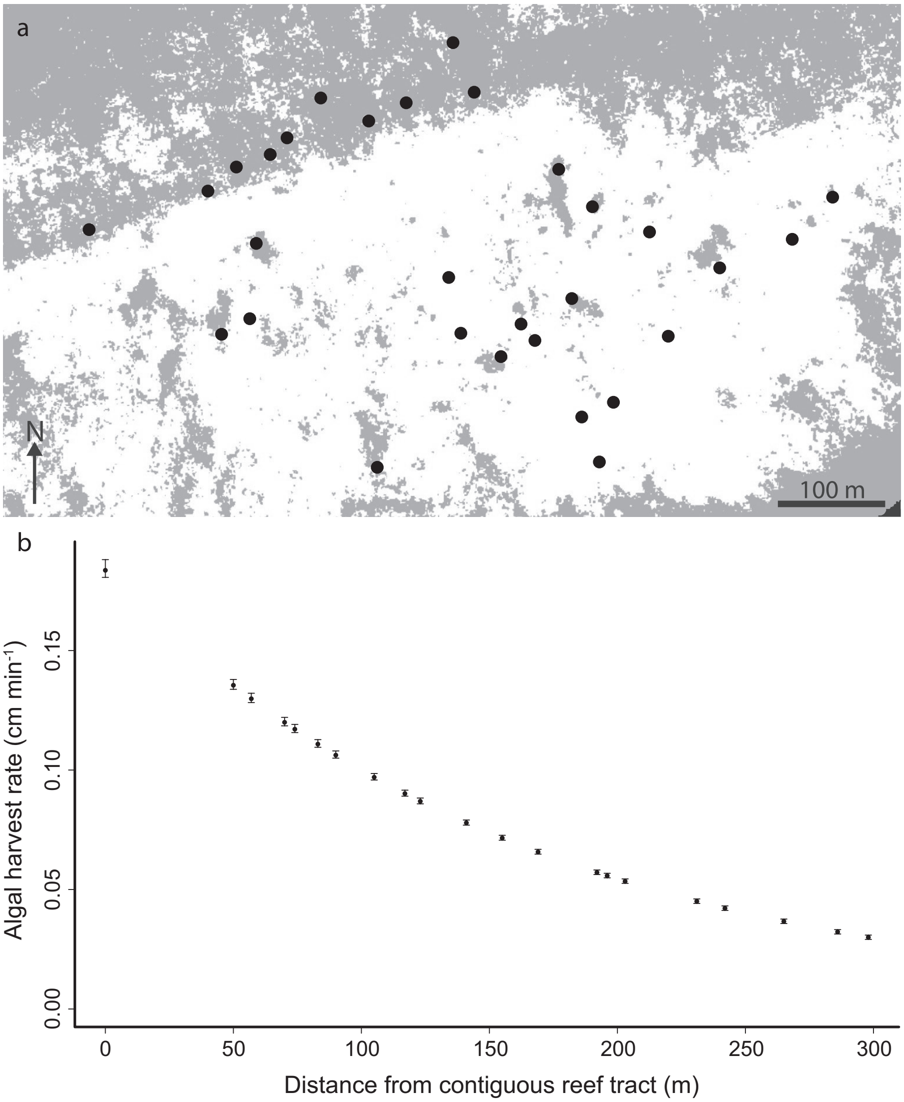

FIG. 1. (a) The location of our study sites (black circles, $n = 30$) for our landscape-scale field survey, overlaid atop a map that designates each pixel as either sand flat (white) or reef (grey) habitat (created with ArcGIS software; ESRI 2011). Ten of the 30 study sites were located within the contiguous reef tract to the northwest, and the shoreline (with associated shallow fringing reef) ran east-west, just south of the mapped region. We used this map to extract landscape-scale predictor variables for our statistical modeling (results summarized in Appendix S3: Table S1). (b) Harvest rates (mean ± 95% confidence intervals) of the macroalga *Acanthophora spicifera* from the best-fit model over distance from the contiguous reef tract (northwest side of the survey area). Reported values are based on four measures over time of algal harvest rate at each of the 30 sites (including 10 sites within the contiguous reef, at 0 distance).

of coral rubble common to sand flat habitats. For our herbivory trials, in addition to using the highly palatable macroalga *Acanthophora spicifera* (used in our survey), we included three more macroalgal species (*Amansia rhodantha*, *Asparagopsis taxiformis*, and *Sargassum pacificum*), as well as filamentous algal turf, to test for species-specific responses (see Appendix S1 for additional rationale). We collected and sorted through individual strands of each macroalga, so that each sample within a species had a similar length, color, thickness, straightness, and, for *S. pacificum*, branch density. We collected algal turf by using a pneumatic drill to extract circular cores (4 cm diameter) of dead coral skeleton completely covered in algal turf from territories guarded by the farmer fish, *Stegastes nigricans*.

For each herbivory trial, we used cable ties and clothespins to attach macroalgae to each cinderblock (see Appendix S1: Fig. S3). We secured the base of each strand of macroalgae in the mouth of a clothespin that was tied to the cinderblock, allowing for a uniform length of each species of macroalgae to be initially exposed to herbivores (exposed length: 5 cm for *Acanthophora spicifera*, *Am. rhodantha*, and *As. taxiformis*; 8 cm for *S. pacificum*). We used cable ties to directly attach cores of algal turf to the cinderblock. At each of the three study locations, we randomly assigned one array to a low initial algal density treatment and the other array to a high initial algal density treatment. To impose the low density treatment at a site, we used one strand of each macroalgal species and one core of algal turf, while we imposed four times that amount for the high density treatment (i.e., four strands per macroalgal species and four cores of algal turf). To control for effects of algal attachment structures, we used the same amount and configuration of cable ties and clothespins for the two density treatments.

We ran herbivory trials for all 10 treatments (5 distances from structural refuge habitat × 2 initial algal densities) at a time for each study location, and we initiated trials at each location on separate days with similar weather conditions of low wind and low cloud cover. We started each herbivory trial in the late morning (between 9:30 and 11:00 h), by attaching the algae to the cinderblocks. We re-measured each strand of macroalgae to the nearest 0.5 cm in situ after 4, 24, 28, and 48 h, to quantify losses due to herbivory. At these same time points, we also assigned each core of algal turf to one of five ordinal categories: 4, no sign of grazing (complete cover of uncropped algal turf: the initial category for all cores); 3, low grazing (some cropping of turf or small bare areas exposed); 2, intermediate grazing (significant cropping of turf and/or larger bare areas exposed); 1, high grazing (all turf cropped and large bare areas exposed); 0, highest grazing (all turf removed; only bare substrate remains). A single observer assigned herbivory categories to all cores of algal turf for all five measurement time points within a trial. After the final measurement (at 48 h), we removed all algal turf cores and any remaining macroalgal strands from each cinderblock. After we completed the first herbivory trial for all three study locations, we switched the algal density treatment assigned to each array and conducted a second trial at each study location, yielding six replicated trials for each of the 10 treatments. Finally, we video recorded a subset of trials to measure: (1) individual bite rate and body size (total length = TL) and total foraging time of all fish species that ate from our experimental units, and (2) the abundance of large piscivorous predators (>35 cm TL), capable of eating the focal fish.

Statistical modeling

We formulated and fit a stochastic death process model to our algal length data (see Appendix S2 for details and derivation and Data S1 for source code) to estimate algal harvest rates. We tested models that assumed that algal harvest rate was determined by either a binomial process, in which algal harvest rate (loss per unit of algae, per unit time; μ_n) decayed exponentially as the amount of algae remaining was reduced, or a Poisson process, in which algal harvest rate was independent of the amount of algae remaining. We further modeled μ_n in standard regression format as either an intercept alone (i.e., null model), representing no effect or the effect of "trial" (for the field experiment), or as a function of one or more categorical or continuous predictor variables. We used the maximum likelihood estimators of our model parameters from the best-fit model to simulate 100 datasets, and we used parametric bootstrapping on these datasets both to verify that our estimators were unbiased and to calculate 95% confidence intervals. We then converted estimates of μ_n from our best-fit statistical models into patch-level algal harvest rates that represent the maximum per-minute harvest rate (i.e., the harvest rate in the first minute, in cm/min), using the following equations (m is the initial amount of algae):

$$\text{Algal loss rate from binomial model} = m(1 - e^{-\mu_n}) \text{ and} \tag{1}$$

$$\text{Algal loss rate from Poisson model} = (1 - e^{-\mu_n}). \tag{2}$$

We used Akaike's Information Criterion (AIC) to determine the best-fit model (lowest AIC) among all models tested for algae remaining over time. We considered alternative models with a difference in AIC (ΔAIC) of <2, relative to the best-fit model, to provide an indistinguishable fit to the data (Burnham and Anderson 2002). We fit linear mixed effects models to our data on the traits of herbivores that we observed visiting our sites, treating site as a random effect (nlme package in R; Pinheiro et al. 2012, R Core Team 2013). We quantified main effects and interactions of our treatments using best-fit models determined with ΔAIC, using the criterion above (see model list in Appendix S3: Table S3). We used residual plots to verify that our data met model assumptions of normality and homoscedasticity.

RESULTS

Landscape-scale survey

We ran models testing the effect of each patch-scale (i.e., within-site) and landscape-scale predictor variable on algal harvest rate (model selection results are summarized in Appendix S3: Table S1). Distance from contiguous reef habitat was the best predictor of algal harvest rate (Fig. 1b, Appendix S3: Fig. S1), which was best fit by a binomial model in our landscape-scale survey (ΔAIC: vs. next-best model, −3.611; vs. null model, −7.945; Appendix S3: Table S1). Our best-fit model showed that from within the contiguous reef to 298 m away, mean algal harvest rate decreased 83.7% (mean ± 95% CI: from 0.184 [+0.04, −0.03] inside the contiguous reef to 0.030 [+0.01, −0.01] cm/min at 298 m away; Fig. 1b). Furthermore, each landscape-scale metric better predicted algal harvest rates than each patch-scale metric characterizing the local conditions of the study site (Appendix S3: Table S1). We expected this result, because we intentionally constrained the ranges of patch-scale metrics across sites; we controlled for patch-level factors to examine effects of landscape-scale factors on herbivory.

Field experiment

Patterns in algal harvest rate differed for each species in our experiment, though inclusion of herbivory trial as a blocking term unanimously improved model fits. For *Acanthophora spicifera* (Fig. 2a) and *Asparagopsis taxiformis* (Fig. 2c), models with harvest rates that declined as algae were depleted (binomial models) and with an interaction between initial algal density and distance from refuge habitat best fit our data (ΔAIC for *Acanthophora spicifera*: vs. next-best model, −3.52; vs. best null, −64.0; ΔAIC for *As. taxiformis*: vs. next-best model, −1.04; vs. best null, −13.3; Appendix S3: Table S2). However, for *As. taxiformis*, three additional models, binomial distance + density (ΔAIC = 1.35), Poisson distance + density (ΔAIC = 1.04), and Poisson distance (ΔAIC = 1.31), provided indistinguishable fits to the data, unanimously indicating a negative effect of distance, though a less clear effect of initial algal density. For both *Amansia rhodantha* (Fig. 2b) and *Sargassum pacificum* (Fig. 2d), models with constant algal harvest rates (independent of remaining algae; Poisson models) and with the main effects of initial algal density and distance from refuge habitat best fit our data (*Am. rhodantha*: ΔAIC: vs. next-best model, −4.24; vs. best null, −8.09; *S. pacificum*: ΔAIC: vs. next-best model, −1.56; vs. best null, −142; Appendix S3: Table S2). However, for *S. pacificum*, the Poisson interaction model provided an indistinguishable fit to the data (ΔAIC = 1.56), suggesting that the positive effect of initial algal density on harvest rate could be reinforced at greater distances from refuge habitat. Finally, algal turf was best fit by the binomial null model (Appendix S3: Table S2), though the binomial distance (ΔAIC = 1.99) and binomial density (ΔAIC = 1.19) models provided indistinguishable fits, suggesting that distance from refuge may have a negative effect and initial algal density a positive effect on harvest rates of turf.

We observed pronounced differences in harvest rates (cm/min) among our macroalgal species. *Acanthophora spicifera* (Fig. 2a) reached a peak average harvest rate that was more than three times greater than that of the three other macroalgal species combined (Fig. 2b–d); these rates exceeded those from our field survey (Fig. 1b). Three out of the four macroalgal species (*Acanthophora spicifera*, *Am. rhodantha*, and *As. taxiformis*) in our experiment exhibited harvest rates that declined with distance from reef habitat, while *S. pacificum* exhibited a slight increase in harvest rate with distance from reef habitat. The quadrupled initial algal density that we imposed as part of our experimental treatments led to clear increases in algal harvest rates only for *Acanthophora spicifera* and *S. pacificum*, for which mean harvest rates increased by a factor of 8.9 (mean ± 95% CI: from 0.126 [+0.17, −0.059] to 1.12 [+1.3, −0.58] cm/min) and 6.9 (0.029 [+0.017, −0.0032] to 0.20 [+0.21, −0.043] cm/min), respectively. The interaction between the effect of isolation from reef habitat and initial algal density for *Acanthophora spicifera* (in contrast to the interaction for *As. taxiformis*; Fig. 2c) arose because harvest rates declined with distance less for high initial algal density patches compared to low initial algal density patches (Fig. 2a). Because of the dominance of the herbivory rate of *Acanthophora spicifera*, this interaction was maintained for harvest rates for all four macroalgal species combined (Fig. 2e), for which the harvest rate decreased over time (Appendix S3: Fig. S2).

We observed a significant increase in average individual bite rate with both greater distance from reef habitat (hereafter, results reported as mean ± 95% CI adjusted for the blocking term “site”: from 0.94 ± 0.07 to 2.16 ± 0.50 bites/s, a mean increase of 230% from −2 [inside the reef] to 30 m, $F_{1,\,581} = 42.65$, $P < 0.0001$) and greater initial density of algae (from 0.91 ± 0.08 to 1.10 ± 0.07 bites/s, a mean increase of 21% from low to high density, $F_{1,\,581} = 10.68$, $P = 0.001$), though the addition of algal density as a second predictor did not improve the model fit (ΔAIC = 0.78), relative to the best-fit model with distance as the predictor variable (Fig. 3a; Appendix S3: Table S3). For total foraging time, we observed a significant interaction between distance from refuge habitat and initial algal density ($F_{1,24} = 4.42$, $P < 0.046$, Appendix S3: Table S3), in which increases in community foraging time from low to high-density treatments were smaller, though proportionally larger, at greater distances from refuge habitat (e.g., from low to high density at −2 m [inside the reef]: 487.3 ± 335.9 s to 1,025.7 ± 294.2 s [210.5% increase] vs. at 20 m: 45.0 s to 110.0 s [244.4% increase]; Fig. 3b). The total length of foraging herbivorous fishes increased significantly with distance from refuge habitat (from −2 m [inside the reef] to 30 m: 13.35 ± 0.32 to 14.88 ± 1.77 cm, respectively: mean increase of 11.5%; $F_{1,\,582} = 45.37$, $P < 0.0001$; Fig. 3c), an effect most pronounced 5 m from the reef, where the mean fish total length peaked at 15.96 ± 0.38 cm. Though we observed a slight increase in fish total length from our low to high algal density treatments (from 14.11 ± 0.43 to 14.57 ± 0.31 cm: mean increase of 3.2%), these effects were not significant (from distance + density model: $F_{1,\,581} = 1.39$, $P = 0.24$). Finally, we verified that individual bite rates of fish: (1) were not correlated with total length ($F_{1,\,582} = 1.83$, $P = 0.18$), and (2) still increased significantly with distance from refuge habitat and with initial algal density, when we standardized bite rates by total lengths (i.e., bite rate × TL^{-1}; distance: $F_{1,\,581} = 15.20$, $P = 0.001$; density: $F_{1,\,581} = 8.20$, $P = 0.004$).

We observed 13 species of fish eating algae from our experimental units (Appendix S4: Figs. S1–S3) and from the substrate surrounding our experimental units. Species from the family Acanthuridae (8 species) dominated the observed assemblage and herbivory activity, comprising 90.4% of visits to our experimental units (i.e., foraging bouts) and 97.7% of bites therein (Appendix S4: Fig. S1, S2). Generally, fish engaged in more foraging bouts and took more bites of algae nearer to the refuge habitat of the reef and in the high (relative to the low) initial algal density treatment (Appendix S4: Figs. S1–S3). Notable exceptions took more bites from sites with low initial algal densities and included *Acanthurus triostegus*, which also more

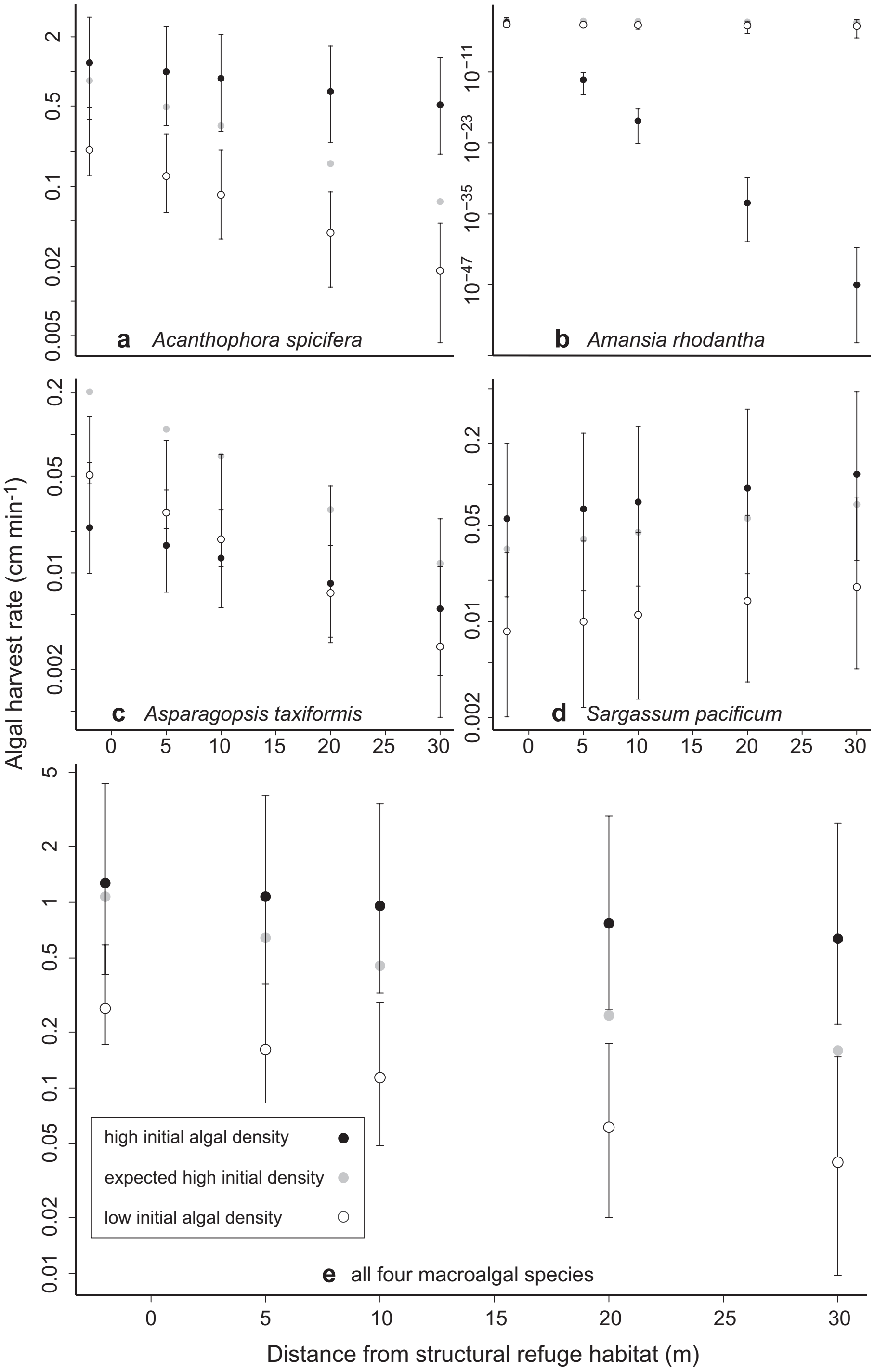

FIG. 2. Harvest rates (mean ± 95% confidence intervals) of macroalgae from the best-fit model for each species of macroalgae (over differing *y*-axis ranges): *Acanthophora spicifera* (a), *Amansia rhodantha* (b), *Asparagopsis taxiformis* (c), and *Sargassum pacificum* (d), and for all macroalgal species combined (e). Our 10 experimental treatments included: five distances from the structural refuge habitat of the coral reef (−2 [inside the reef], 5, 10, 20, and 30 m from the reef edge) crossed with two different initial densities of algae (low [open circles] and high [4× the density of the low treatment; black circles]). Note: grey circles are 4× the mean algal harvest rate for the low initial algal density treatment and represent the expected mean algal harvest rate for the high initial algal density treatment, under the assumption that effects of risk (i.e., distance from refuge habitat) and initial algal density are non-interactive (i.e., independent; see Appendix S1: Fig. S1 for additional details).

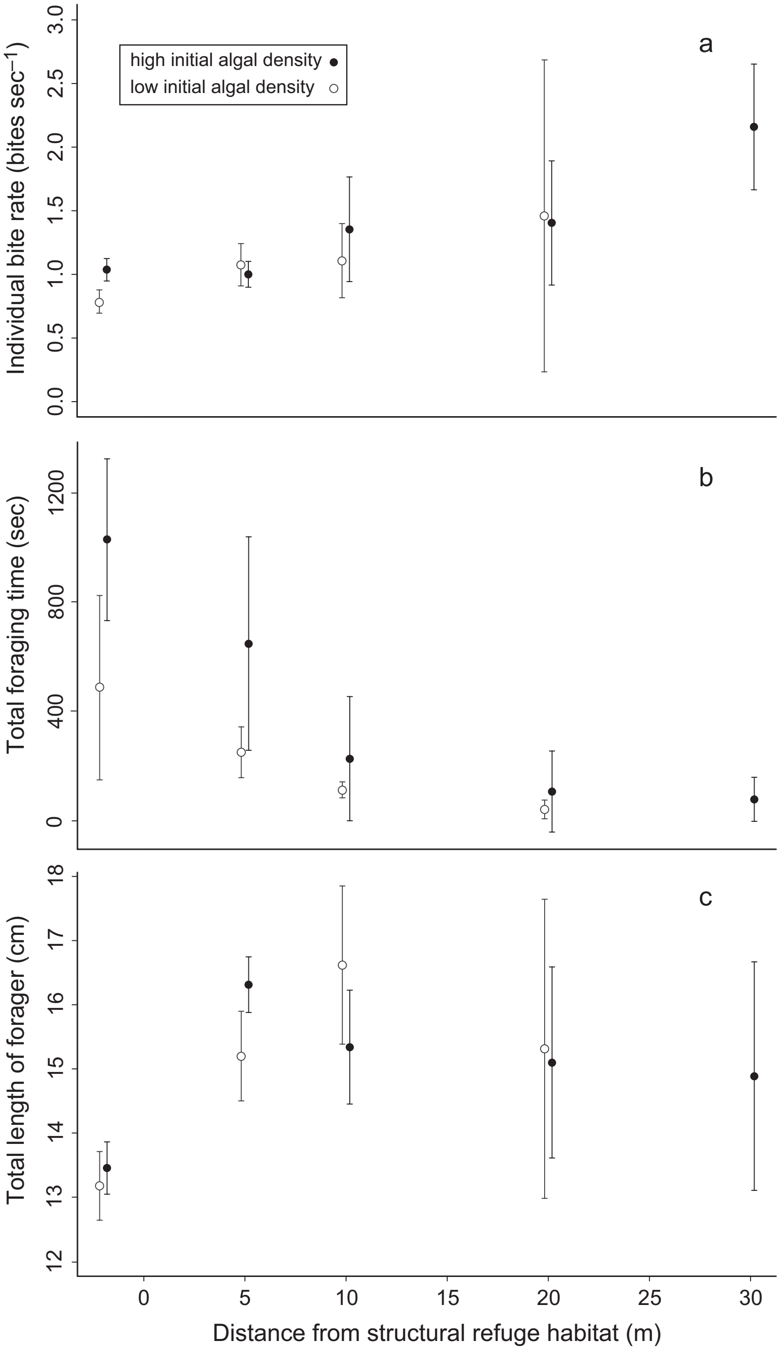

FIG. 3. Traits of foragers (herbivorous reef fishes) observed in our experiment, including individual bite rate (a), total foraging time (i.e., sum of all foraging bout durations for the fish community) per treatment combination (b), and total length of each forager (c), across our 10 treatments: five distances from structural refuge habitat (−2 [inside the reef], 5, 10, 20, and 30 m from the reef edge) crossed with two different initial densities of algae (low [open circles] and high [4× low; black circles]). Values reported are means ± 95% confidence intervals adjusted for the blocking term “site”. Points at each distance are offset to improve visualization. Note that for the low-density, 30-m treatment we observed no foraging from our experimental units.

frequently foraged further from reef habitat, *Acanthurus nigricauda*, which similarly fed exclusively from sites in sand flat habitat, and *Siganus spinus* (Appendix S4: Figs. S1–S3). Generally, the acanthurids took more bites of filamentous algal turf than they took of macroalgae (Appendix S4: Fig. S2), with three notable exceptions: *Naso lituratus* and *Naso unicornis* were responsible for nearly all bites (92.6%) of *S. pacificum*, which both species ate almost exclusively (Appendix S4: Fig. S2c, f), and while *Acanthurus triostegus* ate mostly algal turf from the low initial algal density treatment, in the high initial algal density treatment it ate mostly macroalgae (Appendix S4: Fig. S2b). Conversely, the five non-acanthurid species took more bites of macroalgae than they took of algal turf, and all but *Chlorurus sordidus* took the majority of their bites from *As. taxiformis* (Appendix S4: Fig. S3). We recorded 10 total large, adult piscivore sightings (nine sightings of adult blacktip reef sharks, *Carcharhinus melanopterus*, and 1 sighting of the bluefin trevally, *Caranx melampygus*), all observed passing by experimental units in sand flat habitat.

Discussion

Here we used maximum likelihood to couple observations and an experiment from the field with stochastic process models to reveal that effects of distance from refuge habitat on herbivory depend on initial resource densities. In particular, herbivory of macroalgae declined with distance from refuge (reef structural habitat), but these declines were disproportionately smaller for high-density resource patches than for low-density patches (Fig. 2e). Thus, herbivory rates remained relatively high for high-density patches at more distant sites. This suggests that despite landscapes of fear (sensu Laundre et al. 2001) herbivores can counteract, at least to some extent, increases in resource density, which, in the case of benthic algae in marine systems, can be ecologically detrimental (McCook et al. 2001, Burkholder et al. 2007, Connell et al. 2008). Our findings further indicate that reef fishes incorporate risk and reward into their foraging decisions; they are willing to accept greater risk (i.e., foraging in more distant patches) if those patches provide a greater harvest rate (Fig. 3a). Our landscape-scale survey suggests that the effects observed in our experiment are not restricted to small, artificial reef patches (cinder blocks, in our case) but instead exhibit a general property of characteristically heterogeneous reef landscapes.

Our results on traits of herbivorous fishes foraging from our experimental sites support the conclusion that perceived risk by herbivores drove observed effects of habitat isolation on herbivory. To understand this, let us first consider the costs and benefits of foraging. Optimal foraging theory posits that when an animal chooses to forage, this decision comes with three key costs: the cost of energy spent on foraging (metabolic costs, or C), the cost of not engaging in an alternative activity, such as mating (missed opportunity costs, or MOC), and the cost of being killed (P). Thus, differences in the quitting harvest rate (when the harvest rate of the forager no longer exceeds the combined costs of foraging, and, thus, the forager stops foraging and leaves a patch; H) among patches reflect differences in foraging costs among patches (Brown 1988, Brown and Kotler 2004): $H = C + MOC + P$.

Given that we ran all 10 experimental treatments simultaneously in the same general location for a given trial, and given the close proximity of our treatments relative to the wide movement ranges of the visiting herbivorous fishes (e.g., Meyer and Holland 2005, Welsh and Bellwood 2012), it is reasonable to assume that missed opportunity costs and metabolic costs were equivalent among our study sites for a given trial (Brown et al. 2001, Kilpatrick 2003). Our results also showed that: (1) harvest rates were dependent on resource availability for the majority of observed herbivory (i.e., the binomial model fit best for the greatly preferred algal species *Acanthophora spicifera* [Fig. 2a; Appendix S3: Table S2], which drove patterns in total algal harvest rates [Fig. 2e; Appendix S3: Fig. S2]), and (2) foragers, dominated by acanthurid species with similar size-specific bite sizes (Appendix S4: Fig. S4), significantly increased their bite rates in patches with higher algal density, even when we corrected for forager total length. These observations indicate that our resource patches offered diminishing returns to herbivores, and, thus, quitting harvest rates scaled linearly with our recorded metric of individual average bite rate (Appendix S4: Fig. S5). Consequently, the more than two-fold (1.22 bites/s) increase in individual average bite rate we observed between our within-reef (2 m in from reef edge) patch and our furthest patch from the refuge habitat of the reef (30 m away) largely reflects higher costs of predation (i.e., higher perceived predation risk by herbivores). In addition, we observed a significant, albeit weak, trend toward larger fish total length with increased distance from refuge; this could reflect diminishing predation risk, as prey movement speed (and, thus, escape potential) can increase with body size (Bejan and Marden 2006). Our findings both reinforce and contrast recent work in the Florida Keys: Catano et al. (2016) observed depressed herbivory and higher individual bite rates by herbivores in riskier habitat, but also showed that risk increased with structural complexity of the habitat. This latter distinction likely reflects predominant predator hunting modes, with ambush predators (grouper) in the Keys (Catano et al. 2016) but chase predators (reef sharks) in Mo'orea (Mourier et al. 2012, 2013, Brooks 2016), and suggests that the features that drive landscapes of fear in reef fishes depend on the composition of the predator assemblage.

We observed that distance from refuge habitat reduced the overall herbivory rate of attractive resource patches of benthic macroalgae in a coral reef (Figs. 1b, 3e), but specific herbivory rates differed between our survey and experiment and among algal species within our experiment. First, higher harvest rates of *Acanthophora spicifera* in our experiment (Fig. 3) relative to our survey (Fig. 1b), could be attributed to several factors, including differences in the accessibility/attractiveness of outplanted algae (i.e., survey sites atop large coral colonies were potentially more exposed to predators of herbivores), differences in herbivore or predator density between locations or years, or differences in measurement time points (i.e., algae from surveys were first re-measured at 6 h, while algae from the experiment were re-measured after 4 h). Moreover, the increased variance in algal harvest rates from our experiment, relative to those from our survey, were likely driven by the demographic stochasticity associated with the much smaller size of outplanted algal patches in our experiment (<25% of the amount of *Acanthophora spicifera* used in our survey).

The palatable alga *Acanthophora spicifera* (Littler and Littler 2007) was consumed at the highest rate in our experiment (Fig. 2a) and was observed being eaten by eight herbivorous fish species (Appendix S4: Figs. S2, S3), which included system dominants *Zebrasoma scopas*, *Ctenochaetus striatus*, and *Acanthurus nigrofuscus* (Brooks 2016), and which were responsible for 87.6% of all observed forager visits (Appendix S4: Fig. S1). Consequently, the pattern in *Acanthophora spicifera* harvest rate (Fig. 2a) largely drove the overall pattern in macroalgal harvest rate across treatments (Fig. 2e) and can be thought of as a measure of the maximum relative potential for herbivores to control algae (Littler and Littler 2007). The other three macroalgal species in our experiment were consumed at much lower rates and exhibited different patterns across our experimental treatments, including a negative effect of initial algal density on the harvest rates of *Amansia rhodantha* (Fig. 2b) and *Asparagopsis taxiformis* (Fig. 2c). These patterns could be explained by preferences among algae by herbivore species that also favor particular foraging patch contexts. For example, of the three fish species that took more bites from the low vs. high initial algal density treatment (Appendix S4: Figs. S2, S3), *Acanthurus triostegus* and *A. nigricauda* primarily ate macroalgae from high-density units but primarily ate algal turf from low-density units. This could be driven, in part, by enhanced visual barriers created by macroalgae in high-density units, blocking the surrounding view of potential threats, particularly for fish foraging from centrally located algal turf cores (Appendix S1: Fig. S3). This effect was proposed by Hoey and Bellwood (2011), who showed that algal density suppresses herbivory in much larger patches of algae than those in our experiment, which, in contrast, showed an overall increase in herbivory with algal density. Collectively, these findings suggest that effects of algal density on herbivory may be nonlinear or dependent on algal patch size, in addition to being dependent on herbivore species. Additionally, regarding the positive effect of distance on the harvest rate of *Sargassum pacificum* (Fig. 2d), just two fish species (the only unicornfish we recorded): *Naso lituratus* and *Naso unicornis*, consumed the vast majority of *S. pacificum*. While this observed consumption was restricted to experimental units near the reef edge (i.e., at −2, 5, and 10 m distance; Appendix S4: Figs. S1, S2) during the initial 4-hour period, at later time periods *S. pacificum* was consumed more rapidly at sites farther from the reef edge, driving an overall positive effect of distance from reef on harvest rate (Fig. 2d). Our findings suggest that this later consumption (beyond 4 h) was likely also driven by *N. lituratus* and *N. unicornis*, which commonly form small, conspecific groups (observed in our videos; Randall et al. 1990, Myers 1991), potentially reducing fear of open sand flat habitats by diluting the risk of predation (Foster and Treherne 1981) and enhancing vigilance (Pulliam 1973, Powell 1974). Concordantly, other observed species that commonly form groups (observed in our videos; Randall 1956, Allen and Erdmann 2012): *Acanthurus triostegus* and *A. nigricauda*, were observed foraging most frequently furthest from the reef edge (i.e., 20 and 30 m away; Appendix S4: Figs. S1, S2). Thus, fish species may serve complementary roles in system-wide herbivory, with respect to their selection not only of algae (Rasher et al. 2013), but also of foraging locations across landscapes of fear (Appendix S4: Figs. S1–S3).

In addition to the above differences among algae, *Acanthophora spicifera*, *As. taxiformis* and algal turf harvest rates decreased as the amount of each decreased in a patch, while *Am. rhodantha* and *S. pacificum* exhibited algal harvest rates independent of the amount of algae available. This suggests that these species of algae were perceived differently by herbivores that, perhaps in preference for *Acanthophora spicifera*, algal turf, and, to a lesser extent *As. taxiformis*, may have incidentally fed on *Am. rhodantha* and *S. pacificum* (sensu Emerson et al. 2012), which were subjected to relatively small proportions of observed bites by the fish community (Appendix S4: Figs. S1, S2, but note the exceptions of *N. lituratus* and *N. unicornis* consumption of *S. pacificum*). Furthermore, the pattern of decreasing macroalgal harvest rates over time (Appendix S3: Fig. S2) suggests that, overall, resource patches become less attractive to herbivores as the density of algae (particularly preferred species) declines. Lastly, the ambiguous results revealed for the harvest rate of algal turf, providing support for no treatment effects as well as a positive effect of initial algal density and a negative effect of distance from refuge, could have been driven by logistical limitations. Given the many observed bites of turf across treatments by dominant acanthurid species (Appendix S4: Fig. S2; Poray and Carpenter 2014, Brooks 2016), our re-measurement intervals may have been too long to capture clear among-treatment differences, which may have also been difficult to isolate due to a potentially high measurement error rate associated with our categorical descriptions of turf loss. Collectively, these results suggest that in addition to effects on overall algal density, isolation from the refuge habitat of the reef can indirectly affect the species composition of benthic algae, via herbivore behavior.

Globally, coastal marine ecosystems are experiencing loss and fragmentation of structural refuge habitat formed by foundation species, such as corals (Bellwood et al. 2004), seagrasses (Orth et al. 2006), and kelp (Steneck et al. 2002), due to natural and anthropogenic factors, including storms, pollution, and overharvesting of consumers. Our study suggests that the loss or fragmentation of refuge habitat can reduce consumer control of resources, but this effect can weaken if resource density is higher (Fig. 2a, e) and if consumer communities remain intact. By revealing spatial context dependence in top-down control of resources, our work contributes to the call by Kitchell et al. (1979) and more recently Schmitz et al. (2010) to better understand the potentially fundamental role of consumers in bottom-up processes that affect primary producers. Finally, on a practical note, we would like to point out that ecological studies seldom utilize realistic and nonstandard stochastic models, which help strengthen inference by harnessing information in data more effectively (Strong et al. 1999). In that sense, we hope that our work is also seen as an unpretentious plea for an optimal combination of biological hypotheses, stochastic models, and statistical methods.

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