

Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour

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Summary

1. Predators can exert strong direct and indirect effects on ecological communities by intimidating their prey. The nature of predation risk effects is often context dependent, but in some ecosystems these contingencies are often overlooked.

2. Risk effects are often not uniform across landscapes or among species. Indeed, they can vary widely across gradients of habitat complexity and with different prey escape tactics. These context dependencies may be especially important for ecosystems such as coral reefs that vary widely in habitat complexity and have species-rich predator and prey communities.

3. With field experiments using predator decoys of the black grouper (*Mycteroperca bonaci*), we investigated how reef complexity interacts with predation risk to affect the foraging behaviour and herbivory rates of large herbivorous fishes (e.g. parrotfishes and surgeonfishes) across four coral reefs in the Florida Keys (USA). In both high and low complexity areas of the reef, we measured how herbivory changed with increasing distance from the predator decoy to examine how herbivorous fishes reconcile the conflicting demands of avoiding predation vs. foraging within a reefscape context.

4. We show that with increasing risk, herbivorous fishes consumed dramatically less food (ca. 90%) but fed at a faster rate when they did feed (ca. 26%). Furthermore, we show that fishes foraging closest to the predator decoy were 40% smaller than those that foraged at further distances. Thus, smaller individuals showed muted response to predation risk compared to their larger counterparts, potentially due to their decreased risk to predation or lower reproductive value (i.e. the asset protection principle). Habitat heterogeneity mediated risk effects differently for different species of herbivores, with predation risk more strongly suppressing herbivore feeding in more complex areas and for individuals at higher risk of predation.

5. Predators appear to create a reefscape of fear that changes the size structure of herbivores towards smaller individuals, increases individual feeding rates, but suppresses overall amounts of primary producers consumed, potentially altering patterns of herbivory, an ecosystem process critical for healthy coral reefs.

Key-words: coral reef, landscape of fear, non-consumptive effects, predator–prey interactions, risk effects, rugosity

Introduction

Predators exert important top-down ecological forces by consuming their prey and impacting prey foraging behaviours and habitat use (Lima & Dill 1990; Werner &

Peacor 2003). Research from multiple ecosystems shows the importance of sublethal or non-consumptive effects (NCEs) (also called ‘risk effects’) where predators force prey to balance trade-offs between the benefits of obtaining food and the costs of avoiding predators (Schmitz, Beckerman & O’Brien 1997; Heithaus & Dill 2002; Preisser, Bolnick & Benard 2005; Ripple & Beschta 2007). Ecological context (e.g. habitat structure, species identity) can influence the nature and strength of NCEs and alter the outcome of predator intimidation (Preisser, Orrock &

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Schmitz 2007). It is clear that NCEs are common and a potentially powerful structuring force among ecosystems (Schmitz, Krivan & Ovidia 2004). However, not incorporating the contextual variation in NCEs could impair the ability to understand their impact on community dynamics.

Habitat complexity can shape predator–prey interactions by influencing encounter rates between predators and prey, the likelihood of an attack, and the probability that prey will escape (Lima & Dill 1990). The resulting continuum of risky and safe areas within a prey's environment, the so-called 'landscape of fear' (Laundre, Hernandez & Altendorf 2001), has been demonstrated in terrestrial (Gorini *et al.* 2012) and marine ecosystems (Wirsing *et al.* 2008; Madin, Madin & Booth 2011; Matassa & Trussell 2011). Within this landscape of fear, prey alter their habitat use according to features of the terrain, often avoiding resource rich, but risky, habitats in order to stay safe (Gilliam & Fraser 1987; Schmitz, Beckerman & O'Brien 1997; Heithaus & Dill 2002). For example, following the reintroduction of wolves into Yellowstone National Park, elk (*Cervus elaphus*) reduced their use of preferred grassland foraging habitats, where they were more susceptible to wolf predation, and moved into the protective cover of wooded areas (Creel *et al.* 2005). In seagrass communities, large grazers (sea cows, *Dugong dugon*; sea turtles *Chelonia mydas*) avoided interior habitats of shallow banks with high risk of tiger shark predation, which ultimately had cascading effects on seagrass community composition (Burkholder *et al.* 2013). As predation risk often varies across landscapes, the anti-predator responses of their herbivorous prey could result in cascading effects on plant communities that are heterogeneous across space. Thus, the landscape of fear is a useful framework for developing a mechanistic, community-level understanding of predator–prey interactions (Schmitz 2005).

Despite the complex structural heterogeneity of coral reef ecosystems, the effect of landscape or 'reefscape' elements (i.e. large coral mounds, sand channels, etc.) on predator–prey interactions of reef fishes is poorly understood. Living corals and the underlying matrices of dead coral skeletons form the major structural complexity (often termed 'rugosity') of coral reefs. The few studies examining the influence of structural complexity on reef fish predator–prey interactions suggest that it is likely context dependent. Structure can serve as refuge and increase survival in the presence of predators (Hixon & Beets 1993; Beukers & Jones 1997), but can also limit the visual field and decrease the ability to detect predators (Rilov *et al.* 2007). Whether structure serves as a benefit or detriment to prey may depend on functional traits of the predator (e.g. hunting mode), behavioural attributes of the prey (e.g. escape tactics), and body size of both predator and prey (Heithaus *et al.* 2009; Wirsing, Cameron & Heithaus 2010; Gorini *et al.* 2012). For example, the complexity of highly branching corals can benefit certain taxa that are small enough to hide among its

branches (Beukers & Jones 1997). Yet, for large-bodied species, high complexity areas could impede predator detection and escape, potentially increasing risk.

On coral reefs, herbivorous fishes (e.g. parrotfishes and surgeonfishes) are critical because their grazing removes algal growth and facilitates coral settlement, growth and survivorship (Hughes *et al.* 2007; Mumby *et al.* 2007; Burkepile & Hay 2008). Understanding the spatial distribution of their grazing is important to assess how grazing impact may vary across a reef landscape (Sandin & McNamara 2012). Recent research suggests that predation risk elicits strong behavioural responses in herbivores by altering foraging excursion areas (Madin, Gaines & Warner 2010a), bite rates (Rizzari *et al.* 2014) and the diversity of resources consumed (Catano, Shantz & Burkepile 2014). However, no studies on reefs have examined the potential interactive effects of predation risk and habitat characteristics in mediating herbivore foraging behaviour. Knowing how herbivores respond to variation in risk and structural complexity will help build a more realistic understanding of risk effects in coral reef communities.

We investigated how reef complexity interacts with predation risk to affect the foraging behaviour and spatially explicit impact of large herbivorous fishes (e.g. parrotfishes and surgeonfishes) across four coral reefs in the Florida Keys (USA). In multiple controlled experiments, we used predator decoys of the black grouper (*Mycteroperca bonaci*) to manipulate predation risk in both high and low complexity areas of the reef. We measured how herbivory changed with increasing distance from the predator decoy to examine how herbivorous fishes reconcile the conflicting demands of avoiding predation vs. foraging within a reefscape context. We hypothesized that herbivory would diminish as predation risk increases (i.e. near predator decoys) and that high rugosity areas with more visual obstructions would be perceived as riskier, resulting in stronger suppression of herbivory when predator decoys were present.

Materials and methods

SITE DESCRIPTION

The Florida Keys reef tract is a large bank reef system located approximately 8 km offshore of the Florida Keys, USA. The reefs we sampled were characterized by shallow spur and groove topography and included (Lat., Long.): Molasses Reef (25-005, -80-378), French Reef (25-039, -80-355), South Carysfort (25-209, -80-219), and Pinnacles Reef (24-992, -80-409). Molasses, French and South Carysfort are no-take zones within the Florida Keys National Marine Sanctuary (FKNMS) where fishing has been restricted since 1997 (Bohnsack *et al.* 2009), whereas Pinnacles Reef is open to fishing. The designation of no-take zones has led to increased predator biomass at some of these reefs (Smith *et al.* 2011). Herbivorous fishes (e.g. parrotfish, surgeonfish, etc.) are protected across the entirety of the FKNMS (i.e. in both take and no-take zones), and their populations are robust relative to many other reefs in the wider Caribbean (Burkepile *et al.* 2013a). Trials were conducted during the day

(10 : 00–14 : 00 h) between June and July 2013 on the forereef at depths of 6–8 m.

EXPERIMENTAL DESIGN

Prior to conducting our main experiments, we tested whether fishes would respond to fibreglass models of a black grouper (*M. bonaci*) (ca. 90 cm fork length) (Fig. 1a) either because the decoys represented a threat or simply because they were novel objects. At each reef, we tested responses of fish to three treatments: (i) a grouper decoy; (ii) a decoy control (a plastic carboy with similar dimensions to the grouper decoy) and (iii) a control (no predator decoy or plastic carboy). We anchored grouper decoys and plastic carboys to natural areas of the reef benthos using monofilament line. Trials were separated by a minimum of 30 m at each reef to assure independence. It is unlikely that most reef herbivores, particularly smaller species such as *Sparisoma aurofrenatum* and *Acanthurus bahianus* that were the primary foragers in our study (see Results), would move among trial locations over such distances (Semmens, Brumbaugh & Drew 2005; Welsh, Goatley & Bellwood 2013; Catano *et al.* 2015a). At each reef, two trials were conducted for each of the three treatments producing a total of eight replicates per treatment. We assessed herbivore feeding using standardized assays of a palatable seagrass (*Thalassia testudinum*) placed one metre away from each treatment. Each assay consisted of five blades of seagrass cut to 10 cm, scraped free of epiphytes, and clipped to wooden clothespins (Fig. 1b). Herbivores were allowed to feed on assays for 2 h before we recollected them and measured each seagrass blade to calculate the percentage removed over the course of the trial.

To establish high and low rugosity sites at our four study reefs, we used *in situ* observations in conjunction with remotely sensed rugosity measurements. A LiDAR (Light Detection and Ranging)-derived bathymetric data set provided by the US Geological Survey (USGS) (available online <http://pubs.usgs.gov/of/2007/1395/start.html>) was used to create a map of benthic rugosity (1 × 1 m resolution) with the Benthic Terrain Modeler (a collection of ESRI ArcGIS-based tools available online <http://www.coast.noaa.gov/digitalcoast/tools/btm>). LiDAR-derived rugosity measurements accurately reflect rugosity as measured with traditional chain-transect methods (Kuffner *et al.* 2007). We chose sites with high (mean ± SE: 5.5 ± 0.1) and low (3.9 ± 0.1) LiDAR-derived rugosity values that were located along the reef tract (determined from benthic habitat maps available from the FKNMS (http://floridakeys.noaa.gov/fknms_map/maplibrary.html?s=about) to distinguish reef from non-reef habitats (e.g. seagrass, sand, rubble). We verified the complexity of these locations visually on SCUBA prior to running experiments. Our LiDAR criteria selected high rugosity sites that were structurally complex with large coral mounds, ledges, and other potential visual obstructions and selected low rugosity sites that were considerably flatter (Fig. S1).

At each reef, we used predator decoys to simulate predation risk in high and low complexity sites. We did not include decoy controls (plastic carboys) in these experiments because they did not affect herbivory vs. controls with no carboys (see Results). At increasing distances from the decoy (0.5, 1, 2 and 4 m), we secured seagrass assays as described above and filmed them using GoPro Hero 3 cameras (GoPro, Inc., San Mateo, CA, USA). Trials for predator and rugosity treatments were conducted during both morning (10 : 00–12 : 00) and afternoon (12 : 00–14 : 00) hours at all sites to avoid confounding time of

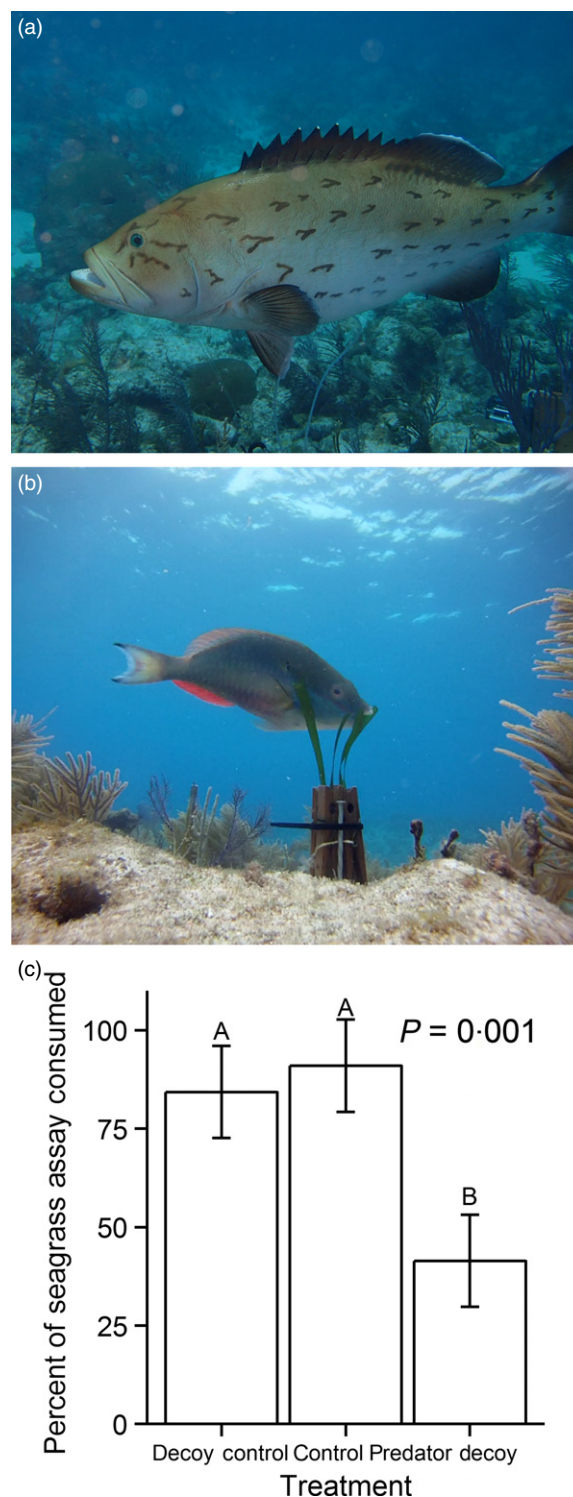


Fig. 1. (a) Predator decoy of black grouper, *Mycteroperca bonaci*, (b) *Sparisoma aurofrenatum* biting assay of *Thalassia testudinum*, and (c) Least square means ± SE for percentage of seagrass consumed adjacent to predator decoy, decoy control or control. Letters above bars represent differences among groups based on Tukey's *post hoc* comparisons.

day with treatment effects. After 2 h, all assays and predator decoys were collected and seagrass blades were measured to calculate the percentage removed. At each reef, we conducted six

trials (three in high rugosity and three in low rugosity areas) in the presence of the predator decoy and six control trials (three in high rugosity areas and three in low rugosity) where the predator decoy was not present ($n = 12$ replicates total per treatment). As with previous experiments, trials at each reef were separated by a minimum of 30 m to assure independence.

Many parrotfish species readily consume *T. testudinum*; however, it is rarely eaten by surgeonfishes or juvenile parrotfishes (Randall 1967). Therefore, in addition to counting bites taken on the seagrass assays in the videos, we counted bites on the benthos from all herbivorous fishes that were within a 25 cm radius of the assay. We estimated the sizes of fishes using markers of known length located in the field of view. We also determined feeding rates of individual fishes by recording the time of a fish's first bite, how many bites they took, and the time of their last bite and divided number of bites by time.

To understand other potential drivers of herbivore foraging behaviour in our experiments, we also quantified territorial damselfishes and potential predators from our video observations. Territorial damselfish can affect how larger herbivorous fish forage by aggressively defending the algal gardens within their territories (Foster 1985). Therefore, we noted the number of territorial damselfish (*Stegastes* and *Microspathodon* spp.) that transected the 25 cm radius around the seagrass assay over the course of the video observation. Most damselfishes have relatively small territories, and they were generally always present in the video frame so most individuals were likely counted only once. Differences in the abundance of predators both within and across reefs could also impact our feeding assays, so we counted predators that passed through the frame to estimate the level of background predation risk. We included only primarily piscivorous adult fishes of the families Carangidae, Lutjanidae, Serranidae and Sphyraenidae that are known to consume adult parrotfishes and surgeonfishes (based on Randall 1967). All counts were standardized by the time of each video observation.

STATISTICAL METHODS

All statistical analyses were conducted using R version 3.0.1 (R Core Team 2013). Parametric assumptions of normality and homoscedasticity were verified using plots of the residuals. To test the effect of the grouper decoy on seagrass consumption, we used a linear mixed model (LMM) with the restricted maximum-likelihood (REML) fitting method to test for differences among the grouper decoy, decoy control and control while accounting for reef nested within protection status as random effects. We used the function `lmer` in the R package `lme4` (Bates *et al.* 2014) for fitting LMMs along with the package `lmerTest` (Kuznetsova, Brockhoff & Christensen 2014) to estimate F statistics and P -values using the Satterthwaite approximation method for denominator degrees of freedom. To assure that time of day did not influence the amount of seagrass consumed, we compared morning and afternoon consumption rates using a Welsh two-sample t -test.

To understand how other potential background factors could influence foraging, we tested whether damselfish and predator abundance observed from video captures varied among reefs and with rugosity (i.e. high and low rugosity) using a two-factor ANOVA. We detected more natural predators at two reefs (see Results), and therefore, we used LMMs fitted with REML to

examine the fixed effects of treatment (i.e. grouper decoy vs. control), rugosity (i.e. high and low rugosity) and their interaction on five foraging metrics: percentage seagrass consumed, the total number of bites on either seagrass or benthos standardized by observation time, size of foraging fishes and individual feeding rates. With this model, we included natural predators as a covariate and reef nested within protection status as random effects. For this analysis, we pooled all distances by calculating the mean of each metric for each trial to understand the overall effect of the decoy vs. the control. In the analysis of individual feeding rates, we also included fish size as a covariate in the model because smaller fishes typically have higher bite rates (e.g. Bonaldo & Bellwood 2008). If interactions between predator treatment and rugosity were significant, we performed Tukey's tests of least square means to determine the sources of those interactions using the function `lsmeans` in the R package `lsmeans` (Lenth & Herva 2015).

To understand how foraging changed with distance from the predator decoy, we used LMMs fitted with REML to examine how the same foraging metrics varied with distance from the grouper decoy (i.e. 0.5, 1, 2, and 4 m) in both high and low rugosity areas, while accounting for reef nested within protection status as random effects. We included rugosity, distance and their interaction as fixed effects. We did these analyses for all fishes and then for the two most frequently observed species, *S. aurofrenatum* and *A. bahianus*. As with the prior analyses, we included fish size as a covariate in the models for individual feeding rates, and we performed *post hoc* Tukey's tests on least square means where there were significant interactions between rugosity and distance.

Results

Herbivores responded to the perceived risk from the grouper decoy and not simply to the introduction of a novel object in the water column. Fishes consumed almost two times more seagrass adjacent to the decoy control (plastic carboy) and control (no carboy or grouper decoy) than adjacent to the grouper decoy (Fig. 1c, $F_{2,33} = 8.74$, $P = 0.001$). There was no statistical difference between the decoy control and the control (Fig. 1c).

The species that fed most frequently on the assays were *S. aurofrenatum*, *A. bahianus*, *Sparisoma viride*, *Acanthurus coeruleus*, *Scarus iserti* and *Sparisoma rubripinne* (in order of decreasing frequency, Fig. S2). *Sparisoma* spp. primarily targeted the seagrass, with 90% of the bites on seagrass from *S. aurofrenatum*, followed by *S. rubripinne* (3%), *S. viride* (3%) and *Sparisoma chrysopterygum* (3%). *Sparisoma*, *Scarus* and *Acanthurus* spp. all took bites on the benthos, with the majority of bites being taken by *S. aurofrenatum* (37%), *A. bahianus* (29%), *S. viride* (10%), *A. coeruleus* (8%), *S. iserti* (6%) and *Scarus taeniopterygus* (5%).

The amount of seagrass consumed was similar in both the morning and afternoon ($t = -0.05$, $P = 0.96$). We did not find evidence for differences in damselfish abundance across reefs ($F_{3,179} = 0.92$, $P = 0.44$) or between high and low rugosity treatments ($F_{1,179} = 1.09$, $P = 0.30$). However, we found significant differences in the

abundance of predators among reefs (Fig. S3, $F_{3,179} = 13.72$, $P < 0.001$) with Molasses and French Reef having higher predator abundance than Pinnacles and South Carysfort according to Tukey *post hoc* tests. Across all reefs, fewer predators were observed in low relative to high rugosity sites ($F_{1,179} = 7.20$, $P = 0.008$). However, natural predator abundance did not influence any of the foraging metrics [percentage of seagrass consumed, bites on seagrass, bites on benthos and individual feeding rates (bites/second)] (Table S1).

The predator decoy influenced multiple foraging metrics. When the grouper decoy was present, the amount of seagrass consumed decreased overall by 46% and was 15% lower in the high relative to low rugosity areas

(Fig. 2a). We found a marginally significant interaction between predator treatment and rugosity ($P = 0.06$) with a 15% greater decline in seagrass consumption in high relative to low rugosity areas when the decoy was present. The decoy reduced the total bites taken on seagrass by 56% in the high rugosity areas but had no effect on total bites in low rugosity areas (Fig. 2b). Similarly, the decoy reduced the total bites taken on the benthos by 43% in the high rugosity areas but had no effect in the low rugosity areas (Fig. 2c). Individual feeding rates were 21% lower when the decoy was present even after accounting for the difference in feeding rates due to fish size (Fig. 2d). Fishes were on average 2 cm smaller when the grouper was present (Fig. 2e) with a trend towards

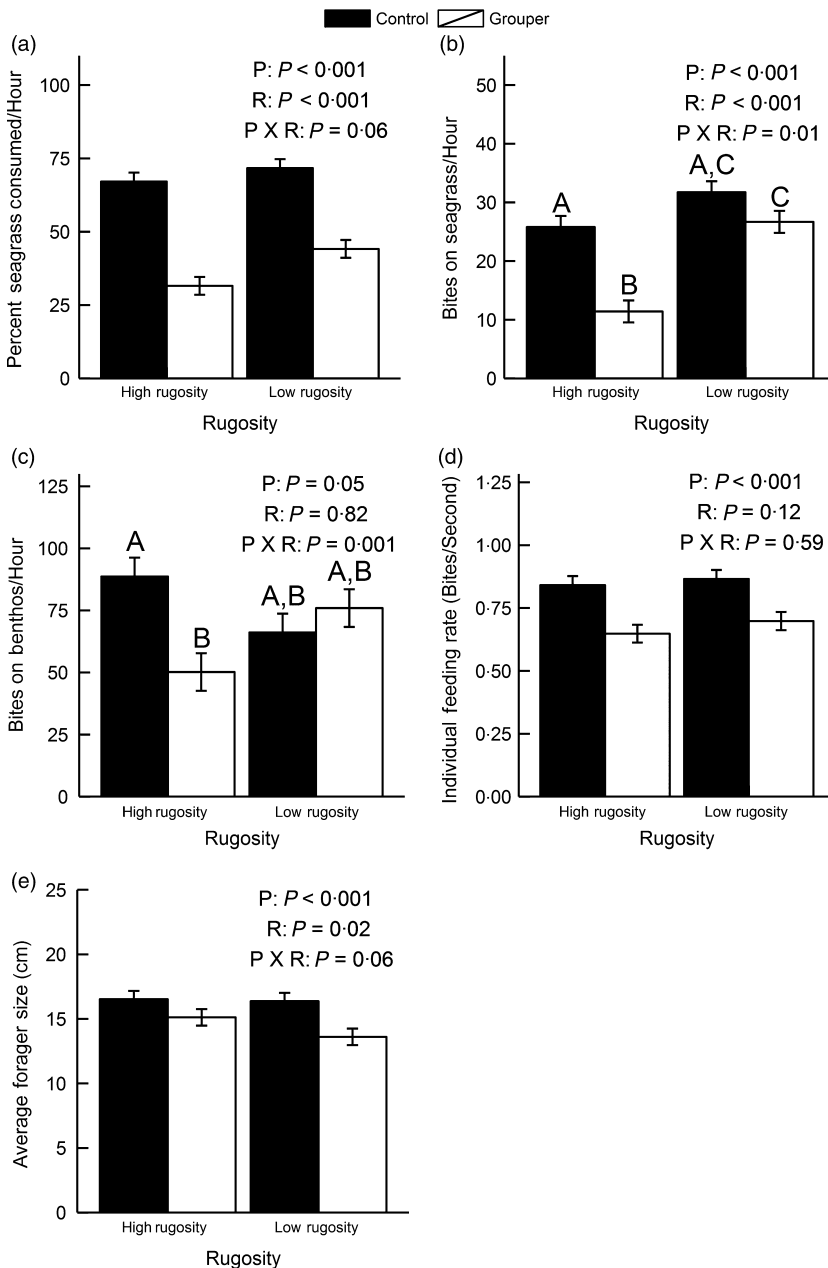


Fig. 2. Least square means (\pm SE) for (a) percentage of seagrass consumed/hour, (b) bites on seagrass/hour, (c) bites on benthos h^{-1} (d) individual feeding rates (bites/minute) and (e) forager size (cm) at high and low rugosity sites and control and grouper treatments. Statistics from linear mixed models showing the effect of the predator decoy (P), rugosity (R) and their interaction (P \times R) (see Table S1 for statistics). Letters above bars represent significant differences among treatments based on Tukey's *post hoc* comparisons.

this pattern being stronger in low rugosity areas (Predator \times Rugosity interaction: $P = 0.06$).

When we tested the spatial effects of the grouper decoy, we found that distance from the decoy influenced all foraging metrics; however, this effect often varied depending on rugosity (Table S2). In both rugosities, the amount of seagrass consumed increased 10 fold between 0.5 m and 4 m from the decoy (Fig. 3a). Proximity to the grouper also had a strong influence on the number of bites on seagrass, which was 40 times greater on average 4 m from the decoy relative to 0.5 m. There was also a strong interaction between rugosity and distance from the decoy, as the number of bites on seagrass was considerably higher (ca. 1.5 \times) in the low relative to the high rugosity areas at both 2 m and 4 m (Fig. 3b). The number of bites on the benthos was

also greater (ca. 10 \times) at 4 m relative to 0.5 m from the decoy but was not different between rugosities (Fig. 3c). Feeding rates of individual fishes declined by ca. 30% between the 0.5 and 4 m distances, even after accounting for differences in feeding rates due to fish size, but this pattern was only in the high rugosity areas (Fig. 3d). There was very little change in feeding rates with distance from the decoy in the low rugosity areas. There was a strong interaction of rugosity and distance on fish size as fishes were on average 6.5 and 2.6 cm smaller in the high vs. low rugosity areas at 0.5 m and 1 m from the decoy areas, respectively (Fig. 3e). Analyses of the size distribution of fishes at 0.5 m and 1 m distances from the decoy showed a similar pattern. In the presence of predator decoys and in high rugosity sites, the size distribution of fishes shifted

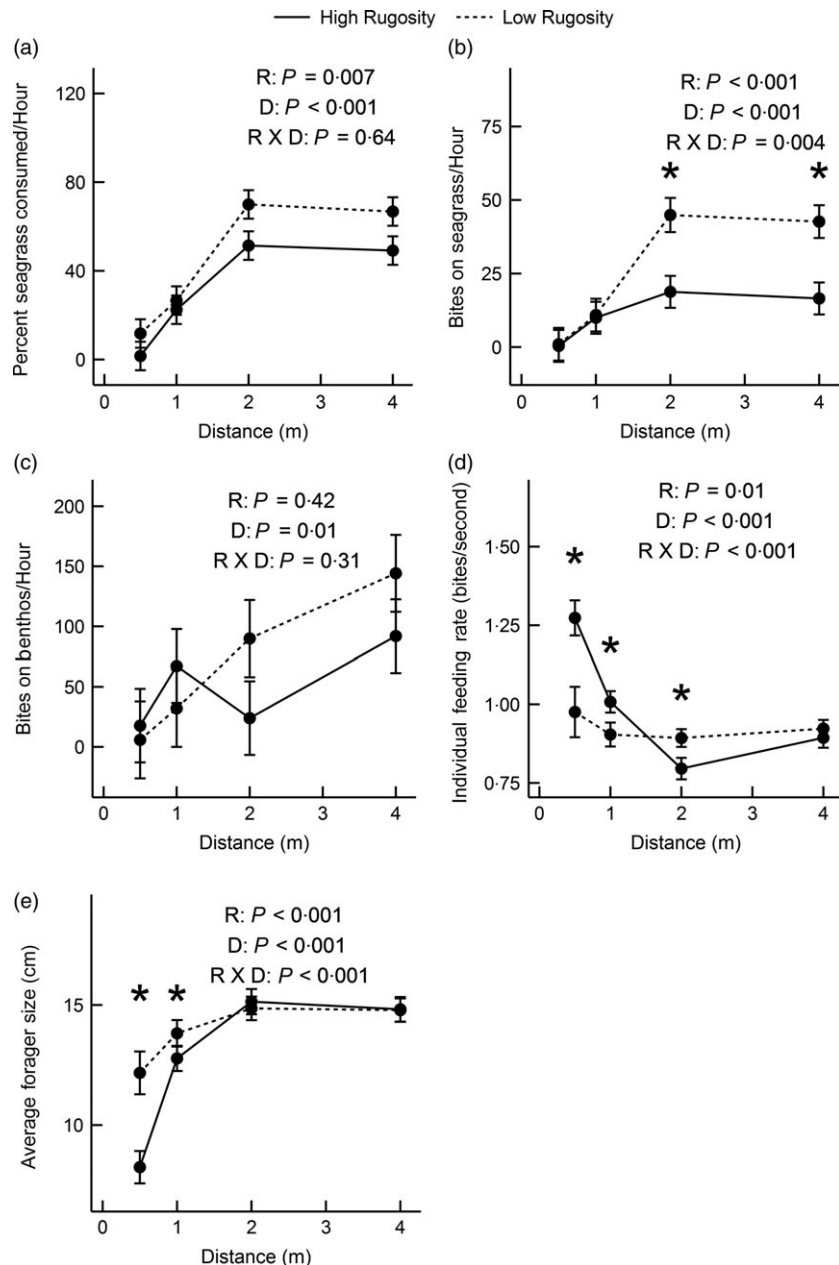


Fig. 3. Least square means (\pm SE) for (a) percentage of seagrass consumed/hour, (b) bites on seagrass/hour, (c) bites on benthos/hour, (d) individual feeding rates (bites/minute) and (e) forager size (cm) at increasing distances from predator model. Statistics from linear mixed models showing the effect of the rugosity (R), distance from decoy (D) and their interaction (R \times D) (see Table S2 for statistics). Asterisks (*) represent significant differences between rugosity treatments based on Tukey's *post hoc* comparisons.

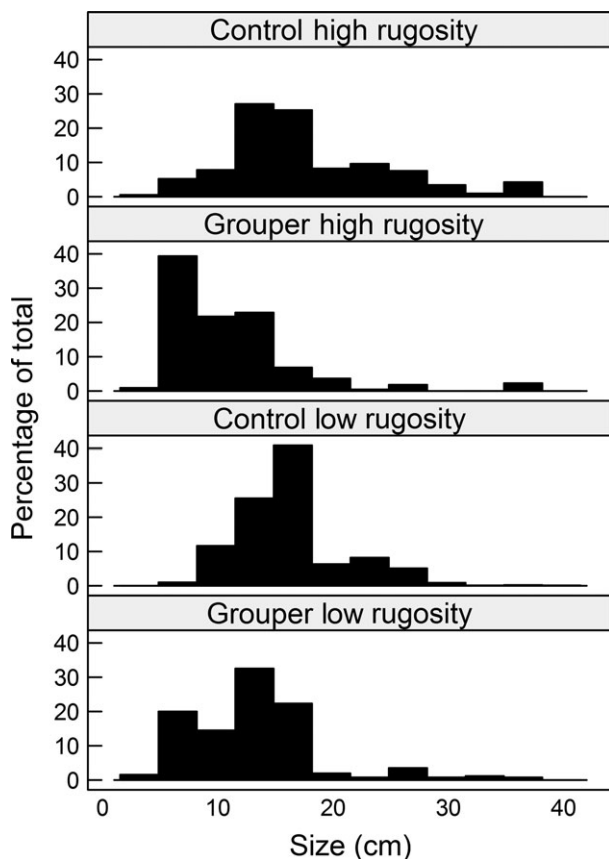


Fig. 4. Percentage of total foraging individuals observed of different-sized fishes near the predator model (0.5 and 1 m) at each predator (i.e. grouper decoy and control) and rugosity (i.e. high and low rugosity) treatment.

towards smaller individuals (Kolmogorov–Smirnov test, Predator: $D = 0.44$, $P < 0.001$, Rugosity: $D = 0.15$, $P < 0.001$) (Fig. 4). Thus, fishes were smaller and fed more rapidly but consumed less food overall the closer they were to the predator decoy, especially in high rugosity areas.

The two most common species, *S. aurofrenatum* and *A. bahianus*, showed feeding patterns similar to those we observed from all species pooled. Individual feeding rates for both species declined with distance from the grouper decoy and were greater in high relative to low rugosity sites at 0.5 m (Table S3, Fig. S4a,b). For both species, total bites per hour was over 10× greater and fishes were ca. 4 cm larger at 4 m relative to 0.5 m from the grouper decoy (Fig. S4c–f). However, for *A. bahianus*, rugosity did not affect either metric, whereas *S. aurofrenatum* were significantly smaller near the decoy and took significantly fewer total bites per hour in the high relative to low rugosity sites.

Discussion

Predators can exert strong influences on prey behaviour and trophic interactions via intimidation across disparate ecosystems (Lima & Dill 1990). However, in coral reef ecosystems, the non-consumptive role of predators has

received less attention (but see Madin *et al.* 2010b; Rizzari *et al.* 2014). Our work suggests that the threat of predation alters both feeding behaviour and top-down impacts of herbivorous fishes. Specifically, we used decoys of large piscivorous fish to show that in risky areas herbivorous fishes consumed ca. 50% less food overall. Interestingly, when fishes did feed near predator decoys they took bites at a faster rate than in areas with lower risk. Furthermore, we show that the effects of risk are dependent on prey size with smaller individuals showing muted responses to predation risk compared to their larger counterparts. Importantly, habitat heterogeneity altered the nature of risk effects, with predation risk more strongly suppressing herbivore feeding in more complex areas. Thus, predators appear to create a reefscape of fear that both changes the size structure of foraging herbivores and decreases their feeding thereby altering patterns in herbivory, an ecosystem process critical for the function of coral reefs.

Our study reinforces the threat-sensitivity hypothesis which predicts that prey will trade off predator avoidance against other activities in a manner that reflects the magnitude of predatory threat (Helfman 1989; Rizzari *et al.* 2014). Herbivores were less willing to feed at closer distances to the predator decoy (i.e. where the magnitude of perceived threat was greater). Furthermore, the risk avoidance behaviours of fishes were remarkably similar across the four reefs that varied substantially in background levels of predation risk (i.e. reefwide predator abundance). Large grouper such as the one depicted by our decoys are relatively rare across reefs in the FKNMS. At the two reefs where we detected the fewest predators, prey perceived the decoy as a potential threat and exhibited avoidance strategies similar to fishes at reefs where predators were more common. Thus, visual predator detection and recognition in herbivorous fishes appears primarily based on unlearned predispositions (Kelley & Magurran 2003). Therefore, prey will likely resume avoidance strategies, which will in turn alter their spatial impact on the benthos, as predators recover in marine protected areas (Smith *et al.* 2011).

In terrestrial systems, landscape features (e.g. valleys, trees, etc.) can be important mediators of predation risk and anti-predator behaviour (Laundre, Hernandez & Altendorf 2001; Valeix *et al.* 2009). For instance, sand dune-dwelling granivorous rodents will alter their use of open and sheltered bush microhabitats depending on the risk of predation (Kotler *et al.* 1993). They utilize open habitats more frequently to avoid snake predators that hide in the bush, but avoid these areas on illuminated nights when owl predation is more likely. Similar to terrestrial systems, landscape features can be important in mediating predator–prey interactions in seagrass habitats (Heithaus *et al.* 2009). However, few studies have investigated the importance of habitat structure in mediating foraging behaviour of herbivores in coral reef ecosystems, even though vulnerability to predation leads to fishes

being hesitant to transverse structurally simple habitats (e.g. sand flats) both within (Turgeon *et al.* 2010) and between reefs (Chapman & Kramer 2000).

Our study suggests that structural complexity of reefs interacts with risk to determine the outcome of foraging decisions. We show that this interaction influences anti-predator behaviour differently depending on the size and identity of foragers. At close proximities to the predator decoy, fishes avoided foraging in both structurally complex and simple habitats. However, grazing remained low in complex areas even at further distances from predator decoys. Although these complex areas may offer places of escape for smaller fishes (Beukers & Jones 1997), most parrotfishes and surgeonfishes are likely too large to hide in the crevices of the reef or among the branches of a coral, and readily flee when threatened (Januchowski-Hartley *et al.* 2011). For these larger fishes, the coral heads and complex reef structure characterizing high rugosity areas likely impede both detection of and escape from predators. Beyond the acute effect of the predator decoy, video analyses also revealed higher predator abundances in complex areas, which may have driven the overall lower rates of herbivory in high rugosity areas regardless of the presence of the predator decoy. These results together suggest that the probability of encountering a predator is greater and the probability of escape is lower in high complexity areas, resulting in greatly altered behavioural patterns of larger herbivores and overall suppression of herbivory in these areas. Thus, we show that the responses of herbivorous fishes to landscape features on a coral reef are similar those of terrestrial herbivores in complex habitats, suggesting that landscapes of fear provide a generalizable framework for predicting trophic interactions across diverse ecosystems (Schmitz 2005; Heithaus *et al.* 2009).

Prey vulnerability can depend on body size, with smaller prey generally subject to more predators and thus greater predation rates (Sinclair, Mduma & Brashares 2003; Preisser & Orrock 2012). On coral reefs, large-bodied parrotfishes often escape predation from gape-limited predators, whereas smaller bodied parrotfishes suffer greater predation rates (Mumby *et al.* 2006). However, for multiple species of reef fishes, there is a positive correlation between body size and wariness in response to predators, suggesting smaller individuals are less risk sensitive (Januchowski-Hartley *et al.* 2011). Our work supports this latter observation because we showed a shift in the size distribution of herbivores towards smaller individuals where predation risk was higher, especially in high rugosity areas. This pattern was consistent when we considered body size distribution across all herbivore species or within species.

There are two primary hypotheses to explain this result. First, small size could be a refuge for prey if predators preferentially consume larger prey that provide more reward with less energy expenditure (Brooks & Dodson 1965). Thus, smaller bodied herbivores may have been less

risk sensitive because they were less desirable targets for a grouper the size of our decoy (ca. 90 cm). Secondly, smaller individuals may be less risk sensitive because they have fewer assets to protect [i.e. the asset protection principle (Clark 1994)] and have more to gain from each foraging episode. Based on this principle, larger bodied herbivores, which have accumulated more assets (e.g. body size, fat reserves, or reproductive potential), have less to gain from each foraging episode, relative to smaller bodied herbivores. These smaller fishes might also be more likely to escape from predators using complex areas as cover, making these areas less risky than they are to larger individuals where complexity could impede their escape. These body size-dependent differences in habitat use appear common across ecosystems because different-sized herbivores often respond differently to the same habitat depending on how it either impedes or facilitates their escape from predation (Burkepile *et al.* 2013b).

Prey vulnerability to predation can also vary depending on prey species. The two most common herbivores we observed, *A. bahianus* and *S. aurofrenatum*, responded similarly to the increasing threat of predation. However, the responses of *S. aurofrenatum* to this threat, in terms of the total bites/hour and size of foragers, were elevated in high rugosity areas, whereas there was no effect of rugosity for *A. bahianus*. *Sparisoma aurofrenatum* may have perceived high rugosity areas as more dangerous because foraging was shifted towards smaller individuals near the decoy and total bites remained lower at all distances compared to low rugosity areas. Landscape features may be more of a driver of anti-predatory behaviour for *S. aurofrenatum* relative to *A. bahianus* because of differences in their escape modes or susceptibilities to predation (Lingle 2002; Wirsing, Cameron & Heithaus 2010). *Acanthurus bahianus*, like other Acanthurids, possess a razorlike scalpel on their caudal peduncle, presumably used in anti-predatory defence, which may make them more likely to forage in potentially risky situations. In contrast, *S. aurofrenatum* do not have a physical anti-predatory defence and mostly rely on escape tactics, potentially making them more likely to avoid complex regions that could hinder their escape. Other studies have shown differences in species' responses to chronic predation risk (i.e. risk integrated over space) (Madin, Gaines & Warner 2010a; Catano, Shantz & Burkepile 2014). Specifically, similar acanthurid species do not show changes in diet or movement on reefs where predator abundance is high (Madin, Gaines & Warner 2010a; Catano, Shantz & Burkepile 2014), whereas *S. aurofrenatum* alter the types of resources they consume (Catano, Shantz & Burkepile 2014), suggesting the latter may be more sensitive to predation risk.

On coral reefs, herbivory plays a key role in preventing algal overgrowth and facilitating coral recruitment, growth and survivorship (Mumby 2006; Hughes *et al.* 2007). Therefore, predators could have indirect effects on benthic communities by altering herbivore behaviour

(Madin *et al.* 2010b). Specifically, predation risk could alter the spatial distribution and intensity of herbivory. On reefs where predators are abundant, herbivores could concentrate their feeding on areas of reef that have inherently less risk, potentially making these areas more suitable for the recruitment and establishment of coral species. Recent models suggest that increasing the spatial concentration of herbivory is more likely to lead to increases in coral recruitment and coral cover relative to areas where the same amount of herbivory is spread across larger areas of reef (Sandin & McNamara 2012). Yet, on reefs where predators are rare, herbivores may be free to forage more widely, thereby diluting herbivory on a reefwide scale and lessening the indirect positive impacts on corals. Additionally, our data suggest that risk from predators results in herbivory that is dominated by smaller herbivores. This shift in the size structure of herbivores could affect the impact of herbivory on the benthos because smaller individuals often have fundamentally different effects on algal communities than do larger individuals (Bonaldo & Bellwood 2008; Plass-Johnson, McQuaid & Hill 2012). To understand how predators influence the intensity and spatial distribution of herbivory, it is critical to consider behaviourally mediated processes because changes to herbivore population sizes and/or their behaviour could ultimately affect coral communities. It is important to note that we show acute responses to the imminent threat of predation and their localized effects on the benthos. Based on this information, we can only hypothesize about the consequences that chronic risk can have on benthic communities across broad spatial and temporal scales.

Our work demonstrates that the threat of predation alters many aspects of herbivore foraging behaviour, thereby influencing the key ecological process of grazing on coral reefs. Based on evidence from multiple disparate ecosystems, it is clear that predators have an important non-consumptive role in affecting community dynamics, and our work is among the first to reinforce this idea in coral reef ecosystems. Furthermore, our work supports the idea that habitat features and prey-specific responses are crucial components to consider when assessing predator–prey interactions and risk effects (Heithaus *et al.* 2009; Wirsing, Cameron & Heithaus 2010; Burkepile *et al.* 2013b). However, global change may be fundamentally altering the nature of these predator–prey interactions, especially on coral reefs. The intense fishing of predators world-wide (Myers & Worm 2003) may reduce the impact that predation risk plays in influencing fish foraging behaviour on reefs (e.g. Madin *et al.* 2010b; Catano, Shantz & Burkepile 2014; Rizzari *et al.* 2014). Further, global and local factors such as climate change, disease and pollution have driven a loss of corals and structural complexity that has profoundly altered reef landscapes (Alvarez-Filip *et al.* 2009). Our data suggest that declines in predator abundance coupled with losses in structural complexity could alter the landscape of fear for herbivorous fishes, thereby influencing the distribution and concentration of

herbivory and the positive indirect effects on corals. Building on existing models of the context dependency of risk effects will help improve our ability to predict how altering the landscape of predation risk will impact coral reefs in an era of global change.

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.8962f> (Catano *et al.* 2015b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Representative panoramic images of a (a) high and (b) low rugosity site.

Fig. S2. Percentage of total foraging individuals observed of different herbivorous fish species at different rugosity (HR: high rugosity, LR: low rugosity) and predator treatments (i.e. grouper decoy and control).

Fig. S3. Predators observed per minute of video observation (Mean \pm SE) at four reefs in high and low rugosity sites.

Fig. S4. Least square means (\pm SE) for (a) and (b) bites/hour on seagrass or benthos, (c) and (d) individual feeding rates (bites/minute) and (e) and (f) forager size (cm) at increasing distances from predator model for *Sparisoma aurofrenatum* and *Acanthurus bahianus*.

Table S1. Summary of LMMs testing for effects of natural predators observed at each site, fish size, predator treatment (i.e.

grouper vs. control), rugosity (i.e. high vs. low) and their interaction on the percentage of seagrass consumed per hour, the bites on seagrass per hour, the bites on benthos per hour, individual feeding rates (bites/second) and fish size.

Table S2. Summary of LMMs testing for effects of fish size, rugosity (i.e. high vs. low), distance from grouper decoy (i.e. 0.5, 1, 2, and 4 m) and their interaction on the percentage of seagrass consumed per hour, the bites on seagrass per hour, the bites on benthos per hour, individual feeding rates (bites/second) and fish size.

Table S3. Summary of LMMs testing for effects of fish size, rugosity (i.e. high vs. low), distance from grouper decoy (i.e. 0.5, 1, 2, and 4 m) and their interaction on bites on seagrass or benthos per hour, individual feeding rates, and forager size for (a) *Sparisoma aurofrenatum* and (b) *Acanthurus bahianus*.