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Andrew G. Bauman

Jovena C. L. Seah

Fraser A. Januchowski-Hartley

Andrew S. Hoey

Jenny Fong

See next page for additional authors

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Authors

Peter A. Todd

National University of Singapore

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Author for correspondence:

Andrew G. Bauman

e-mail: andrew.bauman@nus.edu.sg

†These authors contributed equally to this study.

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Marine biology

Fear effects associated with predator presence and habitat structure interact to alter herbivory on coral reefs

Andrew G. Bauman^{1,†}, Jovena C. L. Seah^{1,†}, Fraser A. Januchowski-Hartley², Andrew S. Hoey³, Jenny Fong¹ and Peter A. Todd¹

¹Experimental Marine Ecology Laboratory, National University of Singapore, Singapore

²Department of Biosciences, Swansea University, Swansea, UK

³ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

AGB, 0000-0001-9260-2153; JCLS, 0000-0002-0488-999X; FAJ-H, 0000-0003-2468-8199; ASH, 0000-0002-4261-5594; JF, 0000-0001-8645-1897; PAT, 0000-0001-5150-9323

Non-consumptive fear effects are an important determinant of foraging decisions by consumers across a range of ecosystems. However, how fear effects associated with the presence of predators interact with those associated with habitat structure remain unclear. Here, we used predator fish models (*Plectropomus leopardus*) and experimental patches of the macroalga *Sargassum ilicifolium* of varying densities to investigate how predator- and habitat-associated fear effects influence herbivory on coral reefs. We found the removal of macroalgal biomass (i.e. herbivory) was shaped by the interaction between predator- and habitat-associated fear effects. Rates of macroalgal removal declined with increasing macroalgal density, likely due to increased visual occlusion by denser macroalgae patches and reduced ability of herbivorous fishes to detect the predators. The presence of the predator model reduced herbivory within low macroalgal density plots, but not within medium- and high-density macroalgal plots. Our results suggest that fear effects due to predator presence were greatest at low macroalgal density, yet these effects were lost at higher densities possibly due to greater predation risk associated with habitat structure and/or the inability of herbivorous fishes to detect the predator model.

1. Introduction

Predators are a key component of many ecosystems and can have a marked influence on ecological processes through both consumptive and non-consumptive (changes in behaviour, physiology or morphology) effects (reviewed in [1,2]). Importantly, changes in prey behaviour (i.e. fear effects) due to predation risk, including altered patterns of habitat use [3,4], feeding rates [5,6] and resources consumed [6,7], can have greater effects on ecosystems than consumptive effects of predators [8]. The nature and magnitude of fear effects can be influenced by a range of factors, including predator identity [9], prey attributes [5], habitat characteristics [6,7] and physical environmental conditions (e.g. water quality [10]). Fear effects will, therefore, vary spatially and temporally [2,4,7,9], and are often heavily dependent on ecological context (e.g. [5,6,8]) altering prey perception and response to risk [4,6,7].

Evidence for fear effects on coral reefs are generally based on the response of fishes to the presence of fish predators or decoy models [3,5,6], or correlative evidence of changes in foraging behaviour among reefs or habitats that differ in the abundance and/or presence of predators [4,11]. For example, macroalgal removal by herbivorous reef fishes has been shown to decline with increasing density of fleshy macroalgae, with declines attributed to the higher abundance of predators

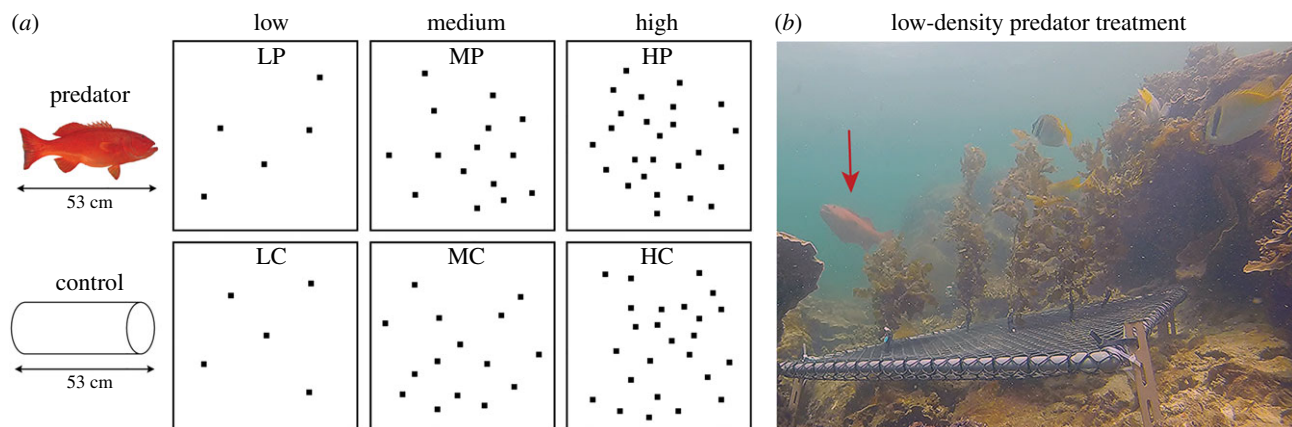


Figure 1. Experimental design: (a) schematic drawing of the spatial arrangement of *S. ilicifolium* assays at three different density levels (low, medium and high) and treatment groups (*P. leopardus* predator model and control). (b) Photograph showing low-density plot with predator fish model (indicated by the red arrow) and *S. virgatus* removing *S. ilicifolium* biomass.

within dense macroalgal beds, or the visual barrier created by the macroalgae making it difficult for herbivorous fishes to detect predators and initiate an escape response (i.e. increased background risk) [4,11]. Despite the potential importance of fear effects associated with both predator presence (i.e. acute risk) and habitat structure (i.e. background risk) in shaping foraging decisions by herbivorous reef fishes, the combined effects of predator presence and macroalgal density on the foraging behaviour of these fishes is largely unknown. Investigating the contextual factors that impact how herbivorous fishes respond to fear effects will facilitate a greater understanding of how environment and animal behaviour interact in coral reef ecosystems. The aim of this study was to determine how fear effects associated with predator presence and macroalgal density shape herbivory on coral reefs. We hypothesize that predator presence (acute risk) and increasing macroalgal density (background risk) interact additively to increase the perception of predation risk by herbivores.

2. Material and methods

We conducted field-based experiments across five consecutive weeks between October and November 2017 on Pulau Satumu, an offshore island of Singapore with a well-developed fringing reef (electronic supplementary material, figure S1). Each week, we transplanted a series of *Sargassum ilicifolium* thalli at three densities: high (25 thalli; approx. 4.0 kg m^{-2}), medium (15 thalli; approx. 2.4 kg m^{-2}) and low (5 thalli, approx. 0.8 kg m^{-2}) to 0.5 m^2 plots positioned haphazardly along the reef crest, the area of highest herbivore activity (3–4 m depth) [12]. We used *S. ilicifolium* because it is the most abundant *Sargassum* species in Singapore [13]. Individual *S. ilicifolium* thalli of similar heights (ca 70 cm) were collected by hand, spun in a mesh bag for approximately 20 s, weighed to the nearest 0.1 g, labelled with a small plastic tag, and allocated randomly to one of the three density treatments. Two replicates of each density treatment were deployed each week, with either a predator model (*Plectropomus leopardus*, 53 cm total length (TL)) or an object control (53 cm length of light grey PVC, 8 cm diameter) placed approximately 1 m from the experimental plots (figure 1). Adjacent plots were separated by a minimum of 15 m, with predator and density treatments allocated randomly among plots. All treatments were deployed between 09:30 and 10:30, with two underwater video cameras (GoPro) mounted on small dive weights placed approximately 1 m from each plot. Cameras recorded continuously for approximately 4 h each day. A 10 cm scale bar was held adjacent to the nearest edge

of each plot for 10 s to allow calibration of fish sizes on the video footage. Three additional *S. ilicifolium* thalli were placed inside exclusion cages (15 cm radius, 100 cm height and 0.5 cm mesh) to control for the effects of handling and translocation.

Cameras were collected after 4 h, and macroalgal assays after 24 h. Following retrieval, each individual thallus was spun and re-weighed as above, and biomass loss (g) calculated per thallus. To estimate *S. ilicifolium* biomass lost due to herbivory, as opposed to handling and translocation effects, we subtracted the proportional loss of biomass from the caged thallus from each of the experimental thalli (following [14]). The first 20 min and last 10 min of each video were discarded to minimize potential diver interference. From the video footage, we recorded the total number of bites, species and estimated TL to the nearest centimetre for each fish observed feeding on *S. ilicifolium* (electronic supplementary material, table S1). Further methodological details are provided in the electronic supplementary material.

We conducted all analyses in R [15], using the *lme4*, *glmer* and *lsmeans* packages [16]. Linear mixed-effect models were fitted to identify differences in the relative and absolute macroalgal biomass removed, coefficient of variation of the biomass lost per thalli within each plot to identify variation in removal rates among thalli, mean bites, total bites and mass-standardized bites. Analysis of biomass removed was based on the pooled *S. ilicifolium* biomass within each plot. Density and predator presence/absence were fixed factors, and day and plot were random factors to account for potential non-independence between plots. Random effects of day and plot (intercept and slope) were tested and Akaike information criterion corrected for small samples sizes (AICc) used to determine the best performing model structure, resulting in day being included in all models, and day and plot in the bites model. Tukey post hoc comparisons were performed using the *lsmeans* package [16]. The proportion of biomass removed was square-root transformed to meet assumptions of normality. We used χ^2 tests to determine whether there were changes in the frequency of species feeding on macroalgae with density and predator presence.

3. Results

(a) *Sargassum* removal

The proportion of *Sargassum* biomass removed decreased with increasing *Sargassum* density (figure 2a), although there was significant density \times predator model interaction. Presence of the predator model reduced the proportion of *Sargassum* biomass removed from low-density plots, but had no detectable effect within the medium or high-density plots (figure 2a and

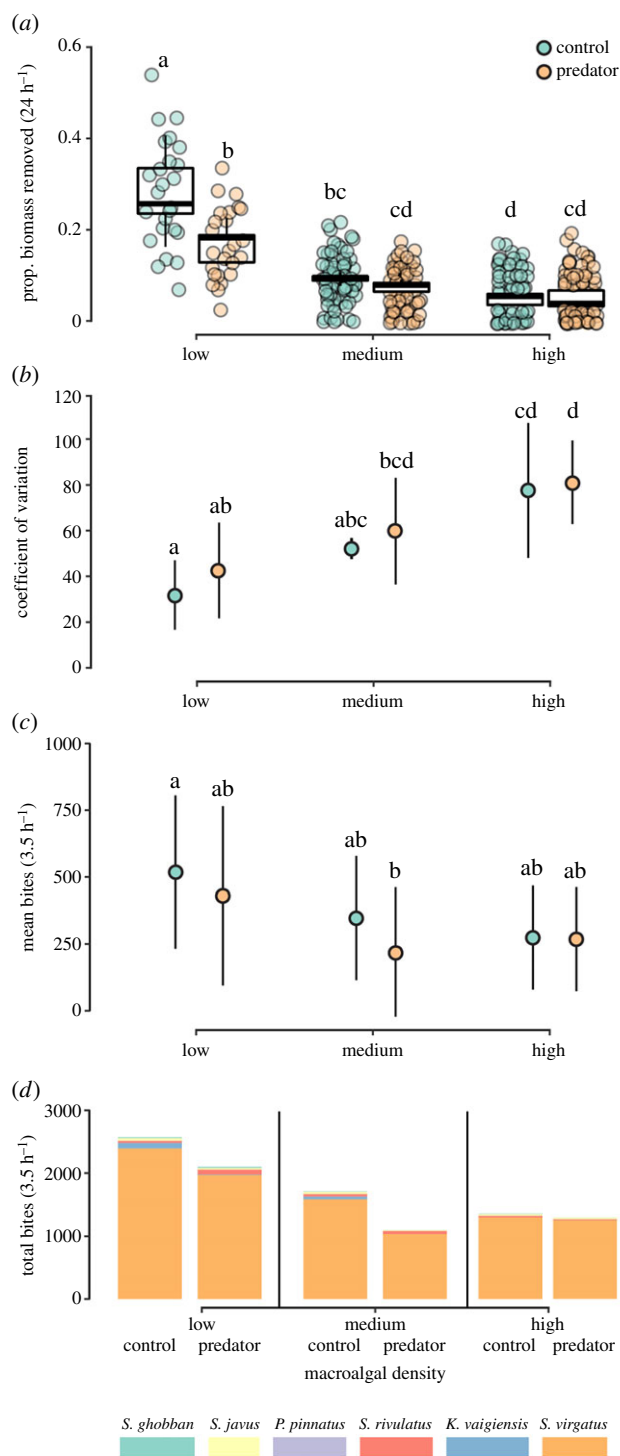


Figure 2. Effect of *S. ilicifolium* density, object controls (teal/left circles) and predator models (orange/right circles) on herbivore foraging behaviour. (a) proportion of macroalgae biomass removed 24 h⁻¹, (b) coefficient of variation, (c) mass-standardized bites 3.5 h⁻¹ and (d) the number of mass-standardized bites taken by all species recorded at each treatment and density. Letters above density treatments indicate significant differences ($p < 0.05$). (Online version in colour.)

table 1). While there was evidence that total (i.e. absolute) biomass removed was generally lower in the presence of the predator model, there were no significant differences in total macroalgal biomass removed among densities (table 1). The coefficient of variation of biomass removed from individual thalli (and therefore heterogeneity in removal within a plot) increased significantly with density, but showed no significant effect of predator presence (figure 2b and table 1).

(b) Bite rates

A total of 10 150 bites by herbivorous fishes were observed from the video footage across all plots. The mean total number of bites plot⁻¹ was significantly greater on low compared to high-density treatments, (figure 2c and table 1). *Siganus virgatus* accounted for greater than 94% of bites across all assays (figure 2d), while *Siganus javus*, *Scarus rivulatus* and *Kyphosus vaigiensis* accounted for the majority of the remaining bites. We found no effect of the predator model on mean total bites within each density treatment, or any differences in feeding by *S. virgatus* among predator treatments, although total bites decreased at high-density treatments. However, the proportion of bites by species other than *S. virgatus* differed between treatments ($\chi_{1,5}^2 = 43.743$, $p < 0.001$), with post hoc comparisons indicating that relative feeding by these species was greatest in low-density plots (irrespective of predator presence) and the medium density control, than the medium-density predator treatment and both high-density treatments. There was no evidence that fish took fewer bites in the presence of the predator model (table 1).

4. Discussion

Despite the recent emphasis on fear effects as a major driver of herbivore foraging behaviour on shallow coral reef ecosystems (e.g. [7,17]), partitioning how herbivores respond to acute (predator presence) and background (habitat-associated) risk remains unexplored. We found daily rates of herbivory, but not shorter-term (3.5 h) herbivore foraging behaviour, was shaped by the interaction between predator- and habitat-associated fear effects. Rates of macroalgal removal (the ‘realized function’ *sensu* [18]) declined with increasing macroalgal density, potentially due to increased visual occlusion by denser macroalgae patches reducing the ability of herbivorous fishes to detect predators, thus increasing their perception of background risk [4]. We also found the presence of a predator model reduced macroalgal removal in low macroalgal density plots, but not in medium- or high-density plots. These results suggest that acute risk due to predator presence were context dependent; being greatest at low macroalgal density, but lost at higher densities due to background risk associated with habitat structure, and/or the inability of herbivorous fishes to detect the predator model.

Acute risk, or the immediate risk an individual experiences while foraging (*sensu* [3]), and background risk, the risk an individual experiences while foraging in complex habitats [6], can lead to more cautious behaviour (i.e. increased vigilance or avoidance), influencing the distribution of foraging intensity [5,7,19]. Such behavioural responses reflect the inherent trade-offs that consumers often make between obtaining food and predator avoidance [1]. Similar to previous studies, our results demonstrate that both acute and background risk can suppress localized herbivory [4,5,6] and impact macroalgal removal, but that these responses may be species-specific, as indicated by our bite-rate data. For example, *S. virgatus* appeared to be less risk averse to both acute (i.e. predator presence) and background risk (i.e. increasing *Sargassum* density) compared to other herbivores of similar or larger body size. The general lack of response by *S. virgatus* to increasing predation risk may be related to the frequent coordinated vigilance behaviour observed by this species (A.G.B. and F.A.J.H. 2017, pers. obs.) and other siganid species, a behaviour that is hypothesized to reduce predation risk while foraging [20,21]. By contrast, previous research from the Great Barrier

Table 1. Results of linear mixed-effects models. All models had day as a random effect. The *lmer* function automatically calculates *t*-tests using Satterthwaite approximations to degrees of freedom.

	fixed effects	estimate	s.e.	d.f.	<i>t</i> -value	Pr (> <i>t</i>)
proportion biomass removed	density (M)	−0.2174	0.0281	20	−7.474	<0.001
	density (H)	−0.3191	0.0281	20	−11.371	<0.001
	predator	−0.1137	0.0281	20	−4.053	<0.001
	predator × density (M)	0.0780	0.0397	20	1.965	0.063
	predator × density (H)	0.1267	0.0397	20	3.191	0.005
total biomass removed	density (M)	5.68	15.10	20	0.376	0.711
	density (H)	−20.84	15.10	20	−1.381	0.183
	predator	−36.16	15.10	20	−2.396	<0.05
	predator × density (M)	14.04	21.35	20	0.658	0.518
	predator × density (H)	42.74	21.35	20	2.002	0.059
variation of biomass removed	density (M)	20.328	8.151	18.794	2.494	<0.05
	density (H)	47.650	8.702	19.129	5.476	<0.001
	predator	10.772	8.151	18.794	1.321	0.202
	predator × density (M)	−3.141	11.528	18.794	−0.272	0.788
	predator × density (H)	−9.111	11.924	18.793	−0.764	0.454
					z-value	
bites plot ^{−1}	density (M)	−0.395	0.204	20	−1.937	0.053
	density (H)	−0.641	0.220	20	−2.911	<0.005
	predator	−0.203	0.193	20	−1.051	0.293
	predator × density (M)	−0.255	0.318	20	−0.800	0.424
	predator × density (H)	−0.156	0.320	20	0.49	0.626
<i>Siganus virgatus</i> bites plot ^{−1}	density (M)	0.195	0.164	20	1.19	0.24
	density (H)	0.608	0.151	20	4.02	<0.001
	predator	0.013	0.174	20	0.07	0.94
	predator × density (M)	−0.057	0.245	20	−0.23	0.82
	predator × density (H)	−0.207	0.219	20	−0.95	0.34

Reef reported that biomass removal of single *Sargassum* assays by herbivorous fishes of similar (*Siganus doliatus*) or even larger body sizes (*Naso unicornis*) was suppressed in the presence of a 48 cm predator (*P. leopardus*) model [5].

Recent research focused on fear effects and reef habitat heterogeneity reports suppressed herbivory in more complex reef habitats due to higher perceived predation risk [6]. Generally, more complex reef habitats are considered beneficial for fish prey because of reduced predation intensity and/or predation risk through the provision of more spatial refuges from predators [11,22]. This study, however, adds to the emerging notion that complex structural features, including those created by large canopy forming macroalgae (e.g. *Sargassum*) increases the fear effects associated with habitat structure and negatively affects the ability of herbivorous fishes to remove macroalgae [4,23]. Evidence suggests that herbivorous fishes avoid reef areas with dense fleshy macroalgae presumably due to greater background risk [4]. Our results revealed similar patterns, with higher density plots of *Sargassum* showing reductions in the removal of macroalgal biomass. Herbivorous fishes may be avoiding areas of high habitat structure because it obstructs their vision, and hence capacity to detect potential predators, and initiate an escape response [22]—so the addition of the predator model had no further impact on macroalgal removal.

We also found decreasing numbers of herbivore species with increasing *Sargassum* density, suggesting that higher macroalgal densities potentially reduce the redundancy of browsing function, even where multiple species are present [24]. Some caution is required when interpreting our results as the predator models we used were stationary, therefore constraining predation risk spatially and possibly providing the herbivorous fish less information on predator intent, thereby obscuring true predator effects on foraging behaviour. Furthermore, these results may vary among reefs due to differences in benthic composition, herbivorous fish assemblages, predator abundance and type, and macroalgae species.

Notably, the effects of *Sargassum* density on herbivory and the rates of macroalgal removal in this study were less pronounced than those reported in previous macroalgal density studies [4]. The perception of higher background risk on herbivorous fishes in our study may have been exacerbated by Singapore's chronic poor water quality (e.g. high turbidity and sedimentation [25]), reducing their ability to detect predators and initiate an escape response. Coral reef fishes rely heavily on visual cues for foraging and predator avoidance [26], and high water turbidity has been shown to amplify predation risk effects by reducing visual detection of predators [27] which can negatively affect both habitat choice and foraging

success [28]. Furthermore, high turbidity has recently been shown to lead to increased vigilance (i.e. more cautious behaviour) and decreased activity in coral reef fish [10] that could potentially reduce foraging rates [28]. Our results suggest that herbivorous fishes' perception of risk is not necessarily additive—the presence of a predator may not significantly change feeding behaviour of the dominant browser, if perception of risk is already high, since increased vigilance may result in fitness costs [29]. It is possible that, while the ecosystem function browsing may decline when macroalgae are abundant, it does not do so linearly. Our findings add to the growing body of literature that emphasize the importance of habitat structure in shaping functional processes, potentially leading to trophic cascades and the persistence of macroalgal stands on coral reefs.

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