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

3

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35 Abstract

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

53

54 Keywords: risk effects, coral reefs, predator-prey interactions, herbivory, *Sargassum*

55

56 1. Introduction

57

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

69

70 Evidence for fear effects on coral reefs are generally based on the response of fishes
71 to the presence of fish predators or decoy models [3,5,6], or correlative evidence of
72 changes in foraging behaviour among reefs or habitats that differ in the abundance
73 and/or presence of predators [4,11]. For example, macroalgal removal by herbivorous
74 reef fishes has been shown to decline with increasing density of fleshy macroalgae,
75 with declines attributed to the higher abundance of predators within dense macroalgal
76 beds, or the visual barrier created by the macroalgae making it difficult for herbivorous
77 fishes to detect predators and initiate an escape response (i.e. increased background
78 risk) [4,11]. Despite the potential importance of fear effects associated with both
79 predator presence (i.e., acute risk) and habitat structure (i.e., background risk) in
80 shaping foraging decisions by herbivorous reef fishes, the combined effects of predator
81 presence and macroalgal density on the foraging behaviour of these fishes is largely
82 unknown. Investigating the contextual factors that impact how herbivorous fishes
83 respond to fear effects will facilitate a greater understanding of how environment and
84 animal behaviour interact in coral reef ecosystems. The aim of this study was to
85 determine how fear effects associated with predator presence and macroalgal density
86 shape herbivory on coral reefs. We hypothesise that predator presence (acute risk) and
87 increasing macroalgal density (background risk) interact additively to increase the
88 perception of predation risk by herbivores.

89

90 2. Material and Methods

91

92 We conducted field-based experiments across five consecutive weeks between October
93 and November 2017 on Pulau Satumu, an offshore island of Singapore with a well-
94 developed fringing reef (electronic supplementary materials, figure S1). Each week, we
95 transplanted a series of *Sargassum ilicifolium* thalli at three densities: high (25 thalli;
96 $\sim 4.0 \text{ kg m}^{-2}$), medium (15 thalli; $\sim 2.4 \text{ kg m}^{-2}$) and low (5 thalli, $\sim 0.8 \text{ kg m}^{-2}$) to 0.5m²
97 plots positioned haphazardly along the reef crest, the area of highest herbivore activity
98 (3–4 m depth) [12]. We used *S. ilicifolium* because it is the most abundant *Sargassum*
99 species in Singapore [13]. Individual *S. ilicifolium* thalli of similar heights (ca. 70 cm)
100 were collected by hand, spun for ~ 20 s, weighed to the nearest 0.1 g, labelled with a
101 small plastic tag, and allocated randomly to one of the three density treatments. Two
102 replicates of each density treatment were deployed each week, with either a predator

103 model (*Plectropomus leopardus*, 53 cm total length) or an object control (53 cm length
104 of light grey PVC, 8 cm diameter) placed ~1 m from the experimental plots (figure 1).
105 Adjacent plots were separated by a minimum of 15 m, with predator and density
106 treatments allocated randomly among plots. All treatments were deployed between
107 09:30 and 10:30, with two underwater video cameras (GoPro) mounted on small dive
108 weights placed ~1 m from each plot. Cameras recorded continuously for ~4 h each day.
109 A 10 cm scale bar was held adjacent to the nearest edge of each plot for 10 s to allow
110 calibration of fish sizes on the video footage. Three additional *S. ilicifolium* thalli were
111 placed inside exclusion cages (15 cm radius, 100 cm height, 0.5 cm mesh) to control
112 for the effects of handling and translocation.

113

114 Cameras were collected after 4 h, and macroalgal assays after 24 h. Following
115 retrieval, individual thalli were spun and re-weighed as above, and biomass loss (g)
116 calculated per thalli. To estimate the *Sargassum* biomass lost due to herbivory, as
117 opposed to handling and translocation effects, we subtracted the proportional loss of
118 biomass from the caged thalli from each of the experimental thalli (following [14]). The first
119 20 min and last 10 min of each video was discarded to minimize potential diver
120 interference. From the video footage we recorded the total number of bites, species, and
121 estimated total length (TL) to the nearest cm for each fish observed feeding on the
122 *Sargassum* (electronic supplementary material, table S1). Further methodological
123 details are provided in the electronic supplementary material.

124

125 We conducted all analyses in R [15], using the *lme4*, *glmer* and *lsmeans* packages
126 [16]. Linear mixed-effect models were fitted to identify differences in the relative and
127 absolute algal biomass removed, coefficient of variation of the biomass lost per thallus
128 within each plot to identify variation in removal rates among thalli, mean bites, total
129 bites and ms-bites. Analysis of biomass removed was based on the pooled *S. ilicifolium*
130 biomass within each plot. Density and predator presence/absence were fixed factors,
131 and day and plot were random factors to account for potential non-independence
132 between plots. Random effects of day and plot (intercept and slope) were tested and
133 Akaike Information Criterion corrected for small samples sizes (AICc) used to
134 determine the best performing model structure, resulting in day being included in all
135 models, and day and plot in the bites model. Tukey post-hoc comparisons were
136 performed using the *lsmeans* package [16]. Proportion of biomass removed was square-

137 root transformed to meet assumptions of normality. We used chi-squared tests to
138 determine whether there were changes in the frequency of species feeding on
139 macroalgae with density and predator presence.

140

141 3. Results

142

143 (a) *Sargassum* removal

144

145 The proportion of *Sargassum* biomass removed decreased with increasing *Sargassum*
146 density (figure 2a), although there was significant density \times predator model interaction.
147 Presence of the predator model reduced the proportion of *Sargassum* biomass removed
148 from low density plots, but had no detectable effect within the medium or high density
149 plots (figure 2a, table 1). While there was evidence that total (i.e. absolute) biomass
150 removed was generally lower in the presence of the predator model, there were no
151 significant differences in total macroalgal biomass removed among densities (table 1).
152 The coefficient of variation of biomass removed from individual thalli (and therefore
153 heterogeneity in removal within a plot) increased significantly with density, but showed
154 no significant effect of predator presence (figure 2b, table 1).

155

156 (b) Bite rates

157

158 A total of 10,150 bites (2,891 ms-bites) by herbivorous fishes were observed from the
159 video footage across all plots. The mean total number of bites plot⁻¹ was significantly
160 greater on low compared to high density treatments, (figure 2c; table 1). *Siganus*
161 *virgatus* accounted for >94% of bites across all assays (figure 2d), while *Siganus javus*,
162 *Scarus rivulatus*, and *Kyphosus vaigiensis* accounted for the majority of the remaining
163 bites. We found no effect of the predator model on mean total bites within each density
164 treatment, or any differences in feeding by *S. virgatus* among predator or density
165 treatments. However, feeding by species other than *S. virgatus* differed between
166 treatments ($\chi_{1,5} = 43.743$, $p < 0.001$), with post-hoc comparisons indicating that feeding
167 by these species was greatest in low density plots (irrespective of predator presence),
168 and the medium density control than the medium density predator treatment, and both

169 high density treatments. There was no evidence that fish took fewer bites in the
170 presence of the predator model, or with increasing macroalgal density (table 1).

171

172 4. Discussion

173

174 Despite recent emphasis on fear effects as a major driver of herbivore foraging
175 behaviour on shallow coral reef ecosystems (e.g. [7,17]), partitioning how herbivores
176 respond to acute (predator presence) and background (habitat-associated) risk remains
177 unexplored. We found daily rates of herbivory, but not shorter-term (3.5 h) herbivore
178 foraging behaviour, was shaped by the interaction between predator- and habitat-
179 associated fear effects. Rates of macroalgal removal (the ‘realized function *sensu*
180 [Bellwood et al. 2019]) declined with increasing macroalgal density, potentially due to
181 increased visual occlusion by denser macroalgae patches reducing the ability of
182 herbivorous fishes to detect predators, thus increasing their perception of background
183 risk. We also found the presence of a predator model reduced macroalgal removal in
184 low macroalgal density plots, but not in medium or high density plots [5,7]. These
185 results suggest that acute risk due to predator presence were context dependent; being
186 greatest at low macroalgal density, but lost at higher densities due to background risk
187 associated with habitat structure, and/or the inability of herbivorous fishes to detect the
188 predator model.

189

190 Acute risk, or the immediate risk an individual experiences while foraging (*sensu*
191 [11]), and background risk, the risk an individual experiences while foraging in
192 complex habitats (*sensu* [X]) can lead to more cautious behaviour (i.e. increased
193 vigilance or avoidance), influencing the distribution of foraging intensity [24]. Such
194 behavioural responses reflect the inherent trade-offs that consumers often make
195 between obtaining food and predator avoidance [6]. Similar to previous studies, our
196 results demonstrate that both acute and background risk can suppress localized
197 herbivory [5,7] and impact macroalgal removal, but that these responses may be
198 species-specific, as indicated by our bite-rate data. For example, *S. virgatus* appeared
199 to be less risk averse to both acute (i.e. predator presence) and background risk (i.e.
200 increasing *Sargassum* density) compared to other herbivores of similar or larger body
201 size The general lack of response by *S. virgatus* to increasing predation risk may be
202 related to the frequent coordinated vigilance behaviour observed by this species (AB

203 and FJH pers. obs.) and other siganid species, a behaviour that is hypothesised to reduce
204 predation risk whilst foraging [25,26]. In contrast, previous research from the GBR
205 reported that biomass removal of single *Sargassum* assays by herbivorous fishes of
206 similar (*Siganus doliatus*) or even larger body sizes (*Naso unicornis*) was suppressed
207 in the presence of a 48 cm predator (*Plectropomus leopardus*) model [X].

208 Recent research focused on fear effects and reef habitat heterogeneity reports
209 suppressed herbivory in more complex reef habitats due to higher perceived predation
210 risk [7]. Generally more complex reef habitats are considered beneficial for fish prey
211 because of reduced predation intensity and/or predation risk through the provision of
212 more spatial refuges from predators [13,27]. This study, however, adds to the emerging
213 notion that complex structural features, including those created by large canopy
214 forming macroalgae, such as *Sargassum*, increases fear effects associated with habit
215 structure negatively affect herbivorous fishes ability to remove macroalgae [12,28].
216 Evidence suggests that herbivorous fishes avoid reef areas with dense fleshy
217 macroalgae presumably due to greater background predation risk [12]. Our results
218 revealed similar patterns within higher density plots of *Sargassum* showing reductions
219 in the removal of assay biomass. Herbivorous fishes may be avoiding areas of high
220 habitat structure because it obstructs their vision, and hence capacity to detect potential
221 predators, and initiate an escape response [27]—so the addition of the predator model
222 had no further impact on macroalgal removal. We also found decreasing numbers of
223 herbivore species with increasing *Sargassum* density, suggesting that higher
224 macroalgal densities potentially reduce the redundancy of browsing function, even
225 where multiple species are present [19]. Some caution is required when interpreting our
226 results as the predator models we used were stationary, therefore constraining predation
227 risk spatially and possibly providing the herbivorous fish less information on predator
228 intent, potentially obscuring true predator effects on foraging behaviour. Further, these
229 results may vary between reefs due to differences in benthic composition, herbivorous
230 fish assemblages, predator abundance and type, and macroalgae species.

231

232 Notably, the effects of *Sargassum* density on herbivory and the rates of macroalgal
233 removal in this study were less pronounced than those reported in previous macroalgal
234 density studies [12]. The perception of higher background risk on herbivorous fishes in

235 our study may have been exacerbated by Singapore's chronic poor water quality (e.g.
236 high turbidity and sedimentation [29]), reducing their ability to detect predators and
237 initiate an escape response. Coral reef fishes rely heavily on visual cues for foraging and
238 predator avoidance [30], and high water turbidity has been shown to amplify predation
239 risk effects by reducing visual detection of predators [31] which can negatively affect
240 both habitat choice and foraging success [32]. Further, high turbidity has recently been
241 shown to lead to increased vigilance (i.e. more cautious behaviour) and decreased
242 activity in coral reef fish [8] that could potentially reduce foraging rates [32]. Our
243 results suggest that herbivorous fishes' perception of risk is not necessarily
244 additive—presence of an predator may not significantly change feeding behaviour of
245 the dominant browser, if perception of risk is already high, since increased vigilance
246 may result in fitness costs [33]. It is possible that, while browsing ecosystem function
247 may decline when macroalgae are abundant, it does not do so linearly. Our findings add
248 to the growing body of literature that emphasise the importance of habitat structure in
249 shaping functional processes, potentially leading to trophic cascades and the stability
250 of macroalgal stands.

251

252 Ethics

253

254 All research carried out abided by Singapore local laws and was done with permission
255 from the Singapore's National Parks Board (NP/PR15-009c).

256

257 Data accessibility

258

259 Data are available from Dryad Digital Repository:

260 <https://datadryad.org/review?doi=doi:10.5061/dryad.m88gq46> [34].

261

262 Author contributions

263

264 A.G.B., J.C.L.S. and P.A.T. conceived and designed the study. A.G.B., J.C.L.S., J.F.

265 F.A.J-H. and A.S.H. collected and/or analysed the data. A.G.B., F.A.J-H and A.S.H.

266 wrote the manuscript with input from J.C.L.S., J.F. and P.A.T. All authors agreed to

267 be accountable for the content herein and gave final approval for publication.

268

269 Competing interests

270

271 We declare no competing interests.

272

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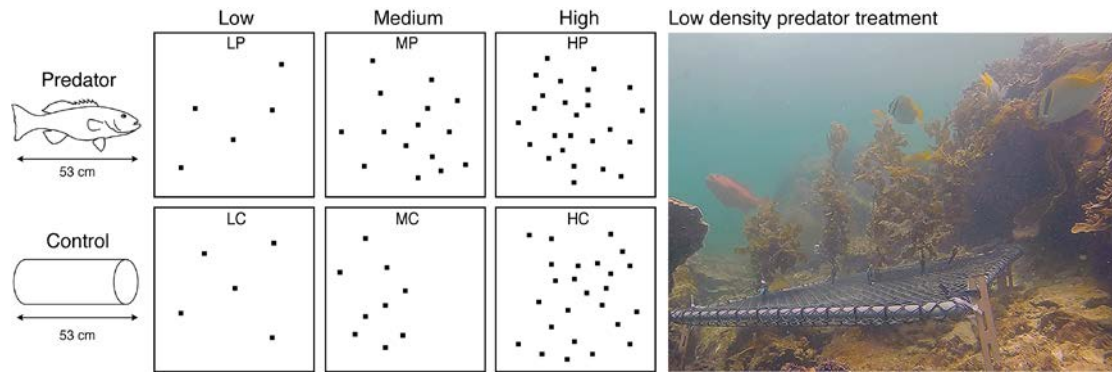
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384 2019 Data from: Fear effects and habitat structure interact to alter herbivore
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386
387

390 Table 1. Results of linear mixed-effects models. All models had day as a random
391 effect.

	Fixed effects	Estimate	Standard Error	df	t-value	Pr (> t)
<i>Proportion removed</i>	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 *	0.0780	0.0397	20	1.965	0.063
	Density (M)					
	Predator *	0.1267	0.0397	20	3.191	0.005
<i>Biomass removed</i>	Density (M)	5.68	15.10	20	0.376	0.711
	Density (H)	-20.84	15.10	20	-1.381	0.1826
	Predator	-36.16	15.10	20	-2.396	0.027
	Predator *	14.04	21.35	20	0.658	0.518
	Density (M)					
	Predator *	42.74	21.35	20	2.002	0.059
<i>Variation</i>	Density (M)	20.328	8.151	18.794	2.494	<0.022
	Density (H)	47.650	8.702	19.129	5.476	<0.001
	Predator	10.772	8.151	18.794	1.321	0.202
	Predator *	-3.141	11.528	18.794	-0.272	0.788
	Density (M)					
	Predator *	-9.111	11.924	18.793	-0.764	0.454
<i>Bites plot⁻¹</i>	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 *	-0.255	0.318	20	-0.800	0.424
	Density (M)					
	Predator *	-0.156	0.320	20	0.49	0.626
<i>Bites plot⁻¹ Sig. virgatus</i>	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 *	-0.057	0.245	20	-0.23	0.82
	Density (M)					
	Predator *	-0.207	0.219	20	-0.95	0.34

393 Figures

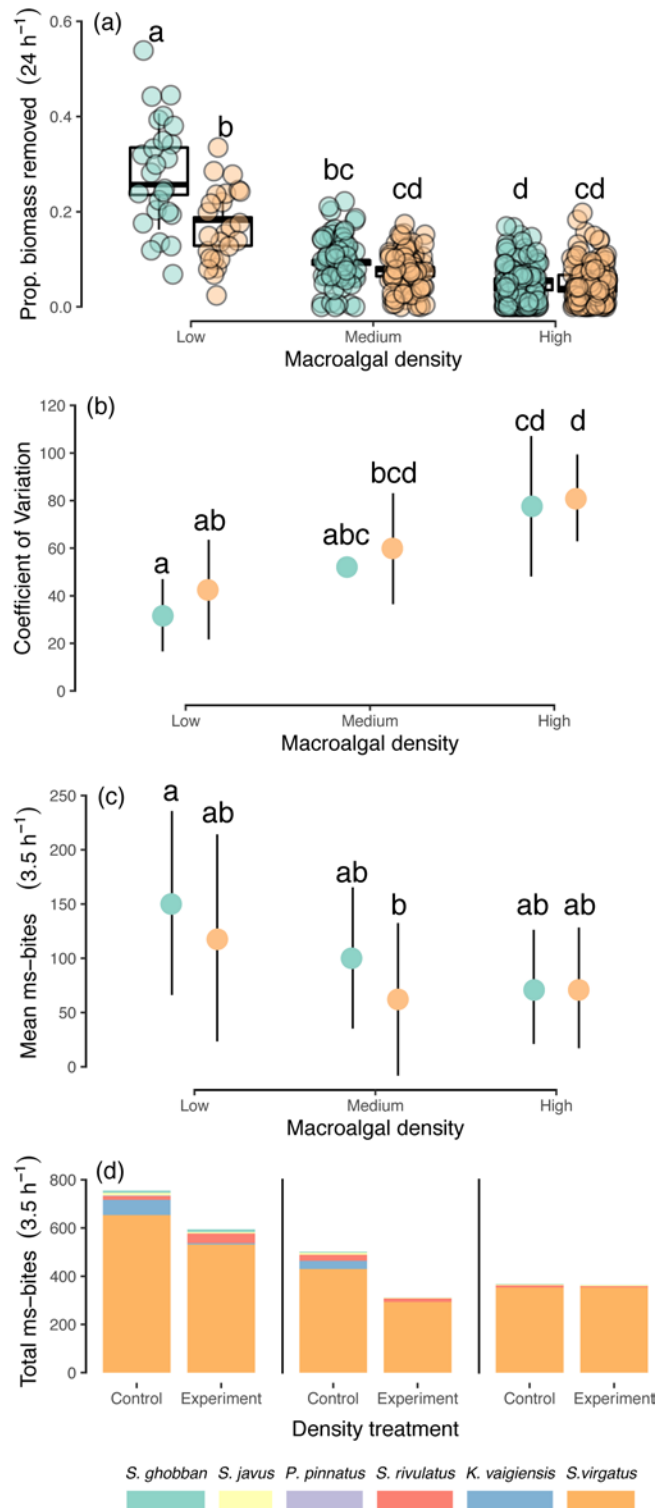
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396 Figure 1. Experimental design: (a) Schematic drawing of spatial arrangement of
397 *Sargassum ilicifolium* assays at three different density levels (low, medium and high)
398 and treatment groups (*Plectropomus leopardus* predator model and control), (b)
399 Photograph showing low density plot with predator fish model (indicated by the red
400 arrow) and *Siganus virgatus* removing *S. ilicifolium* biomass.

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