Paper:

Bauman, A., Seah, J., Januchowski-Hartley, F., Hoey, A., Fong, J. & Todd, P. (2019). Fear effects associated with predator presence and habitat structure interact to alter herbivory on coral reefs. *Biology Letters, 15*(10), 20190409
http://dx.doi.org/10.1098/rsbl.2019.0409

_____

http://www.swansea.ac.uk/library/researchsupport/ris-support/

1   **Fear effects associated with predator presence and habitat structure interact to**

2   **alter herbivory on coral reefs**

3

4   Andrew G. Bauman[1†], Jovena C.L. Seah[1†], Fraser A. Januchowski-Hartley[2], Andrew

5   S. Hoey[3], Jenny Fong[1] and Peter A. Todd[1]

6

7   [1]Experimental Marine Ecology Laboratory, National University of Singapore

8   [2]Department of Biosciences, Swansea University, UK

9   [3]ARC Centre of Excellence for Coral Reef Studies, James Cook University.

10

11   Author for correspondence:

12   Andrew G. Bauman

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

14

15   [†] These authors contributed equally to this study.

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34

Abstract

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 remains 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.

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

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 as significant 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].

69

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 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 hypothesise 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 materials, figure S1). Each week, we transplanted a series of *Sargassum ilicifolium* thalli at three densities: high (25 thalli; ~4.0 kg m^{-2}), medium (15 thalli; ~2.4 kg m^{-2}) and low (5 thalli, ~0.8 kg m^{-2}) to 0.5m^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 for ~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

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 × 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 herbivorours 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

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

Ethics

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

Data accessibility

Data are available from Dryad Digital Repository:
https://datadryad.org/review?doi=doi:10.5061/dryad.m88gq46 [34].

Author contributions

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. 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. wrote the manuscript with input from J.C.L.S., J.F. and P.A.T. All authors agreed to be accountable for the content herein and gave final approval for publication.

283

284

285

286

287   References

288

289   1.   Schmitz OJ, Krivan V, Ovadia O. 2004 Trophic cascades: the primacy of trait-

290   mediated indirect interactions. *Ecol. Lett.* **7**, 153-163. (doi:10.1111/j.1461-

291   0248.2003.00560.x)

292   2.   Helfman GS. 1989 Threat-sensitive predator avoidance in damselfish-

293   trumpetfish interactions. *Behav. Ecol. Sociobiol.* **24**, 47–58.

294   (doi:10.1007/bf00300117)

295   3.   Maziarz M, Piggott C, Burgess M. 2018 Predator recognition and differential

296   behavioural responses of adult wood warblers *Phylloscopus sibilatrix*. *Acta*

297   *Ethol.* **21,** 13–20. (doi:10.1007/s10211-017-0275-2)

298   4.   Stankowich T, Blumstein DT. (2005) Fear in animals: a meta-analysis and

299   review of risk assessment. *Proc. R. Soc. B Biol. Sci.* **272,** 2627–2634.

300   (doi:10.1098/rspb.2005.3251)

301   5.   Rizzari JR, Frisch AJ, Hoey AS, McCormick MI. 2014 Not worth the risk: apex

302   predators suppress herbivory on coral reefs. *Oikos* **123**, 829–836.

303   (doi:10.1111/oik.01318)

304   6.   Lima SL, Dill LM. 1990 Behavioral decisions made under the risk of predation:

305   a review and prospectus. *Can. J. Zool.* **68**, 619–640. (doi:10.1139/z90-092)

306   7.   Catano LB, Rojas MC, Malossi RJ, Peters JR, Heithaus MR, Fourqurean JW,

307   Burkepile DE. 2016 Reefscapes of fear: predation risk and reef hetero-geneity

308   interact to shape herbivore foraging behaviour. *J. Anim. Ecol.* **85**, 146–156.

309   (doi:10.1111/1365-2656.12440)

310   8.   Hess S, Allan BJM, Hoey AS, Jarrold MD, Wenger AS, Rummer JL. 2019

311   Enhanced fast-start performance and anti-predator behaviour in a coral reef fish

312   in response to suspended sediment exposure. *Coral Reefs* **38**, 103–108.

313   (doi:10.1007/s00338-018-01757-6)

314   9.   Creel S, Winnie JA. 2005. Responses of elk herd size to fine-scale spatial and

315   temporal variation in the risk of predation by wolves. Animal Behaviour **69**,

316   1181–1189. (doi:10.1016/j.anbehav.2004.07.022)

317   10.   Valix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F,

318   Fritz H, Macdonald DW. 2009 Behavioural adjustments of African herbivores

319   to predation risk by lions: spatiotemporal variations influence habitat use.

320   *Ecology* **90**, 23–30. (doi:10.1890/08-0606.1)

321   11.   Madin EMP, Gaines SD, Warner RR. 2010 Field evidence for pervasive indirect

322   effects of fishing on prey foraging behavior. *Ecology* **91**, 3563–3571.

323   (doi:10.1890/09-2174.1)

324   12.   Hoey AS, Bellwood DR. 2011 Suppression of herbivory by macroalgal density:

325   a critical feedback on coral reefs? *Ecol. Lett.* **14**, 267–273. (doi:10.1111/j.1461-

326   0248.2010.01581.x)

327   13.   Madin EMP, Madin JS, Booth DJ. 2011 Landscape of fear visible from space.

328   *Sci. Rep.* **1**, 14. (doi:10.1038/srep00014)

329   14.   Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS. 2006 Functional versatility

330   supports coral reef biodiversity. *Proc. R. Soc. B Biol. Sci.* **273**, 101–107

331   (doi:10.1098/rspb.2005.3276)

332   15.   Low JKY, Fong J, Todd PA, Chou LM, Bauman AG. 2019 Seasonal variation

333   of *Sargassum ilicifolium* (Phaeophyceae) growth on equatorial coral reefs. *J.*

334   *Phycol.* (doi:10.1111/jpy.12818)

335   16.   Bauman AG, Hoey AS, Dunshea G, Feary DA, Low J, Todd PA. 2017
336   Macroalgal browsing on a heavily degraded, urbanized equatorial reef system.
337   *Sci. Rep.* **7**, 8352. (doi:10.1038/s41598-017-08873-3)

338   17.   Cronin G, Hay ME. 1996 Susceptibility to herbivores depends on recent history
339   of both the plant and animal. *Ecology* **77**, 1531–1543. (doi:10.2307/2265549)

340   18.   Froese R. Pauly D. *(Eds) (*2017*).* Fishbase*. World Wide Web Electronic*
341   *Publication. Retrieved from: www.fishbase.org.*

342   19.   Hoey AS, Bellwood DR. 2009 Limited functional redundancy in a high
343   diversity system: single species dominates key ecological process on coral reefs.
344   *Ecosystems* **12**, 1316–1328. (doi:10.1007/s10021-009-9291-z)

345   20.   R Core Team (2017) R: A Language and Environment for Statistical
346   Computing. https://www.R-project.org/

347   21.   Lenth RV. 2016 Least-Squares Means: The R Package lsmeans. *J. Stat. Softw.*
348   **69**, 1–33. (doi:10.18637/jss.v069.i01)

349   22.   Rasher DB, Hoey AS, Hay ME. 2017 Cascading predator effects in a Fijian
350   coral reef ecosystem. *Sci. Rep.* **7**:15684. (doi:10.1038/s41598-017-15679-w)

351   23.   Farina, S. *et al.* 2018 Generation and maintenance of predation hotspots of a
352   functionally important herbivore in a patchy habitat mosaic. *Funct. Ecol.* **32,**
353   556–565. (doi:10.1111/1365-2435.12985)

354   24.   Madin EMP, Gaines SD, Madin JS, Warner RR. 2010 Fishing indirectly
355   structures macroalgal assemblages by altering herbivore behavior. *Amer. Nat.*
356   **176**, 785–801. (doi:10.1086/657039)

357   25.   Fox JR, Donelson JM. 2013 Rabbitfish sentinels: first report of coordinated
358   vigilance in conspecific marine fishes. *Coral Reefs* **33**, 253.
359   (doi:10.1007/s00338-013-1108-z)

360   26.   Brandl SJ, Bellwood DR. 2014 Pair-formation in coral reef fishes: an ecological
361   perspective. *Oceanogr. Mar. Biol.* **52**, 1–80.

362   27.   Holbrook SJ, Schmitt RJ. 2002 Competition for shelter space causes density-
363   dependent predation mortality in damselfishes. *Ecology* **83**, 2855–2868.
364   (doi:10.1890/0012-9658(2002)083[2855:cfsscd]2.0.co;2)

365   28.   Mumby PJ, Hastings A, Edwards HJ. 2007 Thresholds and the resilience of
366   Caribbean coral reefs. *Nature* **450**, 98–101. (doi:10.1038/nature06252)

367   29.   Chou LM. 2006. Marine habitats in one of the world's busiest harbours. In: The
368   Environment in Asia Pacific Harbours. pp. 377–391. Springer-Verlag.
369   (doi:10.1007/1-4020-3655-8_22)

370   30.   McFarland WN. 1991 The visual world of coral reef fishes. In: The Ecology of
371   Fishes on Coral Reefs. pp. 16–38. Academic Press.

372   31.   Wenger AS, McCormick MI, McLeod IM, Jones GP. 2013 Suspended sediment
373   alters predator-prey interactions between two coral reef fishes. *Coral Reefs* **32**,
374   369–374. (doi:10.1007/s00338-012-0991-z)

375   32.   Figueiredo BRS, Mormul RP, Chapman BB, Lolis LA, Fiori LF, Benedito E.
376   2016 Turbidity amplifies the non-lethal effects of predation and affects the
377   foraging success of characid fish shoals. *Freshwater Biol.* **61**, 293–300.
378   (doi:10.1111/fwb.12703)

379   33.   Watson M, Aebischer NJ, Cresswell W. 2007 Vigilance and fitness in grey
380   partridges Perdix perdix: the effects of group size and foraging-vigilance trade-
381   offs on predation mortality. *J. Anim. Ecol.* **76**, 211–221. (doi:10.1111/j.1365-
382   2656.2006.01194.x)

383   34.   Bauman AG, Seah JCL, Januchowski-Hartley FA, Hoey AS, Fong J, Todd PA.
384   2019 Data from: Fear effects and habitat structure interact to alter herbivore
385   foraging behaviour. *Dryad Digital Repository.*

386
387

388 Tables

389

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|)
Proportion 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
Biomass removed	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 * Density (M)	14.04	21.35	20	0.658	0.518
	Predator * Density (H)	42.74	21.35	20	2.002	0.059
Variation	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 * 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
Bites plot^{-1} Sig. virgatus	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

392
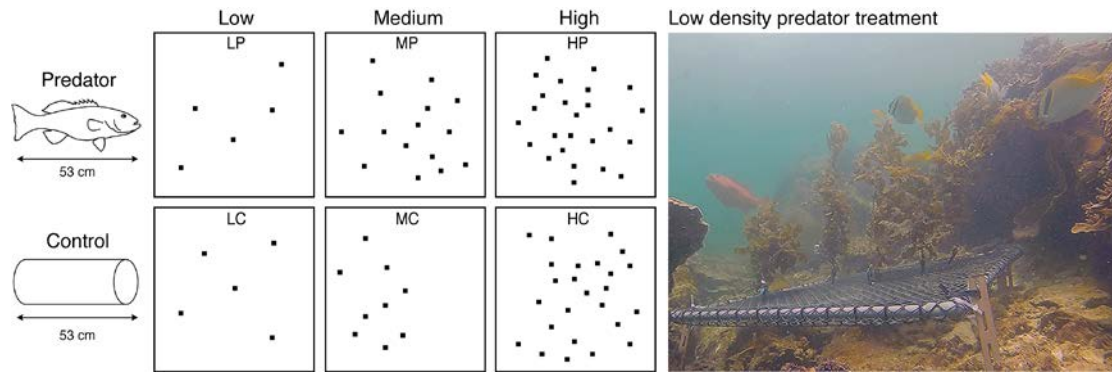
Figures

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.

401
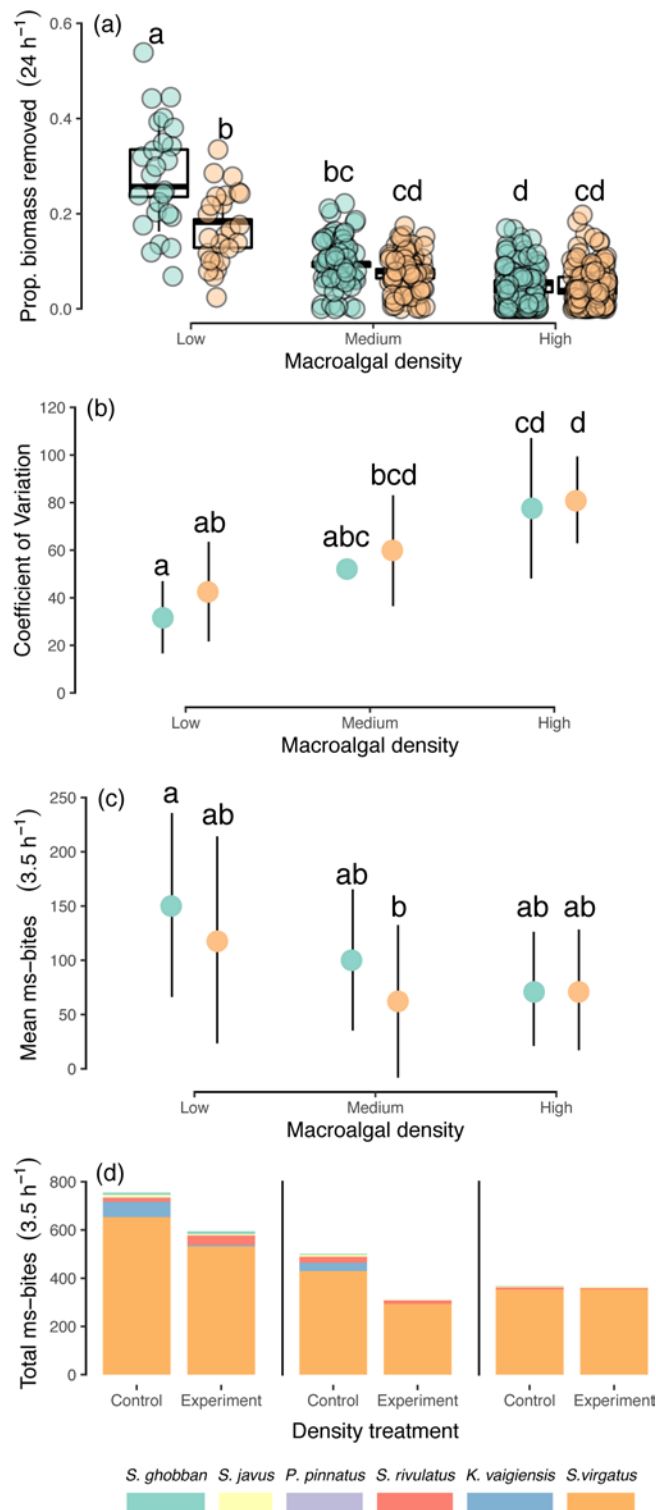
Figure 2. Effect of *Sargassum ilicifolium* density, object controls (teal circles) and predator models (orange circles) on herbivore foraging behaviour. (a) proportion of macroalgae biomass removed 24h[-1], (b) coefficient of variation (c) mass-standardized bites 3.5h[-1], and (d) number of mass-standardised bites taken by all species recorded at each treatment and density. Letters above density treatments indicate significant differences ($p < 0.05$).