

Fear effects and group size interact to shape herbivory on coral reefs

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Abstract

1. Fear of predators ('fear effects') is an important determinant of foraging decisions by consumers across a range of ecosystems. Group size is one of the main behavioural mechanisms for mitigating fear effects while also providing foraging benefits to group members. Within coral reef ecosystems, fear effects have been shown to influence the feeding rates of herbivorous fishes, a key functional group that prevents macroalgal overgrowth. Yet, how fear effects and group size interact to shape macroalgal removal on coral reefs remains unclear.
2. Here, we conducted field-based experiments using models of a common piscivorous fish, the leopard coral grouper *Plectropomus leopardus* and a series of macroalgal *Sargassum ilicifolium* assays positioned at increasing distances from the models (1, 2, 3 and 4 m) on two coral reefs in Singapore to investigate how acute fear effects shape the intensity of herbivory, and whether these effects were influenced by variation in the group size of herbivorous fishes feeding on the assays.
3. We found acute fear effects strongly influenced the foraging behaviour of herbivorous fishes over small spatial scales. Rates of *Sargassum* biomass removal, feeding rates and the total number of individual feeding events were all lower near the predator model. These effects dissipated rapidly with increasing distance from the predator model and were undetectable at a distance of 4 m. We also found generally larger group sizes of herbivorous fishes further from the predator model, presumably reflecting decreased risk. Furthermore, the number of individual bites/event increased significantly with increasing group size for two common browsing fishes, *Siganus virgatus* and *Siganus javus*.
4. Our findings highlight that acute fear effects influence the distribution and intensity of herbivory over small spatial scales. Fear effects also interacted with herbivore group size resulting in changes in the number of individual feeding events and bite rates that collectively shape the realized ecosystem function of macroalgal removal on coral reefs. Group size is an important context-dependent factor that should be considered when examining fear effects on coral reefs.

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KEYWORDS

coral reef fishes, ecosystem function, group size, herbivory, predation risk, predator–prey interactions

1 | INTRODUCTION

Predation is a key process influencing species interactions and the flow of energy through food webs, and hence ecosystem structure and function (Lima & Dill, 1990; Sih et al., 1985). Predators influence prey dynamics and ecological processes through both consumptive and non-consumptive effects (Gaynor et al., 2019; Lima & Dill, 1990). While consumptive effects of predators can have direct effects on prey population abundance, the fear of predators (indirect 'fear effects') can have greater effects on ecosystems (Creel & Christianson, 2008) by eliciting strong behavioural changes in prey foraging (Lima & Dill, 1990; Preisser & Bolnick, 2008) and habitat use (Heithaus & Dill, 2002; Werner & Peacor, 2003). Changes in prey foraging and habitat use from fear effects can lead to declines in fitness through reduced energy acquisition (Werner et al., 1983) and/or increased energy demands (Brown & Kotler, 2004) and ultimately alter the distribution and/or abundance of lower trophic levels through cascading effects (Ripple et al., 2001; Schmitz et al., 2004).

One of the main behavioural mechanisms used by prey to mitigate their vulnerability to predation risk is forming groups (Krause & Ruxton, 2002; Lima, 1995). Group membership can reduce individual predation risk through dilution effects (Foster & Treherne, 1981), enhanced detection of predators (Lima & Dill, 1990; Pulliam, 1973), attack abatement (Turner & Pitcher, 1986) and the confusion effect (Neill & Cullen, 1974), while also enhancing energy acquisition through increased foraging efficiency (Elgar, 1989; Pitcher et al., 1982) and allowing more time for other fitness-improving activities (Lima, 1995). However, with increasing group size, individuals can also incur costs such as competition for resources (Pitcher & Parrish, 1993) and increased conspicuousness (Creel & Creel, 2002) that may attract higher attack rates from predators (Krause & Ruxton, 2002). Despite the prevalence of group formation in animal populations, including fishes across a range of marine ecosystems (Paijmans et al., 2019), we have a limited understanding of how fear interacts with group foraging behaviour of herbivorous coral reef fishes, and whether this influences the spatial distribution and intensity of herbivory on tropical coral reefs.

Herbivorous fishes perform a critical function in coral reef ecosystems, removing fast-growing algae that compete with corals for space. Without top-down control, algae can rapidly colonize open space preventing the settlement, growth and survivorship of corals, thereby limiting the recovery of coral populations following a disturbance (Hughes et al., 2007). Demographic models suggest that the capacity of coral reefs to avoid such shifts is largely dependent on the consumption of algae by the herbivorous fish community (e.g. Mumby et al., 2007). Herbivory on coral reefs is a multifaceted process, carried out by multiple species with different dietary preferences (Choat et al., 2002; Nicholson & Clements, 2021), foraging

behaviours (Streit et al., 2015) and habitat preferences (Hoey & Bellwood, 2010). Accordingly, herbivorous fishes are generally classified into two broad functional groups: 'grazers' which are species that feed on benthic surfaces covered with short algal turfs or epilithic algal matrices (EAM) and 'browsers' which feed on large mature fleshy macroalgae (Green & Bellwood, 2009). Because macroalgae can proliferate on reefs following a disturbance (but see Bruno et al., 2009), the removal of macroalgae by browsers is considered a critical function for preventing and potentially reversing macroalgal phase shifts and promoting reef recovery (Bellwood et al., 2006). Preserving this function has become increasingly important as coral reefs rapidly degrade due to local and global anthropogenic impacts that are exacerbating the expansion of macroalgae across many reef systems (Hughes et al., 2017).

On coral reefs, previous studies of fear effects have associated changes in herbivorous fish foraging rates to spatial and temporal differences in predator presence and/or abundance (Hoey & Bellwood, 2011; Madin et al., 2010; Rasher et al., 2017), the availability of refugia (e.g. grazing halos; Madin et al., 2011) or the presence of static predator models (Bauman et al., 2019; Catano et al., 2016; Rizzari et al., 2014). Combined, these findings suggest that fear effects are important determinants of the spatial and temporal distribution of herbivory on coral reefs (Mitchell & Harborne, 2020). Yet, despite this, no studies have examined how browser foraging behaviour is influenced by changes in group size in the presence of a fish predator. Many herbivorous coral reef fishes form groups (or schools; e.g. Hoey & Bellwood, 2009; Meyer & Holland, 2005; Michael et al., 2013) presumably in part to reduce risk and increase foraging benefits (Gil et al., 2017; Wolf, 1987), which likely affects the delivery of their functional impact. For example, when foraging in groups, browsers have been observed to feed at higher rates and remove greater algal biomass (Michael et al., 2013), and locate and consume macroalgae more rapidly (Gil et al., 2017). Despite group formation among browsers and the function of macroalgal removal on coral reefs, no studies have considered these two factors simultaneously.

Here, we examined how fear effects associated with predator presence shape the spatial distribution and intensity of browsing and how browsing may vary with group size on coral reefs in Singapore. Using a combination of transplanted macroalgal assays, remote video cameras and static models of a common piscivorous fish, the leopard coral grouper *Plectropomus leopardus* we investigated how browsing rates and group size changed with decreasing predation risk (i.e. increasing distance from the models), and the relationship between browser group size and browsing rates. We hypothesized that macroalgal removal would increase with decreasing acute risk, and the formation of larger browser group size closer to the predator model to reduce acute predation risk.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

We conducted field-based experiments between September and October 2016 on Pulau Satumu and Kusu, two off-shore islands in Singapore with well-developed fringing reefs (see Appendix S1, Figure S1). Both reefs have a clearly defined reef crest at 3–4 m depth, and have the highest coral cover (Guest et al., 2016), the lowest macroalgal cover and highest rates of herbivory in Singapore (Bauman et al., 2017; Seah et al., 2021). Each experimental replicate consisted of a series of individual *Sargassum ilicifolium* assays positioned at increasing distances (1, 2, 3 and 4 m) from models of the piscivorous leopard coral grouper (*Plectropomus leopardus*, 53 cm total length, TL) to simulate different levels of acute predation risk, together with two experimental controls (i.e. object control and herbivore exclusion). *Plectropomus leopardus* was selected because this species is common on both Pulau Satumu and Kusu (Lim & Low, 1998; A.G. Bauman, pers. obs.) and has broad diets that include herbivorous fishes (St. John, 1999). The size of the models (53 cm TL) was selected to represent the maximum size of serranids (including *P. leopardus*) observed on Singaporean reefs (A.G. Bauman, pers. obs.). Moreover, predator models of this species of similar and larger sizes (i.e. 48–76 cm TL) have been shown to affect browser foraging behaviour (Great Barrier Reef (GBR): Rizzari et al., 2014; Singapore: Bauman et al., 2019). *Sargassum ilicifolium* was selected because it is the most abundant and widespread *Sargassum* species on Singapore's reefs (Low et al., 2019).

2.2 | Experimental design

Sargassum ilicifolium (hereafter '*Sargassum*') thalli of similar heights (c. 40 cm) were collected daily from a nearby shallow reef flat on Pulau Hantu (Figure S1). Individual thalli were spun in a salad spinner for ~20 s to remove excess water and the wet weight was recorded to the nearest 0.1 g. The initial mass (mean \pm SE) of each thalli was 44.7 ± 8.4 g. For each experimental replicate, six *Sargassum* assays were allocated randomly to one of three treatments: a predator model treatment (four assays positioned 1, 2, 3 and 4 m away from the predator model), one object control treatment (53 cm length of PVC pipe, 8 cm in diameter) with one assay positioned 1 m away where the largest effect on browsing was theorized to occur and a herbivore exclusion treatment (one assay placed inside a 30 cm radius, 100 cm height, 0.5 cm plastic mesh cage; Figure S2). The object control was used to account for the effect of introducing a novel object in the water while the herbivore exclusion cage was used to account for the autogenic losses due to handling and translocation. A negative control treatment (i.e. a series of four assays separated by 1 m without a predator or novel object) was not included in this study because, with replication, there was no conceivable reason why browsing would consistently vary within a 4 m scale in the absence of any object.

Each morning (09:30–10:30) we transplanted two replicates of six *Sargassum* assays (total of 12 assays) haphazardly along the reef crest at ~3–4 m depth at one site (i.e. either Pulau Satumu or Kusu). Predator models were secured ~50 cm above the reef substratum. Individual *Sargassum* assays were subsequently attached to the reef substratum at increasing distances (1, 2, 3 and 4 m) from the predator model. The two additional assays were positioned approximately 20 m (object control) and 30 m (herbivore exclusion control) away from the predator models within the same habitat (i.e. ~3–4 depth along the reef crest; Figure S2). Within each site, experimental replicates were separated by a minimum of 30 m to facilitate independence. This procedure was replicated over four non-consecutive days on each reef ($n = 8$ experimental replicates, with $n = 4$ per reef).

To identify herbivorous fish species feeding on the *Sargassum* assays, a small video camera (GoPro) mounted on a dive weight (2 kg) was positioned approximately 1 m from each of the assays in the predator exposure treatment (i.e. 1, 2, 3 and 4 m from the predator model). We did not film the object control due to logistical constraints (number of working cameras at the time of study), and because this treatment was primarily established to compare the effects of a large novel object versus predator model on macroalgal removal. Filming commenced immediately after the assays and predator models were deployed, with a small scale bar (10 cm) placed adjacent to each assay for 10 s to allow calibration of fish sizes on the videos. All cameras, macroalgal assays and predator models were collected after 4.5 hr. Thus, on each day of the experiment, there were eight cameras per reef, resulting in 144 hr of video observations for each reef (288 hr in total).

Following retrieval, each individual *Sargassum* thalli was spun and re-weighed as above to calculate biomass loss per thallus (Section 2.3). To minimize potential diver interference, the first 20 min and last 10 min of each video were discarded. From the video footage, we recorded the total number of bites, species and estimated TL to the nearest centimetre for each fish feeding, group size per feeding event and total bites per feeding event. Size estimates for each fish were converted to biomass using published length–weight relationships (Hoey et al., 2013; Kulbicki et al., 2005; see Appendix S1, Table S1). A feeding event was recorded every time a fish entered the video frame and fed on *Sargassum*, and the bites from each individual fish were counted until each fish left the video frame. If other fishes entered during the feeding event, bites taken by those individuals were counted and included within the same feeding event. Group feeding was defined as two or more fishes feeding simultaneously during an event (Lukoschek & McCormick, 2000). To account for variation in the feeding impact of individual fishes related to body size, mass-standardized bite impact was calculated as the product of the number of bites and the estimated body mass (kg) for each individual following Hoey and Bellwood (2009).

2.3 | Statistical modelling

Individual assays' positions within each predator exposure treatment replicate (i.e. at 1, 2, 3 and 4 m) were considered non-independent due

to their close proximity, and hence potential exposure to the same individual herbivorous fishes. To account for non-independence, we used a Bayesian mixed modelling approach employing Markov chain Monte Carlo (MCMC) methods for fitting generalized linear mixed models (Hadfield, 2010) with experimental replicate defined as the random effect. To examine the response of herbivorous fishes to the predator model, we compared: (a) changes in *Sargassum* biomass at each position away from the predator model and the object control, (b) herbivorous fish species from the video footage feeding at each assay position from the predator model. For all analyses, assay position was considered an ordinal factor rather than a continuous covariate and the five positions were modelled for analyses of biomass removal (i.e. 1 m from the object control and 1, 2, 3 and 4 m from the predator model).

To examine biomass (g) loss due to herbivory at each assay position, data were first standardized to control for autogenic loss during handling following Cronin and Hay (1996). For individual assays in each replicate, the reductions in macroalgal biomass attributed to herbivory were calculated using the following formula: $[(H_o \times C_f/C_o) - H_f]$ where H_o and H_f were the initial and final wet weights, respectively, of the macroalgal assay exposed to browsing, and C_o and C_f were the initial and final masses of the corresponding assays from the herbivore exclusion treatments. Changes in *Sargassum* biomass were compared by modelling the absolute (g) and relative (proportion) reduction in biomass of replicate assays. In the latter case, proportions were logit transformed (Warton & Hui, 2011). Changes in biomass data were modelled using a Gaussian error structure with site, position and their interaction as fixed effects in initial models.

From the video feeding observations, we modelled the following three response variables: (a) counts of bites per feeding event (bites/event), (b) feeding rates (mass-standardized bites/hr hereafter 'ms-bites') and (c) group size per feeding event (group size/event). Bites/event was modelled to assess whether individual foraging events were affected by distance to the predator models, whereas feeding rates indicated the overall effect of predator on macroalgal removal at each position. Bites/event were modelled for the four most common herbivores (*Siganus virgatus*, *Kyphosus vaigiensis*, *Scarus rivulatus* and *Siganus javus*) using a Poisson error structure. Group sizes >4 were excluded from the analysis due to lack of cases across other explanatory variables. The initial model included the explanatory terms site, group size, assay position, their three-way interaction and pairwise two-way interactions and terms for species and species/group size interaction. Feeding rates were only analysed for *S. virgatus* because this species was responsible for most of the feeding (see Section 3). Feeding rates (ms-bites) were rounded to whole integers to employ a Poisson error structure, and site, assay position and their interaction were used as explanatory variables in the initial model. Analysis of group size (group size/event) was performed for the entire dataset, including group sizes >4, with the initial model including the explanatory terms site, assay position and species, with site/assay position and site/species interactions, using a Poisson error structure.

Models were fit using the MCMCGLMM package, which provides parameter estimates, parameter 95% highest posterior density (HPD) credible intervals and a p -value (pMCMC) corresponding to the smaller of two times the probability that the MCMC parameter estimate is either >0 or <0 (Hadfield, 2010). Model terms were considered significant where one or more levels (for factors) or a co-variate had a pMCMC value <0.05 and parameter estimate 95% HPD's did not include zero. Diffuse, uninformative inverse gamma priors were used for variance components and default priors for fixed effects. Backward model selection was applied from initial models (defined above) by comparing reduced nested models with deviance information criterion (DIC) and model weight. Top ranking models were compared, and the most parsimonious model selected as the simplest model with significant explanatory terms. Results are presented as the predicted posterior means and their 95% HPD credible intervals unless otherwise stated. Comparisons between factor levels in final models were considered statistically significant when prediction 95% HPD's did not overlap prediction estimates of other factor levels. All models were fit using 130,000 iterations, a burn-in of 30,000 iterations and a thinning interval of 50, except for feeding rates and group size, which required longer iterations, burn-ins and thinning intervals due to poor mixing and unacceptably high autocorrelation between thinned samples in models with fewer iterations. Diagnostics were performed by visual inspection of trace plots and ensuring autocorrelation between thinning intervals was low (i.e. at least <0.05). Model comparisons were made using the MuMIn package (Bartoń, 2015). All data were analysed in R (R Core Team, 2017). The R code, full model selection details, parameter estimates, 95% HPD's and pMCMC values are provided in electronic supplementary materials and Bauman et al. (2021).

3 | RESULTS

There were marked increases in both the relative and absolute removal rates of *Sargassum* biomass with increasing distance from the predator model (Figure 1; Figure S3). Mean rates of relative *Sargassum* biomass removal increased >3.5-fold between assays 1 m (4% 4 hr⁻¹) and 4 m (15% 4 hr⁻¹) from the predator model, but were similar between the object control (18% 4 hr⁻¹) and the 4 m assay (Figure 1). The final model for the relative reduction in *Sargassum* biomass included site, assay position and site × assay position interaction, highlighting differences in rates of biomass removal among assay positions within sites (Table S2). The proportion of *Sargassum* biomass removed on Pulau Satumu was significantly higher at the 3 m (20% 4 hr⁻¹; pMCMC = 0.016) and 4 m assay positions (23% 4 hr⁻¹; pMCMC = 0.002), and the object control (22% 4 hr⁻¹; pMCMC = 0.009), than the 1 m (5% 4 hr⁻¹) and 2 m assay positions (7% 4 hr⁻¹; Figure 1A; Table S2). In contrast, the proportion of *Sargassum* biomass removal on Kusu was lower and did not differ between assay positions 2–4 m (model predictions ~8%, 95% HPD's), but all had significantly higher biomass removed than the 1 m assay (4% 4 hr⁻¹) and significantly lower removal than the object control (13% 4 hr⁻¹; Figure 1B).

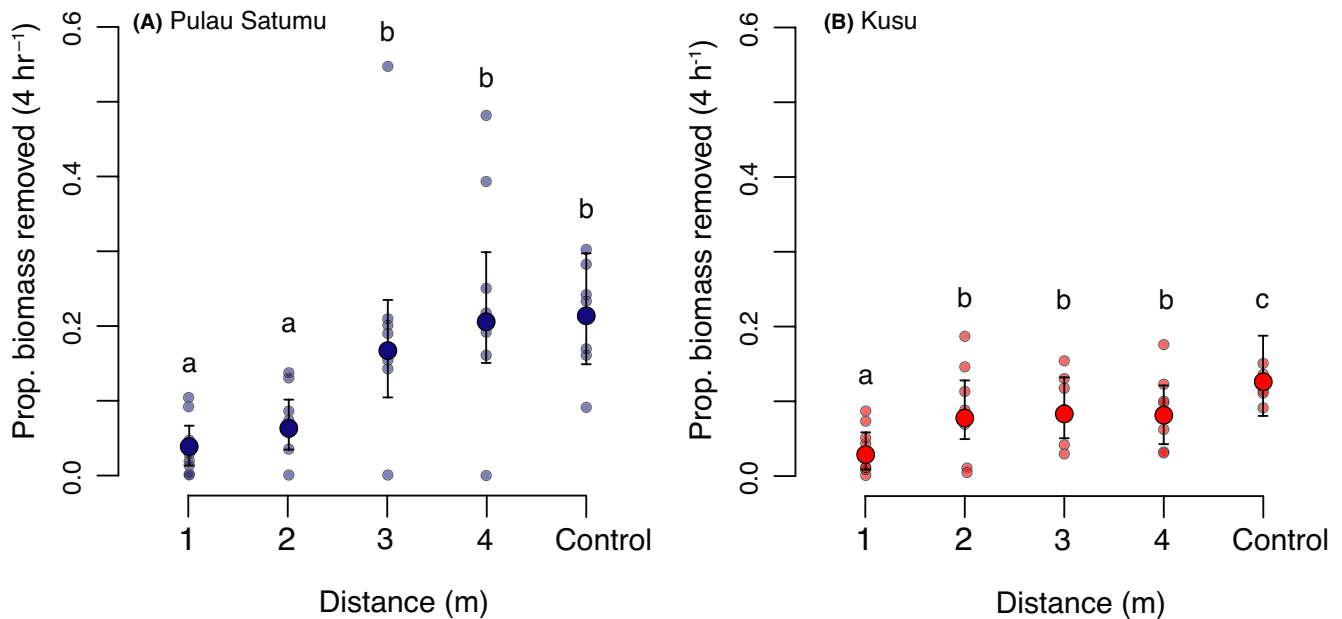


FIGURE 1 The proportion of *Sargassum* biomass removed with increasing distance from the predator model and the object control on (A) Pulau Satumu (blue) and (B) Kusu (red). Larger circles represent model predictions and 95% HPD credible intervals and the smaller circles represent each experimental replicate. Letters above treatments (i.e. distances from predator model and the object control) indicate significant differences. *Note: Sargassum* assays were positioned 1 m from the object control

TABLE 1 Summary of video analysis identifying herbivorous fishes responsible for removing *Sargassum* biomass. Abbreviations: NIFE (Number of individual feeding events) and MGS event⁻¹ (mean group size per event)

Species	NIFE (% total)	Sites present	Replicates present	Total bites (% total)	Total ms-bites (% total)	MGS event ⁻¹ (range)
<i>Siganus virgatus</i>	1,711 (85.72)	P. Satumu, Kusu	16	11,807 (88.85)	3,189.6 (82.8)	2.1 (1–18)
<i>Kyphosus vaigiensis</i>	54 (2.71)	P. Satumu, Kusu	7	575 (4.33)	379.1 (9.84)	3 (1–8)
<i>Scarus rivulatus</i>	85 (4.26)	P. Satumu, Kusu	11	378 (2.84)	131.8 (3.42)	3.2 (1–6)
<i>Siganus javus</i>	84 (4.21)	P. Satumu, Kusu	14	342 (2.57)	66.1 (1.72)	3.1 (1–8)
<i>Scarus ghobban</i>	30 (1.5)	P. Satumu	6	78 (0.59)	55.2 (1.43)	3.1 (1–7)
<i>Siganus canaliculatus</i>	28 (1.4)	Kusu	7	97 (0.73)	27.5 (0.71)	2.3 (1–4)
<i>Siganus punctatus</i>	3 (0.15)	Kusu	2	8 (0.06)	2.0 (0.05)	2.3 (1–3)
<i>Siganus corallinus</i>	1 (0.05)	Kusu	1	3 (0.02)	0.8 (0.02)	1.0 (1–1)

Analysis of the video footage revealed eight herbivorous fish species taking 3,852 ms-bites (13,288 total bites) during 1,996 individual feeding events across all assays (Table 1). Four species (*Kyphosus vaigiensis*, *Scarus rivulatus*, *Siganus virgatus* and *Siganus javus*) were recorded in ~98% of the individual feeding events (hereafter 'IFE's') and accounted for ~97% of ms-bites (Table 1). Feeding among species was highly variable among days, replicates, assay positions and between sites (Figure 2). *Siganus virgatus* was recorded in 1,711 (or 85%) of 1,996 IFEs, fed at each assay position in all 16 replicates (Figure 2) and was responsible for most of the feeding, accounting for 82.8% of the ms-bites (3,189.6 ms-bites, Table 1, Appendix S1). Feeding rates for *S. virgatus* were best explained by site, assay position and their significant interaction (Table S3) with ms-bites/hr increasing with increasing distance from the predator model at both sites, with the magnitude of the difference being greater on Pulau Satumu (Figure 3A,B, Appendix S1).

Proximity to the predator model strongly influenced the number of IFEs and bites/event on *Sargassum* (Figure 4A), with 2.5 times more IFEs and 5 times more bites/event on assays at 4 m (634 IFEs, 1,452 ms-bites) from the predator model relative to 1 m (252 IFEs, 284 ms-bites). Total IFEs and the number of bites per IFE were marginally higher on Pulau Satumu (1,089 IFEs, 2,600 ms bites/event) than Kusu (907 IFEs, 1,252 ms bites/event). Bites/event ranged from 1 to 92 bites, but their distributions were all positively skewed (i.e. the number of bites/event was generally low; Figure 4A). The final bites/event model included assay position, species, group size and a group size × species model interaction (Table S4). Generally, there were significantly fewer bites/event 1 m from the predator model compared to all other assay positions (all pMCMC < 0.001), but no differences in the number of bites/event among assay positions 2, 3 and 4 m though this varied by species (Figure 4B–E). *Kyphosus vaigiensis* took significantly more bites/event at any given group size

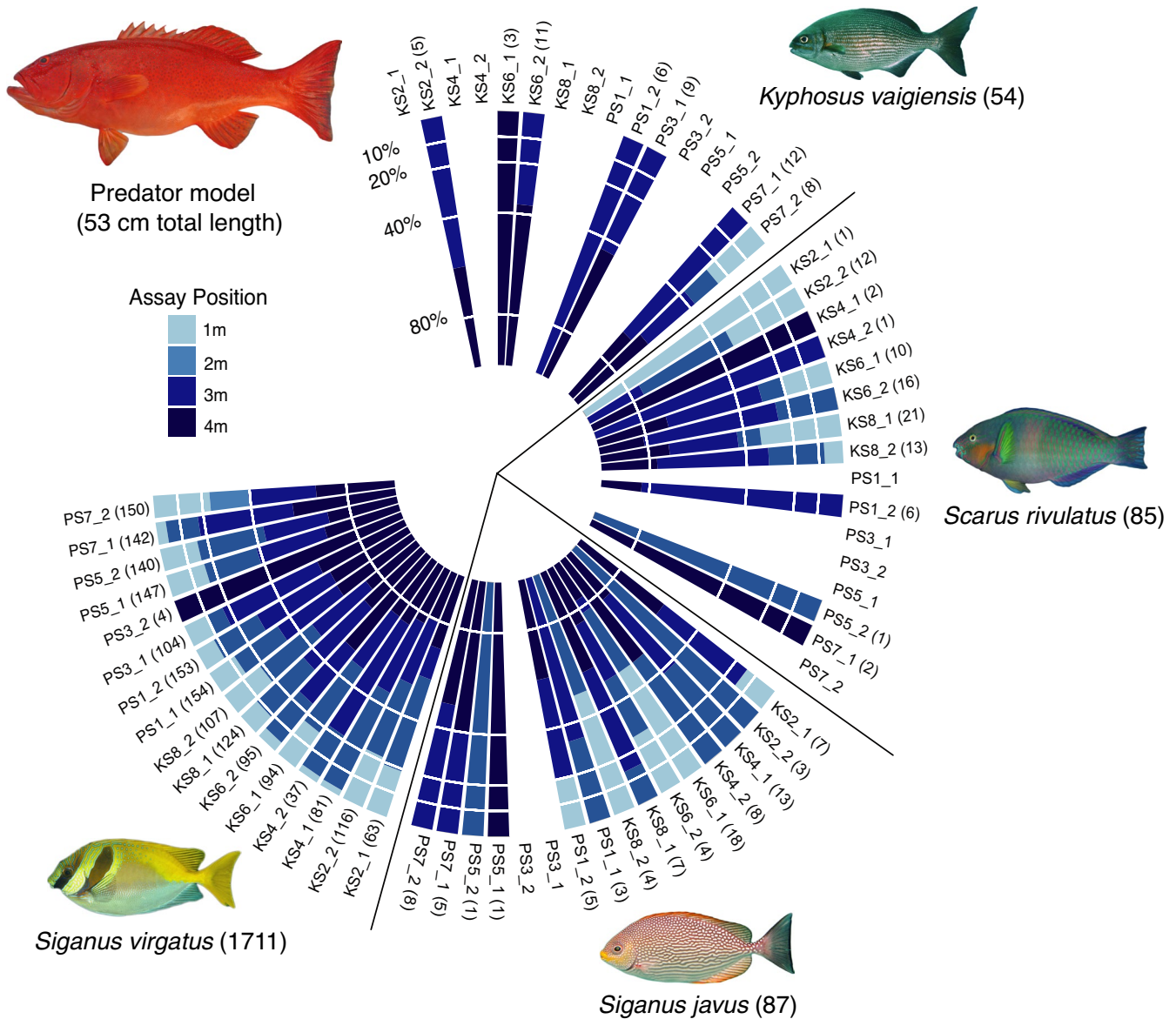


FIGURE 2 Polar histogram of feeding events for the four dominant herbivorous fishes (*Kyphosus vaigiensis*, *Scarus rivulatus*, *Siganus javus* and *Siganus virgatus*). Each bar represents the proportion of feeding events at each assay position in each replicate. Replicates are named according to site (PS = Pulau Satumu; KS = Kusu), day of feeding trial (1–8) and replicate within each day. Numbers in parentheses after each replicate and after species names are the number of feeding events per replicate and the total for each species

than *S. javus* (pMCMC = 0.01) and *S. virgatus* (pMCMC = 0.005), and marginally more than *S. rivulatus* (pMCMC = 0.07, Figure 4B). Bites/event increased significantly with increasing group size for *S. virgatus* (pMCMC = 0.021) and *S. javus* (pMCMC = 0.038), but did not change for *K. vaigiensis* or *S. rivulatus* (Figure 4B–E).

Group feeding events occurred at every assay position on Pulau Satumu and Kusu for *S. virgatus* and *S. javus* but not observed for *K. vaigiensis* at the 1 and 2 m assays at Kusu or for *S. rivulatus* at the 1 m assay on Pulau Satumu (Figure 5A,B). Group sizes per feeding event (group size/event) ranged from 2 to 18 fishes across IFEs, but the majority of groups observed feeding (98%) contained between two and five fishes. Feeding group size was positively related to increasing distance from the predator model at Pulau Satumu but not Kusu (Figure 5C,D) with the most parsimonious model for group

size/event including site, assay position, species and a site assay position interaction (Table S5). There were significantly larger group sizes feeding on *Sargassum* assays at 3 m (pMCMC = 0.014) and 4 m (pMCMC = 0.0063) from the predator model on Pulau Satumu (Figure 5C) compared to Kusu (Figure 5D).

4 | DISCUSSION

Fear effects have increasingly been shown to be important drivers of herbivorous fish foraging behaviour (Mitchell & Harborne, 2020), influencing the spatial and temporal distribution of herbivory on coral reefs (Madin et al., 2010; Rasher et al., 2017; Rizzari et al., 2014), yet how browser foraging behaviour is influenced by group size in the

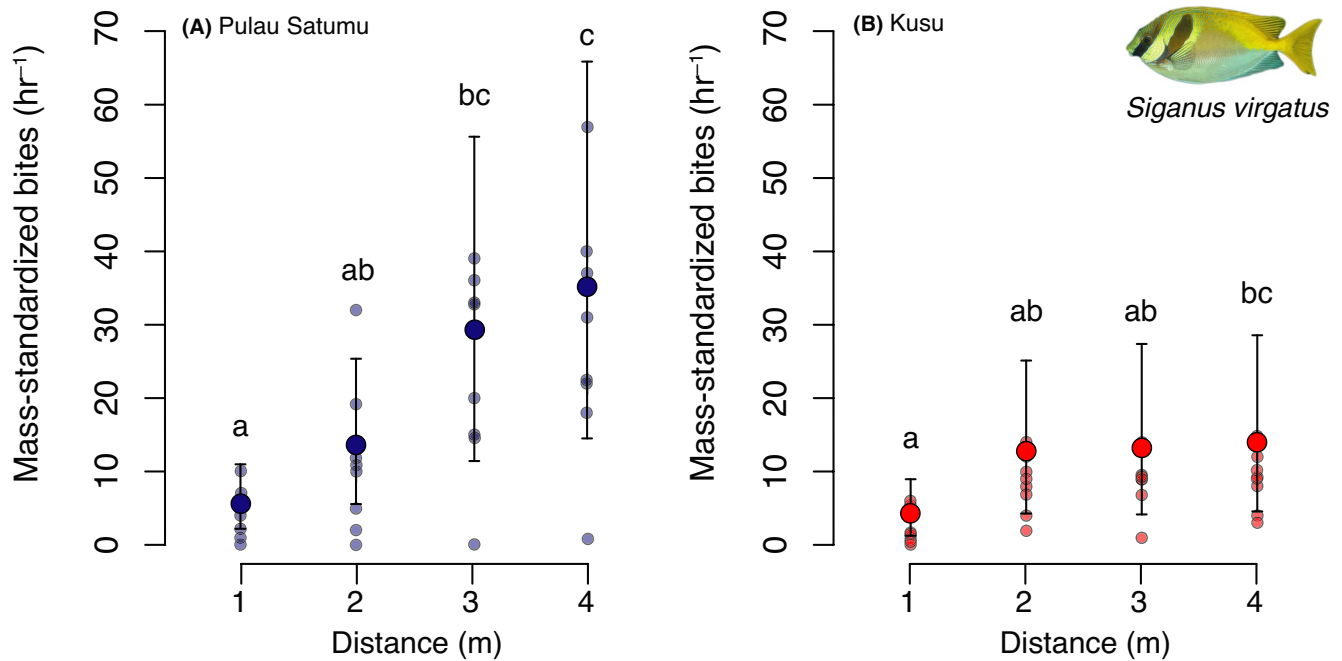


FIGURE 3 Mass standardized bites/hr for *Siganus virgatus* at each assay position on (A) Pulau Satumu (blue circles) and (B) Kusu (red circles). Large circles represent model predictions and 95% HPD credible intervals and the small circles represent each experimental replicate. Letters above distances (i.e. 1, 2, 3 and 4 m) from the predator model indicate significant differences

presence of a predator remains largely unknown. Using predator fish models to simulate acute fear effects, we found that rates of herbivory, the number of individual feeding events (IFE) and feeding rate (ms-bites/hr) were all markedly lower near the predator model, showing that fear effects suppress browsing and impact localized macroalgal removal. Our results show that acute fear effects rapidly dissipate, with no detectable difference in browsing rates 4 m from the predator model relative to the object control. Importantly, we found that both group size and feeding rates of browsing fishes were positively related to distance from the predator model, translating to greater macroalgal removal with increased distance from the predator model. These findings are contrary to our hypothesis and suggest a group size foraging response to low risk rather than an antipredator response to high risk (Creel & Winnie, 2005). Such findings reflect the patterns of group size responses in terrestrial ecosystems where some prey species (e.g. elk, *Cervus elaphus*) have been reported to form larger groups when temporal risk is low but smaller groups when temporal risk is high in order to potentially reduce the risk of detection, encounters and/or attacks (Winnie & Creel, 2007). Notably, two of the dominant browsers in our system, *Siganus virgatus* and *Siganus javus* (f. Siganidae), showed significant increases in group size with distance from the predator model and in the number of individual bites per event with increasing group size. The positive relationship between group size and individual feeding rate may be related to changes in vigilance behaviours that are frequently observed among rabbitfishes—from frequent coordinated vigilance in conspecific pairs (Brandl & Bellwood, 2015) to collective vigilance in larger groups (e.g. Ward et al., 2011). Combined, our results reveal that acute predation risk influences the interaction between

feeding rates and group size in herbivorous reef fishes; and collectively shape the realized ecosystem function of macroalgal removal on coral reefs over small spatial scales.

Evidence from multiple ecosystems shows that spatial variation in predation risk influences where potential prey choose to forage (Gaynor et al., 2019; Laundre et al., 2001). On coral reefs, acute predation risk leads to more cautious herbivore behaviour (i.e. increased vigilance) and/or avoidance of areas in which predators are present (Madin et al., 2010) or likely to be found (Hoey & Bellwood, 2011), thereby influencing the spatial or temporal distribution of foraging intensity (Catano et al., 2017; Rasher et al., 2017) and the amount of algae consumed (Catano et al., 2016; Rizzari et al., 2014). Consistent with previous theoretical (Madin et al., 2010) and empirical studies (Bauman et al., 2019; Catano et al., 2016; Rizzari et al., 2014), we found acute risk reduced browsing and suppressed macroalgal removal. Fear effects rapidly dissipated with increasing distance from the predator model and were undetectable at a distance of 4 m (statistically indistinguishable from the object control). Reduction in algal biomass of assays 4 m from the predator model and near the object control was directly comparable to those of previous studies that deployed *Sargassum* assays in the absence of predator models or objects at these reefs (Bauman et al., 2017; Seah et al., 2021). Likewise, previous predation risk studies in the Florida Keys reported that herbivorous fishes consumed significantly more sea-grass and took between 4 and 40 times more bites on assays 4 m away from larger predator models (grouper *Mycteroperca bonaci* and barracuda *Sphyraena barracuda*, both 90 cm fork length) relative to assays 0.5 m away (Catano et al., 2016, 2017). Our results also revealed no evidence that group size mediated predation risk—that is,

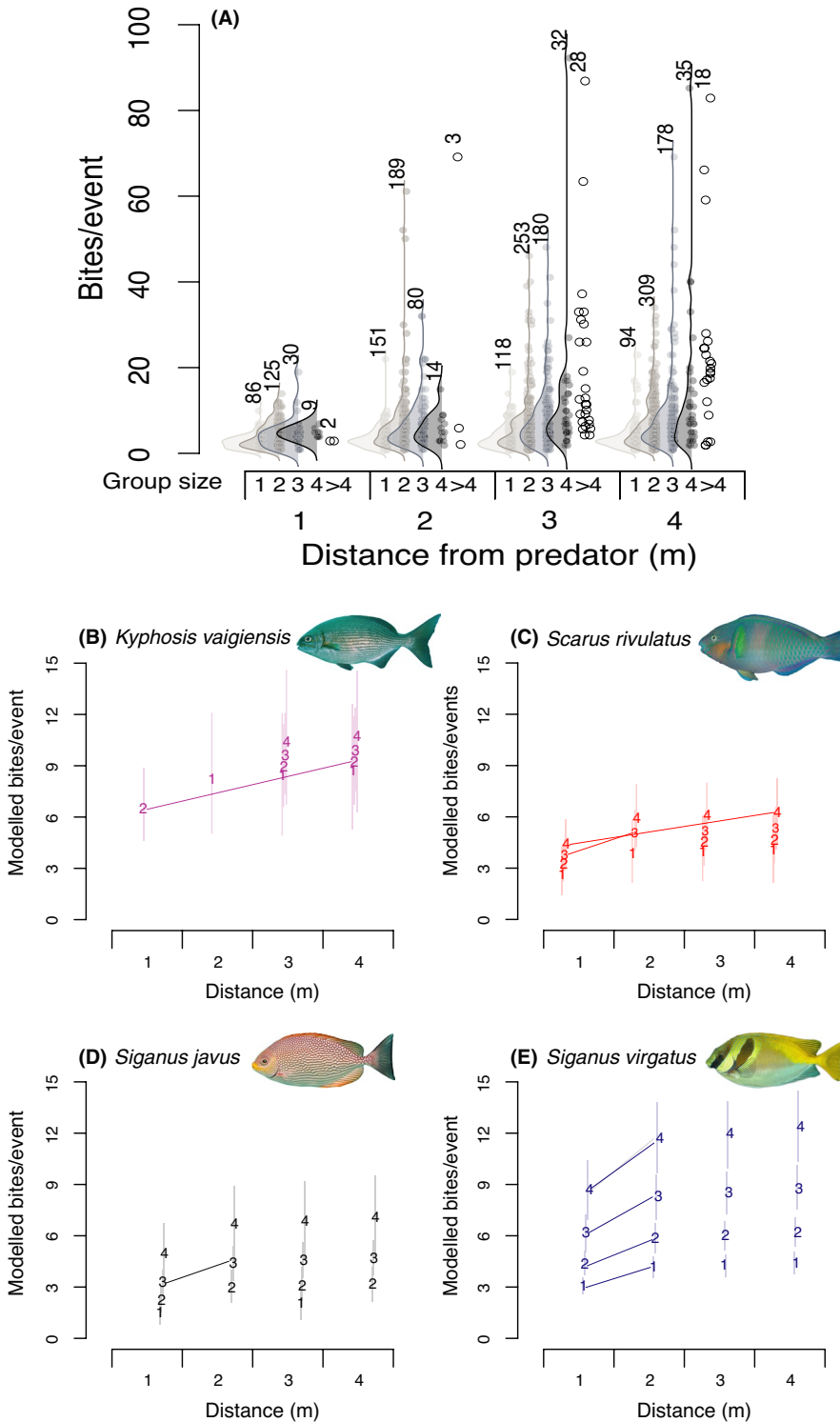


FIGURE 4 Bites per feeding event across assay positions for *Kyphosis vaigiensis*, *Scarus rivulatus*, *Siganus virgatus* and *Siganus javus*. (A) Raw bites/event data for group sizes 1–4 and >4 at each assay position. Distributions are scaleless kernel density for each group size at each assay position (x-axis) where the base of each distribution is raw data offset, numbers indicate the number of cases for each group size category at each assay position. (B–E) Model predictions for group sizes 1–4 for each species. Numbers indicate predictions for that group size at each assay position (x-axis), shaded bars are 95% HPD credible intervals, different species represented by different colours. Solid lines between numbers for each group size in each species indicate a significant difference in model predictions. In all cases where there was a significant difference between 1 and 2 m assay positions, there was also a difference between 1 m and all other assay positions for that group size

the formation of larger groups closer to the predator model as an antipredator defence to reduce risk. In contrast, we found smaller groups of browsers closer to the predator model suggesting that acute risk may generate a mosaic of areas of low browsing where acute risk is high, and areas of high browsing where risk is low (Madin et al., 2010). Spatially concentrated herbivory may lead to increased coral recruitment and coral cover relative to areas where similar rates of herbivory are dispersed (Sandin & McNamara, 2012),

implying that fear-driven changes in browsing could impact recruitment and the recovery of coral populations (Madin et al., 2010). Yet, on predator-poor reefs such as Singapore (Lim & Low, 1998) browsers may disperse their feeding efforts more uniformly over a reef (Madin et al., 2010) potentially affecting the distribution of area suitable for coral settlement (Sandin & McNamara, 2012). Combined our results suggest that the spatial scale over which acute risk influences herbivorous fish foraging behaviour may be considerably smaller

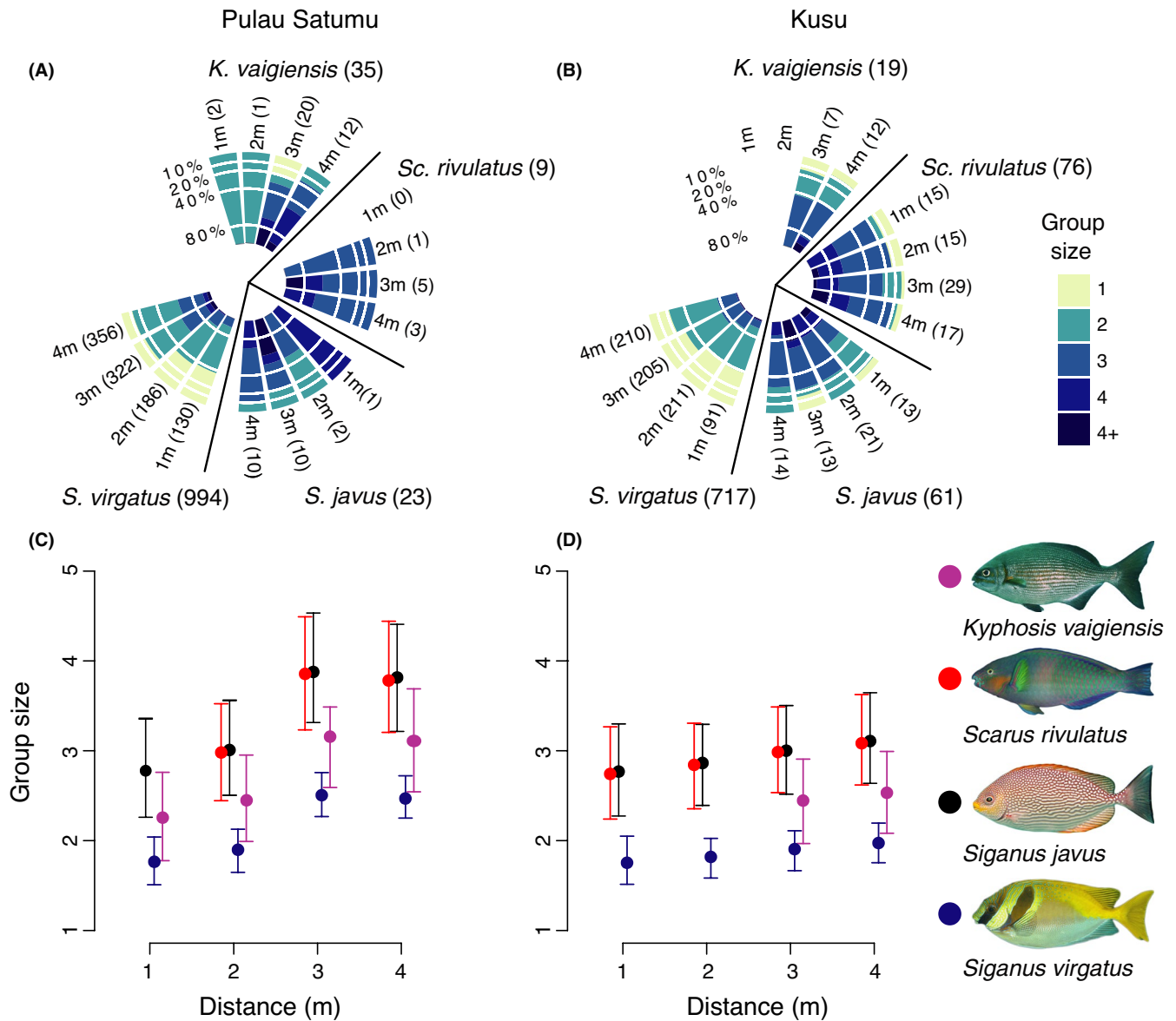


FIGURE 5 Changes in group size for individual feeding events across each assay positions for *Kyphosis vaigiensis*, *Scarus rivulatus*, *Siganus virgatus* and *Siganus javus* at Pulau Satumu (A, C) and Kusu (B, D). Polar histograms of raw group size data at each assay position for each species (A, B). Bars represent the proportion of group sizes at each assay position. Numbers in parentheses after assay position and species names are the total number of feeding events per assay position and the total for each species, respectively. Model predictions and 95% HPD credible intervals for each species (C, D)

than previously suggested, especially if background levels of risk are low, and may be mediated by group foraging.

Acute fear effects on browser foraging behaviour are often context dependent (Catano et al., 2016) and intuitively should vary with predator abundance (Madin et al., 2010), identity (Catano et al., 2017), size (Rizzari et al., 2014) and activity (Rasher et al., 2017) within and among reefs. For example, a previous study reported that larger predator models had a greater effect on herbivore foraging rates than small predator models (Rizzari et al., 2014). Yet, we found that rates of macroalgal consumption on assays 1 m from our predator model (53 cm *P. leopardus*: 4%–5% 4 hr⁻¹) were directly comparable to assays at similar distances from larger predator models (i.e. 76 cm *P. leopardus* and 170 cm reef shark *Carcharhinus melanopterus*)

on the GBR (5%–6% 4.5 hr⁻¹; Rizzari et al., 2014) suggesting our models elicited a similar response. Acute fear effects can also be influenced by local environmental conditions (e.g. high turbidity and sedimentation) that reduce light and the visual perception for both predators and prey (Utne-Palm, 2002). Consequently, the rapid dissipation of acute risk effects in this study may have been exacerbated by the high turbidity and low light conditions on Singapore's reefs (Chou, 2006) reducing browsers ability to visually detect the predator models at greater distances (i.e. 3 and 4 m) which resulted in higher feeding rates at those assay positions. Risk avoidance behaviours can also be modified by predator activity; herbivores may reduce foraging in habitats associated with an influx of larger, mobile predators (e.g. sharks) during specific tidal cycles (e.g. high

tides) presumably due to increased vigilance (Rasher et al., 2017). However, given that *P. leopardus* are opportunistic ambush predators that generally attack prey within a few metres (St. John, 1999), *Sargassum* assays positioned 3–4 m away from the predator models in this study may have attracted browsers increasing the removal of biomass. Notably, these diverse behavioural responses to acute risk are likely to vary among geographic regions, reefs and locations due to differences in herbivorous fish assemblages, identity and abundance of predators, benthic composition and environmental conditions.

Reductions in the removal of *Sargassum* with increasing risk (i.e. near the predator model) coincided with a decrease in group size of foraging fishes. This result is counter to our hypothesis and does not support the generally accepted notion that the formation of larger groups is an antipredator response to increasing predation risk (Krause & Ruxton, 2002; Lima & Dill, 1990). Rather, it may be that larger foraging groups disaggregated into smaller groups in the presence of a predator model to reduce the rates of detection, encounters and/or attacks as observed in some terrestrial species (Creel & Creel, 2002; Creel & Winnie, 2005; Hebblewhite & Pletscher, 2002). Likewise, larger group sizes in this study may have formed as a response to the spatial distribution of the *Sargassum* assays; browsers converged on assays where acute risk was perceived to be lower for the foraging opportunities these areas provided rather than a mechanism of risk dilution (Creel & Winnie, 2005). Alternatively, group size may have been affected by behavioural coupling whereby the presence or action of one individual generates cues that influence the actions of other individuals (e.g. Rosenthal et al., 2015). For example, Gil and Hein (2017) recently reported that herbivorous fishes base their decisions to feed versus flee from predators on the density and actions of other fish (i.e. social cues) within the reefscape, with such behaviours inducing strong temporal correlations in foraging behaviour. Importantly, our findings revealed that acute fear effects can influence browser group sizes over small spatial scales which may help to explain the spatial and temporal variation in macroalgal removal within and among coral reefs.

Our models also showed that acute risk effects on overall group sizes varied among herbivores, but that the four most common browsers observed feeding (*S. virgatus*, *S. javus*, *K. vaigiensis* and *S. rivulatus*) showed broadly similar trends. Of these species, only the rabbitfishes *S. virgatus* and *S. javus* showed marked increases in the number of bites/event with increasing group sizes and decreasing risk. For *S. virgatus*, the dominant consumer of *Sargassum* assays, associated with 85% of the IFEs, results showed that higher removal rates of *Sargassum* were the result of both an increased number of individual fishes feeding within a group and relatively higher individual feeding rates (ms-bites). This foraging response may be related to potential changes in vigilance behaviour with increasing group size (McNamara & Houston, 1992). Coordinated vigilance was commonly observed in foraging rabbitfish pairs in our study, but rarely observed in larger groups of rabbitfishes (>3 individuals, A.G. Bauman, pers. obs.) potentially allowing more time for feeding. Rabbitfishes, including *S. virgatus*, have been observed to display frequent

coordinated vigilance while in pairs (e.g. Brandl & Bellwood, 2015), a behaviour suggested to reduce acute predation risk while foraging (Fox & Donaldson, 2013), but such behaviour can also result in reduced foraging opportunities, particularly when acute risk is high. *Siganus virgatus* also occur in large groups (or schools) on Indo-Pacific reefs (Allen et al., 2003), with groups of up to 18 individuals (of which 15 were recorded feeding) recorded during our study. Theoretical models predict that individual costs of vigilance should decrease and foraging efficiency increases with increasing group size as the role is diluted among a greater number of individuals (Beauchamp, 2019; Bednekoff & Lima, 2004).

While it is beyond the scope of our study to suggest whether behavioural changes from coordinated vigilance in conspecific pairs to collective vigilance in groups occurred in *S. virgatus*, our results do show that group size is an important context-dependent factor that can influence the magnitude of fear effects on browser foraging behaviour over small spatial scales. Most fear effects studies that have investigated acute risk effects on coral reef browsers have not considered group foraging behaviour (Mitchell & Harborne, 2020) and generally tend to aggregate feeding events into a single metric of overall macroalgal removal. By quantifying individual feeding events (IFEs) and integrating browser group sizes, our results provide new insights into how group sizes could act as a mediating variable between fear effects and browsing which may lead to varied consequences of macroalgal removal on coral reefs. Our results also provide further evidence that group foraging among browsers may enhance feeding rates (Michael et al., 2013), and importantly the rates of macroalgal removal (a 'realized function'; Bellwood et al., 2019) within some reef systems. We argue that failing to account for group size effects may lead to overestimating the impacts of acute risk on browser foraging behaviour, and thus its effects on coral communities. However, one important consideration when interpreting our results is that the predator models used in this experiment were stationary, which could concentrate acute predation risk spatially, thereby obscuring the true predator effects on browser foraging behaviour and group size. Nevertheless, further research is warranted to resolve the potential links between group foraging and macroalgal removal on coral reefs, and the degree to which fear effects interact with group size to determine the outcome of foraging decisions.

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AUTHORS' CONTRIBUTIONS

A.G.B., A.S.H. and P.A.T. conceived the study and designed the field experiments; A.G.B., A.S.H., J.F. and I.Z.W.C. collected the ecological

data; G.D. and A.G.B. analysed the data; and A.G.B., A.S.H. and G.D. wrote the manuscript. All authors contributed to interpretation of results and provided editorial comments.

COMPETING INTERESTS

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

R code and data associated with the manuscript are at <https://doi.org/10.5061/dryad.vdncjstf> (Bauman et al., 2021).

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REFERENCES

- Allen, G. R., Steene, R. C., Humann, P., & DeLoach, N. (2003). *Reef fish identification: Tropical pacific*. New World Publications.
- Bartoń, K. (2015). MuMIn: Multi-model inference, version 1.9.0. *R Package*, 1, 18.
- Bauman, A. G., Hoey, A. S., Dunshea, G., Feary, D. A., Low, J., & Todd, P. A. (2017). Macroalgal browsing on a heavily degraded, urbanized equatorial reef system. *Scientific Reports*, 7, 8352. <https://doi.org/10.1038/s41598-017-08873-3>
- Bauman, A. G., Hoey, A. S., Dunshea, G., Fong, J., Chan, I. Z. W., & Todd, P. A. (2021). Data from: Fear effects and group size interact to shape herbivory on coral reefs. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.vdncjstf>
- Bauman, A. G., Seah, J. C. L., Januchowski-Hartley, F. A., Hoey, A. S., Fong, J., & Todd, P. A. (2019). Fear effects associated with predator presence and habitat structure interact to alter herbivory on coral reefs. *Biology Letters*, 15, 20190409. <https://doi.org/10.1098/rsbl.2019.0409>
- Beauchamp, G. (2019). On how risk and group size interact to influence vigilance. *Biological Reviews*, 94, 1918–1934. <https://doi.org/10.1111/brv.12540>
- Bednekoff, P. A., & Lima, S. L. (2004). Risk allocation and competition in foraging groups: Reversed effects of competition if group size varies under risk of predation. *Proceedings of the Royal Society B: Biological Sciences*, 271, 1491–1496. <https://doi.org/10.1098/rspb.2004.2739>
- Bellwood, D. R., Hoey, A. S., Ackerman, J. L., & Depczynski, M. (2006). Coral bleaching, reef fish community shifts and the resilience of coral reefs. *Global Change Biology*, 12, 1587–1594. <https://doi.org/10.1111/j.1365-2486.2006.01204.x>
- Bellwood, D. R., Streit, R. P., Brandl, S. J., & Tebbett, S. B. (2019). The meaning of the term 'function' in ecology: A coral reef perspective. *Functional Ecology*, 33, 948–961. <https://doi.org/10.1111/1365-2435.13265>
- Brandl, S. J., & Bellwood, D. R. (2015). Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes. *Scientific Reports*, 5, 14556. <https://doi.org/10.1038/srep14556>
- Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7, 999–1014. <https://doi.org/10.1111/j.1461-0248.2004.00661.x>
- Bruno, J. F., Sweatman, H., Precht, W. F., Selig, E. R., & Schutte, V. G. W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, 90, 1478–1484. <https://doi.org/10.1890/08-1781.1>
- Catano, L. B., Barton, M. B., Boswell, K. M., & Burkepile, D. E. (2017). Predator identity and time of day interact to shape the risk–reward trade-off for herbivorous coral reef fishes. *Oecologia*, 183, 763–773. <https://doi.org/10.1007/s00442-016-3794-z>
- Catano, L. B., Rojas, M. C., Malossi, R. J., Peters, J. R., Heithaus, M. R., Fourqurean, J. W., & Burkepile, D. E. (2016). Reefscapes of fear: Predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. *Journal of Animal Ecology*, 85, 146–156. <https://doi.org/10.1111/1365-2656.12440>
- Choat, J. H., Clements, K. D., & Robbins, W. D. (2002). The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, 140, 613–623. <https://doi.org/10.1007/s00227-001-0715-3>
- Chou, L. M. (2006). Marine habitats in one of the world's busiest harbours. In E. Wolanski (Ed.), *The environment in Asia Pacific harbours* (pp. 377–391). Springer.
- Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, 23, 194–201. <https://doi.org/10.1016/j.tree.2007.12.004>
- Creel, S., & Creel, N. M. (2002). *The African wild dog: Behavior, ecology and conservation*. Princeton University Press.
- Creel, S., & Winnie Jr, J. A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, 69, 1181–1189. <https://doi.org/10.1016/j.anbehav.2004.07.022>
- Cronin, G., & Hay, M. E. (1996). Susceptibility to herbivores depends on recent history of both the plant and animal. *Ecology*, 77, 1531–1543. <https://doi.org/10.2307/2265549>
- Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, 64, 13–33. <https://doi.org/10.1111/j.1469-185X.1989.tb00636.x>
- Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293, 466–467. <https://doi.org/10.1038/293466a0>
- Fox, J. R., & Donelson, J. M. (2013). Rabbitfish sentinels: First report of coordinated vigilance in conspecific marine fishes. *Coral Reefs*, 33, 253. <https://doi.org/10.1007/s00338-013-1108-z>
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution*, 34, 355–368. <https://doi.org/10.1016/j.tree.2019.01.004>
- Gil, M. A., & Hein, A. M. (2017). Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, 114(18), 4703–4708. <https://doi.org/10.1073/pnas.1615652114>
- Gil, M. A., Zill, J., & Ponciano, J. M. (2017). Context-dependent landscape of fear: Algal density elicits risky herbivory in a coral reef. *Ecology*, 98(2), 534–544. <https://doi.org/10.1002/ecy.1668>
- Green, A. L., & Bellwood, D. R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region*. IUCN working group on Climate Change and Coral Reefs.
- Guest, J. R., Tun, K., Low, J., Vergés, A., Marzinelli, E. M., Campbell, A. H., Bauman, A. G., Feary, D. A., Chou, L. M., & Steinberg, P. D. (2016). 27 years of benthic and coral community dynamics on turbid, highly urbanised reefs off Singapore. *Scientific Reports*, 6, 36260. <https://doi.org/10.1038/srep36260>
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22. <https://www.jstatsoft.org/v033/i02>
- Hebblewhite, M., & Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology*, 80, 800–809. <https://doi.org/10.1139/z02-059>
- Heithaus, M. R., & Dill, L. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, 480–491.

- [https://doi.org/10.1890/0012-9658\(2002\)083\[0480:FAATS P\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0480:FAATS P]2.0.CO;2)
- Hoey, A. S., & Bellwood, D. R. (2009). Limited functional redundancy in a high diversity system: Single species dominates key ecological process on coral reefs. *Ecosystems*, 12, 1316–1328. <https://doi.org/10.1007/s10021-009-9291-z>
- Hoey, A. S., & Bellwood, D. R. (2010). Cross-shelf variation in browsing intensity on the Great Barrier Reef. *Coral Reefs*, 29(2), 499–508. <https://doi.org/10.1007/s00338-010-0605-6>
- Hoey, A. S., & Bellwood, D. R. (2011). Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? *Ecology Letters*, 14, 267–273. <https://doi.org/10.1111/j.1461-0248.2010.01581.x>
- Hoey, A. S., Brandl, S. J., & Bellwood, D. R. (2013). Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: Implications for ecosystem function. *Coral Reefs*, 32, 973–984. <https://doi.org/10.1007/s00338-013-1043-z>
- Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, 546, 82–90. <https://doi.org/10.1038/nature22901>
- Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Motschaniskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase shifts, herbivory and the resilience of coral reefs to climate change. *Current Biology*, 17, 360–365. <https://doi.org/10.1016/j.cub.2006.12.049>
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.
- Kulbicki, M., Gullemot, N., & Amand, M. (2005). A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybiu*, 29, 235–252.
- Laundre, J., Hernandez, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 79, 1401–1409. <https://doi.org/10.1139/cjz-79-8-1401>
- Lim, K. K. P., & Low, J. K. Y. (1998). *A guide to common marine fishes of Singapore*. Singapore Science Centre.
- Lima, S. L. (1995). Back to basics of anti-predatory vigilance: The group-size effect. *Animal Behaviour*, 49, 11–20. [https://doi.org/10.1016/0003-3472\(95\)80149-9](https://doi.org/10.1016/0003-3472(95)80149-9)
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640. <https://doi.org/10.1139/z90-092>
- Low, J. K. Y., Fong, J., Todd, P. A., Chou, L. M., & Bauman, A. G. (2019). Seasonal variation of *Sargassum illicifolium* (Phaeophyceae) growth on equatorial coral reefs. *Journal of Phycology*, 55, 289–296. <https://doi.org/10.1111/jpy.12818>
- Lukoschek, V., & McCormick, M. I. (2000). A review of multi-species foraging associations in fishes and their ecological significance. In *Proceedings of the 9th International Coral Reef Symposium*, Bali, Indonesia, Vol. 1, pp. 467–474.
- Madin, E. M. P., Gaines, S. D., Madin, J. S., & Warner, R. R. (2010). Fishing indirectly structures macroalgal assemblages by altering herbivore behavior. *The American Naturalist*, 176, 785–801. <https://doi.org/10.1086/657039>
- Madin, E. M. P., Gaines, S. D., & Warner, R. R. (2010). Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology*, 91, 3563–3571. <https://doi.org/10.1890/09-2174.1>
- Madin, E. M. P., Madin, J. S., & Booth, D. J. (2011). Landscape of fear visible from space. *Scientific Reports*, 1, 14. <https://doi.org/10.1038/srep00014>
- McNamara, J. M., & Houston, A. I. (1992). Evolutionarily stable levels of vigilance as a function of group size. *Animal Behaviour*, 43, 641–658. [https://doi.org/10.1016/S0003-3472\(05\)81023-1](https://doi.org/10.1016/S0003-3472(05)81023-1)
- Meyer, C. G., & Holland, K. N. (2005). Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acathuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes*, 73, 201–210. <https://doi.org/10.1007/s10641-005-0559-7>
- Michael, P. J., Hyndes, G. A., Vanderklift, M. A., & Vergés, A. (2013). Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Marine Ecology Progress Series*, 482, 227–240. <https://doi.org/10.3354/meps10262>
- Mitchell, M. D., & Harborne, A. R. (2020). Non-consumptive effects in fish predator–prey interactions on coral reefs. *Coral Reefs*, 39, 867–884. <https://doi.org/10.1007/s00338-020-01920-y>
- Mumby, P. J., Hastings, A., & Edwards, H. J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, 450, 98–101. <https://doi.org/10.1038/nature06252>
- Neill, S. R. J., & Cullen, J. M. (1974). Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *Journal of Zoology*, 172, 549–569. <https://doi.org/10.1111/j.1469-7998.1974.tb04385.x>
- Nicholson, G. M., & Clements, K. D. (2021). Ecomorphological divergence and trophic resource partitioning in 15 syntopic Indo-Pacific parrotfishes (Labridae: Scarini). *Biological Journal of the Linnean Society*, 132, 590–611. <https://doi.org/10.1093/biolinnean/blaa210>
- Pajmans, K. C., Booth, D. J., & Wong, M. Y. L. (2019). Towards an ultimate explanation for mixed-species shoaling. *Fish and Fisheries*, 20, 921–933. <https://doi.org/10.1111/faf.12384>
- Pitcher, T., Magurran, A., & Winfield, I. (1982). Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, 10(2), 149–151. <https://doi.org/10.1007/BF00300175>
- Pitcher, T. J., & Parrish, J. K. (1993). The functions of shoaling behaviour. In T. J. Pitcher (Ed.), *The behaviour of teleost fishes* (2nd ed., pp. 363–439). Chapman and Hall.
- Preisser, E. L., & Bolnick, D. I. (2008). The many faces of fear: Comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE*, 3(6), e2465. <https://doi.org/10.1371/journal.pone.0002465>
- Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, 38, 419–422. [https://doi.org/10.1016/0022-5193\(73\)90184-7](https://doi.org/10.1016/0022-5193(73)90184-7)
- R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rasher, D. B., Hoey, A. S., & Hay, M. E. (2017). Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*, 7, 15684. <https://doi.org/10.1038/s41598-017-15679-w>
- Ripple, W. J., Larsen, E. J., Renkin, R. A., & Smith, D. W. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, 102(3), 227–234. [https://doi.org/10.1016/S0006-3207\(01\)00107-0](https://doi.org/10.1016/S0006-3207(01)00107-0)
- Rizzari, J. R., Frisch, A. J., Hoey, A. S., & McCormick, M. I. (2014). Not worth the risk: Apex predators suppress herbivory on coral reefs. *Oikos*, 123, 829–836. <https://doi.org/10.1111/oik.01318>
- Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015). Revealing the hidden networks of interactions in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences of the United States of America*, 112(15), 4690–4695. <https://doi.org/10.1073/pnas.1420068112>
- Sandin, S. A., & McNamara, D. E. (2012). Spatial dynamics of benthic competition on coral reefs. *Oecologia*, 168, 1079–1090. <https://doi.org/10.1007/s00442-011-2156-0>
- Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, 7, 153–163. <https://doi.org/10.1111/j.1461-0248.2003.00560.x>
- Seah, J. C. L., Bauman, A. G., & Todd, P. A. (2021). Temporal variation in macroalgal removal: Insights from an impacted equatorial coral reef system. *Marine Biology*, 168, 2. <https://doi.org/10.1007/s00227-020-03806-7>
- Sih, A., Crowley, P., McPeck, M., Petranka, J., & Strohmeir, K. (1985). Predation, competition and prey communities: A review of field

- experiments. *Annual Review of Ecology and Systematics*, 16, 269–311. <https://doi.org/10.1146/annurev.es.16.110185.001413>
- St. John, J. (1999). Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): Patterns in taxa, size and habitat of prey. *Marine Ecology Progress Series*, 180, 233–246. <https://doi.org/10.3354/meps180233>
- Streit, R. P., Hoey, A. S., & Bellwood, D. R. (2015). Feed characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. *Coral Reefs*, 34, 1037–1047. <https://doi.org/10.1007/s00338-015-1322-y>
- Turner, G. F., & Pitcher, T. J. (1986). Attack abatement: A model for group protection by combined avoidance and dilution. *The American Naturalist*, 128, 228–240. <https://doi.org/10.1086/284556>
- Utne-Palm, A. C. (2002). Visual feeding of fish in a turbid environment: Physical and behavioural aspects. *Marine and Freshwater Behaviour and Physiology*, 35, 111–128. <https://doi.org/10.1080/10236240290025644>
- Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*, 108(6), 2312–2315. <https://doi.org/10.1073/pnas.1007102108>
- Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, 92, 3–10. <https://doi.org/10.1890/10-0340.1>
- Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. C. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64(6), 1540–1548. <https://doi.org/10.2307/1937508>
- Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100. [https://doi.org/10.1890/0012-9658\(2003\)084\[1083:AROTI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1083:AROTI]2.0.CO;2)
- Winnie, J., & Creel, S. (2007). Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, 73, 215–225. <https://doi.org/10.1016/j.anbehav.2006.07.007>
- Wolf, N. G. (1987). Schooling tendency and foraging benefit in the ocean surgeonfish. *Behavioral Ecology and Sociobiology*, 21, 59–63. <https://doi.org/10.1007/BF00324436>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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