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Quantum of fear: Herbivore grazing rates not affected by reef shark presence

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ABSTRACT

Grazing by nominally herbivorous fishes is widely recognised as a critical ecosystem function on coral reefs. However, several studies have suggested that herbivory is reduced in the presence of predators, especially sharks. Nevertheless, the effects of shark presence on grazing, under natural settings, remains poorly resolved. Using ~200 h of video footage, we quantify the extent of direct disturbance by reef sharks on grazing fishes. Contrary to expectations, grazing rate was not significantly suppressed due to sharks, with fishes resuming feeding in as little as 4 s after sharks passed. Based on our observations, we estimate that an average m^2 area of reef at our study locations would be subjected to ~5 s of acute shark disturbance during daylight hours. It appears the short-term impact of reef shark presence has a negligible effect on herbivore grazing rates, with the variable nature of grazing under natural conditions overwhelming any fear effects.

1. Introduction

The feeding activity of nominally herbivorous fishes on coral reefs is widely considered a critical ecosystem function (Bellwood et al., 2019; Brandl et al., 2019). This feeding activity is key for harnessing primary production and cycling nutrients in coral reef ecosystems (Schiettekatte et al., 2022; Robinson et al., 2023), as well as controlling the growth and biomass of algae, which can mediate interactions between benthic biota (Hughes et al., 2007; Rasher et al., 2012). Given the importance of herbivory, a number of studies have identified and explored how a range of factors, including temperature (Carr et al., 2018), sediments (Tebbett et al., 2020a), structural complexity (Vergés et al., 2011), and competitive/territorial interactions (Choat and Bellwood 1985), shape where, and the extent to which, different herbivores feed on coral reefs. In this respect, a growing body of literature has also highlighted the potential importance of predators in mediating herbivorous fish feeding rates through indirect 'fear effects' or non-consumptive effects (e.g. Rizzari et al., 2014; Catano et al., 2016, 2017; Bauman et al., 2019, 2021). As these fear effects may reduce how much herbivores feed, or shape where they feed, these effects could result in cascading ecological consequences on reefs, potentially shaping the distribution of algal biomass (Rasher et al., 2017; Madin et al., 2019).

On coral reefs, sharks are widely viewed as key predatory taxa and, as such, are believed to fulfil a range of important ecological roles, including mediating herbivory via fear effects (Rizzari et al., 2014; Roff et al., 2016; Heithaus et al., 2022). Yet, despite this perceived importance, empirical data on the ecological roles of sharks on coral reefs is relatively limited (Roff et al., 2016; Heithaus et al., 2022). These data limitations may be due to the logistical difficulties that are inherently associated with directly manipulating large predators, as well as the fleeting nature of shark-mediated fear effects (Roff et al., 2016; Mitchell and Harborne 2020). Indeed, most fear effect studies on coral reefs rely on static models of predators, in which the relationship between these models and natural processes can be unclear, or on the examination of fish behaviour across gradients in shark densities, where it can be hard to control for the range of other environmental factors that covary along these gradients (Mitchell and Harborne 2020; Heithaus et al., 2022). As such, our knowledge of how direct, acute (short-term), shark-mediated fear effects shape grazing rates by herbivorous fishes, under natural settings, is surprisingly limited (but see Rasher et al., 2017). This means that even though humans have radically re-shaped shark populations on coral reefs at a global scale (MacNeil et al., 2020; Simpfendorfer et al., 2023), the direct ecological consequences of this mass predator depletion on reefs remain unclear.

Here, we take advantage of a unique opportunity that permitted the direct evaluation of the consequences of reef shark presence on the

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grazing rates of nominally herbivorous fishes. Specifically, we utilised ~200-h of herbivore grazing video footage, under natural conditions, from Australia's Great Barrier Reef (GBR). As this video footage included numerous incidences of reef sharks passing over the area of interest, we were able to directly compare fish grazing rates in short temporal windows before and after the shark passed, and relative to controls. Given that we focused on the same area of reef in each sample, on the same day, and in a close temporal window, this effectively controlled for a range of other variables (e.g. sediment loads [Tebbett et al., 2020a], diel time [Ferreira et al., 1998], and temperature [Smith 2008]) that may shape grazing rates, allowing us to directly compare if the fear effects triggered by the presence of reef sharks had any short-term effects on the grazing intensity that a given area of reef received. Based on prior evidence of shark-mediated fear effects (Rizzari et al., 2014; Rasher et al., 2017), we hypothesised that grazing rates by herbivorous fishes would be significantly reduced around the period of the shark passing relative to control periods. Specifically, our hypothesis is that grazing would be reduced immediately prior to the shark passing due to increased vigilance behaviour once the fish detects a predator and/or immediately after the shark passes due to a period of enhanced 'fear'.

2. Materials and methods

2.1. Field sampling

To quantify the feeding activity of herbivorous fishes, video deployments were conducted at 19 sites across the northern Great Barrier Reef, Australia, in January/February 2021; 2022 (Fig. 1a). At each site, we used underwater video cameras (GoPros) to record parrotfishes, surgeonfishes, and rabbitfishes feeding on turf/CCA covered surfaces on the 'reef crest/edge' habitat in ~2 m of water (following Goatley et al., 2016). To do this a 1 m^2 PVC quadrat was placed haphazardly on low-complexity, horizontal, turf/CCA covered sections of the reef (n = 8–10 replicates at each site at least ~3 m apart) to delineate the survey area. The video cameras were then deployed to include the quadrat in the field of view, and the recording was started. After approximately 10 s, the quadrat was removed, and the site was left undisturbed, with cameras filming for a minimum of 70 min. All filming was conducted between 09:00 and 15:00 to capture the period of greatest herbivorous fish feeding activity and to minimise any temporal variation due to diel-feeding effects (Montgomery et al., 1989; Polunin et al., 1995; Ferreira et al., 1998).

2.2. Video analysis

On initial scanning of the videos, it was noted that both blacktip (*Carcharhinus melanopterus*) and whitetip (*Triaenodon obesus*) reef sharks were observed passing over the 1 m^2 filming area on numerous occasions. This, therefore, presented a unique opportunity to examine herbivorous fish feeding before and after the shark passed over the survey area to assess if there was any short-term 'fear effects' that may affect nominally herbivorous fishes feeding in that area. To do this, we initially scanned all the video footage collected (~200 h) to find suitable instances of shark passes for quantification. A shark pass was deemed suitable if it: a) occurred at least 10 min after the cameras were deployed (to minimise diver effects on herbivorous fish feeding) and there was at least 5 min of video left, and b) the shark passed directly over the 1 m^2 survey area. Importantly, no juvenile sharks were recorded, with all sharks of a size likely to be capable of feeding on the herbivorous fishes of interest (Frisch et al., 2016; Barley et al., 2020).

For each suitable shark pass we recorded the time the shark entered and exited the survey area. The periods of time 5 min immediately before the shark entered the survey area and 5 min immediately after the shark exited the area were subsequently delineated as the 'before' and 'after' sampling periods. Where sharks made repeated passes over the survey area in quick succession (i.e. <2 min) the 'before' period was delineated as before the first pass, while the 'after' period was delineated as after the final pass. Where sharks made repeated passes over the same area after a substantial amount of time had elapsed (>15 min) these were treated as separate passes (5 occurrences). In total, 30 shark passes, in 25 of the videos, across 10 of the sampling sites were analysed (Fig. 1).

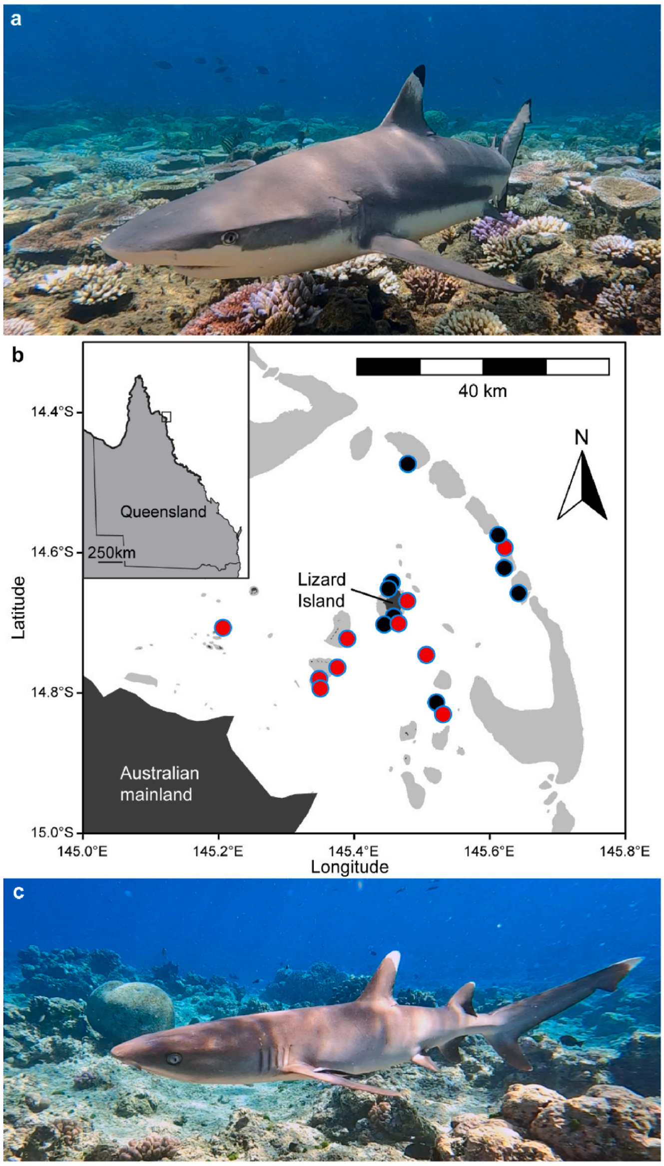

Fig. 1. Study location and shark species observed. Examples of (a) blacktip reef shark (*Carcharhinus melanopterus*) and (c) whitetip reef shark (*Triaenodon obesus*) observed in herbivorous fish grazing videos. (b) Study sites where herbivorous fish grazing videos were deployed in the northern Great Barrier Reef. Red circles denote sites where sharks were recorded in the videos while black circles denote sites where no sharks were recorded.

In the 'before' and 'after' sampling periods we counted all bites delivered by nominally herbivorous (i.e. herbivorous and detritivorous) parrotfishes, surgeonfishes, and rabbitfishes in the survey area, and recorded the time that fishes ceased and commenced feeding relative to the shark pass. All fishes that fed were recorded to species and placed into 5 cm total length (TL) size categories using the quadrat as a reference. Only feeding by fishes >10 cm TL was recorded, so that we focused on fishes that were most likely to be prey for sharks, and most likely to be influenced by the shark presence. Fish size data were subsequently converted to biomass estimates using Bayesian length-weight regression parameters from Fishbase (Froese et al., 2014; Froese and Pauly 2023).

Moreover, we also analysed herbivore feeding (as above) in two different types of randomly selected feeding windows to act as controls. Firstly, Control-A involved quantifying herbivore feeding from randomly selected 5-min sections of video (n = 30) from the same quadrats where a shark was observed passing over the reef. In this case, all 5-min sections occurred a minimum of 10 min before or after a shark had been observed passing over the 1 m^2 area and, therefore, we examined a period when the shark was likely to have no effect while also controlling for spatial variation among plots. Secondly, in Control-B, we recorded herbivore feeding (as above) in 30 randomly selected 5-min sections of video (n = 3 per sampling site for each of the 10 sites of interest) from survey areas where no shark passes were observed.

2.3. Statistical analyses

To test for differences in both the bite rate, and biomass-standardised bite rate, delivered by nominally herbivorous fishes among the feeding observation periods (i.e. before the shark, after the shark, or the two controls) we used separate generalised linear mixed effects models (GLMMs). In both cases, rates were standardised to bites per hour for ease of interpretation. The first model evaluated bite rate as the response variable and was based on a negative binomial distribution with a log-link function, while the second model evaluated biomass-standardised bite rate as the response variable and was based on a tweedie distribution with a log-link function. In both models, the feeding observation period was treated as a categorical fixed effect, while the identity of the feeding observation/quadrat nested within site identity, were treated as random effects to account for the repeated measures of the same location and any lack of spatial independence. Model fit and assumptions were evaluated using residuals via simulation-based model checking procedures (Hartig 2020), which were satisfactory in both cases. Post-hoc pairwise means comparisons with a Tukey's adjustment were also performed in both cases to evaluate differences among feeding observation levels. All statistical analyses were performed in the software R (version 4.2.2; R Core Team 2022) using the *glmmTMB* ((Brooks et al., 2017), *emmeans* (Lenth 2020), and *DHARMa* (Hartig 2020) packages.

3. Results and discussion

Despite hypothesising that grazing rates by herbivorous fishes would be suppressed around the time of a reef shark passing, we found no clear evidence to support this hypothesis (Fig. 2). Indeed, we found no significant differences in herbivorous fish feeding rate, or biomass-standardised feeding rates, either a) before versus after the shark passed over the reef, or b) between either observation period associated with a shark passing over the reef compared to the two different types of control observation periods selected at random (Fig. 2a and b, Tables S1 and S2). Overall, herbivorous fish feeding rates were highly variable (Fig. 2), and this variability may have overwhelmed any short-term fear effects from the presence of sharks as they traversed the reef. Indeed, any fear effect, if present, is likely to be minimal. Notably, most bites observed were delivered by relatively small fishes (average total length weighted by bites = 15.4 cm [fish size range 12.5–47.5 cm]; average mass weighted by bites = 104.7 g [fish mass range 26.5–2039 g]), and in most cases relatively site attached nominally herbivorous fish species (Table S3). As these fish species are highly likely to represent potential prey for the reef sharks observed (Frisch et al., 2016; Barley et al., 2020) we would have expected any significant fear effects to have manifest as reduced feeding; clearly this was not the case. This lack of an effect may be related to the diel mismatch that exists between shark predation and grazing rates on coral reefs.

Feeding rates by herbivorous fishes on coral reefs generally peak around the middle of the day or early afternoon (Montgomery et al., 1989; Polunin et al., 1995), while the extent of reef shark movement (which is often attributed to foraging behaviour) often peaks during crepuscular periods (Papastamatiou et al., 2015; Hammerschlag et al., 2016; Schlaff et al., 2020). Indeed, based on acoustic telemetry data, predation rates on herbivorous reef fishes can be high during crepuscular periods, which may be attributed to predation by reef sharks, while high predation events during daylight hours appear to be driven primarily by other large mobile teleost predators (e.g. carangids) (Khan

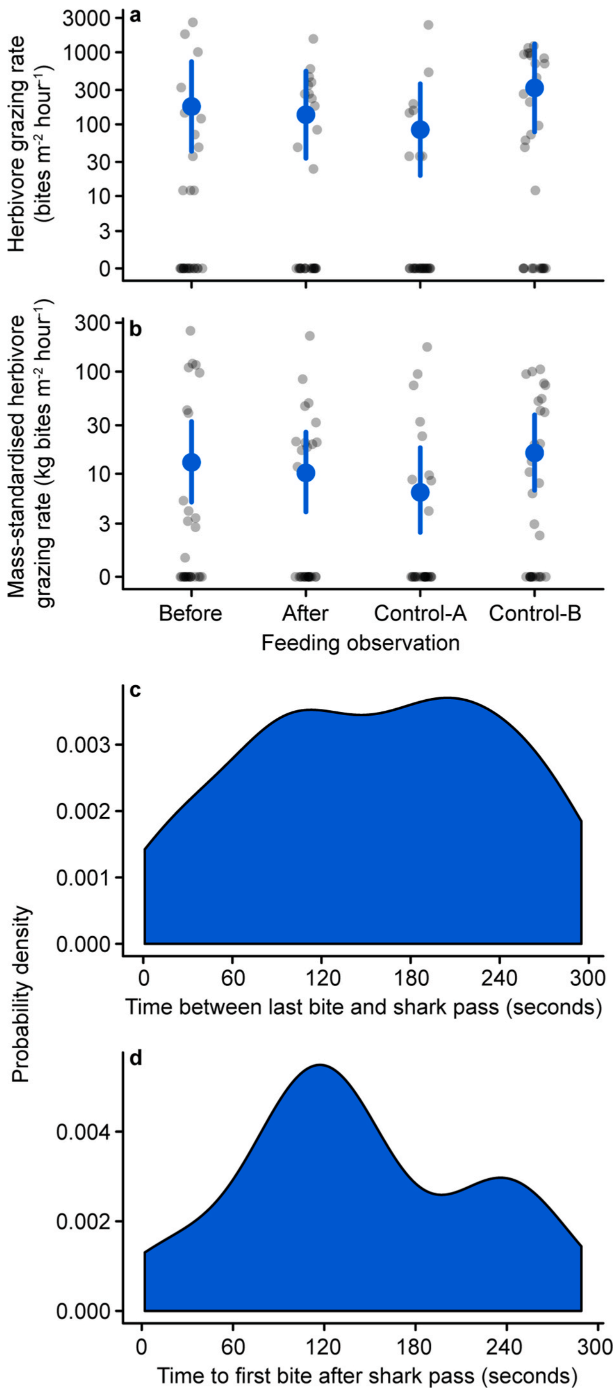

Fig. 2. The (a) grazing rate, and (b) mass-standardised grazing rate, of herbivorous fishes in relation to reef sharks passing over the grazed reef substratum. Before = the 5-min period before a shark passed, after = the 5-min period after the shark had passed, Control-A = randomly selected 5-min periods that occurred at least 10 min before or after a shark passed over the quadrat, and Control-B = randomly selected 5-min control periods from videos where no sharks were observed. The frequency distribution, based on probability density, of (c) the time that elapsed between a herbivorous fish ceasing feeding and a shark passing, and (d) the time that elapsed between a shark passing and a herbivorous fish feeding on the area over which the shark passed.

et al., 2016). Such differences in activity patterns between sharks and reef fishes may be the result of divergence in metabolic rates (Ito et al., 2022), with this mismatch in activity ultimately meaning that the greatest risk for herbivorous fishes may occur outside of major feeding periods. As a result, fear effect disturbances by reef sharks, especially during periods of peak herbivorous fish feeding activity, are likely to be relatively minor with a limited net effect on the grazing intensity that the reef receives. Nevertheless, the potential always exists for high shark abundances to reduce grazing more directly through consumption.

It is important to note that the extent of direct shark disturbance that we document in this study was relatively low. Indeed, given the average shark passes we documented (0.16 m^{-2} h^{-1}), and based on a shark passing over a 1 m^2 area in 3 s, an average 1 m^2 area of reef across our study sites would be expected to receive ~5 s of direct shark disturbance during daylight hours each day. Our results show that this level of short-term disturbance is not sufficient to significantly modify feeding rates by herbivorous fishes in our study system and even if a significant fear effect was documented, such low rates of direct shark disturbance are unlikely to result in a significant suppression of grazing activity. Furthermore, while our rates of direct shark disturbance seem relatively low, the reefs on the GBR where this study was conducted have experienced far lower rates of shark depletion compared to most other coral reef regions around the world (Simpfendorfer et al., 2023). Therefore, the rates of direct shark disturbance that we document are likely to be far higher than would be experienced on many other coral reefs. Nevertheless, shark populations are now a fraction of what they once were, with the densities of sharks on our study reefs still likely to be far lower than those on very remote reefs and/or on reefs in highly enforced protected areas (Robbins et al., 2006; MacNeil et al., 2020). In future research, it would therefore be interesting to explore how grazing varied across a broad range of shark passage rates to determine if shark densities can get high enough to significantly affect grazing. Likewise, documenting grazing rates for longer temporal periods over gradients in shark passage rates would help determine if, and to what extent, grazing rates respond to cumulative shark exposure. Such assessments would help shed light on the ecological role of sharks and how this may have changed following largescale depletion.

Interestingly, our study results contrast markedly with previous research that has documented significant fear effects in herbivorous fishes using models of sharks and other predators (e.g. Rizzari et al., 2014; Catano et al., 2016; Bauman et al., 2021; Asunsolo-Rivera et al., 2023). For example, Rizzari et al. (2014) found that in the presence of a blacktip reef shark model, feeding rates of herbivorous fishes on macroalgae were reduced by ~99.6% relative to treatments without a predator model. While Rizzari et al. (2014) focused on feeding on upright macroalgae assays, and we focused on grazing rates on natural turf-covered reef surfaces (which are two markedly different forms of herbivorous fish feeding on reefs [Tebbett et al., 2023]) the major difference between the two studies is that Rizzari et al. (2014) used a stationary shark model that was deployed for 4.5 h, while our observations were based on natural, mobile, reef sharks. This latter difference may explain the marked contrast in results. Specifically, in our case, reef sharks passed over the 1 m^2 feeding area in approximately 2–3 s, meaning that any fear effects would have been short-term. Indeed, when sharks passed, we did observe a suspension of grazing by herbivores in some cases, and no bites were observed in the 1 m^2 area in the 2–3 s as the shark passed, suggesting that there may have been some level of fear, supporting Rizzari et al. (2014). However, these fear effects appear to have been fleeting given that herbivores ceased feeding on the 1 m^2 area in as little as 1 s before a shark passed (Fig. 2c) and resumed feeding on the 1 m^2 area in as little as 4 s after the shark had passed (Fig. 2d). By contrast, the deployment of a stationary model on the reef for 4.5 h may have magnified these naturally fleeting fear effects (by ~5000-8000-fold based on our observations of shark movement [although this is inherently dependent on shark density and the number of passages on a given reef]) and resulted in an exaggerated suppression of herbivory (as acknowledged by Rizzari et al., 2014). Therefore, caution may be needed when interpreting the magnitude of fear effects from studies based on stationary models (cf. Lima and Bednekoff 1999; Davis et al., 2017).

Beyond fear effect studies based on stationary models, our results also contrast with those of Rasher et al. (2017) who also suggested that herbivory rates were suppressed by fear effects. Notably, the study by Rasher et al. (2017) was also based on natural observations of reef sharks traversing over a reef in Fiji and they observed an average reef shark encounter rate of ~0.025 sightings m^{-2} h^{-1}, which is generally lower than what we observed across reef sites (average 0.16 [range 0–0.8] sightings m^{-2} h^{-1} at each site [based on an hour of footage from each replicate video]). However, as Rasher et al. (2017) highlighted, differences in the context of reefs could hold the key to explaining the differences in observation. Specifically, due to the context (reef topography, tidal cycles, and shark behaviour) of the reef studied in Fiji the herbivorous fishes had extended periods of time in which they could feed in less 'risky' areas and they, therefore, had the potential to avoid feeding in fear 'hot spots' (also see Papastamatiou et al., 2024). The sites examined in our case lacked the same interaction between topography and tidal cycles; all were close to the reef rest/edge, thus providing a deeper refuge if needed. We therefore observed herbivore-shark interactions in a moderately risky environment which is likely to be broadly analogous to the peak herbivore feeding areas on the reef (i.e. the reef crest, upper slope and backreef edge). Importantly, this observation supports the suggestion by Rasher et al. (2017) that the fear effect mechanisms they describe are likely to be limited to specific reef contexts, in places and/or at times of high risk to herbivores (e.g. the inner reef flat [Fox and Bellwood 2007; Bellwood et al., 2018]).

If the reef context in question results in less predictable 'risk', then the need for herbivorous fishes to feed may overwhelm fear of predation (as in the Predation Risk Allocation Hypothesis [Lima and Bednekoff 1999]). In this respect, our results align with those of Davis et al. (2017) who observed very low rates of acute behavioural response in the parrotfish *Chloururs spilurus* to predators (including reef sharks), despite these predators being near the parrotfishes. They also rarely observed any behavioural reaction by herbivorous fishes to the approach or presence of predators. As Davis et al. (2017) suggest, it may be maladaptive for herbivores to suspend feeding or seek shelter each time a predator is present in high predator environments. This is especially true in scenarios where predators may not always pose a threat, such as during different times of the day (as discussed above). Nevertheless, during more risky temporal periods (such as during the evening) or in more vulnerable locations (such as on the reef flat) the predator effect is likely to be greater and may partly account for the limited herbivory in certain habitats (Fox and Bellwood 2007; Rasher et al., 2017).

Beyond fear effects, herbivorous fish grazing can be remarkably variable, with this variability potentially being driven by a complex range of abiotic and biotic factors (Carlson et al., 2017; Streit et al., 2019). It may be that in our case, these other factors, beyond fear effects, were more important in explaining where, and at what rates, fishes graze the reef substratum. In this respect, bottom-up factors such as the quality and quantity of nutritional resources are particularly important in shaping where, and to what extent, different species of herbivorous fishes feed (Carlson et al., 2017; Tebbett et al., 2020a). However, the composition and quality of these nutritional resources, especially those associated with turfs, are also highly variable, including over small (centimetre-scale), spatial scales (Harris et al., 2015; Tebbett et al., 2020b). As such, disentangling how these bottom-up factors shape herbivorous fish feeding requires specific detailed evaluations, often at the level of individual fish or fish species (e.g. Brandl and Bellwood 2016; Carlson et al., 2017; Tebbett et al., 2020a), which was beyond the scope of the present study. Nevertheless, teasing apart the relative importance of these factors under natural settings, and in combination with fear effects, would be an interesting, albeit challenging, avenue for future research.

Overall, our observations on in-situ feeding by herbivores in the presence of mobile reef sharks, suggest that acute fear effects in reef crest/edge locations do not significantly alter herbivorous reef fish feeding rates. These results draw into question the generality of results from studies based on static models and add to the growing body of literature that has explored fear-effects on coral reefs, with results ranging from strong (e.g. Rizzari et al., 2014) to negligible (our case). Clearly, the strength of shark-mediated fear effects appear to be context-dependent on coral reefs, with evidence for significant suppression of herbivore grazing due to fear effects remaining equivocal.

CRediT authorship contribution statement

Sterling B. Tebbett: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sasha I. Faul:** Writing – review & editing, Investigation, Conceptualization, Methodology. **David R. Bellwood:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106442.

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