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Reef-wide evidence that the presence of sharks modifies behaviors of teleost mesopredators

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Abstract. The idea that the presence of sharks impacts the behavior of mesopredatory reef fishes is controversial and lacks clear evidence at reef-wide scales. We compared the abundance and behavior of these reef fishes in response to the presence of reef sharks using Baited Remote Underwater Video System (BRUVS) deployments in two adjacent reef systems where sharks have either been exclusively targeted by fishing or protected by a no-take marine reserve. For a subset of videos, we also compared the behavior of mesopredatory reef fishes immediately before and after the appearance of sharks in the video. On reefs where sharks were more abundant, mesopredatory fishes spent less time swimming in midwater (i.e., away from shelter) and guarding bait compared to reefs where sharks have been selectively removed. The same responses occurred after the appearance of sharks in the video. Reactions to sharks varied both in strength and type among species of mesopredator and were mediated by the availability of shelter on the reef and, for one species, by the levels of activity of the reef sharks. In contrast, we did not find that the presence of sharks influenced the abundance of mesopredators at either reef system across hour-long videos or immediately before and after a shark appeared in the video. Collectively, our findings show that the presence of sharks reduces the propensity of mesopredatory fish to engage in potentially risk-prone behaviors over large spatial scales and that these interactions are mediated by the behavioral characteristics of both predators and prey, and the environment in which they co-occur. Our results are consistent with the idea that sharks as predators or larger competitors initiate changes in the behavior of mesopredatory reef fishes likely to affect trophic structuring within coral reef ecosystems.

Key words: competition; coral reef; fishing; predator–prey interactions; shark; teleosts.

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INTRODUCTION

Predators can exert powerful non-lethal effects on their prey (Brown and Kotler 2004). Behavioral changes by prey that aim to reduce the likelihood of predation, such as increased vigilance, can have negative impacts on prey physiology, energy acquisition, and reproductive output (Boonstra et al. 1998, Sheriff et al. 2009, Oufiero et al. 2011). Ultimately, this can alter energy flows and structuring of communities (Schmitz et al. 2004, Creel and Christianson 2008) across lower trophic levels (Ripple and Beschta 2012, Atwood et al. 2015, Madin et al. 2019). Such alterations in behavior can also occur in small, subordinate carnivores in response to the threat of potentially lethal interactions with larger, dominant competitors of the same or other species (Polis et al. 1989, Palomares and Caro 1999). For example, African wild dogs (*Lycaon pictus*) reduce kleptoparasitic or potentially lethal interactions with larger carnivores via spatial or temporal avoidance of competitively dominant species (Dröge et al. 2017). Given that most ecosystems generally support multiple species of carnivores of a range of sizes, such competitive interactions are ubiquitous and can influence ecosystem structures and functioning in the same way as the threat of predation (Caro and Stoner 2003).

In coral reef systems, the study of behaviors that are likely to be influenced by the risk of predation has largely been confined to small-bodied (>10 cm TL) species that are amenable to manipulation in captive environments (Ferrari et al. 2010, Palacios et al. 2015) or manipulation of predator abundance on patch reefs (Stallings 2008). Some recent work has also used life-sized models of predators to evoke anti-predator/competitor responses in larger herbivorous or mesopredatory reef fishes (Rizzari et al. 2014, Lester et al. 2020). Such experiments are limited both by scale and situation, as they are logistically complex to construct and are thus difficult to replicate among reefs or habitats. This is important because the threat posed by a larger predator can vary with the structural complexity of a habitat, which can provide a refuge for prey or smaller competitors (Madin et al. 2011). Because habitats are patchy, most environments thus consist of a mosaic of both relatively safe and risky areas (the landscape of fear; Laundré et al. 2001) that may influence prey and competitor behavior depending on the perceived level of threat (Heithaus et al. 2008, Smith et al. 2019). Furthermore, the size of prey relative to the size of a predator can also influence the propensity of prey to exhibit anti-predator behaviors. In both terrestrial and marine systems, mortality from predation decreases as body size increases (Sinclair et al. 2003, Cohen et al. 2003). Most predatory fishes ingest food whole (Mihalitsis and Bellwood 2017), so that once prey reach a certain size, they become somewhat invulnerable because of gape-limited predation (Meekan et al. 2018). Individuals larger than this size threshold may not exhibit anti-predator behaviors in the presence of a predator. Instead, these mesopredators may respond to a larger predator as a competitor, rather than potential prey. Conversely, very small prey may also occupy a size refuge to predation because they are relatively cryptic and can be metabolically less profitable to target than larger prey, making them less attractive to predators (Catano et al. 2016).

At larger spatial scales, observational studies provide an alternative to experimental approaches for documenting interactions between sharks and teleost mesopredators. Because these animals often react to the presence of a diver, baited remote video systems (BRUVS) offer an effective means of sampling this community. Furthermore, BRUVS can be deployed across large spatial scales encompassing multiple habitats and preferentially sample predatory species including sharks and large fishes, which are attracted together into the field of view of the camera by the bait. This allows a study to sample multiple species and size classes of predators that are not amenable to captive experiments, across a range of habitats, while at the same time avoiding the potentially confounding presence of an observer (Goetze et al. 2017). Anti-predator and competitive behaviors of mesopredators can be quantified by comparing their behavior prior to and after the appearance of sharks and other large predators in the video, or by comparing behaviors in deployments with and without the presence of sharks. Because the technique is cost effective and easily replicable, it also offers the opportunity of sampling at reef system scales. This allows observations to encompass habitats with differing abundances of reef predators, such as management zones (marine protected areas) and reefs where large predators have been selectively removed due to fishing or have recovered following extirpation. This can provide insights into the impact of anthropogenic threats such as fishing on the trophic interactions and behaviors of predator communities on reefs.

Here, we use this approach to examine evidence for anti-predator and competitive behaviors of mesopredator assemblages in the presence of sharks on the coral reefs of NW Australia. We assume that anti-predator behaviors exhibited by these fishes are likely be similar to those of mesopredators in other systems, where many species display avoidance behavior where the threat of predation is high. For example, elk avoid habitats occupied by wolves (Ripple and

Beschta 2012), dugongs avoid habitats occupied by tiger sharks (Wirsing et al. 2007) and southern stingrays spend more time interacting with baited video systems in shallow habitats where interactions with predatory reef sharks are less likely (Bond et al. 2019). Similarly, mesopredators may choose to occupy habitats that provide better shelter from predators or may be displaced from optimal habitats when there is a higher of risk of predation or competition (Thaker et al. 2011). For these reasons, we focused on abundance, proximity to shelter, and interspecific interactions as behaviors of mesopredatory fishes that were likely to respond to the threat of predation and/or competition.

In order to expand the relevance of our study to a larger spatial scale (hundreds of km), we sampled across two large reef systems that differed in the abundance of reef sharks. The Rowley Shoals and the Scott Reefs are atoll-like reefs that have similar biological, physical and environmental conditions. The Rowley Shoals is a strictly enforced no-take marine reserve established for more than 30 yrs, whereas the shark assemblage of the Scott Reefs has been targeted by fishing for centuries. As a consequence, reef sharks are ~4 times more abundant on the Rowley Shoals than the Scott Reefs (Ruppert et al. 2013, Speed et al. 2018); a difference that is correlated with changes in the abundance, trophic role, and morphology of mesopredatory fishes between these reefs (Barley et al. 2017*a*, *b*, Hammerschlag et al. 2018). At present, it is not known if these differences in mesopredator communities also extend to, or in some cases could be explained by, anti-predator and competitive behaviors. We predicted that the magnitude of any behavioral modification of mesopredators in response to the presence of larger predators will be stronger at the Rowley Shoals, where reef sharks are more abundant, compared to the Scott Reef, where reef shark populations have been selectively removed.

METHODS

Study area

The Scott Reefs (14°0′ S, 121°45′ E) are located ~260 km off the coast of Australia on the edge of the continental shelf. Indonesian fishers have targeted sharks on these reefs for the trade in shark fin for more than two centuries (Russell and Vail 1988). This practice continues today under a Memorandum of Understanding with the Australian Government, where Indonesian fishers are permitted to target sharks at the Scott Reefs using traditional techniques. Fishers also collect a small amount of reef fishes for food.

The Rowley Shoals are also located on the edge of the continental shelf, ~400 km southwest of Scott Reefs, and consist of three large reefs: Imperieuse, Clerke, and Mermaid. They are a well-enforced no-take marine reserve that was established in 1990 and permit only a small amount of charter fishing that mostly targets large pelagic game fish (Speed et al. 2018). Compliance is enforced by regular visits to Rowley Shoals by the Department of Primary Industries and Regional Development. These reefs act as a baseline for intact shark populations in the region of the eastern Indian Ocean (Speed et al. 2018).

Data collection

BRUVS and stereo-BRUVS were deployed around Scott Reef North, Scott Reef South, Imperieuse and Clerke Reefs in September 2016 as part of the Global FinPrint Project (MacNeil et al. 2020; Fig. 1). Totals of 57 and 97 BRUVS were deployed at the Rowley Shoals and Scott Reefs, respectively. These deployments were randomly placed along reef contours in shallow habitats (between 10 m and 30 m depths) and spaced approximately 400 m apart to minimize the overlap of bait plumes. Once on the reef, the BRUVS recorded 60–90 min of video before being retrieved. For full details of deployments see Speed et al. (2018). Of these 154 deployments, 75 were stereo-BRUVS (Rowley Shoals, 28 deployments; Scott Reefs, 47 deployments). Unlike BRUVS, which consist of a single camera, stereo-BRUVS have two cameras on a base bar separated by 70 cm and positioned inwards at an angle of 8 degrees. This configuration allows accurate measurements of distance and size of objects in images recorded by the camera (Harvey and Shortis 1995).

Video analysis

The videos from the BRUVS and stereo-BRUVS deployments were analyzed to test whether the presence of sharks altered the abundance of mesopredatory fish over the entire

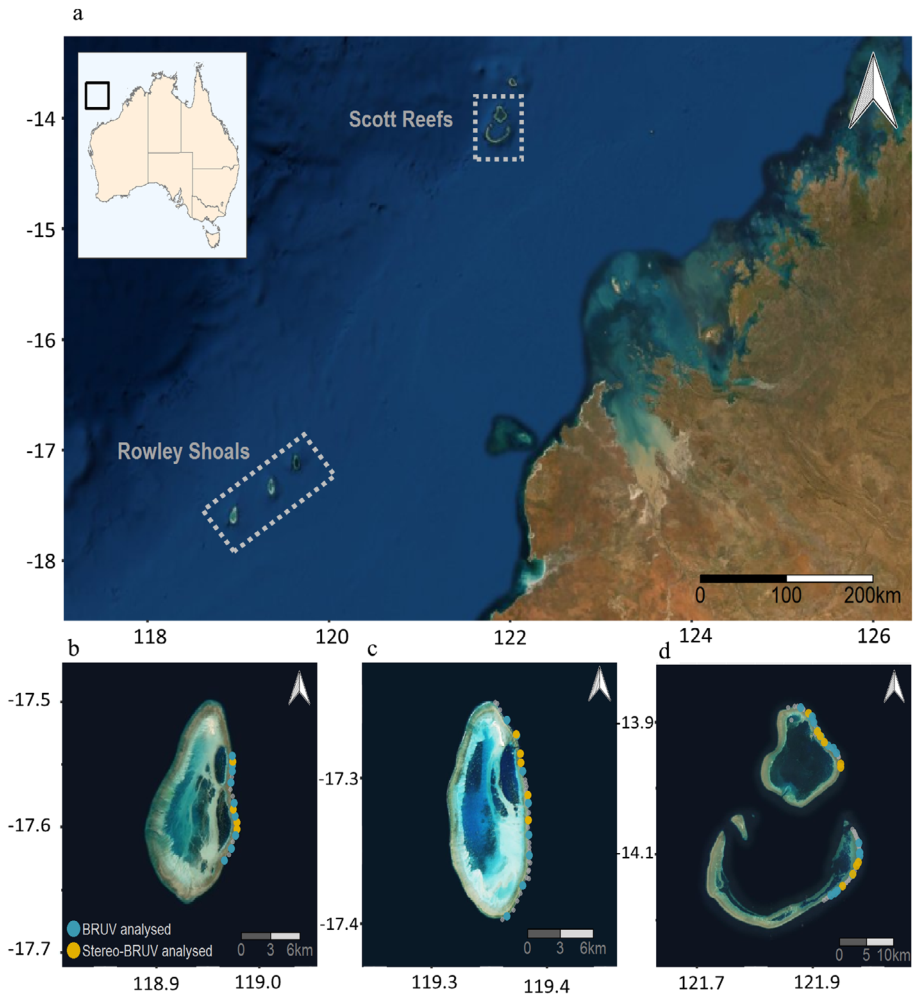

Fig. 1. Northwest region of Australia indicating (a) the location of the Scott Reefs and Rowley Shoals including study site and maps of Stereo-BRUVS and BRUVS deployed by Speed et al. (2018) at (b) Imperieuse Reef, (c) Clerke Reef, and (d) Scott Reefs. Stereo-BRUVS deployments used in our study are shown in yellow, the BRUVS deployments in blue. Gray points show other deployments.

duration of the deployment (60 min), and whether the presence of sharks induced short-term changes in the abundance and behavior of mesopredatory fish in the five minutes immediately following the arrival of a shark. All 154 deployments were initially analyzed for the presence of sharks. Of these videos, a subset of 10 BRUVS videos with sharks present and 10 videos with sharks absent were randomly selected from each of the Scott Reef and the Rowley Shoals deployments, resulting in a total of 40 videos. In these videos, we recorded the MaxN, which is the maximum number of fish observed of any given species in a single frame (Ellis and DeMartini 1995, Willis and Babcock 2000) of each species of mesopredatory fish. All mesopredatory fishes present in the video were categorized into small (≤50 cm TL), medium (50–100 cm TL), and large (>100 cm TL) size classes according to regional estimates of maximum length (TL) on Fishes of Australia (http://fishesofaustralia.net.au; Bray and Gomon 2018) and FishBase (www.fishbase.org; Froese and Pauly 2011, Roff et al. 2019).

To test whether the presence of sharks influenced the behavior and abundance of mesopredatory fishes over short time scales, we analyzed videos from stereo-BRUVS deployments. Those with an unobscured field of view and where a shark was present in some part of the video were used for this analysis, whereas videos where sharks were not present and those that had significant portions of the field of view obscured were excluded. This resulted in 19 videos that we analyzed in two segments: five minutes preceding and the five minutes following the appearance of a shark in the field of view. We choose five-minute segments as this is the amount of time that the behavioral changes induced by sharks are anticipated to persist in other fish species (Klages et al. 2014). In each segment, we recorded the presence of serranids, lutjanids, and lethrinids, the three most abundant families of mesopredators at the Scott Reefs and Rowley Shoals. Species that are difficult to identify from BRUVS were pooled into a single group with other, similar species of the same family. These included *Macolor niger* and *Macolor macularis* (Macolor sp), *Lethrinus olivaceus* and *Lethrinus microdon* (Lethrinus sp), *Monotaxis grandoculis* and *Monotaxis heterodon* (Monotaxis sp), and *Plectropomus laevis* and *Plectropomus maculatus* (Plectropomus sp).We focussed on five species, *Lutjanus bohar, L. decussatus, L. gibbus, Plectropomus spp.,* and *Epinephelus fuscoguttatus* as these occurred in sufficient numbers for analysis. We measured relative abundance of these five species before and after the arrival of a shark in the video using the metric MaxN.

In each of these 5-minute video segments, we measured the fork length and the behavior of each individual of the five mesopredatory reef fishes. We recorded the total time that an individual remained in the field of view and the amount of time spent in midwater (>70 cm above the benthos), near the benthos (<70 cm above the benthos), under shelter and the amount of time an individual spent guarding the bait bag (defined as an individual positioned above the bait bag). Height in midwater was calculated from the distance between the individual and a point on the benthos directly below it at the same distance from the camera. The species and fork length of shark and the number of bites it took from the bait bag were also recorded. All image analysis was conducted using Eventmeasure software (http://seagis.com.au).

Habitat classification

Habitat and vertical relief were analyzed in the program TransectMeasure (http://www.seagis.com.au/transect.html) following the method outlined in McLean et al. (2016). A 5 × 4 grid was overlaid on a high definition image for every individual stereo-BRUVS deployment. The dominant habitat type and relief was characterized within each rectangle using the CATAMI classification scheme (Althaus et al. 2015). Habitat was categorized into hard corals, macroalgae, unconsolidated (sand/rubble), consolidated (rocky bottom), and soft corals. Grid rectangles that were oriented to open water were classified as no biota and removed before analyses. Relief was categorized from 0 (low) to 5 (high) based on Wilson et al. (2007), and values averaged across grids for each deployment. Data were extracted from TransectMeasure software using R code available in Collins et al. (2017).

Statistical analysis

The influence of shark presence on the fish assemblage throughout the entire 60-minute video was tested with PERMANOVA (Anderson et al. 2008). A total of 32 species of mesopredatory fishes were included in this analysis (Appendix S1: Table S1; small size class, 9 species; medium size class, 16 species; large size class, 8 species). We analyzed two factors: shark presence (fixed with two levels: shark present and shark absent) and site (random with four levels: Imperieuse, Clerke, Scott Reef North and Scott Reef South) nested in location (fixed with two levels: Scott Reef and Rowley Shoals; Anderson et al. 2008). This analysis was run for each separate size class of mesopredatory fishes (small, medium and large). For each analysis, Bray-Curtis distances were generated for untransformed data.

The influence of location (the Scott Reefs, Rowley Shoals), continuous habitat covariates (standard deviation of relief, reef cover), shark presence (before or after shark arrival), size of the mesopredator relative to the shark, and the species of shark on the relative abundance of the five mesopredatory fish (MaxN) was analyzed using generalized additive mixed effects models (GAMMs; Lin and Zhang 1999). To account for repeated measures from a single video, we included stereo-BRUVS deployment as a random effect (Harrison 2015). Model selection was based on Akaike Information Criterion (AIC; Akaike 1998) and AIC weights (wAIC; Burnham and Anderson 2004). A full-subsets method was used to fit models of all possible combinations up to a maximum of three independent variables to prevent overfitting (Fisher et al. 2018). The wAIC, which represents probabilities or weights of evidence for each model, was used to aid interpretation of results and identify the best model. Since this analysis generated support for the null model, a separate PERMANOVA was run to test the short-term influence of shark presence on the MaxN of the five most abundant mesopredatory fishes (*Lutjanus bohar*, *L. decussatus*, *L. gibbus*, *Plectropomus* spp., and *Epinephelus fuscoguttatus*). The video was separated into two segments: five minutes before the shark arrived on the video and five minutes immediately after the shark arrived on the video. These two segments of each video were analyzed in a repeated measures design; shark presence (fixed with two levels: shark present or shark absent), location (fixed two levels: Scott Reefs or Rowley Shoals), site (random with four levels: Clerke, Imperieuse, Scott Reef North and Scott Reef South), and stereo-BRUVS deployment (random with 19 levels). Site was nested in location, shark presence was nested in location and site, and stereo-BRUVS deployment was nested in location, site, and shark presence.

To analyze the behavior of mesopredatory fishes in the five minutes before and the five minutes following the presence of sharks in the videos, the influence of location, continuous habitat covariates, shark presence, size of the mesopredator relative to the size of the shark, species of shark, the number of shark bites on the bait bag, and mesopredator abundance (MaxN; Table 1) on the percentage of time mesopredators spent in midwater and the percentage of time mesopredators spent guarding the bait bag were analyzed using generalized additive mixed effects models (GAMMs; Lin and Zhang 1999). Only three species (*L. bohar*, *L. gibbus,* and *E. fuscoguttatus*) occurred in sufficient numbers in the videos for analyses of behavior. To account for repeated measures in a single video, we included stereo-BRUVS deployment as a random effect (Harrison 2015). Model selection was based on Akaike Information Criterion (AIC; Akaike 1998) and AIC weights (wAIC; Burnham and Anderson 2004). A full-subsets method was used to fit models of all possible combinations up to a maximum of three independent variables to prevent overfitting (Fisher et al. 2018). Models with AIC values that differ by less than two units show weak evidence for favoring one over the

Table 1. Dependent and independent variables included in generalized additive mixed effects models.

Variable	Description
Dependent variables	
Time spent in midwater	Percentage of time in the field of view spent >70 cm above the benthos
Time spent guarding bait bag	Percentage of time spent in the field of view positioned immediately next to or above the bait bag
Independent variables	
Mean relief	Mean relief describes the mean height and rugosity of the benthos. Scores range between 1 and 5, where a score of 1 indicates a flat surface and 5 a rock wall
Standard deviation relief	Standard deviation of relief scores
Reef cover	The summed percentage cover of hard coral, soft coral, macroalgae, sponges and unconsolidated habitat (rubble and rocks)
Relative size	Size of the mesopredator (measured by fork length) relative to the size (fork length) of the shark present in the video
Mesopredator abundance	The sum MaxN of mesopredatory fish in the five-minute segments of video before or after sharks were present
Shark presence	Whether a shark was present or absent in the five-minute segment of video
Location	Location of BRUVS deployment. Scott Reef or Rowley Shoals
Shark species	The species of shark *(Carcharhinus amblyrhynchos* or *Triaenodon obesus*) that was present in the video
Number of shark bites	The number of bites of the bait bag

other (Burnham and Anderson 2002). The most parsimonious model was considered to be the model with the fewest variables and lowest estimated degrees of freedom. The wAIC was used to aid interpretation of results. Summed AIC weights were used as a metric of variable importance of each predictor variable across all sets of models (Anderson and Burnham 2002). Although parsimony is useful for hypothesis testing, in the current study we also used importance scores to explore the relationship of all considered predictors and therefore to make broader ecological interpretation not limited to parsimony. We therefore explored and plotted additional models that were highly ranked by $\mathrm{AIC_c}$ (<2 delta $\mathrm{AIC_c}$) and included variables found to be important across all models.

Prior to analysis, the category of unconsolidated habitat was excluded due to strong collinearity with reef cover. Given the high levels of overdispersion, models were fitted to untransformed data using a Tweedie error distribution (Tweedie 1984). The R language for statistical computing (R Core Team 2017) was used for all data manipulation (dplyr, Wickham et al. 2020), analysis (mgcv, Wood 2017), and graphing (ggplot2, Wickham 2016; ggpubr, Kassambara 2020; cowplot, Wilke et al. 2019). Models were constructed, fitted, and compared using the FSSGam package (Fisher et al. 2018).

Results

Mesopredator abundance across 60-minute BRUVS deployments with and without sharks

Two species of sharks were observed (*Carcharhinus amblyrhynchos* $n = 36$ and *Triaenodon obesus* $n = 30$), in the subset of 40 videos where sharks were either present and absent across the entire 60-minute soak time (Appendix S1: Table S2). The presence of sharks did not significantly influence the abundance of mesopredators in any size class. (PERMANOVA, small, Pseudo-$F_{1,34} = 1.57$, $P = 0.13$; medium, Pseudo-$F_{1,35} = 0.96$, $P = 0.52$: large, Pseudo-$F_{1,26} = 1.14$, $P = 0.34$).

Shark assemblages in the stereo-BRUVS deployments

The same species of sharks (*Carcharhinus amblyrhynchos* $n = 7$ and *Triaenodon obesus* $n = 12$) were observed in the 19 Stereo-BRUVS deployments. The fork lengths of these sharks ranged from 63.1 to 96.7 cm (mean = 73.4 ± 7.7 cm) at the Scott Reef and from 75.4 to 110.9 cm (mean = 92.4 cm ± 14.7 cm) at the Rowley Shoals.

Mesopredatory fishes five minutes before and after shark arrival

A total of 336 fishes of the five target species (*Lutjanus bohar* $n = 164$, *L. decussatus* $n = 16$, *L. gibbus* $n = 75$, *Plectropomus* spp $n = 45$ and *Epinephelus fuscoguttas* $n = 36$) were observed in the 10 min segments of videos. The sizes of mesopredatory fishes ranged from 24.1 to 57.6 cm (mean = 38.3 ± 6.1 cm) at the Scott Reefs and from 29.8 to 68.5 cm (mean = 43 ± 7.6 cm) at the Rowley Shoals. Mesopredators ranged from 30% to 85% of the size of the shark appearing in the same video (Fig. 2). The arrival of a shark did not have a significant effect on the short-term (5 min) abundance of mesopredatory fishes (PERMANOVA, Pseudo-$F_{1,29} = 0.27$, $P = 0.89$; Appendix S1: Fig. S1).

Percentage of time spent in midwater

The most parsimonious model for the percentage of time that *L. bohar* spent in midwater was a

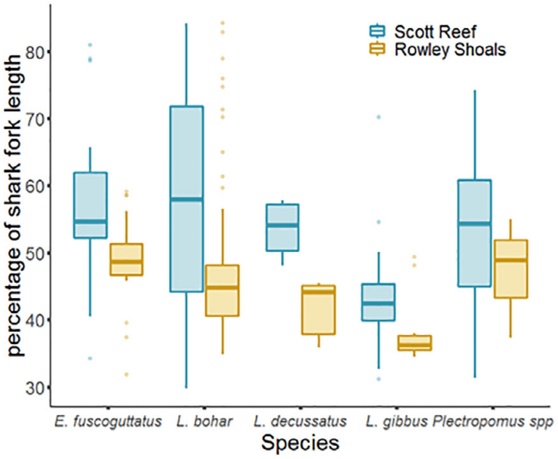

Fig. 2. Fork length of *Epinephelus fuscoguttatuss*, *Lutjanus bohar, L. decussatus, L. gibbus,* and *Plectropomus spp* relative to the fork length of the shark observed in same video segment from stereo-BRUVS deployed at the Scott Reef and Rowley Shoals.

Table 2. Top generalized additive mixed models (GAMMs) for predicting the percentage of time spent in midwater for two species of mesopredatory fishes (*L. bohar* and *L. gibbus*) and percentage of time spent guarding bait bag for the mesopredator species (*E. fuscoguttatus*) at the Scott Reefs and the Rowley Shoals.

Taxa	Best models	R^2	EDF	$\Delta\mathrm{AIC_c}$	$\omega\mathrm{AIC_c}$
Time spent in midwater					
L. bohar	**Mean Relief + Location + Shark presence**	**0.12**	**5**	**0**	**0.10**
	Standard Deviation Relief + No. Shark Bites + Shark Presence	0.13	5.79	0.64	0.08
	Location + Mean Relief x Shark presence	0.14	6.09	0.69	0.07
	No. Shark Bites + Location + Shark Presence	0.11	5.18	0.89	0.06
	No. Shark Bites + Standard Deviation Relief x Shark Presence	0.15	7.44	1.51	0.05
	Mean Relief + Location	0.08	4	1.59	0.05
L. gibbus	**No. Shark Bites + Location**	**0.23**	**4**	**0**	**0.37**
	Relative Size + No. Shark Bites + Location	0.26	5	0.65	0.27
Time spent guarding bait					
E. fuscoguttatus	**Mean Relief + Location x Shark presence**	**0.54**	**6**	**0**	**0.32**
	Relative Size + Shark Presence	0.60	6.42	1.91	0.12

Notes: Difference between lowest reported corrected Akaike Information Criterion ($\Delta\mathrm{AIC_c}$), AIC weight ($\omega\mathrm{AIC_c}$), variance explained (R^2) and effective degrees of freedom (EDF) are reported for model comparisons. Model selection was based on the most parsimonious model within two units of the lowest $\mathrm{AIC_c}$ that had the least parameters. Models ordered by parsimony. Bold values indicate models that were highly ranked by $\mathrm{AIC_c}$ and included variables found to be important across all models.

two-factor model that included mean relief and location (Table 2). There was also strong support (within 2 AIC of the top model) for a three factor model that included mean relief, location and shark presence (Fig. 3a). Model predictions suggested that *L. bohar* spent a smaller percentage of time (~10%) in the midwater at the Rowley Shoals compared to the Scott Reef. The presence of a shark affected the behavior of this species across both reef systems, and *L. bohar* reduced the percentage of time spent in midwater once sharks appeared in the video (Fig. 4b). The percentage of time spent in midwater was also related to the complexity and relief of the benthos, with this species spending a greater percentage of time in midwater at increasing levels of mean relief (Fig. 4c).

The most parsimonious models for the percentage of time that *L. gibbus* spent in midwater included the number of bites that the shark took from the bait bag and location (Table 2). Importance scores also indicated some weak support for the size *of L. gibbus* relative to the size of the shark present in the same video (Fig. 3a). The percentage of time that *L. gibbus* spent in midwater was ~30% less at the Rowley Shoals compared to the Scott Reefs (Fig. 4e). In addition, there was a negative correlation between the percentage of time *L. gibbus* spent in midwater and the number of bites that sharks took from the bait bag (Fig. 4d).

Percentage of time mesopredators spent guarding bait bag

Only *E. fuscoguttatus* spent any appreciable time guarding the bait bag in the videos. The presence of a shark was identified as the most important variable influencing this behavior and was included in both top models (Fig. 3b). The most parsimonious model contained an interaction between reef system and shark presence (Table 2), with the time spent guarding the bait bag declining after a shark appeared in the field of view, but the magnitude of this decline being greater at the Rowley Shoals than the Scott Reefs (Fig. 4g). Mean relief was also identified as an important variable across top-ranked models (Fig. 3b), with *E. fuscoguttatus* spending a greater proportion of time guarding the bait bag as mean relief increased (Fig. 4f).

DISCUSSION

We found that the behaviors of mesopredatory fishes altered in response to the presence of reef sharks. In contrast, we did not find that the presence of any sharks influenced the abundance of common mesopredators in either hour-long videos or in the five-minute segments immediately before and after a shark appeared in video. As expected, the behavioral responses of mesopredators were dependent on the species of mesopredator and were mediated by the

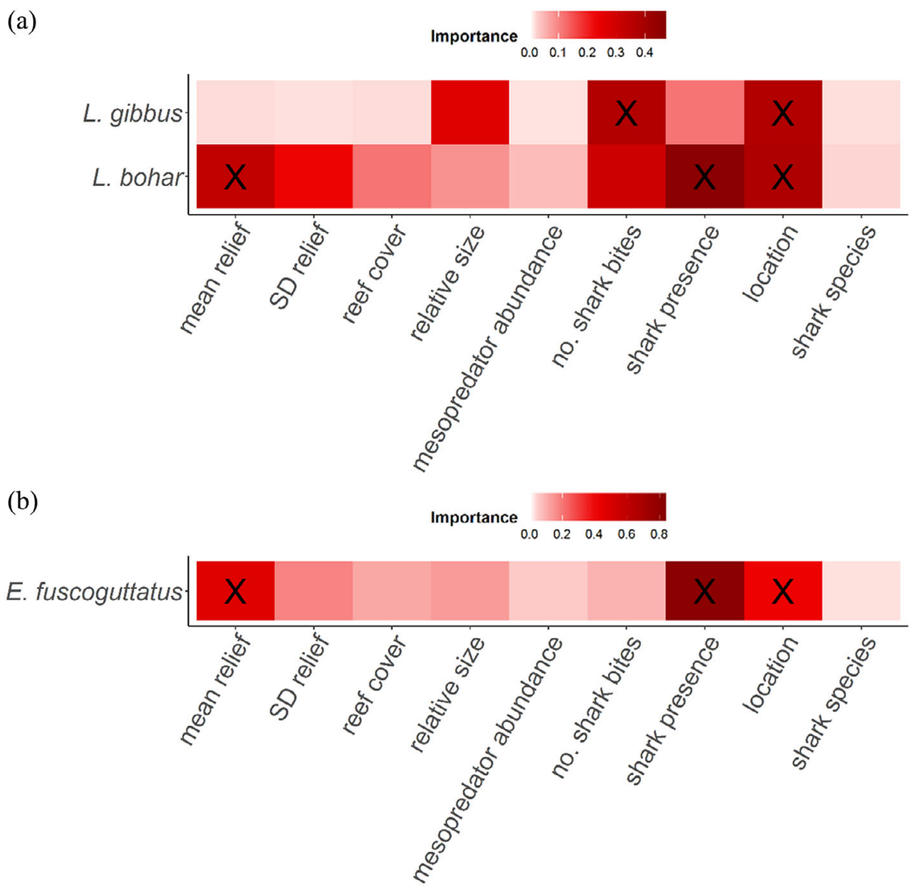

Fig. 3. Importance scores based on summed Akaike weights from full-subsets analysis exploring the influence of nine explanatory variables on (a) the percentage of time spent in midwater by *Lutjanus bohar, L. gibbus* and (b) the percentage of time spent guarding the bait bag by *Epinephelus fuscoguttatus*. A value of 1 indicates that the influence of a variable is high whereas a value of zero indicates no importance. X indicates variables that were included in the most parsimonious model (see Table 2).

availability of shelter on the reef and for one mesopredator, by the levels of activity of the reef sharks. For both *Lutjanus gibbus* and *L. bohar*, the key response to the presence of a shark was a reduction in the amount of time spent swimming in midwater. For *L. bohar*, this change was relatively small (10%), but for the smaller *L. gibbus* time spent in midwater was reduced by over 30%. A primary response of mesopredators to retreat toward shelter near the reef is consistent with the results of a recent study by Lester et al. (2020) who found that many of the same species of mesopredators were more sensitive to the threat of larger predators on a vertical than on a horizontal axis when feeding away from the shelter of a patch reef. They attributed this to the likelihood that predators were able to identify the silhouettes of fishes in midwater, making them vulnerable to attack from below and thus more wary when feeding above the reef than on the seafloor.

It is possible that these behaviors occurred in response to both the threat of predation and to the presence of sharks as a larger and potentially lethal competitor. We did not find evidence that the size of mesopredatory reef fishes relative to the size of the reef shark present in the video influenced the propensity of mesopredators to engage in riskier behaviors. This may have been because the sharks we observed in our stereo-BRUVS deployments were relatively small, as the largest individual (116.38 cm fork length)

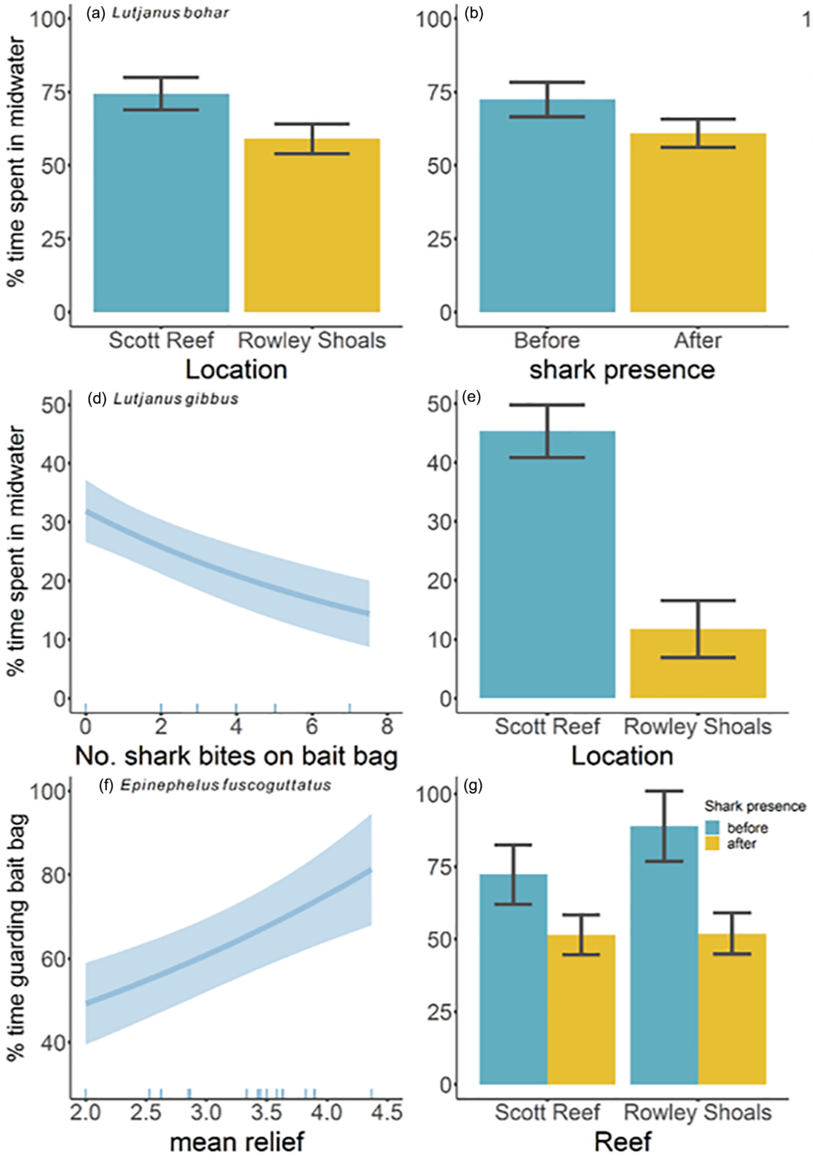

Fig. 4. Plots of the most parsimonious model for percentage of time spent in midwater for *L. bohar* (a–c) and *L. gibbus* (d–e) and the percentage of time spent guarding the bait bag for *E. fuscoguttatus* (f–g) from full-subset GAMM analyses (see Table 2). Error bars and dashed lines indicate standard error. Rug indicate spread of the raw data.

was approximately half of the maximum size recorded for *C. amblyrhynchos*, and all of the individuals of the mesopredatory species were >30% of the size of the sharks in the video (Fig. 2). At this size, mesopredators are likely to attain a refuge from gape-limited predators (Swaisgood et al. 1999, Chivers et al. 2001, Mihalitsis and Bellwood 2017). Although *C. amblyrhynchos* pose a predation threat under some circumstances (e.g., Mourier et al. 2016, Rhodes et al. 2019), their relatively small size in our study suggests that mesopredatory teleosts were responding to sharks as a competitor and rather than a predator. To reduce potentially lethal agonistic interactions or competitive exclusion by dominant competitors, subordinate species use a combination of spatial segregation, temporal segregation, or diet partitioning (Vanak et al. 2013). Our results suggest that reef sharks may evoke similar behavioral changes in mesopredatory teleosts despite the possibility of functional redundancy among species and relatively limited evidence for consumption of mesopredatory teleosts by reef sharks.

Differences in adult size may explain why these species varied in the amount to which individuals responded to the presence of a shark. *L. bohar* is a relatively large mesopredator that grows to 90 cm and there is evidence that at these sizes it may enter a refuge from predation (Barley et al. 2019). Consequently, some of the larger individuals may be less responsive to the presence of sharks, who are viewed only as competitors, rather than a potentially lethal threat. In contrast, *L. gibbus* grows only to 50 cm and is likely to be vulnerable to attack by predators at most sizes; thus, all individuals were likely to display some response. Furthermore, as larger fishes are capable of faster movement (Domenici and Blake 1997), *L. bohar* may need to make smaller adjustments of position in midwater than *L. gibbus* in order to reduce the threat of a predator or larger competitor.

Although *L. bohar* responded to the presence of sharks at the BRUVS, *L. gibbus* mostly reacted to the activity and behavior of these predators and moved toward the reef as the feeding of the sharks increased on the bait bag. There are two possible (non-exclusive) interpretations of this behavior; it may be that the increasing activity of the reef shark increased the perception of threat by *L. gibbus*, so individuals moved toward the shelter of the reef. Alternatively, or in addition, feeding by sharks offered the opportunity for these mesopredators to scavenge on scraps, bringing them down from midwater toward the vicinity of the bait bag. However, the latter seems less likely, since the willingness of *L. gibbus* to approach the bait bag did not increase in the presence of sharks and we did not record any attempts by *L. gibbus* to feed on the bait bag (Appendix S1: Fig. S2). A number of experimental studies have found that behavioral cues from predators enable prey species to respond to predation risk in a threat-sensitive manner (Karplus and Algom 1981, Swaisgood et al. 1999). For example, mosquito fish (*Gambusia holbrooki*) increased swimming speed and acceleration only when predatory jade perch (*Scortum barcoo*) became active and displayed slower swimming speeds within close proximity (Kent et al. 2019). Such threat sensitivity is also an essential attribute for mesopredators, since despite the fact that failing to respond to a threat could lead to injury or death, responding to irrelevant cues can result in lost foraging or reproductive opportunities. These combined and opposing selective pressures mean that mesopredatory species are likely to be acutely sensitive to behaviors that might result in attack by larger predators or competitors and will adjust their risk accordingly.

Unlike the lutjanids, the large serranid, *Epinephelus fuscoguttatus,* did not alter its position in midwater in response to the presence or behavior of sharks. This was not unexpected, since the species mostly swims close to the shelter of the reef. Instead, we found that the amount of guarding behavior of the bait bag declined with the arrival of sharks. Prior to this event, individuals of this species positioned themselves directly over the top or immediately adjacent to the bait bag. On occasion, they could be observed displaying to or chasing other mesopredators of the same or other species away from the bait bag. This behavior declined by 30% at the Rowley Shoals and by 20% at the Scott Reefs once sharks appeared in the video. It was also mediated by the habitat, with more guarding of the bait bag occurring where there was higher relief. This suggests that guarding was risky and that in the presence of a larger predator or competitor, access to shelter was a key variable determining the incidence of this guarding behavior.

The availability of shelter in the face of the threat of predation influences the behavior of many terrestrial and aquatic animals (Cooper and Whiting 2007, Heithaus et al. 2009, Catano et al. 2016). Individuals may be more willing to undertake otherwise risky behaviors that offer energy or reproductive gains when the opportunity for escape from the threat of predation is nearby. Both *L. bohar* and *E. fuscoguttatus* displayed behaviors that suggested that the amount of shelter available on the reef influenced risk-taking behaviors. For *L. bohar,* feeding higher in the water column may allow access to more energy-rich prey such as fishes or squid (Barley et al. 2017*a*), whereas the resource guarding behavior of *E. fuscoguttatus* is likely to ensure that individuals consume a greater proportion of available prey. Interestingly, the behaviors of *L. gibbus* in the presence of sharks were not influenced by relief. Unlike the other species that mostly occur as single individuals (*E. fuscoguttatus*) or small schools (*L. bohar*), *L. gibbus* often occurs in schools of tens to sometimes hundreds of individuals. It may be that this schooling behavior confers some protection against the threat of predation (Pitcher and Parrish 1993) irrespective of the shelter offered by the reef.

We found no evidence that the presence of reef sharks had an effect on our measures of abundance (MaxN) of all mesopredators throughout the entire 60-minute video segment nor the five species of mesopredator in the ten-minute video segments. This suggests that although the presence of sharks modified their behavior, it did not influence the likelihood of these species appearing in the field of view of the camera over the hour-long deployment. As the process of predation is energetically costly there is strong selection for facultative scavenging in nearly all mesopredators (Hammerschlag et al. 2016, Meekan et al. 2018). It may be that the bait bag stimulates this behavior, so that mesopredatory fishes tend to approach within the field of view of the cameras irrespective of the presence of larger predators such as sharks. However, our results show that once in the field of view, they do respond in predictable ways that are likely to reduce the risk of predation and/or competition. These findings are consistent with those of Coghlan et al. (2017), who also found that the presence of larger predatory fishes near a BRUVS bait bag did not influence the abundance of smaller mesopredators. In contrast, Klages et al. (2014) found some evidence that the presence of predators did alter the abundance of smaller species, although this result was both inconsistent in direction (some species increased, others declined in abundance) and among species, with many failing to respond to the presence of a larger competitor. Dunlop et al. (2015) found that larger predators reduced abundance of smaller individuals of some species, although this study used cameras that were downward facing and had a very limited field of view. In this situation, displacement of fish away from the bait bag by a few meters could have resulted in them not being recorded by cameras. In our study, the stereo-BRUVS provided a wide field of view so was less sensitive to any small-scale displacement of fishes away from the bait bag.

Our results suggested that at the Scott Reefs, where sharks have been selectively removed, behavioral responses of teleost mesopredators to the risk of predation and competition were muted compared to those of the same species inhabiting the Rowley Shoals, where populations of these predators are still intact. This outcome is contrary to predictions of the risk allocation theory (Lima and Bednekoff 1999), which suggests that animals should exhibit greatest anti-predator behaviors where risk is brief and infrequent rather than in situations where levels of risk are consistently high. However, empirical tests have provided mixed support for this theory (reviewed by Ferrari et al. 2009), possibly due to circumstances that mediate the relationship between prey boldness and background levels of predation risk (e.g., Ehlman et al. 2019). Furthermore, recent studies of juvenile lemon sharks (*Negaprion brevirostris*) have also shown that individuals from subpopulations where predator abundance was high displayed behaviors likely to reduce risk by being less exploratory and more social compared to individuals from subpopulations with low predator abundance (Dhellemmes et al. 2020). Therefore, it seems possible that an increased presence of sharks as predators/competitors may create a stronger relationship between resource acquisition and safety for mesopredatory fishes at the Rowley Shoals than at the Scott Reefs.

We cannot exclude the possibility that some other unmeasured factor might account for the differences in behavior of mesopredatory fishes we observed between the Scott Reefs and the Rowley Shoals. However, these reef systems are very similar in diversity of reef fish communities and in the physical oceanographic environments they experience. The differences in behaviors we recorded are also accompanied by contrasts in the abundance, trophic role, and morphology of mesopredatory fishes between these reefs (Barley et al. 2017*a*, *b*, Hammerschlag et al. 2018). These occur in a manner consistent with differences in reef shark abundance as a driver of such patterns. Together, this weight of evidence suggests that variation in abundance of these large predators has a predictable and measurable impact on reef fish communities across a broad range of ecological traits and processes.

CONCLUSIONS

Our study has found evidence that presence of reef sharks can change the propensity of large-bodied teleost mesopredatory fishes to engage in potentially risky behaviors over reef-wide scales. However, our results also suggest that interactions between these species are context-dependent and more nuanced than commonly assumed, as they depend upon characteristics of both predators and prey and the environment in which these interactions occur. In addition, when assessing behavioral responses to large-bodied predators or competitors across multiple species, it is likely that these species do not exhibit a uniform response. Given the substantial decline of shark populations in coral reefs and the uncertainty regarding their ecological roles in these environments, it is critical that these factors are taken into account when investigating the effects of these predators on prey populations, or we may underestimate the ecological importance of these predators.

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