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Fishing and Fear Effects Interact to Shape Herbivory on Coral Reefs

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Thesis of Bethany M. Tilton

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

December 2023

Approved:
Thesis Committee

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

Fishing and Fear Effects Interact to Shape Herbivory on Coral Reefs

By
Bethany M. Tilton

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science

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Abstract

Predation influences animal behavior and shapes ecological structure and function through lethal effects and fear effects. On coral reefs, fear effects can alter the distribution and intensity of herbivory by herbivorous reef fishes. This includes the browsing functional group, which potentially reverses macroalgal phase shifts and promotes reef recovery. Herbivory by multiple functional groups may increase on coral reefs through the use of NTZs (no-take zones) but few studies have examined the extent to which small-scale NTZs (< 0.5 km²) influence fear effects and perceived predator presence on reefs. This study aimed to determine whether fear effects on browsers on coral reefs differ between small-scale NTZs and unprotected fished reefs by documenting how browsing fishes respond to predator models stationed on four reefs: two within NTZs (Manta and Twin Peaks) and two outside of these NTZs. We found that there was significantly greater browser presence (MaxN) and total and mass standardized bites in NTZ sites compared to fished sites, and that predator model assays experienced significantly less feeding, with no significant difference between the effect of two predator models that were used. Additionally, macroalgal removal, and total and mass standardized bites differed between the two NTZs, being higher in Manta than in Twin Peaks. Ultimately, we found that small-scale NTZs can potentially result in greater browser biomass and the ecosystem function of macroalgal removal. Further research should explore the usefulness of small-scale NTZs in sustaining other ecosystem functions apart from macroalgal removal on coral reefs.

Keywords: predator-prey interactions, browsers, human impacts, predator models, no-take zones, small-scale marine protected areas, macroalgae removal, ecosystem function, phase shifts

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Introduction

Predation is a key process influencing animal behavior and species interactions, shaping ecological structure and function through both consumptive and non-consumptive effects (reviewed in Lima & Dill, 1990; Gaynor et al., 2019). Consumptive effects (or “lethal” effects) of predators can influence ecological communities and processes by killing individuals, directly removing them from the ecosystem. Predators can also alter prey behavior, physiology, or morphology (Gaynor et al., 2019) through non-consumptive effects (or “fear” effects). Importantly, fear effects may have impacts on ecosystems equal to or larger than those of lethal effects (Creel & Christiansen, 2008; Orrock et al., 2008) by changing prey foraging (Lima & Dill, 1990; Preisser & Bolnick, 2008) and habitat use patterns (Heithaus & Dill, 2002). The specific ways in which fear effects influence ecosystems depend largely on the ecological context (e.g., percent cover from predators, time of day, predator identity, protection status) which can change the specific predator avoidance strategies utilized by prey. Changes in prey (specifically herbivore) foraging and habitat use from fear effects can alter the distribution and/or abundance of herbivore populations, influencing consumption rates of primary producers, thereby influencing rates of primary production and the flow of energy through an ecosystem. On coral reefs, this in turn can drive variation in the consumption of algae across seascapes through behavioral change can result in trophic cascades, where algae is released from predation (e.g., Madin et al., 2010; Rasher et al., 2017). These cascades have the potential to cause phase shifts, thereby potentially permanently altering the function of the ecosystem as a whole (e.g., Pagès et al., 2012; Rasher et al., 2017). Consequently, behavioral changes of herbivores from fear effects have the potential to be wide-reaching across ecosystems; this is evident on coral reefs, where suppression, or release of processes such as through predation-mediated behavior are visually apparent (Madin et al., 2011; DiFiore et al., 2019).

On coral reefs, herbivorous fishes are generally classified into two broad functional groups: ‘grazers,’ which are species that feed on benthic surfaces with short algal turfs, and ‘browsers,’ which feed on large fleshy macroalgae (Green & Bellwood, 2009; Tebbett et al., 2022). Macroalgal overgrowth on coral reefs has the potential to reduce coral “resilience” – the ability of coral reefs to recover from disturbances (e.g., bleaching events and storms *sensu* Hughes et al., 2007) – by

reducing available areas for coral recruitment, thereby hindering the maintenance of relief and structural complexity on coral reefs (Graham et al., 2020). Additionally, certain macroalgae genera, *Sargassum*, may increase microbial abundance and alter microbiome community composition, suppressing coral larvae settlement (Antonio-Martínez et al., 2020; Vermeij et al., 2009). Consequently, browsers are one of the most crucial herbivores to supporting reef resilience because by consuming macroalgae they perform an important function in potentially preventing or even reversing phase shifts to macroalgal domination on reefs (dependent upon the timeframe of domination and macroalgal biomass present) and possibly promoting reef recovery (Bellwood et al., 2006; Puk et al., 2016).

Previous studies on fear effects on coral reefs have shown that changes in browser foraging behavior are often associated with spatial changes in predator presence and/or abundance (e.g., Rizzari et al., 2014; Catano et al., 2016). Areas with healthy predator populations may exhibit spatially-concentrated herbivory resulting from prey species weighing risk of predation against their need to forage (Creel et al., 2005; Creel & Christiansen, 2008). On reefs, this may result in “grazing halos” caused by herbivorous species remaining close to cover due to fear of predation (Madin et al., 2011, 2016). In a fear-dominated reef system, we could see effects similar to those of removing prey species entirely – “hot spots” of fear where prey species avoid foraging altogether (Rasher et al., 2017). Fear effects may also decrease foraging rates, as prey avoid foraging at times or places where predators are likely to be present, ultimately decreasing net primary producer removal (Brown & Kotler, 2004; Lima & Bednekoff, 1999). Consequently, removal of predators through overfishing may result in significant changes to herbivore behavior and primary producer abundance (Rasher et al., 2017).

Overfishing has long been a significant problem on coral reefs, causing reductions in predator (Pauly et al., 1998; Jackson et al., 2001) and prey populations (Edwards et al., 2014; Mumby, 2016; Wakwella et al., 2020) on coral reefs. Overfishing has been shown to lead to an increase in macroalgal cover on some coral reefs (Hughes, 1994), which can reduce reef resilience, leading to a decreased coral cover (Hughes et al., 2010). Macroalgal dominance on coral reefs may be mitigated by implementing Marine Protected Areas (MPAs), which are protected from fishing. MPAs regulate fishing, and certain types of MPAs, known as no-take zones (NTZs) ban fishing

entirely. Protection may also significantly increase macroalgae removal by leading to greater browser abundance in regions where browsers are target species for fishermen and fisheries. There is some evidence that NTZs can effectively restore exploited reef fish populations (e.g., MacNeil et al., 2015), cause higher net herbivory on reefs (Mumby et al., 2006), and result in greater fish size and abundance (Edgar et al., 2014; Pereira et al., 2017); however, current research does not yet clearly support NTZs as effective conservation tools for benthic communities and ecosystems as a whole (particularly those NTZs which cover less than 100 km²; Graham et al., 2020; Strain et al., 2018). Despite this, NTZs may lead to significantly greater herbivory rates and coral cover within the protected area than outside it over the course of several years (e.g., Bonaldo et al., 2017; Mellin et al., 2016).

There has been extensive research examining fear effects on coral reefs and their effect on macroalgal removal (reviewed in Mitchell & Harborne, 2020). However, there is little research examining fear effects in fished areas and NTZs (especially small-scale NTZs), which likely contain large predators whose presence may alter macroalgal removal. NTZs offer an ideal experimental manipulation to investigate interactions between larger coral reef predators and prey, and how these interactions impact reefs. I aimed to determine whether fear effects on browsing herbivorous fishes differs between small-scale NTZs and unprotected, fished areas in Negros Occidental, central Philippines. I also aimed to determine how predator presence may influence removal rates by investigating the effectiveness of small-scale NTZs (< 0.5 km²) in sustaining the key ecosystem function of macroalgal removal. I hypothesized: (i) that browser bite rates and macroalgal removal would be higher in fished areas compared to small NTZs; and (ii) that feeding rates would not differ between predator models and control treatments in fished areas but would in NTZs due to lack of familiarity with large predators in the former compared to the latter.

Methodology

Site description and species

This study was conducted in May 2019 on coral reefs surrounding Danjugan Island in Negros Occidental, central Philippines (9°52'N, 122°22'E; Figure 1). Danjugan is a small (0.43 km²), low-lying, limestone island situated on the west coast of southern Negros with relatively diverse (~278 species) and abundant (~39% cover across reefs) coral communities (Harborne et al., 1996; Wright, 2022). The Danjugan Island Marine Reserve and Sanctuaries (DIMRS; PRRCFI, 2004), established in 2000, includes three small NTZs (each less than 20 hectares), termed “special management areas” (SMAs). Small-scale artisanal fishing with gill nets, spears, and hooks and lines is regulated within the reserve but prohibited within the SMAs (Beger et al., 2004; PRRCFI, 2004).

Four reef sites were selected within the DIMRS to quantify how acute fear effects shape browsing rates (estimated) and the removal of macroalgae (realized ecosystem function; Figure 1). Manta and Twin Peaks are protected from fishing, whereas Bamboo Bridge and Tabon Beach reefs are regularly fished. All four reefs have a well-defined reef crest at 5–6 meters depth, where coral cover ranges from 13.9–39.9% and macroalgae cover is low at 6.7–9.2% (Bauman unpublished data). Manta and Tabon Beach reefs are contiguous, while both Twin Peaks and Bamboo Bridge are isolated by either large areas of sand or other habitat. Each experimental replicate consisted of a series of individual *Sargassum polycystum* assays positioned near two predator models – a leopard coral grouper (*Plectropomus leopardus*, 53 cm total length, TL) and a mangrove snapper (*Lujanus argentimaculatus*, 42 cm TL) – to simulate acute predation risk, and two experimental controls (i.e., object control and herbivore exclusion). The object control (53 cm length of PVC, 8 cm in diameter) was used to account for the effect of introducing a novel object (the predator models and assays) in the water on the reef, and an herbivore exclusion cage (30 cm radius, 100 cm height, 0.5 cm plastic mesh) enclosing an individual assay was used to account for autogenic losses due to handling losses and translocation. *Plectropomus leopardus* was selected because this species is common across the region of Danjugan (Januchowski-Hartley, pers comm), has a broad diet including many herbivorous fish (St. John, 1999), and is commercially valuable in the Philippines (Burgess et al., 2019). Importantly, predator models of this species of similar and larger

sizes (i.e., 48–76 cm TL) have been shown to influence browser foraging behavior (Rizzari et al., 2014; Bauman et al., 2019; 2021). *Lutjanus argentimaculatus* was selected because it has high economic value in Asian coastal fisheries (Leu et al., 2003) and because it is a relatively common piscivorous fish (Abbas et al., 2011) in the study area (Bauman unpublished data). These species were also chosen because they utilize similar hunting strategies on reefs (ambush predation; Gibran, 2007; Chi, 2017). *Sargassum polycystum* was selected because it is one of the most abundant *Sargassum* species on Danjungan reefs, where it can form large monospecific stands (Calumpong et al., 1999).



Figure 1. Map showing study sites on Danjungan Island (Moray was not included in this study). SMAs are outlined with dotted lines. Image taken from Robert Suntay.

Experimental design

Sargassum polycystum (hereafter ‘*Sargassum*’) thalli of similar heights (mean 45 cm) were collected daily from a nearby shallow reef flat adjacent to Tabon reef. Individual thalli were spun in a mesh bag for approximately 30 seconds to remove excess water and the wet weight recorded

to 0.1 g. The initial mass (mean \pm SE) of each thallus was 98.0 ± 8.7 g. For each experimental replicate, five assays were randomly allocated to one of five treatments: two predator treatments (*P. leopardus* and *L. argentimaculatus* predator models), a negative control treatment (i.e., predator-absent), an object control treatment, and an herbivore exclusion control. The negative control consisted of *Sargassum* thallus with no predator model or object control to quantify natural rates of herbivory.

Each morning (~ 08:30–09:30), one experimental treatment was deployed along the reef crest at 5–6 m depth within one fished reef (Bamboo or Taboon) and one protected reef (Manta or Twin Peaks). Within each reef, predator models and controls were secured ~50 cm above the reef substratum. Individual *Sargassum* assays for each treatment were attached to the reef substratum approximately one meter from the model. Adjacent treatments were separated by a minimum of 15 m, with predator and control treatments (i.e., negative control, object control, and caged assay) allocated randomly within reefs each deployment. This procedure was replicated over non-consecutive days a total of five times on Manta and Taboon Beach reefs, four times on Twin Peaks reef, and three times on Bamboo Bridge reef (total 17 experimental replicates).

To identify herbivorous fish species responsible for removing *Sargassum* biomass within each treatment, two underwater video cameras (GoPro Hero 3/4) mounted on weighted stands (2 kg), were positioned crosswise (i.e., diagonally) approximately 1 m away from the assay. This arrangement allowed the entire area and height of the *Sargassum* assay to be viewed. Utilizing video recordings was selected over visual censuses to account for the cautious nature of browsers (see Michael et al., 2013), as well as to decrease the total time deployed, thereby decreasing human impacts on herbivore behavior. Filming commenced immediately after all assays, predator models, and controls were deployed, with a small-scale bar (10 cm) placed adjacent to each assay for ten seconds to allow for estimation of fish sizes on the videos. After approximately four hours all cameras, assays, predator models, and controls were collected (~ 12:30–13:30). A total of 242 hours of footage were recorded.

Following retrieval, each individual *S. polycystum* thalli was spun and re-weighed to calculate biomass loss per thallus. For each video, the first 20 and last 10 minutes were discarded to

minimize potential diver interference. From the video footage, I recorded the total number of bites, species, and estimated TL to the nearest cm for each fish feeding. In instances where individual bite count could not be counted due to a succession of rapid bites without discernable pause, the “foray” was classified as a single bite event (Bellwood & Choat, 1990) and the total bites, length, and species of each fish feeding were not recorded; additionally, during several of these forays, many individuals were obscuring the assay, thereby rendering recording of assay feeding activities impossible. All transient browsing fishes were also counted and identified using MaxN: an index of relative abundance representing the maximum number of individuals of each species seen at one time on a single video frame, and commonly used to avoid double counting of the same individual when analyzing video data (Ellis & DeMartini, 1995). Each 20-minute segment of each video was watched to calculate MaxN of herbivorous fishes in the vicinity of the assays. Prior to analyzing a video, both camera videos for the assay were viewed and, to ensure accuracy of bite count, that which afforded the best view of assay and fish present was chosen for analysis. All data were recorded using Excel.

Data analysis

All data was tested for normality and homogeneity of variances, and all data, save macroalgal biomass removal rates, failed both tests, even with transformations. Therefore, a series of linear mixed effects models (LMEs) were used to examine rates of *Sargassum* removal among reefs, and between protected and fished reefs. Biomass loss for each assay were first standardized to control for autogenic loss during handling following Cronin and Hay (1996). Reductions in macroalgal biomass attributed to browsing 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 *Sargassum* assay exposed to browsing, and C_o and C_f were the initial and final masses of the corresponding assays from the herbivore exclusion controls/treatments. Linear mixed-effect models were used to examine differences in the relative (proportional) loss of *Sargassum* biomass of replicate assays (i.e., the realized function; continuous) among reefs (categorical) and treatments (i.e., two predator models, object control and negative control; categorical). Analysis of macroalgae removed was based on pooled *S. polycystum* biomass across predator model treatments nested within reef with day as a random effect. The best model was selected via AIC_C to account for the small sample size.

Mass standardized bites (hereafter ‘ms-bites’) were calculated by multiplying the total number of bites taken by each individual by the biomass of that individual (kg). Individual biomass was calculated using TL of each feeding individual recorded, along with known length-width relationships for each species recorded (see Kulbicki et al., 2005). Ms-bites were used in lieu of total bites for some analyses because they take fish biomass into consideration, which becomes important when discussing biomass removal.

Total and ms-bites were analyzed using multiple hurdle Generalized Linear Models (GLMs): first, the data was separated into incidences of feeding and no feeding, then a negative-binomial type GLM was performed for total bites taken (count; discrete), and a gamma type GLM was performed for ms-bites taken (continuous). MaxN was analyzed using a negative binomial type GLM (count; discrete). My predictors were the treatment, or type of predator model present (which is categorical), and site or site status (categorical). All analyses were run in the coding program R and RStudio using the packages lmer4, glmmADMB, secr, and emmeans.

Results

Sargassum biomass removal

There were marked differences in the removal rates of *S. polycystum* biomass among Danjungan's reefs ($p < 0.05$; $t_{3,38} = -3.42$, $t_{3,51} = -3.07$, $t_{3,50} = -3.68$, respectively for all reefs compared to Manta) ranging from $< 1\%$ 3.5h^{-1} ($0.8\text{g } 3.5\text{h}^{-1}$) on Bamboo Bridge to 36.0% 3.5h^{-1} ($32.4\text{g } 3.5\text{h}^{-1}$) on Manta. Removal rates were approximately 3.5 times higher on Manta compared to all other sites (LME: $p < 0.05$, $F_{3,50} = 6.23$) but there were no detectable differences between the predator models or negative control (i.e., assay without predator model or novel object) across sites ($p > 0.5$, $F_{2,46} = 0.38$; Figure 2).

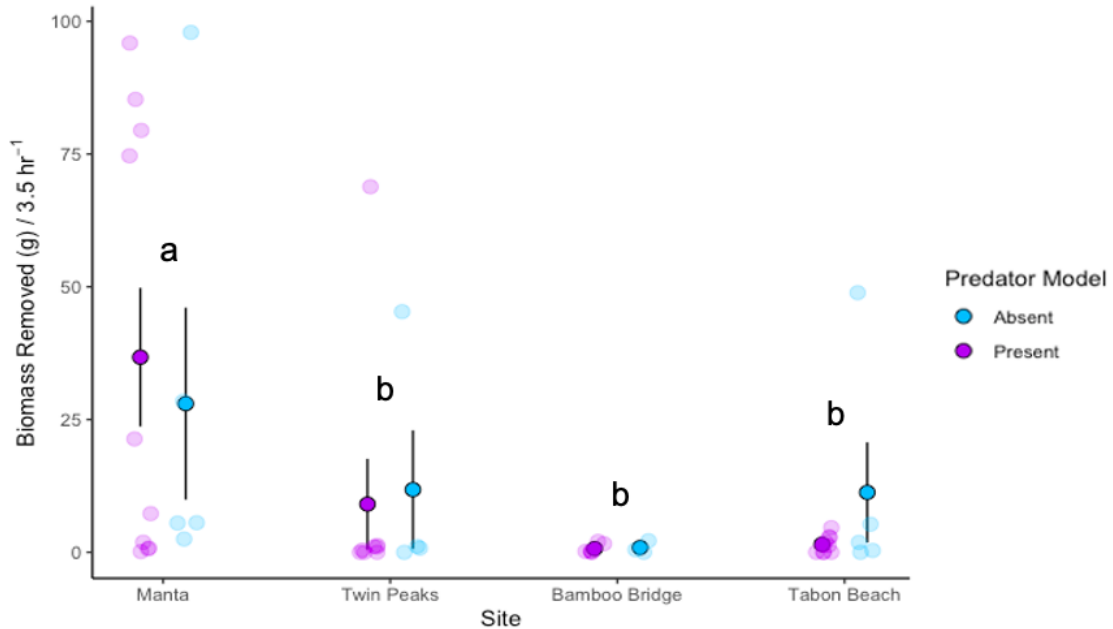


Figure 2. The proportion of *Sargassum* biomass removed 3.5 hr^{-1} across each site and treatment (pooled predator models). Lighter shaded points represent individual replicates. Confidence intervals are standard error. Letters above each site indicate significant differences ($p < 0.05$) between sites.

Bite rates

Analysis of the video footage revealed five herbivorous fish species taking a total of 2,475 bites across all assays. Mean bites per assay ranged from 6.4 ± 3.69 on Bamboo Bridge to 71.9 ± 18.67 on Manta. The most bites recorded on a single assay was 701 (Twin Peaks, *P. leopardus* model present). *N. unicornis* accounted for 1,414 bites (58.4% of all bites recorded; Table 1). Manta

showed significantly more occurrences of feeding than Bamboo Bridge and Tabon Beach (binomial GLM; $p < 0.05$; $z_{3,55} = -1.966$; $z_{3,55} = -2.86$, respectively) but site location did not have an effect on the feeding rates. The presence of a predator model significantly reduced the likelihood that feeding would occur (binomial GLM; $p < 0.05$; $z_{2,55} = 3.08$; Figure 3) but did not affect the number of bites taken ($p > 0.05$).

A total of 3,573.19 ms-bites were recorded across assays and the mean number of ms-bites ranged from 4.75 ± 3.02 (Tabon Beach) to 118.28 ± 108.06 (Twin Peaks); however, the rates of ms-bites did not differ among sites. Two species, *Naso unicornis* and *Naso literatus*, accounted for ~93% of the total ms-bites (3,334; Table 1). The presence of a predator model significantly reduced the likelihood of feeding and ms-bites (binomial GLM; $p < 0.05$, $z_{2,44} = 2.32$; Figure 4).

Table 1. Summary of video analysis including total bites and ms-bites recorded per treatment (predator model), status, site, and species.

Treatment		Species	<i>L. argentimaculatus</i>		<i>P. leopardus</i>		Control	
Status	Site		Total bites	ms-bites	Total bites	Ms-bites	Total bites	ms-bites
NTZ	Manta	<i>Melichthys vidua</i>	151	83.53			65	44.87
		<i>Naso unicornis</i>	44	91.43	260	527.14	308	565.18
		<i>Naso lituratus</i>			171	212.96	171	135.76
	Twin Peaks	<i>Siganus virgatus</i>			3	0.79	336	88.72
		<i>Kyphosus vaigiensis</i>			1	0.79		
		<i>Melichthys vidua</i>					23	4.62
		<i>Naso unicornis</i>			707	1533.67	52	116.86
Fished	Bamboo Bridge	<i>Melichthys vidua</i>					9	4.20
		<i>Naso unicornis</i>					32	66.92
		<i>Naso lituratus</i>					23	19.80
	Tabon Beach	<i>Naso unicornis</i>					9	19.11
		<i>Naso lituratus</i>					58	45.33
		<i>Siganus virgatus</i>					50	11.50

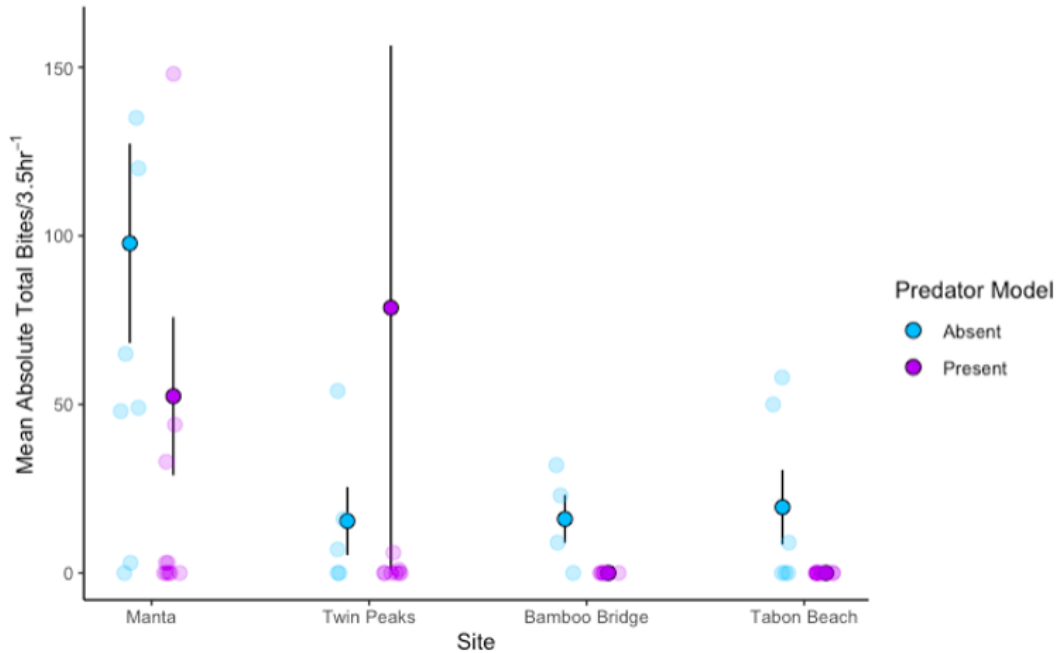


Figure 3. Mean total bites per assay 3.5 hr^{-1} in the presence of a predator model (*Plectropomus leopardus* and *Lutjanidae argentimaculatus*) and the control treatment at each site. Lighter shaded points represent individual replicates. Confidence intervals are standard error.

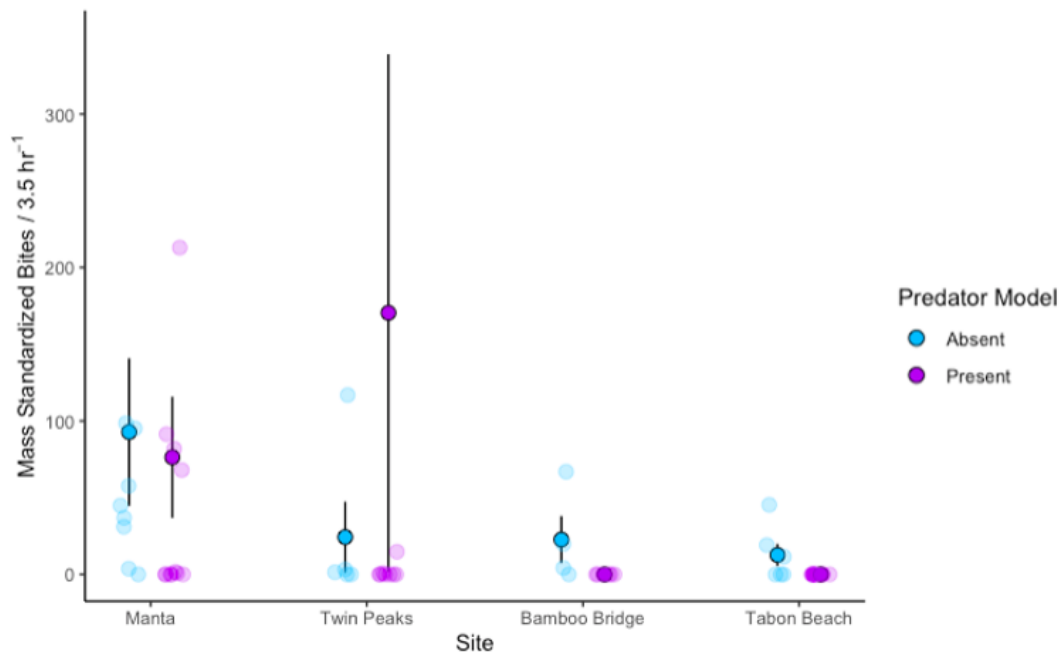


Figure 4. Mass standardized bites per assay 3.5 hr^{-1} in the presence of a predator model (*Plectropomus leopardus* and *Lutjanidae argentimaculatus*) and the control treatment at each site. Lighter shaded points represent individual replicates. Confidence intervals are standard error.

MaxN

A total of 601 individual fishes were recorded across sites. Mean MaxN values per species across sites ranged from 0 (Twin Peaks, *S. virgatus*) to 7.8 ± 3.04 (Manta, *K. vaigiensis*) and differed significantly among sites ($p < 0.05$). Pairwise comparison revealed that MaxN on Manta and Twin Peaks did not differ ($p > 0.05$), whereas MaxN recorded at Bamboo Bridge and Tabon Beach (fished sites) differed significantly from Manta (negative binomial GLM; $p < 0.05$; $z_{3,170} = -4.80$, $z_{3,170} = -2.80$, respectively). MaxN on Tabon Beach did not differ from Twin Peaks ($p > 0.05$) or Bamboo Bridge ($p > 0.05$; Figure 5); Twin Peaks is, however, significantly different from Bamboo Bridge ($p < 0.05$; Figure 5). Treatment was shown to be nonsignificant in explaining variation in MaxN. There were clear differences in abundances of the five browsers present in each site (Figure 6), with *K. vaigiensis* more prevalent in NTZ sites, whereas *N. unicornis* was less prevalent in Bamboo Bridge than in all other sites.

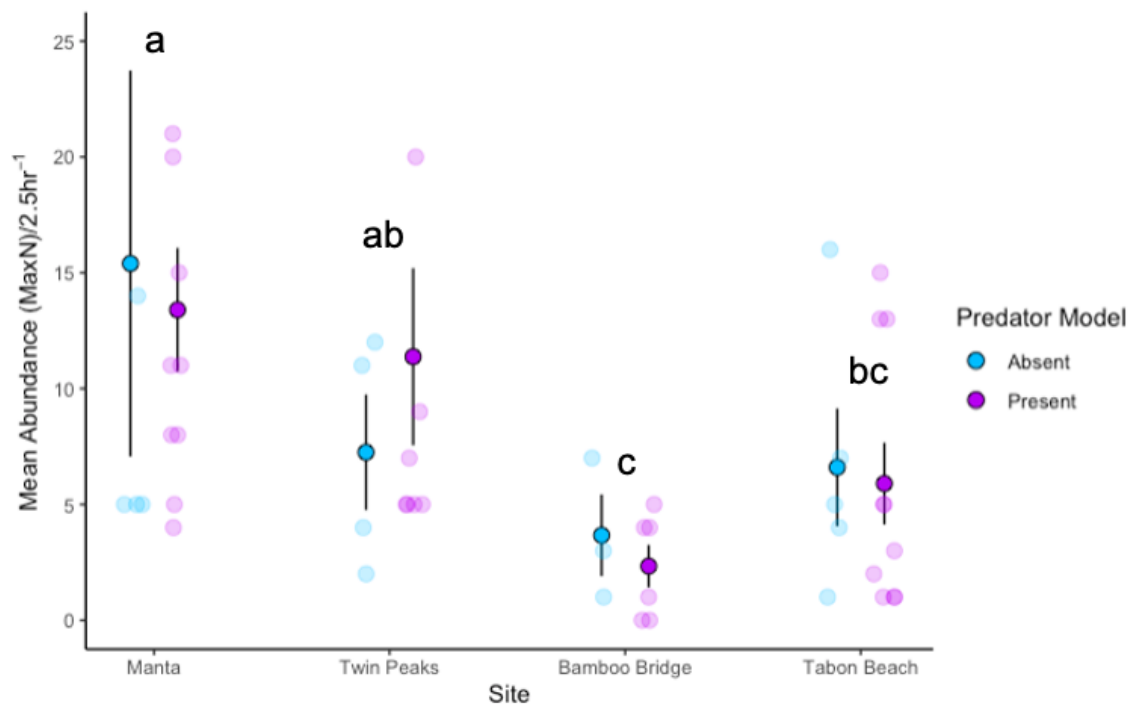


Figure 5. Mean MaxN per assay 2.5 hr^{-1} in the presence of a predator model (*Plectropomus leopardus* and *Lutjanidae argentimaculatus*) and the control treatment at each site. Lighter shaded points represent individual replicates. Confidence intervals are standard error. Letters indicate statistically significant differences ($p < 0.05$) between sites.

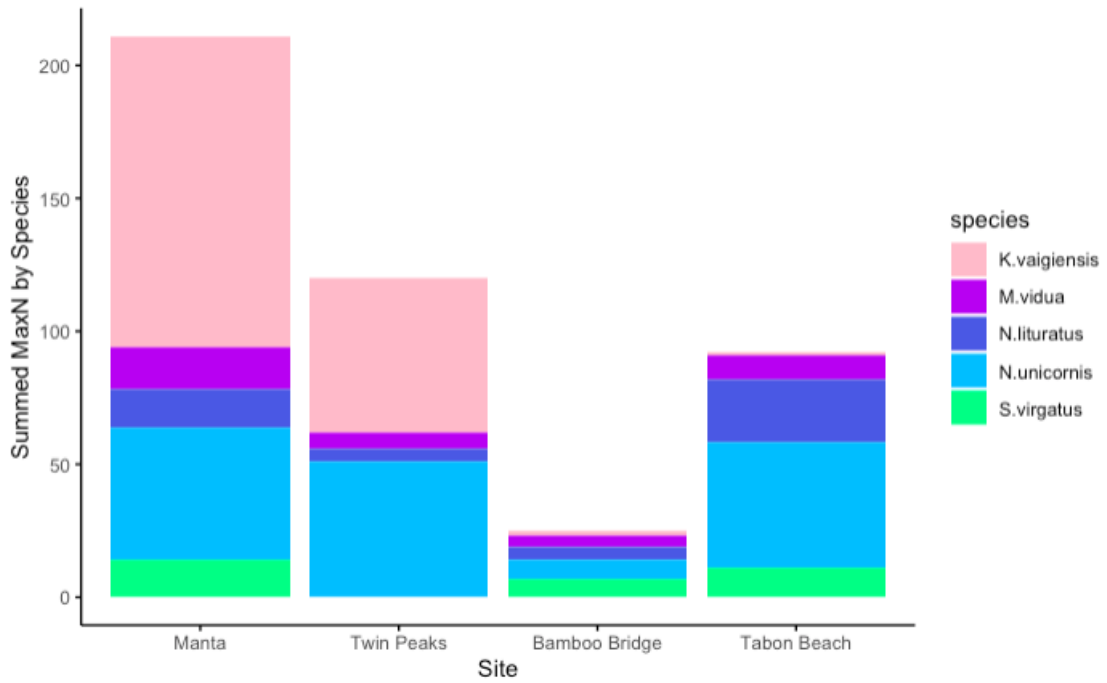


Figure 6. MaxN of each species of browser (*K. vaigiensis*; *M. vidua*; *N. lituratus*; *N. unicornis*; *S. virgatus*) summed by site.

Discussion

Fear effects have been shown to be potentially important drivers of browser foraging behavior and habitat use patterns (Mitchell & Harborne, 2020), influencing the spatial and temporal distribution of macroalgal removal on coral reefs (Madin et al., 2010; Rizzari et al., 2014; Bauman et al., 2021). Yet how browser foraging behavior is influenced by fear effects within small-scale MPAs ($< 1 \text{ km}^2$), and whether critical ecosystem functions are sustained remains unresolved. My results revealed that rates of macroalgal removal (the “realized” function; *sensu* Bellwood et al., 2019), feeding rates (ms-bites hr^{-1}) and the relative abundance of browsing species (MaxN) were all markedly greater within Manta (NTZ) than nearby fished reefs. Notably, despite Danjugan’s small MPA reserves ($< 0.5 \text{ km}^2$), mean macroalgal removal in NTZs (primarily Manta) was 24.5%, 7.5 times greater than in fished sites (3.3% mean removal), and up to 40 times higher when comparing the NTZ with the highest removal (Manta) to the fished site with the lowest removal (Bamboo Bridge). My results also showed that model presence decreased likelihood of feeding and ms-bites, but neither the identity nor size of the predator model (i.e., *P. leopardus* and *L. argentimaculatus*) impacted these factors, and predator model presence did not impact macroalgal removal. Additionally, the number of ms-bites per 3.5 hrs in NTZs was 90.9 ms-bites on average, 10 times greater than in fished sites, which had 8.8 ms-bites on average; furthermore, ms-bite rate in NTZs was up to 25 times higher than in fished sites when comparing the NTZ with the highest ms-bite rate (Twin Peaks) to the fished site with the lowest ms-bite rate (Tabon Beach). While these findings do not identify an impact of acute fear effects on realized function, they suggest that the presence of a predator model does influence some foraging behavior. However, the reduced removal of macroalgae even when browsers are present and lower ms-bite rate in fished sites compared to NTZs suggests that the chronic risk may impact both fish behavior and realized function.

Evidence from multiple ecosystems shows that spatial variation in fear effects influences where prey choose to forage (Gaynor et al., 2019; Laundré et al., 2001). Consistent with previous empirical studies (e.g., Rizzari et al., 2014; Catano et al., 2016; Bauman et al., 2021), my results revealed that acute fear effects reduced browsing rates across reefs but did not impact macroalgal removal. Nevertheless, I also found that the amount of macroalgae removed varied spatially across

reefs, with clear spatial differences between Manta and all other sites. Mean macroalgal removal was 21% in protected sites (Manta and Twin Peaks), which fits with previous studies (REFs). Macroalgal biomass removal on other Indo-Pacific reefs has been shown to be highly variable, ranging from < 10% to 95% removal using similar methods (see Bauman et al., 2021; Bennett & Bellwood, 2011; Hoey, 2010). Variation in macroalgal removal may be due to spatial differences among locations, macroalgal height, density, and cover, habitat structural complexity, browser abundance, or seasonality of these studies (Hoey, 2010; Hoey & Bellwood, 2011). For instance, initial macroalgal assay size utilized varied greatly between these three studies, from 12.5 ± 0.6 (Hoey, 2010) to 200-300g (Bennett & Bellwood, 2011). My macroalgal assays, initially being ~100g, fit within this window. Furthermore, the reefs examined in these studies varied in macroalgal dominance – one study used reefs where macroalgae was dominant (Hoey, 2010) while coral dominated the other reefs – and location relative to the islands – one study focused on an offshore (and therefore exposed) reef (Bauman et al., 2021), while the others studied leeward reefs. My results were comparable to all of these studies, as I utilized both windward (exposed) and leeward reefs. Macroalgal identity was likely not a significant factor between these studies, despite the fact that all three studies cited above utilized different *Sargassum* species. Large spatial variation in macroalgal removal has been seen in several other reef systems such as the Great Barrier Reef (Bennett & Bellwood, 2011), Singapore (Bauman et al., 2017), and the Seychelles Islands (Chong-Seng et al., 2014) and is likely related to other environmental aspects apart from site protection status, as many of these studies utilized sites which did not vary in fishing pressure.

Previous macroalgal removal studies on coral reefs report spatial patterns of higher, but variable, removal rates between small NTZs and adjacent non-protected, fished reefs. For example, a study on small protected areas in Fiji revealed substantially higher browsing rates of *Sargassum* assays in NTZs compared to fished reefs, and greater coral cover in NTZs (Bonaldo et al., 2017). Another study on browsing in fished sites, marine reserves that allow fishing, and NTZs in Kenya found highest browsing rates of *Sargassum* in NTZs, followed by marine reserves, with fished sites showing lowest browsing rates (Knoester et al., 2023). Interestingly, my results showed differences in both bite rate and MaxN between fished sites: Tabon Beach had higher mean bite rates and MaxN than Bamboo Bridge. Tabon Beach's position on the windward, exposed side of Danjugan may have contributed to these spatial differences, as windward reefs have been reported

to have greater fish biomass and primary production than leeward reefs (Marshall & Mumby, 2015). Higher abundance of primary producers could explain these higher bite rates and browser abundance on windward sites compared with their leeward counterparts – browsers will tend toward areas with higher food availability, which tend to be on the windward side.

Comparing between NTZs, macroalgal removal was 2.5 times greater in Manta than Twin Peaks, possibly due to differences in enforcement. Twin Peaks is separated from the populated area of Danjungan which enforces the no-take zone by a hilly area which, in addition to the relative inaccessibility of the site (being on the far side of the island) means poachers likely frequent the area. Manta's higher rates of feeding and macroalgal removal suggest that this reef should be best able to recruit new corals, as macroalgal cover due to reduced browsing would hinder coral recruitment on the other Danjungan reefs; a theory which is supported by the recent finding that Manta alone, when compared with the fished sites, did not see a significant decline in coral cover between 2002–2016 (Twin Peaks was not included in this study; Wright, 2022). This suggests that, when properly enforced, small-scale NTZs may effectively reduce long-term coral degradation. Manta reef should continue to be enforced and all other existing NTZs as well as any future NTZs implemented here should emulate Manta's strict enforcement if they hope to achieve similar effects.

My results revealed that ms-bites per hour were significantly reduced by predator presence, supporting the idea that spatially-concentrated herbivory may be interrupted by predator presence, resulting in herbivores feeding in shorter, more rapid bursts due to fear effects (see Catano et al., 2016; Sandin & McNamara, 2012). Additionally, the fact that macroalgal removal was not impacted by predator presence suggests that browsers may have been taking larger bites in the presence of predator models as an antipredator response. However, browser species are likely playing a role here, because the size of certain browsing species may be too large for the size of the predatory species used in this study to impact their behavior. *N. unicornis*, which made up the majority of all bites taken from the macroalgal assays, was larger than any other browsing species (averaging 46 cm TL), so certain individuals from species *N. unicornis* may not have experienced fear effects as a result of the predator models (*P. leopardus*, the larger of the two, was only 7 cm

larger than the average size of *N. unicornis*, and *L. argentimaculatus*, the smaller of the two, was 4 cm smaller than this average size; therefore, certain *N. unicornis* individuals may not have been threatened by either model). *N. unicornis* has been found to be a dominant browser by similar studies (i.e., Bauman et al., 2021; Hoey & Bellwood, 2009; Rasher et al., 2013) and is a dominant macroalgal browser in many reef regions, removing the vast majority of macroalgae even in systems with high browser diversity (e.g., Hoey & Bellwood, 2009; Rasher et al., 2013). *K. vaigiensis* and *N. lituratus* have been responsible for the majority of feeding in several other coral reef studies (e.g., Bauman et al., 2021; Rasher et al., 2013; Streit et al., 2015), and have also been shown to be highly mobile herbivores, known as mobile links between coral reefs (Welsh & Bellwood, 2014). I found a total of five species of browsers feeding at Danjugan Island between the four sites, with great variation in species dominance between sites. *K. vaigiensis* was dominant in Manta and Twin Peaks but almost entirely absent from Bamboo Bridge and Tabon Beach. *N. unicornis* was second most dominant species in the protected sites and most dominant in Tabon Beach, only showing absence at Bamboo Bridge. The same suite of browsers forages on both sides of the island, according to previous research, but a significantly reduced number of individuals tend to appear at Twin Peaks than Manta site (Aurellado et al., 2009), which matches my results. Browsers are the only functional group of herbivorous fish able to remove macroalgae (Hoey & Bellwood, 2009) therefore allowing for greater coral recruitment (given that macroalgae decreases coral resilience; Hughes et al., 2007; Hoey & Bellwood, 2011). Therefore, this decrease in browser presence and foraging at Twin Peaks compared to Manta suggested by my results could be detrimental to the resilience of corals in Twin Peaks, despite this site's status as an NTZ.

One of the aims of this study was to quantify whether the small-scale NTZs (~ 0.3 km²) around Danjugan Island are effective in maintaining browsing and macroalgal removal, a key ecosystem function. The size requirements for NTZs to be effective have been widely disputed (Claudet et al., 2008; Krueck et al., 2017). In this study, sites protected from fishing had higher MaxN than regularly fished sites, suggesting that small-scale NTZs may be effective in maintaining/sustaining fish biomass. For example, *Kyphosis vaigiensis* was almost entirely absent from fished sites but accounted for nearly 50% of the relative abundance within the NTZ sites. This idea has also been enforced by recent literature, which has found that the implementation of small-scale NTZs has resulted in larger fish size as well as higher abundance, thus further contributing toward the overall

fish biomass (Bonaldo et al., 2017; Espectato et al., 2017). One argument supporting large over small-scale NTZs is that certain target species may have home ranges exceeding the small area (Green et al., 2015; Krueck et al., 2017); for example, mobile links such as *N. unicornis* or *K. vaigiensis* (Welsh & Bellwood, 2014). However, I found *K. vaigiensis* in significantly higher numbers within small-scale NTZs compared with outside them, suggesting that this species can benefit from small-scale NTZs despite its full home range not being covered. Additionally, the implementation of a network of small-scale NTZs may be beneficial toward increasing fish biomass if they are spaced such that fish larvae may be dispersed into separate NTZs (Green et al., 2015), as larvae are not targeted by fishermen. The implementation of further small-scale NTZs at Danjungan would therefore likely result in greater fish biomass by protecting target species from overfishing and allowing for movement of larvae between NTZs, particularly if they were placed strategically at spawning sites (Taylor & Mills, 2013).

Poaching and overfishing of predatory fish has become a major problem in ecosystem management because it has manifold impacts on the ecosystem at large. As fishermen selectively remove the largest specimens of predatory fish, the remainder have increasingly smaller gapes (it is estimated that prey width is limited to 0.6 predator gape size; Gill, 2003), eventually resulting in certain prey individuals becoming too large to be preyed upon by these predators (e.g., Rizzari et al., 2014). This in turn may remove predation risk on certain browsers, thereby potentially reducing the effects of spatially-concentrated herbivory. This likely impacted the results of my study, as the gape limitations of my *P. leopardus* model (TL 53 cm) may have decreased the fear effects of this predator model on larger species such as *N. unicornis* (40-50 cm TL), which may have been too large to be preyed upon by this species.

Ecological contexts such as species of predator (see Catano et al., 2017), size of predator model utilized (see Rizzari et al., 2014), and proximity of models to macroalgal assays (see Bauman et al., 2021) often change how prey evaluate and respond to risk. Interestingly, in this study, browsers did not have significantly different bite rates or abundance in the presence of either model potentially due to small size differences between the predator models used in my study (11 cm difference). In contrast, a previous fear effects study in the Florida Keys reported differences in bite rates while using predator models of similar sizes; however, those species had significantly

different hunting styles (Catano et al., 2017). Both *L. argentimaculatus* (Chi, 2017) and *P. leopardus* (Gibran, 2007) utilize ambush predation, suggesting that predator identity was not the primary reason for the lack of significant difference in browsing rates at one model or the other in my study. Additionally, distance between the assays and predator models may have influenced my results – a previous browser foraging study in Singapore found decreasing foraging with increasing proximity to the predator model (Bauman et al., 2021). My assays were positioned one meter from the predator models; perhaps this immediacy resulted in fewer browsers feeding overall.

Another factor which may have impacted my results is that certain species, such as *K. vaigiensis* or *N. unicornis*, frequently engage in feeding forays – large numbers of fish feeding simultaneously (*sensu* Bellwood & Choat, 1990). A total of 21 forays occurred over the course of this study, during which it became impossible to track the bites taken by each individual fish present; therefore, some potential data was lost. However, given that the majority of these forays were dominated by *N. unicornis* and the forays were evenly spread across NTZs (13 forays) and fished sites (11 forays), the data lost to forays likely would not have significantly altered my results. These species likely engage in these forays as an antipredator response for this very reason – predators would likely find it difficult to track individuals through a large group, just as I found it difficult to do so when attempting to track individual bites from the assay. These forays may have also lessened the fear effects of the predator models for individuals of these species overall, as there is safety in numbers and *K. vaigiensis* in particular would often circle the model as if to confuse the predator. Additionally, I was unable to control for individuals apart from browsing herbivorous fish from feeding on the assays: one replication included minimal macroalgal removal by a sea turtle. This feeding, while unexpected, still performs the function of macroalgal removal on reefs, so this does not constitute a limitation to this study. Lastly, my data has an uneven number of replicates – five for Manta and Tabon, four for Twin Peaks, three for Bamboo Bridge – and for this reason, I was restricted to GLMs for analysis, since they are well-equipped to handle this type of data.

Conclusion

Understanding the relationship between NTZs and rates of macroalgal removal is crucial to potentially mitigating the current degraded state of coral reefs worldwide. The recent concern regarding small-scale NTZs is whether they are able to maintain ecosystem functions despite their small size. Overall, my results indicate that some small-scale NTZs may maintain key ecosystem functions such as macroalgal removal. Higher net macroalgal removal may allow more opportunities for coral recruitment, which could result in healthier coral reefs in Danjungan if the island's NTZs are properly enforced. My results also show that small-scale NTZs have the potential to support higher browser abundance and biomass than fished sites. Consequently, the implementation of further NTZs in this area, regardless of size, could further conserve fish biomass. Additionally, future research should explore whether other ecosystem functions apart from macroalgal removal may be maintained by small-scale NTZs. Ultimately, small-scale NTZs were not shown here to impact browser bite rates but were shown to have higher browser abundance and macroalgae removal than fished sites, suggesting that browsers were taking smaller bites in fished areas than NTZs due to fear effects. Furthermore, fear effects were shown to decrease the likelihood that browsers would feed on macroalgae in a given area. Consequently, the changes to fear effects resulting from the implementation of small-scale NTZs have the potential to significantly impact the occurrence of macroalgal removal and ultimately, coral recruitment and resilience to climate change and other human impacts in the Philippines.

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