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## ENCOUNTER FREQUENCY DOES NOT PREDICT PREDATION FREQUENCY IN TROPICAL DEAD-SHELL ASSEMBLAGES

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**ABSTRACT:** Predation is frequently suggested to be a key biotic process that can shape ecological communities and drive coevolution. The premise behind these hypotheses is that predators select prey to ensure maximum gain per unit effort; for example, by selecting species that are more abundant or accessible. In this study, we tested for predator selectivity in a tropical molluscan assemblage by quantifying the influence of relative abundance (encounter frequency) on predation frequencies. We collected macromollusks (> 4 mm) from 15 sites in three soft-sediment reef lagoons at One Tree Reef (southern Great Barrier Reef, Australia). Dead mollusks were counted and identified to species level (61 species,  $n = 8131$ ), and species predation frequencies were calculated as the proportion of shells with drill holes. We found that in this infauna-dominated community, levels of drilling predation were low (7.14% on average), and there was no evidence that predators selected prey based on encounter frequency. This result was consistent across prey species and lagoons. Thus, drilling predators did not specialize on more accessible prey species and were not a major cause of mortality in this modern macromollusk assemblage. Since drilling gastropods are size selective, lack of selectivity in our samples only applies to the prey size range considered. Detailed studies of prey morphological traits, as well as accounting for predator non-consumptive effects could shed light on the preferences and relevance of drilling gastropods in this soft-sediment carbonate reef assemblage.

### INTRODUCTION

Predation is a key biotic process that shapes communities and the evolution of interacting species (e.g., Vermeij 1993; Leighton 1999). Predation contributes to the flow of energy and resources through communities and ecosystems (Vermeij 1993; Chapin et al. 1997) and can alter the relative abundances of species in lower trophic groups. Changes in relative dominance of trophic groups can impact community structure and function (Paine 1966; Chapin et al. 1997; Duffy 2002; Meyer and Byers 2005). Over generational time scales, improvements in predator effectiveness can also lead to changes in prey defenses (Vermeij 1993). For example, epifaunal tropical gastropods subject to intense predation by crabs have developed thicker shells, smaller apertures and stronger sculpture (Zipser and Vermeij 1978; Bertness and Cunningham 1981). Thus, predators can be important drivers of the evolution of species and communities over time.

Predators have more pronounced effects on community structure and natural selection when predation frequencies are high and predators are selective. For instance, Navarrete and Castilla (2003) showed that gastropod and sea-star predation had a large controlling effect on community structure in Chilean intertidal communities. By removing large numbers of their preferred prey, these predators controlled the population of a bivalve that would otherwise dominate the community. On the other hand, Jones et al. (1992) show that fish predation on mollusks, while omnipresent in tropical reef communities, had very little influence on the molluscan community structure at One Tree Reef. In order to determine what drives predation frequencies, it is important to understand if predators select prey based on community-level or individual-level characteristics. Community characteristics such as prey abundance and life habit primarily determine the accessibility or

probability of encountering prey (Vermeij 1983; Leighton 2002; Leonard-Pingel and Jackson 2013) whereas individual traits such as prey size, shape and mechanical properties largely determine the cost of handling or eating the prey (e.g., Kitchell et al. 1981; Kelley 1988; Kelley and Hansen 1996; Dietl and Alexander 2000; Chiba and Sato 2012; Chattopadhyay et al. 2014). Studies of predation in paleontology have tended to focus on individual-level traits (but see Kelley and Hansen 2006), because community-level data are difficult to collect and can be biased by taphonomic processes. Therefore, focusing on a community-level attribute such as relative abundance can provide new insights into predation.

Given that predation is higher in tropical environments (Dudley and Vermeij 1978; Allmon et al. 1990; Schemske et al. 2009; Visaggi and Kelley 2015; among others), predator selectivity, which leads to more efficient predation, should be more important at low latitudes. Previous research has shown that there is a diversity hotspot for mollusks in Southeast Asian and Australian tropical seas (Crame 2000; Bouchet et al. 2002). One mechanism suggested to maintain this high diversity is higher predation intensities in the tropics relative to other locations (Schemske et al. 2009). Preferential predation on the most abundant species can lead to competitive release that can explain this higher diversity (Menge 1995; Duffy 2002). For example, predation frequencies are high for tropical marine snails that are preyed upon by crabs (Zipser and Vermeij 1978) and paleontological studies have also found evidence for high predation at low latitudes (Vermeij 1980, 1993; Alexander and Dietl 2001). Therefore, tropical communities are an ideal study system in which to study predator selectivity given that mollusks are diverse in these environments, accessible to sample in large numbers, and predation frequencies can be easily quantified from traces in prey shells.

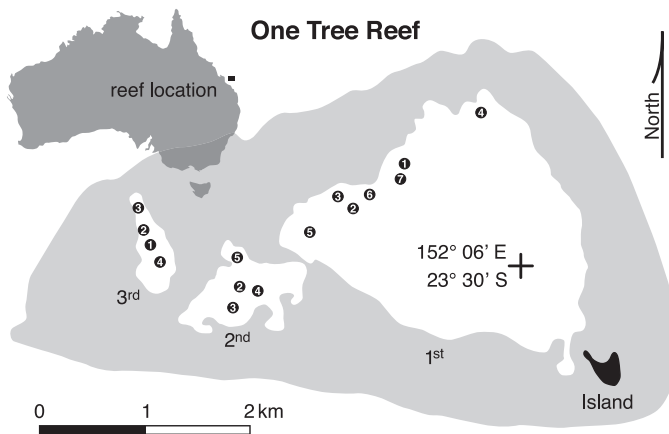


FIG. 1.—Schematic map of One Tree Reef, southern Great Barrier Reef. The reef outline is the shaded gray area, the three lagoons are in white, and One Tree Island in black. Site numbers inside each lagoon agree with the collection sites listed in Table 1. Reef and lagoon outline were traced from Google Earth imagery.

Predator selectivity must be evaluated relative to the prey community, and prey encounter frequencies can be accounted for by using relative abundances of individuals in dead shell assemblages. Prey abundance is a surrogate for the frequency that a foraging predator potentially encounters a prey species (Leighton 2002). The probability of interspecific encounter has a long history; perhaps most familiar to paleontologists is the discussion by Hurlbert in his 1971 paper most commonly referenced for its contributions to rarefaction. A non-selective predator model assumes that all prey are equally available to a predator. So the probability of a predator encountering a particular prey is the prey's relative abundance. Prey abundance can be obtained from dead-shell assemblages (DA) given that extensive research on DA indicates that they are good sources of community-level information (Kelley and Hansen 2006; Kidwell and Tomasovych 2013). Indeed, shell assemblages from the Cretaceous to Pleistocene have been used to show that prey relative abundance was not correlated to drilling frequencies in several bivalve families (Kelley and Hansen 2006). Thus, since it is easier to collect DA than to sample living communities, DA have been widely used as surrogates for living communities.

In this study, we tested for drilling predator selectivity in a tropical molluscan community from One Tree Reef (OTR), southern Great Barrier Reef, Australia (23°20'S, 152°06'E; Fig. 1). The reef crest surrounds three lagoons (roughly 10–13 km<sup>2</sup> in extension; Davies et al. 1976) that have coral patch reefs interspersed with sand (Ludington 1979). Sediment containing dead shells was collected at 15 sites spanning three lagoons. Sites ranged in depth from 4.3 to 6.1 m (ponded depth). At each collection site, four 0.25 m<sup>2</sup> replicate quadrats of 1 m<sup>2</sup> of sediment were sampled by divers using an 80 mm diameter air-lift and 1 mm mesh bags. Only the top 0.1 m of sediment was

## METHODS

### Study Site and Material

removed as examination of deeper sediment failed to recover living mollusks (Kosnik et al. 2015). Sampling was carried out four times in 2012 therefore each site has 16 replicate quadrats.

After collection, samples were wet sieved using a 4 mm sieve. Previous studies (e.g., Kidwell 2001) have found 2 mm sieves to be suitable for mollusks, but at OTR 2 mm sieves were capturing large numbers of juveniles. Since smaller shells have a lower probability of being preserved relative to larger shells (Cooper et al. 2006; Kosnik et al. 2007), we used the fraction retained by a 4 mm sieve to ensure comparability with the fossil record (Kidwell 2001). The death assemblage from one quadrat from each site was sorted; where necessary to achieve sufficient sample size additional replicate quadrats were sorted (Table 1). Individuals were identified to the species level with the aid of published literature (Lamprell and Whitehead 1992; Lamprell and Healey 1998), the Australian Museums' Malacology collections, and mollusk taxonomists. The number of bivalve and gastropod individuals per species were counted. For bivalves, the minimum number of individuals was the number of articulated valves plus the total number of unfragmented right valves.

Given the abundance of dead shell material, encounter rates were calculated for each species using between 2 to 9 replicate quadrats per site (Table 1). Overall, a total of 8131 dead bivalve and gastropod individuals were included in these analyses, representing 61 species from 26 different families (Table 2). These were all the identifiable species present in the dead shell assemblage. Species were separated into life habits using published literature (Lamprell and Whitehead 1992; Beesley et al. 1998; Lamprell and Healey 1998; Table 2). Tellinidae, Lucinidae, Veneridae, Cardiidae, and Galeommatidae bivalves were classified as strictly infaunal (Table 2). Gastropods and the rest of the bivalves were classified as epifaunal given that their feeding habits suggest they are not restricted to the infauna. For example, Nassaridae are scavengers and/or deposit feeders, Haminoecidae are grazers, and Naticidae are mobile predators. Even if naticids are typically classed as infauna, they are not strictly infaunal like the bivalves mentioned above. Therefore, they were grouped together with the rest of the gastropods. Overall, the most abundant taxa were infaunal tellinid bivalves (85.7%), followed by non-tellinid bivalves (7.6%), and gastropods (6.7%) (Table 3).

### Calculation of Predation Frequencies

Predatory drill-holes in the DA were identified using the following criteria: (1) holes of a circular shape and regular outline; (2) holes perpendicular to the shell; and (3) in the case of articulated valves, holes that only go through one of the valves (Kelley et al. 2003; Yanes and Tyler 2009).

Predator selectivity can be readily quantified using drilling predation metrics and taking into account species relative abundances in assemblages or communities (Leighton 2002; Chattopadhyay and Dutta 2013). Predation frequency is usually calculated as the number of individuals of a taxon with a predation trace, divided by the total number of individuals from that same taxon (Lower Taxon Frequency, Kowalewski 2002). This species-level metric can account for selectivity if it is considered relative to the species abundance in a sample. For example, if predators are non-selective, then predation frequency for a given species is constant (slope = 0) irrespective of the prey's relative abundance in the sample. Therefore, to differentiate between selective and non-selective predation the frequency at which predators encounter prey is required. Since all 61 species were used to calculate encounter frequency, drilling frequency was also calculated for all 61 species.

We found no significant differences between predation in right and left valves for tellinids ( $\chi^2 = 0.95$ ,  $df = 3$ ,  $p$  value = 0.81), and no shell had multiple drill holes. Thus, we considered any unfragmented right valve with a drill-hole to be a drilled individual. The three naticid species

TABLE 1.—Total abundance, richness, and sampled area for dead assemblages from different sites. Latitude, longitude and depth are also provided for each site. Depth is ponded depth in meters determined by diver depth gauge and lagoon specific tidal corrections sourced from the Great Barrier Reef Ocean Observing System; asterisk indicates an estimated ponded depth.

Site	Abundance	Richness	Area (m <sup>2</sup> )	Latitude	Longitude	Depth
1 <sup>st</sup> Lagoon, Site 1	955	38	1.75	-23.49159°	152.07444°	4.7m
1 <sup>st</sup> Lagoon, Site 2	181	23	0.5	-23.49461°	152.06969°	4.9m
1 <sup>st</sup> Lagoon, Site 3	334	15	1	-23.49399°	152.06875°	4.9m*
1 <sup>st</sup> Lagoon, Site 4	67	19	0.5	-23.48585°	152.08090°	5.1m
1 <sup>st</sup> Lagoon, Site 5	315	10	1	-23.49677°	152.06587°	4.5m
1 <sup>st</sup> Lagoon, Site 6	127	11	0.5	-23.49406°	152.07054°	5.3m
1 <sup>st</sup> Lagoon, Site 7	100	11	0.5	-23.49214°	152.07440°	4.3m
2 <sup>nd</sup> Lagoon, Site 2	937	30	2.25	-23.50030°	152.06017°	4.9m
2 <sup>nd</sup> Lagoon, Site 3	899	15	2.25	-23.50170°	152.05995°	4.6m
2 <sup>nd</sup> Lagoon, Site 4	110	13	0.5	-23.50043°	152.06168°	5.0m
2 <sup>nd</sup> Lagoon, Site 5	520	23	1	-23.49871°	152.05949°	5.0m
3 <sup>rd</sup> Lagoon, Site 1	1087	24	2	-23.49729°	152.05243°	5.3m
3 <sup>rd</sup> Lagoon, Site 2	1449	35	2	-23.49631°	152.05169°	6.0m
3 <sup>rd</sup> Lagoon, Site 3	758	20	1.5	-23.49468°	152.05145°	6.1m
3 <sup>rd</sup> Lagoon, Site 4	292	14	0.5	-23.49849°	152.05316°	5.7m

present in the samples had a similar size range (Table 3), indicating they could attack the same prey. Therefore, we collectively treat these three naticid species as ‘the predator’, and assess their collective selective/non-selective behavior.

#### Model Selection

A generalized linear mixed-effects model (GLMM) with a binomial response variable (drill hole = 1, no drill hole = 0) was used to determine which explanatory variable best predicted the per species frequency of drill holes. Relative abundance of species in samples (i.e., encounter frequency) and species life habit (infaunal or epifaunal) were included as fixed factors. Species identity and lagoon were included as random factors, and models were tested with and without an effect of relative abundance on species (i.e., random slope). We also included a variable for each replicate as a random factor, because the ratio of model residual deviances to residual degrees of freedom tended to be greater than one, indicating overdispersion. GLMM analyses were carried out using the ‘glmer’ function in the ‘lme4’ package in the statistical programming language R (Version 3.0.2; R Core Team 2013). We used the ‘dropl’ function with chi-squared test to determine which of the fixed factors and interactions to keep in the final model. We used the ‘anova’ function to determine which configuration of random factors to retain. R code and data files are provided as online Supplementary material.

## RESULTS

### Species Life Habits

The overwhelming majority of the species found in the soft sediment assemblages from One Tree Reef were infaunal (93%; Table 2). As a consequence, and given that all potential prey (infaunal or epifaunal) were collected from the same depth (0–0.1 m) and in the same volume of sediment, we considered the ecological differences between what we classified as infaunal and epifaunal species to be minimal. Other studies have found life habit to be an explanatory factor for predation (e.g., Leonard-Pingel and Jackson 2013) but since the absolute majority of taxa had the same life habit, it was excluded as a predictor for predation frequency from the models.

### Predation Frequencies

The most abundant prey species had median predation frequencies between 0 and 10% (*Pinguitellina robusta* (4.4%), *Scissulina dispar* (0.6%),

*Loxoglypta clathrata* (9.3%), *Abranda jeanae* (6.4%), *Ctena bella* (0%), *Fragum fragum* (2.2%); Table 2). Median drilling frequencies for the 61 species ranged from 0% to 100% but this was strongly affected by singletons and species with less than 10 individuals (Table 2). The relative abundance of drilling predators was very low in all three lagoons; 1.87% in First lagoon, 0.57% in Second lagoon, and 0.53% in Third lagoon (Table 3).

#### Model Selection

Species relative abundance was not a significant predictor of drilling frequencies. Model selection based on AIC indicated that the model without relative abundance (AIC = 647.54) was better than the model with relative abundance included as a fixed factor (AIC = 623.72). This indicates that adding relative abundance did not significantly improve the model fit, and therefore knowing prey abundance does not improve our ability to predict predation frequency.

The best model indicated a constant predation frequency of 7.14% (thick black line, Fig. 2). Model selection did not find relative abundance or the intercept to be significant, and the best model included both species and lagoon as random effects (Table 4). The model without the slope term for individual species as a function of relative abundance had lower AIC and BIC than the model with the slope term for individual species (Table 5), suggesting little advantage of including relative abundance as an additional parameter. Predation frequencies of abundant species tended to match the final model whereas species making up less than 2% of the death assemblage had more uncertain predation frequencies, likely due to the low number of individuals from these species that were sampled. In the most extreme case, a species represented in a sample by one individual must have a drilling frequency of either 0% or 100% (Fig. 2). Despite having the most drilling predators, the First lagoon assemblages had the lowest predation frequencies, approximately 4.6% lower than the model average; and despite having fewer drilling predators, the Third lagoon assemblages had the highest rate, approximately 5.3% higher (Tables 3, 4). Overall, the results suggest that drilling predators are not selecting prey based on their abundance across lagoons, and that the most abundant species in the assemblage have drilling frequencies below 10%.

## DISCUSSION

We found no evidence that drilling gastropods were more likely to have drilled more abundant prey in this tropical macromollusk dead shell assemblage. This result was consistent across the 61 species and all

TABLE 2.—Life habit, total number of individuals, number of individuals with drill holes, and drilling frequency (median value between sites) for bivalve and gastropod species from One Tree Reef.

GASTROPODA	Life habit	Total abundance (drilled + undrilled)	Drilled individuals	Drilling frequency
<b>Acteonidae</b>				
<i>Pupa nitidula</i>	Epifaunal	116	35	0.32
<i>Pupa sulcata</i>	Epifaunal	2	1	0.5
<b>Cerithiidae</b>				
<i>Cerithium</i> indet. 1	Epifaunal	1	1	1
Cerithiidae indet. 1	Epifaunal	54	18	0.4
Cerithiidae indet. 2	Epifaunal	15	4	0.14
<b>Columbellidae</b>				
<i>Mitrella ligula</i>	Epifaunal	29	7	0.12
<b>Costellariidae</b>				
Costellariidae indet.	Epifaunal	1	0	0
<b>Eucyclidae</b>				
<i>Herpetopoma atrata</i>	Epifaunal	3	0	0
<i>Herpetotoma aspersa</i>	Epifaunal	4	0	0
<b>Epitonidae</b>				
<i>Epitonium philippinarum</i>	Epifaunal	1	1	1
<b>Fissurellidae</b>				
<i>Emarginula</i> indet.	Epifaunal	17	2	0.06
Fissurellidae indet.	Epifaunal	16	0	0
<b>Haliotidae</b>				
<i>Haliotis</i> indet.	Epifaunal	4	0	0
<b>Haminoeidae</b>				
<i>Atys hyalina</i>	Epifaunal	119	1	0
<i>Atys naucum</i>	Epifaunal	5	1	0.12
<i>Liloa</i> indet.	Epifaunal	1	0	0
<b>Nassaridae</b>				
<i>Nassarius (Niotha) albescens</i>	Epifaunal	1	0	0
<i>Nassarius (Zeuxis) bicallosus</i>	Epifaunal	37	9	0
<i>Nassarius cf. estibus</i>	Epifaunal	15	5	0.33
<b>Naticidae</b>				
<i>Natica (Naticarius) onca</i>	Epifaunal	4	0	0
<i>Notocochlis gualtieriana</i>	Epifaunal	43	1	0
<i>Polinices mammilla</i>	Epifaunal	19	0	0
<i>Tectonatica bougei</i>	Epifaunal	6	0	0
<b>Ranellidae</b>				
<i>Gyrineum lacunatum</i>	Epifaunal	3	0	0
<b>Strombidae</b>				
<i>Strombus gibberulus</i>	Epifaunal	1	0	0
<b>Terebridae</b>				
Terebridae indet.	Epifaunal	1	0	0
<b>Turbinidae</b>				
<i>Astrarium</i> indet.	Epifaunal	1	0	0
<b>Triviidae</b>				
<i>Trivia (Trivirostra) oryza</i>	Epifaunal	5	0	0
<b>Trochidae</b>				
<i>Ethalia guamensis</i>	Epifaunal	6	1	0
<i>Stomatella</i> indet.	Epifaunal	1	0	0
Trochidae indet.	Epifaunal	2	0	0
<b>Turridae</b>				
<i>Lophiotoma acuta</i>	Epifaunal	9	0	0
Gastropoda indet. 1	Epifaunal	1	0	0
Gastropoda indet. 2	Epifaunal	2	1	0
<b>BIVALVIA</b>				
<b>Arcidae</b>				
<i>Barbatia</i> indet.	Epifaunal	2	0	0
<b>Cardidae</b>				
<i>Fragum fragum</i>	Infraunal	246	14	0.02
<i>Microfragum festivum</i>	Infraunal	36	3	0
<i>Nemocardium</i> indet.	Infraunal	5	1	0
<b>Galeommatidae</b>				
<i>Ambuscintilla praemium</i>	Infraunal	16	0	0
<i>Marikellia</i> indet.	Infraunal	4	0	0

TABLE 2.—Continued.

GASTROPODA	Life habit	Total abundance (drilled + undrilled)	Drilled individuals	Drilling frequency
<b>Kelliidae</b>				
<i>Kellia rotunda</i>	Infraunal	1	0	0
<b>Lucinidae</b>				
<i>Ctena bella</i>	Infraunal	264	8	0
<i>Wallucina fijiensis</i>	Infraunal	11	0	0
<b>Mytilidae</b>				
<i>Brachidontes</i> indet.	Epifaunal	3	0	0
<b>Tellinidae</b>				
<i>Abranda jeanae</i>	Infraunal	771	57	0.06
<i>Loxoglypta clathrata</i>	Infraunal	1010	107	0.09
<i>Loxoglypta virgulata</i>	Infraunal	8	1	0.25
<i>Pinguitellina robusta</i>	Infraunal	4119	235	0.04
<i>Scissulina dispar</i>	Infraunal	995	39	0.006
<i>Tellina (Quadrans) gargadia</i>	Infraunal	32	6	0.08
<i>Tellina fijiensis</i>	Infraunal	24	0	0
<i>Tellina</i> indet. 1	Infraunal	2	0	0
<i>Tellina</i> indet. 2	Infraunal	1	0	0
<i>Tellina virgata</i>	Infraunal	8	1	0
<b>Veneridae</b>				
<i>Callista (Striacallista) phasianella</i>	Infraunal	17	1	0
<i>Dosinia amphidesmoides</i>	Infraunal	1	1	1
<i>Pitar (Pitarina)</i> indet.	Infraunal	1	0	0
Venerid indet. 1	Infraunal	1	0	0
Venerid indet. 2	Infraunal	5	1	0
Venerid indet. 3	Infraunal	1	0	0
<i>Bivalvia</i> indet.	Infraunal	2	1	0.5

three of One Tree Reef lagoons (Fig. 2). Differences in predation intensity between lagoons do not reflect differences in the number of predators. Species-level differences in predation frequency only became pronounced for rare species (<2% of sample; Table 2), suggesting that sampling sizes were driving these differences. Nonetheless, species- or individual-level predator selectivity (e.g., based on morphological traits) was not evaluated here and cannot be ruled out. These results suggest that drilling predators are randomly selecting prey at low levels relative to other mortality agents, and therefore unlikely to be playing a major role in structuring this tropical molluscan assemblage through consumption.

Previous contributions have shown that by affecting the abundance of their prey, predators can have an effect on prey populations and ultimately, on community structure (Menge 1995; Duffy 2002). Changes to community structure can in turn affect community function (Chapin et al. 1997), especially if changes in population size affect species with high abundance or biomass. For instance, if predators selectively target prey that are carrying out a specific function in the community, i.e., filter feeding particular nutrients from the water column, predators potentially can affect the nutrient cycling of said community. The magnitude of predatory interactions has also been suggested to be dependent on temperature, where higher temperatures lead to increases in metabolic and consumption rates (Sanford 2002; Dell et al. 2014). The data at hand, however, indicate that regardless the tropical nature of the environment, consumption by these predators does not have a strong effect on reef lagoon communities, as the overall predation rate was 7.14% and predators were not selective for accessible prey. Before drilling predators are assumed to have an important role regulating populations of infaunal species and communities, it is first necessary to demonstrate predator selectivity (e.g., Chattopadhyay and Dutta 2013). Only after non-random predation is demonstrated does it need to be explained.

All the predators found in the samples were naticids, and in most cases the drill-holes had the typical naticid beveled morphology. It is possible

TABLE 3.—Absolute abundance of drilling naticid predators per lagoon. Median size of predators and of the six most abundant species is also shown. More individuals were measured from other samples when needed (e.g., the number of naticid individuals measured exceeds the number used for analyses).

Species	1 <sup>st</sup> Lagoon	2 <sup>nd</sup> Lagoon	3 <sup>rd</sup> Lagoon	Size (mm)	N measured
<b>GASTROPODA</b>					
<b>Naticidae</b>					
<i>Natica (Naticarius) onca</i>	4	0	0	92.71	6
<i>Notocochlis gualtieriana</i>	20	11	12	78.67	38
<i>Polinices mammilla</i>	12	2	5	101.51	17
<i>Natica (Tectonatica) bougei</i>	3	1	2	-	-
<b>BIVALVIA</b>					
<b>Cardidae</b>					
<i>Fragum fragum</i>	99	39	108	87.17	149
<b>Lucinidae</b>					
<i>Ctena bella</i>	75	25	164	38.43	135
<b>Tellinidae</b>					
<i>Abranda jeanae</i>	402	190	179	254.38	196
<i>Loxoglypta clathrata</i>	144	335	531	48.92	115
<i>Pinguitellina robusta</i>	915	1091	2113	138.52	153
<i>Scissulina dispar</i>	115	595	285	101.37	191

however, that by assuming that all drilling predators leave a quantifiable trace we are underestimating predation intensity. Some naticid gastropods consume prey by suffocation without leaving a drill-hole, thus the drilling gastropods in our samples may have consumed prey this way. Experiments carried out in Fiji and Guam on the reef-dwelling naticid *Polinices tumidus* found that this predator killed 15–55% of the prey without leaving a borehole (Vermeij 1980; Ansell and Morton 1987). It is thus possible that *P. mamilla* from One Tree Reef exhibits similar behavior as its congeneric *P. tumidus*. However, given that *N. gualtieriana*, and not *P. mamilla*, was the most abundant predator in this assemblage (Table 3), and that killing by

suffocation has not been documented for this species (boreholes produced in 100% of the attacks,  $n = 14$ ; Ansell and Morton 1987), it is unlikely that we are significantly underestimating predation frequencies. Moreover, other experiments testing for alternative modes of predation in naticids found very little evidence to suggest that suffocation is a pervasive feeding behavior (Visaggi et al. 2013). There are, however, other prey-specific behaviors we may be missing, such as the case of *Atyis hyalina*, a seasonally very abundant gastropod that was never found drilled (Table 2). Since *Atyis* has a big shell aperture, predators could be killing this prey by suffocation instead of drilling its shell.

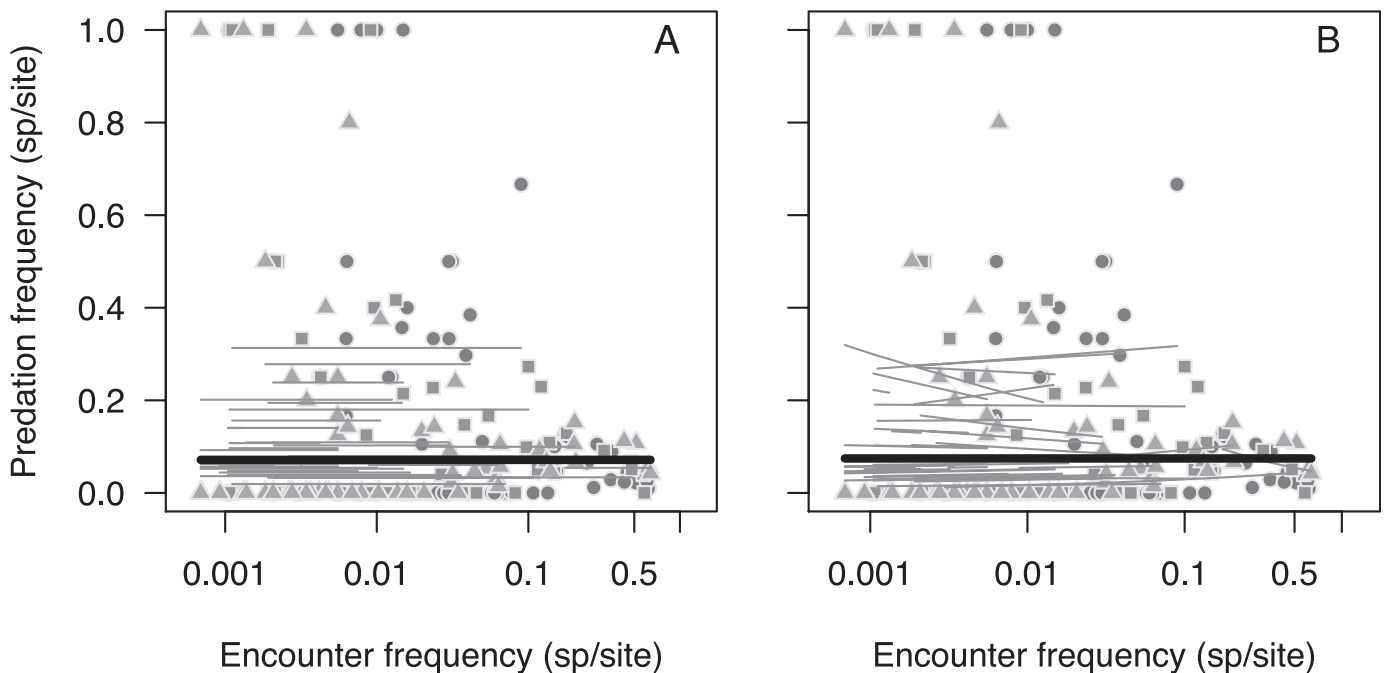


FIG. 2.—Scatterplot of predation frequency and encounter frequency for dead molluscan assemblages. Each symbol represents a species at a site. Circles indicate species in sites from First lagoon, squares indicate species in sites from Second lagoon, and triangles indicate species in sites from Third lagoon. A) The thick dark line is the overall model fit (intercept), and it indicates that the overall value for drilling predation is 7.14%. The thinner lines are the random effects for each species. B) As view A but incorporating a random slope.

TABLE 4.—Summary of generalized linear mixed model statistics for the likelihood of a shell being drilled relative to its encounter frequency. Final best-fit model showing random effects for the slope term for each lagoon and for the different species as a function of relative abundance.

Random effects		
Lagoon	Intercept	
First	-0.163	
Second	0.161	
Third	0.114	
Species	Intercept	Relative abundance
<b>GASTROPODA</b>		
<b>Acteonidae</b>		
<i>Pupa nitidula</i>	1.815	0.042
<i>Pupa sulcata</i>	0.165	-0.189
<b>Cerithiidae</b>		
<i>Cerithium</i> indet. 1	0.375	-0.169
<i>Cerithiidae</i> indet. 1	1.882	0.054
<i>Cerithiidae</i> indet. 2	1.035	-0.006
<b>Columbellidae</b>		
<i>Mitrella ligula</i>	0.117	-0.226
<b>Costellariidae</b>		
<i>Costellariidae</i> indet.	-0.029	0.021
<b>Eucyclidae</b>		
<i>Herpetopoma atrata</i>	-0.121	0.038
<i>Herpetotoma aspersa</i>	-0.130	0.047
<b>Epitoniidae</b>		
<i>Epitonium philippinarum</i>	0.812	-0.071
<b>Fissurellidae</b>		
<i>Emarginula</i> indet.	0.207	-0.020
<i>Fissurellidae</i> indet.	-0.459	0.076
<b>Haliotidae</b>		
<i>Haliotis</i> indet.	-0.081	0.057
<b>Haminoecidae</b>		
<i>Atys hyalina</i>	-1.198	0.073
<i>Atys naucum</i>	0.321	-0.054
<i>Liloa</i> indet.	-0.037	0.012
<b>Nassaridae</b>		
<i>Nassarius (Niotha) albescens</i>	-0.058	0.005
<i>Nassarius (Zeuxis) bicallous</i>	1.844	0.121
<i>Nassarius cf. estibus</i>	1.292	-0.038
<b>Naticidae</b>		
<i>Natica (Naticarius) onca</i>	-0.125	0.036
<i>Notocochlis gualtieriana</i>	-0.522	0.052
<i>Polinices mammilla</i>	-0.484	0.080
<i>Tectonatica bougei</i>	-0.143	0.063
<b>Ranellidae</b>		
<i>Gyrineum lacunatum</i>	-0.074	0.044
<b>Strombidae</b>		
<i>Strombus gibberulus</i>	-0.021	0.022
<b>Terebridae</b>		
<i>Terebridae</i> indet.	-0.022	0.016
<b>Turbinidae</b>		
<i>Astraliium</i> indet.	-0.044	0.009
<b>Triviidae</b>		
<i>Trivia (Trivirostra) oryza</i>	-0.113	0.062
<b>Trochidae</b>		
<i>Ethalia guamensis</i>	0.039	-0.099
<i>Stomatella</i> indet.	-0.029	0.021
<i>Trochidae</i> indet.	-0.062	0.032
<b>Turridae</b>		
<i>Lophiotoma acuta</i>	-0.308	0.065
Gastropoda indet. 1	-0.021	0.022
Gastropoda indet. 2	-0.038	0.034
<b>BIVALVIA</b>		
<b>Arcidae</b>		
<i>Barbatia</i> indet.	-0.061	0.023

TABLE 4.—Continued.

Random effects		
Species	Intercept	Relative abundance
<b>Cardidae</b>		
<i>Fragum fragum</i>	-0.161	0.038
<i>Microfragum festivum</i>	-0.219	-0.105
<i>Nemocardium</i> indet.	0.039	-0.142
<b>Galeommatidae</b>		
<i>Ambuscintilla praemium</i>	-0.327	0.108
<i>Marikellia</i> indet.	-0.098	0.049
<b>Kelliidae</b>		
<i>Kellia rotunda</i>	-0.021	0.022
<b>Lucinidae</b>		
<i>Ciena bella</i>	-1.003	-0.032
<i>Wallucina fijiensis</i>	-0.331	0.070
<b>Mytilidae</b>		
<i>Brachidontes</i> indet.	-0.073	0.047
<b>Tellinidae</b>		
<i>Abranda jeanae</i>	-0.110	-0.051
<i>Loxoglypta clathrata</i>	0.610	0.162
<i>Loxoglypta virgulata</i>	-0.059	-0.067
<i>Pinguitellina robusta</i>	-0.736	-0.571
<i>Scissulina dispar</i>	-0.407	0.251
<i>Tellina (Quadrans) gargadia</i>	0.875	0.007
<i>Tellina fijiensis</i>	-0.620	0.085
<i>Tellina</i> indet. 1	-0.061	0.034
<i>Tellina</i> indet. 2	-0.021	0.022
<i>Tellina virgata</i>	0.085	-0.037
<b>Veneridae</b>		
<i>Callista (Striacallista) phasianella</i>	-0.011	0.037
<i>Dosinia amphidesmoides</i>	0.269	-0.192
<i>Pitar (Pitarina)</i> indet.	-0.036	0.012
<i>Venerid</i> indet. 1	-0.058	0.005
<i>Venerid</i> indet. 2	0.201	-0.066
<i>Venerid</i> indet. 3	-0.048	0.014
<i>Bivalvia</i> indet.	0.260	-0.147

Another biological factor that could be affecting the interpretation of our results is the potential role of hermit crabs 'sequestering' naticid shells. Hermit crabs have been suggested to create anomalies in the abundance of certain shells they occupy (Walker 1989). If this were the case, we would find less naticid predators in the dead shell assemblages than there really are. The samples from One Tree Reef had several live hermit crabs in them (one or two per 0.25 m<sup>2</sup> quadrat) but the great majority of them were occupying highly coiled shells (almost exclusively cerithids) and we never found a living hermit crab using a naticid shell. Thus, even if we cannot discard the role of hermit crabs creating an anomaly in the abundance of naticid shells, the data at hand suggest it is unlikely.

In addition to the drilling predators quantified in this analysis, there are other predators in these soft-sediment communities that can be important causes of mortality. We only have access to records of drilling predation in the dead assemblage but in Recent marine communities, ecologists have carried out research on mollusk predators such as teleost fish, cartilaginous fish, and crabs (e.g., Williams 1982; Jones et al. 1992; Jacobsen and Bennett 2011). More specifically, research also undertaken in the One Tree Reef lagoon showed that predation by three teleost fish did not have a significant impact on the demography or size structure of the benthic mollusk populations (Jones et al. 1992). The authors found that even if these fish were consuming mollusks, it was not sufficient to alter the population dynamics of eight out of ten molluscan prey. Similarly, a study of the stomach contents from over 170 whiptail rays, *Himantura astra*, found mollusks in only 2.2% stomachs of this potential predator (Jacobsen and Bennett 2011). Among the invertebrates, shell-crushing predators such as crabs are known to be important mollusk consumers (Vermeij 1976; Zipser and Vermeij 1978; Bertness 1981). In the

TABLE 5.—Analysis of variance results for comparison between final models with and without a random slope for species.

Model	d.f.	AIC	BIC	logLik	Deviance	$\chi^2$	$\chi^2$ d.f.	Pr ( $\chi^2$ )
Without slope	4	623.72	638.55	-307.86	615.72			
With slope	5	647.54	666.07	-318.77	637.54	0	1	1

samples collected for this study, we found decapods belonging to the Portunidae, Calappidae and Parenthropidae, and some species from these families are known to prey on mollusks (Williams 1982; Lestang et al. 2000). However, given their small size relative to the size of the bivalves, no crab or crab claw found in our same samples would have been capable of crushing a shell retained by the 4 mm sieve (authors' personal observations). We cannot discard that decapod predators influence the population structure of these soft sediments mollusks, however. Even if there are some techniques that have been developed to quantify crushing predation in relation to drilling predation (e.g., Vermeij Crushing Analysis, Stafford and Leighton 2011); given the low drilling frequencies in this system, distinguishing crushing predation from other sources of breakage (i.e., the collection process) could provide ambiguous results, and it exceeded the goals of this study. Still, if crushing predation were important, it would lead to fewer intact shells, and the drilling frequencies here calculated would be inflated. Thus, drilling could be even less important than indicated by these results. Moreover, besides the consumptive effects that predators have in communities, non-consumptive (or trait-mediated) effects are increasingly being recognized as having the same or higher importance (Preisser et al. 2005), particularly in marine environments (Smee and Weissburg 2006; Matassa and Trussell 2011; Gosnell and Gaines 2012). Given that non-consumptive effects can only be quantified in experimental settings, we cannot comment on their potential role in this particular system, yet, it is likely to be important.

A caveat worth considering when interpreting encounter frequency and predator selectivity is a size bias resulting from the 4 mm mesh used to sieve shells. Previous studies have shown that mollusks from tropical, nutrient-poor environments are typically small (e.g., Bouchet et al. 2002; Zuschin and Oliver 2005; Zuschin et al. 2009), suggesting the findings and conclusions from this study should be restricted to macromollusks. If individuals from smaller size fractions had been taken into account, encounter frequencies could have been different and also perhaps selectivity. Visual inspection of the shells captured by 2 mm sieves from our samples suggested however, that they belong to juveniles of the same species found in the 4 mm size fraction. There are mollusks present in the <4 mm fractions, but these individuals represent a minor amount of biomass in the community. In addition, both paleontological and experimental studies have shown positive correlations between predator and prey sizes (e.g., Kelley 1988; Kingsley-Smith et al. 2003; Kowalewski 2004), indicating that the predators and prey within the >4 mm fraction should accurately reflect the predatory dynamics of the >4 mm mollusk fauna sampled. Moreover, this larger size fraction is where the greatest confidence in the fidelity of the dead shell assemblage is, as organisms from smaller size fractions may be lost due to taphonomic factors (Kidwell 2001; Valentine et al. 2006; Archuby et al. 2015).

In addition to finding lack of selectivity for abundant macromollusk species, we also found an overwhelming dominance of infaunal organisms. Tellinids were the most abundant taxa in the studied assemblages, and the predation frequencies observed agree with previous studies that report drilling predation on this family (e.g., Vermeij et al. 1980; Sawyer and Zuschin 2010). Predation frequencies for tellinids from Guam were between 1 and 27% (Vermeij et al. 1980), and 11.6% for tellinids from Bay of Panzano, Italy (Sawyer and Zuschin 2010). The interesting nature of the mollusk community at One Tree Reef, which is dominated by infauna and has low numbers of drilling predators, could

be interpreted as a 'special system' or as a system that is not representative of what is expected from a tropical environment. However, little research has been carried out on soft sediment mollusk communities from Australia and the Indo Pacific (but see Vermeij 1980; Jones et al. 1990; Bouchet et al. 2002), suggesting there is little evidence to substantiate a claim that One Tree Reef is particular in any way. Moreover, One Tree Reef is a Scientific Research Zone in the Great Barrier Reef Marine Park and therefore has been subject to minimal anthropogenic impact. This system thus provides an informative modern analogue to carbonate soft sediments environments preserved in the fossil record.

Lastly, predator selectivity in the fossil record has been extensively studied in an optimal foraging context (e.g., Kitchell et al. 1981; Kelley 1988, 1991; Leighton 2002; Chattopadhyay and Baumiller 2009; Chattopadhyay and Dutta 2013). According to this hypothesis, predators maximize net energy gain per time unit (MacArthur and Pianka 1966; Kitchell et al. 1981; Leighton 2002). For drilling predators, the most time and energy consuming activities are time spent searching and time and energy spent drilling prey. Search time should be negatively correlated to prey density, drilling time should be positively correlated with prey shell thickness (Kitchell 1981; Kelley 1988), and the amount of energy gained should be positively correlated with shell volume or biomass (Kitchell 1981; Powell and Stanton 1985). These three variables are however, measured at different levels. Prey density (search time) is a community-level attribute while mass and thickness are individual-level traits. Here, we looked at the effect of relative abundance (prey encounter rate) on drilling frequencies. Predation frequencies and prey relative abundance were found to be independent, as predators consumed prey at a constant rate. It is worth clarifying the difference between search time and prey encounter rate. Search time includes the time when the predator encounters no prey item, while encounter rate is the probability that the next prey item a predator encounters with be a particular prey item. In this system, search time (mean absolute abundance of *Pinguicellina* per m<sup>2</sup>) is correlated with encounter rate (mean relative abundance of *Pinguicellina* per m<sup>2</sup>) (Pearson correlation,  $r = 0.62$ ,  $p$  value = 0.01,  $df = 13$ ). Given that these two values are positively correlated, prey encounter rate can be an informative (albeit not perfect) estimate of search time. The analyses that we present here provide a first approach to quantify predator selectivity by drilling gastropods. Future studies focused on traits such as shell size, shell shape and shell thickness can shed light on the anti-predatory role they may have on these mollusks, and help understand how they affect or determine predator selectivity (Kitchell et al. 1981; Vermeij 1983; Kelley and Hansen 1993; Leonard-Pingel and Jackson 2013).

Using a modern species-rich dead shell assemblage with taxa that span three orders of magnitude in abundance, we show that drilling predators do not display selectivity for prey species based on encounter frequency. Previous research on rocky hard substrates and intertidal systems has shown that keystone predators disproportionately consume the most abundant prey (Paine 1966; Navarrete and Castilla 2003; Navarrete and Manzur 2008), leading to substantial changes to the structure and functioning of those communities. This important role for predators has also been suggested to have an effect at larger time scales (Vermeij 1993), such as in the ecosystem-wide changes associated to the Mesozoic Marine Revolution (Vermeij 1977; Aberhan et al. 2006; Finnegan et al. 2011). In



contrast, the evidence we present from a tropical dead shell assemblage dominated by infaunal taxa suggests that drilling predators are unlikely to have important direct effects on prey populations. Ultimately, articulating this selectivity approach with individual-level traits used in Optimal Foraging studies, and with detailed analysis of potential non-consumptive effects, can lead to a better understanding of the role of drilling predation in the building and maintenance of this tropical infaunal community.

#### SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: <http://www.sepm.org/pages.aspx?pageid=332>.

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