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PASSIVE DEFENSIVE TRAITS ARE NOT GOOD PREDICTORS OF PREDATION FOR INFAUNAL REEF BIVALVES

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ABSTRACT: Predation is a key biotic interaction that shapes ecological communities. Defensive morphological traits are thought to improve prey survivorship, and knowing which traits aid survivorship is critical to understanding predator-prey dynamics and their impact on community composition. Paleontological studies that use optimal foraging theory and single species experiments suggest that shell size and thickness are traits that affect the outcome of mollusk drilling predation. We analyzed the effectiveness of these morphological traits using a tropical molluscan assemblage from the One Tree Reef lagoon (southern Great Barrier Reef, Australia). Shell mass, shape, thickness, and predation frequency were measured in five bivalve species (n = 804) constituting 80% of the predators' diet. Multiple regression determined that shell mass, shell thickness, and the interaction between the two were important predictors of predation. Drilling was more likely in thinner and larger individuals. However, support for the model that included species identity was markedly stronger, indicating that the morphological traits measured are not general predictors of predation across the five prey species we studied. That is, trait-only models are inadequate for explaining predator-prey dynamics at the community level. Alternatively, active behavioral defenses related to infaunality (like burrowing) appear to be stronger drivers of morphology in this system. Care should be taken when extrapolating results from experiments to communities or large temporal scales, as species with similar traits may not necessarily elicit the same response from predators.

INTRODUCTION

Predators can shape community structure and, on larger time scales, drive the evolution of species and the functioning of ecosystems (Vermeij 1993; Aberhan et al. 2006; Finnegan et al. 2011). By affecting the fitness of their prey, predators lead to changes in prey population dynamics (Meyer and Byers 2005), and over time these changes can modify the relative proportion of different trophic groups in a community (Paine 1966; Duffy 2002). However, individual defensive morphologies that increase prey fitness can modify how predators and prey interact. Therefore, understanding which morphological traits are related to survival can help elucidate how prey affect the selective pressure of predators, and how this two-way interaction impacts community structure.

Anti-predatory morphological traits that improve individual survivorship are more prevalent in the tropics, given that predation tends to be higher at low latitudes (Dudley and Vermeij 1978, Vermeij 1983; Schemske et al. 2009). Physiological processes related to biotic interactions are temperature dependent (Sanford 2002; Dell et al. 2014), and given that metabolic rates are higher in the tropics (Allen et al. 2002), consumption rates increase. Morphological traits such as spines and shell ornamentation (Vermeij 1974; Palmer 1979; Han et al. 2008), thicker shells (Kitchell et al. 1981; Boggs et al. 1984), and larger body size (Kitchell et al. 1981; Kelley 1988; Leonard-Pingel and Jackson 2013; Chattopadhyay et al. 2015) that help defend against predation should therefore be more prominent in these low-latitude environments. The statement regarding body size appears to contradict Bergmann's rule, where a positive association between body mass and latitude is predicted (Blackburn et al. 1999). However, there is little evidence for generalizable body size-latitude relationships among marine bivalves (Berke et al. 2013) so we focus on the role predators may

have on body size instead. If these morphological traits (e.g., ornamentation, shell thickness, and body size) are effective against a predator, or predator guild, and lead to higher fitness, then their effectiveness should span across individuals from different prey species. Thus, the best way to determine which morphologies are more successful against predators is by testing their effectiveness across individuals from different species in the prey community.

Mollusks are ideal candidates for predator-prey studies, because they are a key component of benthic marine communities worldwide. Various surveys and meta-analyses have established that mollusks are exceptionally abundant and diverse at low latitudes (Roy et al. 2000; Bouchet et al. 2002), and that this diversity is both taxonomic and morphological (Roy and Foote 1997; Roy et al. 2001). Even if taxonomic diversity and morphological diversity (disparity) are not always coupled (Roy et al. 2001), mollusks are well-suited for studies of anti-predatory defensive morphologies. The study of morphological traits is particularly tractable for gastropod predators that drill through the shell of their prey because they leave quantifiable evidence of their attack. Also, because drilling predation is ubiquitous among mollusks (Kelley 1988; Kowalewski et al. 1998; Sawyer and Zuschin 2010; Leonard-Pingel and Jackson 2013; Martinelli et al. 2013), valuable insights on the relevance of morphological traits can be inferred from this particular predatory interaction. Extensive paleontological research under the optimal foraging theory framework (MacArthur and Pianka 1966) has shown that morphological traits such as shell size, shape, thickness, and ornamentation can be anti-predatory for mollusks (Vermeij 1974; Palmer 1979; Kitchell et al. 1981; Vermeij 1983; Kelley and Hansen 1993; Han et al. 2008; Leonard-Pingel and Jackson 2013; Chattopadhyay et al. 2015).

Size-limited predation, where larger prey individuals are able to escape predators, is a defensive strategy that influences the size-structure of communities (Osenberg and Mittelbach 1989; Persson et al. 1996; Urban 2007). Evidence for size refuges has been found in a wide array of organisms. For example, mouth gape is a major constraint in the ability of fish to capture prey (Osenberg and Mittelbach 1989; Persson et al. 1996; Ray and Corkum 1997; but see Scharf et al. 2000). Similarly, gape width is also important for fruit-eating birds, mammals, reptiles, and among the invertebrates, sea stars and gastropod predators (Paine 1976; Wheelwright 1985; Jaksic 1989; Karanth and Sunquist 1995; Rodriguez-Robles et al. 1999). For naticid gastropods in particular, predation can be size-limited because naticids use their foot or mesopodium to hold and wrap around their prey (Carriker 1981). If the prey is large, the gastropod cannot hold it properly and the risk of the prey escaping or of drill holes being incomplete increases, as demonstrated by Kitchell et al. (1981). Nevertheless, in terms of optimal foraging, when confronted with prey that have the same energetic cost and demand the same foraging time, predators should prefer larger prey because this maximizes the energy return (Kitchell et al. 1981; Leighton 2002). All else being equal, drilling predators should select larger individuals but a size-refuge would be attained if larger individuals have a lower mortality relative to attack frequency (e.g., Leonard-Pingel and Jackson 2013; Chattopadhyay et al. 2015).

Shell shape influences the ability of predators to seize their prey (Quensen and Woodruff 1997; DeWitt et al. 2000; Lakowitz et al. 2008). Bivalves and gastropods have a wide range of shapes (Raup 1961, 1966; Stanley 1970, 1975), and although it remains largely understudied, this morphological diversity appears to be high in the tropics (Roy et al. 2001). Evidence for morphological evolution driven by predators has been presented in marine, freshwater, and terrestrial mollusks (Seeley 1986; Quensen and Woodruff 1997; DeWitt et al. 2000; Lakowitz et al. 2008). Previous studies that focused on drilling predators found a weak negative relationship with shape, suggesting that elongated shells were drilled less often than equi-dimensional shells (Chattopadhyay et al. 2015); however, this was not significant at the species level (Chattopadhyay et al. 2015). These results suggest that for a given prey size, individuals with spherical shells will be expected to have higher drilling frequencies than individuals with ellipsoidal shells.

Shell thickness is a biomechanical morphological trait that influences energetic costs of drilling for a predator (Kitchell et al. 1981; Boggs et al. 1984). In terms of optimal foraging, for a given prey size, individuals with thicker shells provide a lower energetic gain because the cost of drilling them is higher than the cost of drilling individuals with a thinner shell. Because drilling gastropods dissolve shells by secreting acids and enzymes in addition to scraping shell tissue with their radula (Carriker 1981; Kabat 1990), thicker shells require more acid. Drilling thicker shells or thicker parts of the shell also demands more time (Boggs et al. 1984; Dietl and Herbert 2005), and if gastropods are more vulnerable while drilling (Dietl et al. 2004), they can be at risk of being attacked by predators themselves. There is evidence for behavioral changes in the position of drill holes from wall (thicker) to edge drilling (thinner) when there is higher competition in the environment (Dietl et al. 2004). Still, it is unknown whether drilling gastropods can determine if some shells are thicker than others (Kabat 1990), and there is experimental evidence to suggest that this is not the case, at least for naticids drilling on corbulids (Anderson 1992). Regardless, if gastropods consistently prefer prey with thinner shells, it can be an indication that when in permanent contact with a prey population they can evolve a preference towards thin shells (or other features related to it).

In addition to thickness, other modifications to prey shells such as spines and ribs have been suggested to have an antipredatory role (Vermeij 1974; Palmer 1979; Han et al. 2008). For example, strong sculpture and spines in gastropods can deter shell-crushing crabs (Vermeij 1974; Zipser and Vermeij 1978; Han et al. 2008), and molluscivore fish (Palmer 1979).

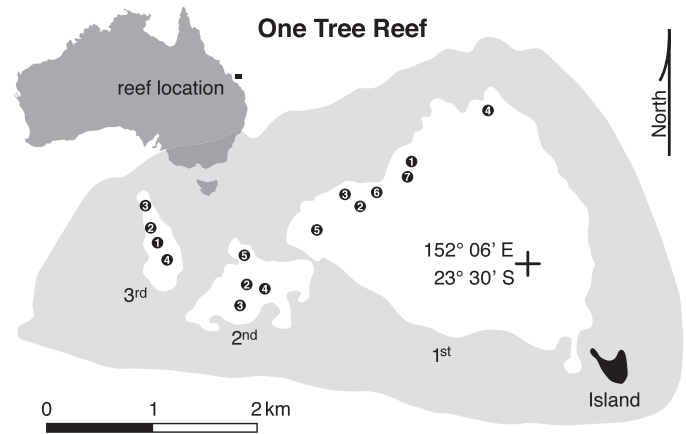


FIG. 1.—Schematic map of One Tree Reef, southern Great Barrier Reef. The reef outline (shaded gray area) surrounds the three lagoons (white), and One Tree Island (black). Numbers inside each lagoon indicate the sites where samples were collected. Reef and lagoon outline were traced from Google Earth imagery.

However, several studies focused on shell ornamentation and drilling predators have found that both ornamentation and spines are ineffective against these gastropods (Feifarek 1987; Harper and Skelton 1993; Willman 2007; Leonard-Pingel and Jackson 2013), which is why these traits are not considered here.

The aim of this study was to determine if morphological traits—i.e., shell size, shell shape, and shell thickness—act as effective defenses against drilling predators in a tropical marine system. Models based on optimal foraging theory and single species experiments suggest that large and thin shells will experience greater predation whereas predators will avoid shells that are too large and too thick. Alternatively, the influence of the morphological traits on predation rates might not be consistent among species; or morphological traits might not be important at all (i.e., predators attack the prey community randomly or based on other, unmeasured factors). This analysis seeks to (1) determine which potentially anti-predatory morphological traits are effective in reducing prey mortality in tropical environments, and (2) establish if these defensive morphological traits are pervasive across the prey community or if there are species-specific variations. The results will lead to a better understanding of the role of passive defensive morphologies, which is key in determining the role of predators in shaping community structure over time.

METHODS

Study Site and Materials

Sampling was carried out at One Tree Reef, southern Great Barrier Reef, Australia (23°20' S, 152°06' E) in 2012. The reef crest surrounds three lagoons (roughly 10–13 km² in extension) that have coral patches interspersed with sand (Ludington 1979). Soft sediments with infaunal organisms were collected at four to seven different sites in each of the three lagoons (Fig. 1). Sites ranged in depth from 4.3 to 6.1 m (ponded depth). At each collection site, divers sampled the top 0.1 m of 1 m² of sediment using an 80 mm diameter air-lift and 1 mm mesh bags.

After collection, samples were wet sieved using a 4 mm sieve. Molluscan material retained by a 4 mm sieve was used because juvenile recruitment pulses were observed in the 2 mm sieve fractions. Given that smaller shells have a lower probability of being preserved relative to larger ones (Kosnik et al. 2007; Cooper et al. 2006), we used the fraction retained by 4 mm sieves to ensure comparability with the fossil record (Kidwell 2001). These dead shell assemblages are representative of Recent fauna as the live-dead agreement is high (Martinelli et al. 2016), and the median age

TABLE 1.—Details about the five study species: family, relative abundance, contribution to the predators' diet, the number of individuals measured, median individual thickness (mm) and shell mass (mg).

Species	Family	Relative abundance	Contribution to predators' diet	Drilling frequency*	Measured individual	Thickness (mm)	Mass (mg)
<i>Abranda jeanae</i>	Tellinidae	11%	13%	6%	196	0.17	121.94
<i>Loxoglypta clathrata</i>	Tellinidae	13%	18%	9%	115	0.19	30.30
<i>Pinguitellina robusta</i>	Tellinidae	58%	38%	4%	153	0.38	89.44
<i>Scissulina dispar</i>	Tellinidae	13%	6%	0.6%	191	0.18	76.44
<i>Fragum fragum</i>	Cardidae	2%	4%	2%	149	0.41	61.00

* from Martinelli et al. 2015

of the assemblages is 19 years (Kosnik et al. 2015). These assemblages have also been previously used to quantify drilling predation and its relation to species relative abundance (Martinelli et al. 2015).

To quantify the effectiveness of potential defensive morphologies we selected a subset of species that contributed most to the diet of drilling predators (Table 1; Fig. 2). The predators' diet was previously estimated as the proportion of each prey species to the total drilled assemblage (Martinelli et al. 2015), and we focus on the five bivalve species with sufficient sample size (> 100 individuals): *Abranda jeanae* (Tellinidae), *Loxoglypta clathrata* (Tellinidae), *Pinguitellina robusta* (Tellinidae), *Scissulina dispar* (Tellinidae), *Fragum fragum* (Cardidae). Gastropods were either not a significant component of the predators' diet, or were not abundant enough to include in the analyses. An alternative approach would have been to also include other taxa of similar size, shape, and thickness that were not found drilled by the predators, and compare these with the species selected. However, those 'potential' species with similar features but without drilling did not exist in the sampled community in numbers that would be informative, or for all the selected traits.

Identification of Predatory Traces

Once the species were selected, a random subset of individuals that contained both drilled (complete) and undrilled individuals of different sizes was used. Predation by drilling predators was assumed successful when the drill holes were complete (i.e., the hole went through the shell). In order to be considered drill holes, the traces had to have a regular circular outline and be perpendicular to the shell (Kowalewski 2002; Kelley et al. 2003; Yanes and Tyler 2009). There were no significant differences between predation on right and left valves ($\chi^2 = 0.95$, p value = 0.81, $df = 3$), and no shell had multiple drill-holes or incomplete drill holes. Therefore, only unfragmented right valves were counted, measured and used to look at predation marks. Any unfragmented right valve with a complete drill-hole was considered a drilled individual. Predation frequency was calculated as the number of drilled individuals of a species, divided by the total number of individuals from that same species (Lower Taxon Frequency, Kowalewski 2002).

Measurement of Anti-Predatory Traits

Shell mass was measured for each individual, with and without a drill hole (804 right valves in total, Table 1). To determine the shell mass of the articulated bivalve at death, individual valve mass was multiplied by two.

Shell shape was measured as the sum of the absolute deviations of x (length), y (height) and z (width) relative to the diameter, d , of a sphere of the same geometric mean size: $([|d - x| + |d - y| + |d - z|] / d)$ to obtain a dimensionless shape metric (following Kosnik et al. 2009).

Shell thickness was measured at the center of each right valve using a thickness gauge. The mid-center position was chosen as a way to standardize data collection between species, as there was no stereotypy for any position of drill holes across all species. Consequently, thickness was measured in the middle of the shell, given that the shell edge is usually

thinner than the center. All linear measurements were made to the nearest 0.01 mm and \log_2 transformed. All the correlation values presented correspond to \log_2 measurements.

Model Selection

A generalized linear model (GLM) with a logit link function and binomial response variable (drill-hole=1, no drill-hole=0) was used to determine if any of the morphological traits, or an interaction between traits had a significant effect on the probability of an individual being drilled. Because mass and shape were strongly collinear (see Results), only mass and thickness were included as predictor variables. To explore species effects, a second GLM was run allowing for species-specific intercepts and mass and thickness slopes. We further ran five species-specific GLMs to assess whether the traits that were good predictors in the pooled species models were the same in the single species models. Overdispersion in all models was checked by calculating the ratio of model residual deviances to residual degrees of freedom. GLM analyses were carried out using the 'glm' function in the 'stats' package in the statistical programming language R (Version 3.0.2, R Core Team 2014). The 'drop1' function with chi-squared test was used to determine which of the fixed factors and interactions to keep for each of the two models. Code and data files are provided as supplementary material.

RESULTS

Correlations Between Measured Variables: Mass, Shape, And Thickness

Shell shape and mass were highly correlated, and larger species tended to be more spherical than smaller species (Pearson correlation, $r = 0.91$, p value < 2.2×10^{-6} , $df = 803$, Fig. 3). As a result, shape was not included in the GLM; however, results were interpreted taking into account that mass is a proxy for shape. Finally, shell thickness and mass (for all measured individuals from all species) were significantly correlated but the correlation coefficient was less than 0.6 (Pearson correlation, $r = 0.45$, p value < 2.2×10^{-6} , $df = 803$), therefore thickness and mass were included in the GLM analyses (Zuur et al. 2010).

Model Selection

The best trait-only model shows that prey with thicker shells and lower mass tend to experience lower levels of mortality by drilling predators (AIC = 548.03, Fig. 4, Table 2). However, when the data points for undrilled and drilled individuals are plotted over the model probabilities this trend is not visually obvious (Fig. 5). Allowing for species effects improved the model (AIC = 536.16, Table 3). Interactions between species and mass, and a three-way interaction between species, mass, and thickness were not significant. The best model indicates that only thickness explains predation frequency for three of the five species (Table 3). Single species models indicated that neither thickness nor mass were consistently good

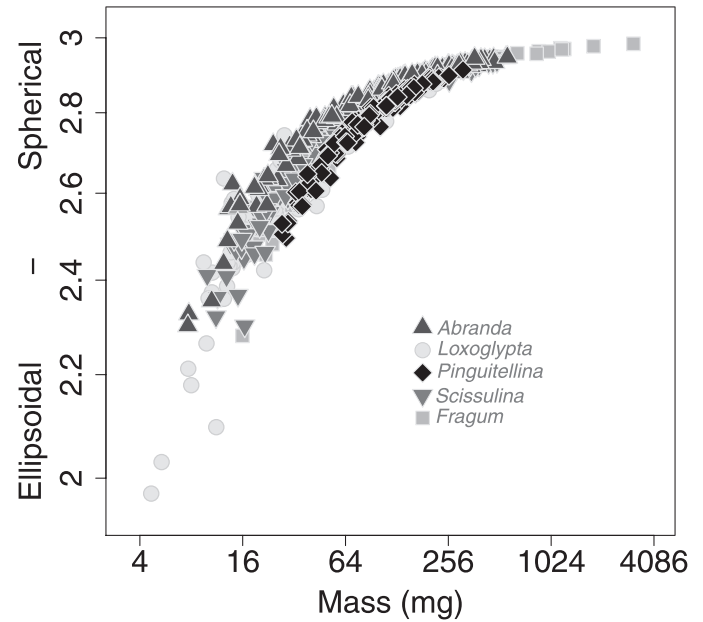
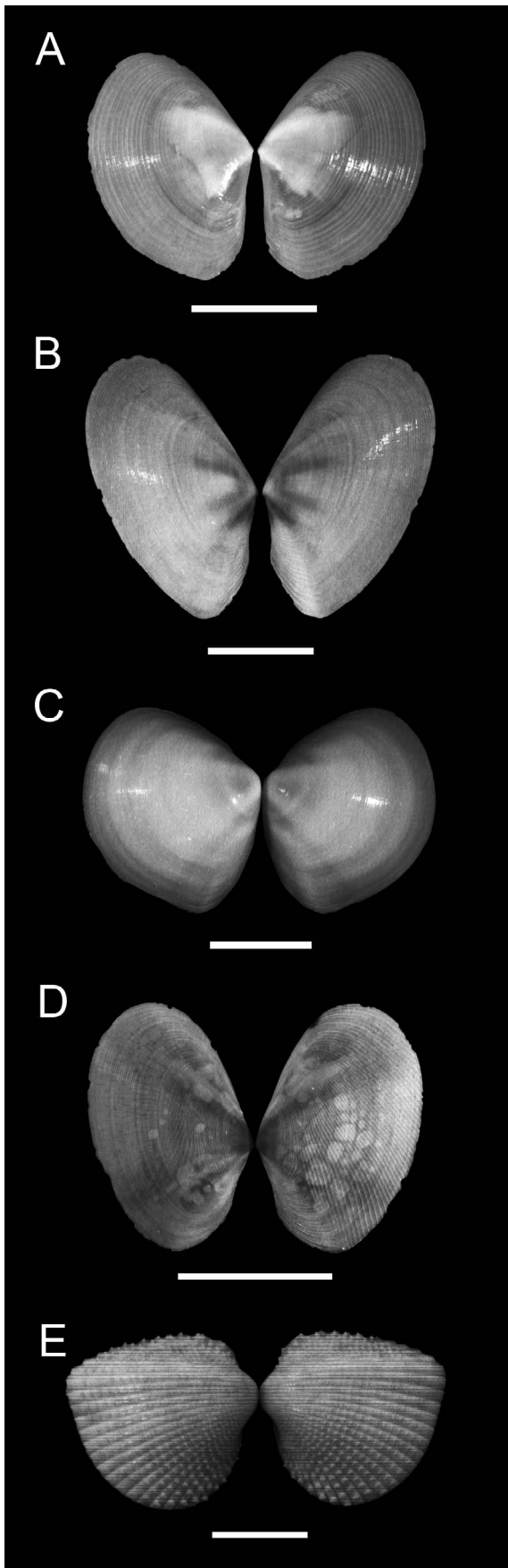


FIG. 3.—Scatterplot showing the correlation between shell shape (from ellipsoidal to more spherical) and shell mass.

predictors for predation among individuals from different species (Table 4). For *Abranda* only mass was a significant predictor, while for *Scissulina* only thickness was significant, for *Loxoglypta* both mass and thickness were significant, for *Pinguitellina* and *Fragum* neither trait was a significant predictor (Table 4).

We found no evidence for overdispersion in residuals for either model as the ratio of model residual deviances to residual degrees of freedom was smaller than 1 in both cases.

DISCUSSION

Using over 800 individuals of key bivalve prey species in a tropical reef-lagoon community, the findings suggest that drilling predators display a mild preference for individual prey based on shell thickness and mass, but these results were not widespread or species independent.

Predator Preference at an Assemblage Level: Shell Thickness and Mass

Despite species-specific differences, there was a tendency for predators to target individuals with thinner shells, a behavior which maximizes net energetic return (Kitchell et al. 1981; Boggs et al. 1984). Drilling shells requires the production of acids and enzymes that dissolve calcium carbonate. This has a metabolic cost (Person et al. 1967), and possibly a 'storage' cost given that boring gastropods have specialized organs to produce and store these chemicals (accessory boring organ or ABO, Carriker 1969, 1981). Histological studies looking at the secretory cells of the ABO have found significantly more mitochondria in the cells of snails that drill relative to other snails (Carriker et al. 1963), suggesting that the metabolic cost is lower if thinner shells are preferred over thicker shells.

Attacking individuals with thinner shells can also reduce the time spent drilling a single prey, which also comes with potential benefits to the predator. Consuming prey quickly enables the predator to consume more

FIG. 2.—Images of the taxa used in this study. All scale bars are 10 mm. A) *Abranda jeanae*. B) *Loxoglypta clathrata*. C) *Pinguitellina robusta*. D) *Scissulina dispar*. E) *Fragum fragum*.

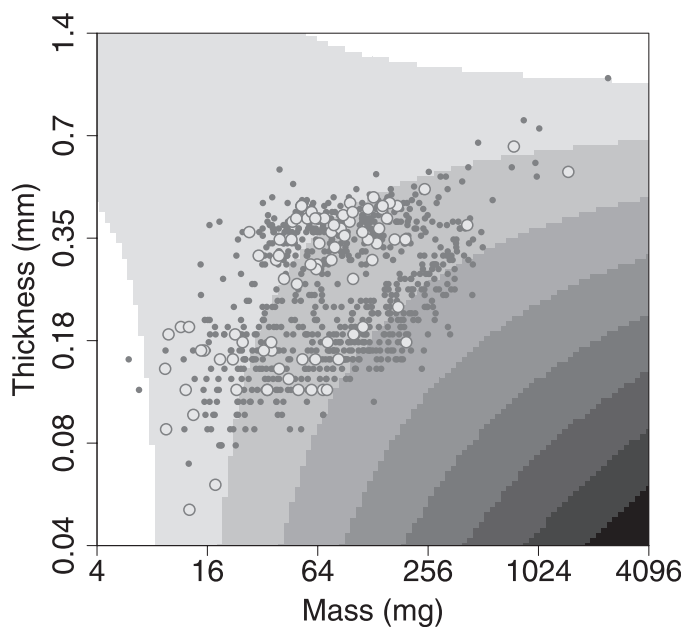


FIG. 4.—Probabilities of predation based on the defensive morphologies model. Lighter shades of gray indicate greater predation probabilities and darker shades of gray indicate lower predation probabilities. Small dots in darker gray represent non-drilled individuals from the five species. Larger light gray dots represent drilled individuals from the five species.

prey per time unit (Boggs et al. 1984), assuming drilling is the rate-limiting step (vs. searching). This is likely given the high density of living mollusks in these reef lagoons (median density: 152 individuals/m², Martinelli et al. 2015). Drilling prey quickly also reduces the time predators are exposed to their own predators, be it conspecifics or predators from a different guild. Given that, in general, selective pressures imposed by predators are stronger than selective pressures by prey (Vermeij 1993), consuming prey quickly would increase the fitness of the predator as it is less exposed to becoming prey itself.

While cost-benefit analyses of drilling predator behavior have also found support for drilling prey with thinner shells (Kitchell et al. 1981; Kelley 1988, 1991; Chattopadhyay and Baumiller 2009), it is unlikely that predators are able to determine shell thickness prior to drilling (Boggs et al. 1984; Kabat 1990). Boring gastropods use their osphradium—a sensory epithelium—to recognize prey chemical cues (Emery 1992). If a predator evolves the ability to associate particular chemical cues with a particular prey species, this could be a mechanism through which predators could select thinner-shelled prey. If, however, gastropods are not able to consistently identify prey depending on their thickness or other cues, it is possible that thicker-shelled individuals have higher fitness (survive failed attacks) than thinner-shelled ones.

Along the same lines, it is interesting to ask why selectivity for a trait varies between prey species. Bivalves with thinner shells are the ones for which thickness was a significant predictor of predation (see Tables 1, 3, 4, Fig. 5). Also, and perhaps more important, the range of shell thickness variation is not the same for all the species (Fig. 5, compare *Pinguitellina* and *Fragum* with the rest). Assuming that predators select thinner-shelled prey, they would not have much variation from which to choose from in *Pinguitellina* and *Fragum*. The findings in this study suggest that for a trait to be informative at a community level, the range of variation in that trait should be similar between species.

Shell mass and shape are also important to drilling predators, but given that these morphological traits are highly correlated (Fig. 3), their relative importance cannot be disentangled. Larger individuals were found to have

TABLE 2.—Summary of generalized linear model statistics for the effects of mass and thickness on the likelihood of a bivalve shell being drilled. (A) The effect of dropping the variables (an interaction) from the full model, with Akaike Information Criterion (AIC) and chi-square statistics, (B) The final predictive model (showing estimates, standard errors and p values). Asterisks (*, **, ***) indicate significance at the 0.05, 0.005 and 0.0005 level, respectively.

A) Variable	d.f.	AIC	Pr (χ^2)
Thickness: Mass	1	548.03	0.005**
B)			
Estimate	SE	p value	
Intercept	-1.523	1.186	0.199
Thickness	0.091	0.174	0.602
Mass	-0.910	0.496	0.066
Thickness: Mass	0.254	0.084	0.002**

greater predation frequencies than smaller individuals, and therefore more spherical individuals had greater predation frequencies than ellipsoidal individuals. There seems to be a relationship between mass and shape throughout ontogeny within a single species as shells generally become more spherical with increasing mass (Fig. 3). Since shell mass and shape were only significant for one species when random slopes were accounted for (Table 3), any further explanation on the relevance of these traits for predators would be highly speculative. A recent paper by Chattopadhyay et al. (2015) also looking at the role of morphological traits found a significant decrease in predation with increasing size (see also Leonard-Pingel and Jackson 2013). However, this conclusion was not supported by a multiple regression presented in the same paper. The same authors found that for shell shape there was significant trend for elongated species to be drilled more often. However, the figures in their paper show that equidimensional species present more drill holes than elongated ones (Chattopadhyay et al. 2015, fig. 3C). Given that in this study individuals (within a species) seem to become more spherical with increasing size, it is possible that the higher drilling observed in larger sizes has more to do with sphericity instead of size, as suggested by Chattopadhyay et al. (2015). It could also well be that the studied prey are in general too vulnerable for small variations in morphology to make a difference to predators. Evidence for this has been found for predation by crabs on gastropods where prey defensive morphologies had a significant effect but this was minor relative to the effect of predator abundance (Stafford et al. 2015). In general there is no strong generalized support for these traits as results vary depending on the analysis or the scale used to test the question. Thus, it is likely that other selective forces, such as an infaunal life habit, or even phylogenetic constraints, are driving shell shape and size.

Active Defenses and the Role of Other Predators

Active defenses such as adopting an infaunal life habit can be key to surviving predators (Vermeij 1977). For example, infaunality has been suggested to evolve as a response to greater predation pressure during the Mesozoic (Vermeij 1977; Aberhan 1994; Aberhan et al. 2006 but see McRoberts 2001), and at the end-Cretaceous mass extinction (Lockwood 2004; Aberhan and Kiessling 2015). In One Tree Reef, the mollusk community is overwhelmingly dominated by infaunal tellinids (86% of the fauna, Martinelli et al. 2015). This bivalve family is well known for its rapid burrowing habits (Stanley 1981; Checa and Jiménez-Jiménez 2003). Tellinids are also amongst the most speciose groups of bivalves (Mikkelsen 2011), and their radiation in the Mesozoic (Stanley 1968) and ecological success in marine environments today may be partly due to this burrowing ability facilitated by long siphons (Mikkelsen 2011) and oblique ribs in their shells (Checa and Jiménez-Jiménez 2003). The dominance of these

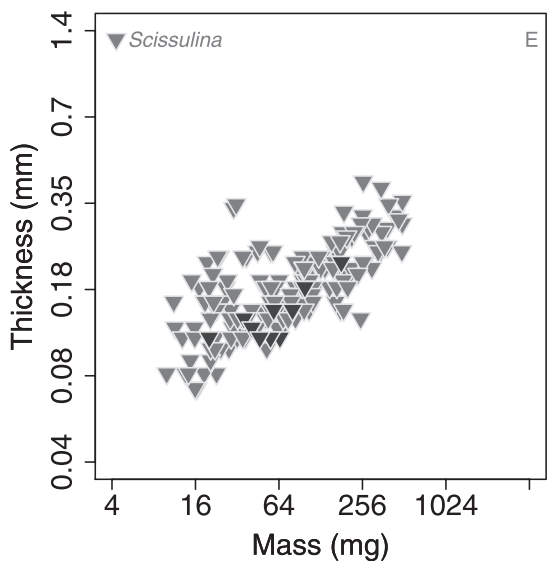
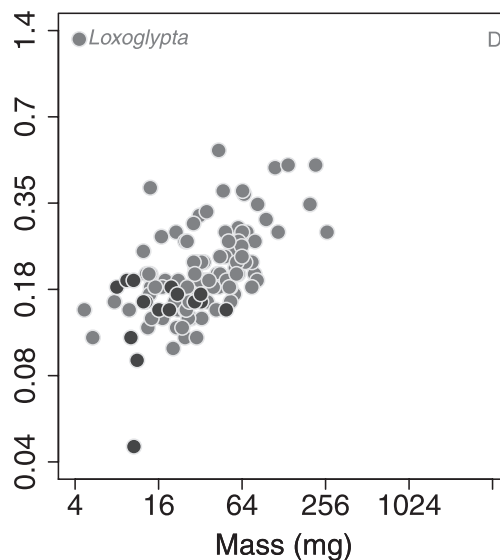
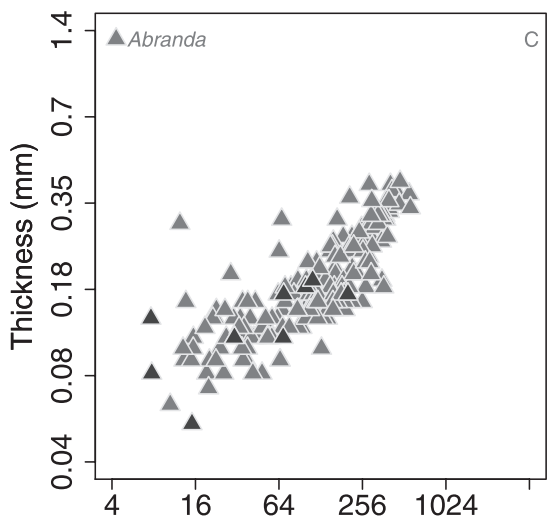
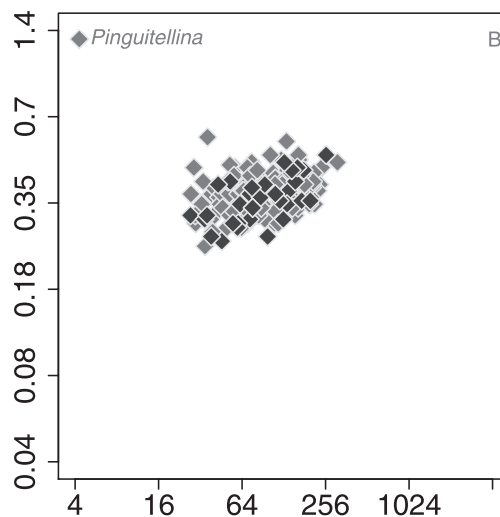
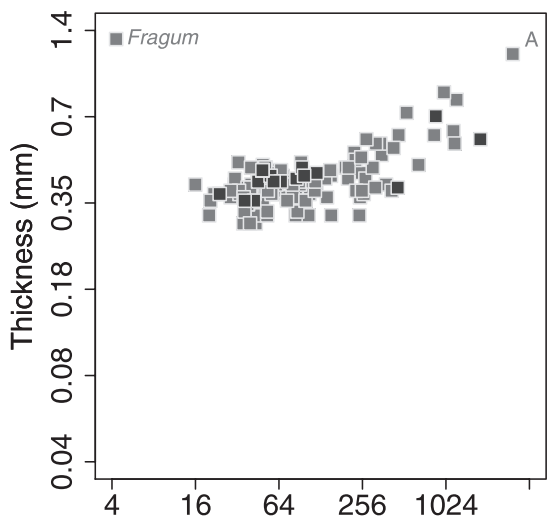


TABLE 3.—Summary of generalized linear model statistics for the effects of mass and thickness on the likelihood of a bivalve shell being drilled accounting for species effects. (A) The effect of dropping variables (and interactions) from the full model, with Akaike Information Criterion (AIC) and chi-square statistics. (B) The final predictive model (showing estimates, standard errors and p values). Asterisks (*, **, ***) indicate significance at the 0.05, 0.005 and 0.0005 level, respectively.

A) Variable	d.f.	AIC	Pr (χ^2)
Thickness: Species	5	536.16	3.188e-06***
B)			
Estimate	SE	p value	
Intercept	-0.730	0.912	0.423
<i>Abranda jeanae</i>	-6.927	2.219	0.002**
<i>Loxoglypta clathrata</i>	-7.978	2.478	0.001**
<i>Pinguitellina robusta</i>	-2.624	1.527	0.086
<i>Scissulina dispar</i>	-6.314	2.259	0.005**
Thickness: <i>Abranda jeanae</i>	-1.740	0.685	0.011*
Thickness: <i>Loxoglypta clathrata</i>	-2.741	0.872	0.002**
Thickness: <i>Pinguitellina robusta</i>	-1.479	0.838	0.077
Thickness: <i>Scissulina dispar</i>	-1.564	0.731	0.032*
Thickness: <i>Fragum fragum</i>	0.976	0.737	0.185

infaunal rapid burrowers in this community could explain why the morphological traits studied were not general predictors of predation. Even if this prediction was not tested, the very low predation rates in this mollusk community (7%, Martinelli et al. 2015) suggest infaunality may be the most important factor. Similar results have been found by Leonard-Pingel et al. (2013) for lower predation in infauna, and especially in tellinids like the dominant group in this study. Interestingly, Chattopadhyay et al. (2015) did not find evidence for lower predation in modern infaunal bivalves from the Red Sea. However, even if those communities were also dominated by infauna, the species composition was markedly different as tellinids only represented 14% of the individuals (Chattopadhyay et al. 2015, table 1).

Finally, drilling gastropods are certainly not the only mollusk predators in this tropical marine community. Crab species from the Portunidae, Calappidae and Paranthropidae families were also found in the same dead shell assemblages. Other studies carried out at One Tree Reef and other areas in the southern Great Barrier Reef indicate that there are both cartilaginous and bony fish that consume mollusks (for a brief review see Martinelli et al. 2015). Regardless, these predators seem to have little effect on the population dynamics of some of the key bivalves species (e.g., Jones et al. 1992). It is possible, however, that these invertebrate and vertebrate consumers are regulating the population dynamics of drilling gastropods in this system, and generating an indirect impact on bivalve populations. Experimental studies on muricids have shown that the presence of a secondary predator can lead to a higher proportion of failed attacks (Chattopadhyay and Baumiller 2007). Similarly, disruptive competition between naticid predators has also been shown to lead to more failed predation attempts in experimental settings (Hutchings and Herbert 2013). These findings from experimental studies thus suggest that behavioral interactions between prey and predators at different trophic levels can have a quantifiable impact on the outcome of predation.

Implications for Experiments Testing for Optimal Foraging

Both marine ecologists and paleobiologists have used optimal foraging theory to test hypotheses using experimental and observational data (e.g.,

TABLE 4.—Summary of generalized linear model statistics for the effects of mass and thickness on the likelihood of each species (A–E) being drilled. The effect of dropping the variables from the full model, with Akaike Information Criterion (AIC) and chi-square statistics is shown first, and the final predictive model (showing estimates, standard errors and p values) follows. Asterisks (*, **, ***) indicate significance at the 0.05, 0.005 and 0.0005 level, respectively.

A) <i>Abranda jeanae</i>	d.f.	AIC	Pr (χ^2)
Variable			
Mass	1	80.991	0.002**
B) <i>Loxoglypta clathrata</i>			
Estimate	SE	p value	
Intercept	1.116	1.294	0.368
Mass	-0.668	0.2315	0.004**
C) <i>Pinguitellina robusta</i>			
Variable	d.f.	AIC	Pr (χ^2)
Thickness	1	80.67	0.024**
D) <i>Scissulina dispar</i>			
Variable	d.f.	AIC	Pr (χ^2)
Thickness	1	81.387	0.016**
E) <i>Fragum fragum</i>			
Variable	d.f.	AIC	Pr (χ^2)
Mass	1	80.67	0.024**
Thickness	1	81.387	0.016**
A) <i>Abranda jeanae</i>			
Estimate	SE	p value	
Intercept	-2.944	3.281	0.369
Mass	-0.806	0.371	0.029*
Thickness	-1.903	0.918	0.038*
B) <i>Loxoglypta clathrata</i>			
Variable	d.f.	AIC	Pr (χ^2)
Thickness	1	164.09	0.073
C) <i>Pinguitellina robusta</i>			
Variable	d.f.	AIC	Pr (χ^2)
Thickness	1	164.09	0.073
D) <i>Scissulina dispar</i>			
Variable	d.f.	AIC	Pr (χ^2)
Thickness	1	80.461	0.028*
E) <i>Fragum fragum</i>			
Variable	d.f.	AIC	Pr (χ^2)
Mass	1	116.10	0.179
Thickness	1	117.73	0.064
A) <i>Abranda jeanae</i>			
Estimate	SE	p value	
Intercept	-7.019	2.070	0.001***
Thickness	-1.556	0.732	0.033*
B) <i>Loxoglypta clathrata</i>			
Estimate	SE	p value	
Intercept	2.918	2.951	0.323
Thickness	-0.332	0.256	0.195
Mass	2.218	1.235	0.072

Kitchell et al. 1981; Boggs et al. 1984; Kelley 1988, 1991; Anderson et al. 1991; Leighton 2002; Chattopadhyay and Baumiller 2009; Chattopadhyay and Dutta 2013). Experiments in aquaria have the benefit that variables can be controlled, but at the same time the simplified environment can lead to modified behaviors (Kabat 1990). The results presented here are from data

FIG. 5.—Scatterplots showing correlation between shell mass and thickness for each species. A) *Fragum fragum*. B) *Pinguitellina robusta*. C) *Abranda jeanae*. D) *Loxoglypta clathrata*. E) *Scissulina dispar*. Species symbols as in Figure 3; symbols in black indicate drilled individuals and symbols in gray indicate undrilled individuals.

collected in the natural system where the interactions play out, and can help link observational and experimental studies. We found that model fits are better when species effects are included (Table 4), and that defensive traits that appear to be significant at an assemblage level cease to be significant when species-specific variations are accounted for (Tables 2, 3, 4). Therefore, if experimentalists seek to obtain results that are informative about how interactions play out in nature, great care needs to be taken to select prey and predator populations because otherwise species-specific preferences may not reflect assemblages or natural communities.

Overall, these results indicate that molluscan morphological traits like mass, shape and thickness are not universally defensive, and that species exhibit different ranges of variation for these traits. This lack of generality in the explanatory power of defensive traits is in agreement with results by Chattopadhyay et al. (2015) from the northern Red Sea, and supports their suggestion that in infaunal mollusks, shell size, thickness, and shape may be more influenced by selective forces other than predators. Stronger interdisciplinary research between marine ecologists and paleobiologists involving experiments and testing of hypotheses with modern, subfossil, and fossil data will help elucidate the role of drilling predators and other selective forces in the assembly of communities in different environments over time.

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SUPPLEMENTAL MATERIAL

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

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