

## THE ROLE OF DRILLING PREDATION IN ISOLATED, NUTRIENT-POOR ECOSYSTEMS: FIRST INSIGHTS FROM RAPA NUI, POLYNESIA

JULIETA C. MARTINELLI,<sup>1</sup> SANDRA GORDILLO,<sup>2,3</sup> M. CARLA DE ARANZAMENDI,<sup>4,5</sup> AND MARCELO M. RIVADENEIRA<sup>6,7</sup>

<sup>1</sup>*School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA*

<sup>2</sup>*Universidad Nacional de Córdoba, Facultad de Filosofía y Humanidades, Museo de Antropologías, Córdoba, Argentina*

<sup>3</sup>*Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Instituto de Antropología de Córdoba (IDACOR), Avda. Hipólito Yrigoyen 174, X5000JHO, Córdoba, Argentina*

<sup>4</sup>*Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Cátedra de Ecología Marina, Av. Velez Sarsfield 299, X5000JJC, Córdoba, Argentina*

<sup>5</sup>*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Diversidad y Ecología Animal (IDEA), Ecosistemas Marinos y Polares (ECOMARES), Av. Velez Sarsfield 299, X5000JJC, Córdoba, Argentina*

<sup>6</sup>*Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Av. Bernardo O'Higgins 877, Coquimbo, Chile*

<sup>7</sup>*Center for Ecology and Sustainable Management of Oceanic Islands, Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile*  
email: [martinellijulieta@gmail.com](mailto:martinellijulieta@gmail.com)

**ABSTRACT:** As a biotic interaction, drilling predation is affected by the evolutionary histories of the predator and prey, as well as the environment. A unique location with distinctive evolutionary histories and environmental conditions is the remote island of Rapa Nui. For mollusks, an evolutionary history in relative isolation has led to high rates of endemism (35–40%), in an area that has some of the most nutrient-poor waters of the global ocean. Here, we use death assemblages collected in Rapa Nui to answer two main questions: (1) How does a pervasive interaction like drilling predation play out in an isolated, oligotrophic marine system? and (2) What role do the environment (exposed vs. sheltered sites) and species traits (feeding, mobility, life habit) play in ‘protecting’ the prey? We predicted that predation would be low relative to other tropical and subtropical islands given the oligotrophic conditions and found that the average drilling frequency (DF) was 5.67% (n = 6122). We observed no significant differences in DF between feeding guilds, mobility types, or life habits. Sheltered sites dominated by the infaunal bivalve *Ctena bella* had higher predation. In terms of passive defenses for *C. bella*, larger body size was not an effective defense against drilling predators. We show that drilling predation in Rapa Nui is lower than in high-latitude regions, and it is dependent on how sheltered or exposed sites are. Historically and currently, Rapa Nui has been subject to multiple anthropogenic stressors, including over-extraction and tourism, making efforts to understand its endemic species and their interactions fundamental.

### INTRODUCTION

Predation is a key biotic interaction that is both affected by evolutionary histories and environmental factors. By reducing prey fitness through mortality and non-lethal predation, predators cause changes in prey species' fitness and population dynamics (Meyer and Byers 2004; Peckarsky et al. 2008; Preisser and Bolnick 2008; Matassa and Trussell 2011; Harper 2016). Through this process, predators become important drivers of species evolution in ecosystems (Vermeij 1977, 1993; Aberhan et al. 2006; Stanley 2008; Finnegan et al. 2011). In addition to evolutionary histories, multiple environmental variables can also determine how predatory interactions play out. Examples of environmental factors that can affect the intensity of biotic interactions are productivity and the energy of the environment. For instance, higher productivity sometimes leads to higher predation (Leibold 1989; Elliott and Leggett 1996; Bohannan and Lenski 2000; Leonard-Pingel and Jackson 2016). In terms of wave energy, wave-swept shores have been linked to lower foraging time and lower predation (Menge 1978; Etter 1996; Gusmao et al. 2018). Temperature can also have a direct impact on predation rates as many physiological processes such as consumption rates are temperature-dependent (Sanford 2002; Dell et al. 2014). In tropical environments where temperatures are high, metabolic rates are also elevated (Allen and Gillooly 2007), and consumption increases (Ashton et al. 2022). This high predatory pressure in marine tropical

environments has been used to explain the presence of passive defensive traits in mollusks such as spines, thicker shells, ornamentation, and larger body size (Vermeij 1974; Palmer 1979; Kitchell et al. 1981; Boggs et al. 1984; Han and Jablonski 2008).

Drilling predation, where a gastropod predator drills a hole through the shell of its prey, presents an ideal system to study the role of passive defensive traits. For example, size-limited predation, where larger prey individuals are able to escape predators, is a defensive passive strategy that influences the size-structure of communities (Osenberg and Mittelbach 1989; Persson 1997; Urban 2007; Aristov and Varfolomeeva 2019). For gastropods, predation is size-limited because some of them use their foot to hold their prey, and if the prey is too large, they cannot hold it (Carriker 1981). If this is considered in terms of optimal foraging however, predators should prefer larger prey because it maximizes their energy return (Kitchell et al. 1981; Leighton 2002). All else being equal, predatory gastropods should select larger individuals until a size refuge by the prey is attained (e.g., Leonard-Pingel and Jackson 2013; Chattopadhyay et al. 2015). Another morphological trait that can be considered a passive defense is shell thickness (Kitchell et al. 1981; Boggs et al. 1984). Individuals with thicker shells have a lower energetic gain for a gastropod predator because the cost of drilling through them is higher than the cost of drilling through individuals with thinner shells.

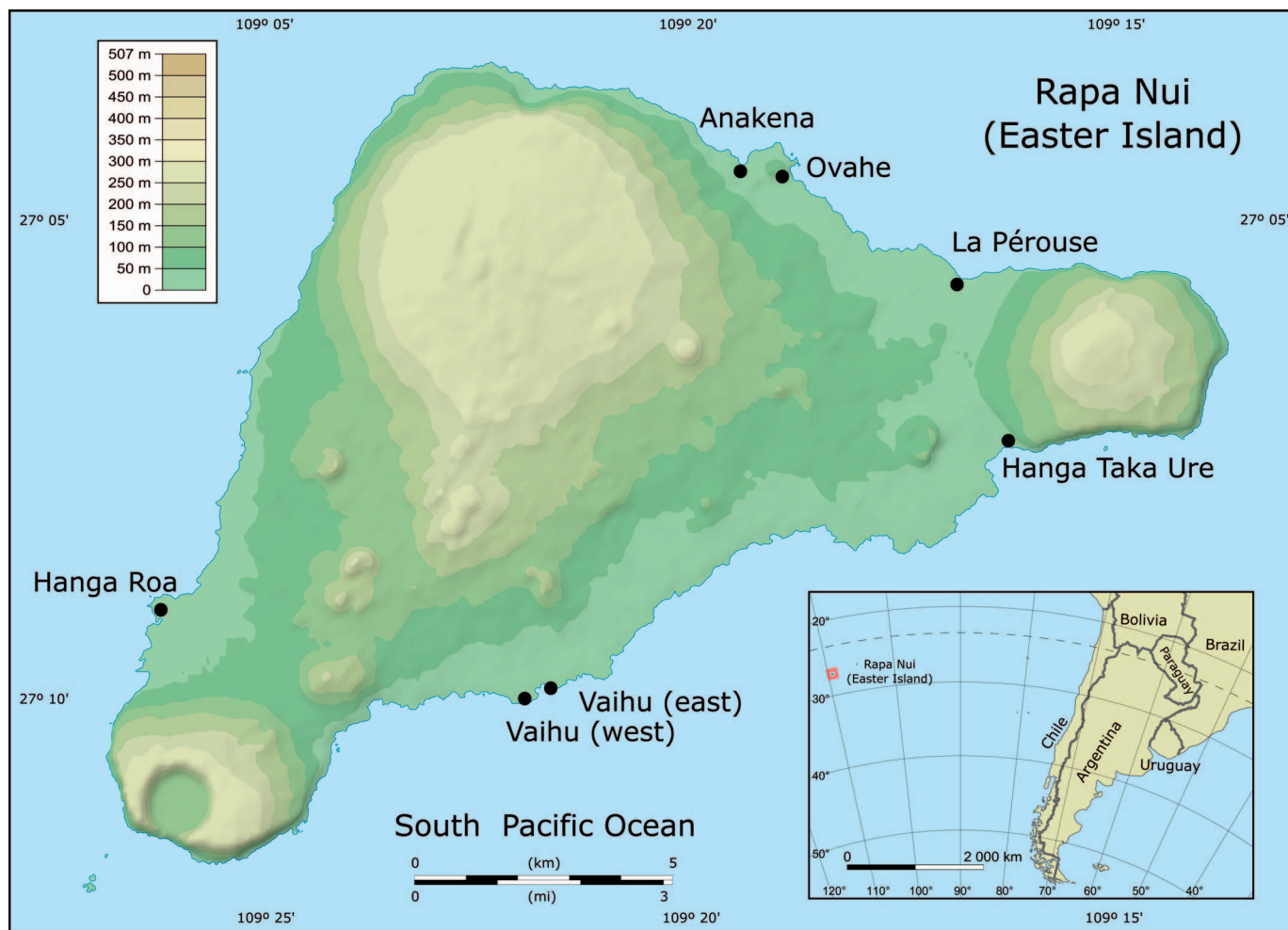


FIG. 1.—Map of Rapa Nui (Easter Island) showing the sites where shells were collected.

Drilling predation also presents the benefit of being well-studied across a wide range of environments, latitudes, and time periods (Vermeij 1993; Kowalewski et al. 1998; Harper and Peck 2003; Kelley et al. 2003; Kowalewski 2004; Leonard-Pingel and Jackson 2013; Martinelli et al. 2013; Visaggi et al. 2013; Chattopadhyay et al. 2015; Martinelli et al. 2015; Visaggi and Kelley 2015; Archuby and Gordillo 2018; Smith et al. 2018; Mondal et al. 2019; Gordillo et al. 2020; Zuschin et al. 2022), for an updated review see (Klompaker et al. 2019), which allows for comparison of predation frequencies between taxa and locations. The existing dataset on drilling predation, however, is still insufficiently detailed to allow us to understand the full range of natural variability in the interaction (Harper 2016), or to allow us to predict how important the role of these predators will be in a given environment (Klompaker et al. 2019). New information from understudied or remote locations helps refine and add to our knowledge.

Oceanic islands that have evolved in more isolation than continental marine environments are of special evolutionary interest to study biotic interactions because of their unique species composition (Whittaker and Fernandez-Palacios 2007). Rapa Nui (Easter Island, Fig. 1) is one of the world's most isolated oceanic islands and this isolation has led to very high rates of endemism among the different marine groups present on the island (Rehder 1980; Boyko 2003; Fernández et al. 2014). Pioneer work by Osorio and Cantuarias (1989) described the intertidal zonation for many molluscs along the Rapa Nui coastline, while Kohn (1978) mentioned for the first time the presence of gastropod predators on the island. The predatory gastropods

include the muricid *Neothasis nesiotis*, *Pisania decapitata engleri*, and *Strigatella flavocingulata* which feed on polychaetes (Kohn 1978).

Today, Rapa Nui's isolation is becoming a thing of the past due to the growing tourism industry and associated human impacts (Figueroa and Rotarou 2016). Historically, the island's natural resources have also been subject to intense over-extraction due to overpopulation (Hunt and Lipo 2009), which might have put a strain on the populations of coastal mollusks. In this context of evolutionary isolation, some of the world's most oligotrophic waters (Morel et al. 2010; Andrade et al. 2014), and human impact, it becomes interesting as well as important for the preservation of an endemic fauna, to understand how predatory interactions play out. An informative first approach is to study drilling predation, as the traces left by drilling gastropods can be easily quantified, requiring no direct intervention or experimentation.

Based on the oligotrophic local conditions (Morel et al. 2010; Andrade 2014), we predict that drilling predation will be lower than in tropical and subtropical regions. Based on the different exposure of the east and west sides of the island to environmental factors such as wave action and winds (Morel et al. 2010; Andrade et al. 2014; Easton et al. 2018; Petit et al. 2021), we predict that drilling predation will be higher in more stable, protected sites in the northwest part of Rapa Nui. We also attempt to determine if morphological traits such as shell size and thickness protect prey against predators, as well as understand whether any prey items are preferred based on their mobility, life habit, or feeding guild. Findings from this study will help comprehend the relative importance of the environmental context and species traits in driving predation and community structure in isolated, nutrient-poor ecosystems.

TABLE 1.—Total number of drilled and undrilled individuals per collection site.

Collection site	Whole individuals	Drilled individuals	DF (%)	Exposure
Anakena	460	47	10.22	Protected
Hanga Roa	841	46	5.47	Protected
Hanga Take Ure	1386	57	4.11	Exposed
La Perouse	743	62	8.34	Protected
Ovahe	785	16	2.04	Protected
Vaihu (east)	215	7	3.25	Exposed
Vaihu (west)	511	21	4.11	Exposed

## METHODS

*Study Site and Sample Collection*

We carried out sampling in Rapa Nui, Polynesia (27°6'S, 109°21'W) in April 2017. The closest continental landmass and island to the east are Chile (~ 3700 km), and the Juan Fernández Islands (~ 3100 km) respectively (Fig. 1). To the west, Ducie Island (Pitcairn Island group) is located ~ 1600 km away. The closest islands to the north are the Galápagos (~ 3800 km).

Sampling was carried out in coastal sites around the entire island to cover as much mollusk diversity as possible (Fig. 1). Wave exposure was variable among sites, with the southeast side of the island being more exposed than the northwest, which is considered more protected (Easton et al. 2018; Petit et al. 2021; Table 1). All the collection sites on Rapa Nui had large volcanic rocks or gravel, and in general, very limited space for shells to accumulate. Most of the shell assemblages we found were located in sand pockets between large volcanic rocks. Only one of our sampling sites, Anakena, is a sandy beach. We collected molluscan specimens manually at six sites on the island (Fig. 1). At each location, we sampled randomly within sand pockets until we collected a minimum of 500 individuals. The sampling effort was equivalent for all sites but there was variability in the abundance of shells that resulted in a range of 500–1200 total counts of shells per site (Table 1). After collection we processed samples through a 4 mm sieve to allow for comparability with the fossil record given that smaller shells have a lower probability of being preserved relative to larger ones (Kidwell 2001; Cooper et al. 2006).

*Species Abundance, Life Habits, Mobility and Feeding Types*

We identified mollusk shells to the species level using published literature (Rehder 1980; Osorio and Cantuarias 1989; Coloma et al. 2004; Spencer et al. 2007; Raines and Huber 2012; Fernández et al. 2014). To understand if predators prefer prey with specific traits, we used prior studies (Kohn 1978; Rehder 1980; Boyko 2003; Raines and Huber 2012) and databases (NMITA database) to classify prey according to their life habits (infaunal or epifaunal), their mobility (mobile, low mobility, sessile) and their feeding type (filter feeders, grazers, scavengers/predators, drilling predators, chemosymbionts, parasites).

*Drilling Frequencies*

We analyzed all unfragmented individuals for the presence of drill holes. For a drill hole to be considered predatory, the trace had to have a regular circular outline and be perpendicular to the shell (Kowalewski 2002; Kelley et al. 2003; Yanes and Tyler 2009). We considered a predatory drill hole to be successful when it was complete (the hole went through the shell). We also quantified the presence of incomplete drill holes (the hole did not go through the shell, it is considered a failed predation attempt), and of multiple drill holes (more than one complete drill hole per shell). To calculate predation frequency, we used the number of drilled individuals per species, divided by the total number of individuals from that same species in a sample (Lower Taxon Frequency; Kowalewski 2002). When calculating predation frequency for bivalves, a correction was applied where only the right shells were considered

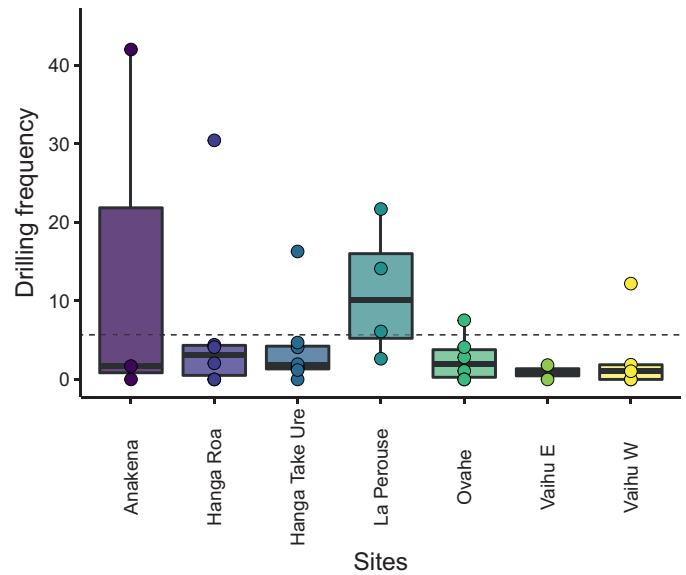


FIG. 2.—Mean drilling frequency per site, calculated with species with  $n \geq 30$ . Each color represents a different site. The horizontal dashed line indicates the pooled drilling frequency value for all individuals. The horizontal bars on the boxplot represent median values, boxes enclose the 25th to 75th percentiles, and whiskers indicate the maximum and minimum values. Dots represent the different species with  $n \geq 30$  at each site.

to avoid overestimating the number of individuals. We calculated these predation frequencies for each site (only pooling data for species with 30 or more individuals; Fig. 2), for the 11 most abundant species (Fig. 3), and for all the pooled life habits, mobility and feeding types (Fig. 4A–4C).

*Testing Which Factors Are Stronger Predictors of Drilling Frequencies*

To determine whether different species traits (feeding mode, mobility, and life habit) or wave exposure of the site (exposed vs protected) were good predictors of drilling frequencies for the different species, we used a generalized

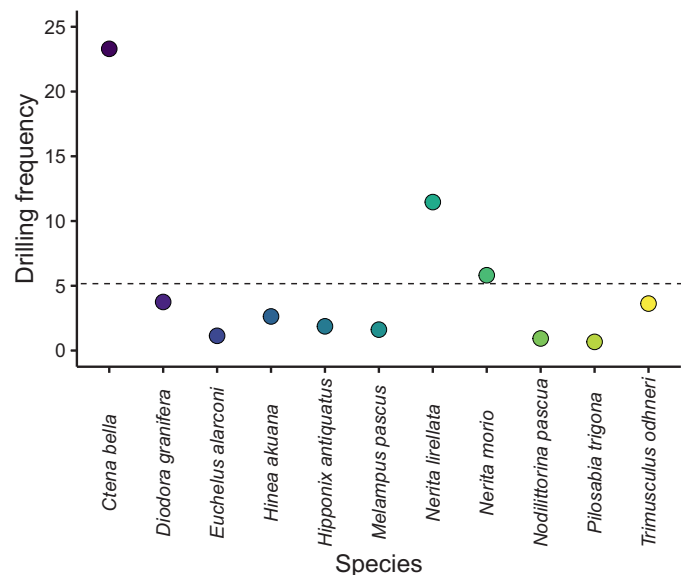


FIG. 3.—Mean drilling frequency per species pooled across all sites ( $n \geq 30$ ). Each species is represented by a different color. The horizontal dashed line indicates the pooled drilling frequency value for all individuals sampled.

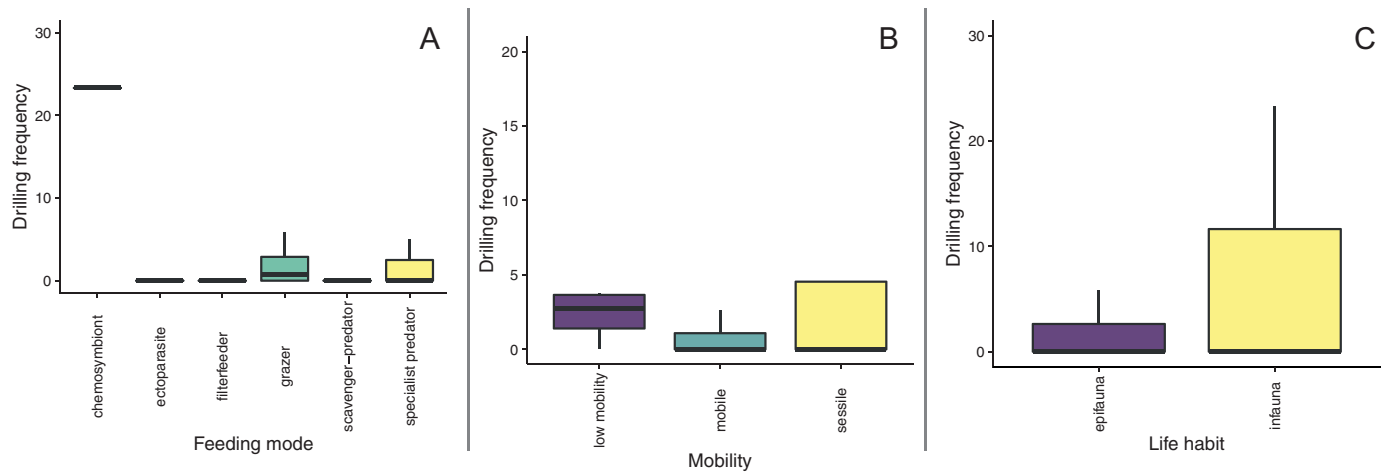


FIG. 4.—Drilling frequency boxplots. **A)** Drilling frequency for mollusks pooled by feeding mode. **B)** Drilling frequency for mollusks pooled by mobility. **C)** Drilling frequency for mollusks pooled by life habit (infauna or epifauna). The horizontal dashed line indicates the pooled drilling frequency value for all individuals. The horizontal bars on the boxplot represent median values, boxes enclose the 25th to 75th percentiles, and whiskers indicate the maximum and minimum values.

linear model (GLM) and modeled the response variable (drilling frequency) with a Poisson distribution to account for the large number of zeros in the dataset. We checked for overdispersion in all models by calculating the ratio of model residual deviances to residual degrees of freedom. We carried out GLM analyses using the ‘glm’ function in the ‘stats’ package in R (R Core Team 2022, vers. 4.2.0). The ‘drop1’ function with chi-squared test was used to determine which of the fixed-factors to keep. Code and data files are provided as supplementary material.

$$Drilling\ Frequency_{i=f(j,k,l,m)} \sim Feeding\ Mode_j + Mobility_k + Life\ Habit_l + Exposure_m$$

To complement the GLM analysis we also carried out four Kruskal-Wallis tests to determine whether drilling frequencies (DF) were significantly different between: (1) exposed or protected sites; (2) life habits; (3) feeding guilds; and (4) mobility types. We chose non-parametric Kruskal-Wallis tests because the distribution of DF was left-skewed due to all the zeros.

**Ctena bella as Prey: Passive Defenses, Site Stereotypy, and the Role of the Environment**

The bivalve *Ctena bella* (Conrad, 1837) (Lucinidae) was the most abundant (n = 455) and drilled prey (DF = 23.3%). Given that it was the most drilled prey species and possibly subject to higher predation pressure, we selected it to test whether prey size or shell thickness conferred any protection from predators. To analyze the relevance of these passive defense traits for *C. bella*, we measured shell size (height, width, length), thickness and mass in individuals from three sites where the species was very abundant (Anakena: n = 148; Hanga Take Ure: n = 253; Hanga Roa: n = 70). Shell thickness was measured with a thickness gauge at the center of the right valve. Linear measurements were made to the nearest 0.01 mm, weight to the nearest 0.01 mg, and all measurements were log<sub>2</sub> transformed. Other relevant biotic information about the species was obtained from online databases (NMITA database: <http://porites.geology.uiowa.edu/database/mollusc/mollusclifestyles.htm>). To determine whether shell size or wave exposure of the site (exposed vs. protected), had a significant effect on the probability of an individual being drilled, we used a generalized linear model (GLM) with a logit link function and binomial response variable (drill-hole = 1, no drill-hole = 0). Shell weight (Pearson’s correlation, r = 0.93, df = 471, p value = 2.2<sup>-16</sup>) and thickness (Pearson’s correlation, r = 0.82, df = 471, p value = 2.2<sup>-16</sup>) were positively significantly correlated with shell length, so they were not included in the models. We checked for overdispersion in all models by calculating the ratio of model

residual deviances to residual degrees of freedom. We carried out GLM analyses using the ‘glm’ function in the ‘stats’ package in R (R Core Team 2022). The ‘drop1’ function with chi-squared test was used to determine which of the fixed-factors to keep. Code and data files are provided as supplementary material.

$$Drilling_{ij} \sim Shell\ size_i + Exposure_j$$

To complement the GLM analysis we also carried out Kruskal-Wallis tests to determine whether DF for *Ctena bella* were significantly different between exposed or protected sites.

**RESULTS**

**Species Abundance, Life Habits, Mobility, and Feeding Types**

The death assemblages yielded 6122 mollusks from nine bivalve and 36 gastropod species. Two of the bivalves are from continental Chile (*Mesodesma donacium* (n = 1), and *Ameghinomya antiqua* (n = 1) and may have been transported to Rapa Nui. The rest of the species have been previously described for the island (Rehder 1980).

Most of the mollusks found are epifaunal (89%), with the exception of *Ctena bella* and the two bivalves from continental Chile. Among the mobility types, 75% of the individuals belong to species with low mobility, 24% were found to be actively mobile, and 1% sessile (Table 2). The dominant feeding type were

TABLE 2.—Relative abundance and mean drilling frequency for each life habit, mobility type, and feeding type of Rapa Nui mollusks.

Trait	Relative abundance	Mean DF (%)
Life habit		
Epifauna	89.4	3.4
Infauna	10.6	11.3
Mobility		
Mobile	24.3	4.3
Low mobility	75.2	2.5
Sessile	0.4	2.2
Feeding type		
Chemosymbionts	10.4	18.8
Ectoparasites	0.1	0
Filter feeders	0.5	1.8
Grazers	85.1	4.1
Scavengers/predators	2.7	2.7
Drilling gastropods	1.1	1.7

TABLE 3.—Abundance of unfragmented and drilled individuals of the 11 most abundant bivalve and gastropod species from Rapa Nui. Drilling frequencies for each species are also shown.

Species	Bivalvia/Gastropoda	Whole individuals	Drilled individuals	DF (%)
<i>Ctena bella</i> (Conrad, 1837)	Bivalvia	455	106	23.3
<i>Diodora granifera</i> (Pease, 1861)	Gastropoda	80	3	3.7
<i>Euchelus alarconi</i> (Rehder, 1980)	Gastropoda	88	1	1.8
<i>Hipponix antiquatus</i> (Linnaeus, 1767)	Gastropoda	749	14	1.8
<i>Melampus pascus</i> (Odhner, 1922)	Gastropoda (Pulmonata)	124	2	1.6
<i>Nerita lirellata</i> (Rehder, 1980)	Gastropoda	253	29	11.5
<i>Nerita morio</i> (G.B. Sowerby I, 1980)	Gastropoda	430	25	5.8
<i>Echinolittorina pascua</i> (Rosewater, 1970)	Gastropoda	322	3	0.9
<i>Pilosabia trigona</i> (Gmelin, 1791)	Gastropoda	299	2	0.7
<i>Hinea akuana</i> (Rehder, 1980)	Gastropoda	1406	37	2.6
<i>Trimusculus odhneri</i> (Hubendick, 1946)	Gastropoda	524	19	3.6

grazers (85%), followed by chemosymbionts (10%) and scavengers/predators (3%, Table 2). Other smaller feeding types also found in the samples were drilling gastropods (1%), filter feeders (0.5%), and ectoparasites (0.5%).

Among drilling gastropods, three potential predators were found: *Pascua citrica* (Muricidae, n = 33), *Neothais nesiotis* (Muricidae, n = 32), and *Morula praecipua* (Muricidae, n = 1). The pooled relative abundance of drilling gastropods per site varied between 0% (Vaihu S) and 2% (Ovahe). Naticid gastropods were not found in the samples.

**Drilling Frequency Per Site and Species**

Mean and median drilling frequency (DF) and standard error for all sites were 5.67% ± 1.61 and 1.90 ± 1.61, respectively. These DF were calculated with the prey species from each site whose n ≥ 30 (Fig. 2). Sites with less than 30 individuals had usually no drilled specimens. Values for the collection sites ranged between 2% (Ovahe) and 10% (Anakena). Only La Perouse and Anakena had DF values higher than the overall mean. The eleven most abundant prey species (n ≥ 30) had DFs between 0.7 and 23% (Fig. 3, Table 3). Drilling frequencies for the 45 species in the samples ranged from 0% to 30% but this was affected by singletons and species with less than 10 individuals.

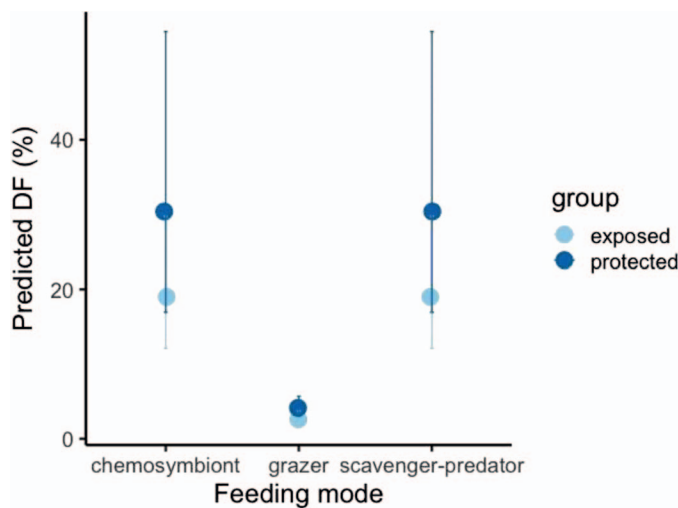


FIG. 5.—Modeling results showing the predicted drilling frequency (DF) for different feeding modes (chemosymbionts, grazers and scavenger/predators) in both exposed and protected sites (shown in light blue and dark blue respectively). The grazers had significantly lower predation than the other two feeding modes (Table 5), and protected sites had significantly higher predation (Table 5).

**Drilling Frequencies for Life Habits, Mobility and Feeding Types**

Infaunal organisms, represented by *Ctena bella*, had the highest drilling frequency (Fig. 4; DF = 23.3%). This DF is also reflected in the feeding types (Fig. 4A) and mobility (Fig. 4B) as *C. bella* is an infaunal lucinid. When we tested for significant differences between groups we found that there were no significant differences between (1) exposed or protected sites (Kruskal-Wallis chi-squared = 0.052, df = 1, p value = 0.819); (2) life habits (Kruskal-Wallis chi-squared = 2.5, df = 1, p value = 0.114); (3) feeding guilds (Kruskal-Wallis chi-squared = 2.5, df = 1, p value = 0.114); or (4) mobility types (Kruskal-Wallis chi-squared = 0.167, df = 1, p value = 0.683).

**Testing Which Factors are Stronger Predictors of Drilling Frequencies**

The generalized linear model showed that beach exposure and feeding mode were significant explanatory predictors of drilling frequencies in mollusks from Rapa Nui (Fig. 5, Table 5). Mollusks with grazing feeding habits had significantly lower drilling frequencies than chemosymbionts and scavengers/predators (Fig. 5). Wave-protected collection sites had significantly higher drilling frequencies than exposed ones (Fig. 5). We found no evidence for overdispersion in residuals for the models as the ratio of model residual deviances to residual degrees of freedom was smaller than 1. Given that these results contradict the Kruskal-Wallis tests, it is likely that their significance is driven by *Ctena bella*, a very abundant infaunal bivalve.

**Ctena bella as Prey: Passive Defenses and the Role of the Environment**

Samples of *C. bella* from Anakena, Hanga Take Ure, and Hanga Roa (Fig. 1) were used for further analyses (Fig. 6). We found that fragmentation rates were below 25% in all sites (Anakena 10%, Hanga Take Ure 9%, Hanga Roa 23%). The DFs for incomplete, complete, and multiple drill holes are presented in Table 4.

The generalized linear model showed that beach exposure was a significant explanatory predictor of drilling predation for *C. bella* but shell mass was not (Fig. 7, Table 6). We found no evidence for overdispersion in residuals for the models as the ratio of model residual deviances to residual degrees of freedom was smaller than 1.

TABLE 4.—Fragmentation and drilling frequencies (incomplete, complete, and multiple) for the bivalve *Ctena bella* in three sites in Rapa Nui.

Site	N	Fragmentation	Incomplete DF	Complete DF	Multiple DF
Anakena	199	10.3%	3%	20.1%	2.5%
Hanga Take Ure	258	9.2%	0.8%	10.8%	2.3%
Hanga Roa	75	22.6%	5.6%	20.7%	2.8%

TABLE 5.—Summary of generalized linear model statistics for the effects of beach exposure, mobility, life habit, and feeding on drilling predation frequencies. (A) The effect of dropping variables 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). Bold text indicates statistical significance.

A—Variable	df	AIC	Pr ( $\chi^2$ )
Beach exposure	1	145.16	<b>0.01216</b>
Mobility	1	138.88	0.97872
Life habit	0	140.88	—
Feeding	1	174.19	<b>2.806<sup>-09</sup></b>
B—Variable	Estimate	SE	<i>p</i> value
Intercept	2.937	0.352	<b>2<sup>-16</sup></b>
Beach exposure	0.470	0.190	<b>0.0134</b>
Mobility	0.007	0.266	0.9787
Life habit	0.012	0.293	0.9672
Feeding	-1.995	0.295	<b>1.55<sup>-11</sup></b>

The results from the Kruskal-Wallis test provided support for the GLM results as the differences in DF between exposed and protected sites were significant (Kruskal-Wallis chi-squared = 21.808, *df* = 1, *p* value = 3.014e-06).

## DISCUSSION

### Low Drilling Frequencies in Rapa Nui

This study provides information on drilling predation from death assemblages in Rapa Nui, one of the most isolated islands on the planet. Given the remoteness of the island and the oligotrophy of its waters, our prediction was that drilling predation would be lower than in other tropical and subtropical regions. In agreement with our prediction, we found that the drilling frequency obtained for mollusks from Rapa Nui (6%) is lower than what has been reported for tropical and subtropical regions such as 12% for modern mollusk assemblages from Brazil (Visaggi and Kelley 2015), 7% for modern infaunal tellinids from Australia (Martinelli et al. 2015), 18% for mollusks from the Miocene in Panama (Fortunato 2007), and 16–27% for large

bivalves from the Neogene in Panama and Costa Rica (Leonard-Pingel and Jackson 2013). The pooled drilling frequency for modern mollusks from Rapa Nui is even lower than the mean drilling intensity of 17% estimated for subtropical mollusk assemblages from the Cretaceous to the Pleistocene (Table 4; Mondal et al. 2019), a time when new predators and prey were evolving in marine communities (Vermeij 1977). The drilling frequencies from our findings are more like drilling intensities reported for high latitude regions in the southern hemisphere (10% for mollusks from the Atlantic coast of Patagonia, (Martinelli et al. 2013), and ~ 2% for limpets from the same coast, (Archuby and Gordillo 2018). These low predation rates in Rapa Nui may be explained by the combination of the subtropical nature of the island (lower temperatures than in tropical environments), the hyper-oligotrophy of the surrounding waters, the harsh environmental conditions and wave action, and the presence of other predators such as fish (Morel et al. 2010; Andrade et al. 2014; Gusmao et al. 2018).

### Environmental Factors and Drilling Predation in Rapa Nui

The relationship between drilling predation and primary production is still not clear (Klompaker et al. 2019), but previous studies have identified primary productivity as a factor that influences predator-prey interactions (Leibold 1989; Bohannon and Lenski 2000). Rapa Nui is located in the South Pacific Gyre, an area that has been described as “the world’s largest oceanic desert” (Morel et al. 2010; Andrade et al. 2014). This region is the most oligotrophic subtropical zone of the global ocean (Morel et al. 2010; Andrade et al. 2014), and that might be one of the reasons why predation is low. A recent study of infaunal invertebrates near coral reefs in Rapa Nui found that wave action and disturbance might be more important than predation in driving local community structure (Gusmao et al. 2018). This finding agrees with our results, where we found that protected sites had significantly higher drilling frequencies than sites exposed to wave action. The coast of Rapa Nui has cliffs and rocks, and there is a lack of intertidal or subtidal ecosystem engineers such as coral reefs or mangroves to protect it, leaving the communities from shallow habitats to face harsh and unstable environments (Gusmao et al. 2018). Hydrodynamic stress has also been suggested as the major driving factor structuring benthic soft-bottom communities on the island (Gusmao et al. 2018). Our results imply that drilling frequencies were significantly affected by exposure to high energy and waves, and this may also explain the preference for



FIG. 6.—Photos of *C. bella* shells with drill holes. The close-up image shows a beveled drill hole. Scale bars = 1 cm.

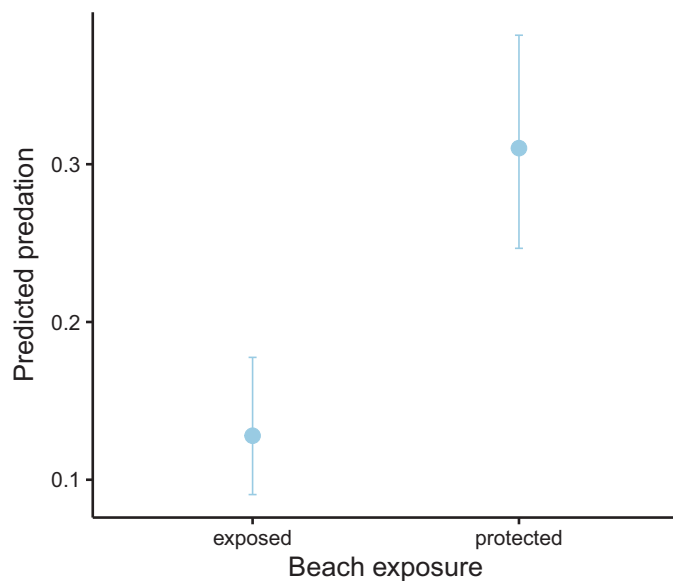


FIG. 7.—Modeling results showing the likelihood of a shell being drilled by predators (0–1) for *C. bella* in both exposed and protected sites. Protected sites had significantly higher predation values (Table 6).

certain life habits. Given that a large proportion of the mollusks in our samples were epifaunal mobile grazers exposed to the environment, it is possible that the infaunal taxa preferred by predators (*Ctena bella*) might be more protected and easier to access and drill in the sediments.

#### Identity of the Drilling Predators

Predation data obtained from death assemblages provide no certainty on which of the predators found was responsible for the drill holes observed. Therefore, the most conservative approach is to attribute the drill holes to the guild of drilling predators, both naticids and muricids (Harper 2016). The only predators found in our samples were muricids, but there are two species of naticids, *Mammilla simiae* and *Notocochlis cernica* that are mentioned by (Rehder 1980) as present in low abundances in Rapa Nui. The mention of these naticids is particularly important given that the main drilled prey, *Ctena bella*, is infaunal. It is possible that we did not find naticids in our samples because they are rare, they got reworked in the sediment due to wave action, or perhaps, *C. bella* may have more semi-infaunal habits in which case it could have been accessible by muricids (see Gordillo and Archuby 2014 for an example of predation of an infaunal venerid by a muricid).

TABLE 6.—Summary of generalized linear model statistics for the effects of beach exposure and shell mass on the likelihood of a *Ctena bella* shell being drilled. **A)** The effect of dropping variables 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). Bold text indicates statistical significance.

A—Variable	df	AIC	Pr ( $\chi^2$ )
Beach exposure	1	487.88	<b>2.178<sup>-05</sup></b>
Mass	1	469.93	0.7723
B—Variable	Estimate	SE	<i>p</i> value
Intercept	-1.976	0.318	<b>5.55<sup>-10</sup></b>
Beach exposure	1.120	0.271	<b>3.74<sup>-05</sup></b>
Mass	0.104	0.360	0.772

#### Passive Defenses

The shells of prey often contain valuable information about the predator's preference and the prey's mechanisms of defense. Optimal foraging theory applied to drilling predation suggests that prey shell thickness and body size can be significant predictor variables for prey survival or predator success (Leighton 2002). The generalized linear model results for *C. bella*, however, do not support this as larger body size or thicker shells did not confer a benefit in terms of survival for *C. bella*.

#### CONCLUDING REMARKS

We provide the first in-depth look at drilling predation in Rapa Nui. This remote island is dominated by species with tropical affinities and endemics that have evolved together in a setting where nutrients in the water are very low, past and present anthropogenic impacts very high, and environmental factors such as wave action and sediment mixing are also very strong. This particular context helps understand the comparatively low predation documented (5.67%). Despite the low drilling frequencies, predators showed a preference for infaunal taxa, particularly *C. bella*. Rapa Nui is under strong human impact, and its endemic molluscan fauna would benefit from some protection as we continue to learn more about these species and their interactions.

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#### SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive:  
<https://www.sepm.org/supplemental-materials>.

#### REFERENCES

- ABERHAN, M., KIESLING, W., AND FÜRSICH, F., 2006, Testing the role of biological interactions in the evolution of Mid-Mesozoic marine benthic ecosystems: Paleobiology, v. 32, p. 259–277.
- ALLEN, A.P. AND GILLOOLY, J.F., 2007, The mechanistic basis of the Metabolic Theory of Ecology: Oikos, v. 116, p. 1073–1077, doi: 10.1111/j.0030-1299.2007.16079.x.
- ANDRADE, I., HORMAZÁBAL, S., AND CORREA-RAMÍREZ M., 2014, Variabilidad espacio-temporal de la clorofila- $\alpha$  satelital en la Provincia de Isla de Pascua, Océano Pacífico Suroriental: Latin American Journal of Aquatic Research, v. 42, p. 871–887.
- ARCHUBY, F.M. AND GORDILLO, S., 2018, Drilling predation traces on recent limpets from northern Patagonia, Argentina: Palaeontologia Electronica, v. 21, doi: 10.26879/620.
- ARISTOV, D. AND VARFOLOMEEVA, M., 2019, Moon snails *Amauropsis islandica* can shape the population of Baltic Clams *Limecola balthica* by size-selective predation in the high-latitude White Sea: Polar Biology, v. 42, p. 2227–2236.
- ASHTON, G.V., FREESTONE, A.L., DUFFY, J.E., TORCHIN, M.E., SEWALL, B.J., TRACY, B., ... AND RUIZ, G.M., 2022, Predator control of marine communities increases with temperature across 115 degrees of latitude: Science, v. 376, p. 1215–1219.
- BOGGS, C.H., RICE, J.A., KITCHELL, J.A., AND KITCHELL, J.F., 1984, Predation at a snail's pace: what's time to a gastropod?: Oecologia, v. 62, p. 13–17.
- BOHANNAN, B.J.M. AND LENSKE, R.E., 2000, The relative importance of competition and predation varies with productivity in a model community: The American Naturalist, v. 156, p. 329–340.
- BOYKO, C.B., 2003, The endemic marine invertebrates of Easter Island: how many species and for how long?, in J. Loret and J.T. Tancredi (eds.), Easter Island: Scientific Exploration into the World's Environmental Problems in Microcosm: Springer US, Boston, 155 p.
- CARRIKER, M.R., 1981, Shell penetration and feeding by Naticacean and Muricacean predatory gastropods: a synthesis: Malacologia, v. 20, p. 403–422, <http://www.vliz.be/imisdocs/publications/ocrd/240294.pdf>.

- CHATTOPADHYAY, D., ZUSCHIN M., AND TOMAŠOVÝCH, A., 2015, How effective are ecological traits against drilling predation? Insights from recent bivalve assemblages of the northern Red Sea: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 440, p. 659–670, doi: 10.1016/j.palaeo.2015.09.047.
- COLOMA, M., MARCHANT, M., MOYANO, H.I., AND RUIZ, V.H., 2004, Moluscos Litorales de Isla de Pascua, Chile, recolectados por la Expedición Cimar 5-Islas Oceánicas I: *Ciencia y Tecnología Del Mar*, v. 27, p. 79–94, <https://www.redalyc.org/pdf/624/62427105.pdf>.
- COOPER, R.A., MAXWELL, P.A., CRAMPTON, J.S., BEU, A.G., JONES, C.M., AND MARSHALL, B.A., 2006, Completeness of the fossil record: estimating losses due to small body size: *Geology*, v. 34, p. 241–244, doi: 10.1130/g22206.1.
- DELL, A.I., PAWAR, S., AND SAVAGE, V.M., 2014, Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy: *The Journal of Animal Ecology*, v. 83, p. 70–84.
- EASTON, E.E., GAYMER, C.F., FRIEDLANDER, A.M., AND HERLAN, J.J., 2018, Effects of herbivores, wave exposure and depth on benthic coral communities of the Easter Island ecoregion: *Marine and Freshwater Research*, v. 69, p. 997–1006.
- ELLIOTT, J.K. AND W.C. LEGGETT, 1996, The effect of temperature on predation rates of a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval Capelin (*Mallotus villosus*): *Journal Canadien des Sciences Halieutiques et Aquatiques*, v. 53, p. 1393–1402.
- ETTER, R.J., 1996, The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.): *Journal of Experimental Marine Biology and Ecology*, v. 196, p. 341–356.
- FERNÁNDEZ, M., PAPPALARDO, P., CASTILLA, J.C., AND RODRÍGUEZ-RUIZ, M.C., 2014, Synthesis of the state of knowledge about species richness of macroalgae, macroinvertebrates and fishes in coastal and oceanic waters of Easter and Salas y Gómez Islands: *Latin American Journal of Aquatic Research*, v. 42, p. 760–802.
- FIGUEROA, B.E. AND ROTAROU, E.S., 2016, Sustainable development or eco-collapse: lessons for tourism and development from Easter Island: *Sustainability: Science Practice and Policy*, v. 8, p. 1093.
- FINNIGAN, S., MCCLAIN C.M., KOSNIK, M.A., AND PAYNE, J.L., 2011, Escargots through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution: *Paleobiology*, v. 37, p. 252–269.
- FORTUNATO, H., 2007, Naticid gastropod predation in the Gatun Formation (late Middle Miocene), Panama: preliminary assessment: *Paläontologische Zeitschrift*, v. 81, p. 356–364.
- GORDILLO, S. AND ARCHUBY, F., 2014, Live-live and live-dead interactions in marine death assemblages: the case of the Patagonian clam *Venus antiqua*: *Acta Palaeontologica Polonica*, v. 59, p. 429–442.
- GORDILLO, S., MALVÉ, M.E., AND MORÁN, G.A., 2020, Naticid drilling predation from tidal flats in Northern Patagonia, SW Atlantic: *Journal of the Marine Biological Association of the United Kingdom*, v. 100, p. 909–919.
- GUSMAO, J.B., LEE, M.R., MACDONALD, I., ORY, N.C., SELLANES, J., WATLING, L., AND THIEL, M., 2018, No reef-associated gradient in the infaunal communities of Rapa Nui (Easter Island)—are Oceanic waves more important than reef predators?: *Estuarine, Coastal and Shelf Science*, v. 210, p. 123–131.
- HAN, C.S. AND JABLONSKI, P.G., 2008, Male mating strategies through manipulation of female-perceived predation risk: a minireview and a hypothesis: *Journal of Ecology and Environment*, v. 31, p. 1–7, doi: 10.5141/jefb.2008.31.1.001.
- HARPER, E.M., 2016, Uncovering the holes and cracks: from anecdote to testable hypotheses in predation studies: *Palaeontology*, v. 59, p. 597–609.
- HARPER, E.M. AND PECK, L., 2003, Predator behaviour and metabolic costs in the Antarctic Muricid Gastropod *Trophon longstaffi*: *Polar Biology*, v. 26, p. 208–217.
- HUNT, T.L. AND LIPO, C.P., 2009, Revisiting Rapa Nui (Easter Island) Ecocide: *Pacific Science*, v. 63, p. 601–616, doi: 10.2984/049.063.0407.
- KELLEY, P., KOWALEWSKI, M., AND HANSEN, T.A., 2003, Predator-Prey Interactions in the Fossil Record: Springer Science and Business Media, Boston, 139 p.
- KIDWELL, S.M., 2001, Preservation of species abundance in marine death assemblages: *Science*, v. 294, p. 1091–1094.
- KITCHELL, J.A., BOGGS, C.H., KITCHELL, J.F., AND RICE, J.A., 1981, Prey selection by naticid gastropods: experimental tests and application to the fossil record: *Paleobiology*, v. 7, p. 533–552.
- KLOMPMAKER, A.A., KELLEY, P.H., CHATTOPADHYAY, D., CLEMENTS, J.F., HUNTLEY, J.W., AND KOWALEWSKI, M., 2019, Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior: *Earth-Science Reviews*, v. 194, p. 472–520.
- KOHN, A.J., 1978, Ecological shift and release in an isolated population: *Conus miliaris* at Easter Island: *Ecological Monographs*, v. 48, p. 323–336.
- KOWALEWSKI, M., 2002, The fossil record of predation: an overview of analytical methods: *The Paleontological Society Papers*, v. 8, p. 3–42.
- KOWALEWSKI, M., 2004, Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): palaeobiological and ecological implications: *The Journal of Molluscan Studies*, v. 70, p. 359–370.
- KOWALEWSKI, M., DULAI, A., AND FÜRSICH, F.T., 1998, A fossil record full of holes: the Phanerozoic history of drilling predation: *Geology*, v. 26, p. 1091–1094.
- LEIBOLD, M.A., 1989, Resource edibility and the effects of predators and productivity on the outcome of trophic interactions: *The American Naturalist*, v. 134, p. 922–949.
- LEIGHTON, L.R., 2002, Inferring predation intensity in the marine fossil record: *Paleobiology*, v. 28, p. 328–342.
- LEONARD-PINGEL, J.S. AND JACKSON, J.B.C., 2013, Drilling intensity varies among Neogene Tropical American bivalvia in relation to shell form and life habit: *Bulletin of Marine Science*, v. 89, p. 905–919.
- LEONARD-PINGEL, J.S. AND JACKSON, J.B.C., 2016, Drilling predation increased in response to changing environments in the Caribbean Neogene: *Paleobiology*, v. 42, p. 394–409.
- MARTINELLI, J.C., GORDILLO, S., AND ARCHUBY, F., 2013, Muricid drilling predation at high latitudes: insights from the southernmost Atlantic: *PALAIOS*, v. 28, p. 33–41.
- MARTINELLI, J.C., KOSNIK, M.A., AND MADIN, J.S., 2015, Encounter frequency does not predict predation frequency in tropical dead-shell assemblages: *PALAIOS*, v. 30, p. 818–926.
- MATASSA, C.M. AND TRUSSELL, G.C., 2011, Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects: *Ecology*, v. 92, p. 2258–2266.
- MENGE, B.A., 1978, Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental harshness: *Oecologia*, v. 34, p. 1–16.
- MEYER, J.J. AND BYERS, J.E., 2004, As good as dead? Sublethal predation facilitates lethal predation on an intertidal clam: *Ecology Letters*, v. 8, p. 160–166.
- MONDAL, S., CHAKRABORTY, H., AND SHUBHABRATA, P., 2019, Latitudinal patterns of gastropod drilling predation intensity through time: *PALAIOS*, v. 34, p. 261–270.
- MOREL, A.H., CLAUSTRE, H., AND GENTILI, B., 2010, The most oligotrophic subtropical zones of the global Ocean: similarities and differences in terms of chlorophyll and yellow substance: *Biogeosciences*, v. 7, p. 3139–3151.
- OSENBERG, C.W. AND MITTELBACH, G.G., 1989, Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods: *Ecological Monographs*, v. 59, p. 405–432.
- OSORIO, C. AND CANTUARIAS, V., 1989, Vertical distribution of mollusks on the rocky intertidal of Easter Island: *Pacific Science*, v. 43, p. 302–315.
- PALMER, A.R., 1979, Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence: *Evolution: International Journal of Organic Evolution*, v. 33, p. 697–713.
- PECKARSKY, B.L., ABRAMS, P.A., BOLNICK, D.I., DILL, L.M., GRABOWSKI, J.H., LUTTBEG, B., ORROCK, J.L., ET AL., 2008, Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions: *Ecology*, v. 89, p. 2416–2425.
- PERSSON, A., 1997, Effects of fish predation and excretion on the configuration of aquatic food webs, *Oikos*, p. 137–146, doi: 10.2307/3546098.
- PETTIT, J.J., GAYMER, C.F., FRIEDLANDER, A.M., AND GUSMAO, J.B., 2021, Humans at the top of the food web: are coastal benthic communities at Rapa Nui affected by fishing?: *Environmental Biology of Fishes*, v. 104, p. 1433–1451.
- PREISSER, E.L. AND BOLNICK, D.I., 2008, The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations: *PLoS One* 3, e2465, doi: 10.1371/journal.pone.0002465.
- R CORE TEAM, 2022, A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org/>.
- RAINES, B. AND HUBER, M., 2012, Biodiversity quadrupled—revision of Easter Island and Salas y Gómez bivalves: *Zootaxa*, v. 3217, p. 1–106.
- REHDER, H.A., 1980, The marine mollusks of Easter Island (Isla de Pascua) and Sala y Gómez: *Smithsonian Contributions to Zoology*, v. 289, p. 1–167.
- SANFORD, E., 2002, Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities: *Integrative and Comparative Biology*, v. 42, p. 881–891.
- SMITH, J.A., HANDLEY, J.C., AND DIETL, G.P., 2018., Effects of dams on downstream molluscan predator-prey interactions in the Colorado River estuary: *Proceedings of The Royal Society, Biological Sciences*, v. 285, p. 20180724, doi: 10.1098/rspb.2018.0724.
- SPENCER, H.G., WATERS, J.M., AND EICHHORST, T.E., 2007, Taxonomy and nomenclature of black nerites (Gastropoda: Neritimorpha: Nerita) from the South Pacific: *Invertebrate Systematics*, v. 21, p. 229–237.
- STANLEY, S.M., 2008, Predation defeats competition on the seafloor: *Paleobiology*, v. 34, p. 1–21.
- URBAN, M.C., 2007, The growth-predation risk trade-off under a growing gape-limited predation threat: *Ecology*, v. 88, p. 2587–2597.
- VERMEIJ, G.J., 1974, Marine faunal dominance and molluscan shell form: *Evolution: International Journal of Organic Evolution*, v. 28, p. 656–664.
- VERMEIJ, G.J., 1977, The Mesozoic Marine Revolution: evidence from snails, predators and grazers: *Paleobiology*, v. 3, p. 245–258, doi: 10.1017/s0094837300005352.
- VERMEIJ, G.J., 1993, *Evolution and Escalation: An Ecological History of Life*: Princeton University Press, Princeton, 544 p.
- VISAGGI, C.C., DIETL, G.P., AND KELLEY, P.A., 2013, Testing the influence of sediment depth on drilling behaviour of *Neverita duplicata* (Gastropoda: Naticidae), with a review of alternative modes of predation by naticids: *The Journal of Molluscan Studies*, v. 79, p. 310–322.
- VISAGGI, C.C. AND KELLEY, P.H., 2015, Equatorward increase in naticid gastropod drilling predation on infaunal bivalves from Brazil with paleontological implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 438, p. 285–299.
- WHITTAKER, R.J. AND FERNANDEZ-PALACIOS, J.M., 2007, *Island Biogeography: Ecology, Evolution, and Conservation*, Oxford University Press, Oxford, 383 p.
- YANES, Y. AND TYLER, C.L., 2009, Drilling predation intensity and feeding preferences by *Nucella* (Muricidae) on limpets inferred from a dead-shell assemblage: *PALAIOS*, v. 24, p. 280–289, doi: 10.2110/palo.2008.p08-074r.
- ZUSCHIN, M., NAWROT, R., DENG, M., GALLMETZER, I., HASELMAIR, A., WÜRZER, S., AND TOMAŠOVÝCH, A., 2022, Scale dependence of drilling predation in the Holocene of the Northern Adriatic Sea across benthic habitats and nutrient regimes: *Paleobiology*, v. 48, p. 462–479.

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