DRILLING INTENSITY VARIES AMONG NEOGENE TROPICAL AMERICAN BIVALVIA IN RELATION TO SHELL FORM AND LIFE HABIT

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ABSTRACT

We calculated the incidence of drilling on bivalve genera from the Neogene fossil record of Panama and Costa Rica to determine differences in predation intensity among groups based on shell architecture, life habit, mobility, and taxonomic affinity. Bulk samples from 28 localities yielded >106,000 bivalve specimens, which were examined for characteristic drilling traces of muricid and naticid gastropods. We calculated the drilling intensity for the 90 most common genera, and characterized the size, ornament, life habit, and mobility for each genus. Large size confers considerable protection from drilling, but shell ornamentation does not. Life habit is strongly linked with drilling intensity. Epifaunal bivalves experience higher predation than infaunal bivalves and shallow burrowers experience higher drilling than deep burrowers. Mobility is also important for epifaunal bivalves; cemented taxa are twice as likely to be drilled as their uncemented counterparts. Our results suggest that bivalve behavior and life habits are more important than shell architecture for defense against drilling predators.

Interactions between predators and prey have long been recognized as major drivers of community evolution and diversification (Darwin 1859, Dawkins and Krebs 1979, Vermeij 1977, 1983, Bambach 1983, Steneck 1983, Roy 1996, Thompson 1998). In the marine realm, escalation, or enemy-driven evolution (Vermeij 1987, 1994), appears to occur more often than does coevolution, or reciprocal evolution (Vermeij 1994, Kelley and Hansen 2001, Dietl and Kelley 2002). The response of molluscan prey to shell-damaging (durophagous) predators is particularly well suited to macroevolutionary studies of predation because of the abundant fossil record of mollusks and the potential for preservation of direct evidence of predation, especially traces such as drill holes and repair scars (Kowalewski 2002 and references therein, Alexander and Dietl 2003, Kelley and Hansen 2003).

Several traits related to shell architecture and life habit are hypothesized to confer protection against predators (Vermeij 1977, 1983, Bambach 1983, Stanley 1988, Alexander and Dietl 2003, Kelley and Hansen 2003). Among bivalves, thick, robust shells and ornamentation such as spines, knobs, and crenulations of valve margins are thought to reduce the probability of a fatal attack by crushing or drilling predators (Stanley 1970, Logan 1974, Vermeij 1978, 1983, Bertness and Cunningham 1981, Kelley 1989, Harper and Skelton 1993, Smith and Jennings 2000, Kelley and Hansen 2001, Alexander and Dietl 2003). Organic rich laminae within bivalve shells (conchiolin) also appear to inhibit drilling and shell breakage (Harper and Skelton 1993, Kardon 1998). Rapid burrowing and the ability of some bivalves to swim by jet propulsion are also interpreted as adaptations to reduce predation. Epifaunal bivalves cemented to a hard substrate may be more difficult for predators to manipulate (Harper 1991). Still other bivalves may escape
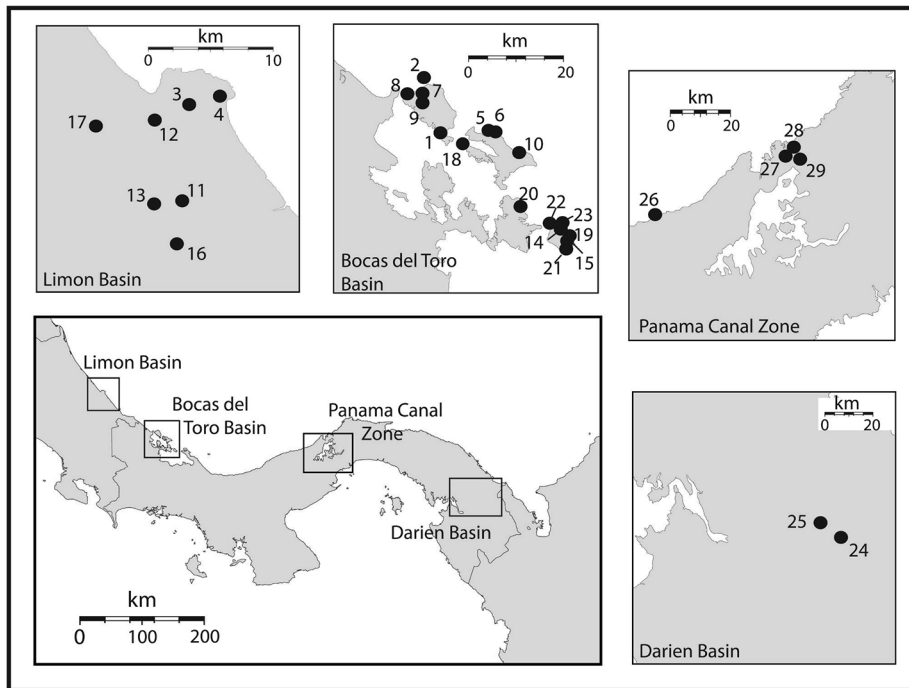
Figure 1. Map of Panama and eastern Costa Rica, with insets showing the four basins from which collections were taken; Limon Basin, Costa Rica; Bocas del Toro Basin, Panama; Panama Canal Zone, Panama; and Darien Basin, Panama. Numbers correspond to faunules listed in Table 1.

predation by boring into hard substrates, nestling (occupying crevices or holes abandoned by other organisms), burrowing deeply into the sediment, or camouflaging themselves with sponges or other encrusting organisms (Stanley 1970, Vermeij 1983, Harper and Skelton 1993, Alexander and Dietl 2003).

These interpretations are compromised, however, because they are based largely upon experimental manipulations of bivalve shells and predators (Harper 1991, Smith and Jennings 2000) or are anecdotal. To address these problems, we used a large quantitative data set of fossil bivalve assemblages to calculate drilling intensities for 90 common genera in the context of data on shell architecture and life mode for the same specimens. Specifically, we tested the hypothesis that bivalves with smaller, less ornamented shells should experience higher predation than their larger, more highly ornamented counterparts. Secondly, we tested the hypothesis that bivalves that can move freely by deep/rapid burrowing or swimming should be drilled less often than bivalves that are epifaunal, cemented, or have otherwise reduced mobility.

Methods

We collected a total of 176 bulk samples from 28 fossil localities termed faunules (O'Dea et al. 2007, Smith and Jackson 2009, Leonard-Pingel et al. 2012) from four basins in northern Panama and eastern Costa Rica (11–0.007 My; Fig. 1, Table 1). All collection localities are interpreted to represent typical nearshore paleoenvironments and samples come from similar lithologic composition (a blue-gray sandy siltstone). In addition, all samples

Table 1. List of faunules including median age, number of bulk samples analyzed, and the number of identifiable bivalve valves sorted and counted. Numbers correspond to localities shown in Figure 1. Ages from O'Dea et al. (2007), Leonard-Pingel et al. (2012), and Fredston-Hermann et al. (2013).

Faunule	Median age (Ma)	No. of samples	No. of bivalve shells	Longitude	Latitude
Lennond (1)	0.007	10	1,292	−82.266350	9.354883
Swan Cay (2)	1.400	11	1,327	−82.299414	9.453347
Empalme (3)	1.600	6	3,646	−83.061250	9.985583
Upper Lomas (4)	1.600	21	14,793	−83.036720	9.991950
Wild Cane Reef (5)	2.050	7	278	−82.167983	9.349978
Wild Cane Key (6)	2.050	4	331	−82.168700	9.351047
Ground Creek *Porites* (7)	2.050	9	2,119	−82.304567	9.416992
Ground Creek Mud (8)	2.050	6	24,476	−82.301983	9.407367
Fish Hole (9)	2.600	4	329	−82.110838	9.318311
Bomba (10)	3.050	10	2,339	−83.066306	9.913861
Quebrada Chocolate (11)	3.100	1	8,438	−83.084728	9.973608
Quitaria (12)	3.500	1	478	−83.085750	9.910228
Cayo Agua: Punta Níspero West (13)	3.550	3	989	−82.031914	9.168555
Cayo Agua: Punta Tiburón–Punta Piedra (14)	3.550	4	998	−82.023775	9.151892
Río Vizcaya (15)	3.550	3	1,651	−83.069381	9.880608
Santa Rita (16)	3.550	6	802	−83.129910	9.970380
Isla Solarte (17)	3.550	3	2,626	−82.218714	9.333214
Cayo Agua: Punta Níspero South (18)	3.550	3	1,922	−82.030579	9.167275
Isla Popa (19)	4.250	6	11,067	−82.107000	9.214520
Cayo Agua: Punta Norte West (20)	4.250	9	3,887	−82.053814	9.178117
Cayo Agua: Punta Piedra Roja West (21)	4.250	10	10,616	−82.016778	9.139444
Cayo Agua: Punta Norte East (22)	4.250	7	1,493	−82.042417	9.174883
Río Chico N17 (23)	6.350	4	5,030	−77.531889	8.257639
Río Tupisa (24)	6.350	3	1,103	−77.610417	8.308611
Río Indio (25)	6.950	11	601	−80.241389	9.179083
Mattress Factory (26)	9.000	2	1,388	−79.830930	9.360060
Isla Payardi (27)	9.600	9	3,184	−79.821389	9.382722
Sand Dollar Hill (28)	11.000	3	1,551	−79.810472	9.351500
Total		176	108,754		

collected came from an inferred paleodepth of ≤100 m. However, the faunules are interpreted to represent a range of paleoenvironments from soft-sediment/sandy bottom substrates to reef and seagrass beds based on sediment composition and faunal assemblages (O'Dea et al. 2007, Johnson et al. 2007, Leonard-Pingel et al. 2012; see Table 2). We recognize the possibility for habitat patchiness to influence predation, but expect overall trends to hold (sensu Sawyer and Zuschin 2010).

Bulk samples were processed and washed on a 2-mm sieve to remove fossil material from the rock matrix and fossils were sorted into gross taxonomic groups. More than 106,000 identifiable bivalves with a hinge and umbo (see Gilinsky and Bennington 1994) were sorted, counted, and identified to genus following Todd (2001). Total valve counts were then halved to obtain the number of bivalve individuals. Valves were examined for the presence of distinctive drilling traces left by predatory gastropods (see Kitchell et al. 1981, Vermeij 1987, Kelley et al. 2001, Leighton 2002, Walker 2007). We did not remove fragmented individuals from the analysis because most individuals were intact with the majority of fragmentation along the edges. With the exception of edge-drilling, which we did not observe in our samples, most drilling on bivalve prey occurs near the central or

umbonal regions of the shell (Kelley 1988, Kingsley-Smith et al. 2003, Dietl et al. 2004, Kowalewski 2004); therefore, we believe that our use of incomplete and fragmented individuals had minimal impact on our calculations. Initially, we distinguished between naticid and muricid drill holes, but because of vagaries in preservation and in the manifestation of drill holes among different shell types (Kowalewski 1993, Kelley and Hansen 2003), we only considered whether a valve had been drilled or not, and not the predator's taxonomic affinity.

We pooled bivalve genera across all samples and time, and calculated the drilling intensity for every bivalve genus with >25 valves by tallying the number of valves displaying at least one drilling trace, and dividing that by the number of individuals of that genus (Kowalewski 2002). The size (small or large based on average adult length found in the literature), ornamentation (low, moderate, high), depth of burial (epifaunal, semiinfaunal, surface infaunal, shallow infaunal, deep infaunal), and mobility (cemented, byssally attached, free living, or variable) were determined for each bivalve genus using the Neogene Marine Biota of Tropical America molluscan life habits database (Todd 2001; see Appendix 1).

Each variable related to shell architecture or life habit was examined in relation to drilling intensity. Pearson's chi-squared tests were used to test for significant differences in relative abundance of drilled and undrilled valves for different shell sizes, among different levels of shell ornamentation, and among different life habits and mobility. To test how habitat influenced drilling trends, we subdivided the faunules into either biogenic (reef or seagrass, see Table 2) or soft-sediment habitats, and analyzed the bivalves from those two habitats for each of the variables listed above. Because multiple chi-squared tests were performed, a stringent Bonferroni correction was applied; all values reported as significant are significant at an alpha of $P < 0.0017$.

For the analyses of shell size and predation frequency, genera were grouped as small (<10 mm) or large (>10 mm) based on average adult lengths (see Appendix 1). The median drilling percentage for each abundant bivalve family (Pectinidae, Cardiidae, Arcidae, Veneridae, Crassinellidae, Osteridae, Glycymeridae, Lucinidae, Corbulidae) was calculated for each faunule. These percentages were compared using a Kruskal-Wallis ANOVA.

Results

Results indicate that size has a significant impact on drilling incidence among all bivalve genera. Small bivalves (those with an adult length <10 mm) were drilled nearly twice as often as larger bivalves (Fig. 2A, Table 3; $\chi^2 = 875.39$, $P < 0.0001$, df = 1). This pattern generally holds within families as well; the percentage of drilled small venerids is slightly higher than that of larger venerids, without Bonferroni correction this would be a significant difference, but with the stringent Bonferroni it is not significant (Fig. 2B, Table 3; $\chi^2 = 8.80$, $P = 0.0030$, df = 1). However, the incidence of drilling upon small lucinids is more than double their larger counterparts (Fig. 2C, Table 3; $\chi^2 = 135.19$, $P < 0.0001$, df = 1).

Drilling percentage differs significantly among all bivalves with low, moderate, or high ornamentation in unexpected ways (Fig. 3A, Table 3). Bivalves with moderate ornamentation experience significantly higher drilling than do bivalves with low ($\chi^2 = 656.87$, $P < 0.0001$, df = 1) or high ($\chi^2 = 461.08$, $P < 0.0001$, df = 1) ornamentation. When only epifaunal bivalves are considered, bivalves with low ornament have drilling percentages significantly lower than both moderate ($\chi^2 = 38.00$, $P < 0.0001$, df = 1) and high ($\chi^2 = 36.20$, $P < 0.0001$, df = 1) ornament groups; moderate and high ornament groups do not show a significant difference

Table 2. Age, inferred paleoenvironment, and environmental data for each faunule. Paleodepths were inferred from either benthic foraminifera or coral assemblages, mean annual range in temperature (MART) was inferred from bryozoan zooid size (O'Dea and Okamura 2000, O'Dea and Jackson 2009). Percent carbonate and mud come from analysis of the sediment, and percent coral shows what percent of the skeletal fossil assemblage was coral. For more information see O'Dea et al. (2007) and Leonard-Pingel et al. (2012).

Faunule	Age (Ma)	Inferred paleoenvironment	Depth (m)	MART (°C)	Carbonate (%)	Mud (%)	Coral (%)
Lennond	0.007	Mixed reef and seagrass	15.0	3.80	85.18	39.03	94.98
Swan Cay	1.400	Reef	100.0	3.22	63.49	20.90	15.74
Empalme	1.600	Reef	20.0	2.82	43.43	32.55	3.45
Upper Lomas	1.600	Reef	75.0	2.82	43.28	21.33	35.70
Wild Cane Reef	2.050	Reef	25.0	4.19	56.40	28.29	67.05
Wild Cane Key	2.050	Mixed reef and seagrass	30.0	4.19	45.76	33.11	52.62
Ground Creek (*Porites*)	2.050	Reef	10.0	4.19	51.41	53.01	93.79
Ground Creek (seagrass)	2.050	Seagrass	10.0	4.19	29.60	30.78	9.45
Fish Hole	2.600	Mixed reef and seagrass	88.0	2.36	19.55	59.34	34.64
Bomba	3.050	Soft sediment	30.0	3.13	68.96	29.78	1.65
Quebrada Chocolate	3.100	Reef	25.0	3.13	31.98	17.22	0.17
Quitaria	3.500	Soft sediment	30.0	3.13	20.83	20.19	2.67
Cayo Agua: Punta Níspero West	3.550	Soft sediment	60.0	7.23	26.10	33.85	1.56
Cayo Agua: Punta Tiburón	3.550	Seagrass	60.0	5.68	32.01	30.14	25.02
Rio Vizcaya	3.550	Soft sediment	12.0	3.13	31.66	15.47	0.19
Santa Rita	3.550	Soft sediment	30.0	5.73	44.40	28.88	5.86
Isla Solarte	3.550	Soft sediment	75.0	6.68	54.10	14.79	3.28
Cayo Agua: Punta Níspero South	3.550	Seagrass	60.0	7.23	26.10	15.34	3.00
Isla Popa	4.250	Soft sediment	50.0	6.65	19.77	56.69	0.02
Cayo Agua: Punta Norte West	4.250	Seagrass	30.0	6.25	15.93	42.59	8.08
Cayo Agua: Punta Piedra Roja West	4.250	Seagrass	42.0	3.52	27.73	18.72	17.32
Cayo Agua: Punta Norte East	4.250	Soft sediment	60.0	4.11	18.87	49.57	1.60
Rio Chico N17	6.350	Soft sediment	30.0	8.67	20.11	36.02	0.00
Rio Tupisa	6.350	Soft sediment	100.0	6.65	15.28	41.20	0.00
Rio Indio	6.950	Soft sediment	25.0	6.77	9.76	12.13	0.09
Mattress Factory	9.000	Soft sediment	28.0	6.18	24.55	35.30	0.25
Isla Payardi	9.600	Soft sediment	27.5	6.18	25.73	47.90	0.00
Sand Dollar Hill	11.000	Soft sediment	27.5	6.18	20.24	8.60	0.43

in drilling percentages within the epifaunal group ($\chi^2 = 2.19$, $P = 0.1392$, df = 1) (Fig. 3B, Table 3).

Relationship to the substrate strongly influences susceptibility of bivalves to predation. Predation intensity is twice as high for epifaunal bivalves as for infaunal bivalves (Fig. 4A, Table 3, $\chi^2 = 362.70$, $P < 0.0001$, df = 1). Corbulids and scallops were removed for this analysis because of their distinctive life habits that obscure the general pattern. Corbulids were excluded because of their anomalous, quasi semi-infaunal life habit (byssal attachment to sediment grains at or just below the sediment surface) and their overwhelmingly high abundance in most samples. Scallops were excluded because of their unique ability to move freely or swim.
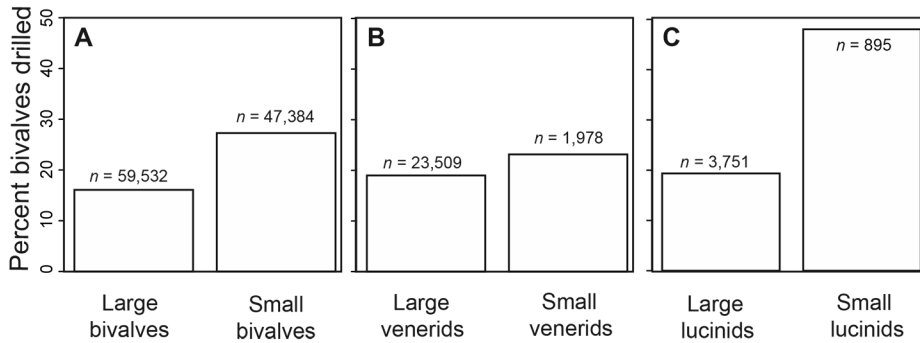
Figure 2. Difference in drilling intensity between large and small bivalves. n indicates the number of individual valves. (A) Average drilling intensity of all small bivalves is significantly higher than that of large bivalves ($\chi^2 = 875.39$, $P < 0.0001$, df = 1). (B) Small venerids experience higher drilling than do large venerids ($\chi^2 = 8.80$, $P = 0.0030$, df = 1). (C) Small lucinids experience significantly higher drilling than do large lucinids ($\chi^2 = 135.19$, $P < 0.0001$, df = 1).

Analysis of drilling and life habit showed that infaunal bivalves with the ability to burrow deeply into the sediment experience significantly less drilling than do bivalves that are shallow burrowers (Fig. 4B, Table 3, $\chi^2 = 2017.77$, $P < 0.0001$, df = 1). Similarly, uncemented epifaunal bivalves are drilled half as often as cemented epifaunal bivalves (Fig. 4C, Table 3; including scallops: $\chi^2 = 330.43$, $P < 0.0001$, df = 1; excluding scallops: $\chi^2 = 48.37$, $P < 0.0001$, df = 1).

These patterns hold when controlling for environment, with two notable exceptions (Table 4). Drilling percentages for infaunal and epifaunal bivalves are not significantly different in biogenic habitats (18.58% and 17.87%, respectively; $\chi^2 = 1.13$, $P = 0.2869$, df = 1). Additionally, uncemented epifaunal bivalves excluding scallops are less frequently drilled than cemented taxa, but the differences are not significant under the selected Bonferroni correction ($\chi^2 = 7.35$, $P = 0.0067$, df = 1).

Taxonomic affinity also influences susceptibility to predation. Drilling percentages differ significantly among abundant bivalve families (Fig. 5; Kruskal-Wallis test: $\chi^2 = 74.01$, $P < 0.0001$, df = 8). Pectinidae (scallops) experience the lowest incidence of drilling with a median drilling percentage of only 0.87%. Several families with different life habits and shell architecture experience similar intermediate levels of drilling (Fig. 5). Families experiencing highest overall drilling intensity are Lucinidae (17.4%) and Corbulidae (21.7%). Corbulids are small and live just beneath the sediment surface. Lucinids are more variable in size and have well developed siphons that allow larger individuals to live well below the sediment surface. The high drilling percentage of lucinids reflects the predominance of small specimens and taxa in our data set.

Discussion

Large size confers a significant refuge from predation. Smaller bivalves experience higher drilling intensities than larger bivalves (Fig. 2). In particular, larger infauna are able to burrow more deeply than smaller infauna (Stanley 1970), and are more difficult for naticid gastropods to manipulate for drilling (Kelley and Hansen 2003 and references therein).

Table 3. Table of percent drilling and *P*-values for comparisons between different shell architecture characteristics, life habits, and mobility of all bivalves. All statistical comparisons were made using Pearson's chi-square test.

Comparison	Percent drilled	*P*-values
Large bivalves	16.08	
Small bivalves	27.27	*P* < 0.0001
Large venerids	18.99	
Small venerids	23.15	*P* = 0.0030
Large lucinids	19.35	
Small lucinids	48.04	*P* < 0.0001
All bivalves		
Low ornament	10.23	
Moderate ornament	26.50	*P* < 0.0001
Low ornament	10.23	
High ornament	17.74	*P* < 0.0001
Moderate ornament	26.50	
High ornament	17.74	*P* < 0.0001
Epifaunal bivalves		
Low ornament	5.01	
Moderate ornamnet	15.37	*P* < 0.0001
Low ornament	5.01	
High ornament	13.26	*P* < 0.0001
Moderate ornament	15.37	
High ornament	13.26	*P* = 0.1392
Infaunal bivalves	8.19	
Epifaunal bivalves	26.70	*P* < 0.0001
Deep infauna	8.19	
Shallow infauna	26.77	*P* < 0.0001
Uncemented epifauna (with scallops)	6.88	
Cemented epifauna	19.76	*P* < 0.0001
Uncemented epifauna (no scallops)	12.75	
Cemented epifauna	19.76	*P* < 0.0001

Extensive ornamentation was a surprisingly ineffective deterrent to drilling predation, although it may be effective against other predators (Logan 1974, Bertness and Cunningham 1981, Vermeij 1987). Among all bivalve life habits, moderate to high ornamentation appears to confer little or no protection against drilling. This is consistent with the hypothesis that surface ornament in infaunal bivalves is more closely related to burrowing (Stanley 1970). High ornamentation also does not appear to deter drilling predation in epifaunal bivalves. Low incidence of predation on epifaunal bivalves with little ornamentation is almost certainly due to their mobility. Highly ornamented epifaunal bivalves do not appear to enjoy any additional protection from drilling predators than their moderately ornamented counterparts. Thus, our results are consistent with experimental studies that suggest the role of
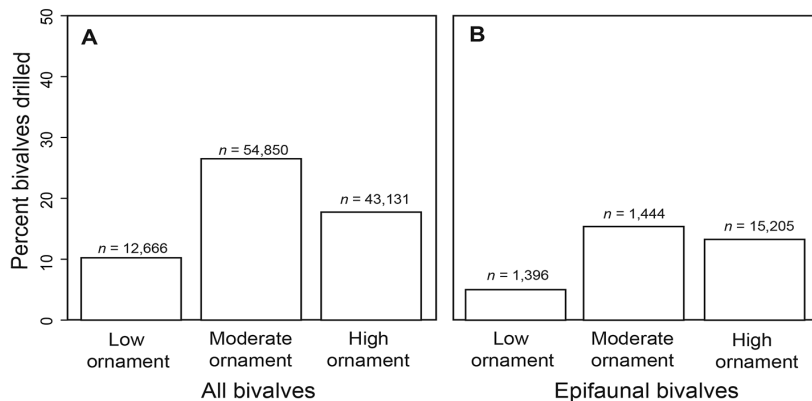
Figure 3. Drilling intensities for bivalve genera with low, moderate, and high shell ornamentation. n indicates the number of individual valves. (A) For all life habits, bivalves with moderate ornament experience significantly higher drilling intensities than do bivalves with low ($\chi^2 = 656.87$, $P < 0.0001$, df = 1) or high ($\chi^2 = 461.08$, $P < 0.0001$, df = 1) ornamentation and bivalves with high ornamentation experience a higher average drilling intensity than bivalves with low ornament ($\chi^2 = 186.43$, $P < 0.0001$, df = 1). (B) Within the epifaunal life habit, bivalves with low ornamentation experience significantly lower drilling intensities than bivalves with either moderate ($\chi^2 = 38.00$, $P < 0.0001$, df = 1) or high ($\chi^2 = 36.20$, $P < 0.0001$, df = 1) ornamentation.

ornament in reducing predation is ambiguous (Carter 1968, Logan 1974, Vance 1978, Feifarek 1987, Harper and Skelton 1993).

Life habit is a very important determinant of bivalve susceptibility to drilling predation. Deep burrowers are drilled less often than shallow burrowers and surface-dwelling infauna. This protection appears to extend even to burrowing naticid predators. Scallops that can swim away from predators experience much lower incidence of predation than any other epifaunal or infaunal bivalves in our sample. In contrast, cemented epifaunal bivalves suffer much higher predation. This may reflect two factors. First, cementation, which acts as a deterrent to some predators (Harper and Skelton 1993, Alexander and Dietl 2003), may not deter drilling gastropods, especially muricid gastropods, which do not manipulate their prey (Harper
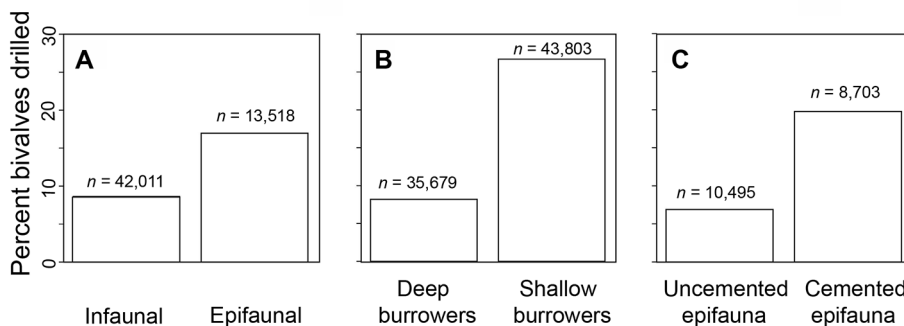

Figure 4. Differences in drilling between different life habits and mobilities of bivalves. n indicates the number of individual valves. (A) The percentage of epifaunal bivalves drilled is twice that of infaunal bivalves ($\chi^2 = 362.70$, $P < 0.0001$, df = 1). (B) The percentage of surface and shallow burrowers drilled is more than three times higher than that of deeply burrowing infaunal bivalves ($\chi^2 = 2017.77$, $P < 0.0001$, df = 1). (C) The percentage of drilling in cemented epifaunal bivalves is more than twice that of uncemented epifaunal bivalves ($\chi^2 = 330.43$, $P < 0.0001$, df = 1).

Table 4. Table of percent drilling and *P*-values for comparisons between different shell architecture characteristics, life habits, and mobility of bivalves within either biogenic or soft-sediment habitats. All statistical comparisons were made using Pearson's chi-square test.

Biogenic habitats			Soft-sediment habitats		
Comparison	Percent drilled	*P*-values	Comparison	Percent drilled	*P*-values
Large bivalves	18.63	$P < 0.0001$	Large bivalves	11.09	$P < 0.0001$
Small bivalves	31.83		Small bivalves	19.62	
All bivalves			All bivalves		
Low ornament	11.56	$P < 0.0001$	Low ornament	6.88	$P < 0.0001$
Moderate ornament	30.38		Moderate ornament	19.72	
Low ornament	11.56	$P < 0.0001$	Low ornament	6.88	$P < 0.0001$
High ornament	20.23		High ornament	11.74	
Moderate ornament	30.38	$P < 0.0001$	Moderate ornament	19.72	$P < 0.0001$
High ornament	20.23		High ornament	11.74	
Infaunal bivalves	18.58	$P = 0.2869$	Infaunal bivalves	9.75	$P < 0.0001$
Epifaunal bivalves	17.87		Epifaunal bivalves	14.43	
Deep infauna	20.25	$P < 0.0001$	Deep infauna	9.29	$P < 0.0001$
Shallow infauna	31.48		Shallow infauna	19.15	
Uncemented epifauna (with scallops)	7.54	$P < 0.0001$	Uncemented epifauna (with scallops)	3.76	$P < 0.0001$
Cemented epifauna	17.20		Cemented epifauna	18.65	
Uncemented epifauna (no scallops)	14.01	$P = 0.0067$	Uncemented epifauna (no scallops)	6.89	$P < 0.0001$
Cemented epifauna	17.20		Cemented epifauna	18.65	

and Skelton 1993, Kelley and Hansen 2003). Second, cemented epifaunal bivalves are often found in reef habitats where drilling intensities are significantly higher than other habitats (Stanley 1970). Our results are similar to those of Sawyer and Zuschin (2010), who also reported that epifaunal bivalves had consistently higher drilling frequencies than infaunal bivalves across a variety of nearshore habitats and that attached epifaunal bivalves experienced higher drilling frequencies than their reclining counterparts. The similarity of these results from different times and geographic localities lends credence to our assertion that bivalve life habits are of fundamental importance in determining their susceptibility to drilling predators.

Bivalve families differ greatly in their overall susceptibility to drilling predators in ways that transcend differences in size, ornamentation, and life habit. Differences in the incidence of drilling among higher taxa are strikingly clear and make intuitive sense because taxonomy reflects many factors at once, including ornamentation, ecology, and shell microstructure. Scallops (Pectinidae), which have crenulated shells and an ability to actively escape predators, are rarely preyed upon by drilling gastropods. In contrast, small bivalves that live right beneath the sediment surface, such as Corbulidae and most lucinids, exhibit the highest incidence of drilling in our study (17.4% and 21.7%, respectively), a pattern that is consistent with other research (Kelley and Hansen 1993, 2006). This is likely due to their life habit and typically small size.
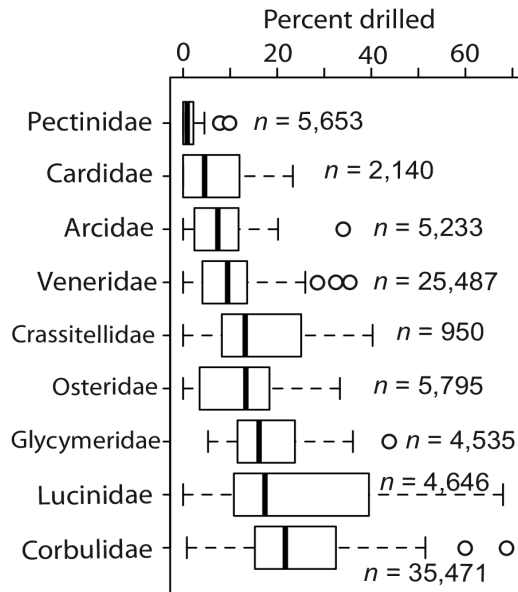
Figure 5. Bivalve genera grouped by taxonomic affinity (families) are significantly different ($\chi^2 =$ 74.01, $P < 0.0001$, df = 8).

Differences among habitats may also be important in determining predation frequency. For example, both Lucinidae and Veneridae are infaunal and similar in range of size and ornament, but exhibit strikingly different incidences of predation. Lucinids predominate in seagrass habitats where drilling percentages are more than double those in unvegetated sandy sediments where venerids are most abundant and drilling frequencies are lower (Sawyer and Zuschin 2010). We see some evidence of this in the analysis of infaunal vs epifaunal drilling proportions within biogenic habitats, where infaunal bivalves have a statistically indistinguishable drilling percentage from epifaunal bivalves. Especially in seagrass beds, small or surface dwelling infaunal bivalves experience unusually high predation (Sawyer and Zuschin 2010).

Higher drilling intensity within seagrass beds also accounts for the higher drilling percentage of uncemented epifauna (not counting scallops) within biogenic environments. Susceptibility to predation based on habitat may therefore be difficult to tease apart from inherent susceptibility based on shell architecture, behavior, and taxonomy. However, we believe that the trends described here are generally true for bivalves from all habitats.

In conclusion, several functional morphological traits of bivalves are related to drilling intensity in ways previously hypothesized, whereas others are not. Shell size, life habit, and mobility strongly influence susceptibility of bivalves to drilling predators, whereas ornamentation does not. Taxonomic affinity integrates the influence of different characters and provides a useful signature of susceptibility to predation that is intuitive and informative. Nevertheless, variability within families is high (Fig. 5) due to variations in predation intensity based on environmental influences such as habitat type.

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Appendix 1. The 90 bivalve genera with a least 25 valves in all samples. The table lists the total number of valves counted in all samples, the percent of the valves with at least one drill hole, and size, ornament, depth, and mobility classifications for each genus.

Genus	Family	No. of valves	Percent drilled	Size	Ornament	Depth	Mobility
Anomia	Anomiidae	299	5.35	Large	High	Epifaunal	Cemented
Acar	Arcidae	162	9.88	Large	High	Epifaunal	Byssally attached
Anadara	Arcidae	3,961	12.62	Large	High	Semi infaunal	Byssally attached
Arca	Arcidae	296	10.81	Large	High	Epifaunal	Byssally attached
Barbatia	Arcidae	827	7.01	Large	Moderate	Epifaunal	Byssally attached
Lunarca	Arcidae	36	11.11	Large	High	Surface infaunal	Variable
Americardia	Cardiidae	32	12.50	Large	High	Shallow infaunal	Free living
Laevicardium	Cardiidae	210	3.81	Large	Low	Shallow infaunal	Free living
Trachycardium	Cardiidae	321	1.25	Large	High	Shallow infaunal	Free living
Trigoniocardia	Cardiidae	1,548	6.85	Large	High	Shallow infaunal	Free living
Cardites	Carditidae	908	19.16	Large	High	Shallow infaunal	Free living
Arcinella	Chamidae	254	14.17	Large	High	Epifaunal	Cemented
Chama	Chamidae	1,085	26.91	Large	High	Epifaunal	Cemented
Caryocorbula	Corbulidae	18,526	35.05	Small	Moderate	Surface infaunal	Byssally attached
Varicorbula	Corbulidae	16,997	25.43	Small	Moderate	Surface infaunal	Byssally attached
Crassinella	Crassatellidae	878	19.59	Small	Moderate	Semi infaunal	Free living
Eucrassatella	Crassatellidae	72	13.89	Large	Moderate	Semi infaunal	Free living
Cardiomya	Cuspidariidae	119	3.36	Small	Moderate	Surface infaunal	Free living
Dimya	Dimyidae	359	57.94	Large	High	Epifaunal	Cemented
Donax	Donacidae	72	0.00	Large	Low	Deep infaunal	Free living
Axinactis	Glycymerididae	65	9.23	Large	High	Semi infaunal	Free living
Tucetona	Glycymerididae	4,471	25.41	Large	High	Semi infaunal	Free living
Hyotissa	Gryphaeidae	253	32.41	Large	High	Epifaunal	Cemented
Isognommon	Isognomonidae	77	10.39	Large	Low	Epifaunal	Byssally attached
Temblornia	Leptonidae	28	0.00	Small	Low	Shallow infaunal	Variable
Ctenoides	Limidae	51	7.84	Large	Moderate	Epifaunal	Byssally attached
Limea	Limidae	29	20.69	Small	High	Epifaunal	Free living
Limopsis	Limopsodae	486	30.45	Small	Moderate	Epifaunal	Byssally attached
Cavilinga	Lucinidae	39	46.15	Large	Moderate	Deep infaunal	Free living
Codakia	Lucinidae	45	26.67	Large	Moderate	Deep infaunal	Free living
Lucina	Lucinidae	2,134	12.84	Large	Moderate	Deep infaunal	Free living
Myrtea	Lucinidae	1,243	28.16	Large	Moderate	Deep infaunal	Free living
Parvilucina	Lucinidae	787	50.06	Small	Moderate	Surface infaunal	Free living
Phacoides	Lucinidae	208	22.12	Large	Moderate	Deep infaunal	Free living
Radiolucina	Lucinidae	106	33.96	Small	Moderate	Surface infaunal	Free living
Mulinia	Mactridae	26	7.69	Large	Low	Deep infaunal	Free living
Crenella	Mytilidae	119	10.08	Small	Moderate	Epifaunal	Byssally attached
Arcopsis	Noetiidae	820	18.54	Large	High	Epifaunal	Byssally attached
Noetia	Noetiidae	225	4.44	Large	High	Semi infaunal	Byssally attached
Sheldonella	Noetiidae	61	19.67	Large	High	Shallow infaunal	Byssally attached
Adrana	Nuculanidae	60	3.33	Large	Moderate	Surface infaunal	Free living
Costelloleda	Nuculanidae	102	3.92	Large	Moderate	Surface infaunal	Free living
Propeleda	Nuculanidae	27	7.41	Large	Moderate	Surface infaunal	Free living
Saccella	Nuculanidae	3,064	10.77	Small	Moderate	Surface infaunal	Free living
Acila	Nuculidae	166	2.41	Large	Moderate	Shallow infaunal	Free living

Appendix 1. Continued.

Genus	Family	No. of valves	Percent drilled	Size	Ornament	Depth	Mobility
Nucula	Nuculidae	2,688	10.71	Small	Low	Surface infaunal	Free living
Varinucula	Nuculidae	128	6.25	Large	Moderate	Shallow infaunal	Free living
Crassostrea	Ostreidae	172	4.65	Large	High	Epifaunal	Cemented
Dendostrea	Ostreidae	5,151	12.89	Large	High	Epifaunal	Cemented
Ostreola	Ostreidae	549	25.87	Large	High	Epifaunal	Cemented
Aequipecten	Pectinidae	40	0.00	Large	High	Epifaunal	Bysally attached
Amusium	Pectinidae	56	3.57	Large	Low	Epifaunal	Free living
Argopecten	Pectinidae	3,765	1.75	Large	High	Epifaunal	Free living
Caribachlamys	Pectinidae	49	4.08	Large	High	Epifaunal	Bysally attached
Cyclopecten	Pectinidae	612	7.52	Small	Low	Epifaunal	Free living
Flabellipecten	Pectinidae	36	0.00	Large	High	Epifaunal	Free living
Leopecten	Pectinidae	482	0.83	Large	Low	Epifaunal	Free living
Leptopecten	Pectinidae	538	0.37	Large	High	Epifaunal	Bysally attached
Pacipecten	Pectinidae	70	22.86	Large	High	Epifaunal	Bysally attached
Spathochlamys	Pectinidae	582	1.37	Large	High	Epifaunal	Bysally attached
Plicatula	Plicatulidae	753	34.53	Large	High	Epifaunal	Cemented
Spondylus	Propeamussiidae	60	13.33	Large	High	Epifaunal	Cemented
Pteria	Pteriidae	169	7.10	Large	Low	Epifaunal	Bysally attached
Yoldia	Sareptidae	108	11.11	Small	Low	Semi infaunal	Free living
Abra	Semelidae	50	4.00	Small	Low	Surface infaunal	Free living
Cumingia	Semelidae	61	13.11	Large	Low	Deep infaunal	Free living
Ervilia	Semelidae	598	16.72	Small	Low	Surface infaunal	Free living
Semele	Semelidae	49	0.00	Large	Low	Deep infaunal	Free living
Tagelus	Solecurtidae	1,240	2.26	Large	Low	Deep infaunal	Free living
Angulus	Tellinidae	853	6.57	Large	Low	Deep infaunal	Free living
Elpidollina	Tellinidae	88	11.36	Large	Low	Deep infaunal	Free living
Eurytellina	Tellinidae	536	8.21	Large	Moderate	Deep infaunal	Free living
Merisca	Tellinidae	563	2.13	Large	Moderate	Deep infaunal	Free living
Moerella	Tellinidae	285	30.88	Small	Low	Surface infaunal	Free living
Strigilla	Tellinidae	85	7.06	Large	Moderate	Deep infaunal	Free living
Tellina	Tellinidae	332	7.23	Large	Low	Deep infaunal	Free living
Felaniella	Ungulinidae	100	18.00	Large	Low	Deep infaunal	Free living
Anomalocardia	Veneridae	55	0.00	Large	Moderate	Deep infaunal	Free living
Chione	Veneridae	15,317	23.24	Large	High	Semi infaunal	Free living
Chionista	Veneridae	36	5.56	Large	High	Shallow infaunal	Free living
Cyclinella	Veneridae	92	4.35	Large	Low	Shallow infaunal	Free living
Dosinia	Veneridae	117	8.55	Large	Moderate	Shallow infaunal	Free living
Gouldia	Veneridae	1,982	23.21	Small	Moderate	Surface infaunal	Free living
Lamelliconcha	Veneridae	302	12.58	Large	Moderate	Shallow infaunal	Free living
Lirophora	Veneridae	839	10.49	Large	High	Shallow infaunal	Free living
Macrocallista	Veneridae	4,405	12.12	Large	Low	Deep infaunal	Free living
Panchione	Veneridae	150	20.00	Large	High	Shallow infaunal	Free living
Pitar	Veneridae	990	13.13	Large	Moderate	Shallow infaunal	Free living
Ventricolaria	Veneridae	73	16.44	Large	Moderate	Shallow infaunal	Free living
Trigonulina	Verticordiidae	70	11.43	Small	Moderate	Surface infaunal	Free living