Taphonomic Bias in Analyses of Drilling Predation: Effects of Gastropod Drill Holes on Bivalve Shell Strength

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The proportion of bivalve shells with drill holes in fossil assemblages is commonly used as a measure of the intensity of predation by drilling gastropods. Previous studies have assumed that drilled and undrilled bivalve shells have equal preservation potentials. We tested this assumption by measuring the mechanical strength of drilled and undrilled valves of the Recent bivalve Mulinia lateralis. *Under compressive loads, drilled valves are significantly weaker than undrilled valves, a difference we attribute to local stress concentrations produced by the presence of the drill hole. Our results suggest that drilled valves may break preferentially and hence inferred patterns of predation may reflect taphonomic as well as biological processes. Careful examination of shell fragments in an assemblage may permit recognition of this type of taphonomic bias.*

INTRODUCTION

Drilling predation by gastropods is a common cause of mortality in shelled mollusks. The frequency of drilled shells in Recent death assemblages is generally considered to be a reliable measure of predation intensity (e.g., Ansell, 1960; Wiltse, 1980; Vermeij, 1980; see Kabat, 1990 for review). Since drilled shells are commonly preserved in the fossil record, similar metrics have been used to quantify drilling predation intensity in fossil assemblages and to study temporal patterns of drilling predation (e.g., Vermeij, 1983, 1987; Hoffman, 1976; Hoffman et al., 1974; Hoffman and Martinell, 1984; Kelley, 1989, 1991; Taylor et al., 1983; Anderson, 1992; see Kabat, 1990 for a review). However, the basic assumption of such an approach is that the preservation potential of drilled and undrilled shells is not significantly different (Kowalewski, 1993; Allmon et al., 1990; Taylor et al., 1983; Dudley and Vermeij, 1978). Despite its widespread acceptance, there are strong theoretical reasons to suspect that this assumption is untenable and, hence, its validity clearly needs to be tested.

In this study, shell strength is defined as the maximum compressive force required to break a shell. Because fragmentation is a common style of damage and a source of taphonomic loss in fossil assemblages (Boyd and Newell, 1972; see review of subsequent literature by Kidwell and Bosence, 1991), the preservation potential of shells must depend, to some extent, on their strength. Thus, in situations where fragmentation is important, drilled and undrilled shells of a species should have similar strengths in order to have similar preservation potentials. This expectation, however, is not consistent with fracture mechanics theory, that states that any notch or hole in a uniformly stressed body acts as a local stress concentrator (see Gordon, 1976 and Wainwright et al., 1982 for discussion), thereby initiating early crack formation and reducing the strength of the body. The stress concentration factor depends on the shape of the hole and is independent of its size (Gordon, 1976). For a circular hole in an elastic plate under an applied stress (S), the stress at the edge of the hole can be theoretically shown to be 3S (Wainwright et al., 1982). Theoretical calculation of the stress concentration factor for a hole in a bivalve shell is much more difficult because the shell has a complex shape and is made of a composite material, the mechanical properties of which are not very well understood (see Wainwright et al., 1982). Thus, testing for differences in shell strength is best approached empirically, comparing measured shell strengths of drilled and undrilled shells.

We test the effects of gastropod drill holes on bivalve shell strength, and thus on preservation potential, by experimentally determining mechanical strengths of drilled and undrilled shells of the Recent bivalve *Mulinia lateralis*. In addition, we test for other potential biases, namely, differences in shell strength between left and right valves, between assemblages collected from two different environments and between dry and rehydrated shells.

MATERIALS AND METHODS

Two bulk samples of disarticulated shells of *Mulinia lateralis* were collected on Seabrook Island, South Carolina, from two environments, a sandy beach (SB) and a tidal channel cutting across the beach (TC). Both samples contained drilled and undrilled left and right valves. Drill holes were all countersunk and typically naticid in character (Carriker and Yochelson, 1968). A third sample

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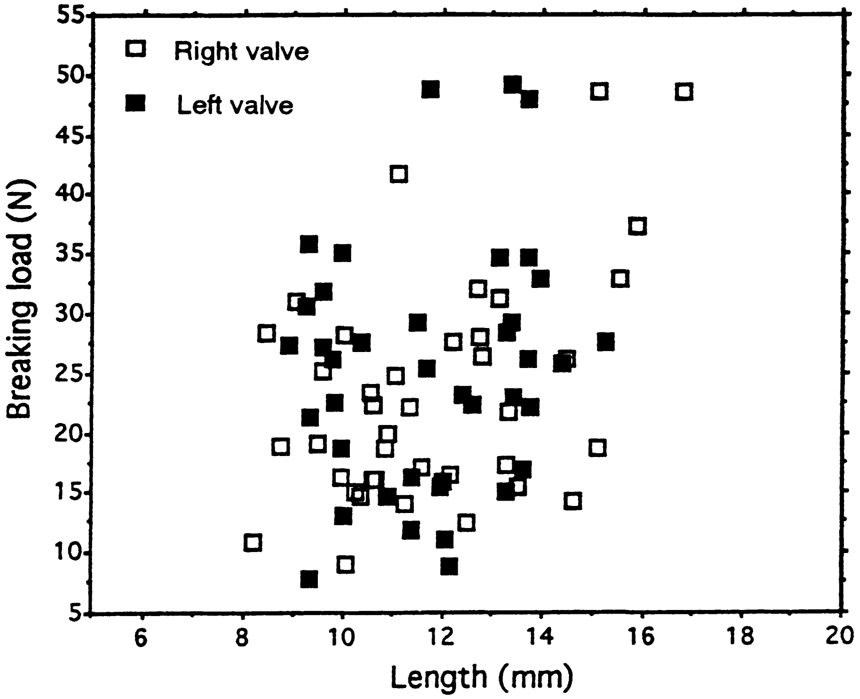

FIGURE 1—Breaking load as a function of length for left and right valves of SB shells (see text). Samples not significantly different (see Table 1).

(TC-H) was prepared by hydrating a subsample of dry undrilled TC shells for four days in artificial sea water.

In order to control for effects due to the position of the drill hole, we only used specimens that had been drilled near the umbo. Because the majority of the shells collected were drilled around the umbo, selection of such shells did not introduce any significant sampling bias. In addition, only shells with no visible evidence of mechanical damage were used. For each valve, the maximum antero-posterior length was measured with digital calipers (±0.01 mm). Each valve was loaded in compression until it broke. The valves were oriented such that the loads were applied perpendicular to the plane of the commissure. The breaking loads for small shells were measured using a small tensometer equipped with a 10 N force transducer, while those for larger shells were measured using a Monsanto tensometer equipped with a compression attachment. A strain gauge attached to the force beam of the tensometer was used to measure the forces (see LaBarbera and Merz, 1992). Signals from the tensometers were amplified and recorded on a Hewlett Packard 7044A X-Y plotter. Precision and accuracy of the force measurements were approximately ±0.5%.

Data analyses were performed using Systat (ver 5.1; Systat Inc., Evanston, IL) on a Macintosh computer. The confidence level for statistical significance was set at 95% or better.

RESULTS

Undrilled Shells

Analysis of covariance (ANCOVA) of regressions of shell strength as a function of length for undrilled valves of *Mulinia lateralis* from the tidal channel indicted that there were no significant differences between the left and right valves for either the dry (TC) or hydrated (TC-H) samples (Table 1). The same result holds for undrilled left and right valves from the beach environment (SB) (Table 1 and Fig. 1). Consequently, we pooled right and left valves within each sample and tested for differences between strength-length regressions for each sample using ANCOVA. No significant differences were found between regressions for undrilled TC and SB shells or between undrilled SB and TC-H shells (Table 1). Similarly no significant differences in strength-length regressions were found when undrilled TC, SB and TC-H shells were analyzed together (Table 1, Fig. 2). However, when strength-length regressions of TC and TC-H shells were compared, the adjusted means were significantly different (TC > TC-H) although the slopes were not (Table 1, Fig. 2).

Comparison of Drilled and Undrilled Shells

For the TC and SB samples, the slopes of the strength-length regressions for the drilled and undrilled specimens were significantly different (Table 1, Fig. 3). The slopes for the drilled shells were significantly lower in each case, indicating that drilled shells, on average, were weaker than undrilled ones. Similar results were obtained when pooled undrilled TC and SB shells were compared to drilled TC and SB shells (Table 1, Fig. 4). Finally, the same pattern was also found when all drilled and undrilled shells were pooled and compared (Table 1, Fig. 4).

DISCUSSION

Relative Strengths of Undrilled Shells

In postmortem assemblages of *Mulinia lateralis*, the relationships between size and shell strength of left and right valves were not significantly different for any of the samples (Table 1, Fig. 1). This suggests that taphonomic losses due to fragmentation (especially due to compaction) should be similar for the two valves of an equivalved species. Hence, any observed differences in the abundance of left and right valves of a single equivalved bivalve species in a fossil assemblage is more likely

TABLE 1—Comparison of measured failure load as a function of length for various samples (see text) of *Mulinia lateralis*. Statistically significant differences ($P < 0.05$) are indicated by asterisk.

Sample	n	ANCOVA probabilities	
		Slopes	Adjusted means
1. Undrilled shells			
Left vs. right valves			
TC shells	49	0.889	0.716
SB shells	78	0.327	0.370
All valves pooled			
TC, SB, TC-H	187	0.494	0.110
TC, SB	127	0.765	0.361
TC, TC-H	109	0.465	0.036*
SB, TC-H	138	0.233	0.225
2. Drilled vs. undrilled			
TC	93	0.035*	
SB	173	0.005*	
TC, SB	266	0.001*	
TC, SB, TC-H	326	0.000*	

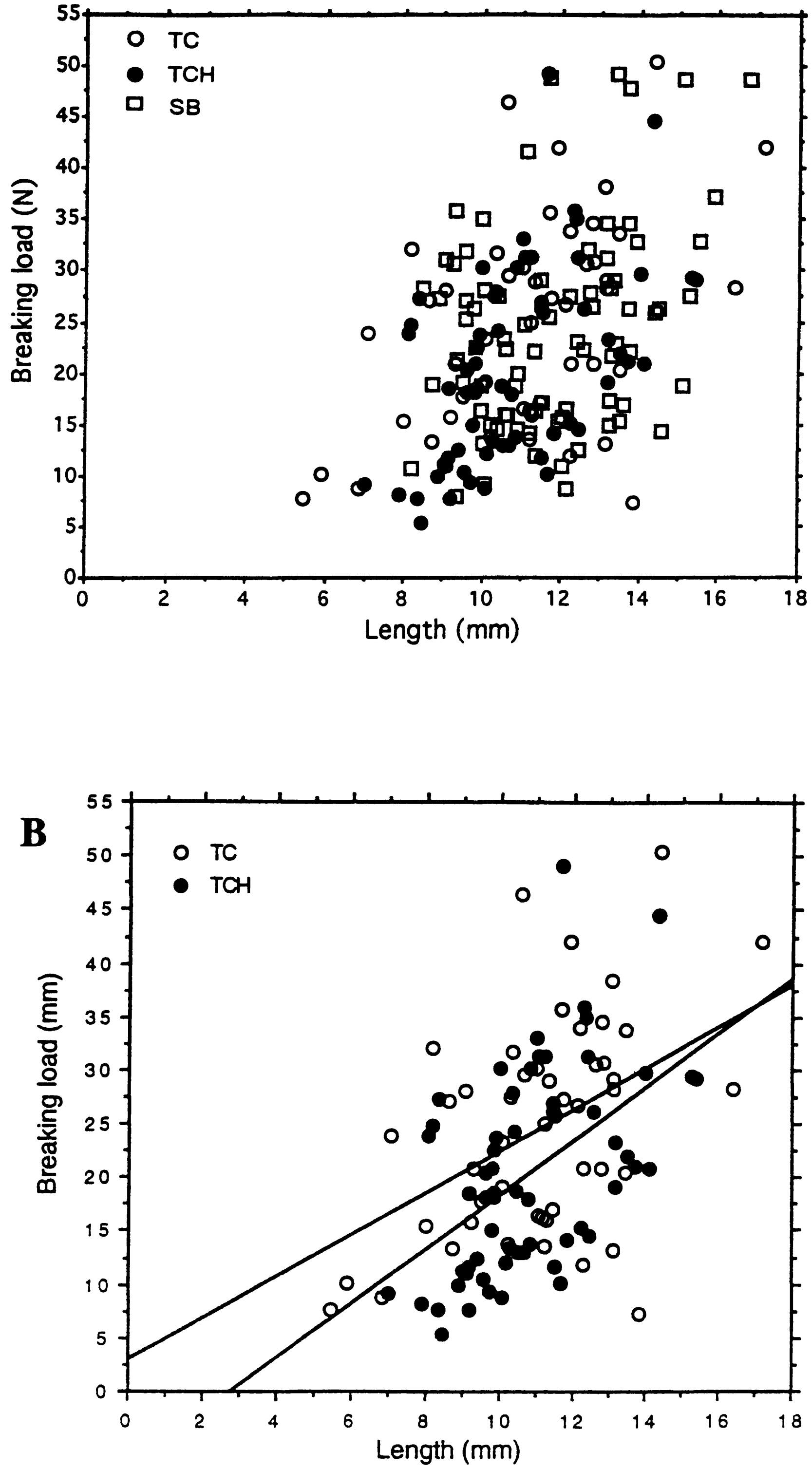

FIGURE 2—Breaking load as a function of length for (A) all undrilled shells (left and right valves pooled) of *Mulinia lateralis*; samples are not significantly different; (B) undrilled TC and TC-H shells; the slopes are not significantly different but the adjusted means are (see text and Table 1).

to be due to differential sorting rather than loss through differential fragmentation.

There were no significant differences in shell strength for dry shells from the two different environments (beach and tidal channel; Table 1). However, rehydrated shells were significantly weaker than dry shells for the tidal channel sample. Currey (1979) demonstrated experimentally that the strength of thin-shelled bivalves can be affected, to some degree, by drying. Our results support this conclusion although, in contrast to the results of Currey (1979), we found that rehydrating reduced the shell strength instead of increasing it.

Comparison of Drilled and Undrilled Shells

The results of this study indicate that, under compressive loads, drilled

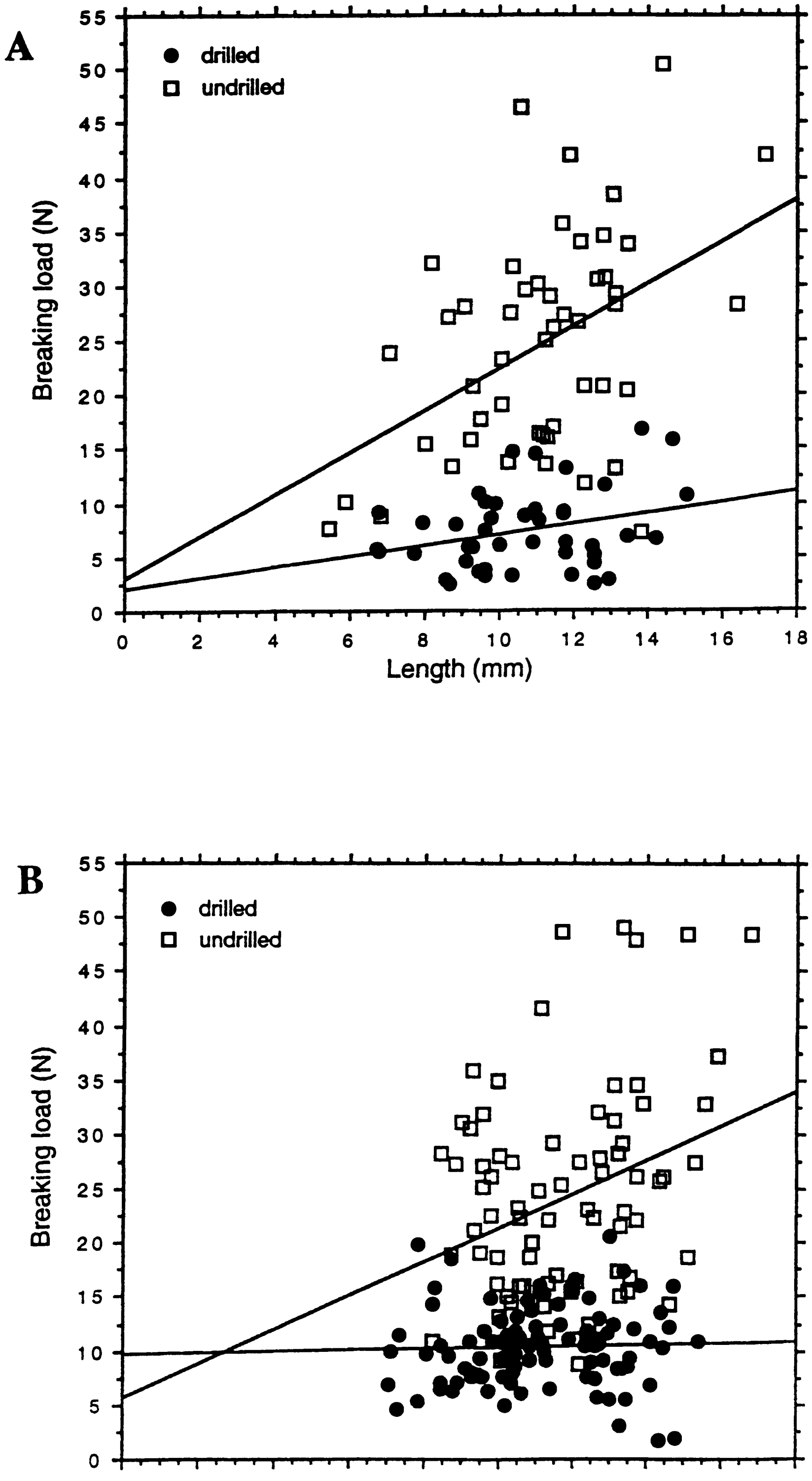

FIGURE 3—Breaking load as a function of length for (A) drilled and undrilled shells from the tidal channel (TC); (B) drilled and undrilled shells from the beach (SB). In both cases the slopes are significantly different (see text and Table 1) indicating that the drilled shells are significantly weaker.

shells of *Mulinia lateralis* are significantly weaker than undrilled ones. These differences can be attributed, primarily, to increased stress concentrations produced by the presence of a drill hole and are entirely consistent with theoretical predictions.

Previous studies of drilling predation have assumed that drilling frequency data convey an original ecological signal. The fact that the drilled and undrilled shells examined here have markedly different mechanical strengths, however, suggests that observed patterns of predation in the fossil record may reflect taphonomic as well as biological processes. Postmortem fragmentation due to compaction has been inferred to be an important source of taphonomic loss of bivalve shells (see Hoffman, 1976 and Kowalewski, 1990, for an example from the Miocene of Poland; also Miller, unpublished data, Eocene of Texas). In situations where postmortem fragmentation is a factor, drilled shells may be preferentially destroyed simply because they are weaker. Patterns of drilling predation observed in these fossil assemblages would, therefore, represent a taphonomically biased record of the original biological signal. The effects of this bias on various aspects of the analysis of drilling predation are discussed below. It should be pointed out that, strictly speaking, our results are valid only for small, thin-shelled, umbonally drilled bivalves under localized compressive loads. It remains to be seen how changes in shell shape, shell thickness, position, completeness and size of the drill hole, and loading regime affect the relationship between drilled and undrilled shells. However, given the magnitude of the strength differences and the theoretical predictions, we would expect similar relative differences in other cases where either shell parameters or drilling sites are different.

Predation Intensity

The frequency of drilled shells in an assemblage is commonly reported as a measure of intensity of drilling gastropod predation (see Kabat, 1990, for a review). Such data have been used to identify preferred prey taxa (e.g., Hoffman and Martinell, 1984; Stanton and Nelson, 1980; Kojumdjieva, 1974) and changes in predator–prey interactions through time (e.g., Vermeij, 1983, 1987; Kelley, 1989, 1991). Long-term changes in drilling frequencies have been interpreted as reflecting the changing importance of this mode of predation in benthic marine communities (see Vermeij, 1987, for review). Although a few studies have considered the potential biasing effects of hydrodynamic sorting (e.g., Lever et al., 1961, 1968; Miller, 1991), most have completely ignored taphonomic biases and none has assessed biases due to differences in mechanical strength.

Our results suggest that in assemblages where postmortem fragmentation is important, preferential loss of the weaker, drilled shells would significantly lower the calculated drilling frequencies and, hence, would lead to underestimates of predation intensities. To illustrate this, we calculated predation intensities as a function of load using our data set. We selected a specific value of load, deleted all drilled and undrilled valves with strengths less than that load, and then calculated the predation intensity (following Vermeij, 1980) based on surviving valves. The results (Fig. 5) show that inferred predation intensity decreases rapidly with increasing load and, hence, differences between actual (i.e., predation intensity for load = 0 N) and calculated intensities can be substantial even at moderate loads. At higher loads (>20 N for our data) only undrilled shells tend to survive and hence drilling frequencies based solely on unbroken shells will give the erroneous impression of an absence of predation. Thus, unless taphonomic biases can be ruled out, calculated drilling frequencies based only on unbroken shells should be interpreted with extreme caution.

Because shell strength varies as a function of size, shape, mass, and microstructure of the shell (see Wainwright et al., 1982), different taxa of bivalves within a given assemblage could suffer varying degrees of tapho-

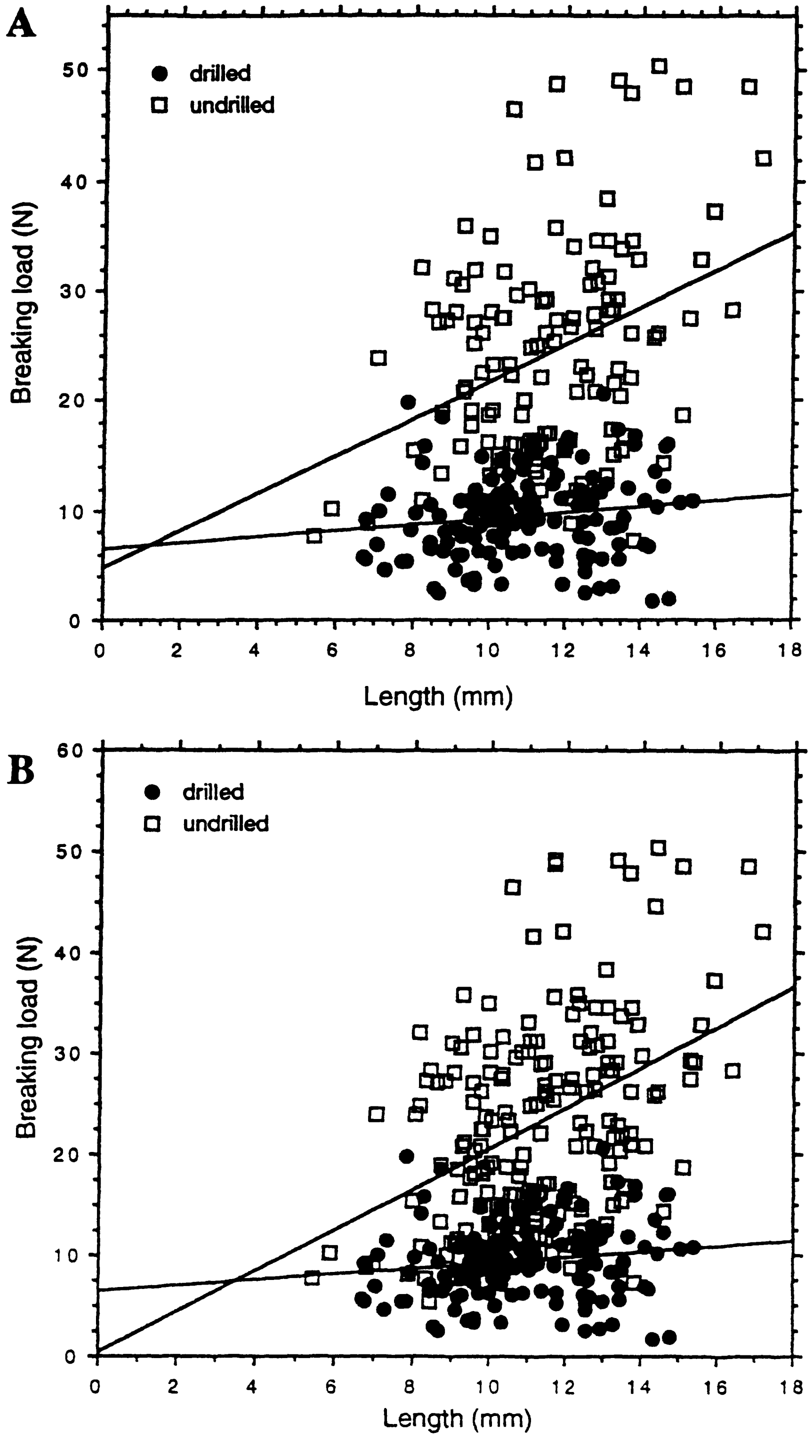

FIGURE 4—Breaking load as a function of length for (A) drilled and undrilled TC and SB shells pooled; (B) drilled and undrilled TC, SB and TC-H shells pooled. In both cases the slopes are significantly different (see text and Table 1) indicating that the drilled shells are significantly weaker.

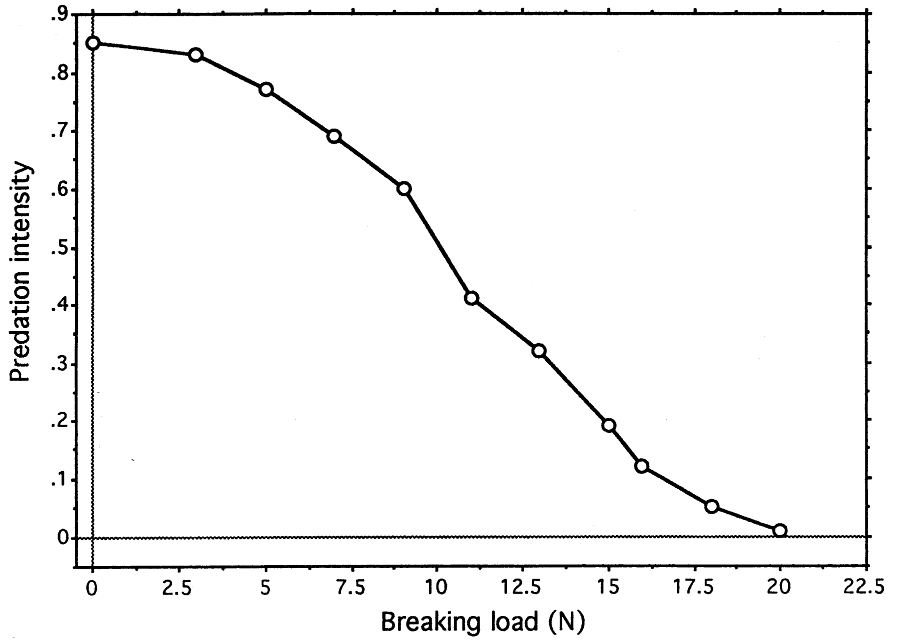

FIGURE 5—Predation intensity calculated as a function of breaking load (see text) for all shells used in this study. Following Vermeij (1980), we define predation intensity as twice the number of drilled whole valves divided by the total number of whole valves.

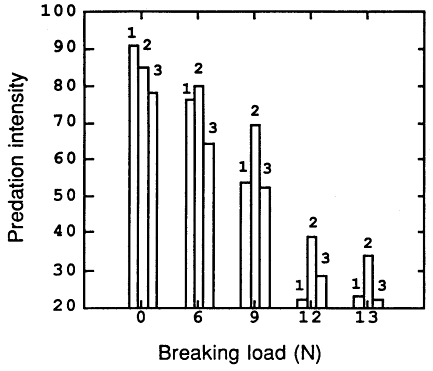

FIGURE 6—Simulated predation intensities as a function of load (see text) for individual size classes. Size class 1 consists of shells of lengths 5–10 mm, size class 2 of lengths 10.01–12 mm and size class 3 of 12.01–14 mm.

nomic loss. Our results suggest the possibility that high variances observed in the proportion of drilled individuals among species and localities (see Vermeij, 1980; Anderson, 1992) may reflect taphonomic rather than (or in addition to) biological signals. The extent of taphonomic loss for each taxon should be estimated individually before interspecific comparisons of predation intensities are undertaken (see below). The inverse relationship between load and drilling frequency also suggests that any systematic temporal trend in compactional regime will tend to alter the inferred temporal pattern of intensity of drilling predation. We think that this is unlikely to be a significant problem for long-term global trends in drilling frequency (e.g., Vermeij, 1987), because on those time scales the changes in compactional regime should be more or less randomly distributed. The problem, nonetheless, needs to be critically examined in future studies.

Optimal Foraging

Several studies have attempted to describe drilling predation in the context of optimal foraging theory, both in Recent assemblages and in the fossil record (Kitchell et al., 1981; Kitchell, 1986; Broom, 1983; Boggs et al., 1984; Kelley, 1988, 1991). Predictions made by optimal foraging models are tested, in part, by comparing the relative availability of size classes of prey to the actual size classes selected (Kitchell et al., 1981; Kelley, 1988). Size frequency distributions of drilled and undrilled shells are required for such analyses.

Figures 3 and 4 show that for all samples, (a) the slope of the strength-size regression line for the undrilled shells is significantly steeper than that of the drilled shells (TC, undrilled = 1.947 ± 0.558, drilled = 0.505 ± 0.261; SB, undrilled = 1.572 ± 0.543, drilled = 0.066 ± 0.188; combined, undrilled = 2.018 ± 0.316, drilled = 0.274 ± 0.162), and (b) for all size classes, the variance in breaking load for the drilled shells is much lower than that for the undrilled shells. These observations suggest that the presence of drill holes disproportionately reduces the strengths of the larger shells. As a result, the difference in mean strengths of drilled and undrilled samples changes with size, with the greatest differences observed in the larger size classes. Consequently, for any given load, larger size classes will preferentially tend to retain intact undrilled shells and, hence, with increasing load, the inferred drilling frequencies for these size classes will be reduced at a faster rate compared

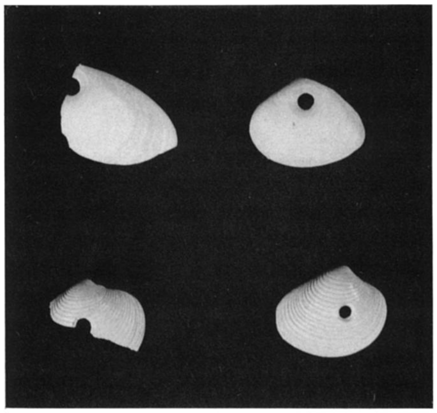

FIGURE 7—Effect of drill hole on fragmentation pattern. Top row: whole and fragmented *Mulinia lateralis*. Fragmentation, in this case, due to experimental loading. Bottom row: whole and naturally fragmented fossil *Cytherea elegaris* from the Eocene of France. Note that fractures pass through drill holes in both cases. All specimens ×2.6.

to the middle size classes. The magnitude of the changes would, of course, depend on the relative slopes of the lines, the variance of the points, and the magnitude of the load, and, hence, would vary from case to case. In general, the end result of this taphonomic bias would be a change in the overall shape of the size frequency distribution (Fig. 6). Thus, in assemblages where this bias exists, size frequency distributions cannot be used to test the predictions of optimal foraging models. In our data, the original size frequency distribution shows maximum predation intensity in the smallest size class and a progressive decrease in predation intensity for the two larger size classes (Fig. 6). In contrast, in the simulated distributions (i.e., when predation intensity for each size class is calculated as a function of load), maximum predation intensity occurs in the middle size class for moderate loads (Fig. 6). Interestingly, the general shape of the altered distributions (maximum predation intensity in the middle size class) is similar to some distributions used to test optimal foraging in the fossil record (e.g., Kitchell et al., 1981; Kelley, 1988). Depending on the nature of the original size distribution of drilled and undrilled shells and the degree of taphonomic overprint, it is possible to make either Type I (rejecting an optimal model when it is true) or Type II (accepting an optimal model when the system is non-optimal) errors while testing optimal foraging models. We are, of course, not suggesting that all interpretations of optimal foraging in the fossil record are artifacts. Optimal foraging is a real biological phenomenon that presumably has its roots in the geologic past. We are simply suggesting that to demonstrate optimal foraging for drilling predators in the fossil record taphonomic biases due to fragmentation must be ruled out first. Our results are relevant only for testing the predictions of the optimal foraging models. Demonstration of prey size selectivity (sensu Kitchell et al., 1981) and calculation of cost-benefit curves are not affected by this type of taphonomic bias.

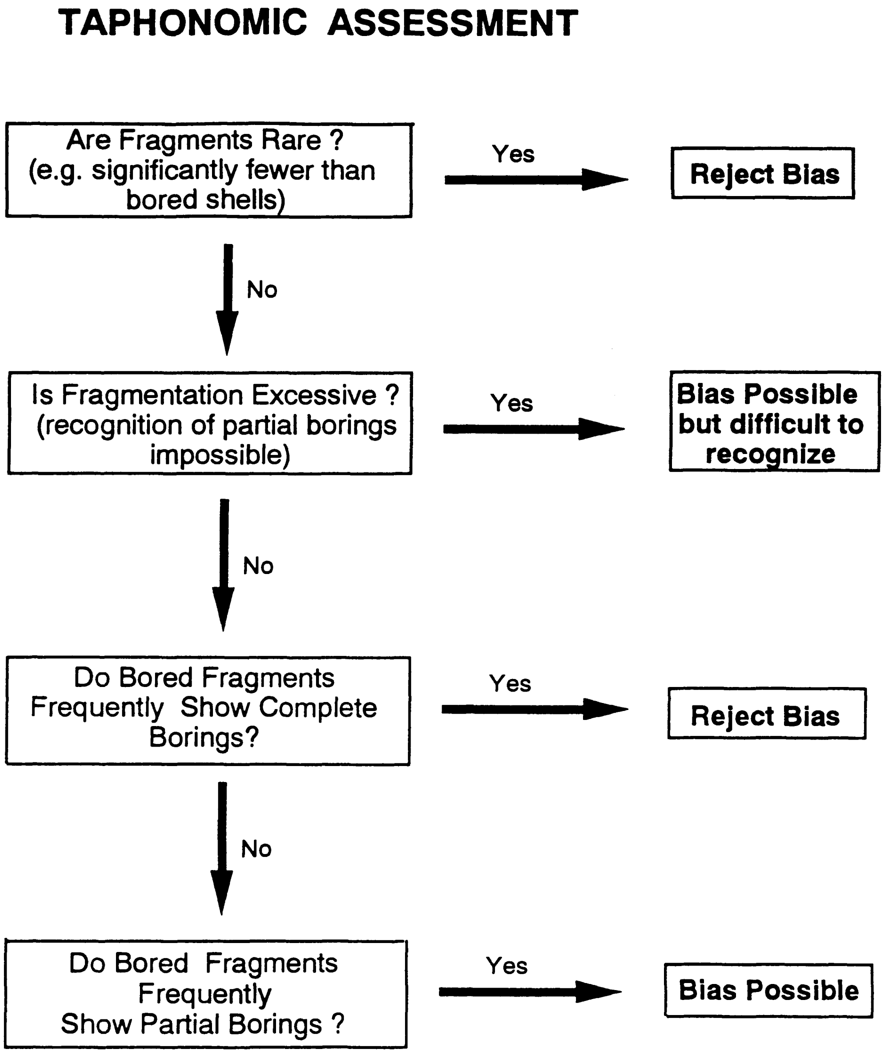

FIGURE 8—Flowchart for assessing the extent of differential taphonomic loss due to the presence of drill holes.

Survivorship Curves and Mortality Patterns

Drilling intensity is often reported as a function of prey size (e.g., Kitchell et al., 1981; Stanton and Nelson, 1980; Stanton et al., 1981; Kojumdjieva, 1974; Hoffman, 1976; Hoffman et al., 1974; Kelley, 1982). In addition, these distributions are also thought to contain important ecological information about the age structure of populations and mortality patterns (Dodd and Stanton, 1990; Craig and Oertel, 1966). For example, Hoffman (1976) used size frequency plots of drilled and undrilled shells to study the mortality patterns of four bivalve species from the Miocene Korytnica Clays of Poland. However, bivalve fragments are abundant in the Korytnica Clays and are thought to have resulted from compactional crushing (Hoffman, 1976). It is obvious that the taphonomic biases discussed earlier also apply to these types of paleoecological studies and hence similar precautions must be taken before size frequency plots are interpreted ecologically.

Assessment of Taphonomic Bias

Causes of fragmentation of mollusc shells include the activity of predators, scavengers, bioturbation, impact during transportation, and postdepositional compaction. Our results suggest that the recognition of taphonomic bias due to fragmentation is crucial in studies of drilling predation. We believe that careful examination of fragmentation patterns should permit an assessment of taphonomic loss resulting from the presence of drill holes. Since a drill hole acts as a local stress concentrator (Wainwright et al., 1982) and initiates crack formation, the theoretical expectation is that when a shell breaks, the fracture should pass through the drill hole. Our experiments confirm this expectation; the drilled shells, almost always, had fractures passing through the drill hole (Fig. 7). Thus, if compaction or other fracturing processes were the primary cause of the loss of drilled shells in a fossil assemblage, one would expect to find a significant number of fragments containing a portion of a drill hole. On the other hand, if fragments were rare compared to the unbroken shells or mostly contained intact drill holes, then one could argue that the presence of the drill hole did not contribute significantly to the shell breakage. These possibilities are summarized here in Figure 8. We recommend examining a large number of fragments and assessing the hypothesis of differential taphonomic loss before considering biological interpretations of calculated drilling frequencies from fossil assemblage. We also suggest that drilling frequencies are best calculated from bulk samples where one can examine a large number of fragments and not from prepared museum specimens where no such information is available.

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