

SHELL REPAIR OF MECHANICALLY INDUCED FRACTURES IN *MERCENARIA* *MERCENARIA* UNDER EXPERIMENTALLY SUBOPTIMUM CONDITIONS

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ABSTRACT Sixty hand-tonged, harvested specimens of *Mercenaria mercenaria* from wild stock in Raritan Bay, New Jersey, measuring 34 to 43 mm in dorsal ventral length, were apportioned among buckets of sediments submerged in predator-excluded flow-through tanks. Experimental sediments simulate substrata found native to hard clams and included: (1) well-sorted sand, (2) pure mud, (3), an admixture of equal volume of shell-free sand and mud, (4) an admixture of 75% sand and 25% shell hash, and (5) an admixture of 75% mud and 25% shell hash. Hand-excavated clams reburrowed monthly for one year. Progressively dysoxic interstitial pore water beneath the sediment interface mediated burrowing conditions. Shells of live specimens in progressively blackened sands became chalky in appearance with ornamentation completely abraded and/or etched away. Upon sacrifice, 30 (50%) specimens revealed fractures in the valve interior that radiated from the ventral (24), posterior (four), and anterior (two) margins, whereas only five of 36 (14%) specimens in the unburrowed "control" group showed anthropogenically (harvesting and machine-sorting) induced microfractures at the ventral margin. Mean annual dorsal-ventral shell accretion was negligible under these experimentally suboptimal conditions. Distribution of fractured specimens among the five experimental substrata is statistically random, although, paradoxically, more clams that reburrowed in mud than sand-shell hash had internally repaired valves. Severity of fractures is evidenced by stuccoed cracks that encroached within a cm of the dorsal hinge and others that bifurcated and deflected through the adductor muscle scars. Converged fractures in one reburrowed specimen removed a large triangular wedge of shell that proved lethal. Nevertheless, repaired fractures did not fail under the strain of repeated re-burrowing.

KEY WORDS: *Mercenaria mercenaria*, burrowing, fracture, repair, abrasion

INTRODUCTION

Lethal and sublethal shell fractures in *Mercenaria mercenaria* have been primarily attributed to durophagous predators. The toll these molluscivores inflict on this commercially valuable species has been reviewed by Krauter (2001). Dredging activity also may sublethally fracture shells of commercially valuable clams as observed in commercially harvested *Glycymeris glycymeris* (Ramsey et al. 2000), *Ensis siliqua* (Gaspar et al. 1994), *Solen* sp. (Bergman & Hup 1992), and *Arctica islandica* (Witbaard & Klein 1994). Scar frequencies have been used to attempt reconstruction of the history of past shellfishing pressure. Another possible non-predatory cause of shell fracture in bivalves is burrowing, although such shell-fracturing mechanical processes have been infrequently investigated experimentally. Checa (1993) illustrated specimens of the thin-shelled deep bivalves *Lutraria lutraria*, *Panopea glycymeris*, and *Solecurtus strigalatus* with scars of repaired cracks induced by reburrowing by individuals that were prone to excavation by winter storm waves.

However, repair of burrowing-induced fractures and its frequency has not been documented in a shallow-burrowing, thicker-shelled, and commercially harvested clam, such as *Mercenaria mercenaria*. The extent to which such mechanically induced fractures can be repaired is unreported. Appreciable abrasion of the ventral margin of *M. mercenaria* has been documented in transplant experiments (Pannella & MacClintock 1968, Rhoads & Pannella 1970, Kennish 1978). Repeated burrowing may chip the commissure margin of some young adults of *M. mercenaria*, thereby providing a site for initiation of dorsally propagated fractures. Conceivably, sediment texture and cohesiveness could influence both sediment loading against the valves (Checa 1993) and/or the likelihood that shell shards become occluded between the valves during the repeatedly opening and adduction of the valves. Reburrowing may provide the additional stress on valves marginally chipped by the commercial excavation, handling, and

sorting processes. Raked specimens, jostling against each other in transport and sorted by conveyor-belt into bags of commercially graded sizes may bear very slightly chipped margins that could become the initiation sites of fractures if the clams are afforded an opportunity to reburrow. Conceivably, sediment texture may be causally related to frequencies of (1) anthropogenically induced microfractures that are propagated through the valve during reburrowing, and/or (2) burrowing-induced microfractures that are further expressed during repeated penetration of the sediment. Sediment texture may also influence interstitial water chemistry mediated by sediment porosity and permeability. Substrates of different mean grain sizes and degree of sorting have different porosity and permeability properties. Suboptimum interstitial conditions beneath the sediment surface where the clam burrows also may influence both shell fracture propagation and the ability of the mantle to repair cracks.

Accordingly, this investigation experimentally focuses on the repair of nonpredatory shell fractures in young adults of *M. mercenaria* that repeatedly burrow into various textured sediments. The testable, refutable null hypotheses are (1) that microfractures possibly initiated by anthropogenic excavation and handling are repaired prior to or during reburrowing activity, (2) that the burrowing process also initiates microfractures that are repairable, (3) repaired fractures withstand the strain induced by reburrowing, (4) that no significant difference in the frequency of fractures results from reburrowing in different textured sediments, and (5) that no significant change in valve thickness and external ornamentation resulted from re-burrowing in different textured sediments.

METHODS AND MATERIALS

Within Raritan Bay, New Jersey–New York, commercial shellfish beds, some situated in depths above effective storm wave base, include sediments characterized as mud, shell, gravel, sand, and sand-mud that host varying densities of *M. mercenaria*. To test

the effect that sediment texture has on shell abrasion, chipping, and fracture-initiation or propagation in *M. mercenaria*, five 12-L buckets of sediment were submerged in each of two 690-L flow through tanks at the NOAA Laboratory at Sandy Hook, New Jersey, which pumps in water from Raritan Bay. Each bucket was filled with a substratum to a 14 cm depth, resulting in the sediment surface recessed about 4 cm from the top of the bucket. Enclosed substrate included one of five types of sediments and shell hash native to Raritan Bay to simulate the various substrata naturally occupied by *M. mercenaria*. The five sediment categories included (1) sieved, intertidal sand void of any gravel size grains and shell fragments, (2) pure mud, (3), an admixture of shell-free intertidal sand (50% by volume) and mud (50% by volume), (4) an admixture of 75% by volume of beach sand and 25% by volume of shell hash, and (5) an admixture of 75% by volume of mud and 25% by volume shell hash. Shell hash included shards of razor clams (*Ensis directus*), blue mussels (*Mytilus edulis*), surfclams (*Spisula solidissima*), and hard clams (*M. mercenaria*) created by mortar and pestle. The longest dimension of any shell shard did not exceed 4 mm. Admixtures of sediment types were thoroughly mixed with a trowel to homogenize the substrates. Two replicates of each substratum were created, one for each flow through tank.

Sixty hand-raked, machine-sorted, specimens of *M. mercenaria* obtained from a depuration plant operating in Raritan Bay were measured dorsal-ventrally (= shell length), and perpendicular to the hinge line at the point of maximum curvature or maximum cross-sectional height (= shell height) to the nearest 0.1 mm by means of electronic vernier calipers. All specimens ranged from 34 to 43 mm in dorsal-ventral length. Initial scrutiny of the specimens revealed no hairline fractures expressed on the valve exteriors. A separate batch of 36 machine-sorted specimens from the depuration plant, measuring 34–41 mm in DV length, were held in an aquarium without sediment for four weeks and then sacrificed to determine if commercial harvesting and handling could have initiated any interior fractures in the shells prior to reburrowing. Among the 60 experimental clams, six specimens were assigned to each of the 10 buckets of substrata and placed reclining on one valve in a clockwork arrangement (12, 3, 6, and 9 o'clock with two specimens at the center) on the sediment in May 1998. Acclimation to the conditions in the tanks occurred during the ensuing summer months. Monitoring of changes in the shell dimensions and external surface appearance commenced in October 1998 and lasted through October 1999.

The flow of water discharged into each tank was maintained at nearly 20 cm/s. Discharge occurred from eight 3-mm diameter perforations along the length of 30-mm diameter pipe that jetted water into the tank. These perforations are too narrow to allow metamorphosed clam predators to enter the tanks. Nevertheless, tanks were checked monthly for incidental invasions. None were found. Water exited the tanks from two vertical oriented, overflow drains at each end of the 70-cm deep tank. Twice a month the dissolved oxygen, salinity, temperature, and pH were recorded for each tank by means of a portable hydrolab. A Marsh McBirney current meter checked the flow velocity jetting from perforations in the tube in the tank twice a month. The tanks were not dosed with any algal extract to enhance clam growth during the experiments.

The clams were excavated by hand from their buckets monthly, and their shell length, and height recorded after any adhering sediment was washed off from the valve exteriors. This procedure was followed monthly from October 1998 until October 1999 when the

clams were sacrificed. No data were collected in May 1999. Dead specimens were cleaned and examined for abrasion, fracture, and repair. No specimen showed infestation with the boring sponge *Cliona* sp.

Fractures and repairs among *M. mercenaria* at the end of experimental interval were described and categorized as to (1) fracture expression (crack visible on interior or exterior of valve, or both), (2) valves affected by fracture (right, left, or both), (3) number of fractures per valve, (4) length of fractures, (5) fracture initiation site at, or very near the valve margin (ventral, posterior, anterior), (6) fracture propagation inward from the valve margin (diagonal, curved, right angled deflections, merging and/or bifurcating), and (7) state of fracture repair (internally stuccoed cracks or unrepaired). A Goodness of fit test determines (1) if sublethal fractures occur randomly among specimens in different textured sediments, (2) if fractures occur randomly around the shell margin (posteriorly, ventrally, or anteriorly), and (3) if fractures propagate in a restricted pathway. A *t* test determined (1) if fractured and unfractured specimens differ according to valve thickness at the ventral margin and (2) if repair condition (stuccoed vs. unrepaired) differs according to fracture length.

Additionally, at the conclusion of the 12-month monitoring period, the valve surface of each surviving clam was examined under magnification and the degree of shell abrasion and/or surficial etching categorized according to the relief of the concentric lamellae as (1) abrasion-negligible, (2) abrasion/etching—slight; wear restricted to ventral area, (3) abrasion/etching—moderate; shiny, bare patches over central and ventral valve area, and (4) abrasion/etching—extensive; obliteration of concentric lamellae over most of valve surface area. It should be noted that abrasion and etching must be distinguished from ontogenetic changes in shell micro-ornament over the valve surface. A swath of the central valve of *M. mercenaria* inherently lacks micro-ornamentation in adulthood, although the entire valve surface of many juveniles to young adults possess fine concentric ribbing.

RESULTS AND ANALYSIS

Among the 36 "control" specimens held in an aquarium and sacrificed after 4 weeks, five showed microfractures radiating dorsally from the ventral margin that were most probably induced anthropogenically during raking, transport, and/or machine-sorting. None showed any signs of repair.

The pH in the experimental tanks holding the sixty specimens fluctuated from 7.0 to 8.0 during the 16 mo interval (Fig. 1). The dissolved oxygen ranged from 3.4 to 6.7 mg/L over the same time frame (Fig. 1). Temperature changed seasonally, peaking in the summer at 25°C, and dropping to a low of 8°C in the winter months (Fig. 1). Salinity fluctuated (sub) parallel with temperature, ranging from a high of 28 ppt in November 98 to a low of 22 ppt in March 99 (Fig. 1). Current velocity from the pipe perforations ranged between 16 cm/s and 24 cm/s over the 16-month interval (Fig. 1).

Of the sixty experimental specimens, 30 were fractured sublethally (Fig. 2A–G) and one lethally (Fig. 2H). Of those fractured sublethally, the crack was visible on the valve interior exclusively in 20 specimens. For 10 specimens, the fracture was evident on both the valve interior and, faintly, on the exterior (Fig. 2A; Table 1). In 12 specimens, the fracture occurred in both opposing valves (Table 1; Fig. 2A). Eleven specimens had a crack in the right valve only and seven had a fracture in the left valve only (Table 1).

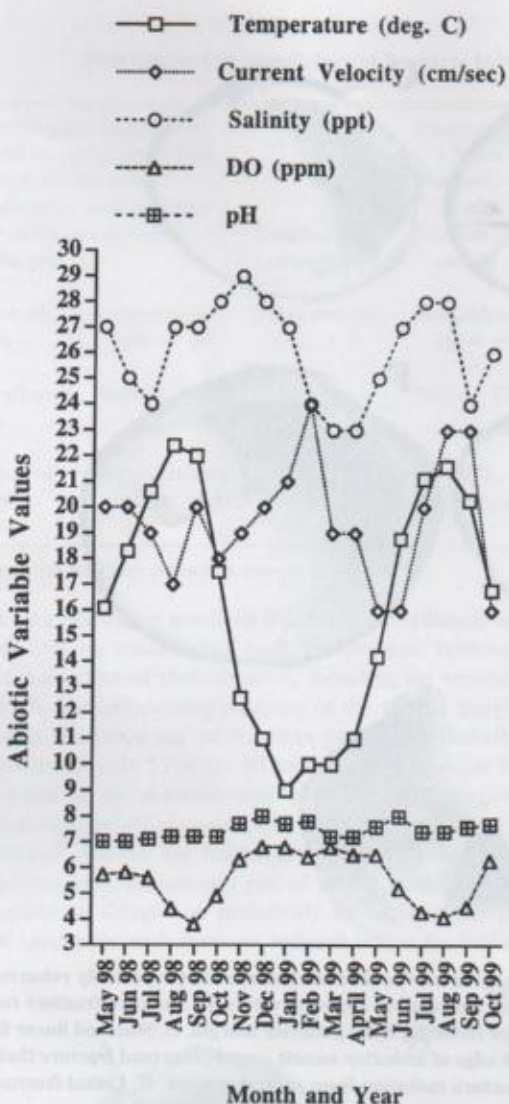


Figure 1. Monthly fluctuations in monitored abiotic variables in flow through tanks with *M. mercenaria* at NOAA laboratory, Sandy Hook, New Jersey.

Fracture length varied from 4 mm to 38 mm. Very long, stuccoed fractures propagated to within 5 mm of the dorsal margin of the clam (Fig. 2B). One specimen had three fractures in one valve and five specimens had two fractures in one valve. Short cracks (5–10 mm) that extended dorsally from or near the ventral margin to the pallial line, but not beyond, were unrepaired (= unstuccoed; Table 1). However, cracks longer than 15mm, extending dorsally beyond the pallial line, were repaired by the mantle (Table 1).

Fractures were initiated at or very near the ventral margin (Fig. 2A and B) in 24 specimens, at the posterior margin (Fig. 2C) in four specimens, and the anterior margin in two specimens. Goodness of fit test revealed that this distribution is nonrandom (Table 1). Thirteen fractures radiated inward on a diagonal from the ventral valve margin, slightly oblique to the dorsal-ventral axis (Fig. 2D; Table 1). Six fractures curved and three had sharp right angle deflections cutting through the edge of the adductor muscle scars in two instances (Fig. 2E–F; Table 1). Two fractures bifurcate near the center of the valve (Fig. 2G). Two cracks converge inward from the ventral margin. One convergence of cracks resulted in a lethal fracture (Fig. 2H).

Thirty-six specimens (62%) have chipped ventral margins. Nevertheless, only 13 of the 30 fractures radiated dorsally from a chipped point on a valve margin (Fig. 3A and B). Resecretion of a small, v-shaped wedge to fill in the chipped ventral margin accompanied mortaring of the fracture in one specimen (Fig. 3C). Seventeen fractures became fainter between the pallial line and the ventral margin, and cannot be traced to the very edge of the shell.

Although the highest frequency of sublethal shell breakage occurred in clams burrowing into pure mud (9 of 12), the distribution of fractures is statistically random (Fig. 4). Ventral margin thickness had no bearing on which valves fractured (Table 1). Fractures were just as likely to be confined to one valve as to be mirrored in both valves (Table 1). Furthermore, valve fractures occurred mostly in mud-burrowing specimens (Fig. 4), and appears to be independent of the degree of external valve abrasion, which is most severe in sand-shell burrowing specimens (Fig. 5). Two thirds of the specimens that burrowed in sand had the concentric lamellae obliterated on all areas of the valves (Fig. 3D), whereas 18 specimens of the 24 that burrowed into mud and mud-shell had only slight ventral abrasion (Fig. 5).

Accretion along the ventral margin was suppressed under these experimental conditions. Mean annual increase in dorsal-ventral shell length varied from only 0.45 mm in clams kept in sand to 1.3 mm for clams kept in mud (Fig. 6). Clams reared in sand and shell-sand showed an annual decrease (<0.05 mm) in cross-sectional shell height whereas clams reared in mud and shell-mud showed an annual increase of ~0.3 mm in cross-sectional shell height (Fig. 7).

DISCUSSION

These experiments indicate that monthly reburrowing by young adults increases the risk of either self-induced shell-breakage or the propagation of fractures induced anthropogenically. The fact that 50% of the experimental clams had fractures when sacrificed but only 14% of the control group had fractures indicates that the burrowing process is responsible for initiation and propagation for many, if not the majority of fractures. These experiments do not, however, indicate a threshold of reburrowing frequencies at which fracturing is likely to be initiated or expressed.

The rate of repair of the fractures also cannot be precisely established, although repair of fractures induced by burrowing possibly occurred between monthly reburrowing episodes. In a separate study, seed of *M. mercenaria* 15–25 mm in dorsal-ventral length were able to rescrete 2- to 3-mm long notches beveled by a high-speed Dremel in the anterior, posterior, and ventral valve margins within 2 weeks while living caged on an intertidal flat in North Carolina (Fig. 8; Alexander & Dietl, in preparation). Serrations or contiguous scallops in the valve posterior (Fig. 3E) may be lethally inflicted on young adult, intertidal *M. mercenaria* by wading birds (Krauter 2001). Conditions on the North Carolina mud-flat subjected to tidal flushing facilitated rapid repair with preclusion of predators. The shell repair processes may have been retarded under suboptimum laboratory conditions at Sandy Hook, New Jersey. Furthermore, internal fractures may be stuccoed (Fig. 2) at a different rate than notches of the valve margin are filled in by rescreted shell (Fig. 8). Nevertheless, the repair of the internal fractures within one month, i.e., between reburrowing sequences, is a realistic estimate given the much shorter time it takes to repair notches around the valve margin.

Regardless of the timing of initiation of the fractures, or their

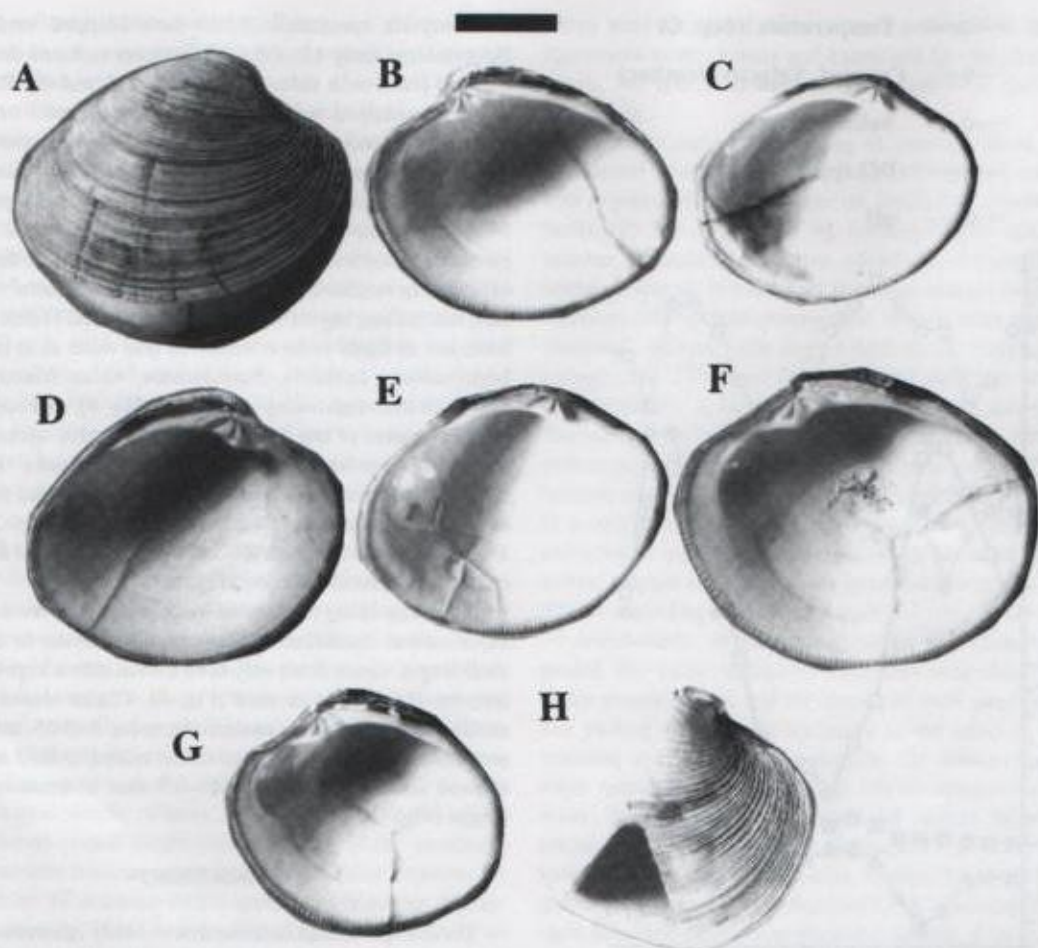


Figure 2. Expression of internal, stuccoed, sublethal fractures, and lethal breakage in valves of *M. mercenaria* that repeatedly reburrowed in sediment. Width of bar = one cm. A, External and internal expression of sublethal fractures in opposing valves. B, Stuccoed fracture radiating from posterior-ventral margin to within 5 mm of dorsal hinge. C, Stuccoed fracture radiating from posterior margin. D, Stuccoed linear fracture from ventral margin. E, Stuccoed ventral fractures that merge and deflect through edge of adductor muscle scar. F, Stuccoed fracture that makes right angle deflection through adductor muscle scar. G, Bifurcating, stuccoed fracture radiating from ventral margin. H, Lethal fractures that merged, resulting in removal of large triangular piece of valve.

propagation, during the months of reburrowing, these experiments complement the experimental results of Checa (1993) who demonstrated that reburrowing only once fractured the valves of the deep-burrowing *Solecurtus strigalatus*. However, fractures in the shallow-burrowing *M. mercenaria* were not necessarily invariably induced by sediment-loading against the hardclam valve exteriors as advocated by Checa (1993) for *S. strigalatus*. First, the experimental hard clam specimens never burrowed deeper than 10 cm (maximum sediment depth 14 cm) in contrast to the deep burrowing (>40 mm beneath the sediment surface), thin shelled clams studied by Checa (1993). Second, three times as many fractures are visible on the interior of the valve rather than the exterior of *M. mercenaria*. Yet all of Checa's (1993) illustrated examples show external expression of the fractures. Eschewing those specimens fractured by anthropogenic handling, these observations are congruent with the argument that closure of the valves on sediment grains or shell shards introduced between the valves fractured the ventral margin and valve interior of many if not most of the specimens.

The high percentage of cracks (67%) that did not propagate from the valve interior to be expressed on the valve exterior indicates that fracture propagation was halted at the annual growth

increment discontinuities in the shell microstructure of *M. mercenaria*. The valve microstructure consists of overlapping layers of crossed lamellar aragonite (Boggild 1930) bounded by organic films (Pannella & Maclintock 1968, Rhoads & Pannella 1970, Kennish 1980). Although all but six of the fractures were initiated near the ventral margin, the fact that 17 of the 30 cracks did not radiate from a chipped point on the valve margins, but instead disappear within 1 to 2 mm of ventral margin, suggests that chipping of the margin is not invariably the progenitor of fractures. The faint expression of the fractures in the area between the pallial line and the ventral margin coincides with the thicker part of the shell relative to shell thickness dorsal to the pallial line. Fractures may have originated dorsal to the pallial line, dissipating before cracking the entire thicker area between the pallial line and the ventral margin.

Although contrasting sediment textures did not statistically significantly differentiate the frequency of fractures among this sample of *M. mercenaria* (Fig. 4), the greater frequency of sublethal fractures among clams that burrowed in mud (nine) vs. sand (three) and shell-mud (six) is counterintuitive. If adduction of the valves upon clasts introduced between the valves during burrowing caused the fractures, the probability of encountering shell

TABLE 1.

Distribution and morphology of fractures induced by burrowing of 60 specimens of *Mercenaria mercenaria*.

Mean ventral valve thickness of fractured vs. unfractured shells	Fractures = 1.5 mm		Unfractured = 1.5 mm		<i>t</i> test; $P = 0.71$; Accept H_0 (means are equal)	
Mean length for stuccoed vs. unplastered shell fractures	Stuccoed = 20 mm		Unplastered = 12 mm			<i>t</i> test; $P < 0.001$; Reject H_0 (means are unequal)
Location of fracture initiation on valve margin	Posterior margin = 4	Anterior margin = 2	Ventral margin = 24		Goodness of Fit; $\chi^2 = 29.6$ with 2 df; Reject H_0 at $P = 0.01$ (nonrandom distribution)	
Expression of fracture	Valve interior only = 20	Valve exterior only = 0	Both sides of valve = 10		Goodness of Fit; $\chi^2 = 20.0$ with 2 df; Reject H_0 at $P = 0.01$ (nonrandom distribution)	
Fracture-affected valves	Right = 11	Left = 7	Both = 12		Goodness of Fit; $\chi^2 = 1.2$ with 2 df; Accept H_0 (distribution random)	
Propagation of fracture	Dorsal-ventrally straight = 5	Dorsal-ventrally curved = 7	Rt. angle deflection = 3*	Merging and branching = 4	Diagonal to dorsal-ventral axis = 13	Goodness of Fit; $\chi^2 = 10.22$ with 4 df; Reject H_0 at $P = 0.05$ (nonrandom distribution)

* Two stuccoed fractures cut across muscle scar area.

shards during burrowing would be highest in the sediment admixtures with 25% by volume shell hash. Furthermore, burrowing in sand increased external shell abrasion, including the ventral margin, (Fig. 5), but any ensuing chipping of the ventral margin did not increase the frequency of fractures propagated dorsally. As previously noted, only 13 of the 30 fractures can be traced from a chipped point on the posterior-ventral margin. One possible explanation is that the initial commercial excavation and handling of the specimens induced the fractures, and more specimens with microfractures were fortuitously placed on the muddy versus the sandy substrata. Given the probability of the low percentage (14%) of specimens with fractures induced before the burrowing

experiment commenced, based on extrapolation from the control group, it is unlikely that a preponderance of the few clams fractured before commencement of the experiments were experimentally placed on mud.

It should be noted that the interstitial water in the sand and sand-shell hash had become blackened during the experiments with accumulated fecal matter in the sediment interstices a few cm beneath the sediment surface before the conclusion of the experiments. This accumulation of organic matter occurred despite hand-tilling of these sediments each month during excavation of the specimens. Valve surfaces became slightly chalky in appearance, but if the valve skeletal microstructure was altered and mechani-

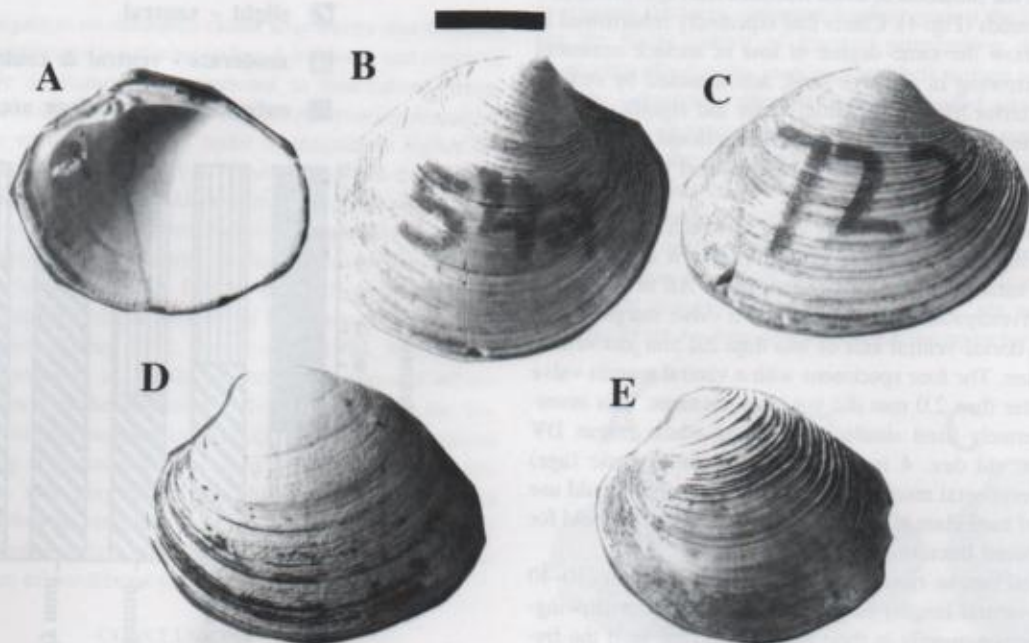
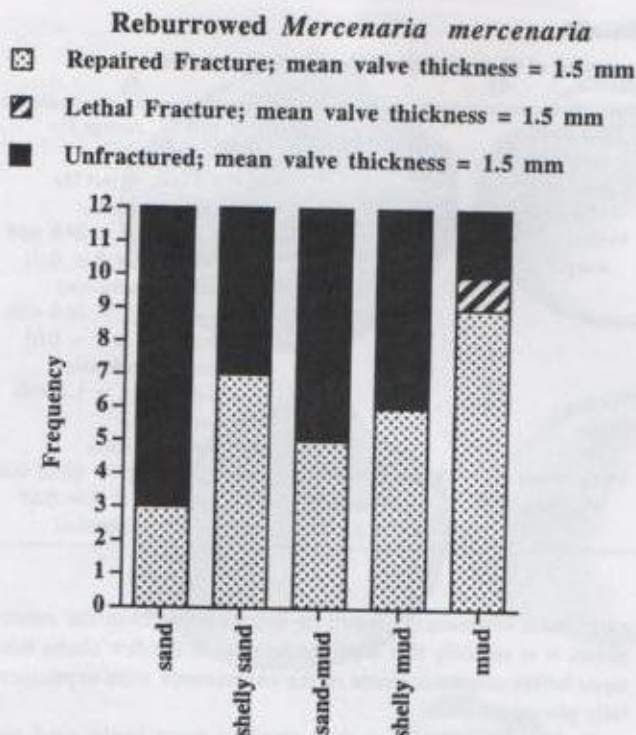


Figure 3. Valves of *M. mercenaria* with chipped margins, rescreted valve wedges, and degree of abrasion following monthly reburrowing into sediment. Width of bar = one cm. A, Specimen with chipped ventral margin from which crack radiates dorsally. B, Ventrally chipped margin with faint expression of dorsally radiating fracture. Note also abrasion of concentric micro-ornament limited to ventral margin of specimen. C, Specimen with secreted wedge at ventral margin filling in small triangular piece of shell removed by cracks. Internally, fractures are stuccoed. D, Complete obliteration of micro-ornament on valve exterior of specimen that monthly reburrowed into sand. E, Predator-induced, contiguous divots at posterior shell margin.



Experimental Sediment Substratum

Figure 4. Frequency of fractures among specimens of *M. mercenaria* that reburrowed monthly in various sediment textures. Distribution is random according to Goodness of Fit test ($\chi^2 = 4.52$ with 4 df).

cally weakened by the change in interstitial water chemistry, it didn't facilitate the initiation of more fractures than specimens that reburrowed in muds (Fig. 4). Clams that repeatedly reburrowed in mud did not show the same degree of loss of surface ornament (Fig. 5). Reburrowing in abrasive sand, accompanied by etching of the shell exterior by the interstitial water did significantly retard the expected annual increase in cross-sectional shell height relative to that shown by clams burrowed in mud and mud-shell hash (Fig. 7).

A valve thickness threshold may exist at which shell fracture due to burrowing does not occur (Table 1), but it could not be unequivocally established by this investigation. All of the specimens in this investigation that cracked had a valve margin thickness along the dorsal-ventral axis of less than 2.0 mm just ventral to the pallial line. The four specimens with a ventral margin valve thickness greater than 2.0 mm did not bear fractures. This investigation deliberately used similar size young adults (mean DV length 37 mm; std dev. 4 mm) to minimize ontogenetic (age) effects on experimental results. Expanded experiments should use a wide range of hard clam sizes to determine if a size threshold for burrowing-induced fracture exists.

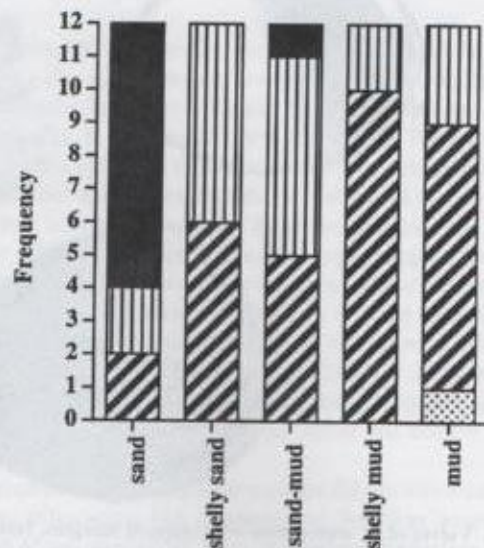
The question can be raised as to whether young adult (30–40 mm in dorsal-ventral length) hard clams show such reburrowing-induced fractures naturally in their native substrata, or if the frequency of repair in the experimental clams is merely an artifact of shell fatigue under suboptimum conditions in sediments in holding tanks where they reburrowed monthly. A specimen of *M. mercenaria* collected from the field shows very similar internal fractures to Figure 3A, but this is only one individual out of 500 specimens re-examined from a collection analyzed for repair scars from

Tuckerton NJ (Alexander & Dietl, 2001). Several specimens have fractures similar to those in Figure 2, but they lack the stuccoed thread-like ridge over the crack. Without the stuccoed repair ridge, it cannot be determined if the crack occurred during the life of the clam or during its post-mortem, transportational history. Greg Dietl (personal communication) forwarded a photograph of a farm-raised hard clam from North Carolina that has an internal fracture and repair in both valves similar to Figure 2B. These anecdotal occurrences of internal, stuccoed fractures from field collections belie the high frequency of fracture and repair found in the experiments. The disparity suggests that the anthropogenic handling of the specimens and/or the strain induced by monthly reburrowing contributed to internal fracturing of the shell in the experiments.

Regardless, these artificial experimental stresses did not preclude repair of the fractures by the mantle tissue. Given that many repairs were probably followed by re-burrowing episodes, the stuccoed repair process is sufficiently strong to enable the overwhelming majority of clams to repeatedly stress the valves during reburrowing without a repaired fracture failing lethally. Whatever the percentage of fractures induced anthropogenically before the reburrowing experiments commenced, which based on the control group could be approximately 14%, or 7 specimens, the repairs withstood the repeated strain in the shell due to reburrowing as many as 12 times. Thirty specimens had fractures in the valves, but only one specimen fatally cracked its valves during monthly reburrowing over a 12-month period (Fig. 2H). The dysoxic pore water beneath the sediment surface, and diminished supply of plankton flowing through the holding tanks may have contributed to the severely retarded accretionary growth (Fig. 6), but these

DEGREE OF VALVE ABRASION

- ☐ negligible
 ▨ slight - ventral
 ▩ moderate - ventral & central
 ■ extensive - all surface area



Experimental Sediment Substratum

Figure 5. Frequency of various degrees of valve abrasion for specimens that reburrowed monthly into various sediment textures.

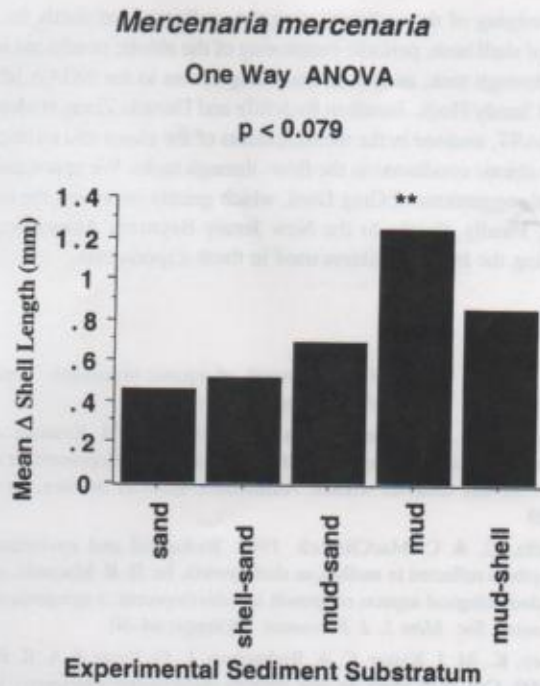


Figure 6. Mean increase (delta mm) in dorsal-ventral length (mm) of specimens of *M. mercenaria* that reburrowed monthly in various textured sediments. **Mean increase is significantly greater than value for sand ($P = 0.01$) and sand-shell ($P = 0.02$) according to Fisher's PSLD test. Mean ventral margin thicknesses are not significantly different among specimens reburrowing into different sediments based on analysis of variance (ANOVA; $P = 0.067$). Sample size = 60.

suboptimum conditions did not prevent the mantle from stuccoing the fractures.

This investigation on hardshell clams also shows that Checa's (1993) investigation on burrowing-induced fractures and repair is not necessarily a phenomenon restricted to thin-valved, deep-burrowing clams, although the frequency of reburrowing necessary to fracture the valves may be an order of magnitude higher for thick shelled clams and less likely to occur naturally in their native habitats. This investigation should prompt bivalve functional morphologists interested in shell biomechanics to search for internally stuccoed fractures in field surveys of shells of a variety of venerids, not just *M. mercenaria*. Just as external shell repairs in commercially valuable clams may be an indicator of shellfishing pressure (Bergman & Hup 1992, Gaspar et al. 1994, Witbaard & Klein 1994, Ramsey et al. 2000), frequency of stuccoed microfractures expressed on the interior of valves may indicate the history of both naturally and anthropogenically caused excavations and reburrowing episodes experienced by a clam population. Repair frequencies also may reflect the physiochemical conditions beneath the sediment surface in which commercially valuable clams reburrowed. Fracture repair may have impact on accretionary growth rates of hardclams yet to reach harvestable sizes.

CONCLUSIONS

Reburrowing into the substrata by *M. mercenaria* may either induce sublethal shell fractures, or further propagate fractures induced by anthropogenic excavation and handling processes. Texture of the sediment (sand, mud, sandy mud, shelly sand, shelly mud) may not necessarily differentiate frequencies of burrowing-

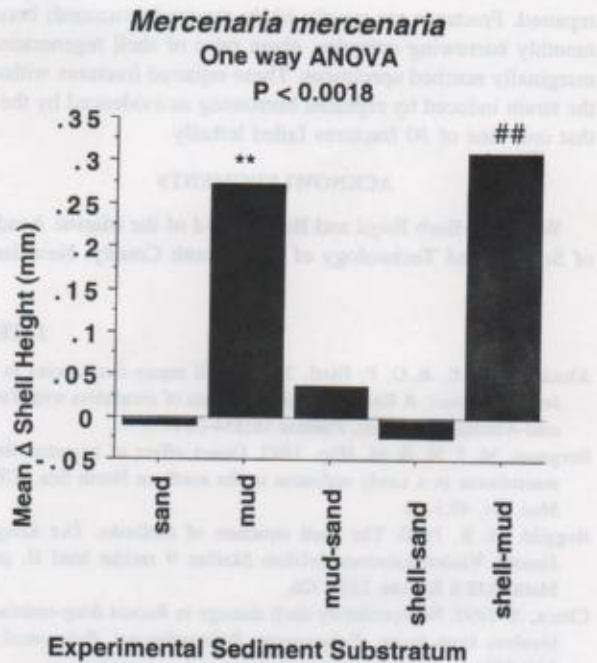


Figure 7. Mean net change (delta mm) in shell height in cross-sectional, lateral profile for *M. mercenaria* that reburrowed monthly in different textured sediments. **Mean value significantly greater vs. sand and sand-shell, ($P < 0.01$), as well as mud-sand ($P = 0.025$) according to Fisher's PSLD test. ##Mean values significantly greater vs. sand, shell-sand, and mud-sand ($P =$ or < 0.01) according to Fisher's PSLD test. Sample sizes = 60.

propagated fractures. Nevertheless, adduction of valves on sediment grains and shell shards can induce the strain that initiates or propagates fractures; sediment-loading against the valve exterior is not the likely culprit of fracture propagation in the shallow-burrowing *Mercenaria mercenaria*. Shell surface micro-ornament may be completely abraded and/or corroded away by repeated reburrowing in organic-rich sands with dysoxic pore water conditions beneath the sediment surface. Nevertheless, such abraded and etched shells are no more susceptible to fractures than shells of clams that repeatedly reburrowed in muds.

Fractures are most often initiated at or very near the ventral margin, rather than shell posterior or anterior margin. Fractures that do not extend dorsal to the pallial line are not likely to be repaired. Fractures may extend beneath the adductor muscle and be

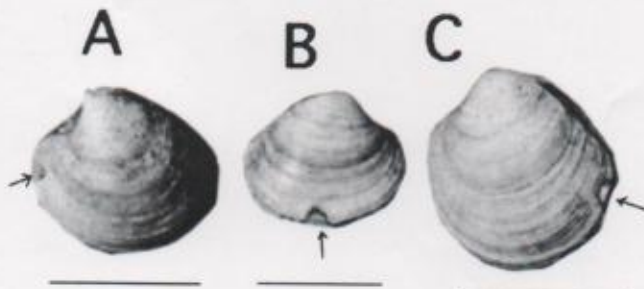


Figure 8. Rescreted shell in notched anterior (A), ventral (B), and posterior (C) margins of seed of *M. mercenaria* after 2 weeks while kept caged on a muddy sand tidal flat near Masonboro Inlet, North Carolina. Notches created by a Dremel in early October 2001. Width of line is 2 cm.

repaired. Fractures are mostly likely repaired (stuccoed) between monthly burrowing episodes, given rates of shell regeneration in marginally notched specimens. These repaired fractures withstand the strain induced by repeated burrowing as evidenced by the fact that only one of 30 fractures failed lethally.

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FIG. 1. Shell repair frequencies in New Jersey bivalves: A Recent baseline for tests of escalation with Tertiary mid-Atlantic congeners. (A) Small notch, (B) medium notch, (C) large notch.