

Dissolution mortality of juvenile bivalves in coastal marine deposits

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Abstract

We evaluate experimentally the effect of carbonate saturation state at the sediment–water interface (SWI) on survivorship of various size classes of the juvenile bivalve *Mercenaria mercenaria*. Populations of 0.2-mm, 0.3-mm, 1-mm, and 2-mm *M. mercenaria* were introduced to sediments realistically undersaturated (experimental, saturation state with respect to aragonite = $\Omega_{\text{aragonite}} = \text{IMP}/K_{\text{sp}}^* = \sim 0.3$) and saturated (control, $\Omega_{\text{aragonite}} = \sim 1.5$) with respect to aragonite in order to evaluate the impact of saturation state and dissolution on survivorship. Linear regression analysis was used to examine mortality within each treatment over time and show significant mortality for each size class in experimental-undersaturated treatments only ($P < 0.05$). Mortality rates in experimental-undersaturated sediments were -11.8 , -4.8 , -1.9 , and -1.1% d^{-1} for the 0.2-, 0.3-, 1.0-, and 2.0-mm bivalves, respectively. Analysis of covariance (ANCOVA) was used to examine differences in mortality between treatments over time and show significantly different mortality rates for the 0.2-, 0.3-, and 1-mm individuals ($P < 0.05$). Dissolution may represent a previously unrecognized yet significant source of mortality for “just-set” juvenile bivalves, particularly the very small individuals that have been largely ignored in recruitment studies to date. Dissolution-induced mortality may help explain the exponential losses of juvenile bivalves following their transition from the pelagic larval phase to the benthic juvenile phase.

Extremely high mortality (>98%) is widespread among settling marine bivalves in nearshore deposits, where exponential loss is common within the first several days to weeks following their full recruitment transition from the pelagic larval phase to the benthic juvenile phase (Thorson 1966; Roegner and Mann 1995; Gosselin and Qian 1997; Hunt and Scheibling 1997; Richards et al. 1999). The exceptionally high mortality rates cause profound change in cohort size, translate to significant alterations of adult bivalve population densities, and presumably are indicative of the selective pressures of evolution. Despite large advances in our overall understanding of factors that control invertebrate recruitment to marine benthic communities (Hadfield 1984; Woodin 1986; Butman et al. 1988; Pawlick 1992; Roegner et al. 1995; Woodin et al. 1998; Marinelli and Woodin 2002), many questions remain regarding factors that cause mortality of early juvenile bivalves following their transition to the benthos. Understanding factors that cause mortality in just-set bivalves is necessary to better resolve questions regarding the discrepancies between settling juvenile abundance and the small numbers of clams that successfully recruit to the adult population.

In this study we consider the effect of carbonate saturation state at the sediment–water interface (SWI) on survivorship of juvenile bivalves following their recruitment from the water column to competent members of the benthos. It is now

widely accepted that the decomposition of sedimentary organic matter can result in extensive dissolution in surficial estuarine sediments underlying waters otherwise supersaturated with respect to biogenic carbonates (calcite and aragonite; Aller 1982; Walter and Burton 1990; Green and Aller 1998, 2001). Sediments in nearshore regions can be undersaturated with respect to carbonates during certain periods of the year and/or in specific locales in the region immediately adjacent to the SWI where shallow burrowing juvenile bivalves congregate following settlement (Zwarts and Wanink 1989). However, the potential effects of sediment saturation state and dissolution on recruitment and survival of just-set bivalves is unknown. If the surface of marine sediment is undersaturated with respect to biogenic carbonates at the time of bivalve settlement, then juveniles might be vulnerable to dissolution immediately following their transition to the benthos. This may be particularly true for recently set bivalves (e.g., 0.2–0.3 mm), since their much greater surface area to volume ratios relative to those of larger individuals (e.g., 1–2 mm) is consistent with greater susceptibility to dissolution (Morse 1983). If dissolution represents a significant source of mortality for juvenile bivalves, there would be broad implications for benthic community recruitment, survivorship, and the coupling between early diagenetic processes and benthic community form and function. Therefore, the purpose of this study was to introduce sediment plugs containing populations of juvenile bivalves to seawater chambers undersaturated and saturated with respect to biogenic carbonates, document several indicators of dissolution, and evaluate survival of bivalves in each treatment as a function of time.

Methods

Experimental design—Surface sediment was collected from an intertidal mud flat along the Southern Maine coast

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(43°49.41'N, 70°4.43'W). This mud flat supports a robust, commercially viable, fishery of the soft shell clam, *Mya arenaria* and the hard shell clam, *Mercenaria mercenaria*. Sediments are composed of fine-grained, silt and clay sized particles, consist of 3–4% organic carbon and 2–4% CaCO₃ by weight, and have an average surface sediment porosity (ϕ) of ≥ 0.9 . The surface 1–2 mm of sediment was collected by gently scraping with a straight edge until ~ 1 liter of mud was gathered. These sediments were stored on ice, transported back to the laboratory, and sieved through a 0.25-mm sieve.

Next, sediment was homogenized by gentle stirring, and aliquots were placed into 120 individual sediment plugs and their surfaces smoothed with a straight edge. Sediment plugs were composed of butyrate disks each with a 25-cm² area routed to an exact depth of 0.6 mm. Sixteen sediment-filled plugs were placed into each of six 50-liter high-density polyethylene tanks containing 30 liters of seawater collected from Portland Harbor, Maine (salinity ≈ 32). Separate populations of 0.2-, 0.3-, 1-, and 2-mm hatchery reared *M. mercenaria* (SeaPerfect/Atlantic Farms) were then each deposited onto four sediment plugs within each chamber. Approximate initial total densities (live and dead) were ~ 250 , 950, 300, and 200 bivalves plug⁻¹ for the 0.2-, 0.3-, 1-, and 2-mm size classes, respectively. With the exception of the 0.3-mm size class, volumetric measurements (instead of counting individual clams) provided roughly the same number of bivalves plug⁻¹ for each size class. The higher number of bivalves in the 0.3-mm size class resulted from an initial mistake in choosing an appropriate volume to give the desired number of bivalves. Despite this high number, densities for each class used in this experiment (80,000–380,000 m⁻²) are similar to field densities reported in the literature (e.g., Hunt et al. 2003). In addition, each chamber contained four plugs with no bivalves. These plugs were used for geochemical measurements taken at each sampling interval. We assume that the shallow plug thickness allowed for rapid diffusive exchange in plugs both with and without bivalves (characteristic diffusion time = minutes), leaving roughly similar geochemical properties in each. This was supported by O₂ microelectrode profiles that showed no difference in pore water O₂ concentrations over the 0.6-mm depth of bivalve and nonbivalve plugs (data not shown).

Overlying water in each seawater chamber was aerated continuously using aquarium pumps. In addition, a gas mixture of 5% CO₂/balance N₂ was introduced into three of the six chambers (termed experimental undersaturated). The CO₂/N₂ gas stream was humidified prior to entering the experimental-undersaturated chambers by allowing gas to first pass through an in-line, water-filled gas saturator. The rate of addition of CO₂/N₂ was predetermined to lower the overlying water pH by ~ 0.7 pH units to a value of ~ 7.1 . The overlying water pH in the three control-saturated chambers remained at ~ 7.8 . The shallow sediment depth in plugs (0.6 mm) meant that water saturation state propagated into sediments and remained nearly identical to values in overlying water (7.0–7.2). Similar pH ranges are common in the near-surface sediments of estuarine deposits and are usually sufficient to lower CO₃²⁻ concentrations below CaCO₃ equilib-

rium values (Aller 1982; McNichol et al. 1988; Green and Aller 1998, 2001).

Both experimental and control seawater treatments were kept at room temperature ($\sim 21^\circ\text{C}$) and continuously aerated. Bivalves were fed daily on a commercially available diatom mixture composed of the flagellates *Isochrysis* (25%), *Pavlova* (20%), and *Tetraselmis* (20%) and the diatom *Thalassiosira weissflogii* (35%) (Post Set 1800, Reed Mariculture). Seawater from each chamber was changed every 3 to 4 d by slowly siphoning out chamber water while simultaneously siphoning in replacement seawater collected from the field. The rates of removal/addition were slow enough to not alter chamber water pH. Following a time-zero sample, sediment plugs were removed every 7 days for a 3-week period from each of the triplicate experiment treatments and each of the triplicate control treatments (i.e., true replicates, no pseudoreplication), sieved through 100- μm mesh, and bivalves preserved in 70% (v/v) ethanol buffered with CaCO₃. Recovered bivalves were stained with Rose Bengal, and live and dead individuals were differentiated and enumerated under a microscope within 48 h of recovery.

Geochemical analysis—During each time point one additional plug (containing no bivalves) was removed from each chamber for geochemical analysis. Plugs were placed into glass Petri dishes and slowly removed from seawater chambers so as not to disrupt the 0.6-mm layer of sediment. A depth-averaged sediment pH was taken using an Accum AB15 pH meter equipped with a Corning rugged combination electrode by inserting the electrode into the sediment while it was still immersed in the Petri dish. Sediment was then transferred using a spatula to an acid-washed and distilled water rinsed 15-ml centrifuge tube and centrifuged for 5 min at 3500 rpm. Pore water was taken up in a 3-cc syringe (total pore water volume ~ 2 ml) and filtered through a 0.45- μm syringe filter, and subsamples were immediately removed for total alkalinity, Cl⁻, and Ca²⁺ analysis. Total alkalinity was determined on a 1-ml aliquot using titration with 0.01N HCl after Edmond (1970). Triplicate Cl⁻ concentrations were measured on 10- μl aliquots using a Labconco digital chloridometer. A 100- μl sample was diluted in La²⁺ (1 mg ml⁻¹) and Ca²⁺ measured by atomic absorption on a Perkin Elmer AAnalyst 300.

Aragonite saturation state—Titration alkalinity, Cl⁻, and pH were used to calculate carbonate ion concentration (CO₃²⁻) at each sampling point in sediment plugs removed for geochemical analysis. CO₃²⁻ was calculated using the first and second dissociation constants of carbonic acid in seawater (Mehrbach et al. 1974) at specific chamber temperature and salinity (21°C, ≈ 32 , Millero 1979). There was no sulfide in any plug. Periodic O₂ profiling using microelectrodes detected O₂ at near-saturated values in chamber water and the presence of O₂ at the base of sediment plugs randomly tested during the experiment (10 random plugs tested, data not shown). The saturation state with respect to aragonite ($\Omega_{\text{aragonite}} = \text{IMP}/K'_{\text{sp}}$) was estimated in sediment pore water by calculating the ion molarity products ($m_{\text{Ca}^{2+}} \times m_{\text{CO}_3^{2-}} = \text{IMP}$) and comparing them to the estimated apparent stoichiometric equilibrium constants (K'_{sp}) according to the

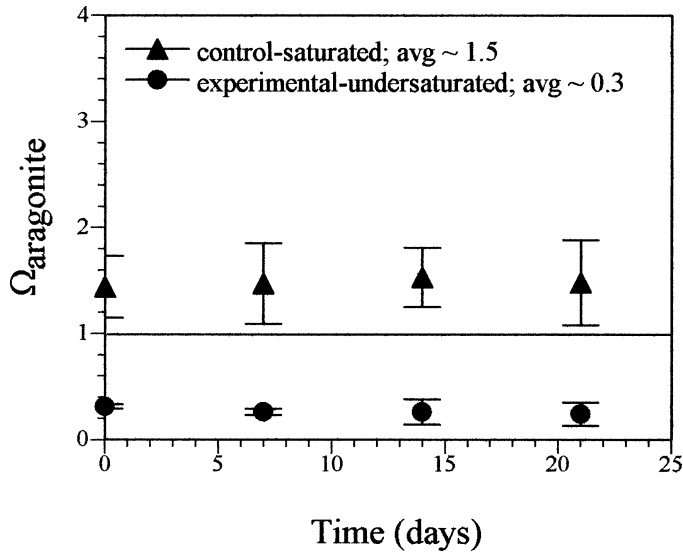


Fig. 1. Average values (\pm SD) of aragonite saturation states in sediment pore water of experimental-undersaturated and control-saturated treatments as a function of time. The horizontal line represents equilibrium with respect to aragonite dissolution and precipitation ($\Omega = 1$). Saturation states >1 are supersaturated and <1 are undersaturated.

temperature and salinity-corrected equations of Gieskes (1974). Saturation states in “geochemical” plugs were assumed to be similar to those in plugs containing bivalves.

Statistical analysis—Linear regression analysis was used on the live and dead assemblages *within* each treatment (control saturated, experimental undersaturated) and for each size class (0.2, 0.3, 1.0, and 2.0 mm) to test the null hypothesis that the change in bivalve numbers as a function of time was zero (i.e., the true slope of bivalve loss as a function of time was zero, the resultant best fit line was horizontal, and mortality/dead shell accumulation in either treatment was not significant). Analysis of covariance (ANCOVA) was used to determine whether treatment (i.e., saturation state) caused significant differences in mortality *between* control-saturated and experimental-undersaturated sediments over time. In this case we tested the null hypothesis that the slopes between treatments were identical (i.e., the lines are parallel and saturation state had no influence on juvenile bivalve mortality).

Results

Geochemical parameters—Aragonite saturation states ($\Omega_{\text{aragonite}}$) in plugs removed for geochemical analysis are shown in Fig. 1. Saturation state over the course of the experiment averaged ~ 1.5 in the control-saturated treatment compared to ~ 0.3 in the experimental-undersaturated treatment ($\Omega = 1$ at equilibrium). Evidence of active CaCO_3 dissolution comes from elevated pore water Ca^{2+} concentrations in experimental-undersaturated sediments relative to control-saturated plugs (Fig. 2).

Bivalve distributions as a function of time—Plots of live and dead bivalve distributions as a function of time for both

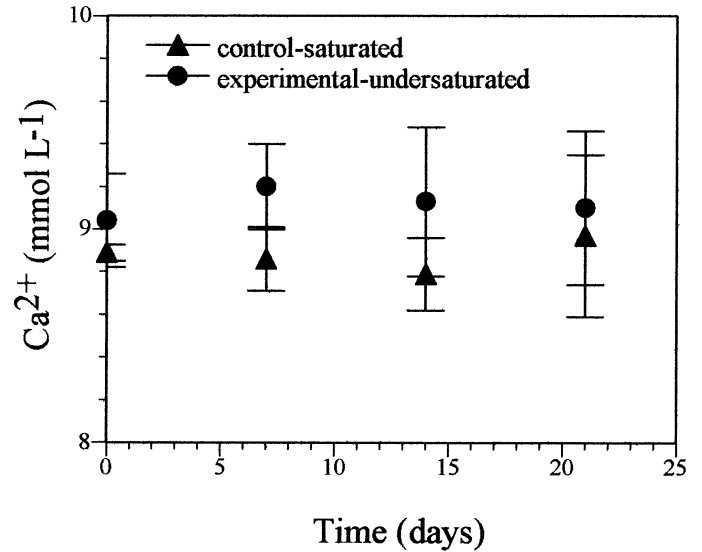


Fig. 2. Average Ca^{2+} concentration (\pm SD) in sediment pore water from experimental-undersaturated and control-saturated treatments. Although error bars overlap between treatments at each sampling point, average values of pore water Ca^{2+} are always higher in undersaturated sediments relative to controls.

control-saturated and experimental-undersaturated treatments are provided in Fig. 3. Linear regression analysis was used to examine mortality within each treatment over time. Results show significant mortality for each size class in experimental-undersaturated treatments only ($P < 0.05$; Table 1). That is, the slopes for live bivalves as a function of time in experimental-undersaturated treatments were significantly different than zero for each size class. Mortality rates in experimental-undersaturated sediments were -11.8 , -4.8 , -1.9 , and -1.1% d^{-1} for the 0.2-, 0.3-, 1.0-, and 2.0-mm bivalves, respectively. Although mortality was also documented for each size class in the control-saturated treatments, the loss of live individuals over the duration of the experiment was never significant ($P > 0.05$; Fig. 3; Table 1). Mortality rates in control-saturated sediments were consistently lower than those of clams reared in undersaturated treatments and were -2.8 , 0.0 , -0.5 , and -0.2% d^{-1} for the 0.2-, 0.3-, 1.0-, and 2.0-mm bivalves, respectively.

Analysis of covariance (ANCOVA) was used to examine differences in mortality between treatments over the duration of the experiment. Results show significant treatment differences in mortality rate for the 0.2-, 0.3-, and 1-mm bivalves. That is, for the 0.2-, 0.3-, and 1-mm juveniles saturation state was critical in determining survival of bivalves over time with experimental-undersaturated sediments significantly increasing mortality rate relative to control-saturated conditions. There was no significant treatment effect for the 2-mm bivalves. ANCOVA data are shown in Table 2.

Qualitative evidence of bivalve dissolution—In addition to quantitative evidence, we observed bivalve activity daily from both treatments by placing random sediment plugs and chamber water into large glass dishes for viewing under a microscope. Within 24 h of the start of the experiment, evidence of external shell dissolution was noted on live bi-

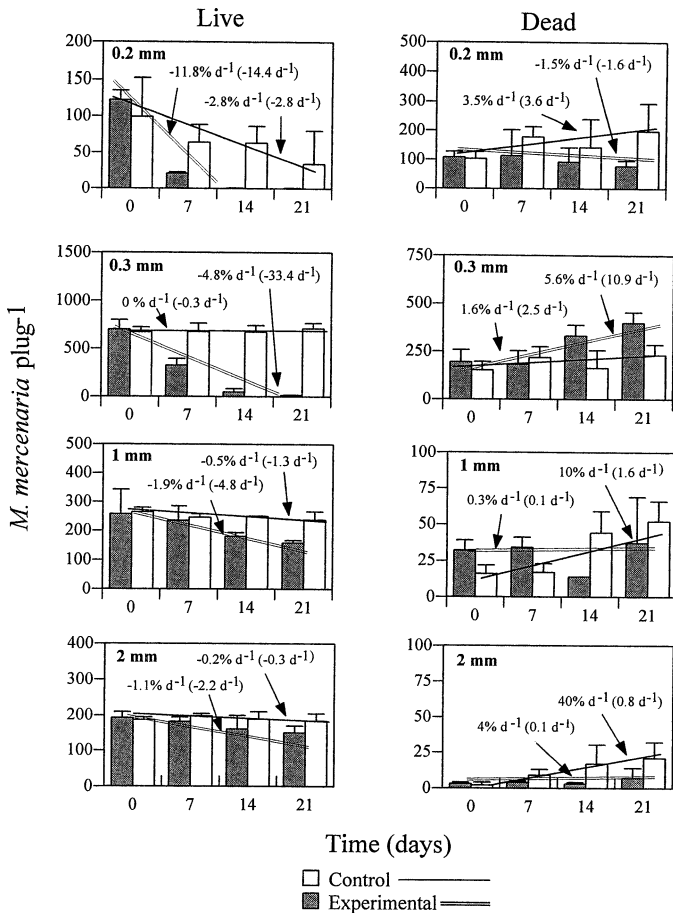


Fig. 3. Mean densities (\pm SD) of live (left column) and dead (right column) *M. mercenaria* in the 0.2-, 0.3-, 1.0-, and 2.0-mm size classes in experimental-undersaturated and control-saturated treatments. Mortality rates and accumulation of dead bivalves are shown as % d⁻¹ for both treatments. Also shown (in parentheses) are the absolute changes in both live and dead bivalve numbers as a function of time.

valves in the 0.2- and 0.3-mm size classes removed from experimental-undersaturated chambers (Fig. 4a,b). There was no obvious dissolution on live individuals in the larger size classes (1 and 2 mm) at this time. Dissolution was obvious by the chalky, flaky appearance of shells and the formation of pits that could be seen under high magnification. Dissolution was not limited to any specific region of the shell but was randomly distributed from the umbo to the shell's leading edge. As the experiment progressed into the second week, external shell dissolution became more obvious on the 0.2- and 0.3-mm individuals in the experimental treatment, with large regions of almost completely dissolved shell seen on almost all remaining bivalves, including most of those still living. Only the proteinaceous matrix into which CaCO₃ is precipitated during shell formation remained visibly intact (Weiner and Hood 1975). Even with their external shell dissolving, it was common to see *M. mercenaria* actively feeding. Throughout the experiment we noted minimal visual evidence of dissolution on the shells of the living larger bivalves (1 and 2 mm) relative to the smaller size

classes, although dissolution was common on the shells of dead bivalves in these larger size classes.

Discussion

In this study, the calculated saturation states indicate that dissolution of biogenic aragonite, the material that composes the shell of *M. mercenaria*, was thermodynamically possible in experimental-undersaturated chambers throughout the experiment ($\Omega < 1$; Fig. 1). Net dissolution was evident by elevated concentrations of pore water Ca²⁺ measured in CO₂-amended treatments (Fig. 2). Results of bivalve distributions with time (Tables 1 and 2; Fig. 3) show that, at least experimentally, small *M. mercenaria* (0.2 and 0.3 mm) are susceptible to dissolution-induced mortality, and at rates substantially higher than older, slightly larger individuals (1 and 2 mm). Although significant treatment differences were seen for the 1-mm bivalves (Table 2), bivalves reared in the experimental-undersaturated treatment had mortality rates 6.2 and 2.6 times less than the 0.2- and 0.3-mm bivalves (Table 1), respectively, suggesting that 1-mm sized clams are better suited to withstand periods of carbonate undersaturation than smaller, more recent sets. Similar initial abundance of bivalves in both control-saturated and experimental-undersaturated treatments for individual size classes excludes the possibility of density-dependent mortality factors in experimental chambers relative to controls (e.g., space/food competition). Likewise, equal additions of mixed diatom culture to all chambers each day should have ensured similar feeding opportunities. High O₂ in overlying water (>90% saturation) from both treatments during the course of the experiment means hypoxic/anoxic conditions did not increase mortality in experimental chambers. With the exception of aragonite saturation state, all known biotic and abiotic factors (e.g., temperature, O₂ concentration, food availability, zero predation pressure, etc.) were similar in both treatments, suggesting that shell dissolution resulted in the higher mortality in experimental-undersaturated sediments.

Dissolution and shell-bearing benthos in nearshore regions—Highly undersaturated sediments, precisely at the location where juvenile bivalves settle and burrow, are common in nearshore, organic-rich deposits (Fig. 5). Despite supersaturated overlying water, undersaturation in sediment pore water can result from multiple processes such as organic matter and mineral oxidation, often coupled with increases in biological particle reworking and sediment irrigation, and the corresponding increase in the acids H₂CO₃, HNO₃, and H₂SO₄ (Aller 1982; Green and Aller 1998, 2001). Although considerable attention has been given to the diagenetic, paleontologic, and elemental cycling implications of carbonate dissolution, the potential effects of saturation state and dissolution on recruitment and survival of living juvenile bivalves remains unknown.

Research on the influence of carbonate undersaturation on shell-bearing benthos has been largely qualitative in nature, with observations of "pitting" around the umbo region of living bivalves as well as the chalky appearance of dissolved areas on discarded shell debris of macrobenthic carbonate organisms (Alexandersson 1975; Aller 1982; Mc-

Table 1. Results from linear regression analysis for live and dead bivalves, from each size class, and for each treatment (Exp = experimental-undersaturated, Ctl = control-saturated). Linear regression analysis was used to determine whether the slope of bivalve numbers versus time was significantly different than zero.

Treatment, size, live or dead	Bivalves d ⁻¹	% d ⁻¹	F	df _n	df _d	P
Exp, 0.2 mm, live	-14.4	-11.8	190.5	1.00	4.00	0.0002
Ctl, 0.2 mm, live	-2.8	-2.8	4.56	1.00	10.00	0.06
Exp, 0.2 mm, dead	-1.6	-1.5	0.82	1.00	10.00	0.39
Ctl, 0.2 mm, dead	3.6	3.5	2.04	1.00	10.00	0.18
Exp, 0.3 mm, live	-33.4	-4.8	66.9	1.00	10.00	<0.0001
Ctl, 0.3 mm, live	-0.3	0	0.56	1.00	10.00	0.47
Exp, 0.3 mm, dead	10.9	5.6	19.6	1.00	10.00	0.0013
Ctl, 0.3 mm, dead	2.5	1.6	1.13	1.00	10.00	0.31
Exp, 1 mm, live	-4.8	-1.9	8.82	1.00	10.00	0.014
Ctl, 1 mm, live	-1.3	-0.5	3.3	1.00	10.00	0.099
Exp, 1 mm, dead	0.1	0.3	0.025	1.00	10.00	0.89
Ctl, 1 mm, dead	1.6	10	4.92	1.00	10.00	0.051
Exp, 2 mm, live	-2.2	-1.1	7.4	1.00	10.00	0.022
Ctl, 2 mm, live	-0.3	-0.2	0.14	1.00	10.00	0.71
Exp, 2 mm, dead	0.1	4	1.02	1.00	10.00	0.34
Ctl, 2 mm, dead	0.8	40	7.53	1.00	10.00	0.03

Nichol et al. 1988). Several quantitative studies have looked at benthic calcareous foraminifera and documented the correlation between temporal fluctuations in foraminifera abundance and calcite undersaturation in sediment pore water (Green et al. 1992, 1993). Multiple studies mention dissolution as a possible mechanism controlling total abundances of foraminifera in salt marshes, bays, and estuaries (Buzas 1965; Bradshaw 1968; Akpati 1975; Murray and Alve 1999). In addition, laboratory experiments show that dissolution impacts survivorship of benthic foraminifera *Elphidium clavatum* and *Buccella frigida* and may increase mortality of the small, ubiquitous bivalves *Nucula annulata* and *Tellina agilis* (Green et al. 1998). Green et al. (1993) speculate that benthic foraminifera may be a useful "indicator organism" of conditions faced by carbonate meiobenthos during recruitment to surficial marine sediments, citing specifically colonizing juvenile bivalves.

Dissolution-induced mortality has implications for existing theories on production–recruitment of shelled benthos and the coupling of biogeochemical processes with benthic community structure. For example, settlement to benthos by some bivalves is not a random process, with some species actively involved in site selection during settlement (Hadfield 1984; Woodin 1986; Butman et al. 1988; Pawlick 1992; Roegner et al. 1995; Woodin et al. 1998; Marinelli and

Woodin 2002). Settling juveniles of *M. mercenaria* are known to reject sediments recently disturbed by removal of the upper several millimeters of the deposit and will accept them again within several hours (Woodin et al. 1995). In organic-rich deposits of many coastal regions, removal of the very surface layer of sediment (≥ 1 mm) will expose reduced metabolites and/or electron-rich mineral phases (e.g., NH_4^+ , Mn^{2+} , Fe^{2+} , FeS) to oxidation, resulting in a pH minimum and, possibly, carbonate undersaturation. Characteristic diffusion times on millimeter length scales are only 10s of minutes, so that a rapid transition back to steady-state conditions will shift the lowered pHs and undersaturated conditions of exposed sediments back toward more alkaline conditions and supersaturated sediments over similar time scales. If carbonate saturation state is a chemical cue for settling larvae, then this thermodynamic shift may explain results of Marinelli and Woodin (2002) that show sediments become "acceptable" to settling bivalves within several hours following disturbance. Undersaturated surface sediments that could dissolve the shell of settling bivalves could be a negative response cue not yet specifically recognized in the literature (Woodin et al. 1993, 1998; Marinelli and Woodin 2002). If saturation state is a factor recruits use to select a habitat, then any physical, biological, or anthropogenic (e.g., trawling) mechanism that disrupts sediments, lowers pH, and results in carbonate undersaturation may impact bivalve recruitment, survivorship, and benthic community structure in these regions.

Evolutionary implications—It is plausible that dissolution of early juveniles represents one of the selective pressures acting on the evolution of the bivalve. Size, not age, determines sexual maturity in *M. mercenaria* (Gosselin and Qian 1997). Data from this study show that, at least using the saturation states evaluated here ($\Omega_{\text{aragonite}} = 0.3$), larger bivalves are far less susceptible to dissolution mortality than smaller size classes, with a quasi-exponential decrease in

Table 2. Results from ANCOVA analysis used to determine whether treatment (i.e., saturation state) caused significant differences in mortality for each bivalve size class.

Clam size (mm)	df	MS	F	df _n	df _d	P
0.2	1	5,075	6.57	1	16	0.021
0.3	1	1,013,000	233.52	1	16	<0.0001
1.0	1	10,170	7.26	1	16	0.016
2.0	1	1,457	2.96	1	16	0.11

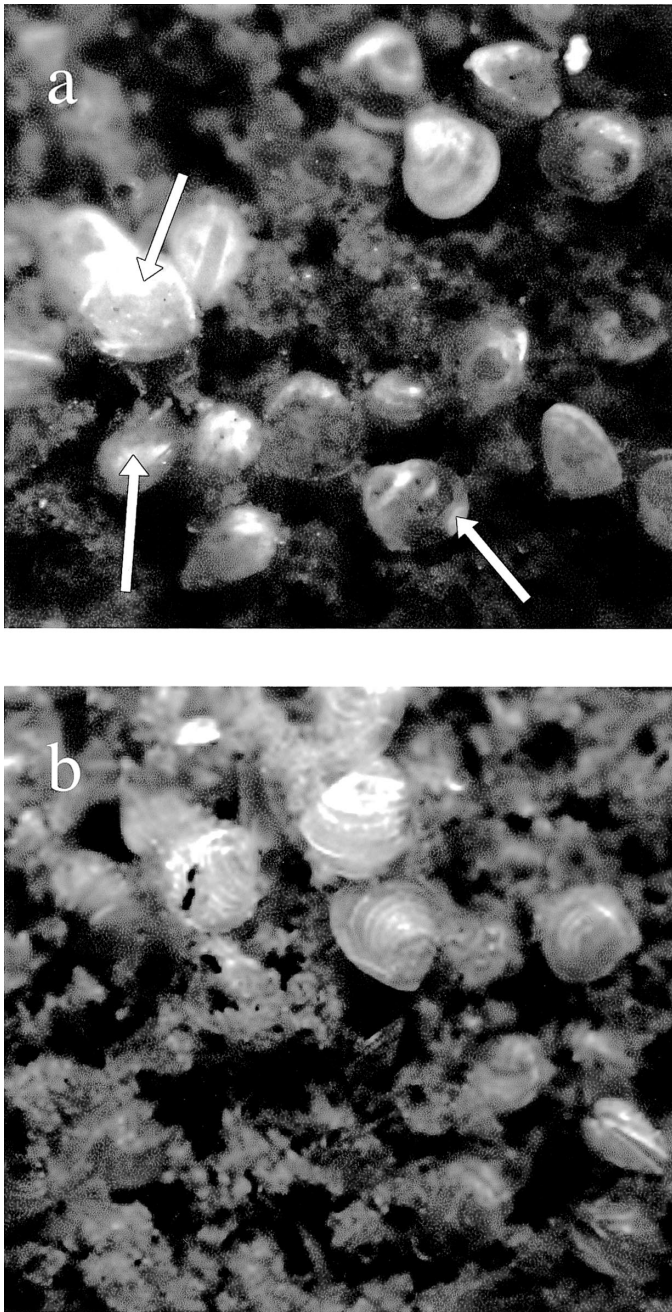


Fig. 4. Photographs of representative 0.3-mm *M. mercenaria* after ~24 h in (a) experimental-undersaturated and (b) control-saturated sediments. Bivalves in undersaturated sediments show evidence of massive external shell dissolution compared to controls (some regions noted by arrows).

mortality rate noted with increasing bivalve size (Fig. 6). Hence, following their transition to the benthos, bivalves capable of rapid growth may be more efficient at overcoming external dissolution during periods of pore water undersaturation and may be better suited to survive this early period of their life history.

Natural log transformation of mortality rate as a function of clam size yields the equation

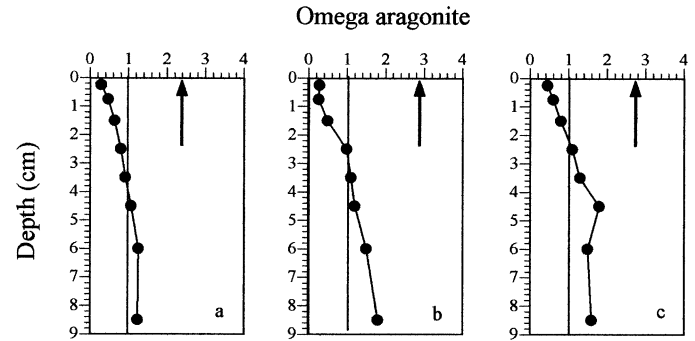


Fig. 5. Sediment saturation state in three coastal estuaries located along the northeastern United States coast. Sediments shown here were recovered during late spring/early summer in (a) Casco Bay estuary, (b) Barnstable harbor, and (c) Long Island sound and all show marked undersaturation from the sediment–water interface to depths of 2–3 cm. Maximum undersaturation occurs adjacent to the SWI in each case with $\Omega_{\text{aragonite}}$ values ranging from ~0.2 to 0.4. Overlying water saturation states are shown by the dark arrow and are supersaturated in each case.

$$\text{Mortality rate, } R (\% \text{ d}^{-1}) = 9.03 \exp^{-1.15 \times \text{size}} \quad (1)$$

and may be a good approximation of dissolution mortality rate faced by small colonizing bivalves under similar saturation states. Equation 1 likely provides a high estimate of dissolution mortality, since the total mortality rates in experimental-undersaturated sediments presumably include background mortality as well (i.e., as documented in control-saturated treatments; Table 1).

Death assemblage modification and palaeontological implications—In the absence of dissolution, loss in sediment plugs of individuals from the living population should translate to increases in the numbers of dead individuals recovered. Absolute loss of 2.8, 0.3, 1.3, and 0.3 live *M. mercenaria* d^{-1} in the 0.2-, 0.3-, 1-, and 2-mm size classes,

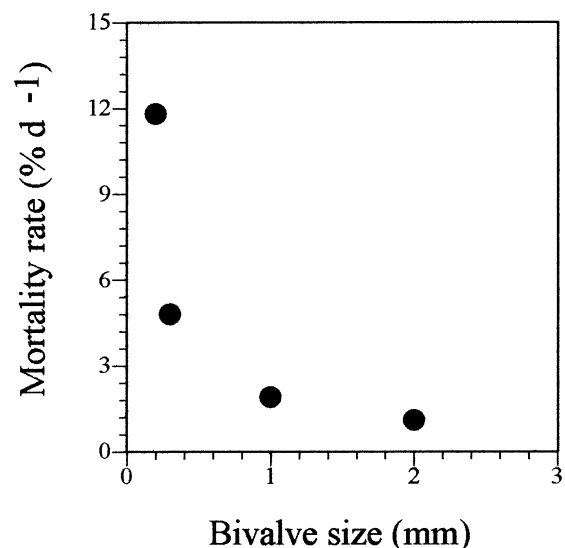


Fig. 6. Mortality rate as a function of bivalve size from experimental-undersaturated sediments.

respectively, in control-saturated treatments ($\Omega = 1.5$) were roughly balanced by additions to the death assemblage of 3.6, 2.5, 1.6, and 0.8 individuals d^{-1} (Table 1; Fig. 3). This near balance suggests that as long as pore waters remain supersaturated with respect to aragonite, juvenile bivalve shells of deceased individuals may be preserved.

In undersaturated chambers, on the other hand ($\Omega = 0.3$), losses of 14.4 and 33.4 live bivalves d^{-1} in the 0.2- and 0.3-mm size classes did not translate to equivalent increases in the death assemblage (Table 1; Fig. 3). In the 0.2-mm bivalve plugs, empty shells declined over the course of the experiment, yielding net losses of 1.6 empty shells d^{-1} . The net loss of shells from the 0.2-mm death assemblage means that dissolution was more rapid than shell replacement from mortality (14.4 d^{-1}). In the 0.3-mm bivalve plugs, loss of 33.4 live *M. mercenaria* d^{-1} in the undersaturated sediments translated to increases of only ~ 11 dead individuals d^{-1} in the death assemblage, suggesting that for this size class dissolution of individual shells was slower than the weekly sampling employed here. Slower rates of dissolution for dead 0.3-mm individuals presumably resulted from greater relative surface area compared to smaller bivalves and were therefore less prone to dissolution according to the standard kinetic rate laws of $CaCO_3$ dissolution (Morse 1983).

In this study the shells of dissolving bivalves were extremely fragile and would not likely withstand the physical rolling or jostling along the sediment surface in intertidal regions (Hunt and Mullineaux 2002), presumably resulting in much faster rates of fragmentation and dissolution in the field relative to the lab. This idea is supported by the fact that shells of dead juvenile bivalves are almost never found in coastal marine deposits, despite the settlement densities of 1,000–200,000 m^2 reported (Elmgren et al. 1986; Hunt and Mullineaux 2002).

Recent evidence suggests that seawater chemistry has oscillated between aragonite and calcite seas over Phanerozoic time (e.g., Harper et al. 1997). During the period dominated by calcite seas, aragonite was soluble and capable of dissolving and so there were likely selective pressures to precipitate a less soluble calcite shell during these periods (Sandberg 1983; Palmer et al. 1988; Harper et al. 1997). Dissolution of aragonitic mollusks during these periods was likely extensive and significantly altered the nature of benthic assemblages recorded in the fossil record (Cherns and Wright 2000). Researchers suggest that evolution of a calcite shell may represent an adaptation to aragonite-corrosive water (Taylor 1973; Harper et al. 1997). If dissolution mortality is an extensive process in coastal regions, it is curious that juvenile bivalves begin their benthic existence shrouded in an aragonite shell and that aragonite undersaturation hasn't selected against this particular mineralogy. However, the aragonite matrix represents a carbonate polymorph that is mechanically stronger than that of calcite (Taylor and Layman 1972). As such, precipitation of an aragonite shell early in a bivalve's life history may represent an evolutionary trade-off, where the structural integrity of aragonite provides greater protection from the biological (e.g., predation) and physical (e.g., hydrodynamics) environment relative to the mortality suffered during seasonal periods of aragonite undersaturation (e.g., Green and Aller 1998, 2001).

Dissolution represents a previously unrecognized source of mortality for just-set juvenile bivalves and may help explain the exponential losses of juvenile bivalves following the transition from the pelagic larval phase to the benthic juvenile phase. Dissolution of recently set bivalves has profound ecological implications since populations may be substantially modified by the thermodynamic conditions encountered by juveniles during their transition from the water column to competent members of the benthos. Relatively small perturbations in the initial populations of settling marine bivalves translate to large alterations of adult populations (Gosselin and Qian 1997; Hunt and Scheibling 1997). This biological–geochemical couple raises interesting questions regarding the role of carbonate chemistry in regulating benthic community composition in nearshore estuarine sediments and merits further investigation.

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