THE VELIGER

The Veliger 45(1):65–70 (January 2, 2002)

Mass Exhumation and Deposition of *Mulinia lateralis* (Bivalvia: Mactridae) on an Intertidal Beach, St. Catherines Island, Georgia, USA

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Abstract. Episodic events which affect populations of marine invertebrate species are rarely documented. We report the catastrophic mass exhumation and deposition of a large aggregation of adult bivalves (*Mulinia lateralis* [Say, 1822]) to a suboptimal habitat on a sandy intertidal beach of St. Catherines Island, Georgia, USA. The displaced population impacted a large area (7000 m^2) of the beach and consisted of similar-sized clams (~13 mm mean shell length). We suggest that the exhumation could have been a result of storm-induced shear stress, an hypoxic event, or other environmental stress on the individuals. Events of this type could have important implications for population dynamics and cohort distribution, fisheries predictions and harvests, and interpretation of fossil assemblages.

INTRODUCTION

On 4 October 1993 we observed a large patch of *Mulinia lateralis* (Say, 1822), the dwarf surfclam, in the intertidal zone on South Beach, near Flag Pond, St. Catherines Island, Georgia (Figures 1, 2). This was a notable occurrence because most adult infaunal bivalves are sedentary, moving long distances only as larvae or stochastically by rafting with eroded substrata, and because *Mulinia lateralis* are normally found subtidally.

Mulinia lateralis typically occurs in near-shore environments along the Atlantic and Gulf coasts of the United States and can be present subtidally in very dense infaunal aggregations. *Mulinia lateralis* can occur episodically and in very high densities (21,000 m^{-2}) subtidally (Santos & Simon, 1980). Santos & Simon (1980) found that an ephemeral population of *M. lateralis* in Tampa Bay, Florida had an average density of approximately 5700 m^{-2} when present. Montagna et al. (1993) reported a population in Laguna Madre, Texas with densities up to 800 m^{-2} soon after recruitment in the spring, and low densities (< 100 m^{-2}) for the majority of the year. Walker & Tenore (1984) found that the density varied with habitat in Wassaw Sound, Georgia. Populations with the highest average density were in sandy mud (10,161 m^{-2}), whereas mud and sand habitats had lower densities (277 m^{-2} and 263 m^{-2}, respectively), but all population densities fluctuated widely. *Mulinia lateralis* populations have not been reported occurring intertidally in such dense live aggregations as we report, and apparently this aggregation was exhumed and deposited.

OBSERVATIONS

The site of the *Mulinia lateralis* accumulation, South Beach, is a medium-energy (silty-sand) beach on the seaward side of St. Catherines Island. St. Catherines Island is a relatively pristine environment as there is little human activity on the island except in a research and conservation compound on the north-west (leeward) portion. Mean tidal amplitude is approximately 2.5 m. High tides were increasing toward a maximum, from +2.1 to +2.6 m mean low water at the time of observation, and this condition had been present during the 5 days preceding our observations. There had been no significant rainfall since 27 September 1993 when 0.2 cm fell (as recorded on Sapelo Island, Georgia). Wind velocity recorded on Sapelo Island had remained below 10 m/sec for the month prior to our observation and reached a velocity of 8.36 m/sec on 30 September 1993.

To quantify the extent of the exhumed population in the intertidal zone, we sampled at ebb tide along a tran-

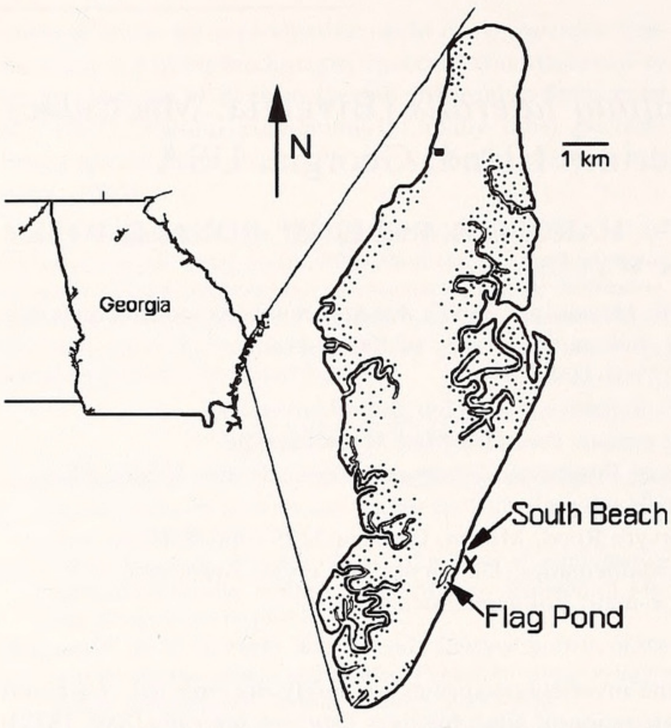

Figure 1. Diagrammatic map of St. Catherines Island, Georgia. Salt marsh is indicated by stippling. The study site is indicated by an X.

Figure 2. *Mulinia lateralis* exposed on South Beach, St. Catherines Island, Georgia on 4 October 1993. The infaunal population extends from high to low tide lines, while the surface clams are aggregated between 42 and 52 meters from the high tide line. *Anadara ovalis* and *Busycon* species are also present. Scale bar represents 1 meter.

sect extending from the wrack line, approximately 80 m landward of the low tide line, to a tide level present 1 hour before maximum low tide. We used circular quadrats of 30 cm diameter (area = 706.5 cm^2) to sample at 2 meter intervals along the transect. All live and dead clams present to a depth of 7 cm were collected. The number of live and dead clams within each quadrat was counted. Where clams were present on the surface, as well as buried, the ratio of surface to subsurface clams was noted.

The exhumed clams covered a large area of the beach (Figure 2). The surface aggregation extended approximately 17 m north to south and 14.5 m east to west (246.5 m^2), whereas the sub-surface accumulation was much larger and extended approximately 87 m north to south from the high intertidal into the subtidal zone (7000 m^2). A large, but unquantified, traction load of live and dead clams also was present in the outgoing tidal swash zone.

Clams occurred on the surface midway between the swash zone and the wrack line, 24–72 m seaward from the high intertidal zone (Figure 3). Within this zone, the greatest density of exhumed clams occurred between 42 and 52 m from the high intertidal zone. The highest density of live clams occurred at 46 m (23,227 live clams m^{-2}; Figure 3). Dead shells were much less abundant, but their distribution paralleled that of the live clams, possibly indicating passive transport or post-depositional mortality. Live clams composed 78.7% of all shells collected. Between 42 and 52 m from the upper intertidal zone, the surface shells (75%) outnumbered the buried shells (Figure 4), but there were no differences in the proportions of dead and live clams in these samples. The mean length of all clams was 12.84 ± 1.17 mm (Figure 5) with no significant ($P < 0.001$) difference between dead and live clams. The majority of live clams examined were sexually mature with ripe gonads.

ACCUMULATION ORIGIN

The mass exhumation of *Mulinia lateralis* reported here was notable because of the limited spatial distribution and because of the very high density of clams involved. Levinton (1970) reported large aggregations of dead valves of this species in Long Island Sound and Narragansett Bay, Rhode Island, and discussed the significance of such dense death assemblages for the fossil record. He suggested that those assemblages were the result of postmortem transport. Other bivalves, notably the surf clam *Spisula solidissima* (Dillwyn, 1817), were observed washed up on New Jersey beaches near their subtidal populations; however, the majority observed during this event were dead or dying (Boyajian & Thayer, 1995). The authors described a storm-deposit of surfclams, and suggested mechanisms of exhumation and deposition, including the hypothesis that storms could remove overlying sediment, increasing the likelihood of subsequent population excavation and size-selective excavation and deposition. Rees et al. (1977) also noted storm-induced strandings of several bivalve species along the coast of North Wales. They stated that wave activity could be a factor in the maintenance of soft bottom benthic associations in near-shore waters.

Although no storms had occurred along the Georgia coast in the month prior to the exhumation event, large waves remain the likely mechanism transporting these

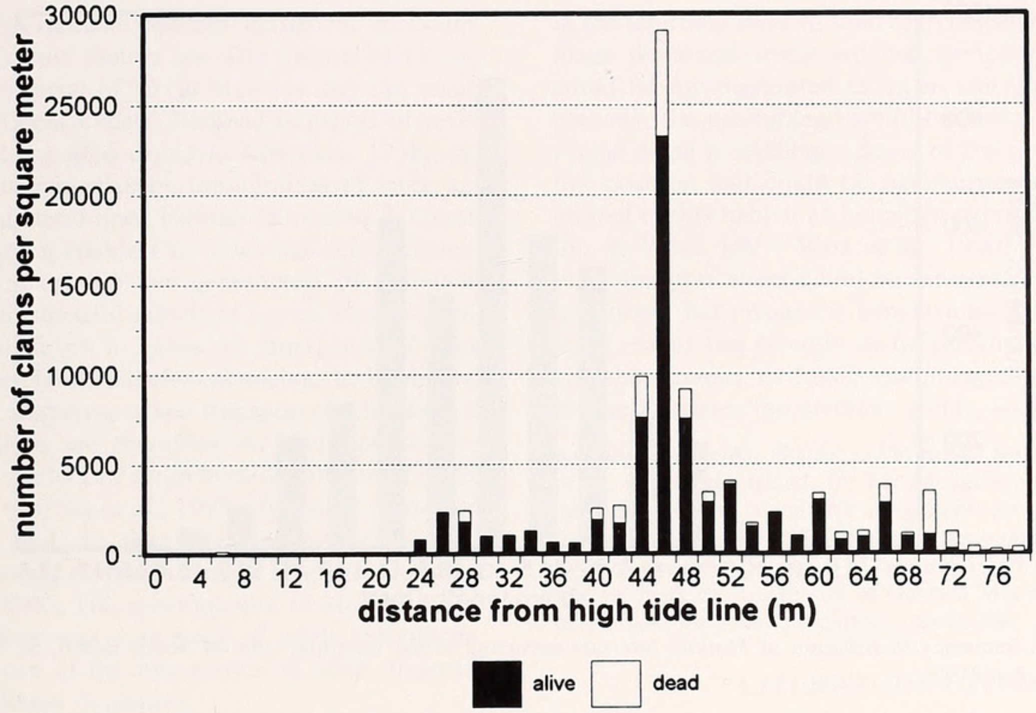

Figure 3. Frequency distribution of *Mulinia lateralis* occurring in the intertidal zone of South Beach, St. Catherines Island, Georgia, on 4 October 1993.

adult megafaunal clams so high into the intertidal zone. Palmer (1988) discussed the importance of passive transport of meiofaunal species and concluded that for such small organisms it is a fairly important mechanism of dispersal of both adults and juveniles. Passive wave-induced movement of any organism involves shear stress, and the larger the organism, the higher the shear stress needed to initiate movement (i.e., erosion) (Denny, 1988). Therefore, a relatively large shear stress, present in large waves or in storm-induced seas, was likely needed to lift

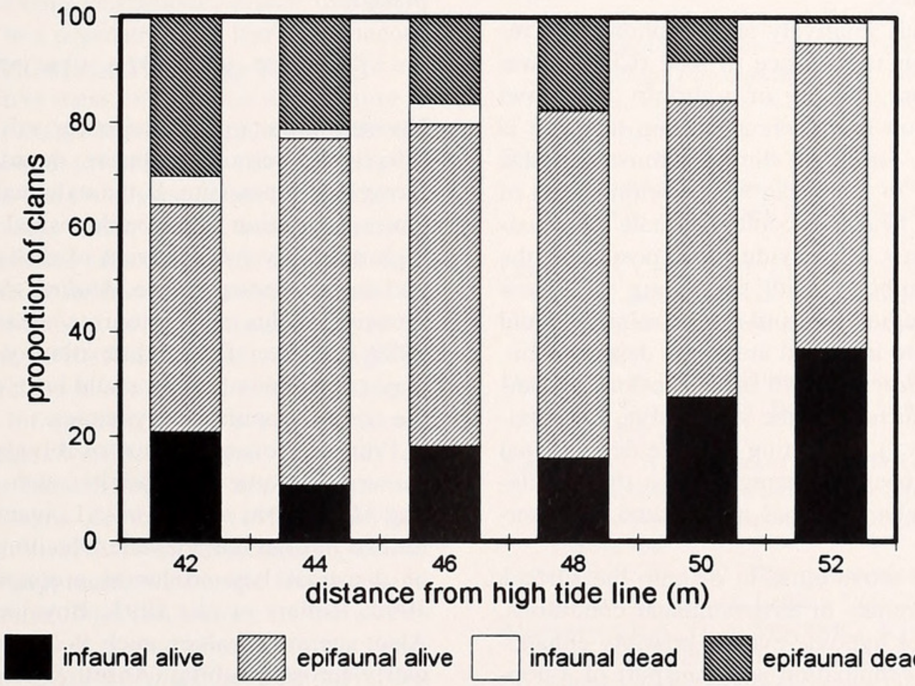

Figure 4. Percent contribution of dead and live *Mulinia lateralis* to surface and infaunal populations occurring in the intertidal zone of South Beach, St. Catherines Island, Georgia, on 4 October 1993.

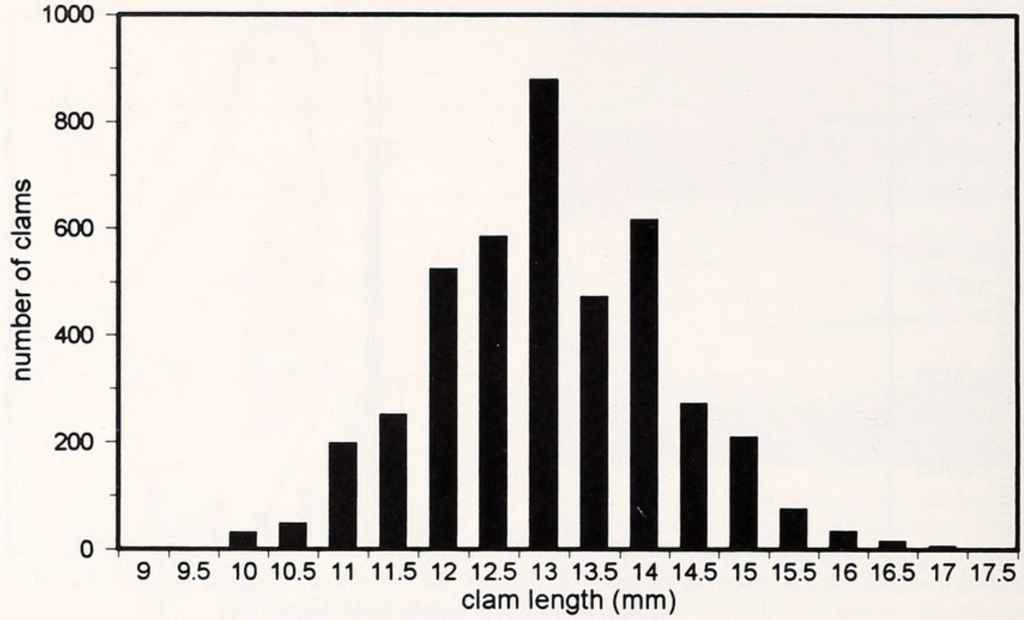

Figure 5. Length-frequency distribution of *Mulinia lateralis* occurring in the intertidal zone of South Beach, St. Catherines Island, Georgia, on 4 October 1993.

and initiate movement of these fairly large clams. Although tidal energy represents a potential source of movement of the clams, the tide prior to the exhumation event was not unusual in magnitude. Other mollusks, including the blood ark (*Anadara ovalis* [Bruguière, 1789]) and whelk species (*Busycon* species), which were much larger (5+ cm length) than *Mulinia lateralis* occurred in patches along the beach on the day of observation, possibly indicating community-wide disturbance, rather than a monospecific disturbance.

Mulinia lateralis has relatively short siphons that require it to remain near the surface to feed (Chalermwat et al., 1991). Therefore, passing of a shrimp otter trawl net over the population (commercial shrimp trawling is important in Georgia, especially during summer months, and occurs frequently in the ocean waters within sight of St. Catherines Island beaches) could facilitate the excavation of large numbers of individuals. Exposure on the sediment surface, combined with the strong tidal flow characteristic of the region or wind-driven mixing, could transport the clams into intertidal areas and deposit them. There were many *M. lateralis* still in suspension and buried just beneath the surface in the swash zone (approximately 1400 clams m^{-2}), indicating that the depositional event may still have been occurring, or that the population was being actively reworked at the time of observation.

Bivalves will often move close to or onto the surface when stressed by extremes in environmental conditions, such as low salinity or hypoxic events, possibly enhancing the likelihood of exhumation and transport of a population (Cleveland, 1991; Richardson et al., 1993). We have no records of subtidal environmental parameters, such as salinity and temperature, for this area, and therefore can only speculate as to what caused the observed phenomenon. It seems unlikely that these clams were transported a long distance before being deposited and were probably from an area relatively nearshore in the vicinity of South Beach. *Mulinia lateralis* typically inhabits sandy-mud substrata (Walker & Tenore, 1984), which are abundant in areas around St. Catherines Island. Most likely, a cojacent population was exhumed and displaced.

EFFECT ON POPULATION DYNAMICS

Events similar to the one observed and described could effectively entrain an entire population of clams and move it to a new site. If the exhumation is extensive, the entire population could be deposited onshore, resulting in high mortality by the stress of dislodgment, desiccation, and extreme temperature. *Mulinia lateralis* is an opportunistic species that colonizes areas quickly (Levinton, 1970), and therefore, exhumation of this type, prior to a major recruitment event, could have short-lived effects on the overall population dynamics.

Previous observations of bivalve movement have shown that some large adults, such as the northern quahog *Mercenaria mercenaria* (Linnaeus, 1758), can be entrained in high energy waters leading to an adjunct mode of dispersal beyond larval propagules (Prezant et al., 1990; Rollins et al., 1992; Boyajian & Thayer, 1995). Also, vagrant bivalves, such as *Donax* species, move regularly across a habitat (Ansell & Truman, 1973). Passive transport resulting in colonization of a habitat can be an important mechanism for population dispersal and establishment for opportunistic species (Emerson & Grant, 1991). Hydrodynamic factors are also known to be important in the dispersal of larval bivalves and can result in patchy recruitment events. Bedload transport of juvenile soft-shell clams *Mya arenaria* Linnaeus, 1758, can affect population dynamics by immigration of large aggregations into underutilized habitats (Emerson & Grant, 1991). The common cockle *Cerastoderma edule* Linnaeus, 1758, lives in the top few centimeters of sediment, and the combined stressful effects of waves, currents, and burial have been shown to cause the emergence of large numbers of these clams, thereby enhancing the likelihood of their passive entrainment and transport (Richardson et al., 1993). Scallops are notorious for their locomotory ability whereby adults can swim horizontally and migrate to new habitats (Carsen et al., 1995). Juveniles, however, swim vertically and are then advected horizontally by currents and possibly moved into more hospitable habitats (Carsen et al., 1995). The accumulation of *Mulinia lateralis* described here was composed of adult individuals, providing evidence of the importance of adult dispersal in bivalve population dynamics.

IMPLICATIONS

Observation and reporting of unexpected ecological phenomena such as the one described here can provide valuable information about population ecology and life history of organisms, as well as information useful for interpretation of fossil assemblages (Boyajian & Thayer, 1995). Although population studies and transplantation experiments provide useful information about a species, unrecorded episodic events can produce effects that could subsequently appear in a population and lead to erroneous conclusions regarding range and cohort dynamics. For example, the size-selective mass exhumation of a portion of a bivalve population could leave a population with the length frequency skewed toward older (or younger) individuals. Future age-class analyses could record this as a low recruitment event, when, in fact, recruitment was normal for the size classes affected by the exhumation.

Interpretation of fossil assemblages could be biased by deposition of large numbers of live animals as well as dead shells (Levinton, 1970; Rollins et al., 1992; Aguirre & Farinati, 1999; Walker & Goldstein, 1999). Although we do not have any information on the post-depositional fate of this assemblage, we do know that the sandy intertidal beach is not ideal habitat for *Mulinia lateralis* (Levinton, 1970). Morris & Rollins (1977) described some life-positioned bivalve fossil assemblages on St. Catherines Island. Interpretation of such fossil assemblages must take into account the history of the assemblage prior to death as well as that after death (taphonomy). The majority of these *M. lateralis* were alive, but their condition could have been weakened by the stresses from exhumation, transport, deposition, and desiccation in the intertidal zone in such high densities. If this assemblage remained intact and was buried on the beach, it could be misinterpreted as an in situ population. Alternatively, the assemblage could be interpreted as a transported death assemblage. Some of the live clams were in life position and could be misinterpreted as having recruited to this habitat as juveniles rather than adults (Rollins & West, 1997; West et al., 1990). There are many ways that this event could be interpreted that could lead to rational but erroneous conclusions. Documentation of these events can provide useful information about a species, community or fossil assemblage, and have bearing on shellfisheries' predictions, yields, and harvests.

Acknowledgments. Thanks to Mr. Royce Hayes, Superintendent of St. Catherines Island, for his on-site support and extensive knowledge of the Island. We are grateful for grant support from the St. Catherines Island Foundation, Incorporated, administered by the American Museum of Natural History. We would also like to thank the University of Georgia Marine Institute on Sapelo Island for access to climatological data.

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