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THE EFFECT OF MORPHOLOGY ON POSTMORTEM TRANSPORTATION OF BIVALVES AND ITS TAPHONOMIC IMPLICATIONS

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ABSTRACT

Fossilized shell assemblages are often the result of postmortem transportation. It is therefore crucial to identify biases introduced due to differences in the hydrodynamic properties of shells to ensure the validity of ecological interpretations. In a flow tank study with the bivalve *Donax scortum* Linnaeus, 1758, we found that shell size, shape, and ornamentation played an important role in dictating the hydrodynamic properties of shells. This study demonstrates that threshold current velocity for the entrainment of a convex-up shell is generally determined by its size, a result corroborating previous findings. We found that a smaller shell is mobilized with a lower velocity compared to a larger one. Additionally, we found ornamentation of a shell also played a significant role in transportation. Unlike previous studies, we have demonstrated that altered smooth shells require a higher velocity for transportation compared to fresh shells with pronounced ornamentation. The movement trajectory of a shell depends on its asymmetry. The right and left valves of a single individual are deflected in distinctly different directions. This study shows that the extent of such deflection is dependent on the size of the valve and the velocity of the flow. Using a simulation based on our experimental data, we have also demonstrated the effect that transportation bias can have in modifying a shell assemblage. The results of this study underscore the concept that the final distribution of shells following a transportation event may yield a bivalve population significantly different from the original one.

INTRODUCTION

Many paleontological studies based on bivalved mollusks utilize assemblage-level data (Chattopadhyay, 2011, 2013; Bardhan et al., 2012). The tacit assumption for using such data is that the information available from the preserved assemblage has not been significantly altered by postmortem processes (Kidwell and Bosence, 1991; Kelley and Hansen, 2003). However, this assumption is not always true. Thus, understanding the implications of taphonomic processes on fossil assemblages is essential to paleontological studies. Postmortem transportation is particularly problematic, and can bias paleoecological studies that compare local diversity and abundance of bivalved mollusks (Kidwell and Bosence, 1991 and reference therein). This study is designed to assess the effect of such transport bias on bivalve shells using experimental data on recent bivalve shell transport.

Previous Studies

Important parameters controlling the hydrodynamic behavior of particles include size, mass, surface roughness, and shape (Vogel, 1994). These variables in turn dictate the entrainment velocity and trajectory of particle movement (Vogel, 1994). During postmortem transportation, molluscan shells behave as particles subjected to fluid flow. Unlike other sedimentary particles, their behavior is difficult to predict primarily because of the complex nature of their shape and variable surface roughness (Miller and Cummins, 1990). Nonetheless, mass is still an important parameter in determining the entrainment velocity of a shell (Spencer, 1963). Allen (1984) established that entrainment is dependent on the fluid force applied and the immersed weight of the shell and thus advocated that higher fluid force will be required to entrain a heavier shell. In a flume experiment, Messina and La Barbera (2004) demonstrated this with recent brachiopod valves wherein differences in mass between brachial and pedicle valves produced significantly different entrainment velocities. However, Kaplan and Baumiller (2000) did not find such differences in transported assemblages of Ordovician brachiopods. Since the majority of bivalved mollusks have two valves of identical mass, they do not show significant difference in entrainment velocities (Miller, 1991; Olivera and Wood, 1997; Chattopadhyay et al., 2006; Chattopadhyay, 2009).

Surface ornamentation is another important factor that influences the nature of fluid flow around a shell (Brenchley and Newall, 1970). Olivera and Wood (1997) have demonstrated the influence of surface roughness on the entrainment velocity of bivalve shells. Dey (2003) also found variation in hydrodynamic behavior between bivalve species with differing degrees of ornamentation.

Apart from size and surface ornamentation, shape plays an important role in deciding the hydrodynamics of a shell. As outlined before, the two valves of a bivalve shell generally do not differ in their mass. However, equivalved shells often show significant difference in the geometry between the shapes of right and left valves. Such symmetry issues, although inconsequential for entrainment velocity, may be important in dictating the movement trajectory and could potentially produce a sorted assemblage. Examples of such disparity in the abundance of right-left valves in bivalve death assemblages have been studied in detail and various hydrodynamic forces identified as causal mechanisms (Nagle, 1964; Frey and Dorjes, 1988; Cadée, 1992). Martin-Kaye (1951) reported a significant variation in the left-right valve ratio of a bivalve species in relation to beach topography from the eastern Trinidad coast. Similar phenomena have been recognized by others (Richter, 1922; Boucot et al., 1958; Kornicker et al., 1963; Lever and Thijssen, 1968; Behrens and Watson, 1969; Frey and Henderson, 1987). These authors concluded that observed deviation in valve ratio resulted from the difference in hydrodynamic properties of left and right valves. However, Shimoyama and Fuuisaka (1992) argued against this explanation. Using computer simulation of shell transport, they claimed that these results can be explained by deviations resulting from relatively small sample sizes.

Conceptual Model for Transport of a Shell

The two main forces that act on a shell in fluid flow are drag force F_D, acting parallel to the direction of the flow, and lift force F_L, acting upward (Fig. 1). The gravitational force, independent of fluid action, is represented by the weight of the shell. When the shell is submerged it experiences a buoyancy force exerted by the fluid, equal to the weight of

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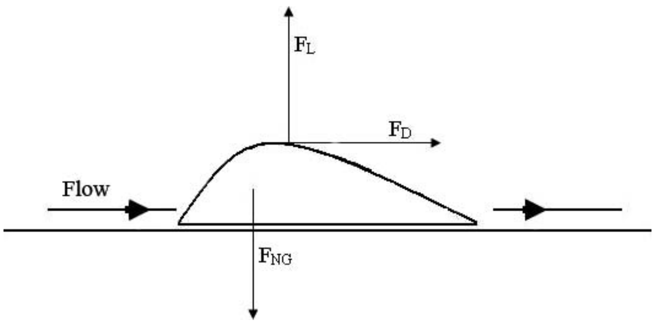

FIGURE 1—Schematic representation of forces acting on a single valve of a disarticulated shell immersed in a fluid flow. F_L = Lift force, F_D = Drag force, F_{NG} = Net gravity force.

displaced volume of the fluid. The net gravity force, F_{NG}, is therefore equal to the difference between the weight and buoyancy force. Drag, lift, and buoyancy can be considered destabilizing forces, whereas weight and friction can be regarded as stabilizing forces. Thus, the stability of a shell in flow depends on the magnitude of drag and lift generated by the fluid, in relation to the friction and net gravity force (Pena et al., 2008). In other words, a shell resting convex up on the bottom, with the umbo pointing upstream, will be entrained when the flow-induced forces overcome stabilizing forces. Since lift helps to reduce frictional force it plays a crucial role in entrainment (Vogel, 1994).

Using the principles discussed above, predictions on the effect of size, surface roughness and shape on entrainment velocity and movement trajectory of a valve can be made. Since mass contributes to the stability of a shell, an increase in entrainment velocity with size can be expected. The effect of surface roughness on entrainment velocity is relatively difficult to predict. It can be argued that the presence of ornamentation will enhance lift by increasing surface roughness. Consequently an ornamented shell should require a low entrainment velocity for destabilization. However, some experimental studies failed to document such a pattern (Olivera and Wood, 1997).

Similarly, the effect of shape on shell transport is challenging to predict. Shape is crucial in determining the movement trajectory of a shell (Miller, 1991). The asymmetry of inequilateral valves results in unequal distribution of drag forces along the surface of a shell and consequently generates torque. This torque may potentially guide the trajectory of movement for asymmetric valves.

Although the effect of morphological factors on transportation of shells can be predicted from simple hydrodynamic principles, it is quite challenging to quantify the extent of such effects without experimental data. In the present study, we have experimentally evaluated the hydrodynamic behavior of shells of *Donax scortum.* We assessed the effect of the following parameters on entrainment velocity and trajectory of movement of *D. scortum* valves: (1) size, (2) ornamentation, (3) right versus left valve. We chose this particular species of bivalve for its broad size range (10–70 mm), highly ornate surface with prominent spines and blades, and pronounced asymmetry in shape (thereby creating highly distinctive right and left valves). Using our experimental data on entrainment velocity and direction of movement, we also developed a quantitative simulation to evaluate the effect of these factors on spatial distribution of shells following postmortem transport.

MATERIALS AND METHODS

Specimens

Bulk samples of *D. scortum* shells were collected from a foreshore beach environment of Chandipur-on-sea, Orissa, India (latitude N

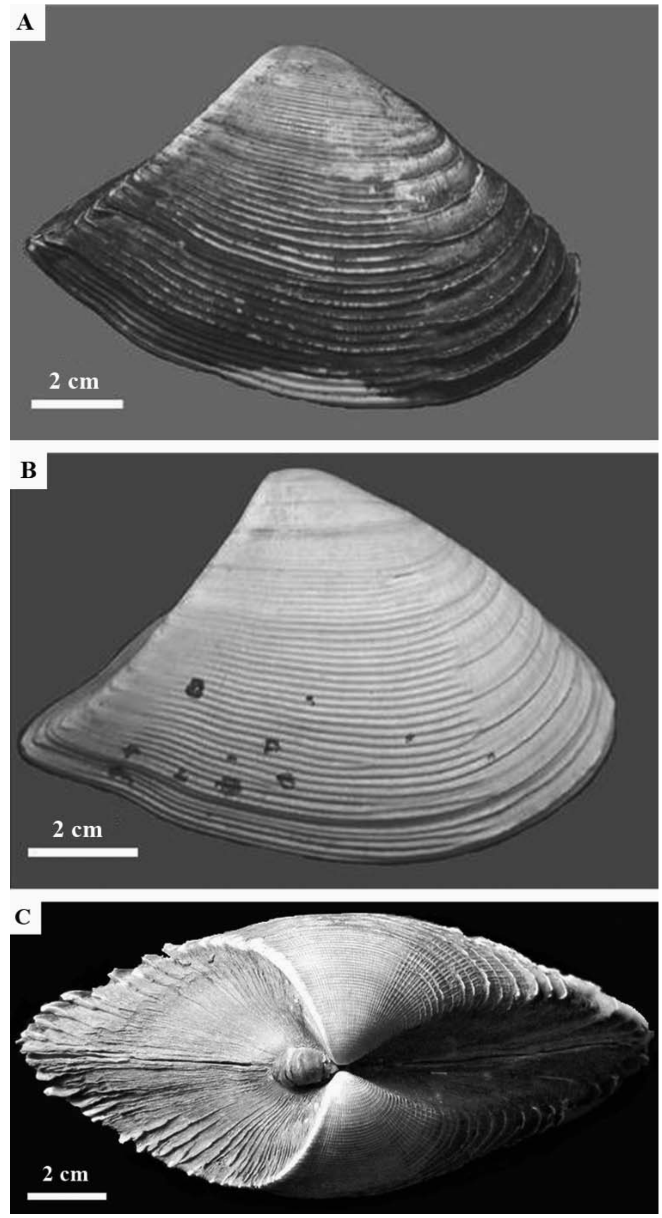

FIGURE 2—Specimens of *Donax scortum*. A) A fresh left valve with well-preserved spines, blades, and periostracum layer. B) An altered left valve with abraded spines, blades, and periostracum layer. C) Dorsal view of an articulated specimen displaying pronounced lunule.

21°27′48.56″, longitude E 87°03′36.58″). Specimens consist of two types of shell; fresh and altered. Fresh specimens include dead shells with well-preserved spines, blades, and periostracum layer but clean of residual soft tissue. Altered specimens had smooth outer shells (Fig. 2). These specimens had lost their ornamentation due to physical abrasion (Fig. 2). Shells were categorized into these two groups by visual inspection. Specimens with intermediate preservation stages were not considered for this study. Articulated fresh shells were disarticulated manually for this study. Right and left valve specimens were identified and separated. Valves with intact umbo and commissural line were selected for the experiment. Anterior-posterior length (L) was measured for each valve using electronic slide calipers (±0.01 mm), and this measure was used as a proxy for size. The mass of each valve was measured using an electronic balance (±0.001 g). A total of 74 disarticulated valves were studied (Table 1).

TABLE 1—Table summarizing the number, average size, and average mass of specimens in each category used in the present study.

	Fresh		Altered	
	Left	Right	Left	Right
Number of specimens	23	25	13	13
Mean size (mm)	41.23	39.68	39.53	41.94
Mean mass (g)	3.53	3.17	2.48	2.98

Flume Design

Experiments were conducted in a closed-circuit laboratory flume housed at the Fluvial Mechanics Laboratory of the Indian Statistical Institute, Kolkata. The dimension of the flume is 10 m × 50 cm × 50 cm. The flume bottom consists of a 2-mm-thick, flat-lying fiber sheet. The detailed design of the flume is discussed in Mazumder et al. (2005). Accurate measurements of flow velocity were obtained using 3-D Micro-Acoustic Doppler Velocimeter (ADV) that measures all three components of velocity with acoustic sensing techniques. The ADV was adjusted to take velocity measurements in the center of the flume approximately 0.3 m downstream of the shell location. The depth of the ADV was fixed, to measure flow velocity at 4 mm from the bottom fiber sheet.

Experimental Protocol

We used 74 valves (48 fresh and 26 altered) for measuring entrainment velocity (Table 1). Each valve was placed in stable flow conditions and turned over several times to release trapped air bubbles from the concave side. They were positioned convex up on a fixed mark at the center and oriented with umbo pointing upstream. This was found to be the most stable configuration; shells reoriented themselves if positioned differently. Each run was conducted by gradually increasing the flow velocity until the valve was entrained. Flow velocity measurements were taken immediately following successful entrainment (i.e., once the valve had moved 30 cm from the starting point). The run was repeated three times for each specimen and the average calculated.

In order to evaluate the trajectory of movement, the angles of deflection of valves in motion were measured. Twenty-one fresh valves were used for this experiment. The run was repeated three times for each specimen and the average recorded. Each shell was positioned at a specific starting point with the umbo pointing upstream in the flume tank (Fig. 3).

Two distances were measured to assess the angle of deviation: (1) the distance of starting point from sidewalls along the starting line (AB), (2) the distance of destination point from starting line along sidewall (BD). The angle of deviation is defined as the angle between the actual path of the shell movement and the mid line (θ).

The angle of deviation is calculated using the following relationships:

$$BD/AB = \tan \varphi$$
$$BD/AB = \tan (90 - \theta)$$
$$BD/AB = 1/\tan \theta$$
$$\theta = \text{archtan} (AB/BD).$$

Simulation to Evaluate Final Shell Distribution

The detailed hydrodynamic properties of individual shells, although important, do not predict the alteration in an assemblage unless we quantify the effect of such transportation on final spatial distribution. Therefore a computer simulation was designed to evaluate spatial distribution of *Donax scortum* shells in unidirectional flow using the experimental results. The character of subpopulations was analyzed and evaluated as to how different they are from the original population.

A population of 20,000 fresh *Donax scortum* valves, equally divided between left and right valves, provides the initial data points. The population was normally distributed in terms of valve size. Each data point had a right-left character, a size value, and a corresponding entrainment velocity (EV). In addition to size and velocity, two variables (i.e., distance R and angle of deviation θ) were also assigned to each data point and initialized to zero to represent their original position. The values of EV, R, and θ were assigned based on their experimental relationship to valve characteristics (size and right- or left-handedness). Next, the original shell population at the origin was subjected to a flow velocity (FV) that distributes the shells. At a particular velocity, the valves would move from the origin only if their entrainment velocity was less than the flow velocity (EV ≤ FV).

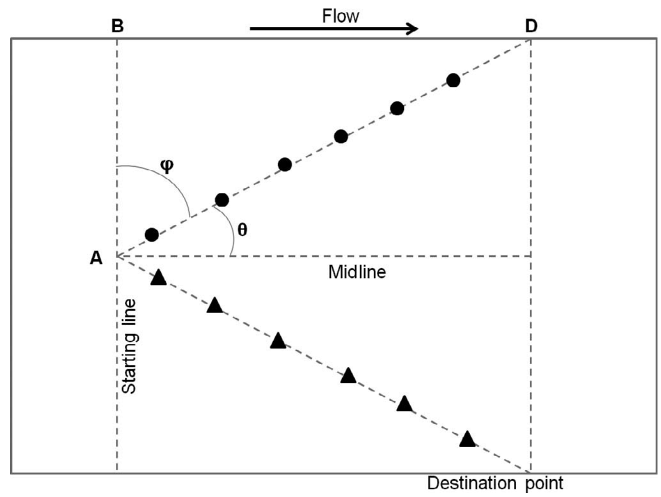

FIGURE 3—Diagram showing the angle measurement technique used for this study in plan view, looking down on the floor of the flume. All the valves use in this experiment were emplaced with their umbo pointing upstream. Solid triangle = left valves, solid circles = right valves.

FV was initially assigned the minimum EV value of the data set. This value of FV was compared with EV for each data point. The value of R and θ changed only if FV > EV. With every unit increment in FV the remaining data points at origin (N) was counted. Then the FV would start from an initial value and increase linearly with a constant increment until a desired maximum velocity was reached. Therefore, a unique N was associated with a maximum FV.

All the valves were subjected to a particular FV for 100 seconds at every increment. The final distance of a valve from the origin depended on size and FV. The direction of the deflection was determined by right- or left-handedness. For calculating the magnitude of angle deviation, the data points were categorized into three size classes: small (<30 mm), medium (30–50 mm), and large (>50 mm). For each size class, the respective empirical relationship between the angle of deviation (θ) and flow velocity (FV) was used.

Nine random samples from the spatial distribution for each unique maximum flow velocity were taken from an area limited by the maximum range of R and θ value for that specific FV. For every random sample, the size distribution of sampled population was calculated and compared to the original population using the Kolmogorov-Smirnov test. Similarly, the right-left ratio for each sample was compared with its original value of 0.5. MATLAB Software was used for creating this simulation and the statistical analyses were done with PAST (Hammer et al., 2001).

RESULTS

Size and Mass

The measured sizes for all valves are normally distributed (Shapiro-Wilk test; fresh: $W = 0.96$, $p = 0.09$; altered: $W = 0.95$, $p = 0.23$). A significant positive correlation (Fig. 4) exists between the size and the

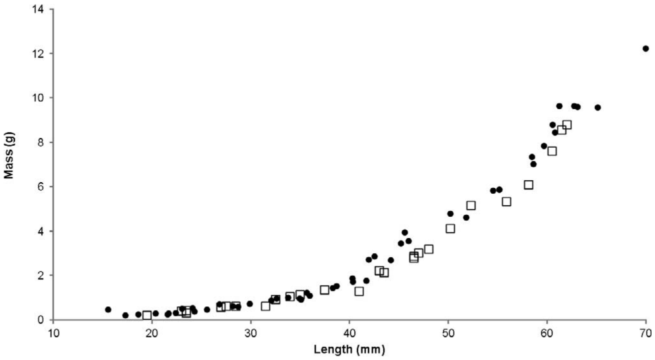

FIGURE 4—Relationship between mass and size of *Donax scortum* shells. Solid circle = fresh shells (N = 48), open square = altered shells (N = 26).

mass of the *Donax scortum* shells (Pearson's product moment correlation). This relationship is true for both fresh specimens (r = 0.94, $p << 0.0001$) and altered specimens (r = 0.93, $p << 0.0001$). There is no significant difference between mean mass for right and left valves in each category (fresh: t = 0.82, p = 0.41; altered: t = 0.49, p = 0.62). The fresh shells are slightly heavier compared to the altered specimens. However, the difference between the means is not statistically significant (t = 1.02, p = 0.31).

Effect of Size

The calculated entrainment velocities for all valves are normally distributed (Shapiro-Wilk test; W = 0.97, p = 0.06). A significant positive correlation (Fig. 5A) exists between the size and the entrainment velocity of the *D. scortum* shells (Pearson's rank order correlation). This relationship is true for both fresh specimens (r = 0.81, $p < 0.0001$) and altered specimens (r = 0.89, $p < 0.0001$).

Effect of Ornamentation

The mean entrainment velocity for fresh shells is significantly lower than for altered specimens (t = −2.64, p = 0.01). In order to compare the entrainment velocities in different classes, we subdivided the specimens in three size classes: small (<30 mm), medium (30–50 mm), and large (>50 mm). For the same size category, entrainment velocity is lower for fresh shells compared to those of the altered shells (Fig. 5B). This difference is statistically significant for all size classes; however, the significance decreases with increasing size (small: t = −3.78, p = 0.001; medium: t = −2.66, p = 0.01; large: t = −1.45, p = 0.05). In the largest size class the difference is only marginally significant.

Effect of Left- or Right-Handedness

There is no significant difference between the mean entrainment velocity for left and right valves (t = 1.8, p = 0.08) (Fig. 5C). The

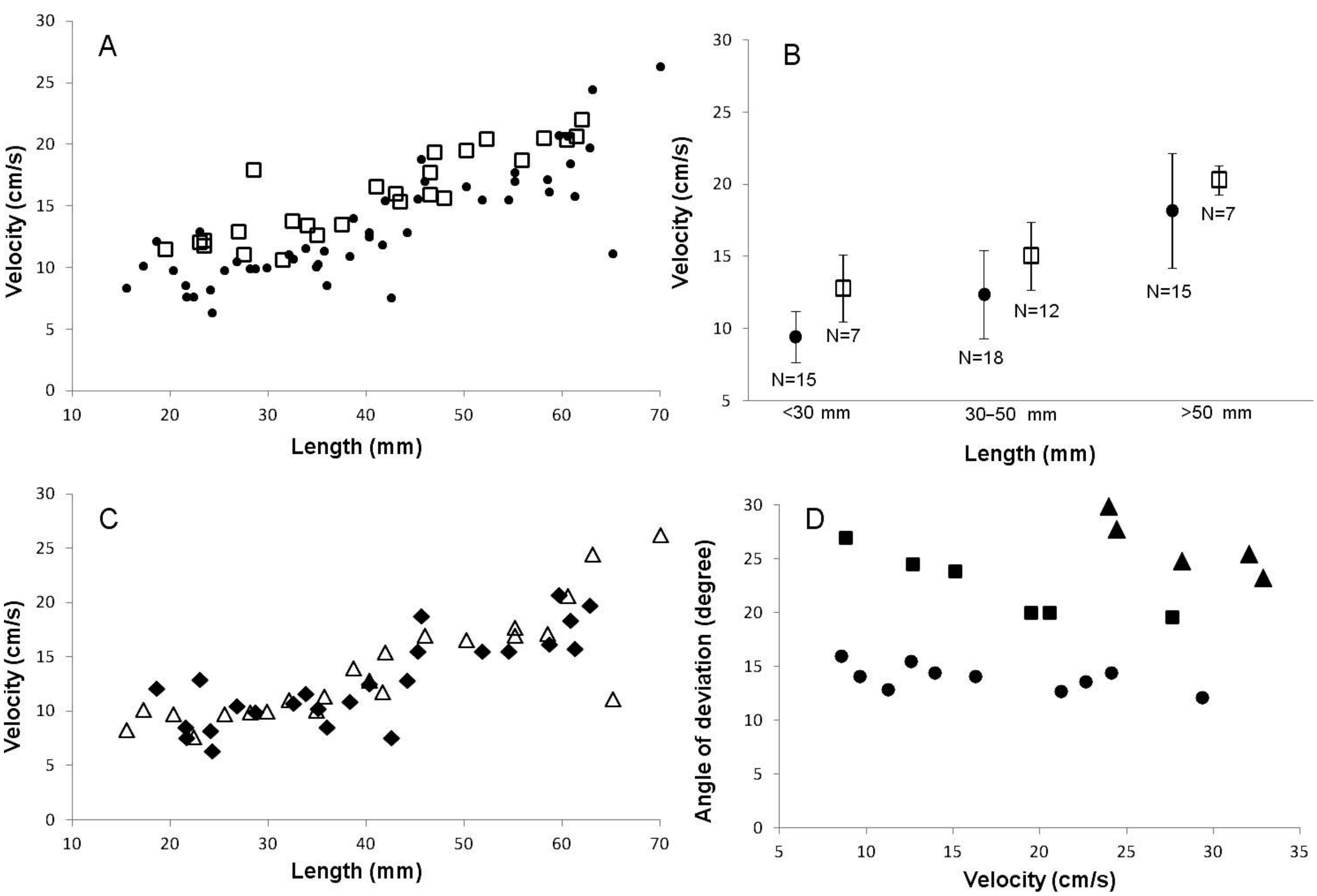

FIGURE 5—A) Plot showing the relationship between entrainment velocity and size. Solid circles = fresh shells (N = 48), open square = altered shells (N = 26). B) Plot showing the difference in average velocity between fresh and altered valves in three size classes. The vertical error bars represent standard error for velocity. N = sample size, solid circle = fresh shells, open square = altered shells. C) Plot showing the relationship between entrainment velocity and size for fresh *D. scortum* shells. Solid rhomb = right valves (N = 25), open triangle = left valves (N = 23). D) Plot showing the relationship between the angle of deviation and the flow for different size classes of *D. scortum* shells. Only the fresh left valves have been used. Circle = small (N = 10), square = medium (N = 6), and triangle = large (N = 5).

TABLE 2—Table summarizing the outcome of multiple regression analysis to evaluate the relative effect of size versus velocity on magnitude of deflection. The analysis is performed on the deflection data of fresh left valves.

	Coefficient	Standard error	*t*	*p*	R^2
Constant	11.698	1.1354	10.304	7.0135E-16	0
Size	0.2975	0.025223	11.795	1.4061E-18	0.6164
Velocity	−0.2244	0.056655	−3.9608	0.00017193	0.082495

direction of the movement of a valve depends on whether it is a right valve or a left valve. The right valves orient themselves toward the left and the left toward the right during entrainment. However, they maintain their orientation after preliminary reorientation. All valves (fresh and altered) show the same pattern. We measured the angle of deviation only for fresh left valve specimens for the ease of measurement. The angle of deviation of a shell is dependent on its size and ambient flow velocity. At a fixed velocity, the angle of deviation increases with size. At a fixed size, the angle of deviation decreases with increasing velocity (Fig. 5D). We ran a multiple regression analysis to evaluate relative effect of size and velocity on deflection (Table 2). The results demonstrate that both size ($p << 0.0001$) and velocity ($p = 0.0002$) significantly contribute to deflection.

Result of Simulation

Graphs with various FV and corresponding N values were plotted (Figs. 6A–C). Each graph presents the spatial distribution of shells at specific velocity range. The number of shells remaining at origin (N) changes with FV. The distance is represented by the contour lines on the graph.

The random samples chosen at various velocities significantly differ from the original population (Kolmogorov-Smirnov test, $p << 0.05$). In order to evaluate the magnitude of such difference the Kolmogorov-Smirnov test statistic (D) of such comparisons were compared against velocity; D is the maximum absolute difference between two cumulative distribution functions (Stephens, 1970). The amount of difference between original and sampled population, manifested by D, is velocity dependent. The range of D values increases with increasing velocity with a nearly constant upper limit for all the velocity values. Thus, there is a negative slope of the lowest D values when plotted against velocity (Fig. 7). The left-right ratio in the sampled population, however, does not have any velocity dependence; it always differs significantly from the original population and shows a binomial distribution characterized by a population of entirely right or left valves.

DISCUSSION

Factors Affecting Entrainment

The effect of morphological factors on entrainment velocity and movement trajectory of a valve was observed. A positive relationship between size and velocity occurs, as predicted from the simple hydrodynamic principle of increasing lift with increasing velocity. However, this mechanism does not explain the observed entrainment velocity difference between fresh and altered samples. Since altered specimens were slightly lighter (although statistically insignificant), it could be expected that equal or lower velocities would be required to entrain altered compared with fresh shells if mass is the dominant factor controlling entrainment. However, the difference between their surface ornamentation may explain this difference in entrainment velocity. Using flow-visualization studies on a corrugated airfoil, Yeung (2006) demonstrated that the trapped vortices for such ornamentation lead to an increase in lift. He also demonstrated that the magnitude of the lift increment depends on the number of such corrugations on the surface. Thus, it can be argued that ornamentation on a fresh shell is responsible for its increased lift; thereby requiring a lower entrainment velocity for destabilization. The smooth surface of shells altered by weathering, on the contrary, requires a much higher entrainment velocity to generate the same amount of lift.

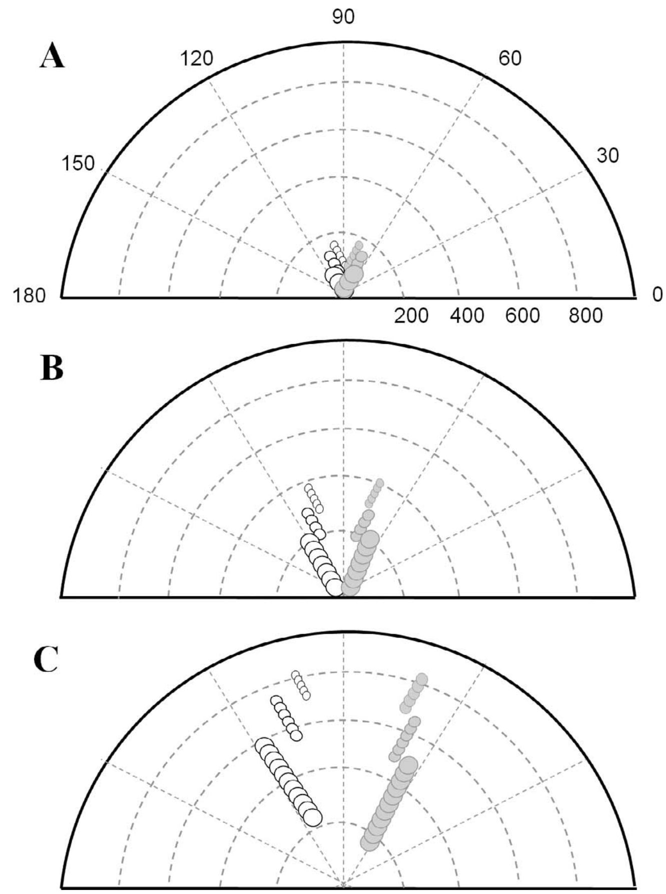

FIGURE 6—Plots representing the distribution of shells from the origin at various velocity ranges based on the simulation results. The contour lines represent the distance from the origin in meters. The contour interval is 200 m and the outermost contour value is 1000 m. The relative size of the symbols represents the size of valves. Solid circle = left valve, open circle = right valve. A) N = 15129, Maximum velocity = 10 cm/s. B) N = 557, Maximum velocity = 20 cm/s. C) N = 0, Maximum velocity = 30 cm/s.

The deflection of a valve results from the torque generated by unequal distribution of drag forces along the surface of an asymmetric shell. The pronounced lunule in *D. scortum* valves (Fig. 2C) creates such force imbalance. The growth of *Donax* is allometric (Mohan et al., 1986), creating a disproportionately large lunule in larger specimens. The larger shells with highly asymmetrical shape are subjected to larger torque. Consequently, larger shells deflect more compared to smaller ones at a fixed velocity. Increase in velocity diminishes the effect of such reorientation and consequently results in decrease in angle of deviation.

Effect of Transportation on Assemblage

Postmortem transport is significantly dependent on various aspects of bivalve shell morphology. As demonstrated by the simulation, this dependence may lead to a spatial distribution of shells that are quite different from the original population. The simulation demonstrated that assemblages affected by low-velocity agents are likely to be substantially different from the original population in terms of their size. With increasing velocity, this difference diminishes since valves of all sizes are transported under high velocity. Thus, in depositional successions deposited under higher-velocity regimes a shell assemblage is more likely to closely resemble the original population than one

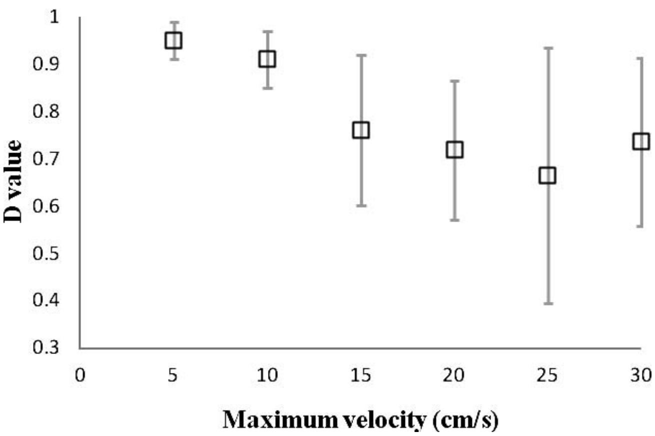

FIGURE 7—Plot representing the relationship between velocity and the K-S statistic D (mean D ± standard error). The D represents the difference between the distributions of sampled population and the original population. All the tests are statistically significant ($p < 0.01$).

deposited under a lower-velocity regime. The right-left proportion, nevertheless, would likely show a highly skewed distribution compared to the original population irrespective of the velocity range. The velocities recorded in this experiment are quite similar to characteristic velocities in low-energy shallow marine shelf systems (Harms, 1979). Morphologically induced taphonomic bias in these assemblages has the potential to create significant problems for analyses of biodiversity, ontogenetics, and predator-prey relationships in these settings.

Studies of biodiversity could be affected by the differential distribution of shells of dissimilar size and symmetry. Species of similar size would be grouped together, misrepresenting the original association. Moreover, symmetrical shells would be transported without deflection (Chattopadhyay, 2009), and occupy different spatial destinations compared with asymmetrical taxa. Hence, species with similar shape would be combined artificially. Although it is possible to identify a deflected assemblage by its biased left-right ratio, it is not easy to identify a lag assemblage of symmetrical shells. In addition to size and symmetry, shell ornamentation would also contribute in the postmortem sorting. Shells with pronounced ornamentations are likely to be separated from less ornate taxa of similar size. All such factors can potentially affect the inferred biodiversity pattern of an area. Transport and size sorting are commonly responsible for altering the true species diversity in modern death assemblages and fossil assemblages (Cadée, 1968; Wolff, 1973; Cummins et al., 1986; Westrop, 1986; Miller et al., 1992; Blob and Fiorillo, 1996; Olszewski and West, 1997). Zuschin et al. (2005), in an analysis of shells from a Miocene tempestie, concluded that the diversity of a bivalve assemblage depends on size sorting and therefore reflects the transport history of the individual bed, not the species richness of the original paleocommunity. Frey and Dorjes (1988) sampled modern beach settings in order to compare the effects of foul-weather processes on fair-weather shell accumulations. They found that the diversity profile depended significantly on wave velocity. Simulation results presented herein suggest that wave velocity also generates a significant difference in the left-right proportion of shells. However, the simulation results also indicate that it would be unlikely to find dominant size sorting under high-energy flow conditions. It would be informative to compare the size-sorting and diversity pattern of assemblages transported under distinctly different flow velocities.

Within a single species, ontogenetic analyses would be challenged due to segregation of different size categories. Bivalve shells often grow allometrically, producing a more ornate shell during later ontogeny. Larger, and concommitantly more ornate, shells would be deflected more and create subassemblages sorted by rough ontogenetic stages.

A size-sorted transported assemblage could also result in complications in the study of predator-prey interactions. Predators often preferentially attack prey of a particular size class. For durophagous and avian predation, wherein the lethal attack destroys the shell, such size selectivity is inferred from the unaffected population (Carter, 1974; Vermeij, 1987; Cadée, 1989). However, transport can modify the size spectrum of an assemblage relative to the original one at its lower or upper bounds. Such modification could generate a superficial absence of larger size classes in transported assemblages and smaller size classes in lag assemblages. This would increase the chance of misdiagnosing the pattern as one created by preferential predatory activity. On a similar note it is worth considering that some predation marks (such as drill hole, repair scar) could perhaps substantially alter the hydrodynamic behavior of a shell as noted by many studies (Lever and Thijssen, 1968; Trewin and Welsh, 1972; Chattopadhyay et al., 2006). Since predation studies in deep time rely heavily on the assumption of the unbiased nature of the assemblage (Kelley and Hansen, 2003, and references therein; Chattopadhyay, 2011; Bardhan et al., 2012; Chattopadhyay and Dutta, 2013), this should be investigated further.

Unlike many other taphonomic agents, however, this transport bias would actually work against time averaging if the extent of shell abrasion increases with time. Due to the differences in morphology and mass between fresh and altered shells, their movement differs. Hence, a time-averaged assemblage, when subjected to relatively low velocity flow, will be sorted by their state of alteration; this will generate subassemblages, each characterized by a unique state of taphonomic alteration.

Transport bias would be more likely to affect assemblages that were subjected to low velocity. The lower flow regime conditions characteristic of shallow marine shelf environments (Harms, 1979) are comparable to the recorded velocities of our experiments. Under high velocity, all the valves would be transported irrespective of their size. Since deflection also decreases with velocity, the amount of seperation between right and left valves would also be expected to diminish. Although the recorded experimental velocities are comparable to natural systems, it is to be noted that they were recorded in a low-friction system. It is possible that the taphonomic biases discussed here would be exacerbated in a natural system with a higher friction sustrate; however, additional research is needed to establish this.

CONCLUSIONS

Bivalve shells, because of their high preservation potential and long evolutionary history, are commonly used by neontologists and paleontologists to explore various ecological and evolutionary questions. Nonetheless, there are comparatively few studies that have looked at the potential taphonomic biases associated with bivalve shell transport. It has been demonstrated herein that hydrodynamic sorting may comprise a significant source of taphonomic bias. Using a recirculation flume, the entrainment velocities of both fresh and altered disarticulated shells of *Donax scortum* were established. The result of the experiment clearly demonstrates that entrainment velocity of a shell depends on its size and the presence or absence of ornamentation. Right- or left-handedness dictates the direction of movement. The magnitude of such deflection is also dependent on size of the shell and velocity of the flow. Computer simulations, based on experimental results discussed herein, illustrate the extent of alteration of bivalve assemblages by various flow velocities and morphologies of the initial assemblages. Additional work is needed to document the nature of bias between taxa, and under varying substrate conditions and flow regimes.

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